

**THE INFLUENCE OF BEHAVIOR ON ACTIVE SUBSIDY
DISTRIBUTION**

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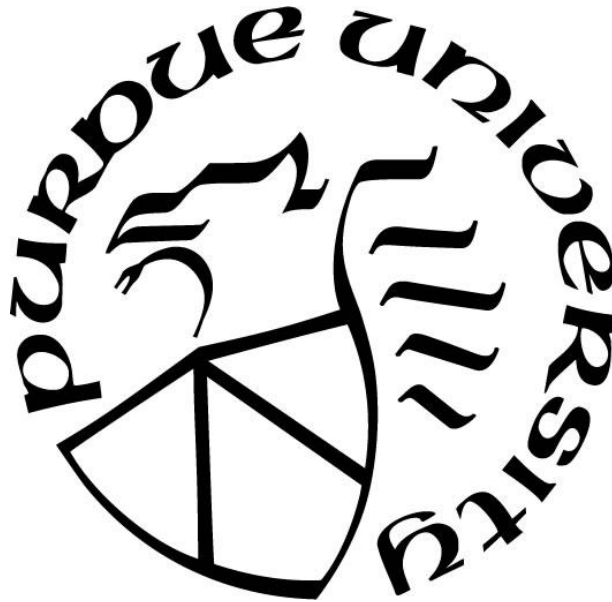
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To Pupsie and our families, friends and mentors for believing in and supporting me

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TABLE OF CONTENTS

| | |
|---|----|
| LIST OF TABLES | 7 |
| LIST OF FIGURES | 8 |
| ABSTRACT | 10 |
| CHAPTER 1. THE STATE OF RESEARCH ON ECOLOGICAL SUBSIDIES | 11 |
| 1.1 Inception, current ideas and knowledge gaps on ecological subsidies | 11 |
| 1.2 References | 19 |
| CHAPTER 2. THE INFLUENCE OF ANIMAL MOVEMENT PATTERN AND MORTALITY MODELS ON THE DISTRIBUTION OF ANIMAL-TRANSPORTED SUBSIDIES | 29 |
| 2.1 Abstract | 29 |
| 2.2 Introduction | 30 |
| 2.3 Methods | 35 |
| 2.3.1 Background | 35 |
| 2.3.2 Design | 36 |
| 2.3.3 Analysis | 38 |
| 2.4 Results | 40 |
| 2.5 Discussion | 44 |
| 2.6 Conclusion | 50 |
| 2.7 References | 51 |
| 2.8 Tables and Figures | 60 |
| CHAPTER 3. THE INFLUENCE OF SOCIAL BEHAVIOR ON THE DISTRIBUTION OF ANIMAL-TRANSPORTED SUBSIDIES | 68 |
| 3.1 Abstract | 68 |
| 3.2 Introduction | 69 |
| 3.3 Methods | 72 |
| 3.3.1 Background | 72 |
| 3.3.2 Design | 73 |
| 3.3.3 Analysis | 75 |
| 3.4 Results | 77 |
| 3.5 Discussion | 80 |

| | |
|--|-----|
| 3.6 Conclusion | 85 |
| 3.7 References | 85 |
| 3.8 Tables and Figures | 95 |
| CHAPTER 4. THE INFLUENCE OF LANDSCAPE HETEROGENEITY ON THE DISTRIBUTION OF ANIMAL-TRANSPORTED SUBSIDIES: A CASE STUDY ON WOOD FROGS IN HARDWOOD FORESTS..... | 104 |
| 4.1 Abstract | 104 |
| 4.2 Introduction..... | 105 |
| 4.3 Methods..... | 108 |
| 4.3.1 Study Site..... | 108 |
| 4.3.2 Empirical data for IBM calibration..... | 109 |
| 4.3.3 Individual Based Model..... | 110 |
| 4.3.3.1 Background..... | 110 |
| 4.3.3.2 Design..... | 112 |
| 4.3.3.3 Simulations | 114 |
| 4.3.3.4 Analysis | 116 |
| 4.4 Results..... | 118 |
| 4.5 Discussion | 121 |
| 4.6 Conclusion | 127 |
| 4.7 References | 127 |
| 4.8 Tables and Figures | 139 |
| CHAPTER 5. ADVANCES IN UNDERSTANDING ACTIVE SUBSIDY SYSTEMS..... | 144 |
| 5.1 Contributions to spatial subsidy research and modeling..... | 144 |
| 5.2 References | 150 |
| APPENDIX A. SUPPLEMENTARY INFORMATION (SI): COMPARING ANIMAL MOVEMENT PATTERNS AND MORTALITY MODELS ON THE DISTRIBUTION OF ACTIVE SUBSIDIES..... | 155 |
| APPENDIX B. SUPPLEMENTARY INFORMATION (SI): EFFECT OF ANIMAL SOCIALITY, MOVEMENT AND MORTALITY ON ACTIVE SUBSIDY DISTRIBUTION..... | 204 |
| APPENDIX C. SUPPLEMENTARY INFORMATION (SI): THE EFFECT OF LANDSCAPE HETEROGENEITY ON ACTIVE SUBSIDY DISTRIBUTION | 256 |

LIST OF TABLES

| | |
|--|-----|
| Table 1 IBM design: state variables with parameter levels (movement behavior and mortality) | 60 |
| Table 2 IBM design: state variables with parameter levels (sociality and movement pattern) | 95 |
| Table 3 IBM design: state variables with parameter levels (landscape heterogeneity and movement pattern)..... | 139 |
| Table 4 Predictor importance and precision for subsidy distribution (movement behavior and mortality) | 166 |
| Table 5 Predictor importance and precision for subsidy distribution metrics (space-based and time-based mortality). | 167 |
| Table 6 Error analysis for subsidy distribution trends (movement behavior and mortality). | 168 |
| Table 7 Predictor importance for subsidy distribution (sociality and movement pattern). | 210 |
| Table 8 Predictor precision for subsidy distribution (sociality and movement pattern)..... | 211 |
| Table 9 Error analysis for subsidy distribution trends (sociality and movement pattern) | 212 |
| Table 10 Predictor importance for subsidy distribution (movement pattern in homogeneous habitats). | 262 |
| Table 11 Predictor precision for subsidy distribution (movement pattern and homogeneous habitats). | 263 |
| Table 12 Predictor importance for subsidy distribution (movement pattern and heterogeneous landscapes). | 264 |
| Table 13 Predictor precision for subsidy distribution (movement pattern and heterogeneous landscapes). | 265 |
| Table 14 Error analysis for subsidy distribution trends (movement pattern and landscape heterogeneity)..... | 266 |
| Table 15 Descriptive statistics for landscape structure predictors..... | 267 |

LIST OF FIGURES

| | |
|--|-----|
| Figure 1 IBM Design concept (subsidy distribution as a function of movement behavior and mortality). | 61 |
| Figure 2 Predictor importance for subsidy distribution (movement behavior and mortality) | 62 |
| Figure 3 Predictor importance for subsidy distribution (space-based vs time-based mortality). . | 63 |
| Figure 4 Synthesis subsidy displacement trends (movement behavior and mortality)..... | 64 |
| Figure 5 Synthesis of subsidy density trends (movement behavior and mortality)..... | 65 |
| Figure 6 Synthesis of subsidy displacement trends (space-based vs time-based mortality). | 66 |
| Figure 7 Synthesis of subsidy density trends (space-based vs time-based mortality). | 67 |
| Figure 8 IBM design concept (subsidy distribution as a function of sociality and movement pattern). | 96 |
| Figure 9 Predictor importance for subsidy distribution (sociality and movement). | 97 |
| Figure 10 Predictor importance for subsidy clustering (sociality and movement). | 98 |
| Figure 11 Synthesis of subsidy displacement trends (sociality and movement). | 99 |
| Figure 12 Synthesis of peak subsidy deposition density trends (sociality and movement)..... | 100 |
| Figure 13 Synthesis of inter-cluster displacement trends (sociality and movement). | 101 |
| Figure 14 Synthesis of cluster size trends (sociality and movement)..... | 102 |
| Figure 15 Synthesis of cluster density trends (sociality and movement. | 103 |
| Figure 16 IBM design concept (subsidy distribution as a function of landscape heterogeneity and movement pattern)..... | 140 |
| Figure 17 Predictor importance for subsidy distribution (landscape heterogeneity and movement pattern)..... | 141 |
| Figure 18 Synthesis of subsidy displacement trends (landscape heterogeneity and movement pattern)..... | 142 |
| Figure 19 Synthesis of subsidy density trends (landscape heterogeneity and movement pattern). | 143 |
| Figure 20 Effect of movement behavior on subsidy displacement..... | 157 |

| | |
|---|-----|
| Figure 21 Subsidy displacement trends (movement behavior and mortality). | 158 |
| Figure 22 Effect of movement behavior on subsidy density. | 159 |
| Figure 23 Subsidy density trends (movement behavior and mortality). | 160 |
| Figure 24 Effect of mortality model on subsidy displacement. | 161 |
| Figure 25 Subsidy displacement trends (space-based vs time-based mortality) | 162 |
| Figure 26 Effect of mortality model on subsidy density. | 163 |
| Figure 27 Subsidy density trends (space-based vs time-based mortality). | 164 |
| Figure 28 Trends in number of dead subsidies (space-based vs time-based mortality). | 165 |
| Figure 29 Subsidy displacement trends (sociality and movement). | 206 |
| Figure 30 Subsidy density trends (sociality and movement). | 207 |
| Figure 31 Subsidy inter-cluster displacement and cluster size trends (sociality and movement). | 208 |
| Figure 32 Subsidy cluster density trends (sociality and movement). | 209 |
| Figure 33 Subsidy displacement trends in homogeneous landscapes. | 258 |
| Figure 34 Subsidy density trends in homogeneous landscapes. | 259 |
| Figure 35 Subsidy displacement trends in heterogeneous landscapes. | 260 |
| Figure 36 Subsidy density trends in heterogeneous landscapes. | 261 |

ABSTRACT

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Title: The Influence of Behavior on Active Subsidy Distribution

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This dissertation investigates the influence of spatially explicit animal behavior active subsidy distribution patterns. Active subsidies are animal-transported consumption and resources transfers from donor to recipient ecosystems. Active subsidies influence ecosystem structure, function and services in recipient ecosystems. Even though active subsidies affect ecosystem dynamics, most ecosystem models consider the influence of spatially-explicit animal behavior on active subsidy distributions, limiting the ability to predict corresponding spatial impacts across ecosystems. Spatial subsidy research documents the need for systematic models and analyses frameworks to provide generally insights into the relationship between animal space use behavior and active subsidy patterns, and advance knowledge of corresponding ecosystem impacts for a variety of taxa and ecological scenarios.

To advance spatial subsidy research, this dissertation employs a combined individual-based and movement ecology approach in abstract modeling frameworks to systematically investigate the influence of 1) animal movement behavior given mortality (chapter 2), 2) animal sociality (chapter 3) and 3) landscape heterogeneity (chapter 4) on active subsidy distribution. This dissertation shows that animal movement behavior, sociality and landscape heterogeneity influence the extent and intensity of active distribution and impacts in recipient ecosystems. Insights from this dissertation demonstrate that accounting for these factors in the development of ecosystem models will consequentially enhance their utility for predicting active subsidy spatial patterns and impacts. This dissertation advances spatial subsidy research by providing a road map for developing a comprehensive, unifying framework of the relationship between animal behavior and active subsidy distributions.

CHAPTER 1. THE STATE OF RESEARCH ON ECOLOGICAL SUBSIDIES

1.1 Inception, current ideas and knowledge gaps on ecological subsidies

Ecological subsidies are resource (e.g., producers, prey, nutrients) and consumption (e.g., predators, pathogens, and parasites) transfers between ecosystems (Polis et al., 1996). Ecological subsidies can alter material and energetic balances between ecosystems and across landscapes with consequences for recipient ecosystem structure, function and services (Nakano and Murakami, 2001). For example, subsidies can influence spatiotemporal patterns of ecological processes such as seed dispersal, contaminant transport and disease transfer (McInturf et al., 2019). Developing adequate tools to model and predict spatial subsidy patterns will therefore enhance our ability to better understand and manage these and many more ecosystem phenomena across landscapes (Earl and Zollner, 2017). Two main categories of ecological subsidies are passive and active subsidies. Passive subsidies are displaced between ecosystems by environmental structure like slope-induced gravity and fluid fluxes like wind currents and runoff (Polis et al., 1996). Active subsidies are animal-transported resources (e.g., prey, and nutrients from dead animals and feces) and consumers (i.e., predators, herbivores and frugivores) from donor to recipient ecosystems (Earl and Zollner, 2017, 2014).

Passive subsidy systems correspond to well understood spatiotemporal patterns in the movement of abiotic transport media (e.g., runoff induced by seasonal precipitation patterns). The hydrologic cycle connects aquatic and terrestrial food webs as environmental fluid systems transport passive subsidies like leaf litter and detritus between surface waters and riparian lands. Organic matter and nutrients from terrestrial ecosystems can be more important for primary and secondary production (e.g., aquatic plants and invertebrates) in surface waters than in situ material

and energy sources (Kraus et al., 2011). Similarly, water movements such as flooding events deposit aquatic resources across terrestrial ecosystems (Brehme et al., 2009; Schindler and Smits, 2017). Corresponding aquatic resource depositions subsidize terrestrial food webs and can drive riparian productivity more than terrestrial nutrient and energy sources (Marczak and Richardson, 2007). Montane, desert and polar ecosystems can be dependent on windborne resource subsidies from distant forest and aquatic ecosystems (Polis et al., 1997). Winds transport pollen, invertebrates, nutrients and detritus hundreds of miles from boreal forests to arctic tundra where they subsidize primary productivity and sustain invertebrate communities (von Stedingk et al., 2008). Passive subsidies generate ecologically important press and pulse disturbances (e.g., eutrophication in lentic systems from terrestrial nutrient transport) that have been thoroughly studied because of well understood transport processes in the environment (McInturf et al., 2019; Polis et al., 1996).

In contrast to passive subsidies, the spatial impacts of active subsidy systems are less understood. Predicting spatiotemporal patterns and corresponding impacts of active subsidies is complicated because it requires knowledge of animal behavior (Earl and Zollner, 2017). Unlike passive subsidies, autonomous animal agents interact with each other and the environment, influencing spatial dynamics and impacts of active subsidy systems (McInturf et al., 2019). Animal space-use can result in nutrient and consumer displacement (Pereira et al., 2014) and affect ecosystem structures like trophic interactions, functions like nutrient cycling and services like pollination (Bartels et al., 2012; Palumbi, 2003). For example, beavers construct dams in ponds, streams, lakes, marshes using woody debris and logs from riparian trees, and beaver dams are significant sources of nutrients and detritus that subsidize aquatic plant and invertebrate communities and stimulate in situ productivity (Malison et al., 2014; McCaffery and Eby, 2016).

The nutrient contribution of beaver dams to aquatic ecosystems can in turn stimulate the emergence of aquatic insects (e.g., dragonflies) and amphibians (e.g., frogs), which are substantial predators on terrestrial invertebrate communities. These consumption subsidies can regulate and suppress provisioning ecosystem services like honey production by bees (Greig et al., 2012; Wesner, 2010). Similarly, bears forage on anadromous salmon in stream ecosystems and transport marine nutrients in carcasses and feces into riparian forests, enhancing primary productivity supporting forest growth that sustains herbivore communities (Quinn et al., 2009). Even though these and many other active subsidy systems are prevalent and important drivers of ecosystem dynamics across landscapes, ecological research on the spatial impacts of active subsidies in recipient ecosystems is limited. Active subsidy research needs to move beyond collections of anecdotes to codify models of general principles and interaction that can be used to forecast corresponding spatial subsidy impacts.

Animals are autonomous agents that can transport subsidies against abiotic flux gradients, engage in conspecific and interspecific interactions, and respond to spatiotemporal variations in resources and risks, influencing the corresponding spatial subsidy distributions and impacts (Earl and Zollner, 2017). Even though the relationship between animal movements, interactions and population distributions are better understood, the influence animal movement on active subsidy patterns in heterogeneous landscapes remain underexplored. Predictive insight into the spatial effects of active subsidies on ecosystems is lacking partly because existing ecosystem models treat space and animal movement implicitly, ignoring important animal behaviors like social interactions (Earl and Zollner, 2017).

Spatial subsidy research relies on ecosystem models with static animal population distributions in binary systems (Guisan and Thuiller, 2005; Hanks et al., 2012; King and With,

2002). Existing ecosystem models treat space explicitly using probability distributions to describe spatial ecosystem patterns resulting from animal space-use (Lele et al., 2013; Marcarelli et al., 2011; Muñoz et al., 2016). Presence-absence, habitat suitability and utilitarian distribution models for instance (Hooten et al., 2016; Scharf et al., 2018) have been used to link animal behavior to population distributions. However, these models ignore the relationship between spatially explicit animal movement and interactions on emerging spatial subsidy impacts (but see (Holdo et al., 2009, 2007)). In contrast, continuous-time, diffusion-based ecological models of animal movements and population distributions (Wolf et al., 2013) ignore the influence of spatial variation in resource and risk distributions on animal movement across landscapes (but see (Moorcroft et al., 2006)). However, these approaches have not been used to study active subsidy systems. The current state of spatial subsidy research does not address if and how active subsidy patterns respond to animal movements, interactions and landscape heterogeneity (Earl and Zollner, 2017). Developing ecosystem models that incorporate spatially explicit animal behavior and landscape heterogeneity can help predict active subsidy distribution and impacts for improved, synergistic wildlife and ecosystem management.

Individual-based modeling (IBM) frameworks are powerful tools (Grimm and Railsback, 2004; Piou et al., 2009) that can be used to examine the relationship between spatially explicit animal movement behavior and active subsidy distributions (Earl and Zollner, 2014). While classical ecosystem models rely on mathematical tractability (e.g., steady-state solutions) and behavioral homogeneity, IBMs accommodate spatiotemporal complexity and behavioral realism (Bauduin et al., 2016; DeAngelis and Mooij, 2005). IBMs provide virtual simulation laboratories for multiple, interactive hypothesis testing suitable for studying complex systems using combinations of sub-models to describe different environments and animal behaviors. IBMs allow

for dynamic sensing and interaction among behaviorally heterogeneous animals and between animals and heterogeneous environments (Tisue and Wilensky, 2004). While classical models control for stochasticity, random effects typically observed in natural systems can be incorporated in IBMs. Incorporating such feature into IBMs, results in observable, measurable spatiotemporal patterns at higher levels of biological and spatial organization emerging from individual animal behaviors and interactions. IBMs have been used to model emergent group level patterns from individual behavior for many taxa including birds, mammals, insects, herptiles and fish (Aben et al., 2014; Bauduin et al., 2016; Dumont et al., 2007; Wallentin, 2017). Stochastic models (Smouse et al., 2010) used in movement ecology can be incorporated in IBMs to simulate the effect of spatially explicit variation animal movement behaviors on active subsidy distribution (Earl and Zollner, 2014).

Animal movement, sociality and landscape heterogeneity have been shown to influence animal movements and the distribution of animal populations (Giuggioli et al., 2013; Morales et al., 2010; Morales and Ellner, 2002), but have not been integrated into a comprehensive framework to assess corresponding ecosystem impacts. The spatial impacts of animal-transported subsidy systems on ecosystem processes, structure, function and services can be better understood when models consider the influence of these factors on active subsidy distributions (Earl and Zollner, 2017; McInturf et al., 2019). In my dissertation, I combine individual-based and movement ecology frameworks to examine if and how active subsidy distributions change with variation in animal movement, sociality and landscape heterogeneity.

Spatial subsidy models that account for the influence of characteristic animal movements in different ecological scenarios could improve our understanding of corresponding ecosystem impacts. Research on how spatial subsidies respond to spatially explicit variation in animal

movement behavior and mortality risk in different ecological contexts (e.g., foraging versus dispersal) is limited (Earl and Zollner, 2017; McInturf et al., 2019). Animal movement behavior and mortality risk can affect animal distributions in landscapes spatial subsidy patterns and impacts across landscapes (Earl and Zollner, 2014). Even though differences in animal movements in different ecological contexts have been shown to affect animal distributions (Jonsen et al., 2005; Lima and Zollner, 1996; Zollner and Lima, 1999), corresponding spatial subsidy distributions and ecosystem impacts from characteristic animal movements and spatiotemporal patterns in mortality risk between foraging and dispersal processes remains under-researched. Animals can also experience variation in mortality risk depending on activity levels and distance travelled (Herbst et al., 2016; Menden-Deuer, 2010; Nielsen et al., 2004). Modeling how active subsidy distributions respond to spatially explicit animal foraging and dispersal movements given spatiotemporal variation in mortality risk can highlight differences between nutrient and consumer subsidy patterns. Models incorporating these considerations will enable the development of predictive tools for differentiating between ecosystem impacts of living and dead organisms in variety of ecological scenarios, including foraging and dispersal.

Ecosystem models that address animal sociality can enhance insights into the relationship between animal movement and spatial subsidies. Even though animal sociality influences animal movements and could affect spatial subsidy patterns and impacts, the relationship between conspecific interactions and spatial subsidies is unknown. Conspecific interactions describe how sociality influences animal behavior (Stamps, 1988; Turchin, 1989). Many species rely on conspecific cues for important ecological processes like determining habitat quality during foraging and dispersal movement with proximal and ultimate consequences for survival (Giuggioli et al., 2013; Holyoak et al., 2008; Stamps, 2001). Animal territoriality or sociality can influence

animal movement behavior as animals avoid or attract conspecifics (Stamps, 1988; Turchin, 1989). This affects animal space-use decisions and fitness during habitat selection, settlement and home range establishment (Giuggioli et al., 2013; Muller et al., 1997). Many taxa exhibit social behavior, including birds, mammals, reptiles, amphibians and insects (Ben-David et al., 1998; Cote and Clobert, 2007; Farrell et al., 2012). Sociality is therefore important for predicting the impact of many active subsidy systems.

Ecosystem models can enrich our understanding about spatial ecosystem effects of spatial subsidy systems by accounting for the influence of landscape heterogeneity. However, connections between landscape heterogeneity and active subsidy distributions have not been explored in spatial subsidy research and corresponding ecosystem models. Landscape heterogeneity influences animal space-use behavior with consequences for individual and population level fitness and survival (Joly, 2019; Patrick et al., 2008). Spatial heterogeneity in the distribution of resources across landscapes can affect animal movement behavior in a variety of ecological processes including foraging and dispersal (Frair et al., 2005; Miramontes et al., 2012). As animals disperse and forage across landscapes, the quality, availability and configuration of habitat affect habitat selection, settlement, home range establishment and mortality (Morales and Ellner, 2002; Rittenhouse and Semlitsch, 2009; Shepard et al., 2013). The proportional composition, quality and structural configuration of a landscape and constituent land cover types affects spatiotemporal patterns in animal behavior and risk (Fahrig, 2007; Morales et al., 2010; Pérez-Barbería et al., 2015; Rodil et al., 2017), potentially resulting in corresponding variations active subsidy distribution and impacts across landscapes. Incorporating animal behavioral and space use responses (e.g., movement, settlement, mortality risk) to habitat and landscape attributes like

proportion and physical connectedness (e.g., cohesion, contagion) in heterogeneous landscapes can increase the value of ecosystem models for spatial subsidy research.

In this dissertation, I develop and use IBMs to examine the influence of animal movement behavior on active subsidy distributions. Chapters 2-4 address how animal movement behavior alters active subsidy distributions in three important ecological contexts with corresponding spatial subsidy scenarios:

Chapter 2: Movement given mortality risk

Chapter 3: Conspecific interactions

Chapter 4: Landscape heterogeneity

The IBMs in my dissertation chapters are generally based on spatial subsidy systems emerging from animal dispersal from a donor to a recipient ecosystem where animals can eat or die, subsidizing recipient ecosystem resources and consumption (Earl, 2012; Earl et al., 2014). In my models, I assume that dispersers cannot return to the donor ecosystem once they enter the recipient ecosystem. This concept applies to many ecological systems including neonate amphibian emergence and breeding dispersal in marine avian systems where dispersers develop traits conducive for fitness and survival in the recipient ecosystem (Blais et al., 2005; Capps et al., 2015; Hocking et al., 2014; Muriel et al., 2016). I develop IBMs and conduct simulations in NetLogo. Depending on the specific ecological question I address in each my three chapters, I adapt the general structure of my IBMs. I assess emergent spatial patterns for consumer (i.e., living) and nutrient (i.e., dead) subsidy displacement and density patterns separately using machine learning methods suited for large simulation data. Displacement and density metrics indicate the respective extents and intensities of emergent nutrient and consumer subsidy distributions. Nutrient subsidy patterns have different consequences than consumer subsidy patterns in recipient ecosystems (Earl

and Zollner, 2017). Nutrient subsidies result in bottom-up trophic impacts while consumer subsidies tend to cause bottom-down effects in recipient ecosystem food webs (Polis et al., 1997, 1996). This will provide greater information on active subsidy distributions to enhance insights into the impacts in important ecological processes and services (e.g., contaminant transport, disease transfer, seed dispersal, nutrient cycling, pollination) for improved wildlife and natural resources management.

1.2 References

- Aben, J., Strubbe, D., Adriaensen, F., Palmer, S.C.F., Travis, J.M.J., Lens, L., Matthysen, E., 2014. Simple individual-based models effectively represent Afrotropical forest bird movement in complex landscapes. *J. Appl. Ecol.* 51, 693–702.
<https://doi.org/10.1111/1365-2664.12224>
- Barocas, A., Golden, H.N., Harrington, M.W., McDonald, D.B., Ben-David, M., 2016. Coastal latrine sites as social information hubs and drivers of river otter fission–fusion dynamics. *Anim. Behav.* 120, 103–114. <https://doi.org/10.1016/J.ANBEHAV.2016.07.016>
- Bartels, P., Cucherousset, J., Steger, K., Eklov, P., Tranvik, L.J., Hillebrand, H., 2012. Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology* 93, 1173–1182. <https://doi.org/10.1890/11-1210.1>
- Bauduin, S., McIntire, E., St-Laurent, M.-H., Cumming, S., 2016. Overcoming challenges of sparse telemetry data to estimate caribou movement. *Ecol. Modell.* 335, 24–34.
<https://doi.org/10.1016/j.ecolmodel.2016.05.004>

- Ben-David, M., Bowyer, R.T., Duffy, L.K., Roby, D.D., Schell, D.M., 1998. Social behavior and ecosystem processes: River Otter latrines and nutrient dynamics of terrestrial vegetation. *Ecology* 79, 2567–2571.
[https://doi.org/10.1890/0012-9658\(1998\)079\[2567:SBAEPR\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1998)079[2567:SBAEPR]2.0.CO;2)
- Blais, J.M., Kimpe, L.E., McMahon, D., Keatley, B.E., Mallory, M.L., Douglas, M.S.V., Smol, J.P., 2005. Ecology: Arctic seabirds transport marine-derived contaminants. *Science* (80-.).
<https://doi.org/10.1126/science.1112658>
- Brehme, C.S., Boarman, W.I., Hathaway, S.A., Herring, A., Lyren, L., Mendelsohn, M., Pease, K., Rahn, M., Rochester, C., Stokes, D., Turschak, G., Fisher, R.N., 2009. Spatial and temporal patterns across an ecological boundary: Allochthonous effects of a young saltwater lake on a desert ecosystem. *J. Arid Environ.* 73, 811–820.
<https://doi.org/10.1016/j.jaridenv.2009.03.002>
- Capps, K.A., Berven, K.A., Tiegs, S.D., 2015. Modelling nutrient transport and transformation by pool-breeding amphibians in forested landscapes using a 21-year dataset. *Freshw. Biol.* 60, 500–511. <https://doi.org/10.1111/fwb.12470>
- Cote, J., Clobert, J., 2007. Social personalities influence natal dispersal in a lizard. *Proc. R. Soc. London B Biol. Sci.* 274.
- DeAngelis, D.L., Mooij, W.M., 2005. Individual-Based Modeling of Ecological and Evolutionary Processes. *Annu. Rev. Ecol. Evol. Syst.*
<https://doi.org/10.1146/annurev.ecolsys.36.102003.152644>
- Dumont, C.P., Himmelman, J.H., Robinson, S.M.C., 2007. Random movement pattern of the sea urchin *Strongylocentrotus droebachiensis*. *J. Exp. Mar. Bio. Ecol.* 340, 80–89.
<https://doi.org/10.1016/j.jembe.2006.08.013>

- Earl, J.E., 2012. Effects of spatial subsidies and canopy cover on pond communities and multiple life stages in amphibians. Submitt. by Univ. Missouri--Columbia Grad. Sch.
- Earl, J.E., Castello, P.O., Cohagen, K.E., Semlitsch, R.D., 2014. Effects of subsidy quality on reciprocal subsidies: how leaf litter species changes frog biomass export. *Oecologia* 175, 209–218. <https://doi.org/10.1007/s00442-013-2870-x>
- Earl, J.E., Zollner, P.A., 2017. Advancing research on animal-transported subsidies by integrating animal movement and ecosystem modelling. *J. Anim. Ecol.* 86, 987–997. <https://doi.org/10.1111/1365-2656.12711>
- Earl, J.E., Zollner, P.A., 2014. Effects of animal movement strategies and costs on the distribution of active subsidies across simple landscapes. *Ecol. Modell.* 283, 45–52. <https://doi.org/10.1016/j.ecolmodel.2014.03.020>
- Fahrig, L., 2007. Non-optimal animal movement in human-altered landscapes. *Funct. Ecol.* 21, 1003–1015. <https://doi.org/10.1111/j.1365-2435.2007.01326.x>
- Farrell, S.L., Morrison, M.L., Campomizzi, A.J., Wilkins, R.N., 2012. Conspecific cues and breeding habitat selection in an endangered woodland warbler. *J. Anim. Ecol.* 81, 1056–1064. <https://doi.org/10.1111/j.1365-2656.2012.01995.x>
- Frair, J.L., Merrill, E.H., Visscher, D.R., Fortin, D., Beyer, H.L., Morales, J.M., 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landsc. Ecol.* 20, 273–287. <https://doi.org/10.1007/s10980-005-2075-8>
- Giuggioli, L., Potts, J.R., Rubenstein, D.I., Levin, S.A., 2013. Stigmergy, collective actions, and animal social spacing. *Proc. Natl. Acad. Sci. U. S. A.* 110, 16904–9. <https://doi.org/10.1073/pnas.1307071110>

- Greig, H.S., Kratina, P., Thompson, P.L., Palen, W.J., Richardson, J.S., Shurin, J.B., 2012. Warming, eutrophication, and predator loss amplify subsidies between aquatic and terrestrial ecosystems. *Glob. Chang. Biol.* 18, 504–514. <https://doi.org/10.1111/j.1365-2486.2011.02540.x>
- Grimm, V., Railsback, S.F., 2004. *Individual-based Modeling and Ecology*, Princeton University Press. <https://doi.org/10.1111/j.1467-2979.2008.00286.x>
- Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8, 993–1009. <https://doi.org/10.1111/j.1461-0248.2005.00792.x>
- Hanks, E.M., Hooten, M.B., Alldredge, M.W., 2012. Continuous-time discrete-space models for animal movement. <https://doi.org/10.1214/14-AOAS803>
- Herbst, S.J., Stevens, B.S., Hayes, D.B., Hanchin, P.A., Post, J., 2016. Estimating walleye (*Sander vitreus*) movement and fishing mortality using state-space models: implications for management of spatially structured populations. *Can. J. Fish. Aquat. Sci.* 73, 330–348. <https://doi.org/10.1139/cjfas-2015-0021>
- Hocking, D.J., Babbitt, K.J., Hocking, D.J., 2014. Amphibian contributions to ecosystem services. *Herpetol. Conserv. Biol.*
- Holdo, R.M., Holt, R.D., Coughenour, M.B., Ritchie, M.E., 2007. Plant productivity and soil nitrogen as a function of grazing, migration and fire in an African savanna. *J. Ecol.* 95, 115–128. <https://doi.org/10.1111/j.1365-2745.2006.01192.x>
- Holdo, R.M., Holt, R.D., Fryxell, J.M., 2009. Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. *Ecol. Appl.* 19, 95–109. <https://doi.org/10.1890/07-1954.1>

- Holyoak, M., Casagrandi, R., Nathan, R., Revilla, E., Spiegel, O., 2008. Trends and missing parts in the study of movement ecology. *Proc. Natl. Acad. Sci. U. S. A.* 105, 19060–5. <https://doi.org/10.1073/pnas.0800483105>
- Hooten, M.B., Buderman, F.E., Brost, B.M., Hanks, E.M., Ivan, J.S., 2016. Hierarchical animal movement models for population-level inference.
- Joly, P., 2019. Behavior in a Changing Landscape: Using Movement Ecology to Inform the Conservation of Pond-Breeding Amphibians. *Front. Ecol. Evol.* 7, 155. <https://doi.org/10.3389/fevo.2019.00155>
- Jonsen, I.D., Flemming, J.M., Myers, R.A., 2005. Robust state-space modeling of animal movement data. *Ecology* 86, 2874–2880. <https://doi.org/10.1890/04-1852>
- King, A.W., With, K.A., 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecol. Modell.* 147, 23–39. [https://doi.org/10.1016/S0304-3800\(01\)00400-8](https://doi.org/10.1016/S0304-3800(01)00400-8)
- Kraus, J.M., Pletcher, L.T., Vonesh, J.R., 2011. Variation in active and passive resource inputs to experimental pools: mechanisms and possible consequences for food webs. *Freshw. Biol.* 56, 491–502. <https://doi.org/10.1111/j.1365-2427.2010.02516.x>
- Lele, S.R., Merrill, E.H., Keim, J., Boyce, M.S., 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. *J. Anim. Ecol.* 82, 1183–1191. <https://doi.org/10.1111/1365-2656.12141>
- Lima, S.L., Zollner, P.A., 1996. Towards a behavioral ecology of ecological landscapes. *Trends Ecol. Evol.* [https://doi.org/10.1016/0169-5347\(96\)81094-9](https://doi.org/10.1016/0169-5347(96)81094-9)

- Malison, R.L., Lorang, M.S., Whited, D.C., Stanford, J.A., 2014. Beavers (*Castor canadensis*) influence habitat for juvenile salmon in a large Alaskan river floodplain. *Freshw. Biol.* 59, 1229–1246. <https://doi.org/10.1111/fwb.12343>
- Marcarelli, A.M., Baxter, C. V., Mineau, M.M., Hall, R.O., 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. *Ecology* 92, 1215–1225. <https://doi.org/10.1890/10-2240.1>
- Marczak, L.B., Richardson, J.S., 2007. Spiders and subsidies: Results from the riparian zone of a coastal temperate rainforest. *J. Anim. Ecol.* 76, 687–694. <https://doi.org/10.1111/j.1365-2656.2007.01240.x>
- McCaffery, M., Eby, L., 2016. Beaver activity increases aquatic subsidies to terrestrial consumers. *Freshw. Biol.* 61, 518–532. <https://doi.org/10.1111/fwb.12725>
- McInturf, A.G., Pollack, L., Yang, L.H., Spiegel, O., 2019. Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors? *Biol. Rev.* brv.12525. <https://doi.org/10.1111/brv.12525>
- Menden-Deuer, S., 2010. Inherent high correlation of individual motility enhances population dispersal in a heterotrophic, planktonic protist. *PLoS Comput. Biol.* 6, e1000942. <https://doi.org/10.1371/journal.pcbi.1000942>
- Miramontes, O., Boyer, D., Bartumeus, F., 2012. The effects of spatially heterogeneous prey distributions on detection patterns in foraging seabirds. *PLoS One* 7, e34317. <https://doi.org/10.1371/journal.pone.0034317>
- Moorcroft, P.R., Lewis, M.A., Crabtree, R.L., 2006. Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *Proc. R. Soc. B Biol. Sci.* 273, 1651–1659. <https://doi.org/10.1098/rspb.2005.3439>

- Morales, J.M., Ellner, S.P., 2002. Scaling up animal movements in heterogeneous landscapes: The importance of behavior. *Ecology* 83, 2240–2247. [https://doi.org/10.1890/0012-9658\(2002\)083\[2240:SUAMIH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2240:SUAMIH]2.0.CO;2)
- Morales, J.M., Moorcroft, P.R., Matthiopoulos, J., Frair, J.L., Kie, J.G., Powell, R.A., Merrill, E.H., Haydon, D.T., 2010. Building the bridge between animal movement and population dynamics. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 365, 2289–301. <https://doi.org/10.1098/rstb.2010.0082>
- Muller, K.L., Stamps, J.A., Krishnan, V. V, Willits, N.H., 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). *Am. Nat.* 150, 650–61. <https://doi.org/10.1086/286087>
- Muñoz, D.J., Miller, D.A.W., Sutherland, C., Grant, E.H.C., 2016. Using Spatial Capture–Recapture to Elucidate Population Processes and Space-Use in Herpetological Studies. *J. Herpetol.* 50, 570–581. <https://doi.org/10.1670/15-166>
- Muriel, R., Morandini, V., Ferrer, M., Balbontín, J., Morlanes, V., 2016. Juvenile dispersal behaviour and conspecific attraction: An alternative approach with translocated Spanish imperial eagles. *Anim. Behav.* 116, 17–29. <https://doi.org/10.1016/j.anbehav.2016.03.023>
- Nakano, S., Murakami, M., 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proc. Natl. Acad. Sci. U. S. A.* 98, 166–70. <https://doi.org/10.1073/pnas.98.1.166>
- Nielsen, S.E., Herrero, S., Boyce, M.S., Mace, R.D., Benn, B., Gibeau, M.L., Jevons, S., 2004. Modelling the spatial distribution of human-caused grizzly bear mortalities in the Central Rockies ecosystem of Canada. *Biol. Conserv.* 120, 101–113. <https://doi.org/10.1016/J.BIOCON.2004.02.020>

- Palumbi, S.R., 2003. Ecological subsidies alter the structure of marine communities. *Proc. Natl. Acad. Sci.* 100, 11927–11928. <https://doi.org/10.1073/pnas.2335832100>
- Patrick, D.A., Harper, E.B., Hunter, M.L., Calhoun, A.J.K., 2008. Terrestrial habitat selection and strong density-dependent mortality in recently metamorphosed amphibians. *Ecology* 89, 2563–74.
- Pereira, L.M., Owen-Smith, N., Moleón, M., 2014. Facultative predation and scavenging by mammalian carnivores: Seasonal, regional and intra-guild comparisons. *Mamm. Rev.* <https://doi.org/10.1111/mam.12005>
- Pérez-Barbería, F.J., Small, M., Hooper, R.J., Aldezabal, A., Soriguer-Escofet, R., Bakken, G.S., Gordon, I.J., 2015. State-Space Modelling of the Drivers of Movement Behaviour in Sympatric Species. *PLoS One* 10, e0142707. <https://doi.org/10.1371/journal.pone.0142707>
- Piou, C., Berger, U., Grimm, V., 2009. Proposing an information criterion for individual-based models developed in a pattern-oriented modelling framework. *Ecol. Modell.* 220, 1957–1967. <https://doi.org/10.1016/j.ecolmodel.2009.05.003>
- Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an Integration of Landscape and Food Web Ecology: The Dynamics of Spatially Subsidized Food Webs. *Annu. Rev. Ecol. Syst.* 28, 289–316.
- Polis, G.A., Holt, R.D., Menge, B.A., Winemiller, K.O., 1996. Time, Space, and Life History: Influences on Food Webs, in: *Food Webs*. Springer US, Boston, MA, pp. 435–460. https://doi.org/10.1007/978-1-4615-7007-3_38
- Quinn, T.P., Carlson, S.M., Gende, S.M., Rich, Jr., H.B., 2009. Transportation of Pacific salmon carcasses from streams to riparian forests by bears. *Can. J. Zool.* 87, 195–203. <https://doi.org/10.1139/Z09-004>

- Rittenhouse, T.A.G., Semlitsch, R.D., 2009. Behavioral response of migrating wood frogs to experimental timber harvest surrounding wetlands. *Can. J. Zool.* 87, 618–625.
<https://doi.org/10.1139/Z09-049>
- Rodil, I.F., Lucena-Moya, P., Jokinen, H., Ollus, V., Wennhage, H., Villnäs, A., Norkko, A., 2017. The role of dispersal mode and habitat specialization for metacommunity structure of shallow beach invertebrates. *PLoS One* 12, e0172160.
<https://doi.org/10.1371/journal.pone.0172160>
- Scharf, A.K., Belant, J.L., Beyer, D.E., Wikelski, M., Safi, K., 2018. Habitat suitability does not capture the essence of animal-defined corridors. *Mov. Ecol.* <https://doi.org/10.1186/s40462-018-0136-2>
- Schindler, D.E., Smits, A.P., 2017. Subsidies of Aquatic Resources in Terrestrial Ecosystems. *Ecosystems.* <https://doi.org/10.1007/s10021-016-0050-7>
- Shepard, E.L.C., Wilson, R.P., Rees, W.G., Grundy, E., Lambertucci, S.A., Vosper, S.B., 2013. Energy Landscapes Shape Animal Movement Ecology. *Am. Nat.* 182, 298–312.
<https://doi.org/10.1086/671257>
- Smouse, P.E., Focardi, S., Moorcroft, P.R., Kie, J.G., Forester, J.D., Morales, J.M., 2010. Stochastic modelling of animal movement. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 365, 2201–11. <https://doi.org/10.1098/rstb.2010.0078>
- Stamps, J., 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. Clobert, J., Danc. E., Dhondt, A. Nichols, J. Dispersal. Oxford Univ. Press. Pages 230-242 in.
- Stamps, J.A., 1988. Conspecific Attraction and Aggregation in Territorial Species. *Am. Nat.* 131, 329–347. <https://doi.org/10.1086/284793>

- Tisue, S., Wilensky, U., 2004. Netlogo: A simple environment for modeling complexity. Conf. Complex Syst. 1–10. <https://doi.org/10.1109/ICVD.2004.1261037>
- Turchin, P., 1989. Population Consequences of Aggregative Movement. *J. Anim. Ecol.* 58, 75. <https://doi.org/10.2307/4987>
- von Stedingk, H., Fyfe, R.M., Allard, A., 2008. Pollen productivity estimates from the forest—tundra ecotone in west-central Sweden: implications for vegetation reconstruction at the limits of the boreal forest. *The Holocene* 18, 323–332. <https://doi.org/10.1177/0959683607086769>
- Wallentin, G., 2017. Spatial simulation: A spatial perspective on individual-based ecology—a review. *Ecol. Modell.* 350, 30–41. <https://doi.org/10.1016/J.ECOLMODEL.2017.01.017>
- Wesner, J.S., 2010. Aquatic predation alters a terrestrial prey subsidy. *Ecology* 91, 1435–1444. <https://doi.org/10.1890/09-1532.1>
- Wolf, A., Doughty, C.E., Malhi, Y., 2013. Lateral diffusion of nutrients by mammalian herbivores in terrestrial ecosystems. *PLoS One* 8, e71352. <https://doi.org/10.1371/journal.pone.0071352>
- Zollner, P.A., Lima, S.L., 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80, 1019–1030. [https://doi.org/10.1890/0012-9658\(1999\)080\[1019:SSFLLI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1019:SSFLLI]2.0.CO;2)

CHAPTER 2. THE INFLUENCE OF ANIMAL MOVEMENT PATTERN AND MORTALITY MODELS ON THE DISTRIBUTION OF ANIMAL-TRANSPORTED SUBSIDIES

2.1 Abstract

Active subsidies are resource transfers between ecosystems by animals navigating landscapes. Subsidies may originate from consumer nutrient deposition or animal carcasses that are deposited in new ecosystems. Animal movement behavior has the potential to significantly mediate the extent and intensity of active subsidies and corresponding ecosystem responses. Animal movement behaviors and mortality can affect active subsidy distributions but have rarely been examined in spatial subsidy models. Movement ecologists typically simulate animal dispersal and foraging movements using variations on random-walk patterns as correlated random walk (CRW) and Lévy walk (LW) respectively. Movement models typically implement mortality as an instantaneous mortality rate (i.e., animal's step-level probability of death). Variation in CRW and LW movement patterns, in combination with mortality probability can change emergent subsidy distributions depending on the mortality probability level. Using a spatially explicit individual-based model (IBM), we quantify how variation in the straightness (i.e. CRW) and step length (i.e. LW) of animal movement patterns, in combination with variation in mortality probability and type, alter the intensity and extent of consumer and nutrient subsidy distributions. Movement pattern and LW scale were dominant determinants of subsidy displacement with more pronounced effects on living (consumer) subsidies. Mortality probability and LW mortality model (i.e., space versus time) strongly predicted subsidy density with stronger effects on dead (nutrient) subsidy deposition patterns. Consumer subsidies were deposited farther and at lower densities than nutrient subsidies. Given lower mortality probability, movements with more variable step lengths displaced both

nutrient and consumer subsidies farther and at lower densities than straighter movements. Movements with more variable step lengths also resulted in greater nutrient subsidy numbers at lower densities with higher mortality probability in spaced-based compared to time-based mortality models. Spatial subsidy models that incorporate interaction between animal movement behavior and mortality conditions enhance insights into animal-transported subsidy distributions.

2.2 Introduction

Animal movement across landscapes can have significant effects on processes and patterns at the ecosystem scale (Doughty et al., 2016). Animal movement can displace resources (e.g., prey, producers, minerals, and nutrients in feces and detritus) and consumers (e.g., predators, pathogens, and parasites) between ecosystems as ecological subsidies (Polis et al., 1997; Quinn et al., 2009). Active subsidies are resources or consumers displaced by animal movement between a donor and a recipient ecosystem and are different from passive subsidies, which are moved by wind and water (Knight et al., 2005; Leroux and Loreau, 2008). Active subsidies can change trophic relationships, alter ecosystem structure and function, and modify material and energetic balances in recipient ecosystems with consequences for ecosystem function and services, including biodiversity maintenance, nutrient cycling and regulation (Ben-David et al., 1998; Farina et al., 2003). Cross-ecosystem subsidies also have implications for the transport of pollutants and pathogens across ecosystem boundaries (Walters et al., 2008).

Despite the significance of active subsidies for ecosystem processes, function and services, there is limited ecological research examining how animal movement behavior and mortality levels influence active subsidy distribution. Even though animal movements have been connected to emergent population patterns, animal movements have not been linked to spatial subsidies and impacts in different ecological scenarios because existing ecosystem models treat movement and

space implicitly (Earl and Zollner 2017, McInturf et al., 2019). For instance, animal foraging movements can result in different subsidy distributions than dispersal search or migratory movements with corresponding variations in ecosystem impact. Most active subsidy research considers space implicitly (Jonsen et al., 2005, 2003; Patterson et al., 2008). Modeling frameworks that do not address the link between mechanistic movement processes and animal distribution patterns can ignore important connections between spatially explicit animal movement and ecosystem-level impacts. Enhancing our understanding of spatially explicit animal movement in the context of active subsidies in ecological landscapes can be critical for species and biodiversity conservation, as well as ecosystem management given global environmental change.

The movement ecology paradigm provides tools to examine how animal movement dynamics in foraging, dispersal and other ecological processes influence emergent scales of active subsidy distributions. Movement ecology frameworks can be used to develop spatially explicit models to predict active subsidy distributions (Earl and Zollner, 2017, 2014) and connect animal movement behavior and space-use processes to spatial subsidy distributions. Movement ecology provides a methodological basis for modeling animal movement as a function of changes in landscape and body morphology, internal state (e.g., hunger, fear, thirst, memory) and external factors (Nathan et al., 2008). Movement models typically do not emphasize ecosystem processes, and thus have not been used to understand the spatiotemporal dynamics of active subsidies in response to animal foraging and dispersal movements. A combination of individual-based and stochastic animal movement and space-use models can yield valuable insights on how movement behavior dynamics influence animal-transported subsidy distributions across landscapes and simplify analyses of complex ecosystem-scale effects (Smouse et al., 2010). Stochastic movement models divide animal trajectories into discrete paths with statistical distributions of step lengths

and turning angles (Codling et al., 2008; Moorcroft, 2012). We can therefore use behaviorally minimalist individual-based modeling (IBM) frameworks with stochastic methods to model complex interactions between dispersal and foraging movement processes and emergent subsidy patterns across scales of biological and ecological organization (Grimm and Railsback, 2012).

Dispersal search patterns and foraging movements are often modeled using correlated random walks (CRW) and Lévy walks (LW), respectively, two dominant stochastic animal movement models (Kareiva and Shigesada, 1983; Viswanathan et al., 1996). However, spatial subsidy researchers have not examined how active subsidy distributions and corresponding ecosystem effects respond to variation in CRW and LW as germane representations of random dynamics in dispersal and foraging movements. CRW is used to model dispersal search movement as uniform distributions of successive, discrete movements sequentially scaled by correlated turning angles (Bergman et al., 2000), and LW is used to model foraging movement with random turning angles scaled by variable step lengths from a heavy-tailed power law distribution (Zhao et al., 2015). The movement ecology literature is replete with contention about the relative efficacy of CRW and LW models as representations of multiscale animal dispersal and foraging movement patterns respectively, in interaction with landscapes and as evolutionarily successful strategies (Benhamou, 2007; Reynolds, 2015, 2008), but the two movement types appear to be consistent with a variety of empirical examples (Codling et al., 2008). Using IBMs with broad parameter spaces to quantify the effects of variation in CRW and LW scaling on active subsidy distributions can highlight their relative and collective relevance for modeling spatially explicit animal movement behavior in a wide array of multispecies foraging and dispersal movement scenarios.

Animal movement behavior can play a critical role in the distribution of foraging and dispersal mortality events in space and related ecological subsidies with ecosystem-scale

consequences (Earl and Zollner, 2014). Models that address how active subsidy distributions respond to different scenarios of spatially explicit stochasticity in movement and mortality dynamics can highlight differences in the scales of dead and living subsidy distributions. Mortality risks in ecological landscapes could impose corresponding consequences for species survival that impact animal movement behavior. Mortality risk is essential for understanding how animals move in different environments (i.e., climate and geomorphology) and communities (i.e., interspecific and intraspecific interactions) (Fahrig, 2007; Schtickzelle et al., 2006). Predators and prey can alter the amount and spatial distribution of consumer (i.e., living) and nutrient (i.e., dead) subsidies in recipient ecosystems when foraging or avoiding predation respectively (Miller et al., 2014; Schmitz, 2008). Predators and scavengers can transport carcasses over varying distances and deposit carrion and feces beyond kill sites (Vizzini et al., 2016). Developing models to study the relative significance and interactive influence of movement behavior dynamics with different mortality conditions on consumer versus nutrient subsidy distributions across a range of ecologically plausible dispersal and foraging scenarios can improve our understanding of the scale and dynamics of corresponding ecosystem effects.

Mortality costs during animal dispersal or foraging movements can change with spatiotemporal variation in the distribution of predation risk and hazardous climatic and environmental conditions (Bastille-Rousseau et al., 2017). Prey can experience spatial variations in predation risk as a function of the distance between refuges in inhospitable landscape matrices or the degree of antipredator vigilance during foraging versus dispersal movements (Kristan and Boarman, 2003; Yoder et al., 2004). Tradeoffs between spatial and temporal mortality costs can influence animal foraging and dispersal movements differently (Zollner and Lima, 2005), which would subsequently affect active subsidy distribution patterns across landscapes. Animals that

cover larger areas foraging or dispersing can encounter more predators and inhospitable habitat conditions (DeCesare, 2012). Similarly, high activity levels can increase the risk of detection by predators and energy expenditure in unfavorable habitat conditions (Martin et al., 2015). Animals that disperse faster through inhospitable areas can therefore reduce temporal predation mortality risk with extended activity times but increase spatial predation mortality risk by covering more ground in less time (Yoder et al., 2004). Depending on the degree of step length variability, foraging animals that move using LW can therefore be more or less susceptible to spatial than temporal mortality risks compared to animals with CRW dispersal search behavior. Considering the relative effects of time-based and space-based scenarios of variation in mortality risk with different degrees of step length variability in model constructions can therefore generate valuable insights into connections between animal movement behavior dynamics and active subsidy distribution.

Our main goal is to quantify the relative importance and interaction between variation in movement pattern scaling and mortality risk for active subsidy distributions. We construct a theoretical IBM with stochastic movement models to investigate how active living and dead subsidy distributions respond to different animal movement dynamics and mortality scenarios. Our model simulates and quantifies emergent spatial extents and intensities of active subsidy distributions from a broad parameter space of CRW and LW scaling for animal dispersal and foraging movement behaviors with changes in mortality probability. We examine the interactive effects between movements with different degrees of LW step length variability and mortality assessed as a function of space versus time. The overarching hypothesis is that the range and spread of active consumer and nutrient subsidy distributions respond notably to spatially explicit variations in animal movement patterns with mortality risk level and function. We expect more

sinuous movements (CRW) to deposit subsidies at higher densities closer to the ecosystem boundary than movements with less variable step lengths (LW), with more pronounced effects on dead than living subsidies at higher mortality probabilities. Given the scale-invariance of LW patterns, movements with more variable step lengths (LW) will likely deposit subsidies farther and at lower densities than straighter movements (CRW) with stronger effects on living than dead subsidies at higher mortalities. We expect higher mortality probabilities to limit subsidy displacement and concentrate living and dead subsidies at higher densities closer to the ecosystem boundary, with greater impact for dead and CRW subsidies compared to living and LW subsidies respectively.

2.3 Methods

2.3.1 Background

We built a simulation model to investigate how variations in animal movement patterns and mortality costs impact the distribution of active living and dead subsidies. We constructed a simple binary world, in which animals initiate movement from a donor ecosystem (natal habitat) and disperse into a recipient ecosystem (adult habitat) with a stochastic chance of death during movement (Earl and Zollner, 2014). This theoretical model applies to many ecological systems including spatial subsidies from amphibian and aquatic insect dispersal and foraging movements in terrestrial landscapes adjacent to source ponds and streams (Capps et al., 2015). Dead individuals provide nutrients, energy, and/or prey to the recipient ecosystems possibly causing bottom-up effects, while living individuals provide a consumer subsidy with potential top-down effects. In our model, individuals could not return to the donor ecosystem after moving into the recipient ecosystem as they undergo ontogenetic or behavioral shifts that are only compatible with the latter habitat. This applies for many species that undergo cross ecosystem natal and breeding

dispersal (e.g., aquatic insects and amphibians) and develop morphological attributes that constrain survival or breeding success in the donor ecosystem (Bishir et al., 2018; Blais et al., 2005).

We made some simplifying assumptions to constrain the modeling process to suit available computer processing speed and storage, as well as for conceptual clarity. We considered only the movement and mortality dynamics of animal-transported subsidies in our model. We assumed that the movement and mortality occur at a small enough time scale that we did not have to consider other demographic processes. We did not account for direct interaction effects between movement behavior and landscape heterogeneity by assuming that animals move and die in a binary world, from a donor to a recipient ecosystem. We also assumed that dead individuals represent nutrient, energy, or contaminant subsidies confined to the location of deposition within the recipient ecosystem to allow us to perform and compare separate analyses of dead and living subsidy distributions. Another assumption we made is that animals have a constant chance of randomly occurring death with each move, and that discrete time is denoted by a single step navigated in the landscape regardless of the rate of movement or distance moved. For movement with variable step lengths (LW) in space-based mortality scenarios, we assumed that mortality can interact with space as a function of the distance covered per step.

Our spatially explicit individual-based model simulation was designed in NetLogo (version 6.0.4) software (Tisue and Wilensky, 2004; Wilensky, 1999), and we analyzed data in program R (version 3.3). Code is available in the supplementary material (Appendix A).

2.3.2 Design

We simulated a binary universe (donor-recipient ecosystem) with 1000 individuals moving outward from the donor ecosystem into an adjacent recipient ecosystem. The simulation environment consists of a vertically wrapped, two-dimensional 1000 (vertical) by 2000 (horizontal)

patch world with the donor ecosystem (1 by 1 patch) centered at the left vertical boundary of the world. A patch is the default unit of square space in NetLogo. Simulation runs were initialized with all individuals randomly distributed in the donor ecosystem. Individuals moved in the recipient ecosystem over 1000 timesteps and were deflected back into the world upon encountering a vertical boundary (Figure 1).

We conducted fully factorial simulations of movement and mortality variable parameter combinations (Table 1) with ten replicate runs per parameter set. Mortality can occur for any individual moving in the recipient ecosystem at any timestep. We quantified and collected population distribution metrics of living and dead individuals on a per-timestep basis but used data values at the 1000th timestep to assess spatial subsidy patterns.

We modeled animal movement behavior as CRW and LW using representative statistical distributions of step lengths and turning angle orientations. At each timestep, individuals select a random step length and turning angle from respective characteristic distributions to navigate from the donor ecosystem start-patch outward and rightward through the adjacent recipient ecosystem. We implemented CRW using a constant one-unit step length and a wrapped Cauchy distribution of degree turning angles $\theta(t)$ for any given timestep (t) as:

$$\theta(t) = \theta(t - 1) + 2 \tan^{-1} \left[\left(\frac{1 - \alpha}{1 + \alpha} \right) \tan(\pi\varphi) \right],$$

where $0 \leq \alpha \leq 1$, and

$$-0.5 \leq \varphi \leq 0.5$$

for a previous turning angle of $\theta(t - 1)$ with φ drawn from a uniform distribution in $[-0.5, 0.5]$ to curb orientational bias by normalizing net displacement to a mean turning angle of 0^0 . We simulated a comprehensive range of CRW patterns from sinuous to straight movement by varying the correlation coefficient (α) (Table 1). CRW movement is straighter as $\alpha \rightarrow 1$ and more sinuous

as $\alpha \rightarrow 0$. We implemented LW using a circular normal turning angle distribution over a range of $[-\pi, \pi]$, and a truncated inverse-power law distribution for the relationship between randomly drawn step lengths $P(s)$ and the minimum step length (s) as:

$$P(s) = \beta s^{-\left(\frac{1}{\mu}\right)}$$

where $1 < \mu \leq 3$, and

$$0 < \beta \leq 1$$

Using a minimum step length of 1, we modeled an inclusive range of LW patterns from high to low step length variability by changing the scaling exponent (μ) (Table 1). LW resembles random walk with near-uniform step lengths as $\mu \rightarrow 3$, and simulates scale-invariant movement as $\mu \rightarrow 1$ with more variable step lengths. We varied the frequency of occurrence of longer step lengths for LW using a normalization constant (β) where $\beta \in \{0.25, 0.5, 1\}$.

We varied the per-timestep likelihood of death using three levels of mortality probability (m) from low to high (Table 1). Individuals draw a random number from a uniform distribution (in $[0, 1]$) at each timestep and die and stop moving if the number drawn is lower than the assigned simulation mortality level for the simulation run. We implemented time-based mortality for CRW and LW as death regardless of step length. We modeled space-based mortality for LW as death as function of step length, per unit of space travelled with each step.

2.3.3 Analysis

We collected displacement and density metrics of living and dead subsidy distribution patterns for each simulation run to assess the effect of variation in movement behavior and mortality (Table 1). These response variables include the number of dead subsidies, the maximum subsidy deposition distance and range, as well as the peak subsidy deposition density and the distance to peak deposition density. The maximum deposition distance is the distance to the

furthest displaced subsidy from the donor-recipient ecosystem boundary. The maximum deposition range is the distance between the furthest and least displaced subsidies from the donor-ecosystem boundary. The peak deposition density is the maximum number of subsidies per density-area demarcated by a radius (a) around each subsidy, where $a \in \{25, 50, 100\}$. The distance to peak density is the distance between the focal subsidy at the location of peak deposition density and the donor-recipient ecosystem boundary. The density area did not affect the outcomes for subsidy distribution metrics.

We used classification and regression trees (CARTs) (Breiman et al., 2017; Therneau et al., 2018) and random forest (Breiman et al., 2011) analyses to compare the effect of variation in movement patterns and mortality types on spatial subsidy distribution metrics. General linear models and other frequentist statistical approaches that require significance testing do not perform well for datasets from individual-based model simulation datasets with large sample sizes (White et al., 2014). High power invariably results in high significance in IBM post hoc analyses. Machine learning-based neural network algorithms like CARTs and random forests are therefore more useful for examining predictor importance and interaction effects in multivariate datasets from IBM simulations. We used random forest analyses to determine the relative importance of predictors for response variables based on the increase in mean square error and split purity (Residual Sum of Squares) from a sample of 2000 random forest fits. We developed random forest models with random sampling and permutation with bootstrapping and bagging on predictor levels fit to response observations. We supported random forest analyses with CARTs to determine natural breaks (splits) and likely outcomes in dependent variable observations in response to interactions in movement and mortality predictor level combinations. The minimum number of dependent variable observations required for a conditional CART split in response to predictor

level combinations was 600 (greater than 10% of the total number of observations). The minimum number of dependent variable observations required for a conditional CART outcome in response to predictor level combinations was 200. We assigned a complexity parameter (C_p) value of 0.001 to select and retain CART fits with response variable splits on predictor combinations that improve the coefficients of determination for CART models by more than 0.1%. We conducted separate analyses on emergent subsidy distributions from variation in CRW and LW movement patterns with mortality probability, and space-based versus time-based mortality with LW step length variability.

We synthesized CART trends into charts. To do this, we grouped CARTs related to subsidy deposition distance and density metrics into respective displacement and density categories. We extracted elements of CARTs that differentiated between outcomes by a minimum of 10% ($n = 2700$) of the total number of observations ($n = 27,000$) based on comparable predictor combinations across subsidy distribution metrics. In the resulting charts, bold lines indicate trends observed in all representative CART figures for each subsidy distribution metric category. Thin lines indicate trends featured in more than one but not all representative CART figures for each subsidy distribution metric category. See supplementary materials (Appendix A) for more detailed CART figures (Figures 21, 23, 25 and 27).

2.4 Results

Scale coefficient and mortality were more important determinants of subsidy displacement and density respectively (Figure 2). Scale coefficient and overall movement pattern (CRW versus LW) strongly predicted maximum subsidy deposition distance, range and peak density distances for living and dead subsidies, but the relative effects on subsidy displacement varied with mortality rate and type. Mortality rate and type strongly predicted the peak deposition densities for both

living and dead subsidies but the effect of mortality on subsidy densities varied with scale coefficient, resulting in different outcomes between living and dead subsidies. Scale coefficient was more important than mortality for predicting the peak deposition densities and distances to peak deposition density locations for living subsidies. Mortality was more significant than scale coefficient for determining the peak deposition densities, but scale coefficient was more important for predicting corresponding distances to peak deposition density locations for dead subsidies. LW scale coefficient strongly predicted the subsidy displacement in both space-based and time-based mortality scenarios, but mortality type (space-based versus time-based) was as important as scale coefficient for predicting the peak deposition density for both living and dead subsidies (Figure 3).

Dead subsidies were generally deposited closer to the shared ecosystem boundary than living subsidies with stronger effects for LW than CRW (Figure 20). LW step length variability had a greater effect on the extent of subsidy displacement than the straightness of CRW (Figure 4). Movements with more variable step lengths ($\mu \in \{1.0, 1.5, \}$) displaced living and dead subsidies farther from the donor-recipient ecosystem boundary resulting in greater maximum subsidy deposition distances and ranges than straighter movements ($\alpha \in \{0.95, 0.99\}$) (Figure 21). Straighter movements deposited subsidies at greater maximum deposition distances and ranges, marginally outperforming intermediate step length variability ($\mu = 2.0$) in low and intermediate mortality scenarios. High mortality limited strong displacement effects of movements with more variable step lengths on living subsidies but enhanced the displacement of dead subsidies. Movements with less variable step lengths ($\mu \in \{2.5, 3.0\}$) generally displaced subsidies closer to the shared ecosystem boundary generating lower maximum subsidy deposition distances and ranges than more sinuous movements ($\alpha \in \{0.5, 0.8\}$). The locations at which peak density occurred were closer to the shared ecosystem boundary for dead subsidies than living subsidies.

Movements with more variable step lengths generated greater distances to peak deposition density than straighter movements for living subsidies. Movements with less variable step lengths resulted in lower distances to peak density for living subsidies than more sinuous movements. For dead subsidies, straighter movements resulted in greater distances to peak deposition density than movements with more variable step lengths. Movements with less variable step lengths generated lower overall distances to peak deposition density for dead subsidies. Dead subsidies were generally deposited at lower densities closer to the shared ecosystem boundary than living subsidies with stronger effects for LW than CRW (Figure 22). Compared to more sinuous movements, movements with less variable step lengths resulted in higher subsidy densities that increased with mortality (Figure 5). Movements with less variable step lengths also deposited living subsidies at higher peak densities than more sinuous movements (Figure 23). Given high mortality, movements with more variable step lengths deposited living subsidies at lower peak densities than straighter movements. In high mortality scenarios, more sinuous movements deposited dead subsidies at greater peak deposition densities than movements with less variable step lengths. For both living and dead subsidies, movements with more variable step lengths and straighter movements generated lower peak deposition densities that further attenuated in low mortality scenarios. For living subsidies, moderate peak deposition densities resulted from straighter movements compared to intermediate step length variability.

Space-based mortality interacted with movements with more variable step lengths to displace subsidies closer to the shared ecosystem boundary than time-based mortality (Figure 6). Increasing space-based mortality however enhanced dead subsidy displacement and attenuated living subsidy displacement (Figure 24). Compared to time-based mortality, space-based mortality interacted with movements with more variable step lengths to deposit subsidies at higher densities

farther from the ecosystem boundary (Figure 7). Movements with less variable step lengths resulted in lower maximum subsidy deposition distances for both living and dead subsidies (Figure 25). High mortality in space-based scenarios generated lower maximum deposition distances and ranges for living subsidies than time-based mortality scenarios. For movements with more variable step lengths, space-based mortality resulted in greater maximum subsidy deposition distances and ranges for dead subsidies than time-based mortality. Movements with more variable step lengths also deposited living subsidies at greater distances to peak density in space-based than time-based mortality scenarios. Movements with less variable step lengths generated lower distances to peak deposition density for living subsidies regardless of mortality type. Dead subsidies were deposited at greater distances to peak density in time-based compared to space-based mortality. Compared to time-based mortality, space-based mortality generally resulted in greater peak subsidy deposition densities (Figure 26). Increasing space-based mortality enhanced peak deposition densities for dead subsidies but attenuated peak deposition densities for living subsidies. For living subsidies from movements with less variable step lengths, space-based mortality generated higher peak deposition densities than time-based mortality (Figure 27). Movements with more variable step lengths resulted in lower peak deposition densities for dead subsidies given high mortality in space-based compared to time-based scenarios. Movements with more variable step lengths generally resulted in more dead subsidies in space-based than time-based mortality scenarios (Figure 28).

In summary, living subsidies were generally deposited farther in more spread-out distributions than dead subsidies across scenarios of movement pattern and scaling as well as mortality level and type. Movements with more variable step lengths therefore displaced subsidies farther from the shared ecosystem boundary at lower densities than straighter movements and high

mortality attenuated displacement effects, with more obvious outcomes for dead than living subsidies. Movements with less variable step lengths also displaced living subsidies closer to the shared ecosystem boundary at lower densities than more sinuous movements and high mortality enhanced concentration effects with more pronounced outcomes for dead than living subsidies. Moderately straight CRW resulted in moderate displacement and densities for both living and dead subsidies, outperforming LW with intermediate step length variability. Compared to time-based mortality, high space-based mortality interacted with movements with more variable step lengths to enhance dead subsidy displacement and density but limit the displacement and density of living subsidies.

2.5 Discussion

We observed differences in the role of movement pattern and mortality on displacement and density of consumer and nutrient subsidies. Subsidy displacement was most strongly influenced by movement behavior, while subsidy concentration was most strongly impacted by mortality. This underscores the importance of addressing animal dispersal and foraging movement behavior relative to variation in mortality risk in developing tools to predict animal-transported subsidy distributions and corresponding ecosystem impacts (Earl and Zollner, 2017; Nathan et al., 2008). Our work models how spatial subsidies might respond to a broad parameter space of ecologically plausible movement and mortality scenarios, serving as a reference for hypothesis testing in empirical studies. Future research examining animal-transported subsidy deposition extents and ranges can use results from our model to anticipate the relative importance of movement behavior and the nature of mortality risk for a wide variety of case studies (Callaway and Hastings, 2002). Mortality may be more important than movement for modeling nutrient subsidy patterns of relatively small-bodied, r-selected species with high mortality rates and low

movement capacities. However, movement may take precedence over mortality for modeling spatial subsidy patterns of larger-bodied k-selected species with relatively low mortality rates and long-range movements. More specifically, our work also provides important insights into the distribution of dead subsidies. It may be intuitive that straighter movements and movements with more variable step lengths displace and spread consumer subsidies more than sinuous movements and movements in recipient ecosystems. However, the effect of mortality risk level and type on corresponding nutrient subsidy displacement and density patterns are less obvious. Our findings demonstrate the importance of understanding how active subsidy distribution patterns and ecosystem impacts can respond to interactions between movement behavior dynamics and variation in the type and level of mortality risk animals experience in a landscape.

Our work underscores potential opportunities for using both LW and CRW appropriately within a common simulation framework to model and predict emergent animal-transported subsidy distribution patterns. The established debate regarding the use of LW and CRW models for simulating different animal movement strategies like foraging and dispersal reinforces the importance of examining how the underlying mechanisms (Benhamou, 2007; Reynolds, 2008) might influence spatial subsidy distribution. We show that relative value of simulating animal movement using patterns driven by step length variability or the degree of sinuosity (CRW) in spatial subsidy modeling applications can vary between and during animal activities like foraging and dispersal. Movement patterns with variable step lengths can be used to model animal subsidy distributions from behavioral intermittence (Bartumeus 2009; Humphries et al., 2016) between or during foraging and dispersal given informational uncertainty about habitat quality and resource distributions in a landscape. We can modulate the degree of step length variability to model different scales of active subsidy distributions emerging from long-range dispersal search

(movements with more variable step lengths) with intermittent foraging and habitat selection (movements with less variable step lengths) given animal uncertainty about resources distributions and patchy habitat quality (Kölzsch et al., 2015; de Jager et al., 2011). Using movement patterns with correlation between step angles to model directional search given animal cognition of the distribution of resources and habitat quality in landscapes could be advantageous. We can vary the degree of correlation between steps to simulate variations in the scale of active subsidy distributions emanating from migration to known refugia (straighter paths) and eventual home range establishment or expansion after habitat prospecting and selection (more sinuous paths) (Fagan and Calabrese, 2014; Roshier et al., 2008). CRW has been used to approximate animal space use and dispersal movement for a variety of species (Smouse et al., 2010; Atwood et al., 2016). LW has also been used to describe variations in animal movement behavior in various species-specific case studies in movement ecology research (Auger-Méthé et al., 2015; Avgar et al., 2013). Implementing CRW and LW in a shared modeling framework to explicitly compare and contrast them can identify the most appropriate tools for describing different animal movement behaviors in empirical and theoretical studies of active subsidy distribution.

We found that step length variability displaced and spread consumer subsidies more than straighter movements and interacted with increasing mortality to enhance corresponding nutrient subsidy densities over smaller areas closer to the ecosystem boundary. Our results also show that increased mortality risk can constrain the displacement and spread of corresponding nutrient subsidies with more pronounced effects on straighter dispersal movements than foraging movement patterns with highly variable step lengths. Our results also provide a starting point for the simulation of animal movement effects on subsidy distribution across the range of parameter space we investigated. For example, seabird and sea turtle prospecting movements in terrestrial

breeding habitats for suitable nesting sites have been simulated using CRW (Hart et al., 2013; Garthe et al., 2016). Seabird and sea turtle nesting colonies deposit considerable numbers of eggs that can be significant nutrient subsidies for plants and animals in terrestrial breeding habitats (Vander Zanden et al., 2012). It might therefore be useful to conceptualize spatial egg deposition patterns at terrestrial breeding sites as outcomes of more sinuous seabird and sea turtle prospecting movement patterns. Similarly, seabird and sea turtle hatchlings disperse from terrestrial breeding and nesting sites across the ocean. Foraging at variable distances over vast ranges, seabirds act as significant consumer subsidies for krill and sea turtles for seaweed. These movements have been approximated with power law distributions (Sims et al., 2008). Spatial subsidy researchers could therefore investigate spatial distributions of emergent seabird and sea turtle neonate distributions as consumer subsidies from terrestrial nesting sites to adjacent oceans based on movement patterns with more variable step lengths.

Animals that move with more variable step lengths displace and spread consumer subsidies over greater areas with reduced local impacts on recipient ecosystems compared to straighter movements. Telemetry-derived bear home range, prospecting and foraging movement data has been approximated with Lévy-like patterns and modeled as a mixed random walk (Gautesstad et al., 1995). Salmon-derived nutrient subsidies to forest ecosystems in bear feces and salmon carcasses supplement scavenger and detritivore consumption with considerable consequences for plant nitrogen uptake at widespread deposition locations (Helfield and Naiman, 2006). Bears deposit salmon carcasses as nutrient subsidies at higher concentrations in riparian forest zones with enhanced local impacts, including supplanting scavenger and detritivore communities (Quinn et al., 2009). Bears also track spatial variation in salmon phenology at variable distances at the watershed scale (Deacy et al., 2016). It would be appropriate to contextualize corresponding

dynamic nutrient subsidy distributions of bear-transported salmon carcasses in riparian forests based on sinuous bear movement patterns with less variable step lengths. Empirical isotope analysis data indicates that bears also deposit feces rich in salmon nutrients at differential distances, augmenting plant nitrogen uptake deep into forests (Swain and Reynolds, 2015). Predicting corresponding nutrient subsidy distributions and scales of ecosystem impact may require using movement patterns with more variable step lengths to simulate bear foraging movements in case studies on the spatial scale and impact of bear-derived salmon nutrient subsidies.

Our results also showed that movements with more variable step lengths deposited more nutrient subsidies at lower densities in space-based compared to time-based mortality scenarios. Given high mortality in space-based instead of time-based mortality scenarios, we observed that consumer subsidy impact increased with step length variability. Increasing step length variability however enhanced the number of nutrient subsidies while attenuating corresponding impact. Compared to time-based mortality, space-based mortality enhanced the displacement extents of nutrient subsidies while constraining the displacement of consumer subsidies with higher step length variability. In space-based but not time-based mortality scenarios, movement patterns with more variable step lengths displaced the location of greatest impact farther from the ecosystem boundary for consumer than for nutrient subsidies. These results are consistent with other observations of sporadic high intensity mortality events occurring at exposed locations of high predation risks across landscapes (Kittle et al., 2015; Rees et al., 2015). It is important to distinguish between space-based and time-based mortality in spatially explicit active subsidy distribution models to improve the prediction accuracy of resulting spatial subsidy impact patterns in response to mortality events and corresponding ecosystem effects in landscape management settings. Variations in the impact of nutrient resources between spatial distributions of space-based

and time-based mortality events can provide ecological cues that affect the distribution of predators and prey resources.

Space-based mortality can occur when animals move through landscapes with limited information or high uncertainty about predation risk or inhospitable habitat conditions. Wildebeest and other ungulate herbivores are substantial and expansive consumer subsidies across Serengeti ecosystems but also contribute significant nutrient subsidies for apex predators with significant top-down trophic benefits for mesopredators and scavengers. Wildebeest collectively migrate and forage along variable spatiotemporal precipitation regimes and patchy grass and forbs resource gradients in the Serengeti (Holdo et al., 2009). This results in movements of high step length variability and corresponding sporadic spatial mortality risks from starvation or predation by apex predators like lions and crocodiles over vast distances along migration routes and around pond refugia in the Serengeti landscape (Palmer et al., 2017). It would be appropriate for subsidy researchers to think of spatial variation in grass cover depressions as outcomes of consumer subsidies and carrion from mortality events as nutrient subsidies for scavengers and plants as wildebeest forage during migration along variable precipitation and grass cover regimes in the Serengeti.

We developed a minimalist theoretical model (IBM) to quantify active subsidy distribution dynamics in response to variation in movement and mortality but future work could increase realism with features like landscape heterogeneity and variation in environmental factors (Wallentin, 2017). Species-specific attributes that can be added to active subsidy distribution models to enhance realism include alternative search strategies (e.g., Foray loops, Archimedean spirals) (Zollner and Lima, 1999) and other factors that influence animal movement like perceptual range (Grant et al., 2018), antipredator vigilance, as well as conspecific and interspecific

interactions (Fletcher, 2006). Another advancement could be to model the role of movement modality (e.g., flying, slithering) and the quality of subsidy deposition as function of animal body size. The distribution of consumer and nutrient subsidies can differ greatly for the same species with consequences for top-down versus bottom-up effects relative to the body-size and navigation mode. Some big animals with large movement can deposit larger amounts of both consumer and nutrient subsidies and over more expansive ranges than smaller animals (Doughty et al., 2016). Future spatial subsidy models could directly account for nutrient subsidy distribution dynamics resulting from the spatial transience of mortality events like the secondary movement and relocation of dead prey by predators or scavengers. Feces and secondary displacements could occur more frequently than direct mortality events, potentially resulting in different spatiotemporal scales of corresponding nutrient subsidy distributions. It would be interesting to examine the differences between space-based and time-based mortality effects on active subsidy distributions by comparing nutrient subsidy deposition patterns from direct mortality to those from fecal matter or carcasses dragged and relocated by scavenger movements. It would also be interesting to test the utility of our theoretical model by parameterizing and pattern-matching (Grimm et al., 2012) with empirical active subsidy distribution, movement and mortality data.

2.6 Conclusion

Predicting the location and impact of active subsidies is useful for making critical decisions to preserve ecosystem integrity, enhancing species and biodiversity conservation efforts, and implementing effective landscape management practices across spatiotemporal scales (Raikow et al., 2011). Subsidies have significant implications for determining the structure and function of ecological communities and thus ecosystem services, including nutrient cycling, metapopulation persistence and connectivity as factors in species conservation, as well as biodiversity maintenance

(Allen et al., 2012). Our model results underscore the importance of movement ecology for predicting the spatial distribution and impact of active subsidies. We show that changing animal movement behavior and scaling patterns, as well as the type and level of mortality risk can lead to variations in active subsidy distribution and impact. Our work advances previous work (Earl and Zollner, 2014) by simulating and quantifying spatial subsidies from two animal movement modeling frameworks instead of one and examining the effect of two types of mortality risk.

2.7 References

- Allen, D.C., Vaughn, C.C., Kelly, J.F., Cooper, J.T., Engel, M.H., 2012. Bottom-up biodiversity effects increase resource subsidy flux between ecosystems. *Ecology* 93, 2165–2174.
doi:10.1890/11-1541.1
- Archer, K.J., Kimes, R. V., 2008. Empirical characterization of random forest variable importance measures. *Comput. Stat. Data Anal.* 52, 2249–2260.
doi:10.1016/J.CSDA.2007.08.015
- Atwood, T.C., Peacock, E., McKinney, M.A., Lillie, K., Wilson, R., Douglas, D.C., Miller, S., Terletzky, P., 2016. Rapid environmental change drives increased land use by an arctic marine predator. *PLoS One* 11, e0155932. doi:10.1371/journal.pone.0155932
- Auger-Méthé, M., Derocher, A.E., Plank, M.J., Codling, E.A., Lewis, M.A., 2015. Differentiating the Lévy walk from a composite correlated random walk. *Methods Ecol. Evol.* 6, 1179–1189. doi:10.1111/2041-210X.12412
- Avagar, T., Mosser, A., Brown, G.S., Fryxell, J.M., 2013. Environmental and individual drivers of animal movement patterns across a wide geographical gradient. *J. Anim. Ecol.* 82, 96–106.
doi:10.1111/j.1365-2656.2012.02035.x

- Bartumeus, F., 2009. Behavioral intermittence, Lévy patterns, and randomness in animal movement. *Oikos* 118, 488–494. doi:10.1111/j.1600-0706.2009.17313.x
- Bastille-Rousseau, G., Gibbs, J.P., Yackulic, C.B., Frair, J.L., Cabrera, F., Rousseau, L.P., Wikelski, M., Kummeth, F., Blake, S., 2017. Animal movement in the absence of predation: environmental drivers of movement strategies in a partial migration system. *Oikos* 126, 1004–1019. doi:10.1111/oik.03928
- Ben-David, M., Bowyer, R.T., Duffy, L.K., Roby, D.D., Schell, D.M., 1998. Social behavior and ecosystem processes: River Otter latrines and nutrient dynamics of terrestrial vegetation. *Ecology* 79, 2567–2571. doi:10.1890/0012-9658(1998)079[2567:SBAEPR]2.0.CO;2
- Benhamou, S., 2007. How many animals really do the Lévy walk? *Ecology* 88, 1962–1969. doi:10.1890/06-1769.1
- Bergman, C.M., Schaefer, J.A., Luttich, S.N., 2000. Caribou movement as a correlated random walk. *Oecologia* 123, 364–374. doi:10.1007/s004420051023
- Breiman, L., Cutler, A., Liaw, A., & Wiener, M., 2011. Package randomForest. Software available at: <http://stat-www.berkeley.edu/users/breiman/RandomForests>.
- Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 2017. Classification and regression trees. doi:10.1201/9781315139470.
- Callaway, D.S., Hastings, A., 2002. Consumer movement through differentially subsidized habitats creates a spatial food web with unexpected results. *Ecol. Lett.* 5, 329–332. doi:10.1046/j.1461-0248.2002.00330.x
- Capps, K.A., Berven, K.A., Tiegs, S.D., 2015. Modelling nutrient transport and transformation by pool-breeding amphibians in forested landscapes using a 21-year dataset. *Freshw. Biol.* 60, 500–511. doi:10.1111/fw.b.12470

- Codling, E.A., Plank, M.J., Benhamou, S., 2008. Random walk models in biology. *J. R. Soc. Interface* 5, 813–34. doi:10.1098/rsif.2008.0014
- De Jager, M., Weissing, F.J., Herman, P.M.J., Nolet, B.A., van de Koppel, J., 2011. Lévy walks evolve through interaction between movement and environmental complexity. *Science* 332, 1551–1553.. doi: 10.1126/science.1201187
- Deacy, W., Leacock, W., Armstrong, J.B., Stanford, J.A., 2016. Kodiak brown bears surf the salmon red wave: direct evidence from GPS collared individuals. *Ecology*. doi:10.1890/15-1060.1
- DeCesare, N.J., 2012. Separating spatial search and efficiency rates as components of predation risk. *Proc. R. Soc. London B Biol. Sci.* 279.
- Doughty, C.E., Roman, J., Faurby, S., Wolf, A., Haque, A., Bakker, E.S., Malhi, Y., Dunning, J.B., Svenning, J.-C., 2016. Global nutrient transport in a world of giants. *Proc. Natl. Acad. Sci. U. S. A.* 113, 868–73. doi:10.1073/pnas.1502549112
- Earl, J.E., Zollner, P.A., 2017. Advancing research on animal-transported subsidies by integrating animal movement and ecosystem modelling. *J. Anim. Ecol.* 86, 987–997. doi:10.1111/1365-2656.12711
- Earl, J.E., Zollner, P.A., 2014. Effects of animal movement strategies and costs on the distribution of active subsidies across simple landscapes. *Ecol. Modell.* 283, 45–52. doi:10.1016/j.ecolmodel.2014.03.020
- Fagan, W.F., Calabrese, J.M., 2014. The correlated random walk and the rise of movement ecology. *Bull. Ecol. Soc. Am.* 95, 204–206. doi:10.1890/0012-9623-95.3.204
- Fahrig, L., 2007. Non-optimal animal movement in human-altered landscapes. *Funct. Ecol.* 21, 1003–1015. doi:10.1111/j.1365-2435.2007.01326.x

- Farina, J.M., Salazar, S., Wallem, K.P., Witman, J.D., Ellis, J.C., 2003. Nutrient exchanges between marine and terrestrial ecosystems: the case of the Galapagos sea lion *Zalophus wollebaecki*. *J. Anim. Ecol.* 72, 873–887. doi:10.1046/j.1365-2656.2003.00760.x
- Fletcher, R.J., 2006. Emergent properties of conspecific attraction in fragmented landscapes. *Source Am. Nat.* 168, 207–219. doi:10.1086/505764
- Garthe, S., Schwemmer, P., Paiva, V.H., Corman, A.-M., Fock, H.O., Voigt, C.C., Adler, S., 2016. Terrestrial and marine foraging strategies of an opportunistic seabird species breeding in the Wadden Sea. *PLoS One* 11, e0159630. doi:10.1371/journal.pone.0159630
- Gautestad, A.O., Mysterud, I., Pelton, M.R., 1995. Complex movement and scale-free habitat use: testing the multi-scaled home-range model on black bear telemetry data. *Ursus*. 10, 219-234
- Grant, T.J., Parry, H.R., Zalucki, M.P., Bradbury, S.P., 2018. Predicting monarch butterfly (*Danaus plexippus*) movement and egg-laying with a spatially-explicit agent-based model: the role of monarch perceptual range and spatial memory. *Ecol. Modell.* 374, 37–50. doi:10.1016/J.ECOLMODEL.2018.02.011
- Grimm, V., Railsback, S.F., 2012. Pattern-oriented modelling: a “multi-scope” for predictive systems ecology. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 367, 298–310. doi:10.1098/rstb.2011.0180
- Hart, K.M., Lamont, M.M., Sartain, A.R., Fujisaki, I., Stephens, B.S., 2013. Movements and habitat-use of loggerhead sea turtles in the northern gulf of mexico during the reproductive period. *PLoS One* 8, e66921. doi:10.1371/journal.pone.0066921
- Helfield, J.M., Naiman, R.J., 2006. Keystone interactions: salmon and bear in riparian forests of alaska. *Ecosystems* 9, 167–180. doi:10.1007/s10021-004-0063-5

- Holdo, R.M., Holt, R.D., Fryxell, J.M., 2009. Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. *Ecol. Appl.* 19, 95–109. doi:10.1890/07-1954.1
- Humphries, N.E., Schaefer, K.M., Fuller, D.W., Phillips, G.E.M., Wilding, C., Sims, D.W., 2016. Scale-dependent to scale-free: daily behavioural switching and optimized searching in a marine predator. *Anim. Behav.* 113, 189–201. doi:10.1016/j.anbehav.2015.12.029
- Jonsen, I.D., Flemming, J.M., Myers, R.A., 2005. Robust state-space modeling of animal movement data. *Ecology* 86, 2874–2880. doi:10.1890/04-1852
- Jonsen, I.D., Myers, R.A., Flemming, J.M., 2003. Meta-analysis of animal movement using state-space models. *Ecology* 84, 3055–3063. doi:10.1890/02-0670
- Kareiva, P.M., Shigesada, N., 1983. Analyzing insect movement as a correlated random walk. *Oecologia* 56, 234–238. doi:10.1007/BF00379695
- Kittle, A.M., Anderson, M., Avgar, T., Baker, J.A., Brown, G.S., Hagens, J., Iwachewski, E., Moffatt, S., Mosser, A., Patterson, B.R., Reid, D.E.B., Rodgers, A.R., Shuter, J., Street, G.M., Thompson, I.D., Vander Vennen, L.M., Fryxell, J.M., 2015. Wolves adapt territory size, not pack size to local habitat quality. *J. Anim. Ecol.* 84, 1177–1186. doi:10.1111/1365-2656.12366
- Knight, T.M., Mccoy, M.W., Chase, J.M., Mccoy, K.A., Holt, R.D., 2005. Trophic cascades across ecosystems. *Nature* 437, 880–883.
- Kölzsch, A., Alzate, A., Bartumeus, F., de Jager, M., Weerman, E.J., Hengeveld, G.M., Naguib, M., Nolet, B.A., van de Koppel, J., 2015. Experimental evidence for inherent Lévy search behaviour in foraging animals. *Proc. R. Soc. London B Biol. Sci.* 282, 20150424. doi:doi.org/10.1098/rspb.2015.0424

- Kristan, W.B., Boarman, W.I., 2003. Spatial pattern of risk of common raven predation on desert tortoises. *Ecology* 84, 2432–2443. doi:10.1890/02-0448
- Leroux, S.J., Loreau, M., 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. *Ecol. Lett.* 11, 1147–1156. doi:10.1111/j.1461-0248.2008.01235.x
- Martin, J., Benhamou, S., Yoganand, K., Owen-Smith, N., 2015. Coping with spatial heterogeneity and temporal variability in resources and risks: adaptive movement behaviour by a large grazing herbivore. *PLoS ONE* 10(2): e0118461.
<https://doi.org/10.1371/journal.pone.0118461>
- McInturf, A.G., Pollack, L., Yang, L.H., Spiegel, O., 2019. Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors? *Biol. Rev.* brv.12525. <https://doi.org/10.1111/brv.12525>
- Miller, J.R.B., Ament, J.M., Schmitz, O.J., 2014. Fear on the move: predator hunting mode predicts variation in prey mortality and plasticity in prey spatial response. *J. Anim. Ecol.* 83, 214–222. doi:10.1111/1365-2656.12111
- Moorcroft, P.R., 2012. Mechanistic approaches to understanding and predicting mammalian space use: recent advances, future directions. *J. Mammal.* 93, 903–916. doi:10.1644/11-MAMM-S-254.1
- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. *Proc. Natl. Acad. Sci. U. S. A.* 105, 19052–9. doi:10.1073/pnas.0800375105
- Palmer, M.S., Fieberg, J., Swanson, A., Kosmala, M., Packer, C., 2017. A ‘dynamic’ landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. *Ecol. Lett.* doi:10.1111/ele.12832

- Patterson, T.A., Thomas, L., Wilcox, C., Ovaskainen, O., Matthiopoulos, J., 2008. State–space models of individual animal movement. *Trends Ecol. Evol.* 23, 87–94.
doi:10.1016/j.tree.2007.10.009
- Polis G.A., Anderson, W.B., Holt, R.D., 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* 28, 289–316. doi.org/10.1146/annurev.ecolsys.28.1.289
- Quinn, T.P., Carlson, S.M., Gende, S.M., Rich, Jr., H.B., 2009. Transportation of Pacific salmon carcasses from streams to riparian forests by bears. *Can. J. Zool.* 87, 195–203.
doi:10.1139/Z09-004
- Raikow, D.F., Walters, D.M., Fritz, K.M., Mills, M.A., 2011. The distance that contaminated aquatic subsidies extend into lake riparian zones. *Ecol. Appl.* 21, 983–990. doi:10.1890/09-1504.1
- Rees, J.D., Webb, J.K., Crowther, M.S., Letnic, M., 2015. Carrion subsidies provided by fishermen increase predation of beach-nesting bird nests by facultative scavengers. *Anim. Conserv.* 18, 44–49. doi:10.1111/acv.12133
- Reynolds, A., 2015. Liberating Lévy walk research from the shackles of optimal foraging. *Phys. Life Rev.* 14, 59–83. doi:10.1016/j.plrev.2015.03.002
- Reynolds, A., 2008. How many animals really do the Lévy walk? *Comment. Ecology* 89, 2347–2351. doi:10.1890/07-1688.1
- Roshier, D.A., Doerr, V.A.J., Doerr, E.D., 2008. Animal movement in dynamic landscapes: interaction between behavioural strategies and resource distributions. *Oecologia* 156, 465–477. doi:10.1007/s00442-008-0987-0

- Schmitz, O.J., 2008. Predators avoiding predation. *Proc. Natl. Acad. Sci.* 105, 14749–14750.
doi:10.1073/pnas.0808033105
- Schtickzelle, N., Mennechez, G., Baguette, M., 2006. Dispersal depression with habitat fragmentation in the bog fritillary butterfly. *Ecology* 87, 1057–65.
- Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W., James, A., Ahmed, M.Z., Brierley, A.S., Hindell, M.A., Morritt, D., Musyl, M.K., Righton, D., Shepard, E.L.C., Wearmouth, V.J., Wilson, R.P., Witt, M.J., Metcalfe, J.D., 2008. Scaling laws of marine predator search behaviour. *Nature* 451, 1098–1102.
doi:10.1038/nature06518
- Smouse, P.E., Focardi, S., Moorcroft, P.R., Kie, J.G., Forester, J.D., Morales, J.M., 2010. Stochastic modelling of animal movement. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 365, 2201–11. doi:10.1098/rstb.2010.0078
- Swain, N.R., Reynolds, J.D., 2015. Effects of salmon-derived nutrients and habitat characteristics on population densities of stream-resident sculpins. *PLoS One* 10, e0116090.
doi:10.1371/journal.pone.0116090
- Therneau, T., Atkinson, B., Ripley, B., & Ripley, M. B. (2018). Package ‘rpart’. *Available online: cran. ma. ic. ac. uk/web/packages/rpart/rpart. pdf (accessed on 20 December 2018).*
- Tisue, S., Wilensky, U., 2004. Netlogo: A simple environment for modeling complexity. *Conf. Complex Syst*, 1–10. doi:10.1109/ICVD.2004.1261037
- Vander Zanden, H.B., Bjorndal, K.A., Inglett, P.W., Bolten, A.B., 2012. Marine-derived nutrients from green turtle nests subsidize terrestrial beach ecosystems. *Biotropica* 44, 294–301. doi:10.1111/j.1744-7429.2011.00827.x

- Viswanathan, G.M., Afanasyev, V., Buldyrev, S. V, Murphy, E.J., 1996. Lévy flight search patterns of wandering albatrosses. *Nature* 381,413–415.
- Vizzini, S., Signa, G., Mazzola, A., 2016. Guano-derived nutrient subsidies drive food web structure in coastal ponds. *PLoS One* 11, e0151018. doi:10.1371/journal.pone.0151018
- Wallentin, G., 2017. Spatial simulation: A spatial perspective on individual-based ecology—a review. *Ecol. Modell.* 350, 30–41. doi: 10.1016/j.ecolmodel.2017.01.017
- Walters, D.M., Fritz, K.M., Otter, R.R., 2008. The dark side of subsidies: adult stream insects export organic contaminants to riparian predators. *Ecol. Appl.* 18, 1835–1841. doi:10.1890/08-0354.1
- Wilensky, U., 1999. NetLogo. Cent. Connect. Learn. Comput. Model. Northwest. Univ. Evanst.
- White, J.W., Rassweiler, A., Samhouri, J.F., Stier, A.C., White, C., 2014. Ecologists should not use statistical significance tests to interpret simulation model results. *Oikos* 123, 385–388. doi:10.1111/j.1600-0706.2013.01073.x
- Yoder, J.M., Marschall, E.A., Swanson, D.A., 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behav. Ecol.* 15, 469–476. doi:10.1093/beheco/arh037
- Zhao, K., Jurdak, R., Liu, J., Westcott, D., Kusy, B., Parry, H., Sommer, P., McKeown, A., 2015. Optimal Lévy-flight foraging in a finite landscape. *J. R. Soc. Interface* 12, 20141158. doi:10.1098/rsif.2014.1158
- Zollner, P.A., Lima, S.L., 2005. Behavioral tradeoffs when dispersing across a patchy landscape. *Oikos* 108, 219–230. doi:10.1111/j.0030-1299.2005.13711.x
- Zollner, P.A., Lima, S.L., 1999. Search strategies for landscape-level interpatch movement. *Ecology* 80, 1019–1030. doi:10.1890/0012-9658(1999)080[1019:SSFLLI]2.0.CO;2

2.8 Tables and Figures

Table 1 *State variables with parameter levels for varying movement behavior and mortality.*

Each simulation run includes a movement pattern (CRW or LW), a corresponding scale coefficient level (correlation coefficient (α) for CRW and scaling exponent (μ) for LW), a space-death setting (true or false indicating space-based versus time-based mortality respectively) and mortality level (i.e., instantaneous rate or probability of death per timestep).

| State Variable | Parameter Levels | | | | | | | | | |
|---|------------------|-----|-----|--------|------|--------------------------|-------|---|-----|---|
| Movement Pattern Scale Coefficient Mortality Space-Death | CRW (α) | | | | | LW (μ) | | | | |
| | 0.5 | 0.8 | 0.9 | 0.95 | 0.99 | 1 | 1.5 | 2 | 2.5 | 3 |
| | 0.00025 | | | 0.0005 | | | 0.001 | | | |
| | TRUE (ON) | | | | | FALSE (OFF ~ Time-death) | | | | |

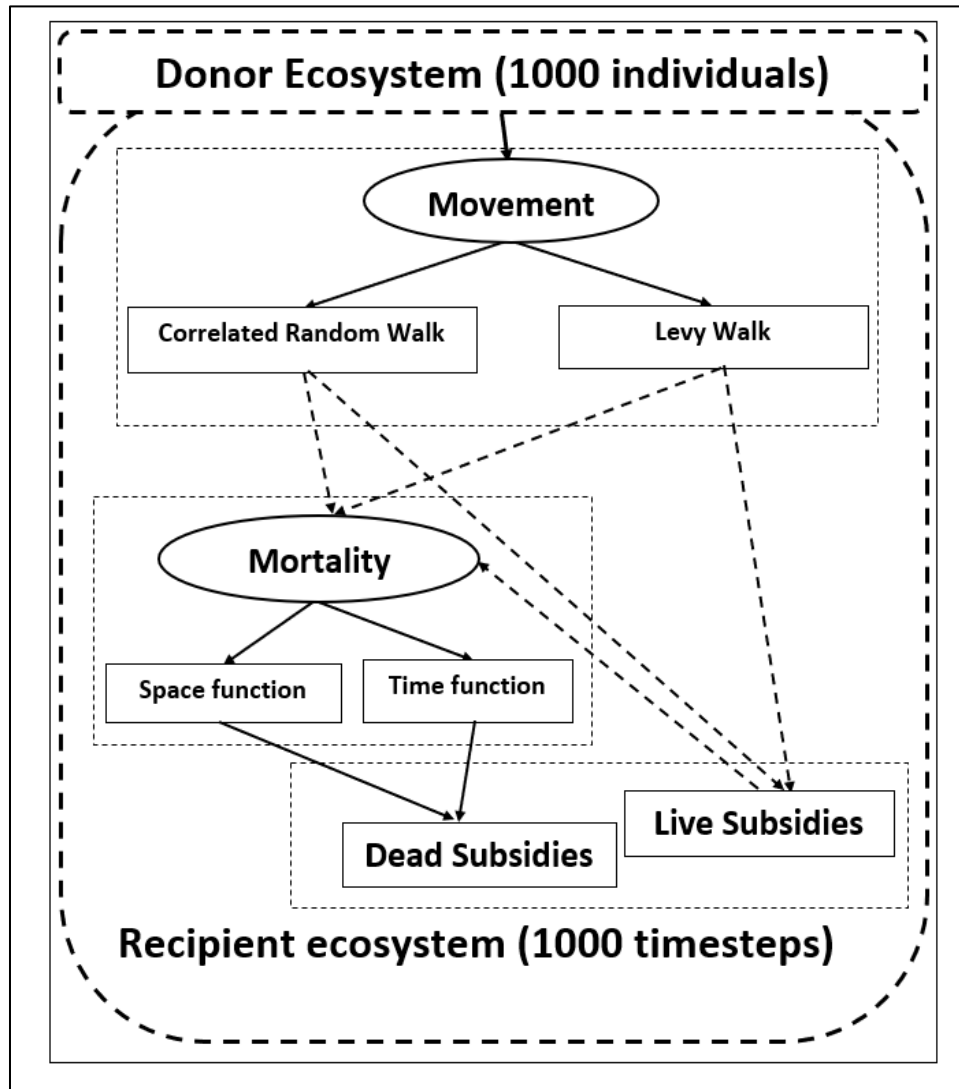


Figure 1 *Design concept*. The conceptual chart of modeling process and procedures. 1000 individuals disperse from donor ecosystem through recipient ecosystem by CRW or LW (as a function of space or time) for a 1000 timestep period as live subsidies, except when they succumb to mortality and become dead subsidies. Individuals move through the recipient ecosystem experiencing space-based or time-based mortality and subsequently depositing living and dead subsidies.

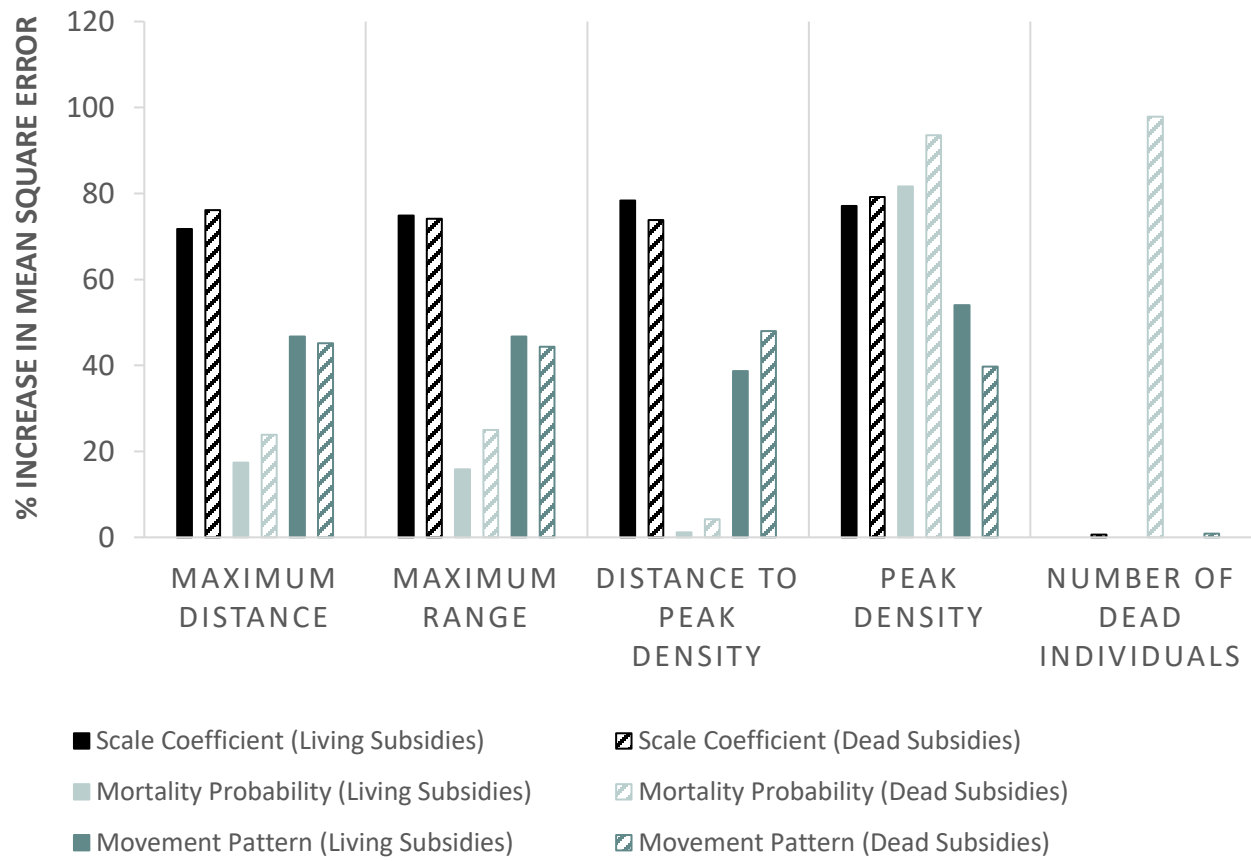


Figure 2 *Random forest model results for impact of movement pattern variation and mortality as a function of time on subsidy distribution.* Percent increase in ANOVA mean square error (%IncMSE) and residual sum of squares (IncNodePurity (RSS)) from randomization permutations on predictor values as a measure of prediction and node split accuracy of random forest model fits. Solid bars represent results for living subsidies and patterned bars represent results for dead subsidies. Taller bars indicate greater predictor importance (See section T in supplementary information for detailed tables with values for variable (%IncMSE) and precision (IncNodePurity (RSS)) (Table 4)).

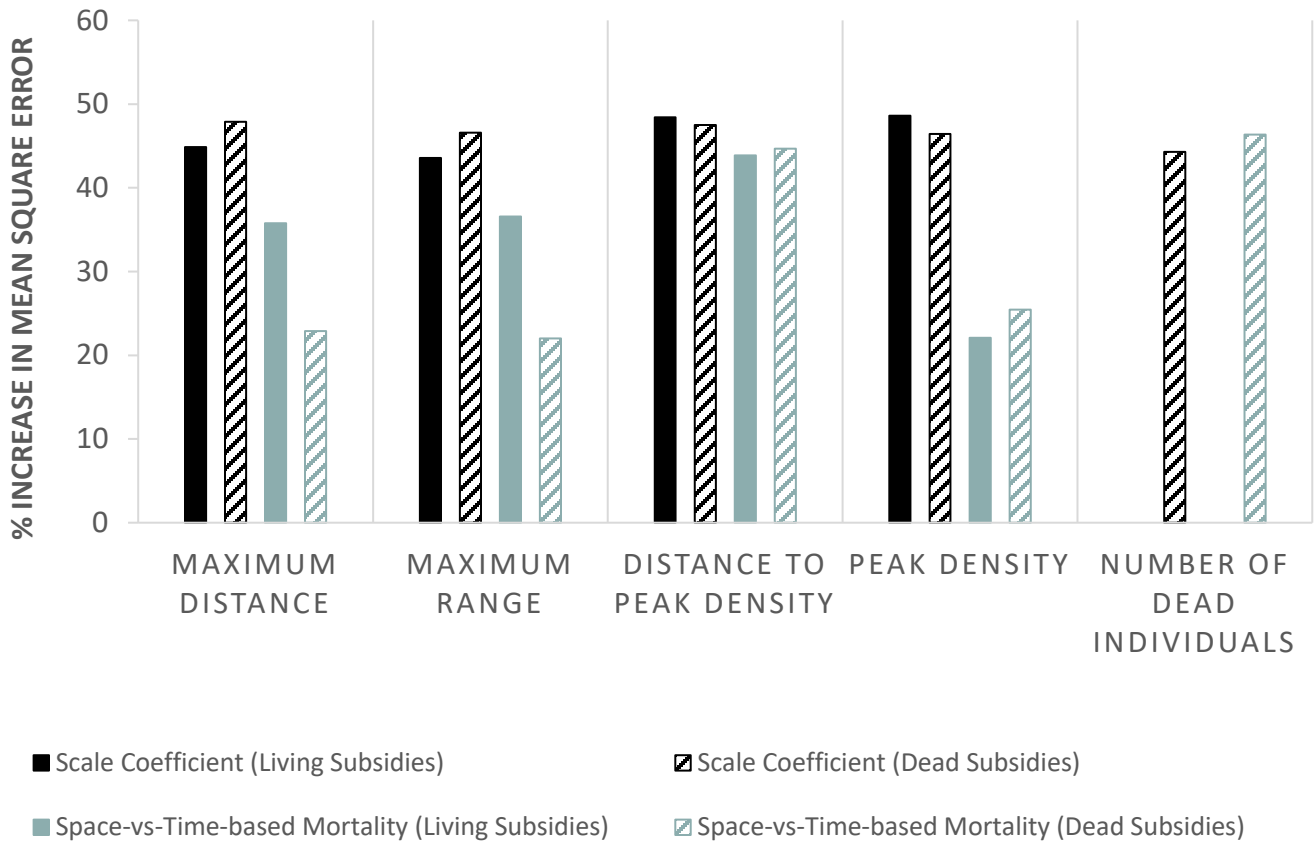


Figure 3 *Random forest model results for impact of LW pattern variation and mortality as a function of space and time on subsidy distribution.* Percent increase in ANOVA mean square error (%IncMSE) and the change in residual sum of squares before and after a split on a predictor at a node (IncNodePurity (RSS)) from randomization permutations on predictor values as a measure of prediction and node split accuracy of random forest model fits. Solid bars represent results for living subsidies and patterned bars represent results for dead subsidies. Taller bars indicate greater predictor importance (See section T in supplementary information for detailed tables with values for variable (%IncMSE) and precision (IncNodePurity (RSS)) (Table 5)).

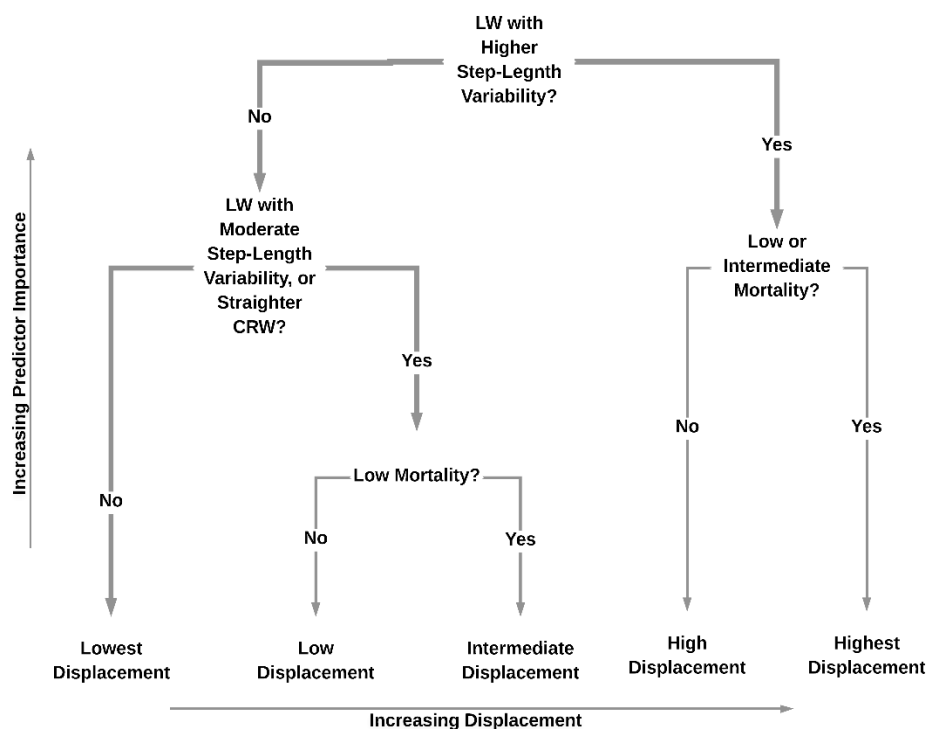


Figure 4 *Synthesis of displacement metrics of subsidy distribution trends (CRW vs LW)*. This chart compares CRW and LW on general CART trends for displacement metrics of active subsidy distribution (maximum subsidy deposition distance, range and distance to peak subsidy deposition density) for living and dead subsidies. Living subsidies were generally displaced farther than dead subsidies. Movements with more variable step lengths resulted in high displacement at low mortality and moderately high displacement at high and intermediate mortalities. Straighter movements and movements with intermediate step length variability resulted in moderate displacement at low and intermediate mortalities, and moderately low displacement at high mortality. More sinuous movements and movements with low step length variability resulted in low displacement limited subsidy displacement the most. Chart relationships delineated with heavy lines represent instances where 6 constituent CARTs agreed while relationships delineated with lighter lines represent instances where at least half but not all constituent CARTs agreed. See figure 21 in supplementary materials (Appendix A) for detailed CARTs synthesized here.

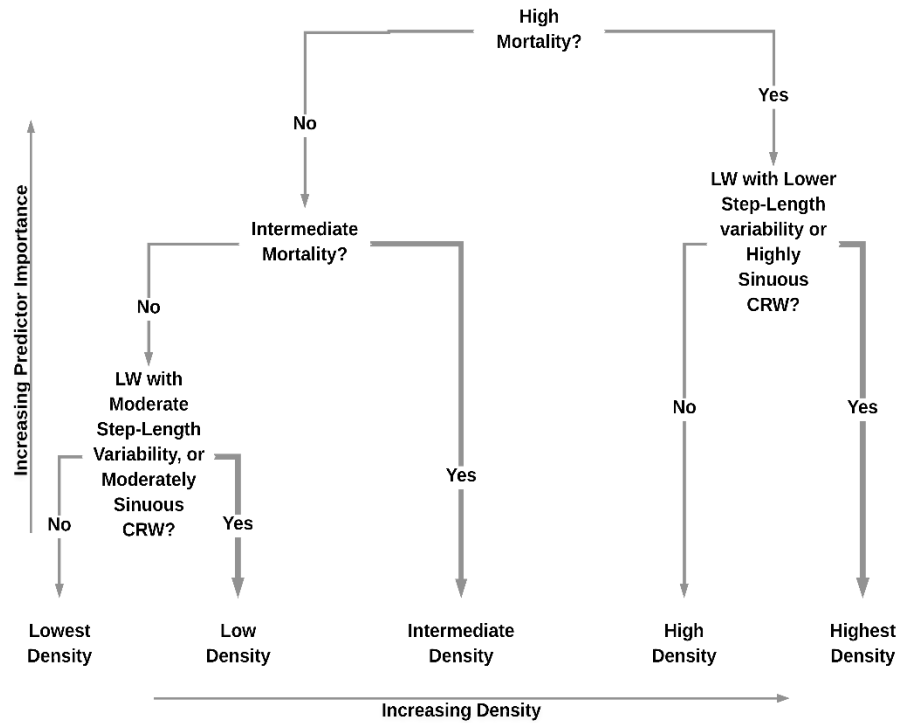


Figure 5 *Synthesis of peak subsidy deposition density trends (CRW vs LW)*. This chart compares CRW and LW on general CART trends for density metric of active subsidy distribution (peak subsidy deposition density) for living and dead subsidies. Dead subsidies were generally deposited at higher densities than living subsidies. High mortality resulted in high subsidy density for more sinuous movements and movements with less variable step lengths. Intermediate mortality generally resulted in moderate subsidy densities. Low mortality resulted in low densities for straighter movements and movements with more variable step lengths. Chart relationships delineated with heavy lines represent instances where 4 constituent CARTs agreed while relationships delineated with lighter lines represent instances where at least half but not all constituent CARTs agreed. See figure 23 in supplementary materials (Appendix A) for detailed CARTs synthesized here.

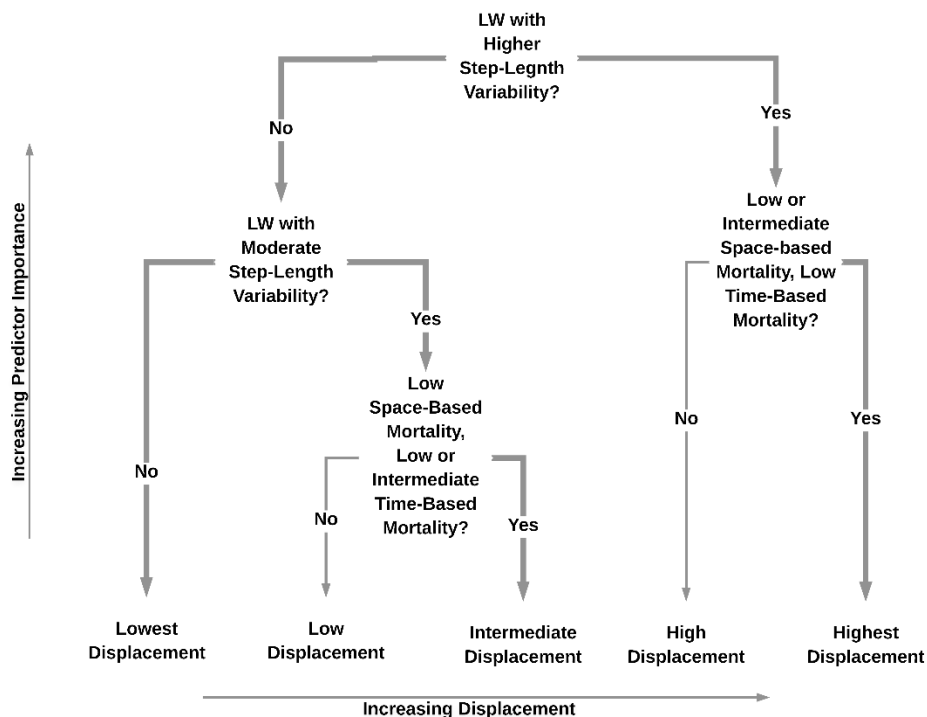


Figure 6 *Synthesis of displacement metrics of subsidy distribution trends (spatial vs temporal mortality on LW)*. This chart compares general CART trends for space-based and time-based mortality on LW step length variability in terms of displacement metrics of subsidy distribution (maximum subsidy deposition distance, range and distance to peak subsidy deposition density) for living and dead subsidies. There were more pronounced effects on dead subsidies than living subsidies. High space-based mortality resulted in intermediate and moderately high displacement for movements with more variable step lengths. Low or intermediate time-based mortality resulted in intermediate and high displacement for movements with more variable step lengths. Movements with less variable step lengths generated low displacement. Chart relationships delineated with heavy lines represent instances where 6 constituent CARTs agreed while relationships delineated with lighter lines represent instances where at least half but not all constituent CARTs agreed. See figure 25 in supplementary materials (Appendix A) for detailed CARTs synthesized here.

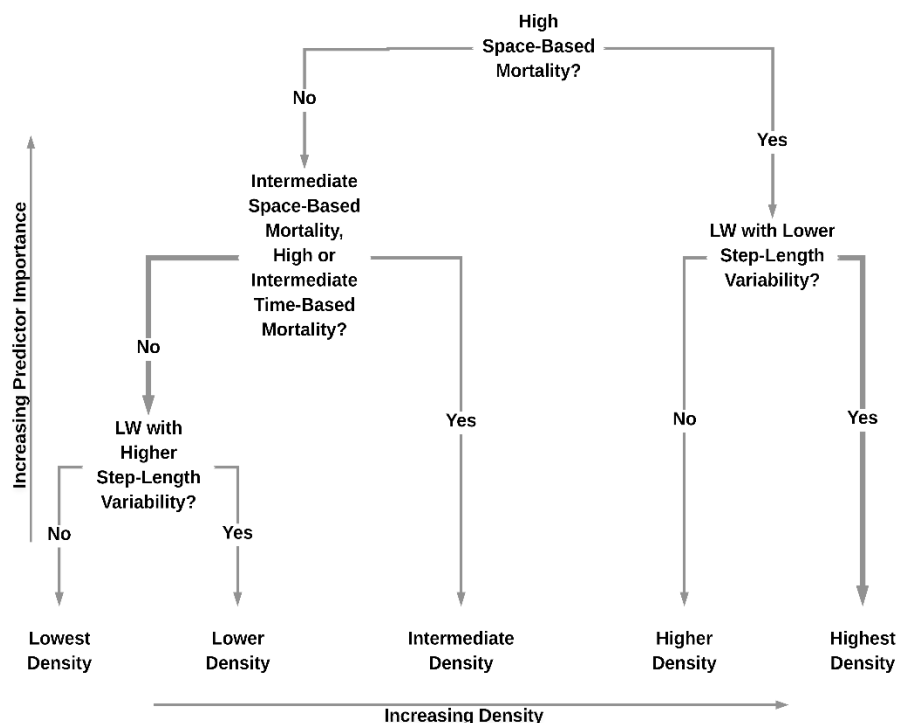


Figure 7 *Synthesis of peak subsidy deposition density trends (spatial vs temporal mortality on LW)*. This chart compares general CART trends for LW space-based and time-based mortality on density metric of subsidy distribution (peak subsidy deposition density) for living and dead subsidies. Living subsidies were generally deposited at lower densities than dead subsidies. High space-based mortality resulted in high density for movement with less variable step lengths compared to moderately high density for movements with more variable step lengths. High and intermediate time-based mortality generally resulted in intermediate densities. More variable step lengths generated low densities in low space-based and time-based mortality scenarios. Chart relationships delineated with heavy lines represent instances where 4 constituent CARTs agreed while relationships delineated with lighter lines represent instances where at least half but not all constituent CARTs agreed. See figure 27 in supplementary materials (Appendix A) for detailed CARTs synthesized here.

CHAPTER 3. THE INFLUENCE OF SOCIAL BEHAVIOR ON THE DISTRIBUTION OF ANIMAL-TRANSPORTED SUBSIDIES

3.1 Abstract

Animal sociality (i.e., conspecific attraction or avoidance) can influence how animals move (i.e., sinuous to straight) across landscapes. Animal movement has been shown to affect active subsidy distributions. Active subsidies are animal-transported resources or consumers across ecosystems that can alter ecosystem structure, function and services including biodiversity and nutrient cycling. However, there is limited research on how animal sociality affects active subsidy distributions through animal movement. We constructed a spatially explicit IBM to quantify the relative influence of variation in animal social and movement behaviors on the extent and intensity of living and dead subsidy distribution. We examined the relative importance of these variables and found that conspecific interaction was important for subsidy density and clustering. Movement was more important for subsidy displacement. Perceptual range and settlement probability had secondary effects on all subsidy distribution metrics. We found that conspecific avoidance spread subsidies further into the recipient ecosystem at lower densities than conspecific attraction. Avoidance scenarios also resulted in greater numbers more, less dense clusters compared to attraction scenarios. Increasing perceptual range and the straightness of movement patterns further enhanced subsidy displacement and spreading in avoidance scenarios but increasing settlement probability attenuated these effects. In attraction scenarios, increasing perceptual range, settlement probability and sinuosity of movement patterns enhanced subsidy density and clustering but limited subsidy displacement. Attraction scenarios generated the most living subsidies in fewer, smaller and denser clusters. Scenarios with no interaction generally resulted in intermediate subsidy deposition patterns compared to attraction and avoidance scenarios. These results confirm

animal sociality influences active subsidy distributions. Incorporating animal sociality and movement behavior in spatial subsidy models can therefore enhance our understanding of active subsidy distributions and corresponding spatiotemporal patterns in ecosystem impacts.

3.2 Introduction

Animal sociality can affect how animals move across landscapes (Stamps et al., 2005; van Gils et al., 2015). Animal movement behavior can alter active subsidy distributions (Earl and Zollner, 2014), but there is limited research on how conspecific interaction affects corresponding active subsidy distributions. Active subsidies are animal consumers and resources transported between ecosystems and can alter landscape level material and energetic balances across landscapes (Polis et al., 1996). Ecological subsidies regulate and support important ecosystem functions and services like nutrient cycling, contaminant transfer, disease spread, and biodiversity maintenance (Polis, 1997). Modeling how sociality influences animal-transported subsidy distributions through animal movement behavior could generate valuable insights on the spatiotemporal dynamics of ecosystem responses to animal movement (Turchin, 1989). Modeling frameworks that consider animal sociality with movement behavior could further enhance planning and decision-making in landscape level wildlife and ecosystem management (Campomizzi et al., 2008; Giuggioli et al., 2013).

Animal sociality is a proximal mechanism for many ecological processes in animal populations (Stamps, 1988). Many species rely on conspecific cues during dispersal to forage, breed, avoid predators, and determine habitat quality and suitability (Stamps, 2001). Conspecific interaction (i.e., attraction or avoidance) describes the effect of animal sociality on space use behaviors like habitat selection and home range establishment (Stamps, 1988). Conspecific interaction influences animal movements and distributions as territorial species avoid conspecifics

while colonial species attract conspecifics with consequences for ecological processes like foraging and dispersal (Giuggioli et al., 2013; Raitanen et al., 2014). Given increased mortality risks and environmental uncertainty associated with dispersal, dispersers benefit from social cues during habitat selection (i.e., settlement and residency) (Pärt et al., 2011; Stamps et al., 2005). The degree of conspecific attraction or avoidance can vary by species with fitness and survival consequences among individuals and populations (Muller et al., 1997; Muriel et al., 2016). For instance, species perceptual ranges can alter space use (Grant et al., 2018; Kittle et al., 2015) and movement behavior (Mueller and Fagan, 2008; Zollner and Lima, 1999), influencing animal responses to conspecific cues of resources and risks in landscapes (Raitanen et al., 2014; Szymkowiak and Kuczyński, 2015). Considering the influence of conspecific interaction as a function of perceptual range on animal movement (Lima and Zollner, 1996; Muriel et al., 2016), habitat selection and settlement (Muriel et al., 2016; Pizzatto et al., 2016) can elucidate connections between animal distributions (Gil et al., 2018) and corresponding spatial subsidies.

Even though reviews in spatial subsidy research document the need to address the impact of animal sociality and movement on ecosystems (Earl and Zollner, 2017), many ecosystem models do not consider the influence of animal interactions on active subsidies. Animal habitat and space use models that consider the sociality focus on one taxon (Guy et al., 2008; Raitanen et al., 2014) and ignore spatially explicit animal movement. In contrast, ecosystem models that incorporate animal movements either ignore animal interactions (Bauduin et al., 2016) or consider sociality in context of a single conspecific interaction scenario (i.e., attraction or avoidance) (Moorcroft and Barnett, 2008). Moreover, research on the ecosystem impacts of species distributions emerging from socially influenced animal behavior is limited (McInturf et al., 2019) because there are no models that consider the interaction between spatially explicit animal sociality

and movement on active subsidy distributions. Ecosystem models that examine variation in animal movements with sociality across a wide range of interaction scenarios can provide general insights into spatial subsidy impacts of animal territoriality and coloniality in a variety of ecological contexts (e.g., habitat prospecting, selection, settlement). Further, spatial subsidy models that examine for the influence of differences in species perpetual ranges on conspecific interactions can be useful for studying spatial subsidy systems across a variety of taxa and ecological communities in real world systems. Models that also account for benefits of conspecific interactions like mitigation of dispersal search mortality risks from socially influenced habitat selection and settlement (Fletcher, 2006) can elucidate differences between nutrient and consumer subsidy patterns.

Movement ecology and Individual-Based Modeling (IBM) approaches (Nathan et al., 2008; Potts et al., 2014; Turchin, 1989; Wallentin, 2017) provide spatially-explicit frameworks to model the influence of animal sociality, perceptual range and movement on active subsidy distribution. Spatially explicit IBMs that incorporate stochastic animal movement, mortality and settlement likelihood as a function of perceptual range and the number of already settled conspecifics provide a novel framework to quantify spatiotemporal dynamics of animal-transported subsidies. In this paper, we construct a spatially explicit IBM to investigate the relative influence of variation in animal social and movement behaviors on active subsidy distribution. Our objective is to quantify the extent and intensity of living and dead subsidy distribution emerging from variation in animal movement patterns and conspecific interaction by settlement as a function of the number of settled conspecifics within perceptual range. We analyze the relative significance of three animal interaction categories (i.e., conspecific attraction, avoidance and no interaction) and settled conspecifics experience reduced mortality risks. We quantify distance, density, and clustering

metrics of subsidy distribution including the maximum deposition distance and range, peak density and distance to peak density, maximum cluster deposition distance, density, radial size, and inter-cluster range. Our overarching hypothesis is that active subsidy distribution patterns likely vary with the type of subsidy (i.e., living, dead), and category of conspecific interaction (i.e., attraction, avoidance, no interaction). Specifically, we predict that depending on perceptual range, conspecific avoidance could spread living subsidies out more than attraction. Settlement and mortality probability could moderate dead subsidy deposition distance, density and clustering effects more than how straight animals move.

3.3 Methods

3.3.1 Background

Our simulation environment consists of a binary world in which animals disperse from a donor ecosystem (natal habitat) to a recipient ecosystem (adult habitat) where settlement or death can occur. Similar ecological system dynamics include amphibians, insect emergence and seabird breeding dispersal between aquatic and proximal terrestrial landscapes (Pittman et al., 2014; Yoder et al., 2004). To simulate ontogenetic shifts from natal to adult habitat in our model, dispersers that enter the recipient ecosystem cannot return to the donor ecosystem as in ecological systems where dispersers develop traits incompatible with donor habitat and adapted to recipient habitat (DeAngelis and Mooij, 2005). We design animal movement as a correlated random walk (CRW). Settlement is a stochastic process where dispersers have a random chance of settling as a function of the number of already settled conspecifics within their perceptual range. We vary the type of conspecific interaction, settlement probability, perceptual range and sinuosity of CRW across corresponding parameter ranges to examine differences in resulting subsidy patterns (Table 2). Living individuals are consumer subsidies to recipient ecosystems that have potential top-down

effects for ecosystem dynamics, whereas dead individuals provide nutrient subsidies with possible bottom-up effects (Andrews and Harvey, 2013).

We assume a highly simplified world of a donor and recipient ecosystem with no spatial heterogeneity to eliminate confounding effects from landscape heterogeneity interacting with movement and conspecific interaction with perceptual range. We do not consider demographic processes in our model because conspecific interactions, movement, and mortality and subsidy distribution dynamics occur at smaller spatiotemporal scales (i.e., natal dispersal event) (Earl and Zollner, 2014). We also assume mortality is lower after settlement due to advantages like lower detection by predators (Szymkowiak and Kuczyński, 2015; van Gils et al., 2015). Dispersers cannot return to the natal zone after entering the recipient ecosystem. In our model, dead individuals become nutrients, energy or contaminant subsidies and remain at the location of death. Settled dispersers remain at the location of settlement in the recipient ecosystem in the model to allow comparison between living and dead subsidies.

We designed our model in the NetLogo software (version 6.0.4) (Tisue and Wilensky, 2004; Wilensky, 1999) simulation environment and used program R (version 3.3) for data analysis.

3.3.2 Design

We implement a vertically wrapped 1000 by 2000 patch (square unit of space in NetLogo) binary landscape in which 1000 individuals disperse from an adjacent donor ecosystem (i.e., 1 patch) centered at the left vertical boundary into the recipient ecosystem during 1000 timesteps. Dispersers move outward through the adult zone (i.e., recipient ecosystem). At each timestep, dispersers orient at random angles drawn from a wrapped Cauchy distribution and move by 1-unit step-lengths for up to 1000 timesteps if an individual does not settle (Figure 8). We vary the degree of sinuosity in disperser movement trajectories by adjusting the correlation between subsequent

turning angles. During movement, individuals have a stochastic chance of settlement and death at each timestep. Individuals cannot move after death but can die after settlement at half the mortality rate prior to settlement in accordance with the assumption that settlement reduces mortality risk.

We implement five levels of baseline settlement probability (φ) as the random chance that any individual settles (Table 2). We model settlement behavior across three levels capturing conspecific interaction (attraction and avoidance) and non-conspecific (null) behavior. We implemented settlement by adjusting the settlement probability across interaction scenarios:

$$\varphi' = \begin{cases} \varphi(n+1), & \text{attraction} \\ \varphi, & \text{null} \\ \frac{\varphi}{(n+1)}, & \text{avoidance} \end{cases}$$

where n = number of settled conspecifics within the perceptual range of dispersers. At each timestep, an unsettled individual draws a random number from a uniform distribution over $[0,1]$ and settles if the number drawn is less than the settlement probability (φ'). We implemented five levels of perceptual range (p) as the radial distance (i.e., number of patches) surrounding the area within which unsettled individuals could sense settled conspecifics (Table 2).

We modeled animal movement using a correlated random walk (CRW). At each timestep, individuals select a turning angle to navigate from the donor ecosystem start-patch outward and through the adjacent recipient ecosystem. We implemented CRW using a constant one-unit step-length and a wrapped Cauchy distribution of turning angles $\theta(t)$:

$$\theta(t) = \theta(t-1) + 2 \tan^{-1} \left[\left(\frac{1-\alpha}{1+\alpha} \right) \tan(\pi\gamma) \right],$$

where $0 \leq \alpha \leq 1$, and

$$-0.5 \leq \gamma \leq 0.5$$

where $\theta(t-1)$ is a previous turning angle and γ is randomly drawn from a uniform distribution over a range of $[-0.5, 0.5]$ to normalize the direction of movement trajectories with the correlation

between successive steps. We simulated a representative range of CRW patterns by varying the scaling coefficient (α) (Table 2). CRW movement is straighter as $\alpha \rightarrow 1$ and more sinuous as $\alpha \rightarrow 0$. Dispersers stop moving after settlement and do not move again for the remainder of the 1000 timestep simulation run.

At each timestep, unsettled dispersers die if the random number drawn is less than the mortality probability (m) where $m = 0.001$, and settled dispersers die if the random number drawn is less than $m = 0.0005$. We conducted simulations using a fully factorial combination among all levels of the state variables and extracted spatial metrics of collective living (i.e., settled and alive) and dead subsidy distribution at the end of each 1000 timestep run. We assessed spatial distribution metrics of both living and dead individuals at the 1000th timestep when all individuals either settled or died to quantify emergent subsidy distribution patterns in the recipient ecosystem.

3.3.3 Analysis

We estimated metrics of emergent subsidy distribution patterns for each run and analyzed living (i.e., settled) and dead subsidy deposition patterns separately. We examined displacement (i.e., maximum subsidy deposition distance, range and distance to peak deposition density), density (i.e., peak deposition density and number of subsidies) and clustering metrics (i.e., maximum cluster size, density and inter-cluster distance). The maximum subsidy deposition distance is the distance from the donor-recipient ecosystem boundary to the furthest displaced subsidy. The maximum subsidy deposition range is the distance between the furthest and least displaced subsidies. The peak subsidy deposition density is the greatest number of subsidies within the area defined by a 100-patch radius (i.e., 10% of the simulation landscape) of each subsidy. The distance to peak density is the distance between the shared ecosystem boundary and the focal subsidy where peak density occurs. We also analyzed clustering patterns in living and dead subsidy deposition

including the number of clusters, the maximum cluster size, cluster displacement and cluster density. We identified members of clusters using a recursive density-based clustering approach where a focal subsidy and the three nearest subsidies within the perceptual range of a subsidy form and grow a cluster. We estimated maximum cluster size as the radial extent of the most spread-out cluster and determined the maximum cluster density as the number of subsidies in the cluster with the greatest number of subsidies. We measured the maximum inter-cluster range as the distance between the furthest and least displaced clusters.

We conducted random forest analyses (Archer and Kimes, 2008; Breiman, 2001) to quantify the relative importance of predictors (i.e., conspecific settlement interaction (i.e., attraction, avoidance, no interaction), perceptual range and movement) to variation in response variables (i.e., subsidy distribution metrics; displacement, density and clustering). To do this, we used bootstrap sampling-with-replacement to perform 2000 iterations of random permutations on predictor observations to develop random forest model fits for response variables. We evaluated the prediction accuracy of resulting random forest models based on the percentage increase in mean square error from resampling predictor data and the corresponding increase in the residual sum of squares as a measure of node purity in random forest trees. We also used classification and regression trees (CARTs) (Breiman, 2017; Therneau and Atkinson, 2015) to analyze relationships between response variables and predictor interactions. We required a minimum of 2000 dependent variable observations (i.e., greater than 5% of the total number of total data observations (i.e., $n = 38,000$) for a node-split or tree outcome in response to predictor level conditions. We applied a complexity parameter (C_p) value of 0.001 to limit overfitting by retaining CARTs that exclude predictor node-splits or outcomes that did not increase the coefficient of determination of CART model fit by more than 0.1%.

We synthesized CART trends into charts. We grouped CARTs related to overall subsidy deposition distance (6 CARTs) and density (4 CARTs), cluster displacement (2 CARTs), cluster size (2 CARTs) and cluster density (4 CARTs) metrics into respective categories. We selected CART elements that differentiated between outcomes by a minimum of 12.5% ($n = 4750$) of the total number of observations ($n = 38,000$) for comparable predictor combinations across groups of subsidy distribution metric. Bold chart lines indicate trends observed in all representative CARTs in each category. Thin lines indicate trends featured in more than one but not all representative CARTs for each category. See supplementary materials for detailed CARTs (Appendix B).

3.4 Results

For both living and dead subsidies, the type of conspecific interaction was generally the most important predictor of deposition quantity, peak density and distance to peak density (Figure 9). Compared to settlement probability, scaling coefficient (i.e., movement behavior) was a better predictor of the peak density and distance to peak density for dead subsidies. However, for living subsidies, settlement probability predicted the peak density and distance to peak density better than scaling coefficient. Conspecific interaction was the most important predictor of the maximum inter-cluster range, cluster density and cluster size for both living and dead subsidies (Figure 10). In order of decreasing predictor importance, perceptual range, scaling coefficient and settlement probability were secondary influences on the maximum inter-cluster range, cluster density cluster size for both living and dead subsidy deposition. Scaling coefficient was the most dominant predictor of subsidy displacement. For both living and dead subsidies, scaling coefficient was a more influential determinant of the maximum subsidy deposition distance and range than conspecific interaction.

The number of living subsidies generally increased with settlement probability due to the decreased probability of mortality with settlement. Conspecific avoidance however generated more dead subsidies than conspecific attraction, particularly for more sinuous movement ($\alpha \leq 0.9$) at higher perceptual range ($p > 5$). Scenarios without conspecific interaction resulted in intermediate numbers of living and dead subsidies. Given lower settlement probability and higher perceptual range, straighter movements ($\alpha > 0.9$) displaced both living and dead subsidies further from the ecosystem boundary in avoidance than attraction scenarios (Figure 11). Compared to avoidance scenarios, attraction resulted in lower maximum subsidy deposition distance, range and distance to peak density given lower settlement probability and perceptual range. Scenarios without conspecific interaction resulted in intermediate subsidy displacement. Attraction scenarios generally resulted in less dense subsidy distributions than avoidance scenarios (Figure 12). Higher settlement probability ($\phi \geq 0.005$) generally resulted in greater peak subsidy deposition density for living subsidies and straighter movement generally resulted in lower peak subsidy deposition density for dead subsidies. Given more sinuous movements at higher settlement probability and perceptual range, attraction scenarios resulted in greater peak subsidy deposition density than avoidance scenarios, particularly for living subsidies. Conspecific avoidance resulted in greater peak deposition density for dead subsidies given more sinuous movement at lower settlement probability ($\phi < 0.005$) and perceptual range. Given straighter movement at higher settlement probability and lower perceptual range ($p \leq 5$), avoidance scenarios and scenarios without conspecific interaction generated intermediate peak subsidy densities.

Given higher perceptual range and settlement probability, scenarios with attraction and without conspecific interaction resulted in the greatest number of living subsidy clusters. Lower settlement probability however reduced the number of living subsidy clusters, resulting in greater

numbers of dead subsidy clusters. In conspecific attraction scenarios, higher settlement probability and perceptual range generally resulted in the lowest number of living subsidy clusters, forming fewer, smaller and denser clusters than avoidance scenarios. Given higher perceptual range, straighter movements generally increased the number of living subsidies in avoidance scenarios with higher settlement probability and increased the number of dead subsidies in attraction scenarios with lower settlement probability. Given higher perceptual range in avoidance scenarios, straighter movement with lower settlement probability resulted in greater inter-cluster displacement for both living and dead subsidies (Figure 13). Sinuous movement in attraction scenarios generally constrained inter-cluster displacement but lower perceptual range and settlement probability reduced this effect. Higher perceptual range in avoidance scenarios generated the largest clusters (Figure 14). Compared to avoidance scenarios and scenarios with no interaction, attraction generated the smallest clusters for both living and dead subsidies. Lower settlement probability however increased cluster sizes for dead subsidies. Given higher perceptual range in attraction scenarios, more sinuous movement with higher settlement probability generated clusters with the greatest living subsidy density (Figure 15). Lower settlement probability and perceptual range however generated clusters with the greatest dead subsidy density. Given higher perceptual range and settlement probability in avoidance scenarios, straighter movements generated clusters with the lowest living subsidy density. Lower settlement probability however resulted in clusters with the lowest dead subsidy density.

In summary, avoidance scenarios spread subsidies further into the recipient ecosystem at lower densities than attraction scenarios. Avoidance scenarios also resulted in more, spread-out, smaller and less dense clusters compared to attraction scenarios. Increasing perceptual range and the straightness of movement patterns further enhanced subsidy displacement and spreading in

avoidance scenarios but increasing settlement probability attenuated these effects. Increasing perceptual range, settlement probability and sinuosity of movement patterns further limited subsidy displacement but enhanced subsidy density and clustering in attraction scenarios. Scenarios with no interaction generally resulted in intermediate subsidy deposition patterns compared to attraction and avoidance scenarios. Living subsidies were generally deposited further and in more spread-out patterns than dead subsidies. Increasing settlement probability, perceptual range and the sinuosity of movement patterns resulted in more living subsidies but attenuated corresponding subsidy displacement with enhanced subsidy densities and increased clustering.

3.5 Discussion

We demonstrate that the relationship of animal sociality and movement behavior to spatial subsidies and associated ecosystem responses depends on the type (e.g., consumer (living), nutrient (dead)) and aspect (e.g., extent, intensity, grouping) of subsidy distribution under consideration. It can be critical to know which type and aspect of subsidy distribution responds more to sociality versus movement given resource and time constraints in researching the ecosystem responses of animal-transported subsidies. We showed that conspecific interactions are more important for assessing the density of consumer subsidies and clustering patterns for both consumer and nutrient subsidies than movement behavior. This is consistent with observations of juvenile ravens in the western Mojave desert where sociality mediates foraging behavior during dispersal search close to natal habitats, resulting in dense consumer subsidy clusters on desert tortoise populations (Kristan and Boarman, 2003; Webb et al., 2009). Similarly, colonial seabirds and sea turtles rely on conspecific cues to locate foraging resources and determine nesting habitat quality with more sinuous movements at terrestrial breeding sites (Garthe et al., 2016; Hart et al., 2013). They deposit large amounts of scat and eggs rich in ocean nutrient subsidies at terrestrial

nesting sites with significant local top-down and bottom-up impacts that enhance coastal vegetation growth and subsidize terrestrial predator diets (Vander Zanden et al., 2012; Wing et al., 2014). Models that account for social interactions can provide more informative predictions of corresponding spatial subsidy impacts for a variety of taxa and ecosystems. Our results also show that movement behavior is more important for the intensity of nutrient subsidy deposition and the extent of consumer and nutrient subsidy deposition in a landscape. This aligns with research showing that territorial bears avoid competing conspecifics by undertaking long range foraging and homing movements to and from streams where they consume anadromous salmon, spreading carcasses in riparian areas and transporting feces rich in ocean nutrients that stimulate vegetation regeneration deep in riparian forests (Quinn et al., 2009). In this active subsidy system, accounting for social influence upon bear movement behavior in ecosystem models can provide adequate predictions of spatial distributions of bear-transported salmon nutrient subsidies to riparian forests ecosystems. Given high data collection costs, spatial subsidy research will benefit from considering the relative importance of animal sociality and movement in different ecological scenarios and prioritizing accordingly.

Spatial subsidy research can improve by considering synergistic interactions between animal sociality and movement on the distribution and impact of animal-transported subsidies across ecosystems. Our results show that spatially explicit interactions between animal sociality and movement influence spatial subsidy patterns. For instance, we found that straighter movements in attraction interactions displaced more consumer subsidies further into the recipient ecosystem, increasing the number, size, density and spread of corresponding nutrient subsidy clusters. This observation is consistent with studies that show that for large herbivore populations (e.g., elephants, zebras, wildebeests) in the Serengeti-Mara grassland ecosystem, socially cued

migrations influence spatial patterns in vegetation turnover (Holdo et al., 2009). For instance, wildebeest migrations along seasonally mediated spatial variations in rainfall and vegetation patterns can result in expansive consumption patterns on grasslands (Musiega and Kazadi, 2004). Migrating wildebeest redistribute nutrients when they deposit dense clusters of feces that stimulate local primary productivity (Holdo et al., 2007), or become prey for apex predators along migration routes (e.g., lions, crocodiles) (Palmer et al., 2017; Subalusky et al., 2017). Ecosystem models that incorporate interactive effects between large herbivore sociality and movement behavior will enable the development of tools to predict spatial impacts of corresponding consumer and nutrient subsidies for improved wildlife and ecosystem management. We also found that straighter movements in avoidance scenarios increased consumer subsidy displacement in large, scattered clusters. This result is consistent with the distribution of kill sites emerging from the foraging movements of territorial lions in the Ngorongoro conservation area (Elliott and Cowan, 1978). Prides in the Ngorongoro crater forage over large territories, resulting in large, sparse kill-site clusters with top-down ecosystem impacts confined to deposition locations (Kissui and Packer, 2004). Developing models to predict consumer subsidy distributions and impacts of territorial apex predators like lions in wildlife and ecosystem management scenarios will require understanding how avoidance interactions influence their foraging movements.

Our model quantified how, animal perceptual range and settlement probability in response to habitat preferences and quality mediates the influence of animal sociality and movement on the distribution of animal-transported subsidies. These results are consistent with other studies that show that variation in animal perceptual range (Zollner and Lima, 1999, 1997) and settlement probability (Stamps et al., 2005) have important secondary influences on movement and sociality that can affect subsidy clustering patterns. Territorial Yellowstone coyotes avoid conspecifics

when foraging over long distances and defending large home ranges (da Luz et al., 2015; Middleton et al., 2013; Pyare and Berger, 2003), which likely results in expansive consumer and nutrient subsidy clusters. Juvenile amphibians and aquatic insects rely on olfactory and visual cues effective over short distances for kin recognition, resulting in straighter dispersal search and sinuous foraging movements (Despland, 2001; Pittman et al., 2014; Sinsch, 2014; Wells, 1977). This low range perceptual range and more sinuous movements informed by dispersal search for refugia generates small but dense amphibian consumer and nutrient subsidy clusters around natal ponds, resulting in strong predator shadows and trophic cascades in local insect communities (Hocking and Babbitt, 2014; McCoy et al., 2009). These examples substantiate the need to account for individual and species variation in perceptual range with animal sociality and movement behavior in models of active subsidy systems. This will improve the utility of such models for predicting spatial patterns and ecosystem impacts in important ecological processes like biological contaminant transport and disease transfer. Aquatic insect and amphibians can transport contaminants and transfer diseases between aquatic and terrestrial ecosystems that destabilize food webs (Kraus et al., 2014), degrade recipient ecosystems (Walters et al., 2008), and affect ecosystem services like nutrient cycling, pollination and pest regulation (Schindler and Smits, 2017). Developing models to predict spatial patterns and impacts of animal-transported contaminants and diseases across ecosystems will require insights on how species perceptual range, movement behavior and sociality influence habitat selection, settlement and contact.

Even though there are some studies that have examined the influence of animal sociality on spacing in animal population distributions (Giuggioli et al., 2013), our work is the first to simulate the influence of animal sociality and movements on active subsidy distributions and impacts. The influence of interaction between animal sociality and movement on spatial subsidies

has important implications for nutrient export and hotspots as well as contaminant impacts in recipient ecosystems. For example, North Atlantic Auk breeding colonies shape spatial patterns in primary productivity in Northwest Greenland, transporting marine nutrients in krill and fish consumption to terrestrial ecosystems as fecal deposition (González-Bergonzoni et al., 2017). Auks rely on conspecific cues to select breeding habitat and nesting sites. Corresponding feces deposition sites show significantly higher primary productivity than surrounding areas, providing vegetation rich in ocean nutrients that musk ox and other large herbivores in the region consume. Auk breeding colonies also deposit significant amounts of nutrients in feces in coastal freshwaters that acidify and degrade coastal freshwater ecosystems. Understanding how sociality in breeding colonies influences seabird movements will enable the development of predictive models to help manage positive and negative impacts of marine nutrient subsidies to terrestrial and freshwater ecosystems.

Our work contributes to spatial subsidy research by being the first IBM to simulate and quantify how spatial subsidies respond to animal movement given sociality and perceptual range across broad range of parameter space, elucidating phenomenological insights into active subsidy systems. Until our research, most spatial subsidy research consisted of collections of empirical anecdotes with single taxon and context (i.e., attraction or avoidance) emphases. We focused on determining the effect of animal sociality and perceptual range with movement and mortality on active subsidy distribution. We made simplifying assumptions to optimize model functionality with computing power and speed (Chapter 2). Model realism can improve by accounting for additional factors like variation in animal body and step size. Move length can be a function of animal body size (e.g., larger animals take bigger steps) or mode of navigation (e.g., flying animals move longer distances) and could affect the extent and impact of active subsidy deposition in

recipient ecosystems or habitats (Earl and Zollner, 2014). To simplify our ability to distinguish between living and dead subsidies, we did not examine secondary movement or relocation of nutrient dead subsidies by agents like scavengers and weather patterns. These variables and concepts were beyond the scope of this work but would provide further insight into how animal sociality and movement behavior influence the distribution of animal-transported subsidies and corresponding ecosystem effects.

3.6 Conclusion

We modeled and showed how spatially-explicit animal sociality can interact with movement behavior and affect emergent spatial consumer and nutrient subsidy distribution patterns. We provided a systematic framework with a comprehensive scenario modeling approach to highlight general principles about how active subsidy distribution and corresponding spatial impacts respond to animal sociality and movement behavior in a variety of abstract but ecologically plausible contexts. Active subsidies can alter ecosystem structure, function and services across landscapes (Earl and Zollner, 2017; Ewers and Didham, 2006). Accounting for animal behavior when examining animal-transported subsidy distributions provides relevant and useful insight into spatiotemporal dynamics of ecosystem impacts. Spatial subsidy models can improve and be more beneficial to spatial subsidy research by accounting for the relative and synergistic influences of animal sociality and movement on active subsidy distributions.

3.7 References

Andrews, K., Harvey, C., 2013. Ecosystem-level consequences of movement: seasonal variation in the trophic impact of a top predator. *Mar. Ecol. Prog. Ser.* 473, 247–260.
<https://doi.org/10.3354/meps10095>

- Archer, K.J., Kimes, R. V., 2008. Empirical characterization of random forest variable importance measures. *Comput. Stat. Data Anal.* 52, 2249–2260.
<https://doi.org/10.1016/J.CSDA.2007.08.015>
- Bauduin, S., McIntire, E., St-Laurent, M.-H., Cumming, S., 2016. Overcoming challenges of sparse telemetry data to estimate caribou movement. *Ecol. Modell.* 335, 24–34.
<https://doi.org/10.1016/j.ecolmodel.2016.05.004>
- Breiman, L., 2017. *Classification And Regression Trees*. Routledge.
<https://doi.org/10.1201/9781315139470>
- Breiman, L., 2001. Random Forests. *Mach. Learn.* 45, 5–32.
<https://doi.org/10.1023/A:1010933404324>
- Campomizzi, A.J., Butcher, J.A., Farrell, S.L., Snelgrove, A.G., Collier, B.A., Gutzwiller, K.J., Morrison, M.L., Wilkins, R.N., 2008. Conspecific Attraction is a Missing Component in Wildlife Habitat Modeling. *J. Wildl. Manage.* 72, 331–336. <https://doi.org/10.2193/2007-204>
- da Luz, M.G.E., Raposo, E.P., Viswanathan, G.M., 2015. And yet it optimizes: Comment on “Liberating Lévy walk research from the shackles of optimal foraging” by A.M. Reynolds. *Phys. Life Rev.* <https://doi.org/10.1016/j.plrev.2015.07.007>
- DeAngelis, D.L., Mooij, W.M., 2005. Individual-Based Modeling of Ecological and Evolutionary Processes. *Annu. Rev. Ecol. Evol. Syst.*
<https://doi.org/10.1146/annurev.ecolsys.36.102003.152644>
- Despland, E., 2001. Role of Olfactory and Visual Cues in the Attraction/Repulsion Responses to Conspecifics by Gregarious and Solitarious Desert Locusts. *J. Insect Behav.* 14, 35–46.
<https://doi.org/10.1023/A:1007845528500>

- Earl, J.E., Semlitsch, R.D., 2012. Reciprocal subsidies in ponds: does leaf input increase frog biomass export? *Oecologia* 170, 1077–1087. <https://doi.org/10.1007/s00442-012-2361-5>
- Earl, J.E., Zollner, P.A., 2017. Advancing research on animal-transported subsidies by integrating animal movement and ecosystem modelling. *J. Anim. Ecol.* 86, 987–997. <https://doi.org/10.1111/1365-2656.12711>
- Earl, J.E., Zollner, P.A., 2014. Effects of animal movement strategies and costs on the distribution of active subsidies across simple landscapes. *Ecol. Modell.* 283, 45–52. <https://doi.org/10.1016/j.ecolmodel.2014.03.020>
- Elliott, J.P., Cowan, I.M., 1978. Territoriality, density, and prey of the lion in Ngorongoro Crater, Tanzania. *Can. J. Zool.* 56, 1726–1734. <https://doi.org/10.1139/z78-237>
- Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev. Camb. Philos. Soc.* <https://doi.org/10.1017/S1464793105006949>
- Fletcher, R.J., 2006. Emergent properties of conspecific attraction in fragmented landscapes. *Source Am. Nat.* 168, 207–219. <https://doi.org/10.1086/505764>
- Garthe, S., Schwemmer, P., Paiva, V.H., Corman, A.-M., Fock, H.O., Voigt, C.C., Adler, S., 2016. Terrestrial and Marine Foraging Strategies of an Opportunistic Seabird Species Breeding in the Wadden Sea. *PLoS One* 11, e0159630. <https://doi.org/10.1371/journal.pone.0159630>
- Gil, M.A., Hein, A.M., Spiegel, O., Baskett, M.L., Sih, A., 2018. Social Information Links Individual Behavior to Population and Community Dynamics. *Trends Ecol. Evol.* <https://doi.org/10.1016/j.tree.2018.04.010>

- Giuggioli, L., Potts, J.R., Rubenstein, D.I., Levin, S.A., 2013. Stigmergy, collective actions, and animal social spacing. *Proc. Natl. Acad. Sci. U. S. A.* 110, 16904–9.
<https://doi.org/10.1073/pnas.1307071110>
- González-Bergonzoni, I., Johansen, K.L., Mosbech, A., Landkildehus, F., Jeppesen, E., Davidson, T.A., 2017. Small birds, big effects: the little auk (*Alle alle*) transforms high Arctic ecosystems. *Proc. R. Soc. B Biol. Sci.* 284, 20162572.
<https://doi.org/10.1098/rspb.2016.2572>
- Grant, T.J., Parry, H.R., Zalucki, M.P., Bradbury, S.P., 2018. Predicting monarch butterfly (*Danaus plexippus*) movement and egg-laying with a spatially-explicit agent-based model: The role of monarch perceptual range and spatial memory. *Ecol. Modell.* 374, 37–50.
<https://doi.org/10.1016/J.ECOLMODEL.2018.02.011>
- Guy, A.G., Bohan, D.A., Powers, S.J., Reynolds, A.M., 2008. Avoidance of conspecific odour by carabid beetles: a mechanism for the emergence of scale-free searching patterns. *Anim. Behav.* 76, 585–591. <https://doi.org/10.1016/j.anbehav.2008.04.004>
- Hart, K.M., Lamont, M.M., Sartain, A.R., Fujisaki, I., Stephens, B.S., 2013. Movements and Habitat-Use of Loggerhead Sea Turtles in the Northern Gulf of Mexico during the Reproductive Period. *PLoS One* 8, e66921. <https://doi.org/10.1371/journal.pone.0066921>
- Hocking, D., Babbitt, K., 2014. Amphibian Contributions to Ecosystem Services. *Herpetol. Conserv. Biol.*
- Holdo, R.M., Holt, R.D., Coughenour, M.B., Ritchie, M.E., 2007. Plant productivity and soil nitrogen as a function of grazing, migration and fire in an African savanna. *J. Ecol.* 95, 115–128. <https://doi.org/10.1111/j.1365-2745.2006.01192.x>

- Holdo, R.M., Holt, R.D., Fryxell, J.M., 2009. Grazers, browsers, and fire influence the extent and spatial pattern of tree cover in the Serengeti. *Ecol. Appl.* 19, 95–109.
<https://doi.org/10.1890/07-1954.1>
- Judy A. Stamps, 1988. Conspecific Attraction and Aggregation in Territorial Species on JSTOR. *Am. Nat.* 131, 329–347.
- Kissui, B.M., Packer, C., 2004. Top–down population regulation of a top predator: lions in the Ngorongoro Crater. *Proc. R. Soc. London. Ser. B Biol. Sci.* 271, 1867–1874.
<https://doi.org/10.1098/rspb.2004.2797>
- Kittle, A.M., Anderson, M., Avgar, T., Baker, J.A., Brown, G.S., Hagens, J., Iwachewski, E., Moffatt, S., Mosser, A., Patterson, B.R., Reid, D.E.B., Rodgers, A.R., Shuter, J., Street, G.M., Thompson, I.D., Vander Vennen, L.M., Fryxell, J.M., 2015. Wolves adapt territory size, not pack size to local habitat quality. *J. Anim. Ecol.* 84, 1177–1186.
<https://doi.org/10.1111/1365-2656.12366>
- Kraus, J.M., Schmidt, T.S., Walters, D.M., Wanty, R.B., Zuellig, R.E., Wolf, R.E., 2014. Cross-ecosystem impacts of stream pollution reduce resource and contaminant flux to riparian food webs. *Ecol. Appl.* <https://doi.org/10.1890/13-0252.1>
- Kristan, W.B., Boarman, W.I., 2003. Spatial pattern of risk of common raven predation on desert tortoises. *Ecology* 84, 2432–2443. <https://doi.org/10.1890/02-0448>
- Lima, S.L., Zollner, P.A., 1996. Towards a behavioral ecology of ecological landscapes. *Trends Ecol. Evol.* [https://doi.org/10.1016/0169-5347\(96\)81094-9](https://doi.org/10.1016/0169-5347(96)81094-9)
- McCoy, M.W., Barfield, M., Holt, R.D., 2009. Predator shadows: complex life histories as generators of spatially patterned indirect interactions across ecosystems. *Oikos* 118, 87–100. <https://doi.org/10.1111/j.1600-0706.2008.16878.x>

- McInturf, A.G., Pollack, L., Yang, L.H., Spiegel, O., 2019. Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors? *Biol. Rev.* brv.12525. <https://doi.org/10.1111/brv.12525>
- Middleton, A.D., Kauffman, M.J., McWhirter, D.E., Jimenez, M.D., Cook, R.C., Cook, J.G., Albeke, S.E., Sawyer, H., White, P.J., 2013. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecol. Lett.* 16, 1023–1030. <https://doi.org/10.1111/ele.12133>
- Moorcroft, P.R., Barnett, A., 2008. MECHANISTIC HOME RANGE MODELS AND RESOURCE SELECTION ANALYSIS: A RECONCILIATION AND UNIFICATION. *Ecology* 89, 1112–1119. <https://doi.org/10.1890/06-1985.1>
- Mueller, T., Fagan, W.F., 2008. Animal distributions and movement behaviors in relation to resource dynamics.
- Muller, K.L., Stamps, J.A., Krishnan, V. V, Willits, N.H., 1997. The effects of conspecific attraction and habitat quality on habitat selection in territorial birds (*Troglodytes aedon*). *Am. Nat.* 150, 650–61. <https://doi.org/10.1086/286087>
- Muriel, R., Morandini, V., Ferrer, M., Balbontín, J., Morlanes, V., 2016. Juvenile dispersal behaviour and conspecific attraction: An alternative approach with translocated Spanish imperial eagles. *Anim. Behav.* 116, 17–29. <https://doi.org/10.1016/j.anbehav.2016.03.023>
- Musiega, D.E., Kazadi, S.-N., 2004. Simulating the East African wildebeest migration patterns using GIS and remote sensing. *Afr. J. Ecol.* 42, 355–362. <https://doi.org/10.1111/j.1365-2028.2004.00538.x>

- Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., Smouse, P.E., 2008. A movement ecology paradigm for unifying organismal movement research. *Proc. Natl. Acad. Sci. U. S. A.* 105, 19052–9. <https://doi.org/10.1073/pnas.0800375105>
- Palmer, M.S., Fieberg, J., Swanson, A., Kosmala, M., Packer, C., 2017. A ‘dynamic’ landscape of fear: prey responses to spatiotemporal variations in predation risk across the lunar cycle. *Ecol. Lett.* <https://doi.org/10.1111/ele.12832>
- Pärt, T., Arlt, D., Doligez, B., Low, M., Qvarnström, A., 2011. Prospectors combine social and environmental information to improve habitat selection and breeding success in the subsequent year. *J. Anim. Ecol.* 80, 1227–1235. <https://doi.org/10.1111/j.1365-2656.2011.01854.x>
- Pittman, S.E., Osbourn, M.S., Semlitsch, R.D., 2014. Movement ecology of amphibians: A missing component for understanding population declines. *Biol. Conserv.* 169, 44–53. <https://doi.org/10.1016/j.biocon.2013.10.020>
- Pizzatto, L., Stockwell, M., Clulow, S., Clulow, J., Mahony, M., 2016. Finding a place to live: conspecific attraction affects habitat selection in juvenile green and golden bell frogs. *Acta Ethol.* 19, 1–8. <https://doi.org/10.1007/s10211-015-0218-8>
- Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an Integration of Landscape and Food Web Ecology: The Dynamics of Spatially Subsidized Food Webs. *Annu. Rev. Ecol. Syst.* 28, 289–316.
- Polis, G.A., Holt, R.D., Menge, B.A., Winemiller, K.O., 1996. Time, Space, and Life History: Influences on Food Webs, in: *Food Webs*. Springer US, Boston, MA, pp. 435–460. https://doi.org/10.1007/978-1-4615-7007-3_38

- Potts, J.R., Mokross, K., Lewis, M.A., 2014. A unifying framework for quantifying the nature of animal interactions. *J. R. Soc. Interface* 11, 20140333–20140333.
<https://doi.org/10.1098/rsif.2014.0333>
- Pyare, S., Berger, J., 2003. Beyond demography and delisting: ecological recovery for Yellowstone's grizzly bears and wolves. *Biol. Conserv.* 113, 63–73.
[https://doi.org/10.1016/S0006-3207\(02\)00350-6](https://doi.org/10.1016/S0006-3207(02)00350-6)
- Quinn, T.P., Carlson, S.M., Gende, S.M., Rich, Jr., H.B., 2009. Transportation of Pacific salmon carcasses from streams to riparian forests by bears. *Can. J. Zool.* 87, 195–203.
<https://doi.org/10.1139/Z09-004>
- Raitanen, J., Forsman, J.T., Kivelä, S.M., Mäenpää, M.I., Välimäki, P., 2014. Attraction to conspecific eggs may guide oviposition site selection in a solitary insect. *Behav. Ecol.* 25, 110–116. <https://doi.org/10.1093/beheco/art092>
- Raposo, E.P., Bartumeus, F., da Luz, M.G.E., Ribeiro-Neto, P.J., Souza, T.A., Viswanathan, G.M., 2011. How landscape heterogeneity frames optimal diffusivity in searching processes. *PLoS Comput. Biol.* 7, e1002233. <https://doi.org/10.1371/journal.pcbi.1002233>
- Schindler, D.E., Smits, A.P., 2017. Subsidies of Aquatic Resources in Terrestrial Ecosystems. *Ecosystems*. <https://doi.org/10.1007/s10021-016-0050-7>
- Sinsch, U., 2014. Movement ecology of amphibians: from individual migratory behaviour to spatially structured populations in heterogeneous landscapes^{1, 2}. *Can. J. Zool.* 92, 491–502.
<https://doi.org/10.1139/cjz-2013-0028>
- Stamps, J., 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. Clobert, J., Danc. E., Dhondt, A. Nichols, J. Dispersal. Oxford Univ. Press. Pages 230-242 in.

- Stamps, J.A., 1988. Conspecific Attraction and Aggregation in Territorial Species. *Am. Nat.* 131, 329–347. <https://doi.org/10.1086/284793>
- Stamps, Krishnan, V. V., Reid, M., 2005. Search costs and habitat selection by dispersers. *Ecology* 86, 510–518. <https://doi.org/10.1890/04-0516>
- Subalusky, A.L., Dutton, C.L., Rosi, E.J., Post, D.M., 2017. Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proc. Natl. Acad. Sci. U. S. A.* 114, 7647–7652. <https://doi.org/10.1073/pnas.1614778114>
- Szymkowiak, J., Kuczyński, L., 2015. Predation-related costs and benefits of conspecific attraction in songbirds--an agent-based approach. *PLoS One* 10, e0119132. <https://doi.org/10.1371/journal.pone.0119132>
- Therneau, T.M., Atkinson, E.J., 2015. An Introduction to Recursive Partitioning Using the RPART Routines, Mayo Foundation. <https://doi.org/10.1017/CBO9781107415324.004>
- Tisue, S., Wilensky, U., 2004. Netlogo: A simple environment for modeling complexity. *Conf. Complex Syst.* 1–10. <https://doi.org/10.1109/ICVD.2004.1261037>
- Turchin, P., 1989. Population Consequences of Aggregative Movement. *J. Anim. Ecol.* 58, 75. <https://doi.org/10.2307/4987>
- van Gils, J.A., van der Geest, M., De Meulenaer, B., Gillis, H., Piersma, T., Folmer, E.O., 2015. Moving on with foraging theory: incorporating movement decisions into the functional response of a gregarious shorebird. *J. Anim. Ecol.* 84, 554–564. <https://doi.org/10.1111/1365-2656.12301>
- Vander Zanden, H.B., Bjorndal, K.A., Inglett, P.W., Bolten, A.B., 2012. Marine-derived Nutrients from Green Turtle Nests Subsidize Terrestrial Beach Ecosystems. *Biotropica* 44, 294–301. <https://doi.org/10.1111/j.1744-7429.2011.00827.x>

- Wallentin, G., 2017. Spatial simulation: A spatial perspective on individual-based ecology—a review. *Ecol. Modell.* 350, 30–41. <https://doi.org/10.1016/J.ECOLMODEL.2017.01.017>
- Walters, D.M., Fritz, K.M., Otter, R.R., 2008. The dark side of subsidies: Adult stream insects export organic contaminants to riparian predators. *Ecol. Appl.* 18, 1835–1841. <https://doi.org/10.1890/08-0354.1>
- Webb, W.C., Boarman, W.I., Rotenberry, J.T., 2009. Movements of Juvenile Common Ravens in an Arid Landscape. *J. Wildl. Manage.* 73, 72–81. <https://doi.org/10.2193/2007-549>
- Wells, K.D., 1977. The social behaviour of anuran amphibians. *Anim. Behav.* 25, 666–693. [https://doi.org/10.1016/0003-3472\(77\)90118-X](https://doi.org/10.1016/0003-3472(77)90118-X)
- Wilensky, U., 1999. NetLogo. Cent. Connect. Learn. Comput. Model. Northwest. Univ. Evanst.
- Wing, S., Jack, L., Shatova, O., Leichter, J., Barr, D., Frew, R., Gault-Ringold, M., 2014. Seabirds and marine mammals redistribute bioavailable iron in the Southern Ocean. *Mar. Ecol. Prog. Ser.* 510, 1–13. <https://doi.org/10.3354/meps10923>
- Yoder, J.M., Marschall, E.A., Swanson, D.A., 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. *Behav. Ecol.* 15, 469–476. <https://doi.org/10.1093/beheco/arh037>
- Zollner, P.A., Lima, S.L., 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80, 1019–1030. [https://doi.org/10.1890/0012-9658\(1999\)080\[1019:SSFLLI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1019:SSFLLI]2.0.CO;2)
- Zollner, P.A., Lima, S.L., 1997. Landscape-Level Perceptual Abilities in White-Footed Mice: Perceptual Range and the Detection of Forested Habitat. *Oikos* 80, 51. <https://doi.org/10.2307/3546515>

3.8 Tables and Figures

Table 2 *State variables with parameter levels incorporated in the individual-based model design.* Type of conspecific interaction, settlement probability, perceptual range and movement (scaling coefficient).

| <i>State Variable</i> | <i>Parameters</i> |
|---|------------------------------------|
| <i>Conspecific interaction</i> | Attraction, Avoidance, None (Null) |
| <i>Settlement probability</i> | 0.001, 0.0025, 0.005, 0.0075, 0.01 |
| <i>Perceptual Range</i> | 1, 3, 5, 7, 10 |
| <i>Movement (CRW scaling coefficient)</i> | 0.5, 0.8, 0.9, 0.95, 0.99 |

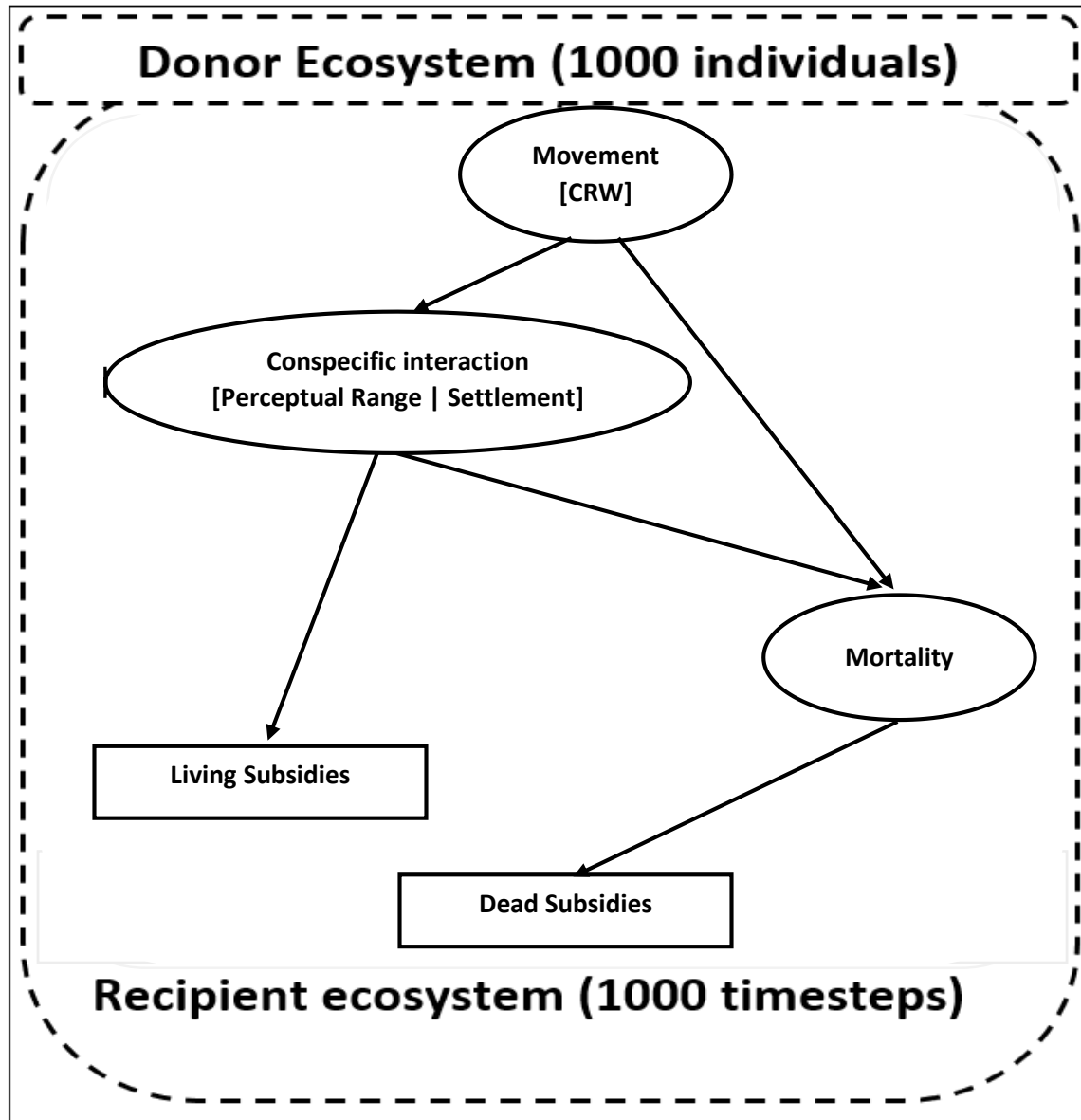


Figure 8 *Design concept. Simulation design, procedure and process flow for IBM sub-models (i.e., movement, conspecific interaction (perceptual range, settlement) and mortality) and outcomes (living and dead subsidies).* Dispersers leave the donor ecosystem and enter the recipient ecosystem, moving with a correlated random walk pattern over 1000 timesteps.

Dispersers die or settle at each time step based on respective mortality or settlement probabilities. Dispersers settlement probability increases as a function of the number of already settled conspecifics within their perceptual range in attraction scenarios. Dispersers settlement probability decreases as a function of the number of already settled conspecifics within their perceptual range in avoidance scenarios. Mortality reduces for settled conspecifics. Settled conspecifics become living subsidies and dead dispersers or conspecifics become dead subsidies in the recipient ecosystem.

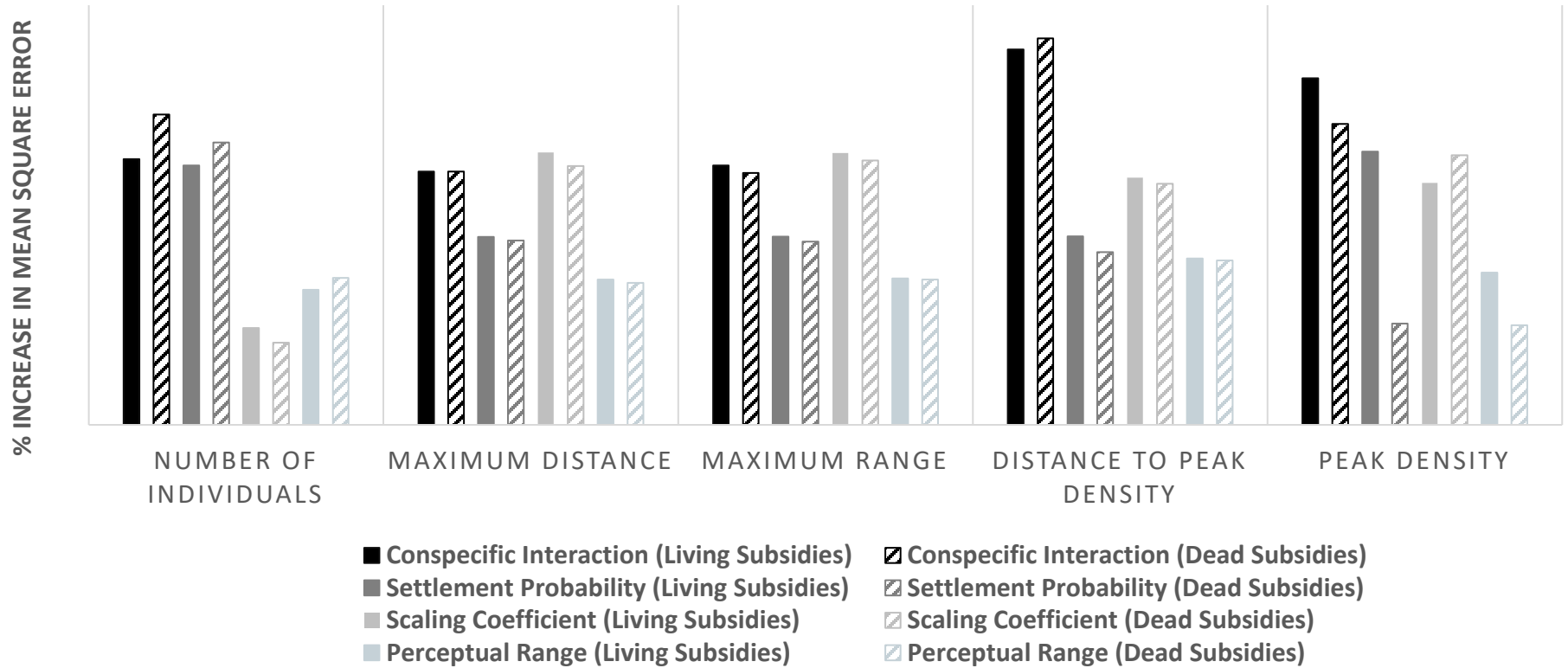


Figure 9 *Increase in percentage means square prediction error for metrics of living (consumer) and dead (nutrient) subsidy distribution.* Values indicate the relative importance as prediction strength of each state variable (conspecific interaction, settlement probability, scaling coefficient and perceptual range) to subsidy distribution; amount (number of living subsidies and number of dead subsidies), displacement (maximum deposition distance, range and distance to peak density), density (peak deposition density). Solid bars represent results for living subsidies and patterned bars represent results for dead subsidies. Taller bars indicate greater predictor importance (See section T in supplementary information (Appendix B) for detailed tables with values for variable (%IncMSE) and precision (IncNodePurity) (Table 7)).

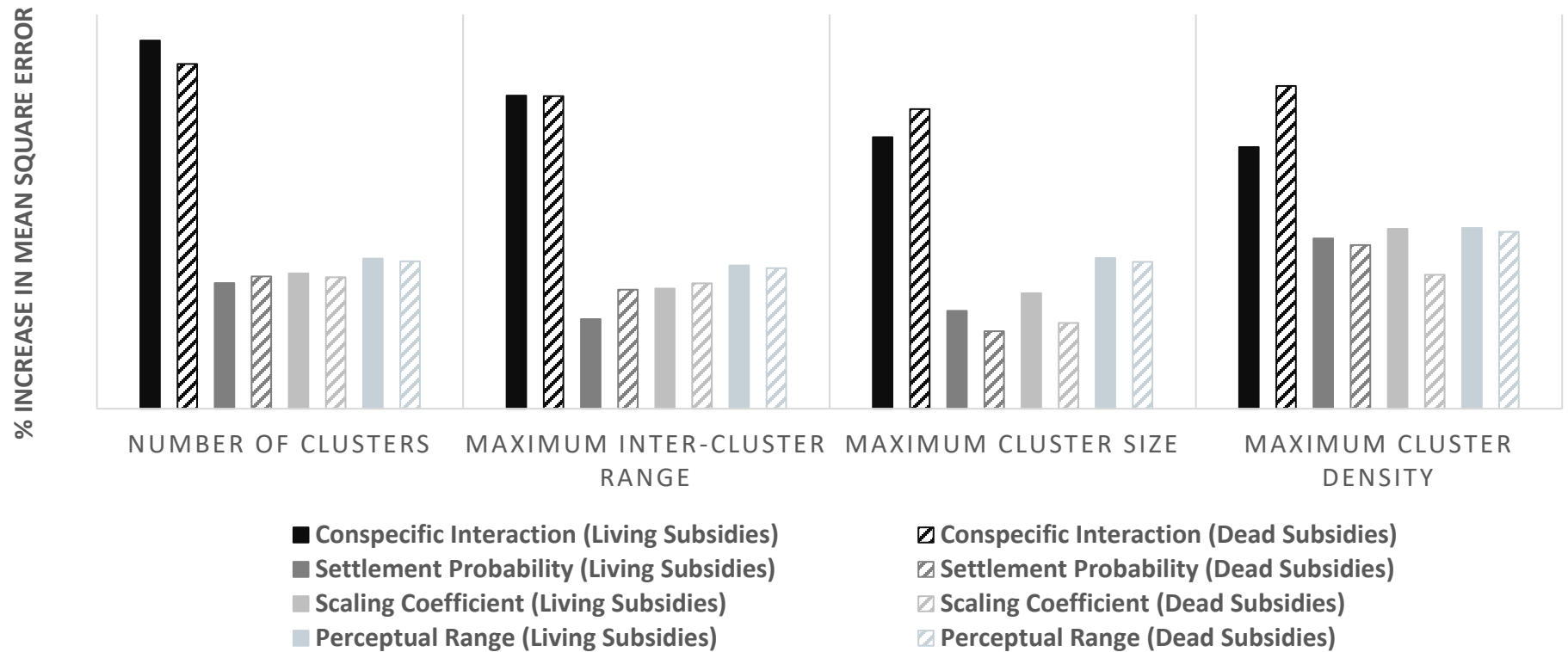


Figure 10 *Increase in percentage means square prediction error for metrics of living (consumer) and dead (nutrient) subsidy distribution.* Values indicate the relative importance as prediction strength of each state variable (conspecific interaction, settlement probability, scaling coefficient and perceptual range) to subsidy distribution; clustering (number of clusters, maximum inter-cluster range, density and size). Solid bars represent results for living subsidies and patterned bars represent results for dead subsidies. Taller bars indicate greater predictor importance. (See section T in supplementary information (Appendix B) for detailed tables with va' for variable importance (%IncMSE) and precision (IncNodePurity) (Table 7))

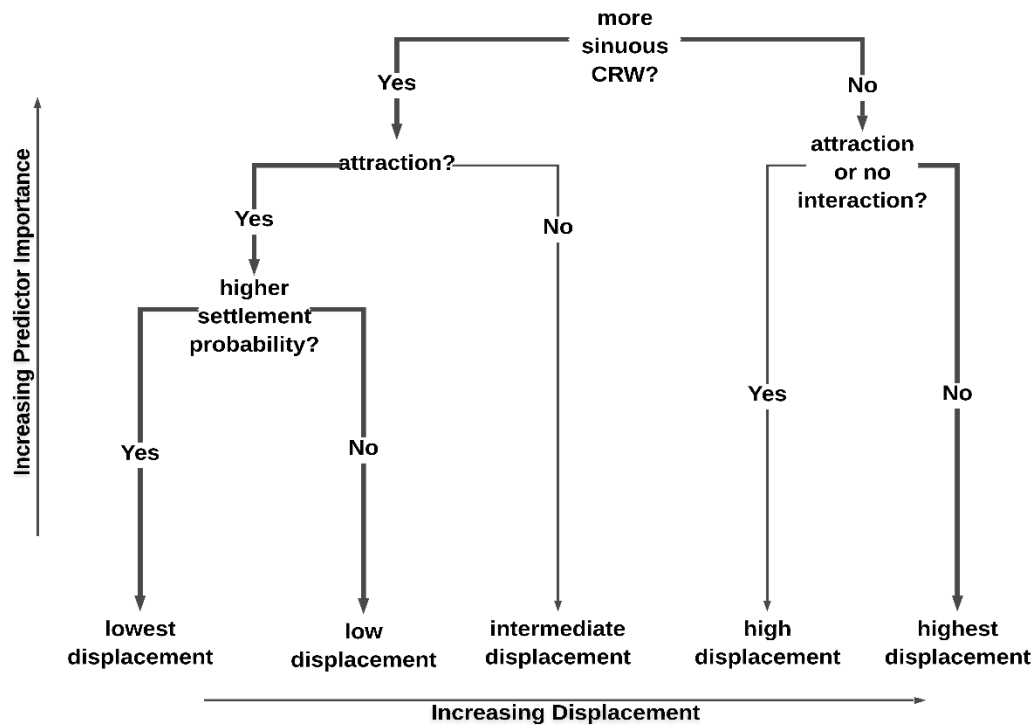


Figure 11 *Synthesis of subsidy displacement trends*. Living subsidies were deposited further than dead subsidies. Given conspecific attraction, more sinuous movements at higher settlement probability and perceptual range generated the least displaced living subsidies with the lowest maximum deposition distance and range from the shared ecosystem boundary. At higher perceptual range and lower settlement probabilities, avoidance scenarios resulted in the greatest distance to peak density for dead subsidies. Scenarios with no interaction resulted in intermediate subsidy displacement. Chart relationships delineated with heavy lines represent instances where 6 representative CARTs agreed while relationships delineated with lighter lines represent instances where at least half but not all constituent CARTs agreed. See figure 29 in supplementary materials (Appendix B) for detailed CARTs synthesized here.

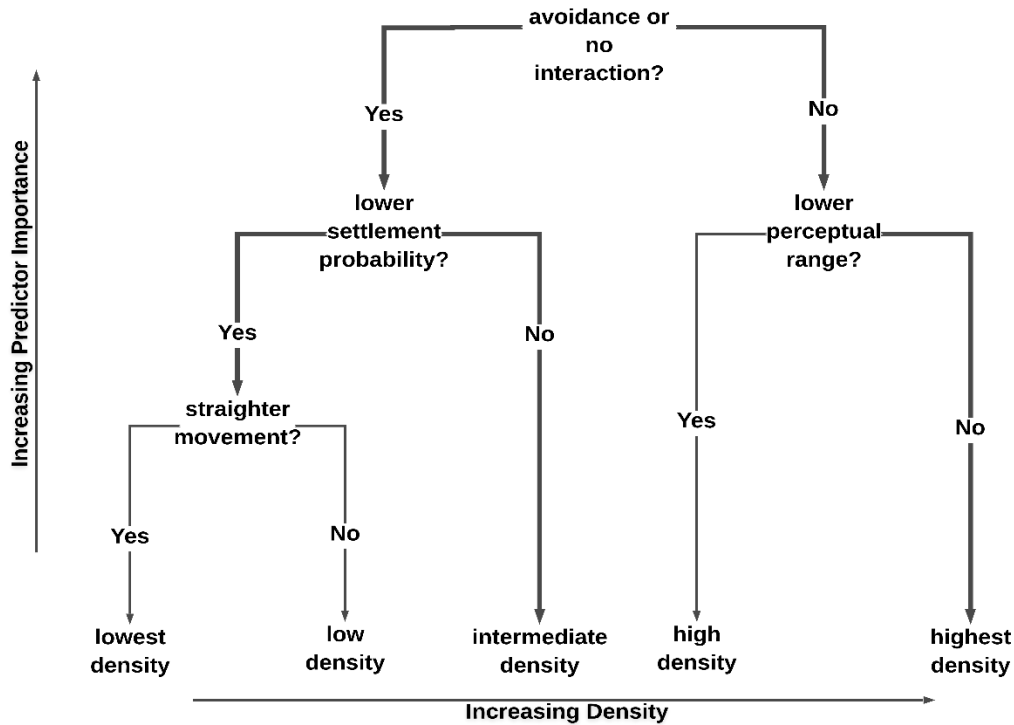


Figure 12 *Synthesis of peak subsidy deposition density trends*. Given straighter movements and lower settlement probabilities, conspecific avoidance and scenarios without conspecific interaction depress the peak deposition density of living subsidies. Conspecific attraction with higher settlement probability and perceptual range resulted in greatest peak deposition density for living subsidies. Given conspecific avoidance and scenarios without conspecific interaction, more sinuous movement and higher settlement probability increases peak deposition for dead subsidies. Chart relationships delineated with heavy lines represent instances where 4 representative CARTs agreed while relationships delineated with lighter lines represent instances where at least half but not all constituent CARTs agreed. See figure 30 in supplementary materials (Appendix B) for detailed CARTs synthesized here.

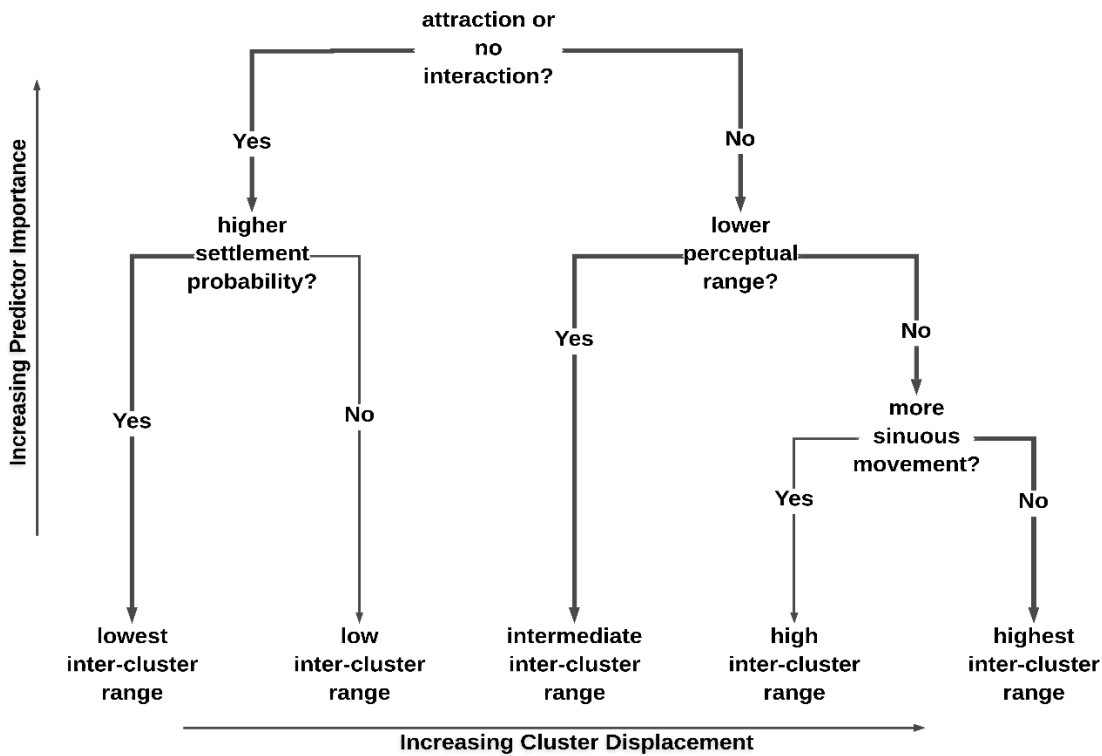


Figure 13 *Synthesis of inter-cluster displacement trends*. Given higher perceptual ranges, straighter movements in conspecific avoidance scenarios resulted in the greatest inter-cluster displacement. Conspecific attraction with higher settlement probabilities resulted in the lowest inter-cluster displacement. Scenarios with no interaction resulted in intermediate inter-cluster displacement. Chart relationships delineated with heavy lines represent instances where 2 representative CARTs agreed while relationships delineated with lighter lines represent instances where at least half but not all constituent CARTs agreed. See figure 31 in supplementary materials (Appendix B) for detailed CARTs synthesized here.

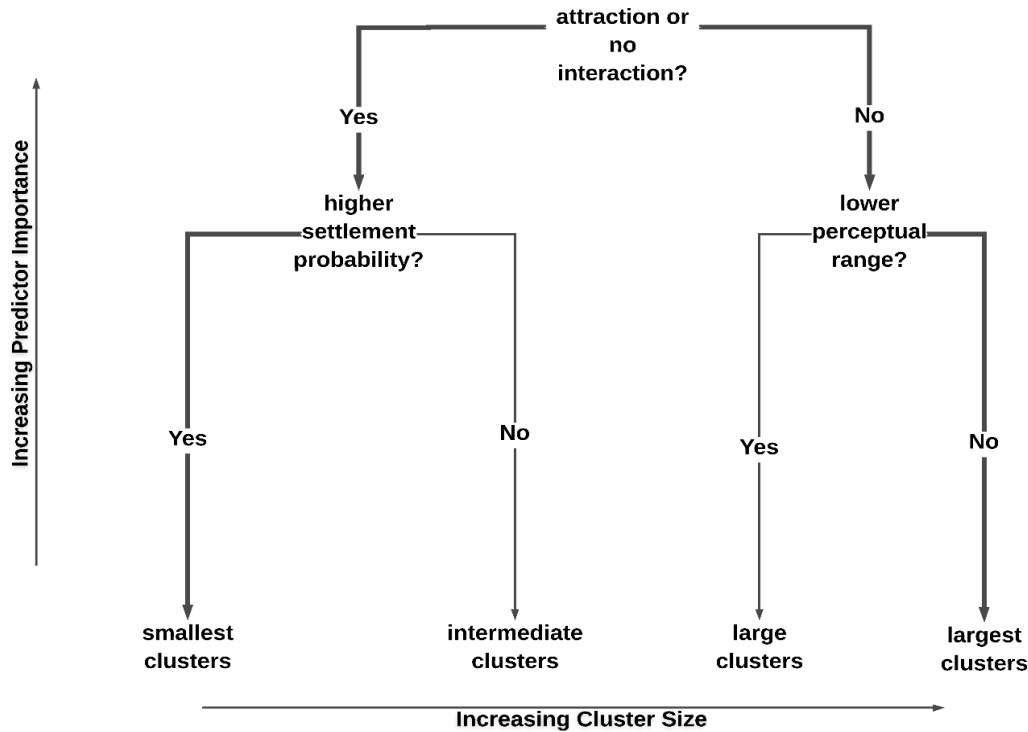


Figure 14 *Synthesis of cluster size trends*. Given lower settlement probability, conspecific attraction resulted in intermediate values for maximum cluster size. Higher settlement probability in scenarios conspecific interaction scenarios and scenarios without interaction constrained maximum cluster size to with smaller clusters for living subsidies than to dead subsidies.

Conspecific avoidance with higher perceptual range resulted in the largest clusters. Chart relationships delineated with heavy lines represent instances where 2 representative CARTs agreed while relationships delineated with lighter lines represent instances where at least half but not all constituent CARTs agreed. See figure 31 in supplementary materials (Appendix B) for detailed CARTs synthesized here.

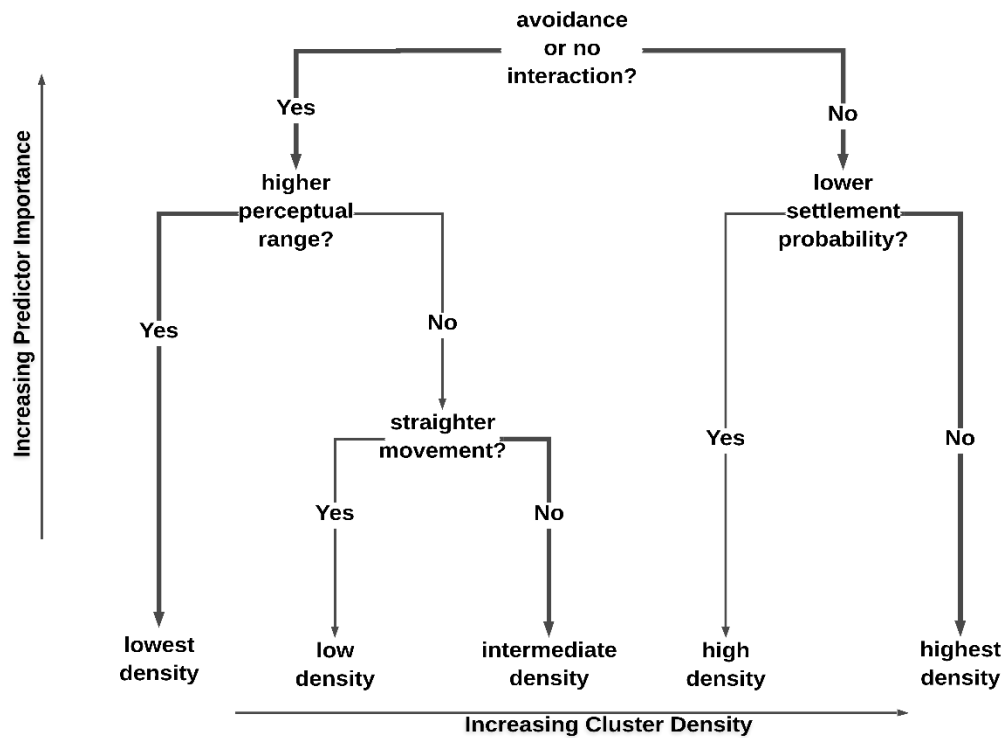


Figure 15 *Synthesis of cluster density trends*. In conspecific attraction scenarios, more sinuous movements and higher settlement probability generated the densest living subsidy clusters. Reducing settlement probability resulted in the greater cluster density for dead subsidies. In avoidance scenarios, cluster density decreased with perceptual range but increased with more sinuous movement. Scenarios with no interaction resulted in intermediate cluster density. Chart relationships delineated with heavy lines represent instances where 4 representative CARTs agreed while relationships delineated with lighter lines represent instances where at least half but not all constituent CARTs agreed. See figure 32 in supplementary materials (Appendix B) for detailed CARTs synthesized here.

CHAPTER 4. THE INFLUENCE OF LANDSCAPE HETEROGENEITY ON THE DISTRIBUTION OF ANIMAL-TRANSPORTED SUBSIDIES: A CASE STUDY ON WOOD FROGS IN HARDWOOD FORESTS

4.1 Abstract

Landscape heterogeneity has been shown to affect animal behavior and space use. The spatial extent and distribution of habitat patches in a landscape can affect animal movement, settlement and mortality, and therefore impact active subsidy distribution. Active subsidies are animal-transported resources and consumers across landscapes. Despite the importance of ecological subsidies for ecosystem structure and services, there is limited research on the influence of landscape heterogeneity on active subsidy distribution. We built an individual-based model (IBM) based on emerging juvenile wood frog movement, settlement and mortality from ponds into surrounding hardwood forests in southern Indiana to examine the effect of landscape heterogeneity on active subsidy distribution. We simulated the effect of variation in virtual animal movement, settlement and mortality on spatial subsidies in homogeneous and heterogeneous recipient ecosystems of open, partial and (or) closed canopy forest habitats. We found that juvenile wood frog movements and subsidy distribution patterns varied significantly with canopy closure. For heterogeneous landscapes, we varied proportional compositions and configurations across canopy closure types. Animal movement behavior was more important than canopy closure for subsidy displacement, and canopy closure was more important than movement for subsidy density. Longer, straighter movement and lower mortality in landscapes with greater proportion and cohesion of closed canopy forest deposited more living juvenile wood frog subsidies at higher density further from source ponds. Given high mortality in landscapes with greater proportion and cohesion of open canopy forest, sinuous movements deposited more dead subsidies at higher densities closer

to the source ponds, but lowering mortality increased dead subsidy displacement and decreased corresponding dead subsidy density. Ecosystem models that incorporate the influence of landscape heterogeneity on animal behavior and space use will generate better predictive insights into corresponding spatial subsidy impacts.

4.2 Introduction

Spatiotemporal variation in the availability and distribution of resources can affect how animals use heterogeneous landscapes (Bleicher, 2017; Morales and Ellner, 2002). Many studies have shown that the proportion and spatial aggregation (e.g., contagion, contiguity, cohesion, clumpiness and interspersed) of quality habitat influences animal movement and distributions in heterogeneous landscapes (King and With, 2002; Shepard et al., 2013). Animals transport ecological subsidies (Polis et al., 1997) between ecosystems as they move across landscapes. Active subsidies are animal-transported resources (e.g., prey, nutrients) and consumers from donor to recipient ecosystems and can change ecosystem structure and function by altering trophic interactions and redistributing materials and energy across landscapes (Earl and Zollner, 2017, 2014). Active subsidies affect important ecosystem services (e.g., nutrient cycling, biodiversity maintenance) that support and regulate ecological communities and processes across ecosystems (Allen et al., 2012; Bagstad et al., 2019). The influence of landscape heterogeneity on animal movement behavior could affect the displacement and density of active subsidies (Ewers and Didham, 2006; Reyna-Hurtado et al., 2012). Understanding how landscape heterogeneity influences active subsidy distributions as a function of animal movement behavior can provide valuable insight on the scale, intensity and extent of corresponding ecosystem impacts (Earl and Zollner, 2017).

Changes in the distribution of resources and risks across landscapes influence animal space use behavior (Bleicher, 2017; Miramontes et al., 2012; Shepard et al., 2013) and likely affect corresponding active subsidy distributions. Recent reviews on the state of spatial subsidy research document the need for systematic studies to develop general insights into the influence of landscape heterogeneity for active subsidy patterns (Earl and Zollner, 2017; McInturf et al., 2019). However, system-level impacts of landscape heterogeneity on spatially-explicit animal behavior and corresponding active subsidy distributions have not been comprehensively addressed in spatial subsidy models. Empirical studies that consider this phenomenon focus on single taxa in specific ecosystems, limiting the development of improved ecosystem models that can be effective for predicting spatial subsidy patterns for a variety of taxa and ecosystems (Moon and Silva, 2013; Schindler and Smits, 2017). Systematic analyses of this phenomenon with abstract case study modeling approaches can help establish more general frameworks and principles of active subsidy systems and corresponding ecosystem impacts. Further, developing systematic models that elucidate how active subsidy distributions change with animal movement behavior in human-altered landscapes can enhance decision-making for land-use planning and wildlife management for multiple species and ecosystems. Most of our understanding of spatial subsidies is based on behaviorally and spatially simplified systems, as existing models assume homogeneous landscapes (Rees et al., 2015; Schreiber and Rudolf, 2008). Such models do not capture important spatial patterns in ecosystem responses to variation in animal movement behavior (Morales and Ellner, 2002; Smouse et al., 2010). Spatially-explicit Individual-Based Models (IBMs) that incorporate random walk concepts can be useful tools for modeling animal movement in response to landscape heterogeneity (Garibaldi et al., 2011; Uno and Power, 2015). IBMs can therefore help to elucidate

corresponding consequences of animal movement on the distribution and impact of animal-transported subsidies (Earl and Zollner, 2014; Chapter 2, 3).

Pond-breeding amphibians provide a useful case study for understanding the influence of movement on the active subsidy distributions in response to landscape heterogeneity. Timber harvest results in spatial heterogeneity in forest canopy density that can alter resident amphibian habitat structure (e.g., refugia locations), movement behavior and related ecological processes (Graeter et al., 2008; Patrick et al., 2006). Timber harvest has been shown to impede dispersal in forest-dwelling amphibians (Popescu et al., 2012; Semlitsch et al., 2009), and landscape heterogeneity in timber harvest around ponds could affect corresponding spatial patterns in amphibian populations. Amphibians consume significant amounts of insects and serve as prey for many terrestrial birds and mammals, transporting substantial nutrient and consumer subsidies during dispersal from aquatic to terrestrial ecosystems (Capps et al., 2015; McCoy et al., 2009). Case studies on how amphibian subsidy distributions respond to forest harvest can inform forest harvest practices that can be applied in other land and species management scenarios (Pittman et al., 2014).

We developed a model of juvenile amphibian movement that changes in response to canopy closure to understand how landscape heterogeneity influences the distribution of dead (nutrient subsidies) and living amphibians (consumer subsidies) in the terrestrial ecosystem surrounding the breeding pond. Our objective was to estimate the effect of landscape heterogeneity on the spatial extent and intensity of active subsidy distributions from juvenile wood frogs (*Lithobates sylvaticus*). We constructed a spatially-explicit IBM to determine how spatial variation in canopy closure as a function of forest harvest intensity in a central U.S. hardwood forest affects emerging juvenile wood frog dispersal parameterized with data we collected on 30 juvenile wood

frogs in southern Indiana. Using the model, we examined how active subsidy distribution patterns vary across canopy closures in homogeneous landscapes and with different proportions and spatial patterns in forest canopy closure in heterogeneous landscapes. We hypothesized that shade from desiccation and cover from predators in large, spatially aggregated, closed canopy forest habitat favors consumer (i.e., living) over nutrient (i.e., dead) subsidy displacement at greater densities further from the donor-recipient ecosystem boundary. We predicted that wood frogs will disperse straighter and faster through patchier, open canopy forests for cover in denser, more continuous canopy forests. As the proportion and continuity of habitat with no canopy cover increases, dispersing juvenile wood frogs should therefore spread dead subsidies further.

4.3 Methods

4.3.1 Study Site

The Hardwood Ecosystem Experiment (HEE) (Figure 16) is designed as a long-term, landscape-level field experiment initiated in 2006 by the Indiana Department of Natural Resources-Division of Forestry for research on Oak-Hickory forest management and regeneration (Swihart et al., 2013). The HEE is in the Brown County Section (BCS) of the Highland Rim Natural Region of south-central Indiana, encompassing Morgan-Monroe and Yellowwood State Forests. The HEE consists of a replicated series of study areas with nine 80 ha management units or areas. The HEE includes three units of control forests with no active management, two even-aged management units (i.e., 10-acre clear-cuts and 3-acre patch-cuts or smaller clear-cuts) and two uneven-aged units (i.e., single tree selection and 10-acre shelterwood).

The wood frog (*Lithobates sylvaticus*) is a common forest-dwelling amphibian species with an expansive geographic range from southern Appalachian mesic forests to the Arctic Circle tundra. The wood frog life cycle includes an aquatic larval stage and ontogenetic shifts to terrestrial

juvenile and adult stages. Wood frogs breed in fish-free vernal pools in late winter in February to March (Berven, 1988; Crouch and Paton, 2000). Adult wood frogs disperse from uplands to breed in low lying ponds and deposit 1000 to 3000 eggs per female (Berven, 1981). Metamorphs emerge from forest ponds in early June into terrestrial juvenile or adult habitat where juveniles disperse into surrounding uplands and mature sexually within 2-3 years of metamorphosis (Berven and Grudzien, 1990; Cornell et al., 1989).

4.3.2 Empirical data for IBM calibration

To parameterize our model, we analyzed landscapes around HEE ponds. We selected 30 ponds with surrounding landscapes that were representative of variation in canopy closure categories [i.e., no canopy (clear-cuts, patch-cuts), partial canopy (shelterwood, single-tree selection) and dense canopy closure (unharvested for 60 years)]. We measured the width and length of the 30 HEE ponds using a range finder to determine the size of virtual ponds in our model. Using ESRI ArcGIS Pro 2.3, we analyzed rasters of land cover within 300 m of each pond (the estimated dispersal range of emerging juvenile wood frogs (Homan et al., 2004)). We calculated descriptive spatial statistics, including overall landscape contagion, contiguity and interspersion with proportional composition, cohesion and clumpiness for each canopy closure category using Fragstats version 4.5 (Mcgarigal et al., 2002). We used resulting estimates of proportional composition and cohesion for the three canopy closure categories to calibrate virtual landscape generation.

We estimated the number of dispersing metamorphs for virtual ponds based on egg mass surveys (counts and estimated clutch size) that we conducted across all 30 HEE ponds in March 2018. At each pond, we randomly sampled 10 egg masses, measuring egg mass volume with a graduated 1000 ml beaker and egg volume with a 10 ml graduated cylinder. We estimated clutch

size as the quotient of the egg mass volume and average egg volume. We generated an estimate of mean juvenile emergence counts for virtual ponds based on premetamorphic survivorship of 0.04 (Berven, 1990).

We parameterized virtual wood frog movement behavior using mean step-lengths and turning angles calculated from the mean vector lengths (i.e., correlation coefficient between turning angles) of 30 juvenile wood frogs we marked and tracked at the HEE in May and June 2018. We captured and marked wood frogs with fluorescent powder. We then released them within 10 m of 9 representative ponds across all three levels of canopy closure with 10 wood frogs released per type of canopy closure. After dusk (~ 2100 hours), we tracked their movements using ultraviolet flashlights (Zollner and Lima, 1997) and marked tracks by placing flags at all turns with angles greater than 5 degrees and used 50 m field tape and lensatic sighting compass to measure net-displacement and bearings from release points. Based on these measurements, we estimated corresponding step lengths and mean vector lengths (i.e., correlation coefficients) for each canopy closure category. Estimations were made using code developed in Python 3.7 (Unpublished, Benjamin Pauli).

4.3.3 Individual Based Model

4.3.3.1 Background

We built an IBM to quantify the effect of landscape heterogeneity on the distribution of living and dead subsidies given variation in movement, settlement and mortality probability. The simulation environment consists of a central pond (natal habitat) surrounded by terrestrial ecosystems with different canopy closure categories (juvenile/adult habitat). Virtual landscapes consist of 15 m by 15 m central ponds based on the estimated mean pond area of 236 m² for the 30 HEE ponds surveyed. Based on habitat types around ponds in the HEE landscape, the canopy

closure categories we considered in our IBM include open canopy (i.e., clear-cuts, patch-cuts), partial canopy (i.e., shelterwood, single-tree) and dense canopy (i.e., forest unharvested for 60 years). The spatial extent of the virtual landscapes was 600 m by 600 m at 1 m² resolution, capturing estimated dispersal and step ranges for emerging juvenile wood frogs from central ponds (Bellis, 1965).

We conducted two sets of simulation experiments in NetLogo (version 6.0.4) software for spatially-explicit agent-based modeling (Tisue and Wilensky, 2004; Wilensky, 1999). In the first experiment, we implemented landscapes with homogeneous landscapes to examine differences in active subsidy distribution across canopy closure categories. We conducted the second set of experiments on heterogeneous landscapes varying the relative proportion and spatial distribution of each canopy closure category. In experiment 1 we focused on quantifying the effect of canopy closure, while in experiment 2, we focused on the effects of the relative proportion and spatial aggregation (i.e., cohesion and clumpiness) of each canopy closure category, and the effects of the overall landscape structure (i.e., contagion, contiguity and interspersation) on active subsidy distribution. These canopy closure metrics describe the tendency of each type of canopy closure to be spatially aggregated across a landscape and overall landscape metrics describe landscape-scale spatial aggregation (McGarigal and Marks, 1995). All of these canopy closure and landscape structure metrics represent spatial habitat and landscape structure attributes that have been shown to affect animal dispersal success (King and With, 2002).

We designed virtual wood frog movement in our model based on the movement behavior of juvenile wood frogs in the three canopy closure categories at the HEE and derived corresponding estimates of settlement and mortality from published work (Cline and Hunter, 2016; Funk et al., 2005; Harper et al., 2015; Patrick et al., 2008; Popescu et al., 2012; Popescu and Hunter,

2011; Rittenhouse et al., 2009; Semlitsch et al., 2009, 2008; Todd et al., 2014). To examine if and how spatial subsidy patterns respond to animal behavior as a function of landscape heterogeneity. Our goal was only to parameterize the model, not to test model output, as such data is very difficult to collect, and no such data sets currently exist. In our model, virtual wood frogs initiate movement from pond edges and disperse into the terrestrial ecosystem (juvenile/adult habitat) where they can move, settle and die during each time step.

We assumed wood frogs behave (i.e., move and settle) and experience mortality differently in each type of canopy closure (Todd et al., 2014), so we implemented different wood frog movement, settlement and mortality probabilities for each canopy closure category. We did not consider demographic processes in our IBM, because we wanted to focus on the scale of post-emergence juvenile dispersal. We assumed that dead subsidies remain at mortality sites as local nutrients or energy and cannot be moved once deposited. We also assumed that settled juvenile wood frogs experience lower movement probability and mortality risk as an advantage of habitat selection and familiarity (Muriel et al., 2016). Another assumption we made is that virtual wood frogs that enter the recipient ecosystem could not return to the donor (i.e., aquatic) ecosystem, consistent with wood frog inability to survive in water after metamorphosis. Dispersing wood frogs become local nutrient subsidies when they die (i.e., dead individuals) and consumer subsidies when they settle and forage (i.e., living individuals), causing potential bottom-up and top-down effects, respectively.

4.3.3.2 Design

Simulations consisted of 2000 virtual juvenile wood frogs dispersing from central virtual ponds into surrounding virtual landscapes. The virtual landscapes included torus boundaries so virtual wood frogs that reach an edge reenter the landscape at the opposite edge to maintain a stable

population of virtual wood frogs within the dispersal range for our model (Campbell Grant et al., 2010). We initialized simulations with virtual wood frogs randomly distributed around the edges of virtual ponds at the origin of the world. We assumed virtual wood frogs moved into and through the recipient ecosystem over approximately 2000 timesteps at 15 minutes per timestep, active for 12 hours per day over a 6-week emigration period (Homan et al., 2004). Virtual wood frogs also have a fixed probability of settlement (i.e., analogous to habitat selection and home range establishment) and death (i.e., analogous to predation mortality) during each 15-minute timestep.

We modeled virtual wood frog movement as a Correlated Random Walk (CRW). We parameterized virtual animal movement in our model within confidence intervals of mean step and vector lengths we calculated from juvenile wood frog movement tracks at the HEE. We varied virtual wood frog turning angles using a wrapped Cauchy distribution of turning angles $\theta(t)$ as:

$$\theta(t) = \theta(t - 1) + 2 \tan^{-1} \left[\left(\frac{1 - \alpha}{1 + \alpha} \right) \tan(\pi\varphi) \right],$$

where $0 \leq \alpha \leq 1$, and

$$-0.5 \leq \varphi \leq 0.5$$

t is a timestep and $\theta(t - 1)$ is the turning angle from a previous timestep. φ is drawn from a uniform distribution over a delta distribution range of $[-0.5, 0.5]$ to normalize the direction of movement trajectories to a null orientation angle. CRW movement is straighter as $\alpha \rightarrow 1$ and more sinuous as $\alpha \rightarrow 0$.

We varied for each type of canopy closure based on corresponding estimates of annual survivorship, settlement and movement probabilities from previous studies (Cline and Hunter, 2016; Funk et al., 2005; Harper et al., 2015; Patrick et al., 2008; Popescu et al., 2012; Popescu and Hunter, 2011; Rittenhouse et al., 2009; Semlitsch et al., 2009, 2008; Todd et al., 2014). We

determined baseline mortality, settlement and movement probabilities (δ) for 15-minute timesteps from annual estimates as:

$$\delta = 1 - (1 - \beta)^{1/z}$$

where β = annual probability estimate

$z = 35040$ (i.e. number of 15 minute timesteps in a year)

We determined final mortality and settlement probabilities for simulations and iteratively incremented baseline rates by 10% until all dispersers died or settled during the 2000 timestep duration. Each disperser draws a random number from corresponding uniform distributions (in $[0,1]$) at each timestep and moves, dies or settles if the number drawn is lower than the movement, mortality or settlement probability level for the simulation run. In our model, settled individuals die at fixed decremented rates corresponding to each canopy closure category to account the advantage of habitat selection and familiarity.

4.3.3.3 Simulations

In our experiments, we simulated and quantified spatial subsidy patterns emerging from virtual wood frog movement, settlement and mortality in experiment 1: forests with homogeneous canopy closure (i.e., open canopy, partial canopy or closed canopy) and experiment 2: heterogeneous forests of mixed canopy closure categories with different proportional compositions and spatial aggregation characteristics. We compared effects of overall landscape attributes including proportion and aggregation characteristics by type of canopy closure, to the influence of animal movement, settlement and mortality on resulting active subsidy distribution patterns.

In experiment 1, we simulated wood frog movement, settlement and mortality on homogeneous virtual landscapes of with single canopy closure categories and compared resulting subsidy distribution patterns. We varied movement, settlement and mortality probabilities across

three levels (i.e., high, medium and low) in each canopy closure category (Table 1). We generated 7,290 homogeneous landscapes assuming a fully factorial design of canopy closure, virtual juvenile wood frog movement, settlement and mortality probabilities with reduced rates from settlement (i.e., 3 levels each) at 10 replicates per parameter combination. We used predictor importance analysis (see Analysis section) results from experiment 1 to determine and select parameters that were most important for subsidy distribution. We varied selected parameters in experiment 2 and kept remaining parameters (i.e., settlement, movement probability) fixed within by type of canopy closure.

In experiment 2, we simulated wood frog movement, settlement and mortality in heterogeneous landscapes with mixed canopy closure categories and examined resulting subsidy distribution patterns. We generated heterogeneous virtual landscapes using forest proportions drawn from random uniform distributions with up to 50% partial canopy forest and 50% no canopy forest with remaining proportions as dense canopy forest. To do this, we used package NLMR in program R version 3.5.3 to generate heterogeneous virtual landscapes based on a modified random clusters approach (Saura and Martínez-Millán, 2000). We created virtual landscapes at a 15 m² resolution (i.e., 40 by 40 grid) based on the mean aerial extent of a mature oak tree canopy (Muth and Bazzaz, 2003). We analyzed resulting virtual landscapes using package Landscapemetrics in program R version 3.5.3 to extract Fragstats-based descriptive spatial statistics (i.e., including overall landscape contagion, contiguity and interspersion with proportional composition, clumpiness and cohesion of canopy closure categories). Prior to simulating movement, we re-grid resulting rasters to 1 m² resolution (600 by 600 grid) using package Raster in program R version 3.5.3 to capture the limited spatial scale at which wood frogs interact with forest landscapes

(Sinsch, 2014). Based on the average area of the 30 HEE ponds we surveyed (236 m²), we included a 15 m by 15 m virtual pond at the center of each virtual heterogeneous landscape.

Based on variable importance (see Analysis) results of experiment 1, we implemented fixed settlement and movement probabilities at intermediate levels, and varied mean step lengths, mean vector lengths and mortality probability for each canopy closure category in experiment 2. We. To vary settlement and movement probabilities, we randomly drew parameters from uniform distributions within 95% confidence intervals of (Table 3). Each replicate simulation run was a unique heterogeneous virtual landscape with a unique draw of mean step lengths, mean vector lengths and mortality probabilities drawn from corresponding confidence intervals. We generated 200,000 virtual heterogeneous landscapes assuming a fully factorial experimental design with five levels of mean step and vector lengths, and mortality for each canopy closure category at one replicate per parameter combination.

4.3.3.4 Analysis

After each simulation run, we collected displacement and density metrics of living and dead subsidy distribution patterns. The response variables included the number of dead subsidies and the maximum subsidy deposition distance and range, the peak subsidy deposition density and the distance to peak deposition density for both living and dead subsidies. The maximum deposition distance is the distance to the most displaced subsidy from the donor-recipient (i.e., pond-terrestrial) ecosystem boundary. The maximum deposition range is the distance between the furthest and least displaced subsidies from the donor-recipient ecosystem boundary. The distance to peak density is the distance to the focal subsidy at the location of peak deposition density from the donor-recipient ecosystem boundary, and the peak deposition density is the maximum number

of subsidies per area demarcated by a radius (a) of 60 m (i.e., 10% of total landscape area) around each subsidy.

In experiment 1, we used MANOVA to analyze all subsidy distribution metrics for significant differences between canopy closure categories. We used ANOVA coefficients to determine the significance of movement, settlement and mortality variables on each subsidy distribution metric. For each response variable, we conducted Tukey multiple comparison tests to determine significant pairwise differences between canopy closure categories. In experiment 2, we used classification and regression trees (CARTs) (Therneau and Atkinson, 2015) and random forest (Breiman et al., 2017) analyses to compare the effect of variation in overall forest contagion, contiguity and interspersion, and the relative proportions, cohesion and clumpiness across canopy closure categories with movement, mortality and settlement on subsidy distribution metrics. We used random forest analyses to determine the relative importance of predictors for response variables based on the increase in percentage mean square error and split purity (residual sum of squares) from 2000 random forest model fits. We developed random forest models with random sampling and permutation with bootstrapping and bagging on predictor levels fit to response observations. We supported random forest analyses with CARTs to determine natural breaks (splits) and likely outcomes in dependent variable observations in response to interactions in movement and mortality predictor level combinations. The minimum number of dependent variable observations required for a conditional CART split in response to predictor level combinations was 600 (greater than 10% of the total number of observations). The minimum number of dependent variable observations required for a conditional CART outcome in response to predictor level combinations was 200. We assigned a complexity parameter (C_p) value of 0.001 to select and retain CART fits with response variable splits on predictor combinations that improve

the coefficients of determination for CART models by more than 0.1%. We extracted elements of CARTs that differentiated between outcomes by a minimum of 10% of the total number of observations based on comparable predictor combinations across subsidy distribution metrics. We conducted separate analyses on emergent subsidy distributions from variation in CRW and LW movement patterns with mortality probability, and space-based versus time-based mortality with LW step length variability.

We synthesized CART trends into charts. To do this, we grouped CARTs related to subsidy deposition distance and density metrics into respective displacement (i.e., 6 CARTs) and density (i.e., 4 CARTs) categories. In the resulting charts, bold lines indicate trends observed in all representative CART figures for each subsidy distribution metric category. Thin lines indicate trends featured in more than one but not all representative CART figures for each subsidy distribution metric category. See supplementary materials for all the component carts that were synthesized in our results.

4.4 Results

Comparing subsidy distribution metrics across homogenous landscapes from experiment 1, all displacement and density metrics of subsidy distribution were significantly different across canopy closure categories (*MANOVA*; $F > 30.56$, $p < 0.001$). Both displacement and density metrics were also significantly different across canopy closure categories (*ANOVA*; $F_{2,7278} > 30.55$, $p < 0.001$). All response variables were significantly different for pairwise comparisons among forest treatments (*Tukey – HSD*; $p < 0.001$) except for the distance to peak density for both living and dead subsidies. Canopy closure was the most dominant predictor of density-based metrics (i.e., number and peak deposition density) of living and dead subsidy distribution (Figure

17; Appendix C Tables 12 and 13). Canopy closure was also the most influential predictor of displacement-based metrics (i.e., maximum deposition distance, range and distance to peak density) of dead subsidy distribution. Mean step and vector lengths strongly predicted the extent of living subsidy displacement. Mortality probability was an important secondary predictor and settlement probability was generally the least important variable for both displacement and density metrics of living and dead subsidy distribution.

In experiment 1, low mortality scenarios in closed canopy forests resulted in the greatest living subsidy displacement (Figure 16). Given higher and intermediate mortality, smaller steps resulted in the lowest living subsidy displacement. However, straighter movements attenuated this effect and resulted in intermediate living subsidy displacement. Denser canopy closure generally reduced living and dead subsidy displacement from the shared ecosystem boundary but lower mortality enhanced dead subsidy displacement. Living subsidy density increased with canopy closure (Supplementary information, Appendix C). Density-based metrics for dead subsidies were highest in open canopy forest, lowest in closed canopy forest and intermediate for partial canopy forest.

In heterogeneous habitats from experiment 2, the proportion and cohesion of open canopy forest was the most influential predictor of density-based metrics of living and dead subsidy distribution (Figure 17). The proportion and cohesion of closed canopy forest were important secondary predictors of density-based metrics of living and dead subsidies. Overall landscape contagion and interspersions also strongly predicted density-based metrics of living and dead subsidy distribution. Mean step and vector lengths in closed canopy forest were generally the most important predictors for displacement-based metrics of living and dead subsidy distribution. Mortality probability in closed and partial canopy forest was an important secondary predictor

living subsidy displacement. Mean step and vector length in open canopy forest were important determinants of displacement-based metrics of dead subsidy distribution.

In experiment 2, living subsidy displacement was highest for longer, straighter movements given lower mortality in landscape with a greater proportion of closed canopy forest with higher cohesion (Figure 18). Lower mortality in partial canopy forest resulted in intermediate living subsidy displacement. Longer, straighter movement in landscapes with a greater proportion of open canopy forest with higher cohesion resulted in the furthest displacement dead subsidies. Higher mortality and straighter movement in landscapes with greater proportions and cohesion of closed canopy forest resulted in greater distances to peak dead subsidy deposition density. Straighter movement resulted in greater distances to peak density for living subsidies in landscapes with greater proportions of open canopy forest. Given lower mortality in closed canopy forest, the highest living subsidy densities occurred in landscapes with lower proportions of open canopy forest and higher closed canopy forest cohesion (Figure 19). Higher mortality and straighter movement in open canopy forest with higher cohesion resulted in the least dense subsidy distributions. More sinuous movement in landscapes with higher proportion and cohesion of open canopy forests resulted in the greatest dead subsidy densities. Higher mortality in landscapes with higher proportion of partial canopy forest resulted in intermediate dead subsidy density. Given lower mortality, the least dense dead subsidy distributions resulted from straighter movement in landscapes with greater proportion and cohesion of closed canopy forests.

In summary, subsidy distribution patterns were significantly different across forest treatment. Mean step and vector lengths mattered more for subsidy displacement and mortality mattered more for subsidy density. Mortality was generally the second most influential for juvenile wood frog subsidy distribution patterns. Overall landscape contagion and interspersions also

predicted subsidy distribution patterns but with less influence than proportional composition and cohesion of canopy closure categories. Longer, straighter movement and lower mortality in landscapes with greater proportion and cohesion of closed canopy forest deposited more living juvenile wood frog subsidies at higher density further from source ponds. Higher mortality in landscapes with greater proportion and cohesion of open canopy forest, sinuous movements deposited more dead subsidies at higher densities closer to the source ponds, but lowering mortality increased dead subsidy displacement and decreased corresponding dead subsidy density. Partial canopy forests generated intermediate living and dead subsidy displacement and density.

4.5 Discussion

This research provides a systematic analysis of the influence of landscape heterogeneity on active subsidy distributions across a broad parameter space using an ecologically informed abstract modeling approach. Our work provides general insights towards a unifying framework for improving the utility of ecosystem models in spatial subsidy research. Our models demonstrate that spatial subsidy models that account for landscape heterogeneity can improve our understanding of corresponding subsidy distributions and impacts in natural ecosystems. Landscape heterogeneity affects subsidy deposition patterns, because animal space use depends on habitat type (Morales and Ellner, 2002). Despite established evidence of the influence of landscape structure on animal space use and movement (Morales and Ellner, 2002), there is limited information on the connection between landscape structure and active subsidy distributions. My work is the first that links spatial subsidies to the influence of landscape heterogeneity on animal movements using a combination of individual-based and movement ecology approaches. Our results from simulating the effect of landscape heterogeneity on juvenile wood frog subsidy distributions show that the relative proportional compositions, spatial configuration and suitability

of multiple habitat types influences emergent spatial subsidy patterns. Consumer and nutrient subsidy distributions vary with animal mortality, movement and settlement behavior as a function of corresponding spatial heterogeneity in habitat structure (e.g., quality, spatial extent and configuration). Animals move further in heterogeneous landscapes with larger proportions and greater aggregation (i.e., cohesion, contagion) of favorable habitat, displacing corresponding nutrient and consumer subsidies at higher densities further into recipient ecosystems. This is consistent with urban wetland research showing that amphibian species abundance, richness and regulation of invertebrate pest populations varies with the extent and density of green space foliage, and decreases as impervious surface cover and structural complexity increases (Hamer and McDonnell, 2008).

Spatial subsidy models can enrich our understanding of the ecosystem impact of animal nutrient and consumer subsidy distribution in processes like animal-mediated seed dispersal by accounting for the influence of landscape heterogeneity on animal movement, mortality and habitat space use. Our results show that consumer subsidies move further in landscapes with greater proportions and cohesion of more favorable habitat, indicating that landscape heterogeneity can affect consumer and nutrient subsidy distribution in ecological processes such as animal-mediated seed dispersal. Many frugivorous birds and primates consume and disperse significant amounts of fruit and seeds deep into large, continuous closed canopy forests compared to smaller dispersal kernels in fragmented forest habitats (Da Silveira et al., 2016; Link and Di Fiore, 2006; Saavedra et al., 2014). Striped-cheek greenbuls in the Tanzanian Usambara Mountains consume *Letonychia* tree fruits and disperse seeds into large, continuous tropical forests in the Amani Nature Reserve over twice as far as they do in adjacent forests interspersed with tea plantations (Cordeiro and Howe, 2003). Similarly, spider monkey communities in the Lacadona-Maya rainforest in

southeastern Mexico deposit nutrient subsidies at high densities around sleeping trees and sites deep into tropical rainforest and away from interspersing rural farmlands and human settlements (González-Zamora et al., 2012). Droppings facilitate forest regrowth and plant species diversity near abandoned farmland, but forest regeneration declines with spider monkey movement and the spatial extent of forested habitat as human settlement and farmland cover increases.

Proportional composition and spatial aggregation of land cover types across different degrees of favorability in heterogenous landscapes influences the consumer subsidy distribution. Maintaining large, continuous forested habitat via silvicultural management can enhance dispersal and survival, as well as persistence and genetic diversity for organisms whose movements are extremely sensitive to timber harvest (Cobben et al., 2012; Litvaitis and Villafuerte, 1996). Our results show that given low mortality, straighter movement in landscapes with greater proportion and spatial aggregation of suitable habitat resulted in juvenile wood frog consumer subsidy deposition at higher densities further from source ponds. Many amphibian species rely on large tracts of closed canopy forests to provide cover from desiccation and predator detection during natal dispersal and breeding migrations between ponds and the surrounding terrestrial landscape (Chelgren and Adams, 2017). Amphibian consumers disperse and regulate invertebrate agricultural pest communities farther from source ponds into rural farmlands with greater proportion of connected closed canopy habitat (Khatriwada et al., 2016). Amphibian consumer subsidy spread and corresponding impacts on invertebrate herbivore and pollinator communities affects plant productivity (McCoy et al., 2009). Heterogeneous forests with greater proportion and cohesion of closed canopy forests around ponds can enhance amphibian dispersal and increase corresponding spatial extents and impacts of potential trophic cascades. Accounting for variation

in animal dispersal in response to variability in the spatial extents and aggregation of quality habitat can improve our understanding of corresponding consumer subsidy distributions and impact.

Landscape heterogeneity as proportional composition and spatial aggregation of unfavorable habitat affects nutrient subsidy distribution and related ecosystem impacts like nutrient hotspots with corresponding spatial variability in primary production (Polis et al., 1997; Polis and Strong, 1996). Incorporating reduced-impact logging approaches in silvicultural and general landscape management practices can enhance nutrient subsidy spread by limiting attenuating effects of clearcutting on the dispersal success and survival of species that are sensitive to timber harvest (Putz et al., 2008). This is consistent with our finding that mortality in landscapes with greater proportion and spatial aggregation of unsuitable habitat constrained animal dispersal success and resulted in dense nutrient subsidy distributions close to pond-forest ecosystem boundaries. Conservation-based timber harvest practices like large, continuous closed canopy forest buffers around source ponds or populations, as well as single tree selections and patch-cuts to provide transition habitats with partial canopy forests can mitigate impacts upon animal dispersal (Freidenfelds et al., 2011; Veysey Powell and Babbitt, 2015). Using a mix of silvicultural and landscape management approaches could enhance species diversity as function of habitat preference and resource selection by specialist species. For instance, while crown-dwelling frugivorous and insectivorous birds respond negatively to dense canopy forest, lower branch dwellers like nectarivores and granivores respond positively to selective logging (Burivalova et al., 2015; Thiollay, 1997). Landscape heterogeneity could therefore affect the spatial extent and impact of nutrient subsidy feedback (e.g., vegetation growth at latrine sites) as a function of variation in species habitat preferences. Spatial subsidy research can provide insights into landscape-scale subsidy impact by considering the influence of heterogeneity in unfavorable

habitat matrix composition (Haynes and Cronin, 2004) and configuration on dispersal movements (Cline and Hunter, 2016) and spatial subsidy impacts.

Our research provides a foundation for connecting spatial impacts of aquatic insect and amphibian contaminant transport, disease transfer and nutrient export to movement behavior influenced by spatial heterogeneity in habitats of different quality across landscapes. While variation in microhabitat and microclimate conditions with forestry practices has been shown to affect amphibian and aquatic insect movements and habitat selection (French and McCauley, 2019; Volpe et al., 2016), no research explored effects on subsidy spatial patterns prior to our work. Emerging amphibians have been shown to transport bioaccumulated trace elements (e.g., heavy metals) as well as diseases (e.g., chytridiomycosis, ranavirus) from aquatic to terrestrial ecosystems (Harper and Petranka, 2006; Kolby et al., 2015; Unrine et al., 2007). Our research demonstrates that predicting spatial impacts of amphibian-transported contaminants and disease transfer in terrestrial food webs and metapopulations will require knowledge about how amphibian behavior changes with habitat and landscape structure. A 21-year study on naturally occurring wood frog populations in central hardwood forest revealed a mean net export of 12.8 kg carbon (C), 3.5 kg nitrogen (N) and 1 kg phosphorous (P) in the form of emerging juveniles from a single pond (Capps et al., 2015). The study suggests that vernal pools are subsidy hotspots that transform low quality nutrients like leaf litter into high quality nutrients like amphibians and macroinvertebrates, which move into forest landscapes. However, factors affecting the spatial distribution of these nutrients are unclear, impeding our ability to predict and understand the spatial impacts of amphibian related ecosystem services. A similar perspective could be presented for the role of these animals in pest control (Hocking et al., 2014). Our work shows that considering emerging aquatic insects and amphibian behavior in response to spatial variation in microhabitat and

overall landscape structure will improve estimates of the spatial distribution and impact of nutrient export in wildlife and ecosystem management scenarios.

To improve model realism in future work, active subsidy models should account for spatial subsidy responses to the influence of habitat edges on animal movement behavior and mortality. Animals move differently and experience different mortality conditions at habitat edges compared to interior habitat, resulting in corresponding variability in active subsidy distributions (Frair et al., 2005; Heim et al., 2015; Pittman et al., 2013; Popescu and Hunter, 2011; Walston and Mullin, 2008). Therefore, different movement behavior or mortality conditions at habitat edges could affect active subsidy distributions if animals avoid unfavorable habitat by either moving along or away from habitat edges. Demographic processes and animal body size could also affect the animal movement behavior and the amount of nutrient deposition from mortality events (Briggs et al., 2012; Demi et al., 2012; Peterman et al., 2013). Accounting for body size from variation in resource distributions as a function of landscape heterogeneity in our model could affect resulting nutrient and consumer subsidy deposition patterns differently. Considering secondary and tertiary movement of carcasses by scavengers could also influence nutrient subsidy deposition patterns in response to habitat heterogeneity (Earl and Zollner, 2017). In future work, pattern-matching model-based subsidy distributions to field observations of spatial subsidy patterns will help test model improvements in real-world applications. Spatial subsidy models that consider edge effects, animal body size, demographic processes and potential spatial transience of nutrient subsidies as a function of scavenger or other secondary movements can be more useful for estimating the location and impact of nutrient subsidies in landscape and wildlife management scenarios.

4.6 Conclusion

We used an individual-based model of juvenile dispersal from forest ponds into surrounding landscapes in central hardwood forests to show that landscape heterogeneity is an important factor for active subsidy distribution. We demonstrated that the relative proportion and spatial aggregation of favorable to unfavorable habitat can affect the extent and intensity of living and dead subsidy distributions via animal movement, settlement and mortality. Greater proportional composition and spatial aggregation of higher quality habitat in heterogeneous landscapes displaces consumer subsidies further and at higher densities in recipient ecosystems. Nutrient subsidy displacement and deposition densities decrease in heterogeneous landscapes with higher proportional compositions and spatial aggregation of lower quality habitat types. Spatial subsidy research can improve our understanding of how animal movements impact ecosystems by accounting for the influence on landscape heterogeneity.

4.7 References

- Allen, D.C., Vaughn, C.C., Kelly, J.F., Cooper, J.T., Engel, M.H., 2012. Bottom-up biodiversity effects increase resource subsidy flux between ecosystems. *Ecology* 93, 2165–2174. <https://doi.org/10.1890/11-1541.1>
- Bagstad, K.J., Semmens, D.J., Diffendorfer, J.E., Mattsson, B.J., Dubovsky, J., Thogmartin, W.E., Wiederholt, R., Loomis, J., Bieri, J.A., Sample, C., Goldstein, J., López-Hoffman, L., 2019. Ecosystem service flows from a migratory species: Spatial subsidies of the northern pintail. *Ambio*. <https://doi.org/10.1007/s13280-018-1049-4>
- Bellis, E.D., 1965. Home Range and Movements of the Wood Frog in a Northern Bog. *Ecology* 46, 90–98. <https://doi.org/10.2307/1935261>

- Berven, K.A., 1990. Factors Affecting Population Fluctuations in Larval and Adult Stages of the Wood Frog (*Rana Sylvatica*). *Ecology* 71, 1599–1608. <https://doi.org/10.2307/1938295>
- Berven, K.A., 1988. Factors Affecting Variation in Reproductive Traits within a Population of Wood Frogs (*Rana sylvatica*). *Copeia* 1988, 605. <https://doi.org/10.2307/1445378>
- Berven, K.A., 1981. Mate Choice in the Wood Frog, *Rana Sylvatica*. *Evolution* (N. Y). 35, 707–722. <https://doi.org/10.1111/j.1558-5646.1981.tb04931.x>
- Berven, K.A., Grudzien, T.A., 1990. Dispersal in the Wood Frog (*Rana Sylvatica*): Implications for Genetic Population Structure. *Evolution* (N. Y). 44, 2047–2056. <https://doi.org/10.1111/j.1558-5646.1990.tb04310.x>
- Bleicher, S.S., 2017. The landscape of fear conceptual framework: definition and review of current applications and misuses. *PeerJ* 5, e3772. <https://doi.org/10.7717/peerj.3772>
- Breiman, L., Friedman, J.H., Olshen, R.A., Stone, C.J., 2017. Classification and regression trees, Classification and Regression Trees. <https://doi.org/10.1201/9781315139470>
- Briggs, A.A., Young, H.S., McCauley, D.J., Hathaway, S.A., Dirzo, R., Fisher, R.N., 2012. Effects of spatial subsidies and habitat structure on the foraging ecology and size of geckos. *PLoS One* 7, e41364. <https://doi.org/10.1371/journal.pone.0041364>
- Burivalova, Z., Lee, T.M., Giam, X., ekercio lu, C.H., Wilcove, D.S., Koh, L.P., 2015. Avian responses to selective logging shaped by species traits and logging practices. *Proc. R. Soc. B Biol. Sci.* 282, 20150164–20150164. <https://doi.org/10.1098/rspb.2015.0164>
- Campbell Grant, E.H., Nichols, J.D., Lowe, W.H., Fagan, W.F., 2010. Use of multiple dispersal pathways facilitates amphibian persistence in stream networks. *Proc. Natl. Acad. Sci. U. S. A.* 107, 6936–40. <https://doi.org/10.1073/pnas.1000266107>

- Capps, K.A., Berven, K.A., Tiegs, S.D., 2015. Modelling nutrient transport and transformation by pool-breeding amphibians in forested landscapes using a 21-year dataset. *Freshw. Biol.* 60, 500–511. <https://doi.org/10.1111/fwb.12470>
- Chelgren, N.D., Adams, M.J., 2017. Inference of Timber Harvest Effects on Survival of Stream Amphibians Is Complicated by Movement. *Copeia* 105, 712–725. <https://doi.org/10.1643/CE-16-573>
- Cline, B.B., Hunter, M.L., 2016. Movement in the matrix: substrates and distance-to-forest edge affect postmetamorphic movements of a forest amphibian. *Ecosphere* 7, e01202. <https://doi.org/10.1002/ecs2.1202>
- Cobben, M.M.P., Verboom, J., Opdam, P.F.M., Hoekstra, R.F., Jochem, R., Smulders, M.J.M., 2012. Landscape prerequisites for the survival of a modelled metapopulation and its neutral genetic diversity are affected by climate change. *Landsc. Ecol.* 27, 227–237. <https://doi.org/10.1007/s10980-011-9676-1>
- Cordeiro, N.J., Howe, H.F., 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proc. Natl. Acad. Sci.* <https://doi.org/10.1073/pnas.2331023100>
- Cornell, T.J., Berven, K.A., Gamboa, G.J., 1989. Kin recognition by tadpoles and froglets of the wood frog *Rana sylvatica*. *Oecologia* 78, 312–316. <https://doi.org/10.1007/BF00379103>
- Crouch, W.B., Paton, P.W.C., 2000. Using Egg-Mass Counts to Monitor Wood Frog Populations. *Wildl. Soc. Bull.* <https://doi.org/10.2307/3783845>
- Da Silveira, N.S., Niebuhr, B.B.S., Muylaert, R. de L., Ribeiro, M.C., Pizo, M.A., 2016. Effects of Land Cover on the Movement of Frugivorous Birds in a Heterogeneous Landscape. *PLoS One* 11, e0156688. <https://doi.org/10.1371/journal.pone.0156688>

- Demi, L.M., Simon, K.S., Coghlan, S.M., Saunders, R., Anderson, D., 2012. Anadromous alewives in linked lake–stream ecosystems: do trophic interactions in lakes influence stream invertebrate communities? *Freshw. Sci.* 31, 973–985. <https://doi.org/10.1899/11-124.1>
- Earl, J.E., Zollner, P.A., 2017. Advancing research on animal-transported subsidies by integrating animal movement and ecosystem modelling. *J. Anim. Ecol.* 86, 987–997. <https://doi.org/10.1111/1365-2656.12711>
- Earl, J.E., Zollner, P.A., 2014. Effects of animal movement strategies and costs on the distribution of active subsidies across simple landscapes. *Ecol. Modell.* 283, 45–52. <https://doi.org/10.1016/j.ecolmodel.2014.03.020>
- Ewers, R.M., Didham, R.K., 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biol. Rev. Camb. Philos. Soc.* <https://doi.org/10.1017/S1464793105006949>
- Frair, J.L., Merrill, E.H., Visscher, D.R., Fortin, D., Beyer, H.L., Morales, J.M., 2005. Scales of movement by elk (*Cervus elaphus*) in response to heterogeneity in forage resources and predation risk. *Landsc. Ecol.* 20, 273–287. <https://doi.org/10.1007/s10980-005-2075-8>
- Freidenfelds, N.A., Purrenhage, J.L., Babbitt, K.J., 2011. The effects of clearcuts and forest buffer size on post-breeding emigration of adult wood frogs (*Lithobates sylvaticus*). *For. Ecol. Manage.* 261, 2115–2122. <https://doi.org/10.1016/J.FORECO.2011.03.005>
- French, S.K., McCauley, S.J., 2019. The movement responses of three libellulid dragonfly species to open and closed landscape cover. *Insect Conserv. Divers.* *icad.12355*. <https://doi.org/10.1111/icad.12355>

- Funk, W.C., Greene, A.E., Corn, P.S., Allendorf, F.W., 2005. High dispersal in a frog species suggests that it is vulnerable to habitat fragmentation. *Biol. Lett.* 1, 13–16.
<https://doi.org/10.1098/rsbl.2004.0270>
- Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M., 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecol. Lett.* 14, 1062–1072. <https://doi.org/10.1111/j.1461-0248.2011.01669.x>
- González-Zamora, A., Arroyo-Rodríguez, V., Oyama, K., Sork, V., Chapman, C.A., Stoner, K.E., 2012. Sleeping Sites and Latrines of Spider Monkeys in Continuous and Fragmented Rainforests: Implications for Seed Dispersal and Forest Regeneration. *PLoS One* 7, e46852.
<https://doi.org/10.1371/journal.pone.0046852>
- Graeter, G.J., Rothermel, B.B., Gibbons, J.W., 2008. Habitat Selection and Movement of Pond-Breeding Amphibians in Experimentally Fragmented Pine Forests. *J. Wildl. Manage.* 72, 473–482. <https://doi.org/10.2193/2006-330>
- Hamer, A.J., McDonnell, M.J., 2008. Amphibian ecology and conservation in the urbanising world: A review. *Biol. Conserv.* 141, 2432–2449.
<https://doi.org/10.1016/J.BIOCON.2008.07.020>
- Harper, E.B., Patrick, D.A., Gibbs, J.P., 2015. Impact of forestry practices at a landscape scale on the dynamics of amphibian populations. *Ecol. Appl.* 25, 2271–84.

- Harper, E.M., Petranka, J.W., 2006. RANAVIRUS IN WOOD FROGS (*RANA SYLVATICA*): POTENTIAL SOURCES OF TRANSMISSION WITHIN AND BETWEEN PONDS. *J. Wildl. Dis.* 42, 307–318. <https://doi.org/10.7589/0090-3558-42.2.307>
- Haynes, K.J., Cronin, J.T., 2004. Confounding of patch quality and matrix effects in herbivore movement studies. *Landsc. Ecol.* 19, 119–124. <https://doi.org/10.1023/B:LAND.00000021721.41349.85>
- Heim, O., Treitler, J.T., Tschapka, M., Knörnschild, M., Jung, K., 2015. The Importance of Landscape Elements for Bat Activity and Species Richness in Agricultural Areas. *PLoS One* 10, e0134443. <https://doi.org/10.1371/journal.pone.0134443>
- Hocking, D.J., Babbitt, K.J., Hocking, D.J., 2014. Amphibian contributions to ecosystem services. *Herpetol. Conserv. Biol.*
- Homan, R.N., Windmiller, B.S., Reed, J.M., 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. *Ecol. Appl.* 14, 1547–1553. <https://doi.org/10.1890/03-5125>
- Khatiwada, J.R., Ghimire, S., Paudel Khatiwada, S., Paudel, B., Bischof, R., Jiang, J., Haugaasen, T., 2016. Frogs as potential biological control agents in the rice fields of Chitwan, Nepal. *Agric. Ecosyst. Environ.* 230, 307–314. <https://doi.org/10.1016/J.AGEE.2016.06.025>
- King, A.W., With, K.A., 2002. Dispersal success on spatially structured landscapes: when do spatial pattern and dispersal behavior really matter? *Ecol. Modell.* 147, 23–39. [https://doi.org/10.1016/S0304-3800\(01\)00400-8](https://doi.org/10.1016/S0304-3800(01)00400-8)

- Kolby, J.E., Ramirez, S.D., Berger, L., Richards-Hrdlicka, K.L., Jocque, M., Skerratt, L.F., 2015. Terrestrial Dispersal and Potential Environmental Transmission of the Amphibian Chytrid Fungus (*Batrachochytrium dendrobatidis*). *PLoS One* 10, e0125386. <https://doi.org/10.1371/journal.pone.0125386>
- Link, A., Di Fiore, A., 2006. Seed dispersal by spider monkeys and its importance in the maintenance of neotropical rain-forest diversity. *J. Trop. Ecol.* <https://doi.org/10.1017/S0266467405003081>
- Litvaitis, J.A., Villafuerte, R., 1996. Factors Affecting the Persistence of New England Cottontail Metapopulations: The Role of Habitat Management. *Wildl. Soc. Bull.* 24, 686–693.
- McCoy, M.W., Barfield, M., Holt, R.D., 2009. Predator shadows: complex life histories as generators of spatially patterned indirect interactions across ecosystems. *Oikos* 118, 87–100. <https://doi.org/10.1111/j.1600-0706.2008.16878.x>
- McGarigal, Cushman, S., Neel, M., Ene, E., 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps.
- McGarigal, K., Marks, B.J., 1995. FRAGSTATS: spatial pattern analysis program for quantifying landscape structure., Gen. Tech. Rep. PNW-GTR-351. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 122 p. <https://doi.org/10.2737/PNW-GTR-351>
- McInturf, A.G., Pollack, L., Yang, L.H., Spiegel, O., 2019. Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors? *Biol. Rev.* brv.12525. <https://doi.org/10.1111/brv.12525>

- Miramontes, O., Boyer, D., Bartumeus, F., 2012. The effects of spatially heterogeneous prey distributions on detection patterns in foraging seabirds. *PLoS One* 7, e34317.
<https://doi.org/10.1371/journal.pone.0034317>
- Moon, D.C., Silva, D., 2013. Environmental heterogeneity mediates a cross-ecosystem trophic cascade. *Ecol. Entomol.* 38, 23–30. <https://doi.org/10.1111/j.1365-2311.2012.01398.x>
- Morales, J.M., Ellner, S.P., 2002. Scaling up animal movements in heterogeneous landscapes: The importance of behavior. *Ecology* 83, 2240–2247. [https://doi.org/10.1890/0012-9658\(2002\)083\[2240:SUAMIH\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[2240:SUAMIH]2.0.CO;2)
- Muriel, R., Morandini, V., Ferrer, M., Balbontín, J., Morlanes, V., 2016. Juvenile dispersal behaviour and conspecific attraction: An alternative approach with translocated Spanish imperial eagles. *Anim. Behav.* 116, 17–29. <https://doi.org/10.1016/j.anbehav.2016.03.023>
- Muth, C.C., Bazzaz, F.A., 2003. Tree canopy displacement and neighborhood interactions. *Can. J. For. Res.* 33, 1323–1330. <https://doi.org/10.1139/x03-045>
- Patrick, D.A., Harper, E.B., Hunter, M.L., Calhoun, A.J.K., 2008. Terrestrial habitat selection and strong density-dependent mortality in recently metamorphosed amphibians. *Ecology* 89, 2563–74.
- Patrick, D.A., Hunter, M.L., Calhoun, A.J.K., 2006. Effects of experimental forestry treatments on a Maine amphibian community. *For. Ecol. Manage.* 234, 323–332.
<https://doi.org/10.1016/J.FORECO.2006.07.015>
- Peterman, W.E., Rittenhouse, T.A.G., Earl, J.E., Semlitsch, R.D., 2013. Demographic network and multi-season occupancy modeling of *Rana sylvatica* reveal spatial and temporal patterns of population connectivity and persistence. *Landsc. Ecol.* 28, 1601–1613.
<https://doi.org/10.1007/s10980-013-9906-9>

- Pittman, S.E., Osbourn, M.S., Semlitsch, R.D., 2014. Movement ecology of amphibians: A missing component for understanding population declines. *Biol. Conserv.* 169, 44–53.
<https://doi.org/10.1016/J.BIOCON.2013.10.020>
- Pittman, S.E., Semlitsch, R.D., Shannon Pittman, C.E., 2013. Habitat type and distance to edge affect movement behavior of juvenile pond-breeding salamanders.
<https://doi.org/10.1111/jzo.12055>
- Polis, G.A., Anderson, W.B., Holt, R.D., 1997. Toward an Integration of Landscape and Food Web Ecology: The Dynamics of Spatially Subsidized Food Webs. *Annu. Rev. Ecol. Syst.* 28, 289–316.
- Polis, G.A., Strong, D.R., 1996. Food Web Complexity and Community Dynamics. *Am. Nat.* 147, 813–846. <https://doi.org/10.1086/285880>
- Popescu, V.D., Hunter, M.L., 2011. Clear-cutting affects habitat connectivity for a forest amphibian by decreasing permeability to juvenile movements. *Ecol. Appl.* 21, 1283–1295.
<https://doi.org/10.1890/10-0658.1>
- Popescu, V.D., Patrick, D.A., Hunter, M.L., Calhoun, A.J.K., 2012. The role of forest harvesting and subsequent vegetative regrowth in determining patterns of amphibian habitat use. *For. Ecol. Manage.* 270, 163–174. <https://doi.org/10.1016/J.FORECO.2012.01.027>
- Putz, F.E., Sist, P., Fredericksen, T., Dykstra, D., 2008. Reduced-impact logging: Challenges and opportunities. *For. Ecol. Manage.* 256, 1427–1433.
<https://doi.org/10.1016/J.FORECO.2008.03.036>
- Rees, J.D., Webb, J.K., Crowther, M.S., Letnic, M., 2015. Carrion subsidies provided by fishermen increase predation of beach-nesting bird nests by facultative scavengers. *Anim. Conserv.* 18, 44–49. <https://doi.org/10.1111/acv.12133>

- Reyna-Hurtado, R., Chapman, C.A., Calme, S., Pedersen, E.J., 2012. Searching in heterogeneous and limiting environments: foraging strategies of white-lipped peccaries (*Tayassu pecari*). *J. Mammal.* <https://doi.org/10.1644/10-MAMM-A-384.1>
- Rittenhouse, T.A.G., Semlitsch, R.D., Thompson, F.R., 2009. Survival costs associated with wood frog breeding migrations: effects of timber harvest and drought. *Ecology* 90, 1620–1630. <https://doi.org/10.1890/08-0326.1>
- Saavedra, F., Hensen, I., Beck, S.G., Böhning-Gaese, K., Lippok, D., Töpfer, T., Schleuning, M., 2014. Functional importance of avian seed dispersers changes in response to human-induced forest edges in tropical seed-dispersal networks. *Oecologia* 176, 837–848. <https://doi.org/10.1007/s00442-014-3056-x>
- Saura, S., Martínez-Millán, J., 2000. Landscape patterns simulation with a modified random clusters method. *Landsc. Ecol.* 15, 661–678. <https://doi.org/10.1023/A:1008107902848>
- Schindler, D.E., Smits, A.P., 2017. Subsidies of Aquatic Resources in Terrestrial Ecosystems. *Ecosystems.* <https://doi.org/10.1007/s10021-016-0050-7>
- Schreiber, S., Rudolf, V.H.W., 2008. Crossing habitat boundaries: coupling dynamics of ecosystems through complex life cycles. *Ecol. Lett.* 11, 576–587. <https://doi.org/10.1111/j.1461-0248.2008.01171.x>
- Semlitsch, R.D., Conner, C.A., Hocking, D.J., Rittenhouse, T.A.G., Harper, E.B., 2008. Effects of Timber Harvesting On Pond-Breeding Amphibian Persistence: Testing The Evacuation Hypothesis. *Ecol. Appl.* 18, 283–289. <https://doi.org/10.1890/07-0853.1>

- Semlitsch, R.D., Todd, B.D., Blomquist, S.M., Calhoun, A.J.K., Gibbons, J.W., Gibbs, J.P., Graeter, G.J., Harper, E.B., Hocking, D.J., Hunter, M.L., Patrick, D.A., Rittenhouse, T.A.G., Rothermel, B.B., 2009. Effects of Timber Harvest on Amphibian Populations: Understanding Mechanisms from Forest Experiments. *Bioscience* 59, 853–862.
<https://doi.org/10.1525/bio.2009.59.10.7>
- Shepard, E.L.C., Wilson, R.P., Rees, W.G., Grundy, E., Lambertucci, S.A., Vosper, S.B., 2013. Energy Landscapes Shape Animal Movement Ecology. *Am. Nat.* 182, 298–312.
<https://doi.org/10.1086/671257>
- Sinsch, U., 2014. Movement ecology of amphibians: from individual migratory behaviour to spatially structured populations in heterogeneous landscapes. *Can. J. Zool.* 92, 491–502.
<https://doi.org/10.1139/cjz-2013-0028>
- Smouse, P.E., Focardi, S., Moorcroft, P.R., Kie, J.G., Forester, J.D., Morales, J.M., 2010. Stochastic modelling of animal movement. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 365, 2201–11. <https://doi.org/10.1098/rstb.2010.0078>
- Swihart, R.K., Saunders, M.R., Kalb, R.A., Haulton, G.S., Charles H., eds. M., 2013. The Hardwood Ecosystem Experiment: a framework for studying responses to forest management. Gen. Tech. Rep. NRS-P-108. Newt. Square, PA U.S. Dep. Agric. For. Serv. North. Res. Station. [CD ROM] 350 p. 108, 1–350.
- Therneau, T.M., Atkinson, E.J., 2015. An Introduction to Recursive Partitioning Using the RPART Routines, Mayo Foundation. <https://doi.org/10.1017/CBO9781107415324.004>
- Thiollay, J.-M., 1997. Disturbance, selective logging and bird diversity: a Neotropical forest study. *Biodivers. Conserv.* 6, 1155–1173. <https://doi.org/10.1023/A:1018388202698>

- Todd, B.D., Blomquist, S.M., Harper, E.B., Osbourn, M.S., 2014. Effects of timber harvesting on terrestrial survival of pond-breeding amphibians. *For. Ecol. Manage.* 313, 123–131.
<https://doi.org/10.1016/J.FORECO.2013.11.011>
- Uno, H., Power, M.E., 2015. Mainstem-tributary linkages by mayfly migration help sustain salmonids in a warming river network. *Ecol. Lett.* 18, 1012–1020.
<https://doi.org/10.1111/ele.12483>
- Unrine, J.M., Hopkins, W.A., Romanek, C.S., Jackson, B.P., 2007. Bioaccumulation of trace elements in omnivorous amphibian larvae: Implications for amphibian health and contaminant transport. *Environ. Pollut.* 149, 182–192.
<https://doi.org/10.1016/J.ENVPOL.2007.01.039>
- Veysey Powell, J.S., Babbitt, K.J., 2015. Despite Buffers, Experimental Forest Clearcuts Impact Amphibian Body Size and Biomass. *PLoS One* 10, e0143505.
<https://doi.org/10.1371/journal.pone.0143505>
- Volpe, N.L., Robinson, W.D., Frey, S.J.K., Hadley, A.S., Betts, M.G., 2016. Tropical Forest Fragmentation Limits Movements, but Not Occurrence of a Generalist Pollinator Species. *PLoS One* 11, e0167513. <https://doi.org/10.1371/journal.pone.0167513>
- Walston, L.J., Mullin, S.J., 2008. Variation in amount of surrounding forest habitat influences the initial orientation of juvenile amphibians emigrating from breeding ponds. *Can. J. Zool.* 86, 141–146. <https://doi.org/10.1139/Z07-117>
- Zollner, P.A., Lima, S.L., 1997. Landscape-Level Perceptual Abilities in White-Footed Mice: Perceptual Range and the Detection of Forested Habitat. *Oikos* 80, 51.
<https://doi.org/10.2307/3546515>

4.8 Tables and Figures

Table 3 *State variables with parameter values used in individual-based model simulations.* In experiment 1, state variable parameters varied across Low, Medium (Mid) and High levels corresponding to homogeneous virtual landscapes with a single canopy closure category. Except for movement settlement probability in experiment two, state variable parameters were randomly selected from a random uniform distribution between Low and High values corresponding to each canopy closure category in heterogeneous landscapes. We fixed movement and settlement probabilities at Mid-level for all experiment 2 runs because experiment 1 showed that they their influence on subsidy distribution metrics was generally limited compared to the other state variables.

| <i>State Variables</i> | Canopy Closure Category | | | | | | | | |
|-----------------------------------|--------------------------------|------------|-------------|-----------------------|------------|-------------|----------------------|------------|-------------|
| | Open Canopy | | | Partial Canopy | | | Closed Canopy | | |
| | <i>Low</i> | <i>Mid</i> | <i>High</i> | <i>Low</i> | <i>Mid</i> | <i>High</i> | <i>Low</i> | <i>Mid</i> | <i>High</i> |
| Mean Vector Length (MVL) | 0.52 | 0.67 | 0.82 | 0.41 | 0.52 | 0.63 | 0.14 | 0.3 | 0.46 |
| Mean Step Length (MSL) (m) | 0.26 | 0.39 | 0.52 | 0.23 | 0.27 | 0.31 | 0.18 | 0.28 | 0.38 |
| Mortality Probability | 0.005 | 0.0075 | 0.01 | 0.001 | 0.0025 | 0.005 | 0.00075 | 0.001 | 0.0025 |
| Settlement Probability | 0.0005 | 0.00075 | 0.001 | 0.001 | 0.0025 | 0.005 | 0.0025 | 0.005 | 0.0075 |
| Movement Probability | 0.5 | 0.55 | 0.6 | 0.7 | 0.75 | 0.8 | 0.9 | 0.95 | 0.99 |

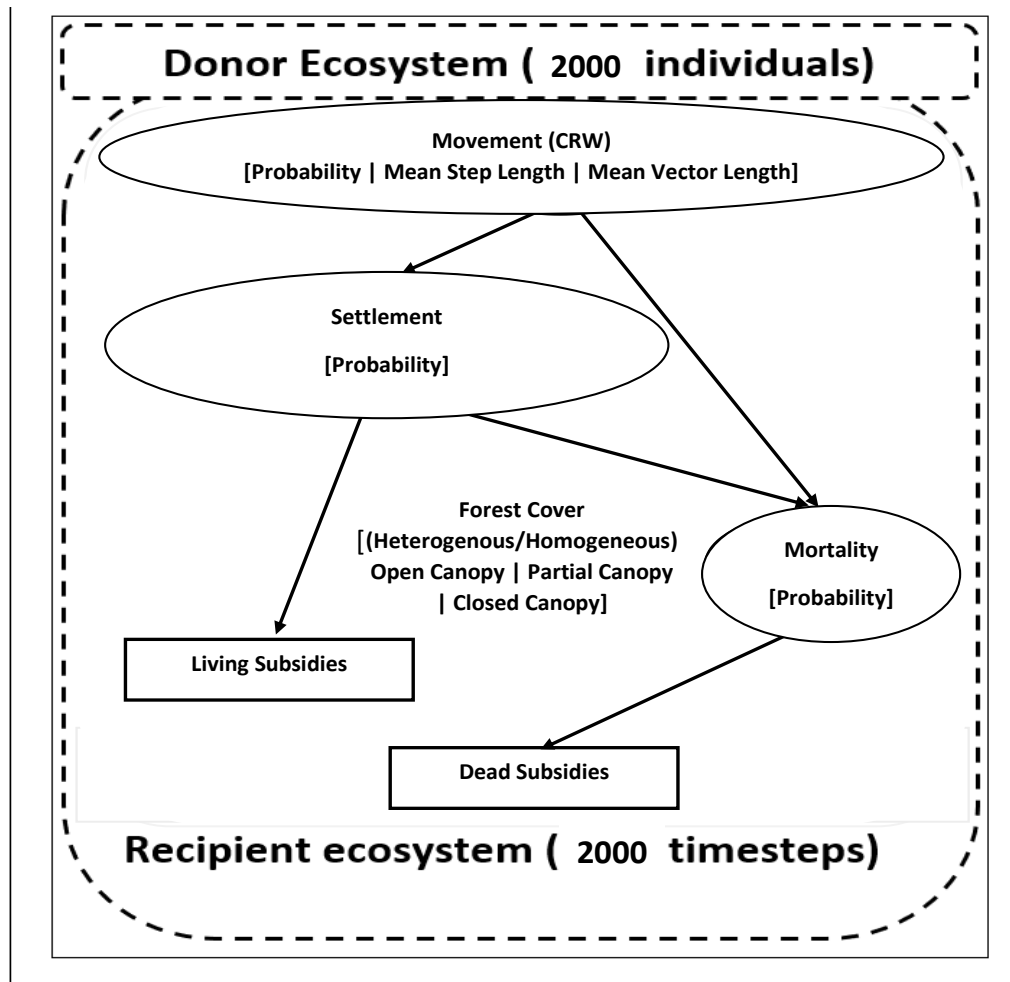


Figure 16 *Design concept: Simulation design, procedure and process flow for IBM sub-models (i.e., movement, settlement and mortality) and outcomes (i.e., living and dead subsidies).*

Recipient ecosystem consists of homogeneous or heterogeneous forest canopy closure categories: open, partial and closed canopy. Movement was implemented in simulations using per-step movement probability and correlated random walk (CRW) based on per-step mean step and vector lengths derived from HEE juvenile wood frog track surveys by canopy density. We implemented per-step probabilities of mortality and settlement that varied with canopy closure category and occurred stochastically as dispersers travelled through recipient ecosystem. Living subsidies settle and mortality results in dead subsidies.

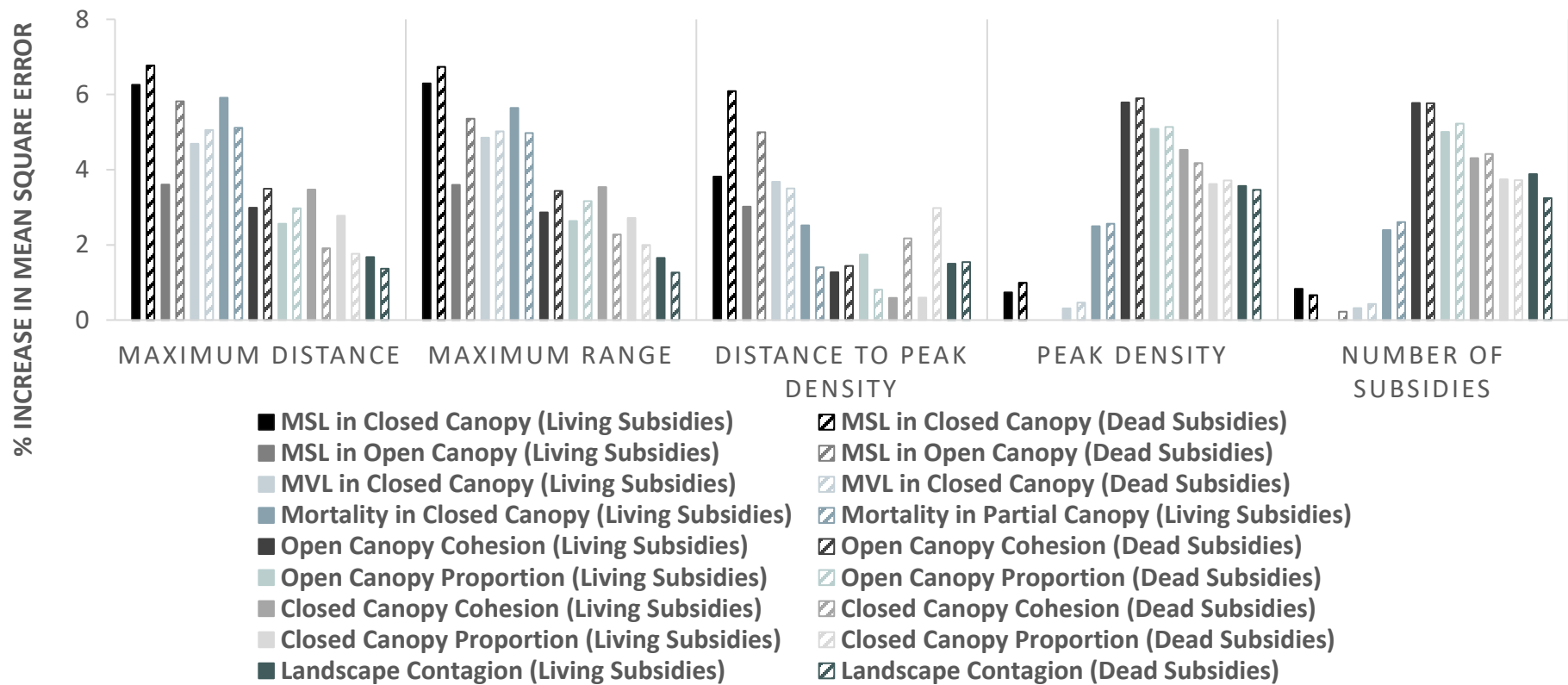


Figure 17 *Predictor importance measured as increase in percentage mean square prediction error for most influential metrics of living (consumer) and dead (nutrient) juvenile wood frog subsidy distribution in heterogeneous landscapes (i.e., experiment 2). Larger values indicate greater importance. Animal movement behavior is more important for subsidy displacement than landscape heterogeneity and landscape heterogeneity is more important for subsidy density than animal movement behavior. Solid bars represent results for living subsidies and patterned bars represent results for dead subsidies. Taller bars indicate greater predictor importance (See section T in supplementary information (Appendix C) for detailed tables with values for variable (%IncMSE) and precision (IncNodePurity) (Table 12)).*

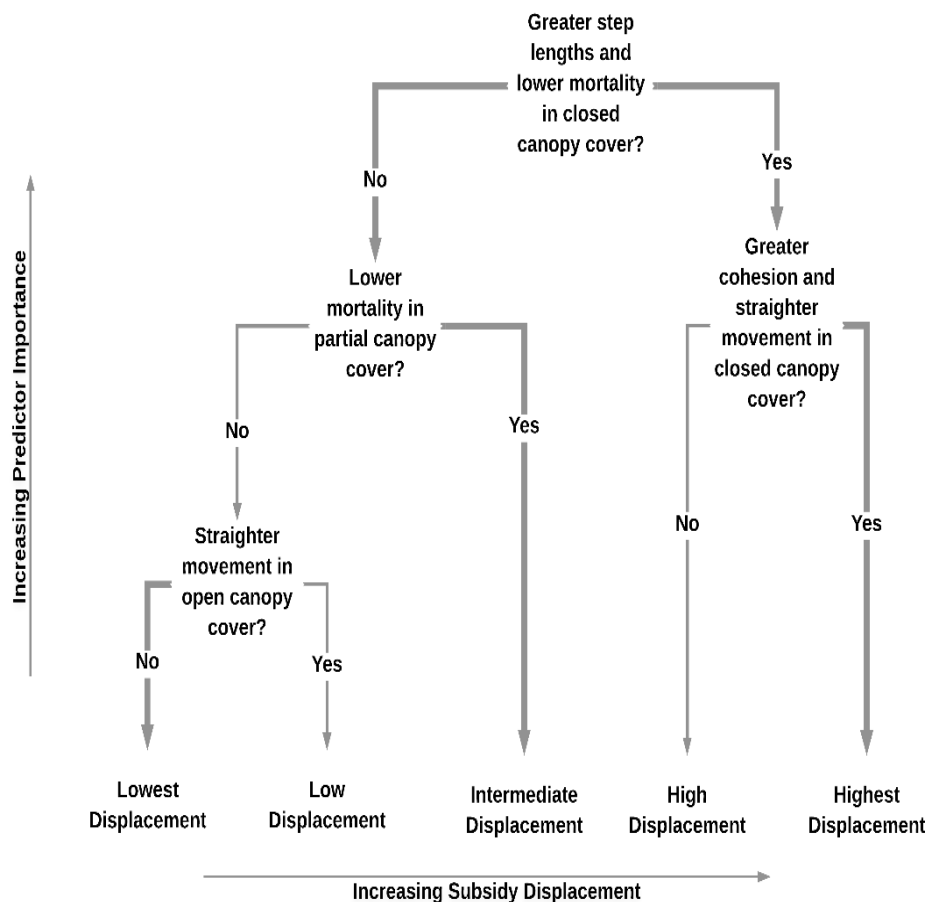


Figure 18 *Synthesis of subsidy displacement trends in heterogeneous landscapes.* Given lower mortality and straighter movements with greater step lengths in heterogeneous forests, greater cohesion of closed canopy habitat resulted in greater subsidy displacement. Lower mortality in partial canopy habitat generated intermediate subsidy displacement. Straighter movement in open canopy displaced subsidies farther into recipient ecosystems, particularly for dead subsidies. Chart relationships delineated with heavy lines represent instances where 6 representative CARTs agreed while relationships delineated with lighter lines represent instances where at least half but not all constituent CARTs agreed. See figure 35 in supplementary materials (Appendix C) for detailed CARTs synthesized here.

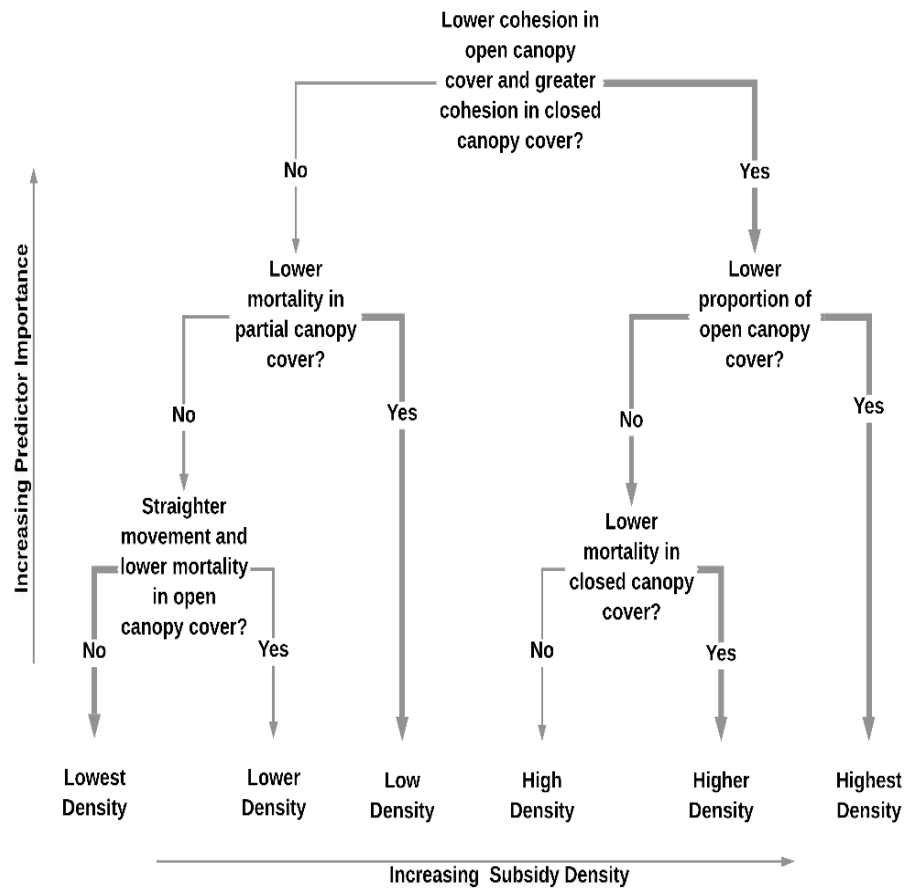


Figure 19 *Synthesis of peak subsidy deposition density trends in heterogeneous landscapes.* Given lower mortality and greater cohesion in closed canopy in heterogeneous forests, lower cohesion and proportion of open canopy habitat generated the greatest subsidy deposition densities. Lower mortality in partial canopy forest resulted in intermediate subsidy deposition densities, particularly for living subsidies. More sinuous movement and higher mortality in closed canopy habitat resulted in greater subsidy deposition density, particularly for dead subsidies. Chart relationships delineated with heavy lines represent instances where 4 representative CARTs agreed while relationships delineated with lighter lines represent instances where at least half but not all constituent CARTs agreed. See figure 36 in supplementary materials (Appendix C) for detailed CARTs synthesized here.

CHAPTER 5. ADVANCES IN UNDERSTANDING ACTIVE SUBSIDY SYSTEMS

5.1 Contributions to spatial subsidy research and modeling

Ecological subsidies are ubiquitous in natural ecosystems and can affect ecosystem structure, function and services (Palumbi, 2003; Polis et al., 1996). Animal movements can result in active consumer and nutrient subsidy displacement across ecosystems (Earl and Zollner, 2017). Our understanding of active subsidy impacts on ecosystems is limited, because classical ecological and ecosystem models treat movement and space implicitly (Earl and Zollner, 2017; McInturf et al., 2019; Scharf et al., 2018). The results presented in chapters 2 to 4 of this dissertation provide a unique contribution because they combine individual based and movement ecology methods in novel modeling frameworks to investigate the influence of spatially explicit animal movement, sociality and landscape heterogeneity on spatial subsidies towards enhancing our understanding of ecosystem impacts (Earl and Zollner, 2014). In the three core chapters of this dissertation, I quantified and examine if and how active subsidy distributions vary in response to spatially explicit animal movement in three important ecological contexts: 1) Movement given mortality 2) Conspecific interaction and 3) Landscape heterogeneity.

I established that spatial subsidy models can improve insights into spatial subsidy impacts by considering ecological differences in animal movement behavior (e.g., foraging, dispersal) and mortality (e.g., spatial risk, temporal risk). In the second chapter of my dissertation, I demonstrated that animal movements interact with mortality risk to generate greater nutrient than consumer subsidy impacts closer to ecosystem boundaries. I showed that as mortality risk increases, straighter dispersers generate more displaced and spread out nutrient subsidy patterns than foragers with more sporadic movements. A key insight was that increasing mortality risk with the rate of

movement or distance travelled by foraging animals enhances corresponding subsidy displacement and spread. CRW and LW have been used to represent animal foraging and dispersal movements across taxa with a rich tradition of scholarly debate about the relative viability of each approach (Benhamou, 2007; Reynolds, 2015). IBM frameworks of spatial subsidy systems that employ both CRW and LW in movement models where each is most appropriate in terms of animal life history, can better elucidate and differentiate ecosystem impacts of nutrient and consumer subsidies from foraging and dispersal.

In the third chapter of my dissertation, I demonstrated that that accounting for animal movement behavior given territorial and social interactions in spatial subsidy models will enhance our understanding of variation in corresponding active subsidy patterns and impacts. My results indicated that animal sociality interacts with movement behavior to influence active subsidy distributions. My work showed that for social animals, settlement influenced by conspecifics generates denser consumer than nutrient subsidy patterns closer to ecosystem boundaries. Further, social animals with high perceptual range generate fewer, smaller clusters with greater subsidy density, but straighter dispersal movements increase cluster sizes and subsidy spread. In contrast, for territorial species, I showed that straighter dispersal movements in territorial species generate larger clusters with lower subsidy density, particularly for animals with higher perceptual range. I conclude that differences in subsidy patterns emerging from different conspecific interaction scenarios are strongly influenced by perceptual range and how straight animals move. Spatial subsidy models that consider animal interactions in determining corresponding ecosystem impacts will be more insightful than ecosystem models that exclude the influence of animal sociality.

Spatial subsidy models can improve by accounting for the effect of the relative quality, proportion and spatial aggregation of multiple constituent habitat types on animal space-use,

fitness and survival. My fourth chapter demonstrates that landscape heterogeneity influences spatial subsidy patterns and impacts by affecting animal movement, settlement and mortality. I showed that active subsidy displacement and spread increases with the quality, proportional composition and spatial aggregation (i.e., cohesion) of habitat types as well as overall landscape structure (i.e., contagion). I showed that movement (i.e., mean step and vector lengths) matters more for subsidy displacement, but the proportion and physical connectedness (i.e., cohesion) of habitat types are more important for subsidy impact. Longer, straighter movements in landscapes with greater proportion and physical connectedness of higher quality habitats (e.g., closed and partial canopy) generate denser consumer subsidies far from donor ecosystems. I also demonstrated that greater mortality in landscapes with greater proportion and aggregation of lower quality habitat types (e.g., closed and partial canopy) spreads out nutrient subsidies closer to donor ecosystems. Spatial subsidy models should consider animal sociality to improve insights on ecosystem impacts. Accounting for sociality will enhance the predictive power of ecosystem models in active subsidy systems.

My research provides a methodological road map for incorporating stochastic movement models in IBMs to generate powerful tools for modeling the spatial subsidy impacts of animal behavior. Prior to my work, there were no ecosystem models that consider ecological differences in spatiotemporally explicit animal movement and mortality (Earl and Zollner, 2014), sociality or landscape heterogeneity on corresponding active subsidy distributions and impact even though animal behavior is important for spatial subsidies. My research reveals that spatial subsidy patterns and ecosystem impacts respond to spatially explicit animal behavior and that the magnitude and extent of these response is far greater than previously appreciated. Spatial subsidy systems are ubiquitous and important drivers of cross-ecosystem structure, function and services. Ecosystem

models can be more useful for assessing the spatial subsidy impacts in wildlife and ecosystem management by considering the influence of animal movement, interactions in heterogeneous landscapes on active subsidies. Spatial subsidy research can improve by integrating individual-based and movement ecology frameworks to generate modeling tools suitable for examining connections between individual animal behavior and emergent ecosystem impacts.

My work shows that the intensity and extent of spatial subsidy impacts varies with animal movement, sociality and landscape heterogeneity. The role of behavior and landscape heterogeneity in active subsidy distributions has implications for predicting the impact of biologically transported contaminants across ecosystem boundaries. For instance, bears and seabirds that forage on contaminated fish can transport biomagnified aquatic pollutants like heavy metals when they disperse into and deposit feces and carcasses in riparian terrestrial ecosystems (Blais et al., 2005; Braune et al., 2005; Gregory-Eaves et al., 2007). My work shows that predicting spatial patterns in contaminated feces and carcass deposition will require understanding how bear and seabird foraging and dispersal movements vary with respective territorial and social interactions, as well as heterogeneity in habitat quality and structure to manage and mitigate ecosystem impacts. Similarly, aquatic insects bioaccumulate and transport contaminants like persistent organic pollutants to terrestrial ecosystems where they become prey, resulting in biomagnification of pollutants in terrestrial food webs (Kraus et al., 2014; Schindler and Smits, 2017). Contaminant transfer in prey can control predator populations and cause ecotoxicological effects that destabilize food webs in recipient terrestrial ecosystems (Jones et al., 2013; Schiesari et al., 2018). Developing effective models to predict spatial patterns in bottom-up effects caused by bioaccumulated contaminants requires knowledge of animal behaviors and interactions given resource and risk heterogeneity (French and McCauley, 2019). Pollutants transported in active

subsidies from aquatic to terrestrial ecosystems can affect economically important recreational ecosystem services (e.g., bird watching) and human health (e.g., contaminated anadromous fish consumption) (Walters et al., 2008).

My research provides groundwork to develop tools to predict the spread and spatial impact of animal-transported diseases across ecosystem boundaries based on knowledge about the relationship between animal behavior and spatial subsidy patterns. Active subsidies can transport pathogens and spread diseases that affect species conservation and ecosystem health (Pereira et al., 2014). For instance, anthropogenic, climatic and ecohydrologically driven amphibian movement spreads the fatal chytridiomycosis disease among populations (Dodd, 2009). Infected amphibians transport chytrid fungus spores as they move between aquatic and terrestrial ecosystems across landscapes, spreading chytridiomycosis to healthy amphibian populations (Harper and Petranksa, 2006). Furthermore, pathogen and disease spread by active vectors or subsidies can have greater impacts on species that exhibit social behavior. For example, amphibian species that interact with conspecifics in events such as explosive breeding assemblages can influence the impact of chytridiomycosis and other infectious diseases (Giuggioli et al., 2013; Semlitsch, 2008). Horizontal disease transmission has also been shown to increase with aggregation and contact in scavenger communities (Mateo-Tomás et al., 2015). Scavengers like vultures and hyenas are important for nutrient cycling when they consume and break down carcasses into labile nutrient forms, controlling toxicity and disease spread (Atwood et al., 2016; Subalusky et al., 2017). Examining scavenger movement behavior and conspecific interaction at carcasses can improve our understanding of pathogen and disease spread and conservation of scavenger communities.

My research provides a foundation for connecting spatial impacts of consumer and nutrient export to movement behavior influenced by spatial heterogeneity in habitat quality and structure across landscapes. This has implications for nutrient and consumer subsidy patterns in relation to ecosystem processes like nutrient cycling and hotspots. Heterogeneity influences the distribution of resources and risks in a landscape with corresponding effects on movement behavior (Bleicher, 2017; Joly, 2019). The influence of landscape heterogeneity on animal movements therefore affects important animal space use processes like dispersal and foraging, habitat prospecting and selection, settlement and home range establishment with fitness and survival consequences (Crowley et al., 2019; Miramontes et al., 2012; Sinsch, 2014). A 21-year study indicates a net amphibian nutrient export to terrestrial ecosystems but suggests that factors affecting the corresponding spatial impact remain confounding (Capps et al., 2015). This impedes our ability to predict the spatial distribution of related ecosystem services like nutrient cycling (Hocking et al., 2014). More broadly, my work provides a general systematic template for developing predictive models to determine the spatial distribution and impact of animal-transported subsidies based on movement, sociality and landscape heterogeneity.

In conclusion, my dissertation demonstrates that animal behavior (i.e., movement and sociality) and landscape heterogeneity affect corresponding active subsidy distributions and impacts in recipient ecosystems. My work established that these factors should be considered in spatial subsidy models to enhance their value as predictive tools in research for wildlife and ecosystems management. This is particularly relevant in situations where collection of data on the ground has high operational or ecological costs (e.g., species of concern, cryptic organisms, diseases and contaminant transfer scenarios). Future models should also address how subsidy impact changes with subsidy quality as a function of the size and elemental body composition of

consumer and nutrient subsidies respectively (Demi et al., 2012). Incorporating the possibility of disperser returns to donor ecosystems (e.g., philopatric breeding dispersal) in future models could provide additional insights into the spatial impacts of feedback loops generated by reciprocal subsidies between aquatic and terrestrial ecosystems (Bartels et al., 2012). Active subsidies are ubiquitous, prevalent and important for ecosystems structure, processes, functions and services. As my dissertation research has shown, animal movement, sociality and space use in relation to landscape heterogeneity plays important and quantifiable role in the distribution and impact of active subsidies. Spatial subsidies research will therefore improve our ability to predict spatial distributions and manage corresponding ecosystem impacts by accounting for the influence of animal behavior and landscape heterogeneity.

5.2 References

- Atwood, T.C., Peacock, E., McKinney, M.A., Lillie, K., Wilson, R., Douglas, D.C., Miller, S., Terletzky, P., 2016. Rapid Environmental Change Drives Increased Land Use by an Arctic Marine Predator. *PLoS One* 11, e0155932. <https://doi.org/10.1371/journal.pone.0155932>
- Bartels, P., Cucherousset, J., Steger, K., Eklov, P., Tranvik, L.J., Hillebrand, H., 2012. Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. *Ecology* 93, 1173–1182. <https://doi.org/10.1890/11-1210.1>
- Benhamou, S., 2007. How many animals really do the Lévy walk? *Ecology* 88, 1962–1969. <https://doi.org/10.1890/06-1769.1>
- Blais, J.M., Kimpe, L.E., McMahon, D., Keatley, B.E., Mallory, M.L., Douglas, M.S. V, Smol, J.P., 2005. Arctic Seabirds Transport Marine-Derived Contaminants. *Science* (80-.). 309, 445–445. <https://doi.org/10.1126/science.1112658>
- Bleicher, S.S., 2017. The landscape of fear conceptual framework: definition and review of

current applications and misuses. PeerJ 5, e3772. <https://doi.org/10.7717/peerj.3772>

- Braune, B.M., Outridge, P.M., Fisk, A.T., Muir, D.C.G., Helm, P.A., Hobbs, K., Hoekstra, P.F., Kuzyk, Z.A., Kwan, M., Letcher, R.J., Lockhart, W.L., Norstrom, R.J., Stern, G.A., Stirling, I., 2005. Persistent organic pollutants and mercury in marine biota of the Canadian Arctic: An overview of spatial and temporal trends. *Sci. Total Environ.* <https://doi.org/10.1016/j.scitotenv.2004.10.034>
- Capps, K.A., Berven, K.A., Tiegs, S.D., 2015. Modelling nutrient transport and transformation by pool-breeding amphibians in forested landscapes using a 21-year dataset. *Freshw. Biol.* 60, 500–511. <https://doi.org/10.1111/fwb.12470>
- Crowley, P.H., Trimmer, P.C., Spiegel, O., Ehlman, S.M., Cuello, W.S., Sih, A., 2019. Predicting Habitat Choice after Rapid Environmental Change. *Am. Nat.* 193, 619–632. <https://doi.org/10.1086/702590>
- Demi, L.M., Simon, K.S., Coghlan, S.M., Saunders, R., Anderson, D., 2012. Anadromous alewives in linked lake–stream ecosystems: do trophic interactions in lakes influence stream invertebrate communities? *Freshw. Sci.* 31, 973–985. <https://doi.org/10.1899/11-124.1>
- Dodd, C.K., 2009. *Amphibian ecology and conservation : a handbook of techniques.*
- Earl, J.E., Zollner, P.A., 2017. Advancing research on animal-transported subsidies by integrating animal movement and ecosystem modelling. *J. Anim. Ecol.* 86, 987–997. <https://doi.org/10.1111/1365-2656.12711>
- Earl, J.E., Zollner, P.A., 2014. Effects of animal movement strategies and costs on the

distribution of active subsidies across simple landscapes. *Ecol. Modell.* 283, 45–52.

<https://doi.org/10.1016/j.ecolmodel.2014.03.020>

French, S.K., McCauley, S.J., 2019. The movement responses of three libellulid dragonfly species to open and closed landscape cover. *Insect Conserv. Divers.* icad.12355.

<https://doi.org/10.1111/icad.12355>

Giuggioli, L., Potts, J.R., Rubenstein, D.I., Levin, S.A., 2013. Stigmergy, collective actions, and animal social spacing. *Proc. Natl. Acad. Sci. U. S. A.* 110, 16904–9.

<https://doi.org/10.1073/pnas.1307071110>

Gregory-Eaves, I., Demers, M.J., Kimpe, L., Krümmel, E.M., Macdonald, R.W., Finney, B.P., Blais, J.M., 2007. Tracing salmon-derived nutrients and contaminants in freshwater food webs across a pronounced spawner density gradient. *Environ. Toxicol. Chem.* 26, 1100.

<https://doi.org/10.1897/06-402R.1>

Harper, E.M., Petranka, J.W., 2006. Ranavirus in Wood Frogs (*Rana Sylvatica*): Potential Sources of Transmission within and between Ponds. *J. Wildl. Dis.* 42, 307–318.

<https://doi.org/10.7589/0090-3558-42.2.307>

Hocking, D.J., Babbitt, K.J., Hocking, D.J., 2014. Amphibian contributions to ecosystem services. *Herpetol. Conserv. Biol.*

Joly, P., 2019. Behavior in a Changing Landscape: Using Movement Ecology to Inform the Conservation of Pond-Breeding Amphibians. *Front. Ecol. Evol.* 7, 155.

<https://doi.org/10.3389/fevo.2019.00155>

Jones, T.A., Chumchal, M.M., Drenner, R.W., Timmins, G.N., Nowlin, W.H., 2013. Bottom-up

- nutrient and top-down fish impacts on insect-mediated mercury flux from aquatic ecosystems. *Environ. Toxicol. Chem.* 32, 612–618. <https://doi.org/10.1002/etc.2079>
- Kraus, J.M., Schmidt, T.S., Walters, D.M., Wanty, R.B., Zuellig, R.E., Wolf, R.E., 2014. Cross-ecosystem impacts of stream pollution reduce resource and contaminant flux to riparian food webs. *Ecol. Appl.* <https://doi.org/10.1890/13-0252.1>
- Mateo-Tomás, P., Olea, P.P., Moleón, M., Vicente, J., Botella, F., Selva, N., Viñuela, J., Sánchez-Zapata, J.A., 2015. From regional to global patterns in vertebrate scavenger communities subsidized by big game hunting. *Divers. Distrib.* <https://doi.org/10.1111/ddi.12330>
- McInturf, A.G., Pollack, L., Yang, L.H., Spiegel, O., 2019. Vectors with autonomy: what distinguishes animal-mediated nutrient transport from abiotic vectors? *Biol. Rev.* brv.12525. <https://doi.org/10.1111/brv.12525>
- Miramontes, O., Boyer, D., Bartumeus, F., 2012. The effects of spatially heterogeneous prey distributions on detection patterns in foraging seabirds. *PLoS One* 7, e34317. <https://doi.org/10.1371/journal.pone.0034317>
- Palumbi, S.R., 2003. Ecological subsidies alter the structure of marine communities. *Proc. Natl. Acad. Sci.* 100, 11927–11928. <https://doi.org/10.1073/pnas.2335832100>
- Pereira, L.M., Owen-Smith, N., Moleón, M., 2014. Facultative predation and scavenging by mammalian carnivores: Seasonal, regional and intra-guild comparisons. *Mamm. Rev.* <https://doi.org/10.1111/mam.12005>
- Polis, G.A., Holt, R.D., Menge, B.A., Winemiller, K.O., 1996. Time, Space, and Life History:

- Influences on Food Webs, in: Food Webs. Springer US, Boston, MA, pp. 435–460.
https://doi.org/10.1007/978-1-4615-7007-3_38
- Reynolds, A., 2015. Liberating Lévy walk research from the shackles of optimal foraging. *Phys. Life Rev.* 14, 59–83. <https://doi.org/10.1016/j.plrev.2015.03.002>
- Scharf, A.K., Belant, J.L., Beyer, D.E., Wikelski, M., Safi, K., 2018. Habitat suitability does not capture the essence of animal-defined corridors. *Mov. Ecol.* <https://doi.org/10.1186/s40462-018-0136-2>
- Schiesari, L., Leibold, M.A., Burton, G.A., 2018. Metacommunities, metaecosystems and the environmental fate of chemical contaminants. *J. Appl. Ecol.* <https://doi.org/10.1111/1365-2664.13054>
- Schindler, D.E., Smits, A.P., 2017. Subsidies of Aquatic Resources in Terrestrial Ecosystems. *Ecosystems.* <https://doi.org/10.1007/s10021-016-0050-7>
- Semlitsch, R.D., 2008. Differentiating Migration and Dispersal Processes for Pond-Breeding Amphibians. *J. Wildl. Manage.* 72, 260–267. <https://doi.org/10.2193/2007-082>
- Sinsch, U., 2014. Movement ecology of amphibians: from individual migratory behaviour to spatially structured populations in heterogeneous landscapes. *Can. J. Zool.* 92, 491–502. <https://doi.org/10.1139/cjz-2013-0028>
- Subalusky, A.L., Dutton, C.L., Rosi, E.J., Post, D.M., 2017. Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proc. Natl. Acad. Sci. U. S. A.* 114, 7647–7652. <https://doi.org/10.1073/pnas.1614778114>
- Walters, D.M., Fritz, K.M., Otter, R.R., 2008. The dark side of subsidies: Adult stream insects export organic contaminants to riparian predators. *Ecol. Appl.* 18, 1835–1841. <https://doi.org/10.1890/08-0354.1>

APPENDIX A. SUPPLEMENTARY INFORMATION (SI): COMPARING ANIMAL MOVEMENT PATTERNS AND MORTALITY MODELS ON THE DISTRIBUTION OF ACTIVE SUBSIDIES

Section S: Supplementary Results

- ❖ Means annotated boxplots of subsidy distribution metrics (Displacement (deposition distance and range) and Impact (peak deposition density and distance) for living and dead subsidies) by:
 - Movement pattern (CRW vs LW)
 - LW Mortality type (Space-based vs Time-based)
- ❖ Classification and Regression Trees (CARTs) of subsidy distribution metrics (Displacement (maximum distance, range and distance to peak density)) and Impact (peak density), with leaves containing mean response values, number (n) and percentage (%) of data points resulting from predictor split:
 - Nodes containing predictor splits for movement scaling (correlation coefficient (CRW) and scaling exponent (LW)) and mortality:
 - Correlation coefficients (more sinuous to straighter) - 0.5, 0.8, 0.9, 0.95, 0.99
 - Scaling exponent (high to low scale-invariance) – 1.0, 1.5, 2.0, 2.5, 3.0
 - Mortality (Low to High) – 0.00025, 0.0005, 0.001
 - LW Movement scaling (scaling exponent) and Mortality type (Space-based versus Time-based):
 - Mortality type (High to Low, as function of space and time) – Space.a.00025, Space.b.0005, Space.c.001, Time.d.00025, Time.e.0005, Time.f.001

-Section T: Random Forest and CART Error Analysis

- ❖ Subsidy distribution metrics by % IncMSE, IncNodePurity (RSS), % variance explained and misclassification rate for:
 - Movement pattern (CRW & LW) with mortality as a function of time | LW pattern with mortality as a function of space and time

Section U: Model Construction

- ❖ Model Overview, Design Concepts, Details (ODD) description:
 - Overview: Purpose, State variables and scale, Process overview and scheduling
 - Design concepts: Emergence, Sensing, Interaction, Stochasticity, Observation
 - Details: Initialization, Inputs, Sub-models

-Section V: Code

- ❖ Code:
 - Model construction: NetLogo Version 6.0.4 Code
 - NetLogo Model description and function
 - Data processing and analysis: R version 3.5.1

-CART Response Variable Notation: number of dead subsidies: *dead.count*, maximum living subsidy deposition distance: *live.max.dist*, maximum dead subsidy deposition distance: *dead.max.dist*, maximum living subsidy range: *live.range*, maximum dead subsidy range: *dead.range*. peak living subsidy deposition density: *live.peak.dens*, peak dead subsidy deposition density: *dead.peak.dens*, distance to peak living subsidy deposition density: *live.peak.dens.dist*, distance to peak dead subsidy deposition density: *dead.peak.dens.dist*

Section S: Supplementary Results

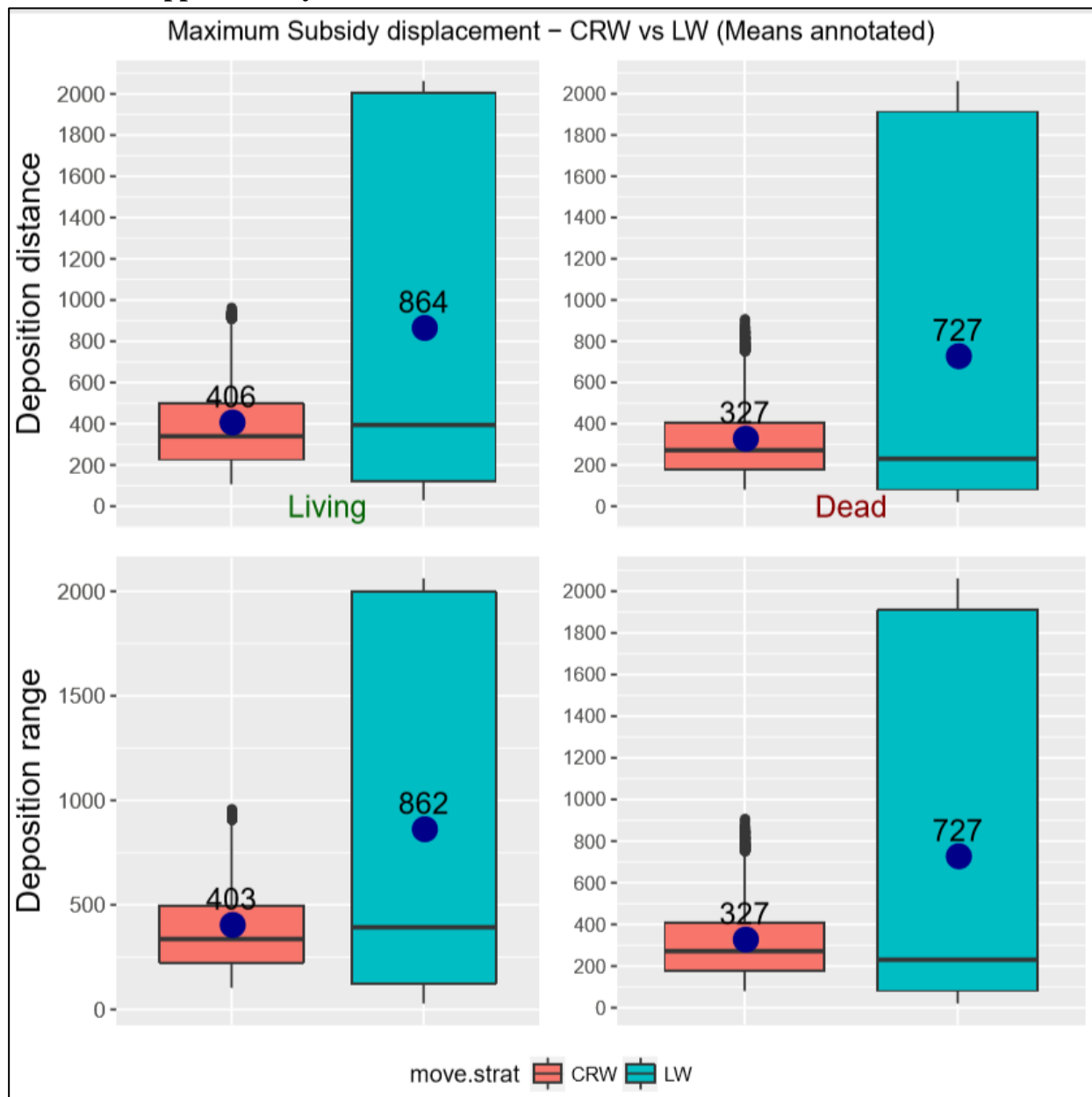


Figure 20 Comparing the effect of movement pattern on subsidy distribution metrics for both living and dead subsidies. LW subsidies are further displaced (maximum distance and range) and with higher impact (peak density and peak density distance) than CRW subsidies. Living subsidies are also further displaced with lower impact than dead subsidies.

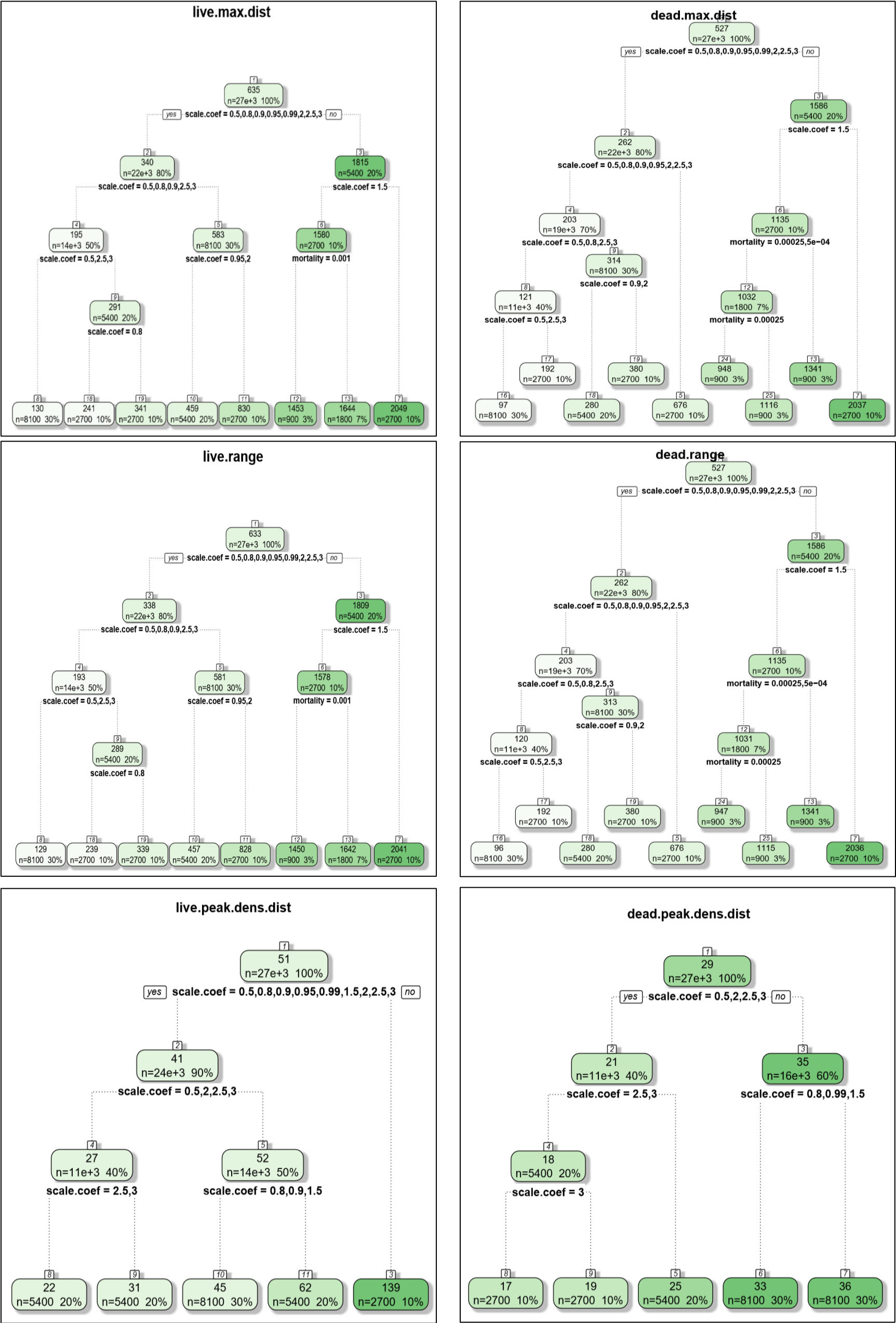


Figure 21 More scale-invariance (LW) and straighter (CRW) movements deposit subsidies further (maximum distance and range) than less scale-invariance and more sinuous movements, with scale-invariance movements outperforming straighter movements and attenuated by high mortality. Higher scale-invariance and straighter movements result in higher distances to peak density for both living and dead subsidies, attenuated by intermediate and high mortality for living subsidies.

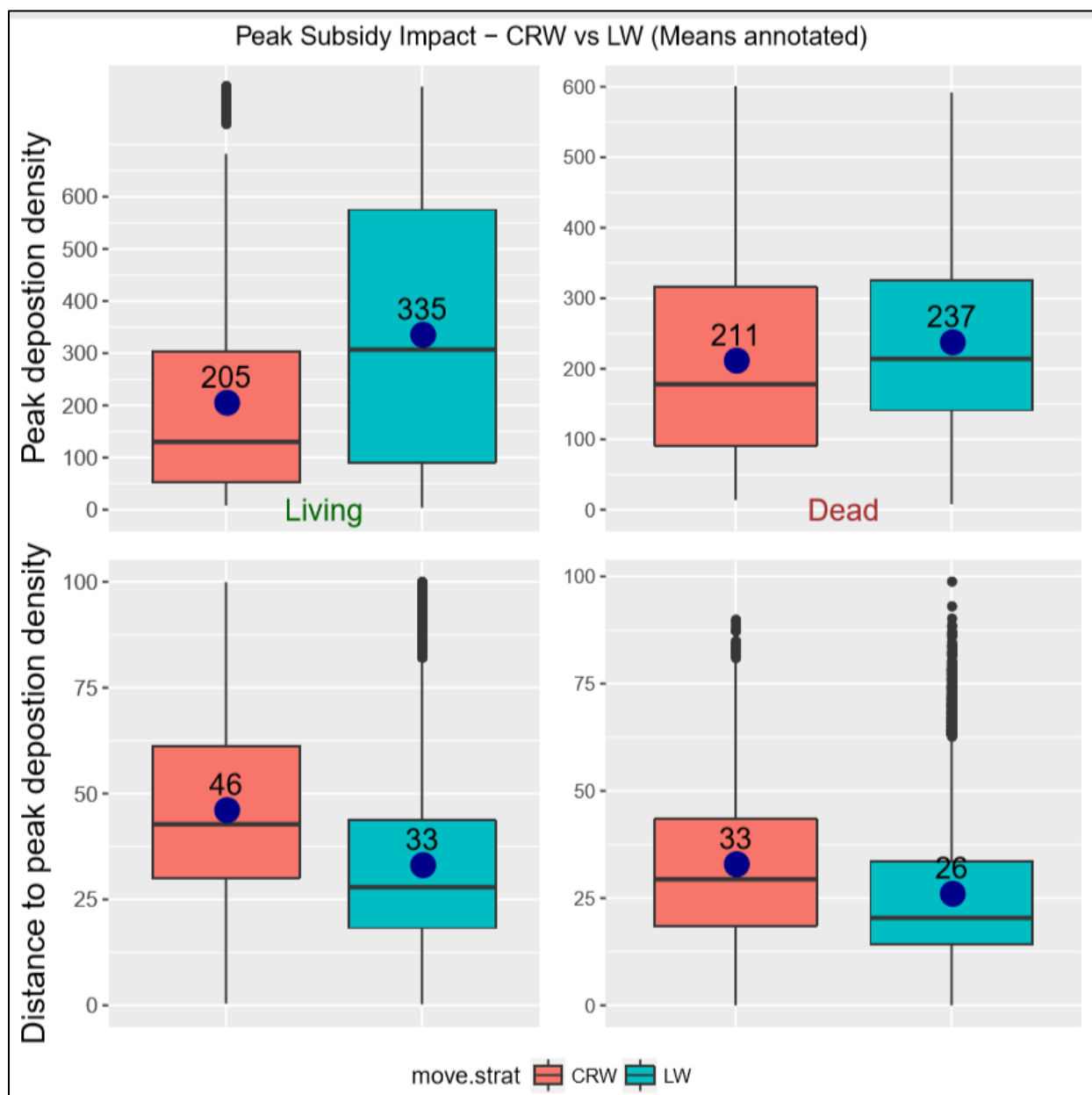


Figure 22 Comparing the effect of movement pattern on subsidy distribution metrics for both living and dead subsidies. LW subsidies are further displaced (maximum distance and range) and with higher impact (peak density and peak density distance) than CRW subsidies. Living subsidies are also further displaced with lower impact than dead subsidies.

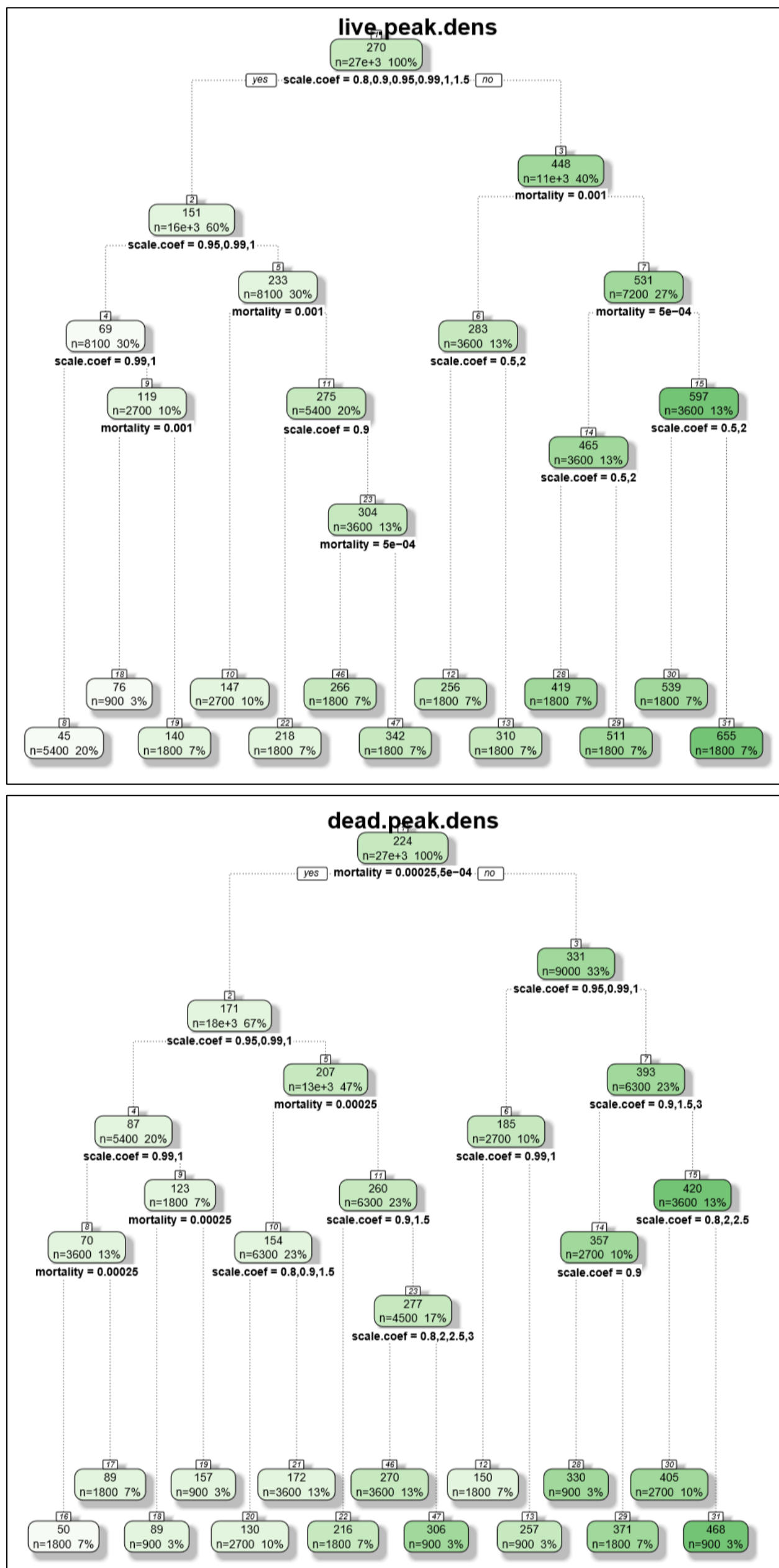


Figure 23 Lower scale-invariance movements (LW) and more sinuous movements (CRW) result in higher peak densities of living subsidies, attenuated by high mortality. High mortality leads to higher peak densities of dead subsidies, attenuated by high-scale invariance and straighter movements.

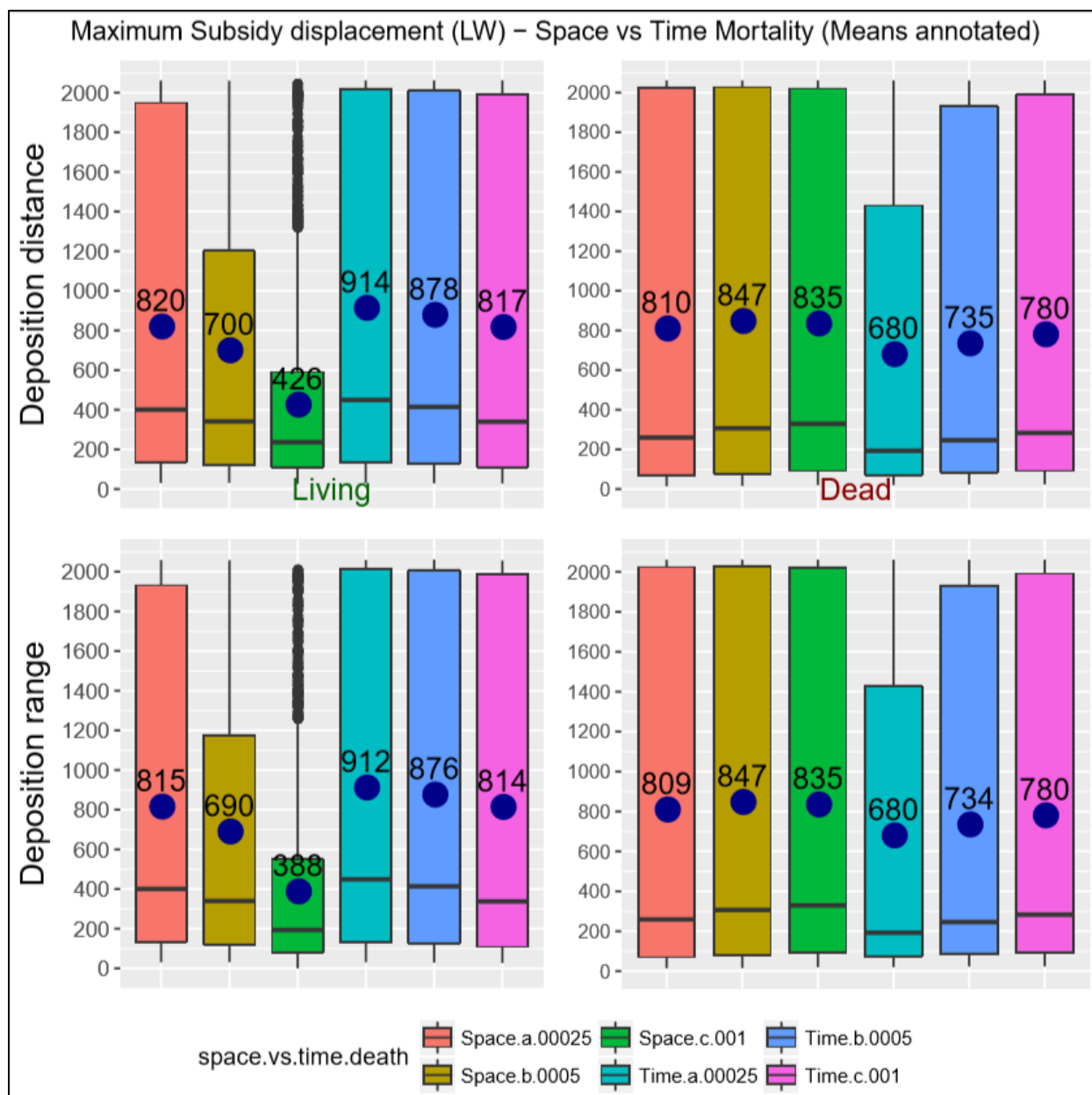


Figure 24 Space-based mortality further attenuates displacement (maximum distance and range) of living LW subsidies and enhances the displacement of dead LW subsidies, compared to time-based mortality. Living LW subsidies are further displaced than dead LW subsidies.

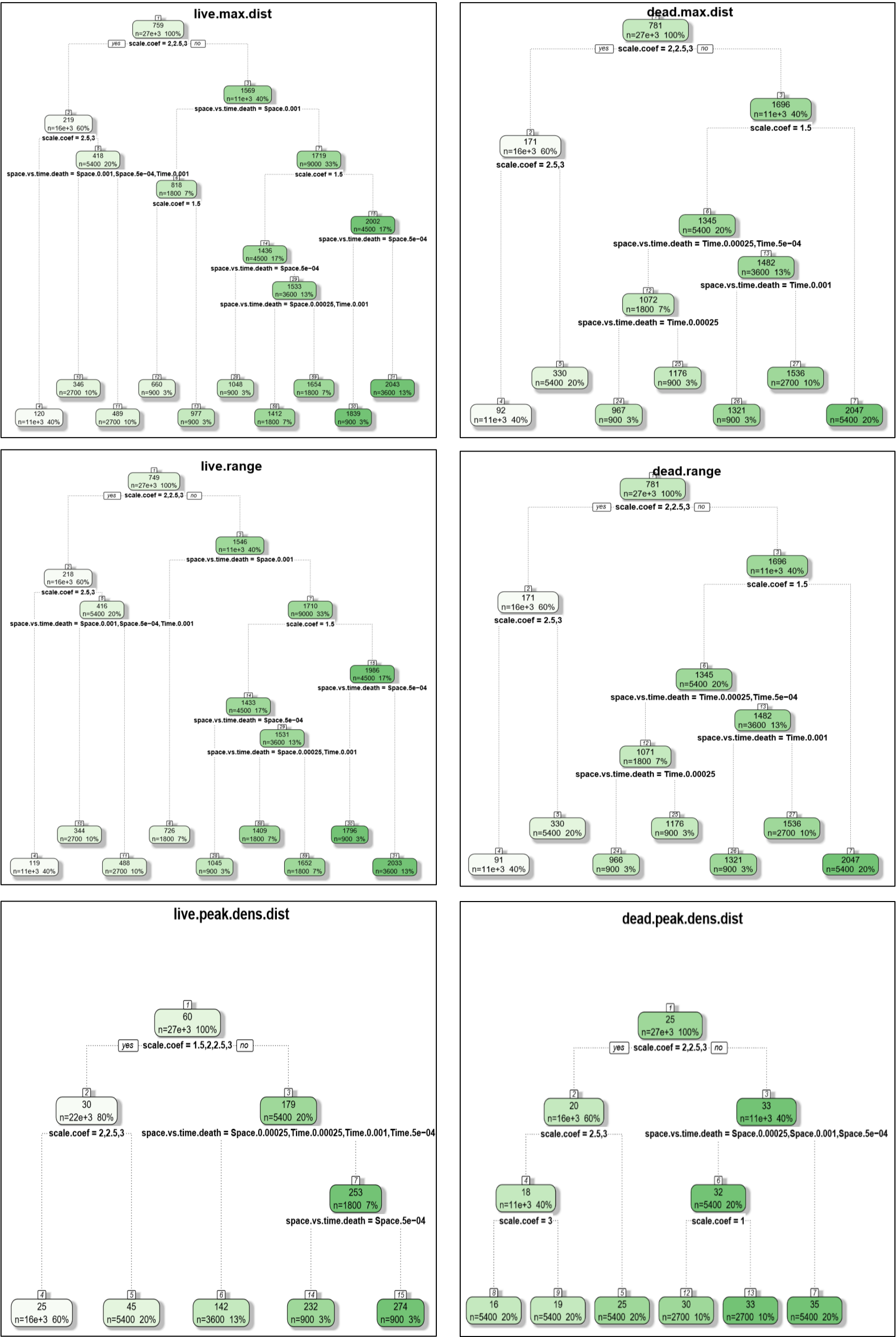


Figure 25 High space-based mortality attenuates displacement (maximum distance and range) for higher scale-invariance movements for living LW subsidies, and lower time-based mortality attenuates displacement of dead LW subsidies. Mortality as a function of space versus time has minimal impact on subsidy impact as peak density distance. Higher scale-invariance movements result in higher distance to peak density for both living and dead subsidies with enhanced effects for living subsidies.

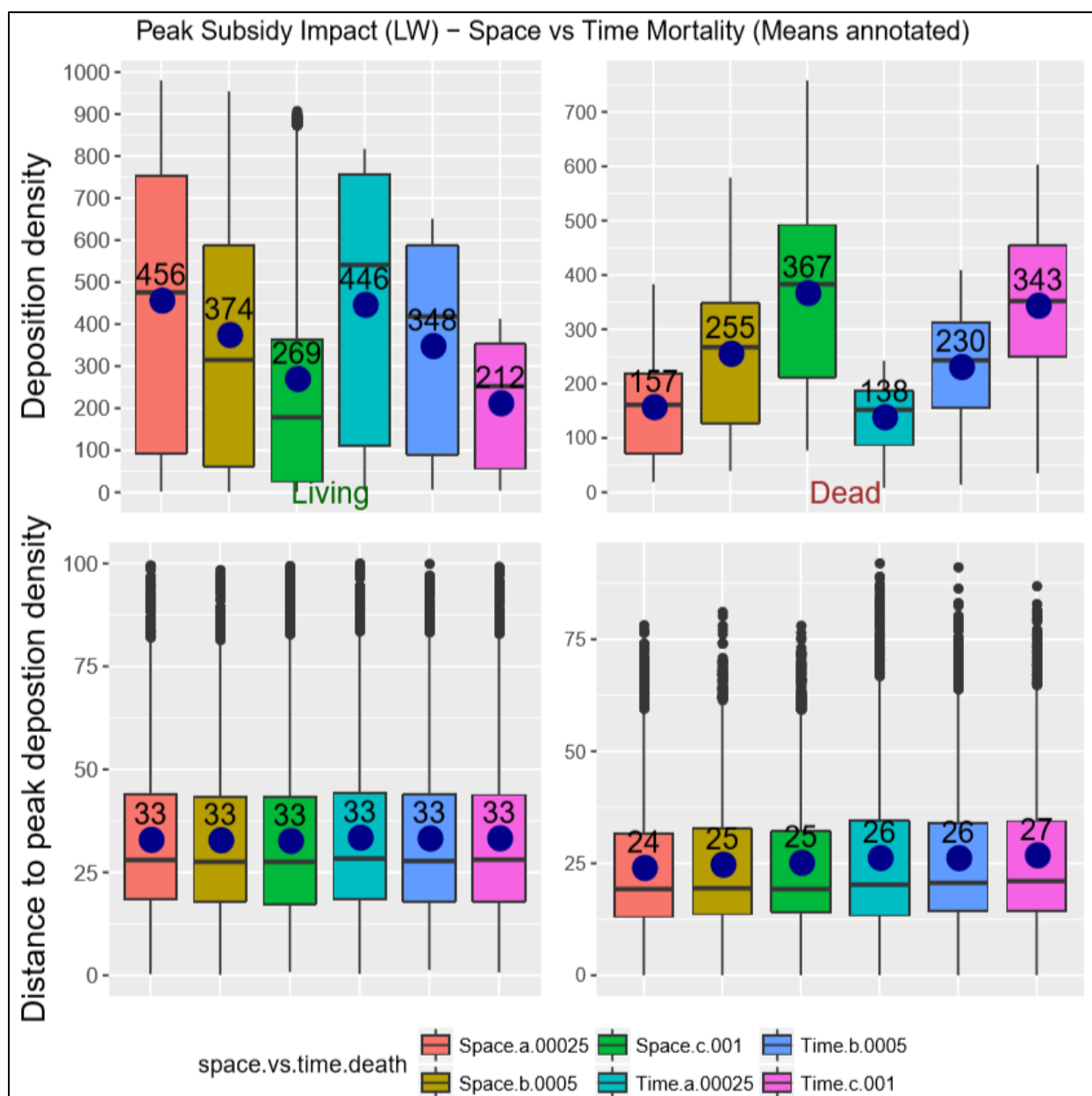


Figure 26 Space-based mortality leads to higher peak densities and peak density distances for living LW subsidies and lower impact for dead LW subsidies, compared to time-based mortality. Higher mortality results in higher subsidy impact.

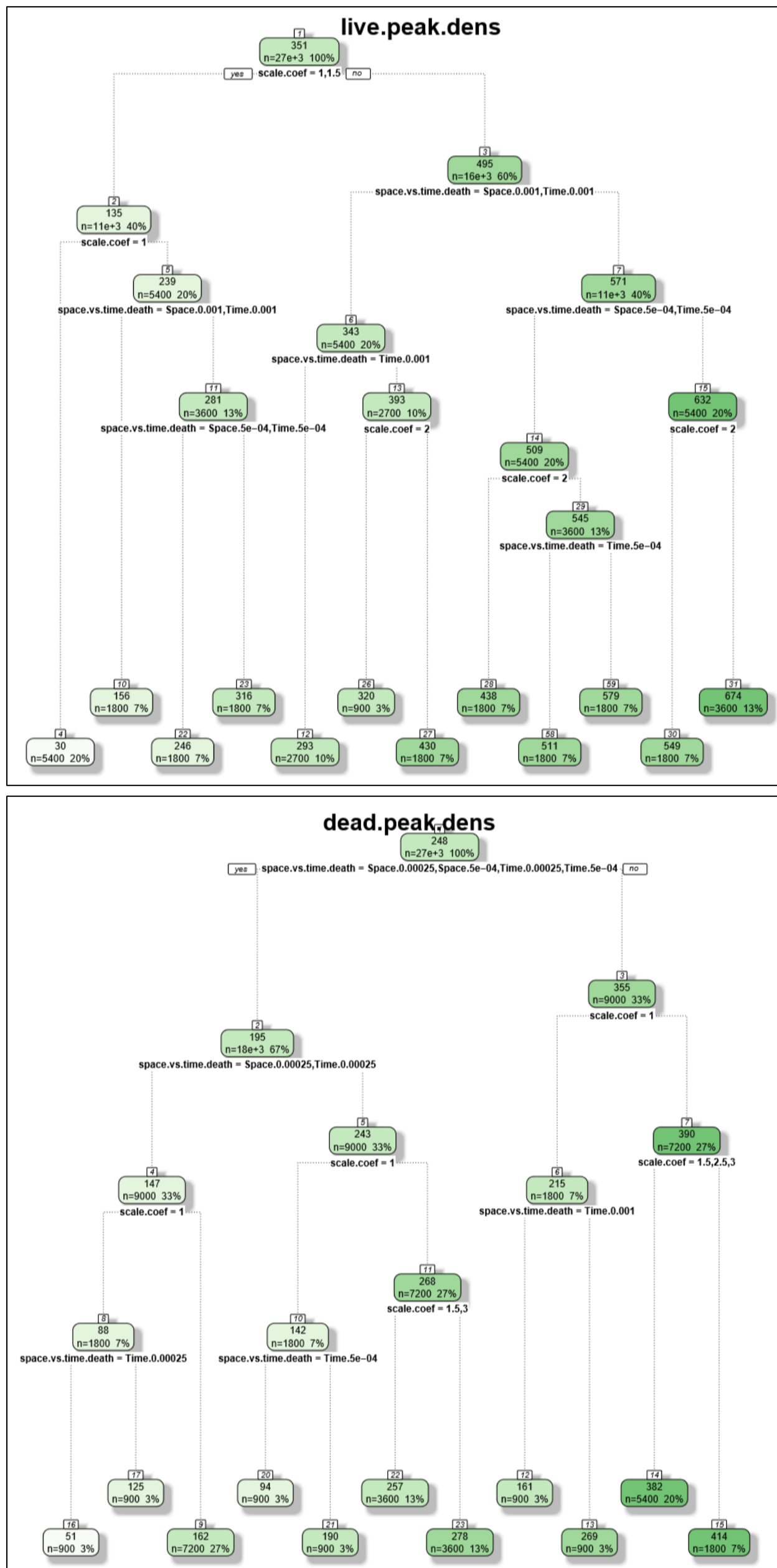


Figure 27 Lower scale-invariance movements at high space-based and time-based mortality attenuates the impact (peak density) for living LW subsidies. High space-based mortality attenuates the impact of low-scale-invariance movements and time-based mortality enhances the impact of high-scale-invariance movements of dead LW subsidies.

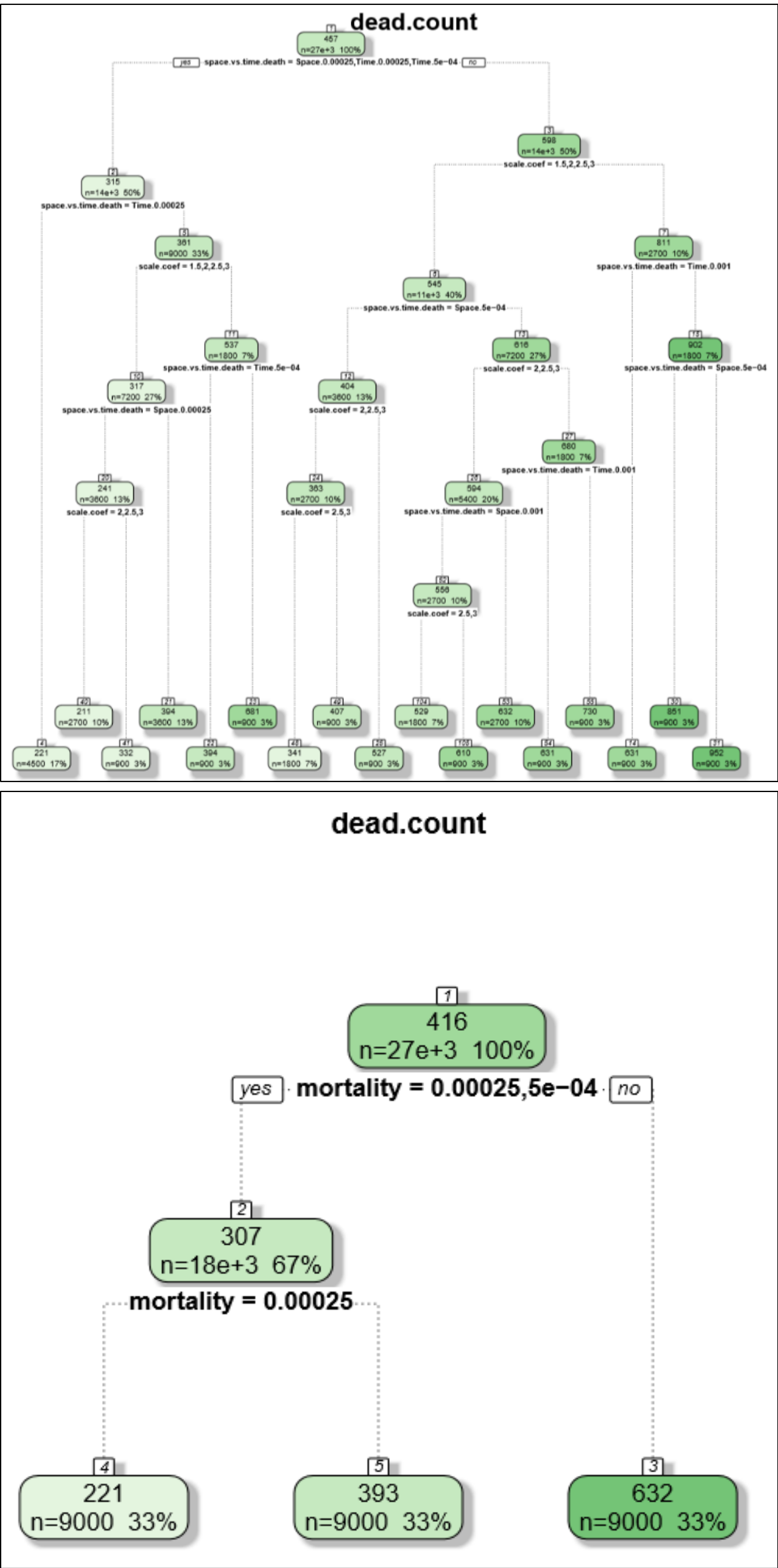


Figure 28 At high mortality, LW with more variable step lengths results in more dead subsidies in space-based than time-based scenarios. LW with less variable step lengths generate fewer dead subsidies given low space-based mortality but result in moderate numbers of nutrient subsidies at intermediate space-based mortality. In time-based mortality only scenarios, however, high mortality causes the largest numbers of dead subsidies, intermediate mortality causes intermediate numbers of dead subsidies and low mortality causes the least number of dead subsidies respectively.

Section T: Random Forest and CART Error Analysis

Table 4 *Random forest model results for impact of movement pattern variation and mortality as a function of time on subsidy distribution.* Percent increase in ANOVA mean square error (%IncMSE) and residual sum of squares (IncNodePurity (RSS)) from randomization permutations on predictor values as a measure of prediction and node split accuracy of random forest model fits. Higher %IncMSE and IncNodePurity (RSS) values indicate higher prediction capacity for a given independent variable in the model fit and for node splits in the random forest model.

| Predictor | Scale Coefficient | | Mortality Probability | | Movement Pattern | |
|--|--------------------------|-------------|------------------------------|-------------|-------------------------|-------------|
| | Living | Dead | Living | Dead | Living | Dead |
| % Increase in Mean Square Error | | | | | | |
| <i>maximum subsidy deposition distance</i> | 71.70 | 76.10 | 17.40 | 23.88 | 46.71 | 45.19 |
| <i>subsidy deposition range</i> | 74.86 | 74.09 | 15.83 | 25.01 | 46.72 | 44.35 |
| <i>peak density</i> | 77.06 | 79.16 | 81.62 | 93.52 | 53.99 | 39.69 |
| <i>distance to peak density</i> | 78.37 | 73.82 | 1.18 | 4.24 | 38.71 | 47.98 |
| <i>number of dead</i> | | 0.66 | | 97.85 | | 0.88 |
| Increase in Node Purity | | | | | | |
| <i>maximum subsidy deposition distance</i> | 6.49E+09 | 5.67E+09 | 1.02E+07 | 1.94E+07 | 7.19E+08 | 5.37E+08 |
| <i>subsidy deposition range</i> | 6.60E+09 | 5.59E+09 | 1.01E+07 | 2.00E+07 | 7.16E+08 | 5.35E+08 |
| <i>peak density</i> | 4.43E+08 | 9.37E+07 | 1.22E+08 | 1.31E+08 | 5.87E+07 | 2.71E+06 |
| <i>distance to peak density</i> | 1.86E+07 | 8.07E+05 | 5.50E+04 | 3.88E+03 | 5.03E+05 | 1.57E+05 |
| <i>number of dead</i> | | 1.13E+05 | | 5.12E+08 | | 1.30E+04 |

Table 5 *Random forest model results for impact of LW pattern variation and mortality as a function of space and time on subsidy distribution*. Percent increase in ANOVA mean square error (%IncMSE) and the change in residual sum of squares before and after a split on a predictor at a node (IncNodePurity(RSS)) from randomization permutations on predictor values as a measure of prediction and node split accuracy of random forest model fits. Higher % increase in MSE and increase in Node Purity values indicate higher prediction capacity for a given independent variable in the model fit and for node splits in the random forest model.

| <i>Predictor</i> | <i>Scale Coefficient</i> | | <i>Space-vs-Time-based Mortality Model</i> | |
|--|--------------------------|-------------|--|-------------|
| <i>Subsidy Type</i> | <i>Living</i> | <i>Dead</i> | <i>Living</i> | <i>Dead</i> |
| % Increase in Mean Square Error | | | | |
| <i>maximum subsidy deposition distance</i> | 44.85 | 47.90 | 35.78 | 22.90 |
| <i>subsidy deposition range</i> | 43.57 | 46.59 | 36.58 | 22.00 |
| <i>peak density</i> | 48.41 | 47.51 | 43.87 | 44.67 |
| <i>distance to peak density</i> | 48.61 | 46.42 | 22.10 | 25.44 |
| <i>number of dead</i> | | 44.28 | | 46.36 |
| Increase in Node Purity | | | | |
| <i>maximum subsidy deposition distance</i> | 6.21E+09 | 7.92E+09 | 4.09E+08 | 7.72E+07 |
| <i>subsidy deposition range</i> | 5.73E+09 | 7.55E+09 | 4.84E+08 | 5.03E+07 |
| <i>peak density</i> | 4.70E+08 | 3.41E+07 | 1.01E+08 | 8.56E+07 |
| <i>distance to peak density</i> | 4.90E+07 | 5.81E+05 | 2.87E+06 | 1.37E+04 |
| <i>number of dead</i> | | 9.92E+07 | | 3.17E+08 |

Table 6 %Variance explained and Misclassification error rate for all CARTs. CARTs explained over 45% of the variance with under 35% misclassification error for maximum subsidy deposition distance and range as well as peak deposition density and the number of dead subsidies. CARTs explained over 30% of the variance with under 45% misclassification error for the distance to peak subsidy density. Noise caused by the stochastic implementation of movement and mortality variation in the model construction contributes to unexplained variance and misclassification.

| <i>Predictor</i> | <i>CRW & LW with Time-based Mortality</i> | | <i>LW with Space-based vs Time-based Mortality</i> | |
|--|---|-------------|--|-------------|
| | <i>Living</i> | <i>Dead</i> | <i>Living</i> | <i>Dead</i> |
| % Variance Explained | | | | |
| <i>maximum subsidy deposition distance</i> | 62.4 | 60.9 | 77.5 | 75.7 |
| <i>subsidy deposition range</i> | 61.3 | 61.7 | 79.3 | 74.7 |
| <i>peak density</i> | 58.8 | 51.6 | 46.4 | 57.2 |
| <i>distance to peak density</i> | 41.6 | 44.7 | 34.4 | 35.1 |
| <i>number of dead</i> | | 82.5 | | 57.2 |
| Misclassification error rate (%) | | | | |
| <i>maximum subsidy deposition distance</i> | 13.4 | 13.2 | 9.6 | 12.2 |
| <i>subsidy deposition range</i> | 14.5 | 12.9 | 10.5 | 11.8 |
| <i>peak density</i> | 24.8 | 33.2 | 34.4 | 33 |
| <i>distance to peak density</i> | 38.5 | 30.1 | 42.6 | 33.8 |
| <i>number of dead</i> | | 20.7 | | 7.1 |

Section U: Model Construction - Overview, Design Concepts, Details (ODD) Protocol

1. Overview

1.1 Purpose

Ecological subsidies are consumer and resource transfers by animal movements across ecosystems and landscapes. This model is an IBM simulation to investigate how variations in animal movement patterns and mortality costs impact the distribution of active living and dead subsidies. The model quantifies the spatial extents and intensities of active subsidy distributions from a broad parameter space of animal dispersal and foraging movement patterns in a variety of mortality scenarios. It consists of a simple binary world, in which animals initiate movement from a donor ecosystem (natal habitat) and disperse into a recipient ecosystem with the stochastic chance of death during movement. Examples of ecological systems with similar dynamics include spatial subsidies from amphibian and aquatic insect dispersal and foraging movements in terrestrial landscapes adjacent to source ponds and streams. Dead individuals provide nutrients, energy, and/or prey to the recipient ecosystems possibly causing bottom-up effects, while living individuals provide a consumer subsidy with potential top-down effects.

1.2 State variables and scales

The model comprises of three hierarchical levels: individual, population and environment. The simulation environment consists of a binary landscape: donor ecosystem and recipient ecosystem. Individuals are characterized by the state variables: movement strategy, scale coefficient, mortality, space-death. Movement strategies refer to models that describe animal movement behavior. The model generates virtual animal movement patterns using one of two common movement strategies used to develop virtual animal movement trajectories: CRW (CRW) (i.e. paths determined by variation in turning angle correlation between steps) and LW (LW) (i.e. paths determined by variation in step lengths). Depending on the movement strategy, different ranges of scale-coefficient generate variation in animal movement patterns and scales. The mortality function determines the type of death that virtual animals undertaking LW movement experience (i.e. as a function of space (dependent on step-length) or time (regardless of the step-length)).

1.3 Process overview and scheduling

Based on combinations of movement rules to generate different movement behaviors, virtual animals move from the donor to the recipient ecosystem where they can die depending on the level of mortality (Figure 1 in Manuscript). 1000 virtual animals randomly orient in the donor ecosystem at the start of a simulation. Depending on the movement strategy and corresponding scaling coefficients (5 levels per movement strategy) engaged, individuals select a random step-length and (or) a turning angle from representative distributions to negotiate a move, repeating this procedure at each timestep to generate successive moves and trajectories for over 1000 equal timesteps. Based on the global mortality level and function, individuals have a random chance of dying at any timestep during movement. Some individuals live (living subsidies) and others die (dead subsidies) by the end of the simulation.

2. Design Concepts

2.1 Emergence

Different living and dead subsidy distribution (deposition) patterns emerge from variation in virtual animal movement behavior and paths over the duration of simulations. The model does not explicitly account for adaption and fitness-seeking as the aim is to quantify emergent spatial distribution patterns based on a comprehensive spectrum of ecologically plausible variation in animal movement patterns and mortality scenarios. Implicit adaptation occurs in animals drawing random step lengths and (or) random turning angles to negotiate movement based on different movement strategies and scales. Implicit fitness-seeking occurs as animals randomly die or live based on the level and type of mortality risk.

2.2 Sensing

Virtual animals are aware of their movement strategy and move accordingly. The model includes the assumption that individual virtual animals know their next move based on the turning angles and (or) step lengths they draw from representative distributions of the different movement strategies at each timestep. Individuals are aware of their state (dead or alive) and know to keep moving as long as they are alive but stop moving when they die.

2.3 Interaction

Virtual animals interact with the environment as living or dead subsidies. Individuals are aware of their state (dead or alive) and location (2D-x,y-coordinates) in the recipient ecosystem at any given timestep. The model incorporates a fully factorial combination of movement and mortality parameter levels. Each virtual animal is aware of its neighbors within an area demarcated by a prescribed model radius.

2.4 Stochasticity

Virtual animals draw random step lengths and (or) turning angles from representative distributions related to the movement strategies engaged. Virtual animal trajectories or paths therefore emanate from stochastically generated movement patterns. Each virtual animal also has a stochastic chance of death if a random number they draw from a uniform probability distribution over [0,1] at each timestep is less than the global mortality level.

2.5 Observation

Metrics of active subsidy displacement and density extracted from spatial distributions at the end of each simulation include: maximum subsidy deposition distance and range, the peak density and the distance to peak density. The maximum subsidy deposition distance is the distance from the donor-recipient ecosystem boundary to the furthest displaced subsidy. The maximum subsidy deposition range is the distance between the most and least displaced subsidies. The peak density is the greatest concentration of subsidies in the recipient ecosystem and the distance to peak density is the distance to the focal location where the peak density occurs. The model accounts for the distribution of living and dead subsidies separately.

3. Details:

The model was designed in NetLogo (version 6.0.4) software (Tisue and Wilensky, 2004; Wilensky, 1999)

3.1 Initialization

The environment is a binary-universe (donor-recipient ecosystem) that consists of a two-dimensional 1000 (vertical) by 2000 (horizontal) patch world (wrapped vertically) with a deflective vertical boundary and the origin centered at the left vertical boundary of the world (a patch is a unit space in the NetLogo world). Simulations were initialized with all individuals randomly distributed in a designated start-patch in the donor ecosystem at the origin of the world. 1000 virtual animals moved outward from the donor ecosystem into an adjacent recipient ecosystem over a duration of 1000 timesteps. Individuals could not return to the donor ecosystem once they entered the recipient ecosystem.

3.2 Inputs

Model inputs include the number of virtual animals and simulation duration (set to 1000 individuals and 1000 timesteps). Model inputs also include the movement strategy, scaling coefficient, mortality level and mortality type (Table 1 in Manuscript). The model includes a normalization constant and density-area radius (a) (See section 3.3. Sub-models). The model allows users to vary the minimum step length for LW and the mean step length for CRW (set to a length of 1 patch per step).

3.3 Sub-models

Animal movement behavior as CRW and LW consist of representative statistical distributions of step lengths and turning angle orientations. At each timestep, individuals select a random step length and turning angle from respective characteristic distributions to navigate from the donor ecosystem start-patch outward and rightward through the adjacent recipient ecosystem. CRW consists of a constant one-unit step length and a wrapped Cauchy distribution of turning angles $\theta(t)$ as:

$$\theta(t) = \theta(t-1) + 2 \tan^{-1} \left[\left(\frac{1-\alpha}{1+\alpha} \right) \tan(\pi\varphi) \right],$$

$$0 \leq \alpha \leq 1$$

$$-0.5 \leq \varphi \leq 0.5$$

$\theta(t-1)$ is a previous turning angle and φ is drawn from a uniform distribution over a delta distribution range of $[-0.5, 0.5]$ to normalize the initial direction of movement trajectories to a null orientation angle. CRW features a comprehensive range of movement patterns from sinuous to straight movement with a correlation coefficient (α) over five levels, where $\alpha \in \{0.5, 0.8, 0.9, 0.95, 0.99\}$ (Table 1 in Manuscript). CRW movement is straighter as $\alpha \rightarrow 1$ and more sinuous as $\alpha \rightarrow 0$. LW consists of a circular normal turning angle distribution over a range of $[-\pi, \pi]$, and a truncated inverse-power law distribution for the relationship between randomly drawn step lengths $P(s)$ and the minimum step length (s) as:

$$P(s) = \beta s^{-\left(\frac{1}{\mu}\right)}$$

$$1 < \mu \leq 3$$

$$0 < \beta \leq 1$$

With a minimum step length of 1, LW patterns range from high to low step length variability with scaling exponent (μ) variation across five levels, where $\mu \in \{1.0, 1.5, 2, 2.5, 3.0\}$ (Table 1 in Manuscript). LW resembles Brownian motion with near-uniform step lengths as $\mu \rightarrow 3$,

and simulates scale-invariant movement as $\mu \rightarrow 1$ with more variable step lengths. A normalization constant (β) is used to vary the frequency of occurrence of longer step lengths where $\beta \in \{0.25, 0.5, 1\}$.

The per-timestep likelihood of death varies across three levels of mortality probability (m) from low to high, where $m \in \{0.00025, 0.0005, 0.001\}$. Individuals draw a random number from a uniform distribution ($[0, 1]$) at each timestep and die and stop moving if the number drawn is lower than the assigned simulation mortality level for the simulation run. The model incorporates time-based mortality for CRW and LW as death regardless of step length, and space-based mortality for LW as death as function of step length, per unit of space travelled with each step.

Section V: Code

-Model Construction - NetLogo Version 6.0.4

-Code Tab in NetLogo

```
; Daniel Bampoh
; Simulation Experimentation Code
; January 10, 2019
```

; The following simulation experimentation code implementation explores the relevance of animal movement strategies (LW and CRW) as well as mortality risk type (temporal versus spatial) to ; their cross-ecosystem spatial distribution and impact as active vector subsidies. The world requires the user to build in buttons, sliders, monitors and plots ; in the NetLogo interface to support ; functionality of procedures – The model requires Behavior-Space mode to conduct batch simulations - see submission attachments for code with interactive interface and model use details

```
globals [ start-patch dead-count death-spots live-max-dist dead-max-dist live-mean-dist dead-
mean-dist live-range dead-range live-min-dist dead-min-dist live-peak-dens-entity
dead-peak-dens-entity live-peak-dens dead-peak-dens live-peak-dens-dist dead-peak-dens-dist ] ;
global variable settings, including (from right to left) the start patch for turtles,
; the number of dead turtles, the maximum distance for live and dead turtles, the minimum distance
for live and dead turtles, the range for live and dead turtles, the peak density
; for live and dead turtles, and the distance to peak density for live and dead turtles respectively
turtles-own [ orient reorient step ] ; assigns two variables "orient" (sets turtle direction) and "step"
(determines length of turtle's move in set direction) of turtles
```

to setup ; procedure to reset NetLogo interface once setup button is pressed after one run of various code procedures

```
ca ; clears the world
resize-world 0 2000 -500 500 ; resizes the NetLogo world to preferred specifications
set dead-count 0 ; sets the value of dead-count to zero for counting when code runs
ask patches ; code within ensuing squared brackets gives initialization commands to patches to
setup foundational world interface for running simulations
[
  ifelse (pxcor > 1) or (pycor > 0.5) or (pycor < -0.5) ; creates a unit-space natal patch that is 1
unit wide along the x-axis (starting at origin (0,0), to the left boundary of the
```

```

; world), and 0.5 units above and below the origin along the y-axis
[set pcolor green] ;sets the color of place in the world, outside of the natal patch boundary to
green
[set pcolor blue] ;sets the color of the natal patch brown
]
crt number-turtles ; creates assigned number of turtle dispersers
[
setxy ( 0 + random 1) (-0.5 + random 1) ;randomly positions the each of the thousand turtles
within and immediately around the natal patch
set heading random 360 ; sets the initial direction of the turtles to a random angle between 0 and
360 degrees
set color black ; sets the color of each of the 100 turtles to red
set size 3 ; sets the size each of the 1000 turtles to red
set shape "turtle" ; assigns a "turtle" shape to each of the 100 turtles
set start-patch patch-here ; sets the start patch for turtles
]
reset-ticks ; resets timesteps to 0 when setup button is pressed
set death-spots patches with [ pcolor = brown ] ; sets patch color at turtle death locations from
green to brown
end ; end of setup procedure

```

```

to-report turning-angle-range [ #min #max ] ; function for determining the initial turning angle
preceding any given move as a random floating number within a specified range
report #min + random-float ( #max - #min ) ; calculates and reports range of turning angles for
turtles to undertake during movement
end ; end of turning angle range calculation and reporting procedure

```

```

to-report turning-angles-dist [ #correlation ]
let turning-angle ( ( 1 - #correlation ) * tan( 180 * ( random-float 1 - 0.5 ) ) ) / ( 1 + #correlation )
report 180 - ( 2 * atan 1 turning-angle )
end
;to-report Weibull-dist [ #shape #scale #mean-step-length ] ; function defining a Weibull
distribution of correlated random walk step lengths by the mean step length, and shape
;and scale parameters of the distribution
;set mean-move-length #mean-step-length ; assigns the move length of the correlated random
walk to the mean step length of the Weibull distribution function that represents it
;let mean-step-length ( ( #shape / #scale ) * ( ( #mean-step-length / #scale ) ^ ( #shape - 1 ) ) *
exp ( ( #mean-step-length / #scale ) ^ ( #shape ) ) ) ; calculates the step
; length of the correlated random walk based on the shape and scale parameters, as well as the
mean step length of the Weibull distribution
;report mean-step-length ; produces the step length for correlated random walk
;end ; end of Weibull distribution calculation and reporting procedure for defining turtle correlated
random walk (CRW) step-length

```

```

to-report power-law-dist [ #norm-const #min-step-length #scale-exp ] ; function defining a power
law distribution for LW based on the normalization constant, the

```

```

; minimum step length and the scaling exponent of the distribution
set scale-exp #scale-exp ; sets the scaling exponent of the power law distribution function to a
randomly generated scaling exponent variable
let randomizer random-float 1
let min-step-length ( #norm-const * #min-step-length * ( 1 - randomizer ) ^ ( - 1 / #scale-exp ) ) ;
calculates the minimum step length executed by LW subsidies from
;the normalization constant, scaling exponent and minimum step length of the power law function
report min-step-length ; produces the step length for the LW
end ; end of power-law distribution for calculation and reporting procedure for defining turtle LW
step length

```

```

to write-csv [ #filename #items ] ; function that allows that creates a csv file for writing data to
using filename and items (list entry) as variables
if is-list? #items and not empty? #items ; #items is a list of the data (or headers!) to write
[ file-open #filename ; opens file for output export into file as input by given filename
set #items map quote #items ; quote non-numeric items
ifelse length #items = 1 [ file-print first #items ] ; print the items
[file-print reduce [ [?1 ?2] -> (word ?1 "," ?2) ] #items ] ; if only one item, print it
file-close ; close file once output export is complete (when code stops running)
]
end ; end of procedure for exporting essential simulation output to comma-separated-value file

```

```

to-report quote [ #thing ] ; function that allows for string formatted entries to be included in
inverted commas as listable items in the csv file so that row/column headings,
;as well as no-value numbers may be added
ifelse is-number? #thing ; queries whether reported entry is a number
[ report #thing ] ; reports number if entry is a number
[ report (word "\"" #thing "\"") ] ; reports text in quotes if entry is text so that it can be recognized
as a string
end ; end of entry formatting procedure for simulation output export to csv

```

```

to Pass-Away-Time ; procedure for determining incurred turtle mortality (time-based) per timestep
as turtles navigate world regardless of movement strategy (Levy or CRW)
let chances-time random-float 1 ; set the chances of death to a random floating-point number
between 0 and 1
if chances-time <= mortality[ ; determine if the chances of death supersede that of the fixed
mortality level
set pcolor brown ; set the color of the patch at the location of the turtle death to brown
set dead-count dead-count + 1 ; adds 1 onto the original value of dead-count parameter to track
turtle death
die ; kill the turtle
]
end ; end of the procedure for assessing turtle cumulative mortality as a function of constant
instantaneous (discrete) per-timestep hazard

```

to Pass-Away-Space ; procedure for calculating the per-step incurred turtle mortality (space-based_ per timestep as turtles navigate world regardless of movement strategy
; (Levy or CRW)

let int-step round step ; rounds the step-lengths generated for turtles to the nearest whole number and assigns them as a variable

let count-up 1 ; sets a counter, starting at 1

while ; looped set of instructions assigned to each turtle in brackets following the ensuing bracket statement, given the condition in them

[

count-up <= int-step ; while the counter is less than the number of times the rounded turtle step-lengths is divisible by 1, the statements in ensuing brackets are

;conducted

]

[

set count-up count-up + 1

let chances-space random-float 1 ; assign a random number floating point number (from a uniform-random distribution) between 0 and 1 to each turtle as its mortality

;level in each unit move

if chances-space <= mortality [; if statement on the condition that the random mortality value assigned to each turtle is below the specified mortality rate for all turtles

; and if condition is satisfied then the following statements are performed

set pcolor brown ; turn all patches upon which turtle whose randomly generated mortality exceeds the specified mortality (hazard) rate to brown

set dead-count dead-count + 1 ; increase the dead-count value by 1

die ; instructs turtle to die

]

]

end ; end of procedure for assessing turtle mortality as a function of constant per-step hazard mortality rate as function of space

to Pass-Away ; procedure to invoke either time or space-based mortality functions as when corresponding interface switch is turned on or off

ifelse space-death ; queries if switch at interface names space-death is turned on

[

Pass-Away-Space

]

[; calls the space-based mortality function to orchestrate turtle deaths as a function of constant per-step hazard rate, variable on distance from the start patch of the

;world

Pass-Away-Time ; otherwise maintains regular per-timestep mortality at constant hazard rate regardless of distance of turtles from origin of world

]

end ; ends procedure to operate switch that operates alternating between time and space-based (distance assessment) cumulative mortality on constant hazard function

to Corr-Rand-Move ; movement procedure for CRW

```

set orient turning-angles-dist corr-eff
set heading heading + one-of [-1 1] * orient ; sets the CRW turtle heading or orientation to
random angle selected from the wrapped Cauchy distribution
set step mean-move-length
fd step ;advances forward by assigned mean step length
end ; end of movement procedure for CRW

to Corr-Export-n-Plot-Live ; procedure for simulation data and plot generation for living CRW
subsidies
  let corr-max-distance max [ distance start-patch ] of turtles ; calculates the maximum turtle
distance from the start patch
  let corr-min-distance min [ distance start-patch ] of turtles ; calculates the minimum turtle
distance from the start patch
  let corr-range ( corr-max-distance - corr-min-distance ) ; calculates range of turtles (difference
between maximum and minimum turtle distance from the start patch)
  let corr-peak-density-turtle max-one-of turtles [ count turtles with [ distance myself < density-
area ] ] ; locates turtle with maximum number of surrounding turtles by
; selected surrounding radial distance or range
  let corr-peak-density [ count turtles with [ distance myself < density-area ] ] of corr-peak-density-
turtle ; counts number of turtles around located peak density turtle as
; density and determines the maximum occurrence as peak subsidy density analogue
  let corr-peak-density-distance [ distance start-patch ] of corr-peak-density-turtle ; determines
distance from the start-patch (origin of world) to the location of turtle at
; the center of the area of peak subsidy density of CRW subsidies
  if ticks <= duration ; while the number of timesteps is greater than 0 and less than the prescribed
limit (duration at interface) perform the code content in the ensuing
; square brackets
[ ; comma separated output to command center window
  output-type "CorrMaxDistance" output-type "," output-type corr-max-distance output-type ","
  output-type "CorrRange" output-type "," output-type corr-range output-type ","
  output-type "CorrPeakDensity" output-type "," output-type corr-peak-density output-type ","
  output-type "CorrDistancetoPeakDensity" output-type "," output-type corr-peak-density-
distance output-type ","
  write-csv "CorrRandWalkLiveResults.csv" ( list "Corr Max Distance" corr-max-distance
  "Corr Range" corr-range
  "Corr Peak Density" corr-peak-density
  "Corr Distance to Peak Density" corr-peak-density-distance )
; writes maximum turtle displacement, turtle displacement range, turtle peak density and
distance to peak density to a csv file dubbed CorrRandomWalk, per timestep
  set-current-plot "CRW Live Dispersal" ;sets the CRW plot to be updated with each tick
  set-current-plot-pen "corr-max-distance"
  set-plot-pen-color black ; set plot pen color to black
  plot corr-max-distance ; plots the maximum turtle distance covered by the turtles doing
CRW at each timestep or tick
  set-current-plot-pen "corr-range"
  set-plot-pen-color blue ; set plot pen color to blue

```



```

    plot corr-range ; plots the range of distances covered by turtles doing CRW at each timestep
or tick
    set-current-plot-pen "corr-peak-density-distance"
    set-plot-pen-color red ; set plot pen color to red
    plot corr-peak-density-distance ; plot the distance to peak density of turtles doing CRW at
each timestep or tick
    set-current-plot-pen "corr-peak-density"
    set-plot-pen-color green ; set the plot pen color to green
    plot corr-peak-density ; plot the peak density of turtles doing CRW at each timestep or tick
(per prescribed area)
]

```

end ; end of procedure for simulation data and plot generation for living CRW subsidies

to Corr-Export-n-Plot-Dead ; procedure for simulation data and plot generation for dead CRW subsidies

```

    set death-spots patches with [ pcolor = brown ] ; sets all patches where turtle deaths occur to the
from the color green to the color brown
    if dead-count >= 1 [ ; asks if the number of locations of turtle deaths is greater than unity
    let corr-max-dead-distance max [ distance start-patch ] of death-spots ; determines the maximum
distance among locations of turtle deaths from the world origin or
    ;start-patch
    let corr-min-dead-distance min [ distance start-patch ] of death-spots ; determines the minimum
distance among locations of turtle deaths from the world origin or
    ;start-patch
    let corr-dead-range ( corr-max-dead-distance - corr-min-dead-distance ) ; determines the range
(difference between maximum and minimum distances) among locations of turtle
    ;deaths from world origin or start-patch
    let corr-peak-dead-density-patch max-one-of death-spots [ count death-spots with [distance
myself < density-area ] ] ; determines the center patch at peak density (by
    ; density-area parameter) or patches where turtle deaths occur as locale of peak density
    let corr-peak-dead-density [count death-spots with [ distance myself < density-area ] ] of corr-
peak-dead-density-patch ; determines the number of death patches at the
    ;location of peak death patch density, based on density-area criterion
    let corr-peak-dead-density-distance [ distance start-patch ] of corr-peak-dead-density-patch ;
determines the distance from the start-patch or world origin to the location
    ; of peak death patch density
    if ticks <= duration ; while the timesteps increase
    [ ; comma separated output to command center window
    output-type "CorrMaxDeadDistance" output-type "," output-type corr-max-dead-distance
output-type ","
    output-type "CorrDeadRange" output-type "," output-type corr-dead-range output-type ","
    output-type "DeadCount" output-type "," output-type dead-count output-type ","
    output-type "CorrPeakDeadDensity" output-type "," output-type corr-peak-dead-density output-
type ","
    output-type "CorrDistancetoPeakDeadDensity" output-type "," output-type corr-peak-dead-
density-distance output-print " "

```

```

write-csv "CorrRandWalkDeadResults.csv" ( list "Corr Max Dead Distance" corr-max-dead-
distance
  "Corr Dead Range" corr-dead-range
  "Corr Peak Dead Density" corr-peak-dead-density
  "Corr Peak Dead Density Distance" corr-peak-dead-density-distance )
; writes maximum turtle displacement, turtle displacement range, turtle peak density and
distance to peak density to a csv file dubbed CorrRandomWalk, per timestep
; for dead turtles
set-current-plot "CRW Dead Dispersal"
set-current-plot-pen "corr-max-dead-distance"
set-plot-pen-color black ; set plot pen color to black
plot corr-max-dead-distance ; plots the maximum turtle distance covered by the turtles doing
CRW at each timestep or tick
set-current-plot-pen "corr-dead-range"
set-plot-pen-color blue ; set plot pen color to blue
plot corr-dead-range ; plots the range of distances covered by turtles doing CRW at each
timestep or tick
set-current-plot-pen "corr-peak-dead-density-distance"
set-plot-pen-color red ; set plot pen color to red
plot corr-peak-dead-density-distance ; plot the distance to peak density of turtles doing CRW
at each timestep or tick
set-current-plot-pen "corr-peak-dead-density"
set-plot-pen-color green ; set the plot pen color to green
plot corr-peak-dead-density ; plot the peak density of turtles doing CRW at each timestep or
tick (per prescribed area)
set-current-plot-pen "dead-count"
set-plot-pen-color grey ; sets the plot pen color for the count of the number of dead turtles to
grey
plot dead-count ; plots the count of the number of dead turtles
]
]
end ; end of procedure for simulation data and plot generation for dead CRW subsidies

to Correlated-Random-Walk ; the "move" procedure to be executed by a turtle performing CRW
set move-strat "CRW"
ask turtles [
  Corr-Rand-Move ; execute CRW movement strategy for turtles
  Pass-Away ; call mortality function as needed based on state of interface switch (on, time-based
or off, space (distance)-based cumulative mortality assessed on constant
;per-step hazard rate))
]
Corr-Export-n-Plot-Live ; outputs and plots results subsidy distribution for living turtles
executing CRW movement strategy
Corr-Export-n-Plot-Dead ; outputs and plots results subsidy distribution for dead turtles
executing CRW movement strategy
tick ; proceed a timestep

```

```

if ticks = duration ; queries if the number of timesteps exceeds the assigned duration
[
  let corr-simfile-label random-float 1.0 ; creates a random number to assign to output file names
  ask turtles [ ; plots living CRW dispersers locations and distances
    set-current-plot "CRW Disperser locations"
    set-current-plot-pen "corr-live-location"
    set-plot-pen-color green
    plotxy xcor ycor ; plots x and y location of living CRW dispersers relative to origin of world
    set-current-plot "CRW Disperser Distances"
    set-current-plot-pen "corr-live-distance"
    set-plot-pen-color blue
    plot distance start-patch ; plots distance of living CRW dispersers from start-patch
  ]
  ask death-spots [ ; plots dead CRW dispersers locations and distances
    set-current-plot "CRW Disperser Locations"
    set-current-plot-pen "corr-dead-location"
    set-plot-pen-color brown
    plotxy pxcor pycor ; plots x and y locations of dead CRW dispersers relative to origin of world
    set-current-plot "CRW Disperser Distances"
    set-current-plot-pen "corr-dead-distance"
    set-plot-pen-color red
    plot distance start-patch ; plots distance of dead CRW dispersers from start-patch
  ]
  export-output (word "corr-output" corr-simfile-label ".csv") ; exports output csv file
  export-world (word "corr-input" corr-simfile-label ".csv") ; exports world/ parameter
initialization to csv file
  export-interface (word "corr-interface" corr-simfile-label ".png") ; exports graphic of interface
as .png file
  export-all-plots (word "corr-plots " corr-simfile-label ".csv") ; exports plot data to csv file
  stop ; if so, stop the simulation run
]
end ; end CRW turtle procedure

to Levy-Flight-Move ; movement procedure for LW
  set orient turning-angle-range 0 360 ; sets the turning angle orientation or direction of LW for
each turtle at the start of each move to a randomly generated
  ; angle between 0 and 360 degrees
  set heading heading + one-of [-1 1] * orient ; set direction of movement of turtle
  set step power-law-dist norm-const min-move-length scale-exp ; derives the LW step length
from the power law distribution with a normalization constant
  ; of 0.5, a minimum step length of 0.5 and a scaling exponent of 3
  fd step ; moves the turtle forward by the step length described above, as executed in a LW
end ; end of movement procedure for LW subsidies

to Levy-Export-n-Plot-Live ; procedure for simulation data and plot generation for living LW
subsidies

```

```

let levy-max-distance max [ distance start-patch ] of turtles ; calculates the maximum turtle
distance from the start patch
let levy-min-distance min [ distance start-patch ] of turtles ; calculates the minimum turtle
distance from the start patch
let levy-range ( levy-max-distance - levy-min-distance ) ; determines range of levy-walk turtles
let levy-peak-density-turtle max-one-of turtles [ count turtles with [ distance myself < density-
area ] ] ; locate turtle with greatest number of surrounding turtles within
;prescribed area or region
let levy-peak-density [ count turtles with [ distance myself < density-area ] ] of levy-peak-
density-turtle ; determines the number of surrounding turtles for the located
;turtle with the highest number of turtles around it as the peak subsidy density analogue
let levy-peak-density-distance [ distance start-patch ] of levy-peak-density-turtle ; determines
the distance from the origin of the world to the location of the turtle at
;the center of peak subsidy density of LW subsidies
if ticks <= duration ; while the number of timesteps is greater than 0 and less than the prescribed
limit (duration at interface) perform the code content in the ensuing
;square brackets
[ ; comma separated output to command center window
output-type "LevyMaxDistance" output-type "," output-type levy-max-distance output-type ","
output-type "LevyRange" output-type "," output-type levy-range output-type ","
output-type "LevyPeakDensity" output-type "," output-type levy-peak-density output-type ","
output-type "LevyDistancetoPeakDensity" output-type "," output-type levy-peak-density-
distance output-type ","
write-csv "LevyWalkLiveResults.csv" ( list "Levy Max Distance" levy-max-distance
"Levy Range" levy-range
"Levy Peak Density" levy-peak-density
"Levy Distance to Peak Density" levy-peak-density-distance )
; writes maximum turtle displacement, turtle displacement range, turtle peak density and
distance to peak density to a csv file dubbed LevyWalk, per timestep
set-current-plot "LW Live Dispersal" ; sets the LW plot to be updated with each tick
set-current-plot-pen "levy-max-distance"
set-plot-pen-color black ; sets the plot pen color to black
plot levy-max-distance ; plots the maximum turtle distance covered by the turtles doing LW
at each timestep or tick
set-current-plot-pen "levy-range"
set-plot-pen-color blue ; sets the plot pen color to blue
plot levy-range ; plots the range of turtle LW subsidies at each timestep or tick
set-current-plot-pen "levy-peak-density-distance"
set-plot-pen-color red ; sets the plot pen color to red
plot levy-peak-density-distance ; plots the distance to peak subsidy density of LW subsidies
at each timestep
set-current-plot-pen "levy-peak-density"
set-plot-pen-color green ; sets the plot pen color to green
plot levy-peak-density ; plots the peak subsidy density of turtle LW subsidies at each timestep
or tick (per prescribed area)
]

```

end ; end of procedure for simulation data and plot generation for living LW subsidies

to Levy-Export-n-Plot-Dead ; procedure for simulation data and plot generation for dead LW subsidies

set death-spots patches with [pcolor = brown] ; sets patches where turtle deaths occur from the color green to the color brown

if dead-count >= 1 [; asks if the number of locations of turtle deaths is greater than unity

let levy-max-dead-distance max [distance start-patch] of death-spots ; determines the maximum distance among locations of turtle deaths from the world origin or

; start-patch

let levy-min-dead-distance min [distance start-patch] of death-spots ; determines the minimum distance among locations of turtle deaths from the world origin or

;start-patch

let levy-dead-range (levy-max-dead-distance - levy-min-dead-distance) ; determines the range (difference between maximum and minimum distances) among locations of turtle

;deaths from world origin or start-patch

let levy-peak-dead-density-patch max-one-of death-spots [count death-spots with [distance myself < density-area]] ; determines the center patch at peak density (by

; density-area parameter) or patches where turtle deaths occur as locale of peak density

let levy-peak-dead-density [count death-spots with [distance myself < density-area]] of levy-peak-dead-density-patch ; determines the number of death patches at the

; location of peak death patch density, based on density-area criterion

let levy-peak-dead-density-distance [distance start-patch] of levy-peak-dead-density-patch ; determines the distance from the start-patch or world origin to the location

; of peak death patch density

if ticks <= duration ; while timesteps increase but remain beneath prescribed duration limit

[; comma separated output to command center window

output-type "LevyMaxDeadDistance" output-type "," output-type levy-max-dead-distance output-type ","

output-type "LevyDeadRange" output-type "," output-type levy-dead-range output-type ","

output-type "LevyDeadCount" output-type dead-count output-type ","

output-type "LevyPeakDeadDensity" output-type "," output-type levy-peak-dead-density output-type ","

output-type "LevyDistancetoPeakDeadDensity" output-type "," output-type levy-peak-dead-density-distance output-print " "

write-csv "LevyWalkDeadResults.csv" (list "Levy Max Dead Distance" levy-max-dead-distance

"Levy Dead Range" levy-dead-range

"Levy Peak Dead Density" levy-peak-dead-density

"Levy Peak Dead Density Distance" levy-peak-dead-density-distance)

; writes maximum turtle displacement, turtle displacement range, turtle peak density and distance to peak density to a csv file dubbed CorrRandomWalk, per timestep for

; dead turtles

set-current-plot "LW Dead Dispersal" ; sets the LW plot to be updated with each tick

set-current-plot-pen "levy-max-dead-distance"

set-plot-pen-color black ; set plot pen color to black

```

    plot levy-max-dead-distance ; plots the maximum turtle distance covered by the turtles doing
    CRW at each timestep or tick
    set-current-plot-pen "levy-dead-range"
    set-plot-pen-color blue ; set plot pen color to blue
    plot levy-dead-range ; plots the range of distances covered by turtles doing CRW at each
    timestep or tick
    set-current-plot-pen "levy-peak-dead-density-distance"
    set-plot-pen-color red ; set plot pen color to red
    plot levy-peak-dead-density-distance ; plot the distance to peak density of turtles doing CRW
    at each timestep or tick
    set-current-plot-pen "levy-peak-dead-density"
    set-plot-pen-color green ; set the plot pen color to green
    plot levy-peak-dead-density ; plot the peak density of turtles doing CRW at each timestep or
    tick (per prescribed area)
    set-current-plot-pen "dead-count"
    set-plot-pen-color grey ; sets the plot pen color for the count of the number of dead turtles to
    grey
    plot dead-count ; plots the count of the number of dead turtles
  ]
]
end ; end of procedure for simulation data and plot generation for dead LW subsidies

```

to Levy-Walk ; the "move" procedure to be executed by turtles performing the LW

```

  set move-strat "LW"
  ask turtles [
    Levy-Flight-Move ; execute LW movement strategy for turtles
    Pass-Away ; call mortality function as needed based on state of interface switch (on, time-based
    or off, space (distance)-based cumulative mortality assessed on constant
    ;per-step hazard rate))
  ]
  Levy-Export-n-Plot-Live ; outputs and plots results of subsidy distribution for living turtles LW
  movement strategy
  Levy-Export-n-Plot-Dead ; outputs and plots results of subsidy distribution for living turtles
  executing LW movement strategy
  tick ; proceed a timestep
  if ticks = duration ; queries if the number of timesteps exceeds the assigned duration
  [
    let levy-simfile-label random-float 1.0 ; assigns export output file floating-point number
    identifiers
    ask turtles [ ; plots locations and distances of living LW dispersers
      set-current-plot "LW Disperser locations"
      set-current-plot-pen "levy-live-location"
      set-plot-pen-color green
      plotxy xcor ycor ; plots x and y locations of living LW dispersers relative to the origin of the
      world
      set-current-plot "LW Disperser Distances"
    ]
  ]

```

```

set-current-plot-pen "levy-live-distance"
set-plot-pen-color blue
plot distance start-patch ; plots distances of living LW dispersers from the start-patch
]
ask death-spots [ ; plots locations and distances of dead LW dispersers
set-current-plot "LW Disperser Locations"
set-current-plot-pen "levy-dead-location"
set-plot-pen-color brown
plotxy pxcor pycor ; plots x and y locations of dead LW dispersers relative to the origin of the
world
set-current-plot "LW Disperser Distances"
set-current-plot-pen "levy-dead-distance"
set-plot-pen-color red
plot distance start-patch ; plots distances of dead LW dispersers from the start-patch
]
export-output (word "levy-output" levy-simfile-label ".csv") ; exports output to csv file
export-world (word "levy-input" levy-simfile-label ".csv") ; exports world/ initialization
parameters to csv file
export-interface (word "levy-interface" levy-simfile-label ".png") ; exports interface graphic
as .png file
export-all-plots (word "levy-plots " levy-simfile-label ".csv") ; exports plot data to csv file
stop ;if so, stop the simulation run
]
end ; end LW turtle procedure

```

```

to output ; output procedure for reporting results
set live-max-dist max [ distance start-patch ] of turtles ; calculates the maximum turtle distance
from the start patch
set live-min-dist min [ distance start-patch ] of turtles ; calculates the minimum turtle distance
from the start patch
set live-mean-dist mean [ distance start-patch ] of turtles ; calculates the mean turtle distance from
the start patch
set live-range ( live-max-dist - live-min-dist ) ; calculates range of turtles (difference between
maximum and minimum turtle distance from the start patches)
set live-peak-dens-entity max-one-of turtles [ count turtles with [ distance myself < density-
area ] ] ; locates turtle with maximum number of surrounding turtles by selected
; surrounding radial distance or range
set live-peak-dens [ count turtles with [ distance myself < density-area ] ] of live-peak-dens-entity ;
counts number of turtles around located peak density turtle as density
; and determines the maximum occurrence as peak subsidy density analogue
set live-peak-dens-dist [ distance start-patch ] of live-peak-dens-entity ; determines distance from
the start-patch (origin of world) to the location of turtle at the center
; of the area of peak subsidy density of CRW subsidies
set death-spots patches with [ pcolor = brown ]
if count death-spots >= 1 [

```

```

    set dead-max-dist max [ distance start-patch ] of death-spots ; calculates the maximum turtle
distance from the start patch
    set dead-min-dist min [ distance start-patch ] of death-spots ; calculates the minimum turtle
distance from the start patch
    set dead-mean-dist mean [ distance start-patch ] of death-spots ; calculates the mean turtle
distance from the start patch
    set dead-range ( dead-max-dist - dead-min-dist ) ; calculates range of turtles (difference between
maximum and minimum turtle distance from the start patch)
    set dead-peak-dens-entity max-one-of death-spots [ count death-spots with [ distance myself <
density-area ] ] ; locates turtle with maximum number of surrounding turtles by
    ; selected surrounding radial distance or range
    set dead-peak-dens [ count death-spots with [ distance myself < density-area ] ] of dead-peak-
dens-entity ; counts number of turtles around located peak density turtle as
    ; density and determines the maximum occurrence as peak subsidy density analogue
    set dead-peak-dens-dist [ distance start-patch ] of dead-peak-dens-entity ; determines distance
from the start-patch (origin of world) to the location of turtle at the center
    ; of the area of peak subsidy density of CRW subsidies
]
end ; end of results reporting procedure

```

```

to move-turtles ; procedure for batch implementation of both movement strategies in sequence
    if move-strat = "CRW" [ ; checks condition that movement strategy chooser is set to CRW
conditions for simulation
        Corr-Rand-Move ; execute CRW movement strategy for turtles
    ]
    if move-strat = "LW" [ ; Checks condition that movement strategy chooser is set to LW conditions
for simulation
        Levy-Flight-Move ; calls the simplified LW movement strategy procedure for batch
experimentation
    ]
end ; end of sequential batch experimentation implementation of LW procedure

```

```

to go ; procedure performs batch simulations of movement strategies in sequence
    if ticks <= duration [ ; checks the condition that the time passed is less than allotted simulation
duration
        ask turtles [
            move-turtles ; moves turtles according to different movement strategies for duration in
sequence
            Pass-Away ; call mortality function as needed based on state of interface switch (on, time-
based or off, space (distance)-based cumulative mortality assessed on constant
            ;per-step hazard
        ]
        output ; outputs values for reporting
        tick ; a progression of unit timestep in simulation run
    ]
    backup-sim-output ; backs up all simulation results to working directory

```


end ; end of batch simulations

to do-plots ; procedure that runs plots of results of results in sequence

if move-strat = "CRW" [; checks the condition that the current movement strategy choice for simulation is a CRW

Corr-Export-n-Plot-Live ; outputs and plots results subsidy distribution for living turtles executing CRW movement strategy

Corr-Export-n-Plot-Dead ; outputs and plots results subsidy distribution for dead turtles executing CRW movement strategy

]

if move-strat = "LW" [; checks condition that current movement strategy choice for simulation is LW

Levy-Export-n-Plot-Live ; outputs and plots results of subsidy distribution for living turtles LW movement strategy

Levy-Export-n-Plot-Dead ; outputs and plots results of subsidy distribution for living turtles executing LW movement strategy

]

end ; end of plotting procedure

to backup-sim-output ; procedure that backs up all simulation data including inputs and outputs

if ticks = duration [; queries if the number of timesteps exceeds the assigned duration

let simfile-label random-float 1.0 ; creates a random number to assign to output file names

if move-strat = "CRW"[; checks the condition that the current movement strategy choice for simulation is a CRW

ask turtles [; plots locations and distances of living CRW dispersers

set-current-plot "CRW Disperser locations"

set-current-plot-pen "corr-live-location"

set-plot-pen-color green

plotxy xcor ycor ; plots x and y locations of living CRW dispersers relative to the origin of the world

set-current-plot "CRW Disperser Distances"

set-current-plot-pen "corr-live-distance"

set-plot-pen-color blue

plot distance start-patch ; plots the distances of living CRW dispersers from the start-patch

]

ask death-spots [; plots location and distances of dead CRW dispersers

set-current-plot "CRW Disperser Locations"

set-current-plot-pen "corr-dead-location"

set-plot-pen-color brown

plotxy pxcor pycor ; plots x and y locations of dead CRW dispersers relative to the origin of the world

set-current-plot "CRW Disperser Distances"

set-current-plot-pen "corr-dead-distance"

set-plot-pen-color red

plot distance start-patch ; plots the distances of dead CRW dispersers from the start-patch

]

```

    export-output (word "corr-output" simfile-label ".csv") ; exports output csv file
    export-world (word "corr-input" simfile-label ".csv") ; exports world/ parameter
initialization to csv file
    export-interface (word "corr-interface" simfile-label ".png") ; exports graphic of interface
as .png file
    export-all-plots (word "corr-plots " simfile-label ".csv") ; exports plot data to csv file
]
if move-strat = "LW"[ ; checks the condition that the current movement strategy choice for
simulation is a CRW
ask turtles [ ; plots the locations and distances of living LW dispersers
set-current-plot "LW Disperser locations"
set-current-plot-pen "levy-live-location"
set-plot-pen-color green
plotxy xcor ycor ; plots the x and y locations of living LW dispersers from the origin of the
world
set-current-plot "LW Disperser Distances"
set-current-plot-pen "levy-live-distance"
set-plot-pen-color blue
plot distance start-patch ; plots the distances of living LW dispersers from the start-patch
]
ask death-spots [ ; plots the locations and distances of dead LW dispersers
set-current-plot "LW Disperser Locations"
set-current-plot-pen "levy-dead-location"
set-plot-pen-color brown
plotxy pxcor pycor ; plots the x and y locations of dead LW dispersers relative to the origin of
the world
set-current-plot "LW Disperser Distances"
set-current-plot-pen "levy-dead-distance"
set-plot-pen-color red
plot distance start-patch ; plots the distances of dead LW dispersers from the start-patch
]
    export-output (word "levy-output" simfile-label ".csv") ; exports output to csv file
    export-world (word "levy-input" simfile-label ".csv") ; exports world/ initialization
parameters to csv file
    export-interface (word "levy-interface" simfile-label ".png") ; exports interface graphic
as .png file
    export-all-plots (word "levy-plots " simfile-label ".csv") ; exports plot data to csv file
]
]
end

```

-Model Use:

-Info Tab in NetLogo

What is it?

AniMovSub is a spatiotemporally explicit individual-based model that simulates the effect of animal movement and mortality on animal-transported (active) subsidy distribution. The model simulates animal movement patterns and mortality risks and extracts information about emergent spatial distributions. The model computes displacement and density metrics of spatial distributions of a population of virtual animals moving from a donor ecosystem to a recipient ecosystem.

How it works

Animals are randomly oriented from the central location (donor ecosystem) at the left vertical boundary of the world and move outward and rightward into the adjacent region (recipient ecosystem). Users can simulate movement and mortality for up to 1000 virtual animals over a period of up to 1000 timesteps. The model also allows the user to choose between correlated random walk (CRW) and Lévy walk (LW) movement patterns and different mortality risk levels. Users can change the straightness of correlated random walk movement patterns by adjusting the correlation coefficient and alter the degree of step length variability of Lévy walk movement patterns by adjusting the scaling exponent over a comprehensive range of options for each movement type. Users can also adjust the global chance of death for moving animals in the model. The plots show how living and dead subsidy distribution metrics change with each timestep for each movement type. Subsidy distribution metric include the number of dead subsidies, the maximum subsidy deposition distance (furthest displaced subsidy) and range (distance between furthest and least displaced subsidy), the peak density (greatest density of subsidies) and distance to peak density (distance to the location where the greatest density of subsidies occurs).

How to use it

Specify model inputs (adjust corresponding sliders, switches or choosers - in permitted [ranges]): Number of dispersers (number-turtles - [0,1000]), duration (duration - [0,1000]), Movement strategy (move-strat - [CRW|LW]), correlation coefficient to vary CRW turning angles (corr-eff - [0:1]), scaling exponent to vary LW step lengths (scale-exp - [0,1]), mean step length for CRW (mean-move-length - [1:5]), minimum step length for LW [min-move-length - [0,1]), mortality level/probability (mortality - [0:0.002]), death as a function of space of time (space-death - [on|off]), radius of patches circumscribing area for peak density estimation (density-area - [0:100]), normalization constant to vary LW frequency of longer step length (norm-const - [0:1]). Upon making desired adjustments, click the "CRW" or "LW" button for dispersers to move according to either CRW or LW from donor ecosystem start patch (brown patch) at center of left vertical boundary of world into adjacent recipient ecosystem (green area). Alternatively, click the "Go" button for dispersers to execute both movement patterns one after the other.

Things to notice

First thing to notice is the movement of dispersers from the donor ecosystem or patch into the adjacent recipient ecosystem of the world as the simulation progresses. Note that different parameter combinations result in different virtual animal movement and distribution patterns, particularly depending on movement strategy and scaling coefficients. Note that when dispersers return into the world at the opposite edges if or when they reach either horizontal edge of the world but bounce off vertical edges. Note that patches where dispersers die turn red, marking the location of death for the duration of the simulation. Dead dispersers no longer move. Notice

updating plots CRW ("Corr-") and LW ("Levy-") dispersal subsidy distribution metrics: maximum dispersal distance ("-max-distance") and range ("-range") as well peak density ("-peak-density") and distance to peak density (peak-density-distance), for living ("-live-") and dead ("-dead-") subsidies respectively. Also notice plots for the locations ("-location") and total distances traveled (-distance) by CRW ("Corr-") and LW ("Levy-") for all living ("-live-") and dead ("-dead-") at the end of simulation duration. Also notice the "dead-count" monitor that updates the number of dead subsidies as the simulation progresses. Observe trends for subsidy distribution metrics in plots and monitors. See "CorrRandomWalk" and "LevyWalk" files in working directory for full results of subsidy distribution metrics by CRW and LW respectively.

Things to try

The model is most useful for performing batch simulations in behavior space (Ctrl+Shift+B). Users can edit a comprehensive list of all model variables to include specific levels of each for fully factorial batch simulations with data output to the working directory. Move scaling coefficient sliders CRW ("corr-eff") and LW ("scale-exp") from left to right and observe how virtual animal movement and subsidy distribution patterns change. Move mortality slider from left to right and observe changes in the number and distribution of dead virtual animals (red patches) and black virtual animals living turtles (black virtual animals), as well as the dead-count monitor. Also observe trends in plots. For LW, switch space-death on or off and observe how the numbers of distribution of dead virtual animals (red patches) changes between the two states.

Extending the model

Users can use a Weibull distribution to generate dynamic variation in CRW step lengths around mean-move-lengths instead of using constant step lengths. See commented block of corresponding code and remove comment marks (i.e. semi colon) to experiment. Users may also use other step length and turning angle distributions, run simulations and observe how living and dead subsidy distribution patterns respond. Users can also change world-wrapping or torus conditions and observe corresponding changes in subsidy distribution patterns. The same can be done with the size of the world or the respective donor and recipient ecosystem sizes. Change the range of the turning angle range for LW in the code tab, run simulations and observe how resulting subsidy distribution patterns respond.

NETLOGO FEATURES

The backup-sim-output procedure uses the "export" function in NetLogo to export pictures and details of the world and interface as well as all output and plots at the end of the simulation to the user working directory for troubleshooting, error checking and proofing purposes.

Related models

Related models include:

- Jackson, HB, Fahrig L. What size is a biologically relevant landscape? Landscape Ecology.
- Wilensky, U. (1999). NetLogo. <http://ccl.northwestern.edu/netlogo/>. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.

Credits and references

-Earl, J. E., & Zollner, P. A. (2017). Advancing research on animal-transported subsidies by integrating animal movement and ecosystem modelling. *Journal of Animal Ecology*, 86(5), 987-997.

-Earl, J. E., & Zollner, P. A. (2014). Effects of animal movement strategies and costs on the distribution of active subsidies across simple landscapes. *Ecological Modelling*, 283, 45-52.

Data Processing R version 3.5.1

```
##### Daniel Bampoh #####
```

```
##### Data Preparation Code - Prepare raw data from NetLogo batch simulation in behavior space #####
```

```
### set working drive for analysis code updates and output
setwd("/:Working_Directory")
```

```
# create a list of files for which data is to be collated into a single file
```

```
file_list
```

```
list.files(path="C:/Users/chipmunk/Desktop/DBamp_Diss_Research/DissCh1SimsQ1",
           pattern=".txt")
```

```
file_list # report file list
```

```
# collate data in all files in folder location
```

```
for (file in file_list){
```

```
  # if the merged dataset doesn't exist, create it
```

```
  if (!exists("dataset")){
```

```
    dataset <- read.csv(file, skip = 6, header=TRUE, sep=",")
```

```
  }
```

```
  # if the merged dataset does exist, append to it
```

```
  if (exists("dataset")){
```

```
    temp_dataset <- read.csv(file, skip = 6, header=TRUE, sep=",")
```

```
    dataset<-rbind(dataset, temp_dataset)
```

```
    rm(temp_dataset)
```

```
  }
```

```
}
```

```
dataset
```

```
names(dataset)
```

```
dim(dataset)
```

```
# write raw dataset to working directory
```

```
write.csv(file= "RawDataSetNew.txt", x=dataset, row.names = F)
```

```
# select every 1000th step
```

```
new.dataset <- dataset[dataset$X.step == 1000,]
```

<-

```

new.dataset
names(new.dataset)
dim(new.dataset)

# remove unnecessary information for analysis
final.dataset <- subset(new.dataset, select=c(X.run.number., duration, min.move.length,
                                             number.turtles, mean.move.length,X.step.))
final.dataset <- as.data.frame(sapply(final.dataset, function(x) gsub("\\", "", x)))
names(final.dataset)
dim(final.dataset)
str(final.dataset)
summary(final.dataset)

# write final dataset to working directory
write.csv(file= "WorkingDataSet.txt", x=final.dataset, row.names = F)
AniMovSubDat <- read.csv("WorkingDataSet.txt", header = TRUE, sep = ",")
AniMovSubDat
names(AniMovSubDat)
dim(AniMovSubDat)
str(AniMovSubDat)
summary(AniMovSubDat)

# order data by movement pattern and mortality variables, then save to working directory
AniMovSubDat <- AniMovSubDat[with(AniMovSubDat, order(move.strat, mortality)),]
AniMovSubDat
write.csv(file = "SortedWorkingDataSet.txt", x=AniMovSubDat, row.names = F)
AniMovSubDatMain <- read.csv("SortedWorkingDataSet.txt", header = TRUE, sep = ",")
AniMovSubDatMain
names(AniMovSubDatMain)
dim(AniMovSubDatMain)
str(AniMovSubDatMain)
summary(AniMovSubDatMain)

# select CRW data and save as separate file to working directory
CRWAniMovSubDatMain <- AniMovSubDatMain[AniMovSubDatMain$move.strat == "CRW",]
CRWAniMovSubDatMain <- subset(CRWAniMovSubDatMain, select = -c(scale.exponent))
names(CRWAniMovSubDatMain)
dim(CRWAniMovSubDatMain)
str(CRWAniMovSubDatMain)
summary(CRWAniMovSubDatMain)
write.csv(file= "CRWDataSet.txt", x=CRWAniMovSubDatMain, row.names = F)

# select LW data and save as separate file to working directory
LWAniMovSubDatMain <- AniMovSubDatMain[AniMovSubDatMain$move.strat == "LW",]
LWAniMovSubDatMain <- subset(LWAniMovSubDatMain, select = -c(corr.eff))
names(LWAniMovSubDatMain)

```

```

dim(LWAniMovSubDatMain)
str(LWAniMovSubDatMain)
summary(LWAniMovSubDatMain)
write.csv(file= "LWDataSet.txt", x=LWAniMovSubDatMain, row.names = F)

##### Data Analysis – CRW and LW given Time-based mortality #####
# print all results to text file
sink("Results.txt", append=TRUE, split=TRUE)

### install r packages for random forest and classification analysis
install.packages("randomForest")
install.packages("rpart")
install.packages("rpart.plot")
install.packages("sandwich")
install.packages("party")
install.packages("rattle")
install.packages("ggplot2")
install.packages("gridExtra")

### load package libraries
library(randomForest)
library(sandwich)
library(party)
library(rpart)
library(rpart.plot)
library(RGtk2)
library(rattle)
library(RColorBrewer)
library(ggplot2)
library(gridExtra)

### combine CRW and LW datasets, adjoining respective scale coefficient variables into single
scale coefficient column for analysis
# read in separate CRW data file
CRWAniMovSubDat <- read.csv("CRWDataSet.txt", header = TRUE, sep = ",")
CRWAniMovSubDat
  names(CRWAniMovSubDat)
  dim(CRWAniMovSubDat)
  str(CRWAniMovSubDat)
  summary(CRWAniMovSubDat)

# read in separate LW data file
LWAniMovSubDat <- read.csv("LWDataSet.txt", header = TRUE, sep = ",")
LWAniMovSubDat
  names(LWAniMovSubDat)

```

```

dim(LWAniMovSubDat)
str(LWAniMovSubDat)
summary(LWAniMovSubDat)

# combine CRW and LW files into single file with shared scale coefficient variable column
names(CRWAniMovSubDat)[1] <- "scale.coef"
names(LWAniMovSubDat)[1] <- "scale.coef"
AniMoveSubDatMainRF <- rbind(CRWAniMovSubDat, LWAniMovSubDat)
names(AniMoveSubDatMainRF)
dim(AniMoveSubDatMainRF)
str(AniMoveSubDatMainRF)
summary(AniMoveSubDatMainRF)

# write output to single csv file in working directory and read back into R
write.csv(file= "AniMoveSubDatFin.txt", x=AniMoveSubDatMainRF, row.names = F)
AniMovSubDatRF <- read.csv("AniMoveSubDatFin.txt", header = TRUE, sep = ",")
AniMovSubDatRF
names(AniMovSubDatRF)
dim(AniMovSubDatRF)
str(AniMovSubDatRF)
summary(AniMovSubDatRF)

# write output to file and read back in R under different name
write.csv(file= "AniMoveSubDatFinalx.txt", x=AniMovSubDatRF, row.names = F)
AniMovSubDatFinalx <- read.csv("AniMoveSubDatFinalx.txt", header = TRUE, sep = ",")

# convert continuous to categorical independent variables to factors
AniMovSubDatFinalx.num2fact <- c('scale.coef', 'density.area', 'mortality', 'norm.constant')

# convert independent variables to factor data types and dependent variables to numerical data
types
AniMovSubDatFinalx.int2num <- c('dead.count', 'live.peak.dens', 'dead.peak.dens')
AniMovSubDatFinalx[,AniMovSubDatFinalx.num2fact] <-
lapply(AniMovSubDatFinalx[,AniMovSubDatFinalx.num2fact] , factor)
AniMovSubDatFinalx[,AniMovSubDatFinalx.int2num] <-
lapply(AniMovSubDatFinalx[,AniMovSubDatFinalx.int2num] , as.numeric)
AniMovSubDatFinalx
names(AniMovSubDatFinalx)
dim(AniMovSubDatFinalx)
str(AniMovSubDatFinalx)
summary(AniMovSubDatFinalx)

# Plot means-annotated boxplots of displacement-based metrics as dependent variables against
movement strategy

fun_mean <- function(x){

```



```
return(data.frame(y=mean(x),label=mean(x,na.rm=T))))}
```

```
p1 <- ggplot(AniMovSubDatFinalx,aes(x=move.strat,y=live.max.dist)) +
  geom_boxplot(aes(fill=move.strat)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y..,
digits=0))) +
  labs(y = "Deposition distance") +
  scale_y_continuous(breaks = seq(0, 2000, by = 200)) +
  annotate("text", label = 'Living', x = 1.5, y = 0, color = "darkgreen", cex = 5) +
  theme(axis.ticks.x = element_blank(),
        axis.text = element_text(size = 10),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),
        legend.position = "none")

p2 <- ggplot(AniMovSubDatFinalx,aes(x=move.strat,y=dead.max.dist)) +
  geom_boxplot(aes(fill=move.strat)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y..,
digits=0))) +
  #labs(y = "Maximum deposition distance") +
  scale_y_continuous(breaks = seq(0, 2000, by = 200)) +
  annotate("text", label = 'Dead', x = 1.5, y = 0, color = "darkred", cex = 5) +
  theme(axis.ticks.x = element_blank(),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),
        axis.title.y = element_blank(),
        legend.position = "none")

p3 <- ggplot(AniMovSubDatFinalx,aes(x=move.strat,y=live.range)) +
  geom_boxplot(aes(fill=move.strat)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y..,
digits=0))) +
  labs(y = "Deposition range") +
  #scale_y_continuous(breaks = seq(0, 600, by = 100)) +
  theme(axis.ticks.x = element_blank(),
        axis.text = element_text(size = 10),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),
        legend.position = "none")
```

```
p4 <- ggplot(AniMovSubDatFinalx,aes(x=move.strat,y=dead.range)) +
  geom_boxplot(aes(fill=move.strat)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y..,
digits=0))) +
  #labs(y = "Maximum deposition distance") +
  scale_y_continuous(breaks = seq(0, 2000, by = 200)) +
  guides(fill=guide_legend(title = "Movement pattern")) +
  theme(axis.ticks.x = element_blank(),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),
        axis.title.y = element_blank(),
        legend.text = element_text(size=15),
        legend.title=element_text(size=15),
        legend.position = c(0,0.1))
```

collate all displacement-related boxplots into multifigure graphic

```
pdf("generalresultsdispCRWLWTimeMort.pdf")
grid.arrange(p1, p2, p3, p4, nrow = 2, ncol = 2, top = "Maximum Subsidy displacement CRW-
LW-Time-Mort (Means annotated)")
dev.off()
```

Plot means-annotated boxplots of density-based metrics as dependent variables against movement strategy

```
p5 <- ggplot(AniMovSubDatFinalx,aes(x=move.strat,y=live.peak.dens)) +
  geom_boxplot(aes(fill=move.strat)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y..,
digits=0))) +
  labs(y = "Peak deposition density") +
  scale_y_continuous(breaks = seq(0, 600, by = 100)) +
  annotate("text", label = 'Living', x = 1.5, y = 0, color = "darkgreen", cex = 5) +
  theme(axis.ticks.x = element_blank(),
        axis.text = element_text(size = 10),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),
        legend.position = "none")
```

```
p6 <- ggplot(AniMovSubDatFinalx,aes(x=move.strat,y=dead.peak.dens)) +
  geom_boxplot(aes(fill=move.strat)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
```

```

stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y..,
digits=0))) +
#labs(y = "Deposition density") +
scale_y_continuous(breaks = seq(0, 600, by = 100)) +
annotate("text", label = 'Dead', x = 1.5, y = 0, color = "brown", cex = 5) +
theme(axis.ticks.x = element_blank(),
      axis.text.x = element_blank(),
      axis.title = element_text(size = 15),
      axis.title.x = element_blank(),
      axis.title.y = element_blank(),
      legend.position = "none")

```

```

p7 <- ggplot(AniMovSubDatFinalx,aes(x=move.strat,y=live.peak.dens.dist)) +
  geom_boxplot(aes(fill=move.strat)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y..,
digits=0))) +
  labs(y = "Distance to peak deposition density") +
  #scale_y_continuous(breaks = seq(0, 600, by = 100)) +
  #ylim(0,100)
  #scale_y_continuous(breaks = seq(0, 600, by = 100)) +
  theme(axis.ticks.x = element_blank(),
        axis.text = element_text(size = 10),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),
        legend.position = "none") +
  ylim(0,100)

```

```

p8 <- ggplot(AniMovSubDatFinalx,aes(x=move.strat,y=dead.peak.dens.dist)) +
  geom_boxplot(aes(fill=move.strat)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y..,
digits=0))) +
  #labs(y = "Maximum deposition distance") +
  scale_y_continuous(breaks = seq(0, 100, by = 25)) +
  guides(fill=guide_legend(title = "Movement pattern")) +
  theme(axis.ticks.x = element_blank(),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),
        axis.title.y = element_blank(),
        legend.text = element_text(size=15),
        legend.title=element_text(size=15),
        legend.position = c(0,0.1))

```

```

# collate all density-related boxplots into multifigure graphic

pdf("generalresultsdensCRWLWTimeMort.pdf")
grid.arrange(p5, p6, p7, p8, nrow = 2, ncol = 2, top = "Peak Subsidy Impact CRW-LW-Time-Mort
(Means annotated)")
  #top=textGrob("Peak Subsidy Impact (Means annotated)",
  #gp=gpar(fontsize=20,font=3)))
dev.off()

### assign dependent variables to array, leave out variables not relevant for analysis
dvnamesx <- paste(names(subset(AniMovSubDatFinalx[,c(7:19)],
  #select = -c(live.min.dist, dead.min.dist))),
  sep = ','))
dvnamesx
str(dvnamesx)

### random forest and CART analysis on data without addressing space-based mortality effects
attach(AniMovSubDatFinalx)

### empty list for CART and random forest model output
CARTtreemodelsx <- list() # CART
RFtreemodelsx <- list() # random forest

### reassign independent variables and leave out variables not relevant for analysis
ivnamesx <- paste(names(subset(AniMovSubDatFinalx[,c(1:6)],
  select = -c(density.area, space.death, norm.constant))),
  collapse = ' + ')
ivnamesx
str(ivnamesx)

### run random forest and classification models
#function of space (x)
for (y in dvnamesx){
  formx <- as.formula(paste(y, "~", ivnamesx))
  CARTtreemodelsx[[y]] <- rpart(formx, data = AniMovSubDatFinalx, method = "anova",
    control = rpart.control(minsplit = 600, minbucket = 200, cp = 0.001))
  RFtreemodelsx[[y]] <- randomForest(formx, data = AniMovSubDatFinalx,
    improve = 0.001, doBest = TRUE, importance = TRUE, ntree = 2000)
}

### model results summaries for CART and random forest models
CARTtreemodelsx.summary <- lapply(CARTtreemodelsx, summary)
CARTtreemodelsx.printcp <- lapply(CARTtreemodelsx, printcp)
CARTtreemodelsx.plotcp <- lapply(CARTtreemodelsx, plotcp)
CARTtreemodelsx.rsq <- lapply(CARTtreemodelsx, rsq.rpart)
CARTtreemodelsx.results <- lapply(CARTtreemodelsx, print)

```

```

RFtreemodelsx.results <- lapply(RFtreemodelsx, print)
RFtreemodelsx.imp <- lapply(RFtreemodelsx, randomForest::importance)
RFtreemodelsx.imp

### random forest and CART tree plots
# save CART plots to working directory by dependent variable
pdf('MoveScaleMortCRWLWCART.pdf')
for (var in names(CARTtreemodelsx)){
  #dev.new()
  fancyRpartPlot(CARTtreemodelsx[var][[1]], main = var)
}
dev.off()

# prune CART plots by complexity parameter (Cp) and save to working directory by dependent
variable
pdf('MoveScaleMortCRWLWCARTPruned.pdf')
for (var in names(CARTtreemodelsx)){
  #dev.new()
  fancyRpartPlot(prune(CARTtreemodelsx[var][[1]],
                        cp
                        =
CARTtreemodelsx[var][[1]]$cptable[which.min(CARTtreemodelsx[var][[1]]$cptable[, "xerror"])
, "CP"]),
                main = var)
}
dev.off()

# save variable importance plots for random forest models to working directory by dependent
variables
pdf('MoveScaleMortCRWLWRandForsVarImp.pdf')
for (var in names(RFtreemodelsx)){
  # dev.new()
  varImpPlot(RFtreemodelsx[var][[1]], main = var)
}
dev.off()

detach(AniMovSubDatFinalx)

### Data Analysis – LW with space-based versus time-based mortality ###

### Prepare raw data from NetLogo batch simulation in behavior space using -Data Preparation-
code format ###

### read in prepped dataset for analysis
# read in separate LW data file
LWAniMovSubDat2 <- read.csv("LWDataSet2.txt", header = TRUE, sep = ",")

```

```

LWAniMovSubDat2
names(LWAniMovSubDat2)
dim(LWAniMovSubDat2)
str(LWAniMovSubDat2)
summary(LWAniMovSubDat2)

# relabel scale coefficient variable
names(LWAniMovSubDat2)[1] <- "scale.coef"
AniMoveSubDatMainRF2 <- LWAniMovSubDat2
names(AniMoveSubDatMainRF2)
dim(AniMoveSubDatMainRF2)
str(AniMoveSubDatMainRF2)
summary(AniMoveSubDatMainRF2)

# write file to working directory
write.csv(file= "NewAniMoveSubDatFin2.txt", x=AniMoveSubDatMainRF2, row.names = F)
AniMovSubDatRF2 <- read.csv("NewAniMoveSubDatFin2.txt", header = TRUE, sep = ",")
AniMovSubDatRF2
names(AniMovSubDatRF2)
dim(AniMovSubDatRF2)
str(AniMovSubDatRF2)
summary(AniMovSubDatRF2)

# Convert all independent variables to factors and dependent variable to numerical data types
write.csv(file = "AniMoveSubDatFinalz.txt", x=AniMovSubDatRF2, row.names = F)
AniMovSubDatFinalz <- read.csv("AniMoveSubDatFinalz.txt", header = TRUE, sep = ",")
names(AniMovSubDatFinalz)[6] <- "death.function"
levels(AniMovSubDatFinalz$death.function)[match("false",levels(AniMovSubDatFinalz$death.
function))] <- "Time"
levels(AniMovSubDatFinalz$death.function)[match("true",levels(AniMovSubDatFinalz$death.f
unction))] <- "Space"
AniMovSubDatFinalz$space.vs.time.death <- do.call(paste,
c(AniMovSubDatFinalz[c("death.function", "mortality")], sep = "."))
AniMovSubDatFinalz <- AniMovSubDatFinalz[,c(1,2,3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18)]
AniMovSubDatFinalz <- AniMovSubDatFinalz[,c(1,2,18,4,5,7,8,9,10,11,12,13,14,15,16,17)]
AniMovSubDatFinalz.num2fact <- c('scale.coef', 'density.area', 'norm.constant',
'space.vs.time.death')
AniMovSubDatFinalz.int2num <- c('dead.count', 'live.peak.dens', 'dead.peak.dens')
AniMovSubDatFinalz[,AniMovSubDatFinalz.num2fact] <-
lapply(AniMovSubDatFinalz[,AniMovSubDatFinalz.num2fact], factor)
AniMovSubDatFinalz[,AniMovSubDatFinalz.int2num] <-
lapply(AniMovSubDatFinalz[,AniMovSubDatFinalz.int2num], as.numeric)
AniMovSubDatFinalz
names(AniMovSubDatFinalz)
dim(AniMovSubDatFinalz)
str(AniMovSubDatFinalz)

```

```

summary(AniMovSubDatFinalz)
###

# Plot all displacement-related means-annotated boxplots

p9 <- ggplot(AniMovSubDatFinalz,aes(x=space.vs.time.death,y=live.max.dist)) +
  geom_boxplot(aes(fill=space.vs.time.death)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y...,
digits=0))) +
  labs(y = "Deposition distance") +
  scale_y_continuous(breaks = seq(0, 600, by = 100)) +
  annotate("text", label = 'Living', x = 3.5, y = 0, color = "darkgreen", cex = 5) +
  theme(axis.ticks.x = element_blank(),
        axis.text = element_text(size = 10),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),
        legend.position = "none")

p10 <- ggplot(AniMovSubDatFinalz,aes(x=space.vs.time.death,y=dead.max.dist)) +
  geom_boxplot(aes(fill=space.vs.time.death)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y...,
digits=0))) +
  #labs(y = "Maximum deposition distance") +
  scale_y_continuous(breaks = seq(0, 600, by = 100)) +
  annotate("text", label = 'Dead', x = 3.5, y = 0, color = "darkred", cex = 5) +
  theme(axis.ticks.x = element_blank(),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),
        axis.title.y = element_blank(),
        legend.position = "none")

p11 <- ggplot(AniMovSubDatFinalz,aes(x=space.vs.time.death,y=live.range)) +
  geom_boxplot(aes(fill=space.vs.time.death)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y...,
digits=0))) +
  labs(y = "Deposition range") +
  scale_y_continuous(breaks = seq(0, 600, by = 100)) +
  theme(axis.ticks.x = element_blank(),
        axis.text = element_text(size = 10),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),

```

```

axis.title.x = element_blank(),
legend.position = "none")

p12 <- ggplot(AniMovSubDatFinalz,aes(x=space.vs.time.death,y=dead.range)) +
  geom_boxplot(aes(fill=space.vs.time.death)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes(label=round(..y..,
digits=0))) +
  #labs(y = "Maximum deposition distance") +
  scale_y_continuous(breaks = seq(0, 600, by = 100)) +
  guides(fill=guide_legend(title = "Movement pattern")) +
  theme(axis.ticks.x = element_blank(),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),
        axis.title.y = element_blank(),
        legend.text = element_text(size=12),
        legend.title = element_text(size=12),
        legend.position = "bottom")
grid.arrange(p9, p10, p11, p12, nrow = 2, ncol = 2,
             top=textGrob("Maximum Subsidy displacement (Means annotated)",
                          gp=gpar(fontsize=20,font=3)))

# Compile multifigure graphic of displacement-related plots

pdf("generalresultsdispLWSpaceTimeMort.pdf")
grid.arrange(p9, p10, p11, p12, nrow = 2, ncol = 2, top = "Maximum Subsidy displacement – LW-
Space-Time-Mort (Means annotated)")
dev.off()

# Plot all density-related means-annotated boxplots

p13 <- ggplot(AniMovSubDatFinalz,aes(x=space.vs.time.death,y=live.peak.dens)) +
  geom_boxplot(aes(fill=space.vs.time.death)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y..,
digits=0))) +
  labs(y = "Deposition density") +
  scale_y_continuous(breaks = seq(0, 600, by = 100)) +
  annotate("text", label = 'Living', x = 3.5, y = 0, color = "darkgreen", cex = 5) +
  theme(axis.ticks.x = element_blank(),
        axis.text = element_text(size = 10),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),

```



```

legend.position = "none")

p14 <- ggplot(AniMovSubDatFinalz,aes(x=space.vs.time.death,y=dead.peak.dens)) +
  geom_boxplot(aes(fill=space.vs.time.death)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y..,
digits=0))) +
  #labs(y = "Maximum deposition distance") +
  scale_y_continuous(breaks = seq(0, 600, by = 100)) +
  annotate("text", label = 'Dead', x = 3.5, y = 0, color = "brown", cex = 5) +
  theme(axis.ticks.x = element_blank(),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),
        axis.title.y = element_blank(),
        legend.position = "none")

p15 <- ggplot(AniMovSubDatFinalz,aes(x=space.vs.time.death,y=live.peak.dens.dist)) +
  geom_boxplot(aes(fill=space.vs.time.death)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y..,
digits=0))) +
  labs(y = "Deposition distance") +
  scale_y_continuous(breaks = seq(0, 600, by = 100)) +
  theme(axis.ticks.x = element_blank(),
        axis.text = element_text(size = 10),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),
        legend.position = "none") +
  ylim(0,100)

p16 <- ggplot(AniMovSubDatFinalz,aes(x=space.vs.time.death,y=dead.peak.dens.dist)) +
  geom_boxplot(aes(fill=space.vs.time.death)) +
  stat_summary(fun.y = mean, geom="point",colour="darkblue", size=5) +
  stat_summary(fun.data = fun_mean, cex = 5, geom="text", vjust=-0.7, aes( label=round(..y..,
digits=0))) +
  #labs(y = "Maximum deposition distance") +
  scale_y_continuous(breaks = seq(0, 100, by = 25)) +
  guides(fill=guide_legend(title = "Movement pattern")) +
  theme(axis.ticks.x = element_blank(),
        axis.text.x = element_blank(),
        axis.title = element_text(size = 15),
        axis.title.x = element_blank(),
        axis.title.y = element_blank(),
        legend.text = element_text(size=12),

```

```

legend.title = element_text(size=12),
legend.position = "bottom")

pdf("generalresultsdensLWSpaceTimeMort.pdf")
grid.arrange(p1, p2, p3, p4, nrow = 2, ncol = 2, top = "Maximum Subsidy Density LW-Space-
Time-Mort (Means annotated)")
dev.off()

### assigns dependent variable
dvnamesz <- paste(names(subset(AniMovSubDatFinalz[,c(6:16)],
                             select = -c(live.min.dist, dead.min.dist))),
                  sep = ',')
dvnamesz
str(dvnamesz)

### random forest and classification analysis on data addressing space-based mortality effects
attach(AniMovSubDatFinalz)

### lists for model results
CARTtreemodelsz <- list() # CART
RFtreemodelsz <- list() # random forest

### assigns independent variable
ivnamesz <- paste(names(subset(AniMovSubDatFinalz[,c(1:5)],
                             select = -c(density.area, norm.constant))),
                  collapse = ' + ')
ivnamesz
str(ivnamesz)

### random forest and CART models accounting for the effects of death as a function of space (z)
for (y in dvnamesz){
  formz <- as.formula(paste(y, "~", ivnamesz))
  CARTtreemodelsz[[y]] <- rpart(formz, data = AniMovSubDatFinalz, method = "anova",
                               control = rpart.control(minsplit = 600, minbucket = 200, cp = 0.001))
  RFtreemodelsz[[y]] <- randomForest(formz, data = AniMovSubDatFinalz,
                                     improve = 0.001, doBest = TRUE, importance = TRUE, ntree = 2000)
}

### random forest and CART model summaries
CARTtreemodelsz.summary <- lapply(CARTtreemodelsz, summary)
CARTtreemodelsz.printcp <- lapply(CARTtreemodelsz, printcp)
CARTtreemodelsz.plotcp <- lapply(CARTtreemodelsz, plotcp)
CARTtreemodelsz.rsq <- lapply(CARTtreemodelsz, rsq.rpart)
CARTtreemodelsz.results <- lapply(CARTtreemodelsz, print)
RFtreemodelsz.results <- lapply(RFtreemodelsz, print)

```

```

RFtreemodelsz.imp <- lapply(RFtreemodelsz, randomForest::importance)
RFtreemodelsz.imp

### random forest and CART tree plots
pdf('MoveScaleDeathFuncSpaceTimeLWCART.pdf')
for (var in names(CARTtreemodelsz)){
  #dev.new()
  fancyRpartPlot(CARTtreemodelsz[var][[1]], main = var)
}
dev.off()

pdf('MoveScaleDeathFuncSpaceVsTimeLWCARTPruned.pdf')
for (var in names(CARTtreemodelsz)){
  #dev.new()
  fancyRpartPlot(prune(CARTtreemodelsz[var][[1]],
    cp
    CARTtreemodelsz[var][[1]]$cptable[which.min(CARTtreemodelsz[var][[1]]$cptable[, "xerror"]),
    "CP"]),
    main = var)
}
dev.off()

# random forest variable importance plots
pdf('MoveScaleDeathFuncSpacevsTimeLWRandForsVarImp.pdf')
for (var in names(RFtreemodelsz)){
  #dev.new()
  varImpPlot(RFtreemodelsz[var][[1]], main = var)
}
dev.off()

detach(AniMovSubDatFinalz)

```

APPENDIX B. SUPPLEMENTARY INFORMATION (SI): EFFECT OF ANIMAL SOCIALITY, MOVEMENT AND MORTALITY ON ACTIVE SUBSIDY DISTRIBUTION

-Section S: Supplementary Results

- ❖ Classification and Regression Trees (CARTs) of subsidy deposition distribution metrics (Displacement (maximum distance, range and distance to peak density)), Density (peak density), and Clustering (maximum cluster count, size, density, and inter-cluster distance), with leaves containing mean response values, number (n) and percentage (%) of data points resulting from predictor split:
 - Nodes containing predictor splits for movement scaling (correlation coefficient (CRW)):
 - Correlation coefficients (more sinuous to straighter) - 0.5, 0.8, 0.9, 0.95, 0.99
 - Settlement probability (Low likelihood to High likelihood) – 0.001, 0.0025, 0.005, 0.0075, 0.01
 - Perceptual Range (Low to High) – 1, 3, 5, 7, 10

-Section T: Random Forest and CART Error Analysis

- ❖ Subsidy distribution metrics by % IncMSE, IncNodePurity (RSS), % variance explained and misclassification rate for:
 - Movement pattern (CRW) and conspecific interaction: settlement probability, perceptual range

Section U: Model Construction

- ❖ Model Overview, Design Concepts, Details (ODD) description:
 - Overview: Purpose, State variables and scale, Process overview and scheduling
 - Design concepts: Emergence, Sensing, Interaction, Stochasticity, Observation
 - Details: Initialization, Inputs, Sub-models

-Section V: Code

- ❖ Code:
 - Model construction: NetLogo Version 6.0.4 Code
 - NetLogo Model description and function
 - Data processing and analysis: R version 3.5.1

-CART Response Variable Notation

Number of dead subsidies: *dead.count*, maximum living subsidy deposition distance: *live.max.dist*, maximum dead subsidy deposition distance: *dead.max.dist*, maximum living subsidy range: *live.range*, maximum dead subsidy range: *dead.range*, peak living subsidy deposition density: *live.peak.dens*, peak dead subsidy deposition density: *dead.peak.dens*, distance to peak living subsidy deposition density: *live.peak.dens.dist*, distance to peak dead subsidy deposition density: *dead.peak.dens.dist*, number of living subsidies: *consp.count / live.count*, number of living subsidy clusters: *cluster.count.live*, number of dead subsidy clusters: *cluster.count.dead*, maximum living subsidy cluster density: *max.clust.dens.live*, maximum dead subsidy cluster density:

max.clust.dens.dead, maximum living subsidy cluster size: *max.clust.size.live*, maximum dead subsidy cluster size: *max.clust.size.dead*, maximum living subsidy inter-cluster distance: *max.dist.interclust.live*, maximum dead subsidy inter-cluster distance: *max.dist.interclust.dead*

Section S: Supplementary Results

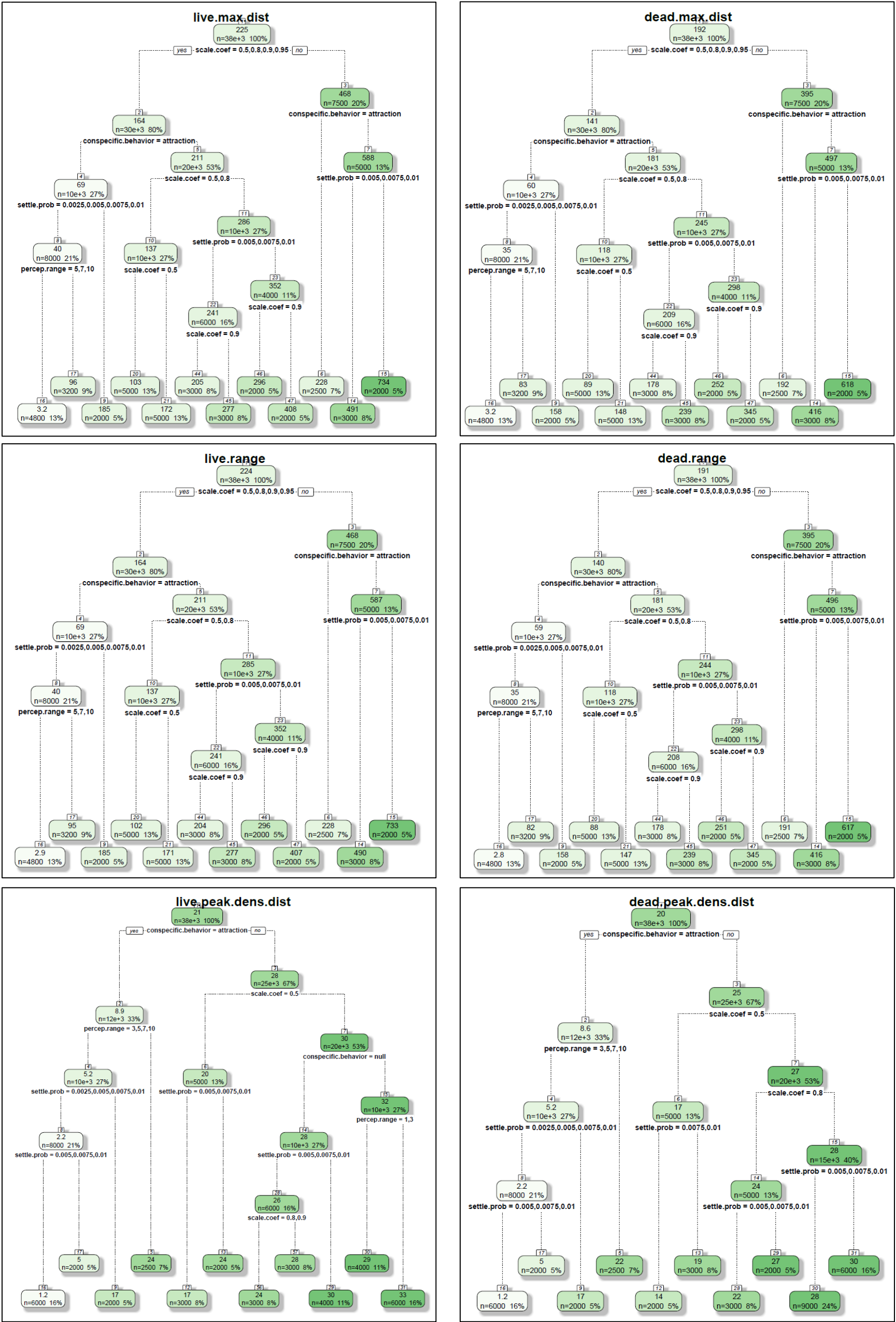


Figure 29 Living subsidies were deposited further than dead subsidies. Given conspecific attraction, more sinuous movements at higher settlement probability and perceptual range generated the least displaced living subsidies with the lowest maximum deposition distance and range from the shared ecosystem boundary. At higher perceptual range and lower settlement probabilities, avoidance scenarios resulted in the greatest distance to peak density for dead subsidies. Scenarios with no interaction resulted in intermediate subsidy displacement.

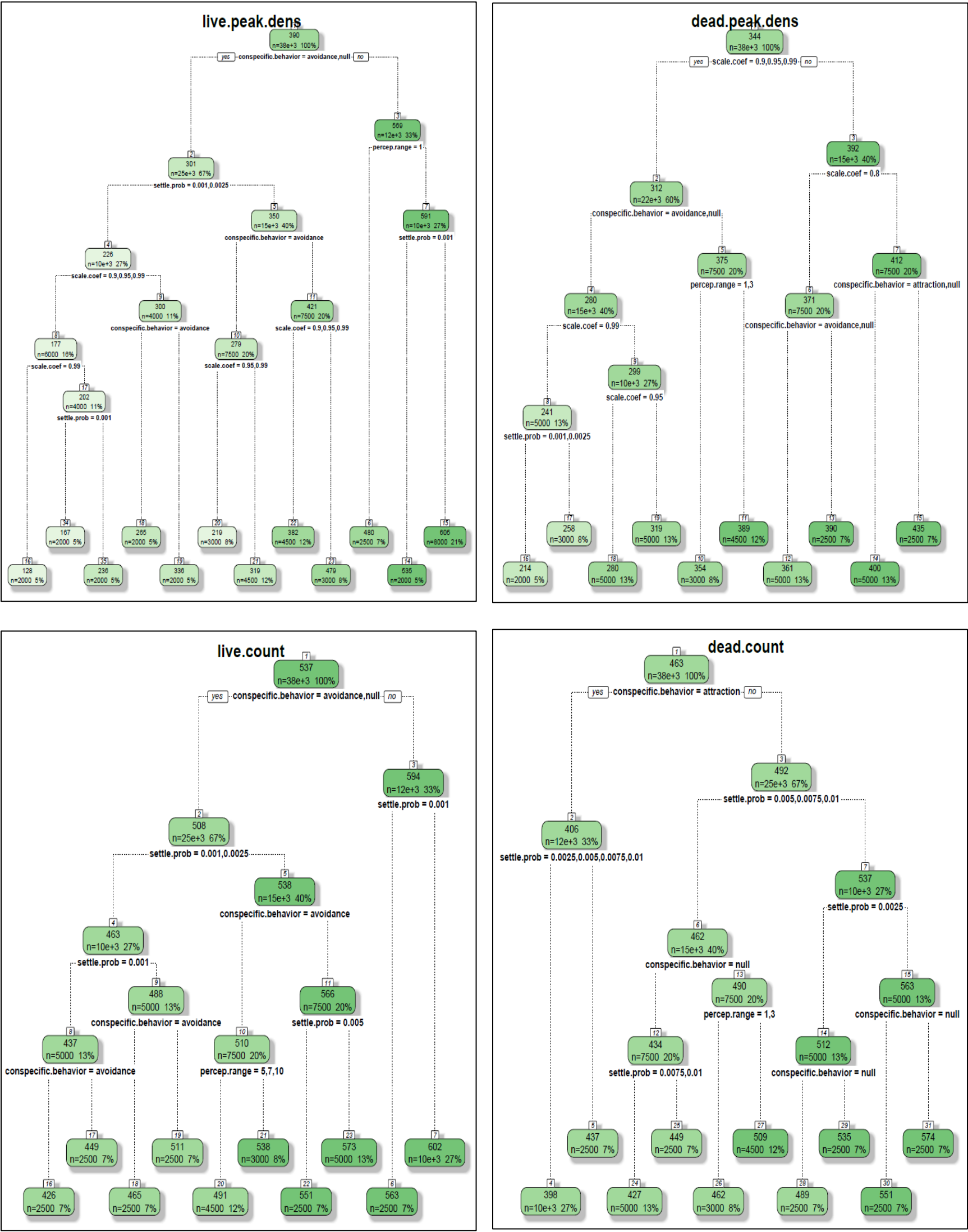


Figure 30 Given straighter movements and lower settlement probabilities, conspecific avoidance and scenarios without conspecific interaction depress the peak deposition density of living subsidies. Conspecific attraction with higher settlement probability and perceptual range resulted in greatest peak deposition density for living subsidies. Given conspecific avoidance and scenarios without conspecific interaction, more sinuous movement and higher settlement probability increases peak deposition for dead subsidies.

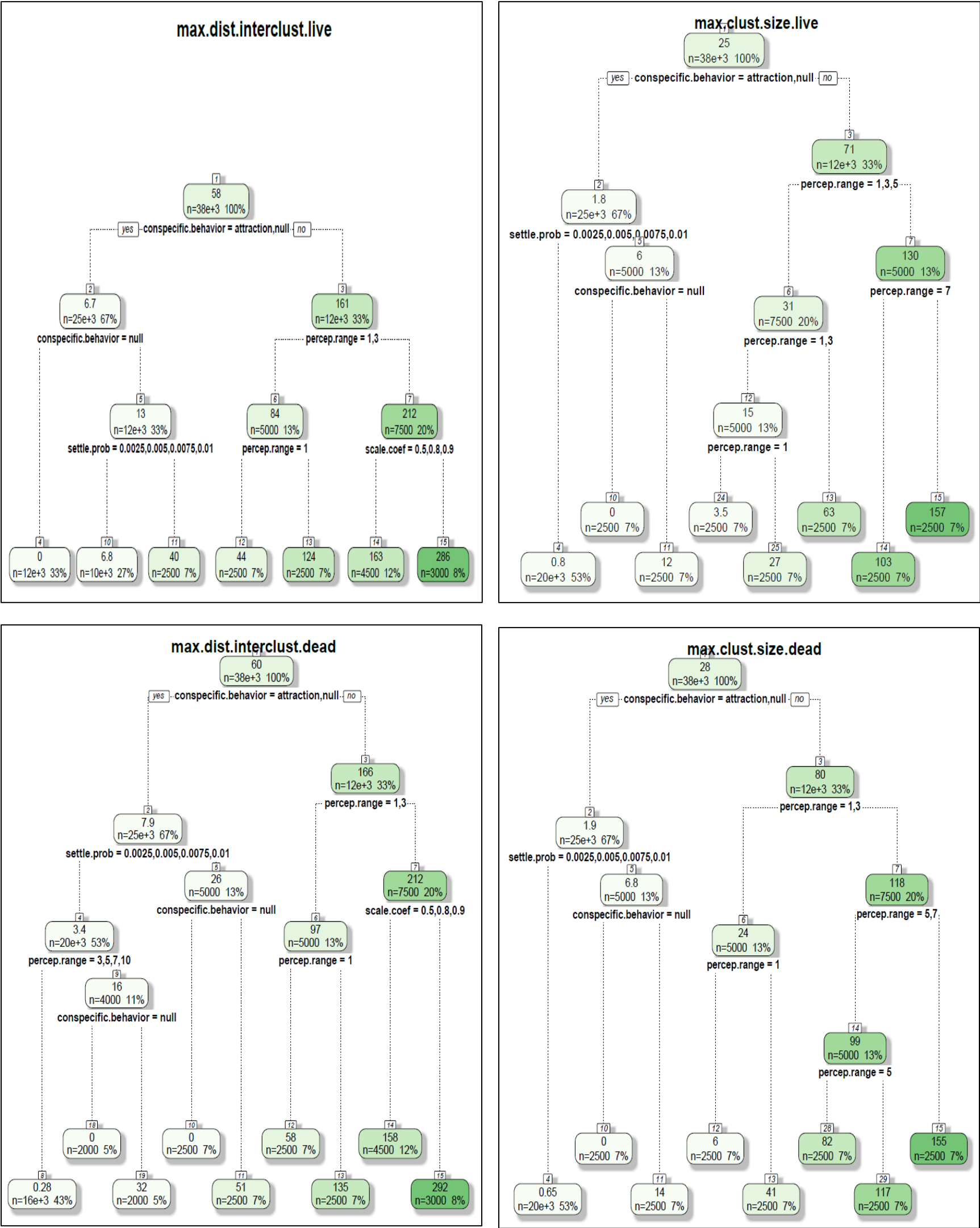


Figure 31 Given higher perceptual ranges, straighter movements in conspecific avoidance scenarios resulted in the greatest inter-cluster displacement. Conspecific attraction with higher settlement probabilities resulted in the lowest inter-cluster displacement. Scenarios with no interaction resulted in intermediate inter-cluster displacement.



Figure 32 Given lower settlement probability, conspecific attraction resulted in intermediate values for maximum cluster size. Higher settlement probability in scenarios conspecific interaction scenarios and scenarios without interaction constrained maximum cluster size to with smaller clusters for living subsidies than to dead subsidies. Conspecific avoidance with higher perceptual range resulted in the largest clusters.

Section T: Random Forest and CART Error Analysis

Table 7 *Increase in percentage means square prediction error (%IncMSE) for metrics of living (consumer) and dead (nutrient) subsidy distribution.* Values indicate the relative importance as prediction strength of each state variable (conspecific interaction, settlement probability, scaling coefficient and perceptual range) to subsidy distribution; amount (number of settled subsidies and number of dead subsidies), displacement (maximum deposition distance, range and distance to peak density), density (peak deposition density) and clustering (number of clusters, maximum inter-cluster range, density and size). Larger values indicate higher predictor importance.

Percentage increase in mean square error of subsidy deposition distribution metric by state variable

| <i>State Variable</i> | <i>Conspecific Interaction</i> | | <i>Settlement Probability</i> | | <i>Scaling Coefficient</i> | | <i>Perceptual Range</i> | |
|---|--------------------------------|-------------|-------------------------------|-------------|----------------------------|-------------|-------------------------|-------------|
| <i>Subsidy Distribution metric</i> | <i>Living</i> | <i>Dead</i> | <i>Living</i> | <i>Dead</i> | <i>Living</i> | <i>Dead</i> | <i>Living</i> | <i>Dead</i> |
| Number of subsidies | 126.61 | 147.86 | 123.66 | 134.54 | 46.15 | 39.17 | 64.41 | 70.07 |
| Maximum deposition distance | 120.71 | 120.72 | 89.60 | 87.79 | 129.77 | 123.37 | 69.19 | 67.64 |
| Maximum deposition range | 123.66 | 120.06 | 89.65 | 87.28 | 129.52 | 125.93 | 69.72 | 69.27 |
| Peak deposition density distance | 178.86 | 184.24 | 89.78 | 82.25 | 117.75 | 114.93 | 79.22 | 78.41 |
| Peak deposition density | 165.22 | 143.39 | 130.19 | 48.25 | 115.34 | 128.45 | 72.58 | 47.46 |
| Number of subsidy clusters | 186.78 | 174.91 | 63.72 | 67.02 | 68.60 | 66.64 | 76.15 | 74.75 |
| Maximum inter-cluster range | 158.88 | 158.51 | 45.37 | 60.37 | 60.88 | 63.63 | 72.62 | 71.21 |
| Maximum cluster size | 137.74 | 151.95 | 49.57 | 39.24 | 58.61 | 43.53 | 76.45 | 74.55 |
| Maximum cluster density | 132.66 | 163.78 | 86.40 | 83.06 | 91.22 | 67.92 | 91.60 | 89.64 |

Table 8 *Prediction precision as increase in node purity (residual sum of squares) (IncNodePurity (RSS)) in metrics of living (consumer) and dead (nutrient) subsidy distribution.* Values indicate the relative importance as prediction accuracy of each state variable (conspecific interaction, settlement probability, scaling coefficient and perceptual range) to subsidy distribution; amount (number of settled subsidies, number of dead subsidies), displacement (maximum deposition distance, range, distance to peak density), density (peak deposition density) and clustering (number of clusters, maximum inter-cluster range, density and size). Larger values indicate higher predictor precision.

Increase in node purity of living and dead subsidy deposition distribution metric by state variable

| <i>State Variable</i> | <i>Conspecific Interaction</i> | | <i>Settlement Probability</i> | | <i>Scaling Coefficient</i> | | <i>Perceptual Range</i> | |
|---|---------------------------------------|--------------------|--------------------------------------|--------------------|-----------------------------------|--------------------|--------------------------------|--------------------|
| <i>Subsidy Distribution metric</i> | <i>Living</i> | <i>Dead</i> | <i>Living</i> | <i>Dead</i> | <i>Living</i> | <i>Dead</i> | <i>Living</i> | <i>Dead</i> |
| Number of subsidies | 1.63E+08 | 1.07E+06 | 1.47E+08 | 3.05E+07 | 3.21E+06 | 2.69E+06 | 3.85E+06 | 5.95E+07 |
| Maximum deposition distance | 2.59E+08 | 1.88E+08 | 1.37E+08 | 9.12E+07 | 5.25E+08 | 3.62E+08 | 3.17E+07 | 2.35E+07 |
| Maximum deposition range | 2.63E+08 | 1.88E+08 | 1.36E+08 | 9.08E+07 | 5.25E+08 | 3.65E+08 | 3.16E+07 | 2.46E+07 |
| Peak deposition density distance | 2.83E+06 | 2.20E+06 | 3.42E+05 | 2.78E+05 | 4.03E+05 | 4.36E+05 | 2.94E+05 | 2.62E+05 |
| Peak deposition density | 5.34E+08 | 3.14E+07 | 9.22E+07 | 2.79E+06 | 6.25E+07 | 6.23E+07 | 1.71E+07 | 1.65E+06 |
| Number of clusters | 2.16E+06 | 1.45E+06 | 2.21E+04 | 2.04E+04 | 1.02E+05 | 7.75E+04 | 1.70E+05 | 1.35E+05 |
| Maximum inter-cluster range | 1.77E+08 | 1.82E+08 | 2.87E+06 | 5.13E+06 | 1.42E+07 | 1.77E+07 | 2.12E+07 | 1.70E+07 |
| Maximum cluster size | 3.88E+07 | 4.73E+07 | 6.66E+05 | 1.90E+05 | 1.14E+06 | 6.93E+05 | 1.32E+07 | 1.19E+07 |
| Maximum cluster density | 1.78E+08 | 4.13E+08 | 2.41E+07 | 1.01E+07 | 2.59E+07 | 2.90E+07 | 6.51E+07 | 7.14E+07 |

Table 9 %Variance explained and Misclassification error rate for all CARTs. CARTs collectively explained over 40% of the variance with under 35% misclassification error for subsidy displacement, density and clustering. Noise caused by the stochastic implementation of movement and mortality variation in the model construction contributes to unexplained variance and misclassification.

| <i>Predictor</i> | <i>Conspecific Interaction with Movement</i> | |
|--|--|-------------|
| | <i>Living</i> | <i>Dead</i> |
| % Variance Explained | | |
| <i>maximum subsidy deposition distance</i> | 79.1 | 78.6 |
| <i>maximum subsidy deposition range</i> | 78.9 | 78.4 |
| <i>Peak subsidy deposition density</i> | 61.7 | 51.9 |
| <i>distance to peak subsidy deposition density</i> | 44.2 | 42.5 |
| <i>number of subsidies deposited</i> | 82.3 | 79.3 |
| <i>maximum inter-cluster distance</i> | 79 | 80.1 |
| <i>maximum cluster size</i> | 79.1 | 81.2 |
| <i>maximum cluster density</i> | 58.4 | 73.0 |
| <i>maximum number of clusters deposited</i> | 77.8 | 76.8 |
| Misclassification error rate (%) | | |
| <i>maximum subsidy deposition distance</i> | 30.1 | 31 |
| <i>maximum subsidy deposition range</i> | 30.8 | 31.1 |
| <i>peak subsidy deposition density</i> | 30.6 | 26.8 |
| <i>distance to peak subsidy deposition density</i> | 27.4 | 29.8 |
| <i>number of subsidies deposited</i> | 13.5 | 17.8 |
| <i>maximum inter-cluster deposition distance</i> | 16.9 | 17.1 |
| <i>maximum cluster size</i> | 13.5 | 9.6 |
| <i>maximum cluster density</i> | 25.3 | 23.7 |
| <i>maximum number of clusters deposited</i> | 25.5 | 30.2 |

Section U: Model Construction - Overview, Design Concepts, Details (ODD) Protocol

4. Overview

4.1 Purpose

Ecological subsidies are consumer and resource transfers by animal movements across ecosystems and landscapes. This model is an IBM simulation to investigate how variations in animal movement and sociality with mortality impact the distribution of living and dead subsidies. The model quantifies the spatial extents and intensities of active subsidy distributions from a broad parameter space of animal dispersal movement and foraging movement patterns with a variety of conspecific interaction and mortality scenarios. It consists of a simple binary world, in which animals initiate movement from a donor ecosystem (natal habitat) and disperse into a recipient ecosystem with the stochastic chance of settlement and/or death during movement, depending on their perceptual range. Examples of ecological systems with similar dynamics include spatial subsidies from amphibian and aquatic insect dispersal and foraging movements from source ponds and streams into adjacent terrestrial landscapes. Dead individuals provide nutrients, energy, and/or prey to the recipient ecosystems possibly causing bottom-up effects, while living individuals are consumers with potential top-down effects.

4.2 State variables and scales

The model comprises of three hierarchical levels: individual, population and environment. The simulation environment consists of a binary landscape: donor ecosystem and recipient ecosystem (1000 by 2000 unit-space universe). Individuals are characterized by the state variables: conspecific interaction, settlement probability, perceptual range, movement strategy, scale coefficient and mortality probability as function settlement, space and time. Conspecific interaction occurs across three scenarios; attraction, null (i.e., no interaction) and avoidance affecting dispersers spatial subsidy patterns in the recipient ecosystem, depending on their movement behavior, settlement probability and perceptual range. There are two models that vary the strength of conspecific interaction varies around the baseline settlement probability as a function of the number of settled dispersers around a focal disperser in motion; a multiplicative and an exponential model. Movement strategies refer to models that describe animal movement behavior. The model generates virtual animal movement patterns using one of two common movement strategies: CRW (CRW) (i.e. paths determined by variation in turning angle correlation between steps) and LW (LW) (i.e. paths determined by variation in step lengths). Depending on the movement strategy, different ranges of scale-coefficient generate variation in animal movement patterns and scales. The mortality function determines the type of death that virtual animals undertaking LW movement experience (i.e. as a function of space (dependent on step-length) or time (regardless of the step-length)). Settled animals can experience an incremented or decremented mortality rate denoting variation in the effect of conspecific interaction on virtual animal survival.

4.3 Process overview and scheduling

Based on combinations of movement rules to generate different movement behaviors, virtual animals move from the donor to the recipient ecosystem where they can die depending on the level of mortality (Figure 1 in Manuscript). 1000 virtual animals randomly orient in the donor ecosystem at the start of a simulation. Depending on the movement strategy and corresponding scaling coefficients (5 levels per movement strategy) engaged, individuals

select a random step-length and (or) a turning angle from representative distributions to negotiate a move, repeating this procedure at each timestep to generate successive moves and trajectories for over 1000 equal timesteps. Based on the global mortality level and function, individuals have a random chance of dying at any timestep during movement. Some individuals live (living subsidies) and others die (dead subsidies) by the end of the simulation.

5. Design Concepts

5.1 Emergence

Different living and dead subsidy distribution (deposition) patterns emerge from different conspecific interaction scenarios, variation in virtual animal settlement probability, perceptual range, movement behavior and mortality probability. The model does not explicitly account for adaption and fitness-seeking as the aim is to quantify emergent spatial distribution patterns based on a comprehensive spectrum of ecologically plausible variation in animal movement behavior and conspecific interaction with perceptual range, as well as settlement and mortality probabilities. Adaptation occurs implicitly in animals drawing random step lengths and/or turning angles to negotiate movement based on different movement strategies and scales. Implicit fitness-seeking occurs as animals randomly settle with decremented or incremented mortality rates depending on the conspecific interaction scenario, perceptual range and settlement probability with level and type (i.e. space versus time) of mortality risk.

5.2 Sensing

Virtual animals are aware of their movement strategy and move accordingly. Depending on perceptual range, dispersing virtual animals also sense the number of settled conspecifics around them and adjust their settlement probability accordingly. The IBM also includes the assumption that individual virtual animals know their next move based on the turning angles and (or) step lengths they draw from representative distributions of the different movement strategies at each timestep. Individuals are aware of their state (dead or alive) and know to keep moving as long as they are alive but stop moving when they settle or die. Once settled, dispersers sense an increase or decrease in survivorship depending on the set effect of conspecific interaction on survival in the model.

5.3 Interaction

Virtual animals interact with the environment as living or dead subsidies. Individuals are aware of their state (dead or alive) and location (2D-x, y-coordinates) in the recipient ecosystem at any given timestep. Living dispersers also interact with each other. Dispersers in motion interact with settled dispersers by avoiding them or settling in their vicinity depending on the perceptual range. The model incorporates a fully factorial combination of conspecific interaction scenarios and strengths, movement behavior and perceptual ranges, settlement and mortality probability parameter levels.

5.4 Stochasticity

Virtual animals draw random step lengths and (or) turning angles from representative distributions related to the movement strategies engaged. Virtual animal trajectories or paths therefore emanate from stochastically generated movement patterns. Depending on the

conspecific interaction scenario and perceptual range, each disperser has a stochastic chance of settlement or death if a random number they draw from a uniform probability distribution over $[0,1]$ at each timestep is less than the global mortality and settlement probability.

5.5 Observation

Metrics of active subsidy displacement and density extracted from spatial distributions at the end of each simulation include: maximum subsidy deposition distance and range, the peak density and the distance to peak density, the number of clusters that form, the maximum cluster size and density, as well as the maximum inter-cluster range for both living and dead subsidies. The maximum subsidy deposition distance is the distance from the donor-recipient ecosystem boundary to the furthest displaced subsidy. The maximum subsidy deposition range is the distance between the most and least displaced subsidies. The peak density is the greatest concentration of subsidies in the recipient ecosystem and the distance to peak density is the distance to the focal location where the peak density occurs. The maximum cluster size is the radial extent of the most spread-out cluster and the maximum cluster density is the number of subsidies in the cluster with the greatest number of subsidies. The maximum inter-cluster distance is the distance between the least and most displaced clusters. The model accounts for the distribution of living and dead subsidies separately.

6. Details:

The model was designed in NetLogo (version 6.0.4) software (Tisue and Wilensky, 2004; Wilensky, 1999)

6.1 Initialization

The environment is a binary-universe (donor-recipient ecosystem) that consists of a two-dimensional 1000 (vertical) by 2000 (horizontal) patch world (wrapped vertically) with a deflective vertical boundary and the origin centered at the left vertical boundary of the world (a patch is a unit space in the NetLogo world). Simulations were initialized with all individuals randomly distributed in a designated start-patch in the donor ecosystem at the origin of the world. 1000 virtual animals moved outward from the donor ecosystem into an adjacent recipient ecosystem over a duration of 1000 timesteps. Individuals could not return to the donor ecosystem once they entered the recipient ecosystem. Dispersers have global perceptual range, mortality and settlement probabilities. Settled dispersers have a fixed decremented or incremented mortality rate depending on the set effect of conspecific interaction on survival.

6.2 Inputs

Model inputs include the number of virtual animals and simulation duration (set to 1000 individuals and 1000 timesteps). The type and strength of conspecific interaction, perceptual range and settlement probability are also model inputs (see section 3.3 Sub-models). Model inputs also include the movement strategy, scaling coefficient, mortality level and mortality type (Table 1 in Manuscript). The model includes a normalization constant and density-area radius (a) (See section 3.3. Sub-models). The model allows users to vary the minimum step length for LW and the mean step length for CRW (set to a length of 1 patch per step).

6.3 Sub-models

Animal movement behavior as CRW and LW consist of representative statistical distributions of step lengths and turning angle orientations. At each timestep, individuals select a random step length and turning angle from respective characteristic distributions to navigate from the donor ecosystem start-patch outward and rightward through the adjacent recipient ecosystem. CRW consists of a constant one-unit step length and a wrapped Cauchy distribution of turning angles $\theta(t)$ as:

$$\theta(t) = \theta(t-1) + 2 \tan^{-1} \left[\left(\frac{1-\alpha}{1+\alpha} \right) \tan(\pi\varphi) \right],$$

$$0 \leq \alpha \leq 1$$

$$-0.5 \leq \varphi \leq 0.5$$

$\theta(t-1)$ is a previous turning angle and φ is drawn from a uniform distribution over a delta distribution range of $[-0.5, 0.5]$ to normalize the initial direction of movement trajectories to a null orientation angle. CRW features a comprehensive range of movement patterns from sinuous to straight movement with a correlation coefficient (α) over five levels, where $\alpha \in \{0.5, 0.8, 0.9, 0.95, 0.99\}$ (Table 1 in Manuscript). CRW movement is straighter as $\alpha \rightarrow 1$ and more sinuous as $\alpha \rightarrow 0$. LW consists of a circular normal turning angle distribution over a range of $[-\pi, \pi]$, and a truncated inverse-power law distribution for the relationship between randomly drawn step lengths $P(s)$ and the minimum step length (s) as:

$$P(s) = \beta s^{-\left(\frac{1}{\mu}\right)}$$

$$1 < \mu \leq 3$$

$$0 < \beta \leq 1$$

With a minimum step length of 1, LW patterns range from high to low step length variability with scaling exponent (μ) variation across five levels, where $\mu \in \{1.0, 1.5, 2, 2.5, 3.0\}$ (Table 1 in Manuscript). LW resembles Brownian motion with near-uniform step lengths as $\mu \rightarrow 3$, and simulates scale-invariant movement as $\mu \rightarrow 1$ with more variable step lengths. A normalization constant (β) is used to vary the frequency of occurrence of longer step lengths where $\beta \in \{0.25, 0.5, 1\}$.

The per-timestep likelihood of death varies across three levels of mortality probability (m) from low to high, where $m = n \times 0.001$, where n is the decrementing/ incrementing factor depending on set effect (i.e. negative or positive) of conspecific interaction on the survivorship of settled dispersers ($n=1$ for moving dispersers). Individuals draw a random number from a uniform distribution ($[0, 1]$) at each timestep and die and stop moving if the number drawn is lower than the assigned simulation mortality level for the simulation run. The model incorporates time-based mortality for CRW and LW as death regardless of step length, and space-based mortality for LW as death as function of step length, per unit of space travelled with each step.

Conspecific interaction occurs as settlement given baseline settlement probability (φ) that is the random chance that any individual settles depending on the conspecific interaction scenario and perceptual range (Table 1 in manuscript). We model settlement behavior across three levels capturing conspecific interaction (attraction and avoidance) and non-conspecific (null) behavior. We implemented settlement by adjusting the settlement probability across interaction scenarios:

$$\varphi' = \begin{cases} \varphi(n+1), & \text{attraction} \\ \varphi, & \text{null} \\ \frac{\varphi}{(n+1)}, & \text{avoidance} \end{cases}$$

where n = number of settled conspecifics within the perceptual range of dispersers

At each time-step, an unsettled individual draws a random number from a uniform distribution over $[0,1]$ and settles if the number drawn is less than the settlement probability (φ'). We implemented five levels of perceptual range (p) as the radial distance (i.e., number of patches) surrounding the area within which unsettled individuals could sense settled conspecifics (Table 1).

Section V: Code

-Model Construction - NetLogo Version 6.0.4

-Code Tab in NetLogo

```
; Daniel Bampoh
; Investigating the impact of variation in animal movement Strategy and type of mortality risk on
the spatial distribution of subsidies
; Simulation Experimentation Code (NetLogo 6.0.4)
; June 29, 2017
```

```
; The following simulation experimentation code implementation explores the relevance of animal
movement strategies (Levy Walk and Correlated Random Walk), conspecific behavior
; and mortality risk to their cross-ecosystem spatial distribution and impact as active vector
subsidies.
```

```
extensions [ dbscan ] ;loads extension for density-based cluster assessment algorithm
globals [ start-patch live-max-dist dead-max-dist live-min-dist dead-min-dist live-range dead-
range live-peak-dens-entity dead-peak-dens-entity dead-turt settle-turt live-count
live-peak-dens dead-peak-dens live-peak-dens-dist dead-peak-dens-dist consp-count consp-
max-dist consp-min-dist consp-range consp-peak-dens-entity black-turt live-turt
consp-peak-dens consp-peak-dens-dist dead-mean-dist num-neighbors consp-settle dead-count
non-consp-count cluster-count-live max-clust-dens-live mean-clust-dens-live
min-clust-dens-live max-clust-size-live mean-clust-size-live min-clust-size-live mean-dist-
interclust-live max-dist-interclust-live min-dist-interclust-live live-mean-dist
db-clusters-live db-clusters-dead cluster-count-dead max-clust-dens-dead mean-clust-dens-dead
min-clust-dens-dead max-clust-size-dead mean-clust-size-dead min-clust-size-dead
mean-dist-interclust-dead max-dist-interclust-dead min-dist-interclust-dead undead-fraction] ;
global variable
;settings, including (from right to left) the starting patch for turtles, the number of dead turtles,
the maximum distance for live and dead turtles, the minimum distance for
;live and dead turtles, the range for live and dead turtles, the peak density for live and dead turtles,
and the distance to peak density for live and dead turtles respectively
turtles-own [ orient reorient step my-neighbors ] ; assigns two variables "orient" (sets turtle
direction) and "step" (determines length of turtle's move in set direction) of turtles
```

to setup ; procedure to reset netlogo interface once setup button is pressed after one run of various code procedures

```

ca ; clears the world
resize-world 0 2000 -500 500 ; resizes the netlogo world to prescribed specifications
set dead-count 0 ; sets the value of dead-count to zero for counting when code runs
ask patches ; code within ensuing square brackets gives initialization commands to patches to
setup foundational world interface for running simulation experimentation
[
  ifelse (pxcor > 1) or (pycor > 0.5) or (pycor < -0.5) ; creates a natal patch that is 10 units wide
  along the x-axis (starting at origin (0,0), to the left boundary of the
  ; world), and 10 units above and below the origin along the y-axis
  [set pcolor green] ; sets the color of place in the world, outside of the natal patch boundary to
  green
  [set pcolor blue] ; sets the color of the natal patch yellow
]
crt number-turtles ; creates a 1000 turtle dispersers
[
  pu ; pen-up, do not trace path of turtles
  setxy ( 0 + random 1) (-0.5 + random 1) ; randomly positions the each of the thousand turtles
  within and immediately around the natal patch
  set heading random 360 ; sets the initial direction of the turtles to a random angle between 0 and
  360 degrees
  set color black ; sets the color of each of the 100 turtles to yellow
  set size 3 ; sets the size each of the 1000 turtles to yellow
  set shape "turtle" ; assigns a "turtle" shape to each of the 100 turtles
  ; set pen-size 0.1 ; sets size of trajectory trace for dispersers
  set start-patch patch-here ; sets the start patch to be the patch that each turtle is in at the start of
  each walk run
]
reset-ticks ; resets timesteps to 0 when setup button is pressed
set dead-turt turtles with [ color = red ] ; sets patch color at turtle death locations from green to
yellow
set live-turt turtles with [ color != red ]
end ; end of setup procedure

```

to-report turning-angle-range [#min #max] ; function for determining the initial turning angle preceding any given move as a random floating number within a specified range

```

report #min + random-float ( #max - #min ) ; calculates and reports range of turning angles for
turtles to undertake during movement
end ; end of turning angle range calculation and reporting procedure

```

to-report turning-angles-dist [#correlation] ; wrapped Cauchy turning distribution function for correlated random walk with correlation coefficient as input

```

let turning-angle ( ( 1 - #correlation ) * tan ( 180 * ( random-float 1 - 0.5 ) ) ) / ( 1 + #correlation ) ;
wrapped Cauchy distribution formula

```

```

report 180 - ( 2 * atan 1 turning-angle ) ; orientation randomizer
end ; end of correlated random walk wrapped Cauchy distribution function

```

```

to-report power-law-dist [ #norm-constant #min-step-length #scale-exponent ] ; function defining
a power law distribution for levy walk based on the normalization constant, the
; minimum step length and the scaling exponent of the distribution
set scale-exponent #scale-exponent ; sets the scaling exponent of the power law distribution
function to a randomly generated scaling exponent variable
let randomizer random-float 1
let min-step-length ( #norm-constant * #min-step-length * ( 1 - randomizer ) ^ ( - 1 / #scale-
exponent ) ) ; calculates the minimum step length executed by levy walkers from
;the normalization constant, scaling exponent and minimum step length of the power law function
report min-step-length ; produces the step length for the levy walk
end ; end of power-law distribution for calculation and reporting procedure for defining turtle levy
walk step length

```

```

to write-csv [ #filename #items ] ; function that allows that creates a csv file for writing data to
using filename and items (list entry) as variables
if is-list? #items and not empty? #items ; #items is a list of the data (or headers!) to write
[ file-open #filename ; opens file for output export into file as input by given filename
set #items map quote #items ; quote non-numeric items
ifelse length #items = 1 [ file-print first #items ] ; print the items
[file-print reduce [ [?1 ?2] -> (word ?1 "," ?2) ] #items] ; if only one item, print it
file-close ; close file once output export is complete (when code stops running)
]
end ; end of procedure for exporting essential simulation output to comma-separated-value file

```

```

to-report xcor-mean [ xcors ] ; reports mean x-coordinate location of a patch or turtle set relative
to edges of the world
let angles map [ x -> 360 * (x - (min-pxcor - 0.5)) / world-width ] xcors ; maps out the mean x-
coordinate location
let mean-x mean map cos angles ; determines the cosine of mean x-coordinate location to
determine position relative to horizontal edge
let mean-y mean map sin angles ; determines the sine of mean x-coordinate location to determine
position relative to vertical edge
report (atan mean-y mean-x) / 360 * world-width + (min-pxcor - 0.5) ; determines mean position
relative to edges of world
end ; end of mean x-position calculation function

```

```

to-report ycor-mean [ ycors ] ; reports mean y-coordinate location of a patch or turtle set relative
to edges of the world
let angles map [ y -> 360 * (y - (min-pycor - 0.5)) / world-height ] ycors ; maps out the mean y-
coordinate location
let mean-x mean map cos angles ; determines the cosine of mean y-coordinate location to
determine position relative to horizontal axis

```

```

let mean-y mean map sin angles ; determines the sine of mean y-coordinate location to determine
position relative to vertical axis
report (atan mean-y mean-x) / 360 * world-height + (min-pycor - 0.5) ; determines mean position
relative to edges of world
end ; end of mean x-position calculation function

```

```

to-report cluster-distance [ cluster1 cluster2 ] ; reports location or distance of conspecific clusters
relative to each other in world
let x1 xcor-mean [ xcor ] of turtle-set cluster1 ; determines x-coordinate location of first cluster
let y1 ycor-mean [ ycor ] of turtle-set cluster1 ; determines y-coordinate location of first cluster
let x2 xcor-mean [ xcor ] of turtle-set cluster2 ; determines x-coordinate location of second cluster
let y2 ycor-mean [ ycor ] of turtle-set cluster2 ; determines y-coordinate location of second cluster
report sqrt ((x1 - x2) ^ 2 + (y1 - y2) ^ 2) ; determines distance between first and second cluster
end ; end of interclust-live distance function

```

```

to-report quote [ #thing ] ; function that allows for string formatted entries to be included in
inverted commas as listable items in the csv file so that row/column headings,
;as well as no-value numbers may be added
ifelse is-number? #thing ; queries whether reported entry is a number
[ report #thing ] ; reports number if entry is a number
[ report (word "\"" #thing "\"") ] ; reports text in quotes if entry is text so that it can be recognized
as a string
end ; end of entry formatting procedure for simulation output export to csv

```

```

to-report radial-extent [ cluster ] ; report function for the radial extent of a conspecific cluster
report max map [ ; reports function for cluster
a -> max map [ ; maps the maximum distance of the spread of a conspecific cluster
b -> [
distance a ] of b ; considers the distance of spread across a cluster
]
cluster ; cluster radial extent identifier
]
cluster ; reported cluster radial extent value
end

```

```

to Pass-Away-Time ; procedure for determining incurred turtle (time-based) per timestep as turtles
navigate world regardless of movement strategy (Levy or CRW)
let chances-time random-float 1 ; set the chances of death to a random floating-point number
between 0 and 1
if ( color = black ) [
if ( chances-time <= mortality ) [ ; determine if the chances of death supersede that of the fixed
mortality level
set color red ; set the color of the patch at the location of the turtle death to yellow
set dead-count dead-count + 1 ; adds 1 onto the original value of dead-count parameter to track
turtle death
;die ; kill the turtle

```

```

    ]
  ]
  if ( color = yellow ) [
    ;if ( num-neighbors > 1 ) [
    ;if ( density-dependence = "positive" ) [
      if ( conspecific-survival = "positive-effect" ) [
        ; if ( chances-time <= ( mortality / num-neighbors ) ) [
          if ( chances-time <= ( mortality / 2 ) ) [
            set color red
            set dead-count dead-count + 1
            set consp-count consp-count - 1
            ;die
          ]
        ]
      ;if ( density-dependence = "negative" ) [
        if ( conspecific-survival = "negative-effect" ) [
          ; if ( chances-time <= ( mortality * num-neighbors ) ) [
            if ( chances-time <= ( mortality * 2 ) ) [
              set color red
              set dead-count dead-count + 1
              set consp-count consp-count - 1
              ;die
            ]
          ]
        ]
      ;]
    ]
  ]
  if ( ticks = ( duration ) ) [
    if ( non-consp-count > 0 ) [
      if ( color = black ) [
        die
      ]
    ]
  ]
]
end ; end of the procedure for assessing turtle cumulative mortality as a function of constant
instantaneous (discrete) per-timestep hazard

```

to Pass-Away-Space ; procedure for calculating the per-step incurred turtle mortality (space-based_ per timestep as turtles navigate world regardless of movement strategy (Levy or CRW)

let int-step round step ; rounds the step-lengths generated for turtles to the nearest whole number and assigns them as a variable

let count-up 1 ; sets a counter, starting at 1

while ; looped set of instructions assigned to each turtle in brackets following the ensuing bracket statement, given the condition in them

```

[
  count-up <= int-step ; while the counter is less than the number of times the rounded turtle step-
lengths is divisible by 1, the statements in ensuing brackets are conducted

```

```

]
[
  set count-up count-up + 1
  let chances-space random-float 1 ; assign a random number floating point number (from a
uniform-random distribution) between 0 and 1 to each turtle as its mortality
  ;level in each unit move
  if ( chances-space <= mortality ) [ ; if statement on the condition that the random mortality value
assigned to each turtle is below the specified mortality rate for all turtles and if condition is satisfied
then the following statements are performed
    set color red ; turn all patches upon which turtle whose randomly generated mortality exceeds
the specified mortality (hazard) rate to yellow
    set dead-count dead-count + 1 ; increase the dead-count value by 1
    ;die ; instruct turtle to die
  ]
]
end ; ends of procedure for assessing turtle mortality as a function of constant per-step hazard
mortality rate as function of space

```

to Pass-Away ; procedure to invoke either time or space-based mortality functions as when corresponding interface switch is turned on or off

```

;ask turtles with [ color = black ] [ ; just added this line
ifelse space-death ; queries if switch at interface names space-death is turned on
[
  Pass-Away-Space
]
[ ; calls the space-based mortality function to orchestrate turtle deaths as a function of constant
per-step hazard rate, variable on distance from starting patch of
  ;world
  Pass-Away-Time ; otherwise maintains regular per-timestep mortality at constant hazard rate
regardless of distance of turtles from origin of world
]
;]
end ; ends procedure to operate switch that operates alternating between time and space-based
(distance assessment) cumulative mortality on constant hazard function

```

to settle

```

set my-neighbors ( other turtles with [ color = yellow ] ) in-radius percep-range
set num-neighbors count my-neighbors
if ( color = black ) [
  let rand-settle random-float 1
  if ( conspecific-behavior = "attraction" ) [
    if ( conspecific-effect = "multiplicative" ) [
      set consp-settle ( settle-prob * ( num-neighbors + 1 ) )
    ]
    if ( conspecific-effect = "exponential" ) [
      set consp-settle ( 1 - ( ( 1 - settle-prob * ( num-neighbors + 1 ) ) ^ ( num-neighbors + 1 ) ) )
    ]
  ]
]

```

```

]
]
if ( conspecific-behavior = "avoidance" ) [
  if ( conspecific-effect = "multiplicative" ) [
    set consp-settle ( settle-prob / ( num-neighbors + 1 ) )
  ]
  if ( conspecific-effect = "exponential" ) [
    set consp-settle ( 1 - ( ( 1 - settle-prob / ( num-neighbors + 1 ) ) ^ ( 1 / ( num-neighbors +
1 ) ) ) )
  ]
]
]
if ( conspecific-behavior = "null" ) [
  set percep-range 0
  set num-neighbors 0
  set consp-settle settle-prob
]
if ( rand-settle <= consp-settle ) [
  set consp-count consp-count + 1
  set color yellow
]
]
end

```

to Corr-Rand-Move ; movement procedure for correlated random walk

```

;pen-down ; marks the path traveled by each turtle while performing correlated random walk
set orient turning-angles-dist corr-eff ; assigns turtle orientation to a random turning angle from
the wrapped Cauchy distribution function based on a correlation
;coefficient of 0.5 and mean turning angle of 90 degrees
set heading heading + one-of [-1 1] * orient ; sets the correlated random walk turtle heading or
orientation to random angle selected from the Cauchy distribution
;set step weibull-dist norm-constant scale-exponent mean-move-length ; sets a scaled step length
to be chosen from a Weibull distribution function
set step mean-move-length
fd step ;advances forward a scaled multiple of selected step length
end ; end of movement procedure for correlated random walk

```

to Find-Corr-Consp-Clusters-n-Plot

```

let settle-turtles turtles with [ color = yellow ]
if ( count settle-turtles > 3 ) [
  let clusters dbscan:cluster-by-location live-turt 3 percep-range
  (foreach clusters range length clusters [ [g i] ->
    foreach g [
      t -> ask t [
        set label i
      ]
    ]
  ]
]

```

```

))
let corr-num-clusters length clusters
if (corr-num-clusters ) > 1 [
  let corr-max-cluster-density max map length clusters
  let corr-mean-cluster-density mean map length clusters
  let corr-min-cluster-density min map length clusters
  let corr-max-cluster-size max map radial-extent clusters
  let corr-mean-cluster-size mean map radial-extent clusters
  let corr-min-cluster-size min map radial-extent clusters
  let corr-mean-dist-interclust-live mean map [ c1 ->
    mean map [ c2 ->
      cluster-distance c1 c2
    ] remove c1 clusters ; Get distance to all other clusters but c1
  ] clusters
  let corr-max-dist-interclust-live max map [ c1 ->
    max map [ c2 ->
      cluster-distance c1 c2
    ] remove c1 clusters ; Get distance to all other clusters but c1
  ] clusters
  let corr-min-dist-interclust-live min map [ c1 ->
    min map [ c2 ->
      cluster-distance c1 c2
    ] remove c1 clusters ; Get distance to all other clusters but c1
  ] clusters
  if ( ticks <= duration ) ; while the number of timesteps is greater than 0 and less than the prescribed
  limit (duration at interface) perform the code content in the ensuing
  ; square brackets
  [ ; comma separated output to command center window
    output-type "CorrNumberClusters" output-type "," output-type corr-num-clusters output-type
    ","
    output-type "CorrMaxClusterDensity" output-type "," output-type corr-max-cluster-density
    output-type ","
    output-type "CorrMeanClusterDensity" output-type "," output-type corr-mean-cluster-density
    output-type ","
    output-type "CorrMinClusterDensity" output-type "," output-type corr-min-cluster-density
    output-type ","
    output-type "CorrMaxClusterSize" output-type "," output-type corr-max-cluster-size output-
    type ","
    output-type "CorrMeanClusterSize" output-type "," output-type corr-mean-cluster-size output-
    type ","
    output-type "CorrMinClusterDensity" output-type "," output-type corr-min-cluster-density
    output-type ","
    output-type "CorrMeaninterclust-Distance" output-type "," output-type corr-mean-dist-
    interclust-live output-type ","
    output-type "CorrMaxinterclust-Distance" output-type "," output-type corr-max-dist-interclust-
    live output-type ","

```



```

output-type "CorrMininterclust-Distance" output-type "," output-type corr-min-dist-interclust-
live output-type ","
write-csv "CorrClustRandWalkLiveResults.txt" ( list "NumberClusters" corr-num-clusters
"Corr Max Cluster Density" corr-max-cluster-density
"Corr Mean Cluster Density" corr-mean-cluster-density
"Corr Min Cluster Density" corr-min-cluster-density
"Corr Max Cluster Size" corr-max-cluster-size
"Corr Mean Cluster Size" corr-mean-cluster-size
"Corr Min Cluster Size" corr-min-cluster-size
"Corr Mean interclust Distance" corr-mean-dist-interclust-live
"Corr Max interclust Distance" corr-max-dist-interclust-live
"Corr Min interclust Distance" corr-min-dist-interclust-live)
; writes maximum turtle displacement, turtle displacement range, turtle peak density and
distance to peak density to a csv file dubbed CorrRandomWalk, per timestep
set-current-plot "CRW Cluster Density Metrics" ;sets the correlated random walk plot to be
updated with each tick
set-current-plot-pen "corr-num-clusters"
set-plot-pen-color red ; set plot pen color to black
plot corr-num-clusters ; plots the maximum turtle distance covered by the turtles doing
correlated random walk at each timestep or tick
set-current-plot-pen "corr-max-cluster-density"
set-plot-pen-color blue ; set plot pen color to blue
plot corr-max-cluster-density ; plots the range of distances covered by turtles doing
correlated random walk at each timestep or tick
set-current-plot-pen "corr-mean-cluster-density"
set-plot-pen-color yellow ; set plot pen color to yellow
plot corr-mean-cluster-density ; plot the distance to peak density of turtles doing correlated
random walk at each timestep or tick
set-current-plot-pen "corr-min-cluster-density"
set-plot-pen-color grey ; set plot pen color to yellow
plot corr-min-cluster-density ; plot the distance to peak density of turtles doing correlated
random walk at each timestep or tick
set-current-plot "CRW Cluster Size Metrics"
set-current-plot-pen "corr-max-cluster-size"
set-plot-pen-color black ; set the plot pen color to green
plot corr-max-cluster-size ; plot the peak density of turtles doing correlated random walk at
each timestep or tick (per prescribed area)
set-current-plot-pen "corr-mean-cluster-size"
set-plot-pen-color green ; set plot pen color to yellow
plot corr-mean-cluster-size ; plot the distance to peak density of turtles doing correlated
random walk at each timestep or tick
set-current-plot-pen "corr-min-cluster-size"
set-plot-pen-color orange ; set plot pen color to yellow
plot corr-min-cluster-size ; plot the distance to peak density of turtles doing correlated
random walk at each timestep or tick
set-current-plot "CRW Inter-cluster Metrics"

```

```

    set-current-plot-pen "corr-mean-dist-interclust"
    set-plot-pen-color black ; set the plot pen color to green
    plot corr-mean-dist-interclust-live ; plot the peak density of turtles doing correlated random
walk at each timestep or tick (per prescribed area)
    set-current-plot-pen "corr-max-dist-interclust"
    set-plot-pen-color red ; set plot pen color to yellow
    plot corr-max-dist-interclust-live ; plot the distance to peak density of turtles doing
correlated random walk at each timestep or tick
    set-current-plot-pen "corr-min-dist-interclust"
    set-plot-pen-color yellow ; set plot pen color to yellow
    plot corr-min-dist-interclust-live ; plot the distance to peak density of turtles doing correlated
random walk at each timestep or tick
  ]
]
]
end ; end of procedure for simulation data and plot generation for living correlated random walkers

```

to Corr-Export-n-Plot-Live ; procedure for simulation data and plot generation for living correlated random walkers

```

let live-corr-turtles turtles with [ color != red ]
if ( count live-corr-turtles >= 1 ) [
  let corr-max-distance max [ distance start-patch ] of live-corr-turtles ; calculates the maximum
turtle distance from the starting patches
  let corr-min-distance min [ distance start-patch ] of live-corr-turtles ; calculates the minimum
turtle distance from the starting patches
  let corr-range ( corr-max-distance - corr-min-distance ) ; determines range of levy-walk turtles
  let corr-peak-density-turtle max-one-of live-corr-turtles [ count live-corr-turtles with [ distance
myself < density-area ] ] ; locate turtle with greatest number of surrounding turtles within
;prescribed area or region
  let corr-peak-density [ count live-corr-turtles with [ distance myself < density-area ] ] of corr-
peak-density-turtle ; determines the number of surrounding turtles for the located
;turtle with the highest number of turtles around it as the peak subsidy density
  let corr-peak-density-distance [ distance start-patch ] of corr-peak-density-turtle ; determines
the distance from the origin of the world to the location of the turtle at
;the center of peak subsidy density of correlated random walkers
  if ( ticks <= duration ) ; while the number of timesteps is greater than 0 and less than the
prescribed limit (duration at interface) perform the code content in the ensuing
  ; square brackets
  [ ; comma separated output to command center window
    output-type "CorrMaxDistance" output-type "," output-type corr-max-distance output-type ","
    output-type "CorrRange" output-type "," output-type corr-range output-type ","
    output-type "CorrPeakDensity" output-type "," output-type corr-peak-density output-type ","
    output-type "CorrDistancetoPeakDensity" output-type "," output-type corr-peak-density-
distance output-type ","
    write-csv "CorrRandWalkLiveResults.txt" ( list "Corr Max Distance" corr-max-distance
"Corr Range" corr-range

```

```

"Corr Peak Density" corr-peak-density
"Corr Distance to Peak Density" corr-peak-density-distance )
; writes maximum turtle displacement, turtle displacement range, turtle peak density and
distance to peak density to a csv file dubbed CorrRandomWalk, per timestep
set-current-plot "CRW Live Dispersal" ;sets the correlated random walk plot to be updated
with each tick
set-current-plot-pen "corr-max-distance"
set-plot-pen-color black ; set plot pen color to black
plot corr-max-distance ; plots the maximum turtle distance covered by the turtles doing
correlated random walk at each timestep or tick
set-current-plot-pen "corr-range"
set-plot-pen-color blue ; set plot pen color to blue
plot corr-range ; plots the range of distances covered by turtles doing correlated random
walk at each timestep or tick
set-current-plot-pen "corr-peak-density-distance"
set-plot-pen-color red ; set plot pen color to yellow
plot corr-peak-density-distance ; plot the distance to peak density of turtles doing correlated
random walk at each timestep or tick
set-current-plot-pen "corr-peak-density"
set-plot-pen-color green ; set the plot pen color to green
plot corr-peak-density ; plot the peak density of turtles doing correlated random walk at each
timestep or tick (per prescribed area)
]
]
end ; end of procedure for simulation data and plot generation for living correlated random walkers

```

to Corr-consp-Export-n-plot

```

if ( count turtles with [ color = yellow ] ) >= 1 [
let consp-corr-max-distance max [ distance start-patch ] of turtles with [ color = yellow ]
let consp-corr-min-distance min [ distance start-patch ] of turtles with [ color = yellow ]
let consp-corr-range ( consp-corr-max-distance - consp-corr-min-distance )
let consp-corr-peak-density-turtle max-one-of turtles with [ color = yellow ] [ count turtles with
[ distance myself < density-area and ( color = yellow ) ] ]
let consp-corr-peak-density [ count turtles with [ distance myself < density-area and ( color =
yellow ) ] ] of consp-corr-peak-density-turtle
let consp-corr-peak-density-distance [ distance start-patch ] of consp-corr-peak-density-turtle
if ( ticks <= duration ) ; while the number of timesteps is greater than 0 and less than the
prescribed limit (duration at interface) perform the code content in the ensuing square brackets
[ ; comma separated output to command center window
output-type "conspCorrMaxDistance" output-type "," output-type consp-corr-max-distance
output-type ","
output-type "conspCorrRange" output-type "," output-type consp-corr-range output-type ","
output-type "conspCorrPeakDensity" output-type "," output-type consp-corr-peak-density
output-type ","
output-type "conspCorrDistancetoPeakDensity" output-type "," output-type consp-corr-peak-
density-distance output-type ","

```

```

write-csv "conspCorrRandWalkLiveResults.txt" ( list "consp Corr Max Distance" consp-corr-
max-distance
"consp Corr Range" consp-corr-range
"consp Corr Peak Density" consp-corr-peak-density
"consp Corr Distance to Peak Density" consp-corr-peak-density-distance )
; writes maximum turtle displacement, turtle displacement range, turtle peak density and
distance to peak density to a csv file dubbed CorrRandomWalk, per timestep
set-current-plot "CRW conspecific Subsidies" ;sets the correlated random walk plot to be
updated with each tick
set-current-plot-pen "consp-corr-max-distance"
set-plot-pen-color black ; set plot pen color to black
plot consp-corr-max-distance ; plots the maximum turtle distance covered by the turtles
doing correlated random walk at each timestep or tick
set-current-plot-pen "consp-corr-range"
set-plot-pen-color blue ; set plot pen color to blue
plot consp-corr-range ; plots the range of distances covered by turtles doing correlated
random walk at each timestep or tick
set-current-plot-pen "consp-corr-peak-density-distance"
set-plot-pen-color red ; set plot pen color to yellow
plot consp-corr-peak-density-distance ; plot the distance to peak density of turtles doing
correlated random walk at each timestep or tick
set-current-plot-pen "consp-corr-peak-density"
set-plot-pen-color green ; set the plot pen color to green
plot consp-corr-peak-density ; plot the peak density of turtles doing correlated random walk
at each timestep or tick (per prescribed area)
]
]
end

```

to Corr-Export-n-Plot-Dead ; procedure for simulation data and plot generation for dead correlated random walkers

```

let dead-turtles turtles with [ color = red ] ; sets patch color at turtle death locations from green to
yellow
if ( count dead-turtles >= 1 ) [ ; asks if the number of locations of turtle deaths is greater than
unity
let corr-max-dead-distance max [ distance start-patch ] of dead-turt ; determines the maximum
distance among locations of turtle deaths from the world origin or
;start-patch
let corr-min-dead-distance min [ distance start-patch ] of dead-turt ; determines the minimum
distance among locations of turtle deaths from the world origin or
;start-patch
let corr-dead-range ( corr-max-dead-distance - corr-min-dead-distance ) ; determines the range
(difference between maximum and minimum distances) among locations of turtle
;deaths from world origin or start-patch
let corr-peak-dead-density-patch max-one-of dead-turt [ count dead-turt with [distance myself <
density-area ] ] ; determines the center patch at peak density (by

```

```

; density-area parameter) or patches where turtle deaths occur as locale of peak density
let corr-peak-dead-density [count dead-turt with [ distance myself < density-area ] ] of corr-peak-
dead-density-patch ; determines the number of death patches at the
; location of peak dead subsidy density, based on density-area criterion
let corr-peak-dead-density-distance [ distance start-patch ] of corr-peak-dead-density-patch ;
determines the distance from the start-patch or world origin to the location
; of peak death patch density
if ( ticks <= duration ) ; while the timesteps increase
[ ; comma separated output to command center window
output-type "CorrMaxDeadDistance" output-type "," output-type corr-max-dead-distance
output-type ","
output-type "CorrDeadRange" output-type "," output-type corr-dead-range output-type ","
output-type "DeadCount" output-type "," output-type dead-count output-type ","
output-type "CorrPeakDeadDensity" output-type "," output-type corr-peak-dead-density output-
type ","
output-type "CorrDistancetoPeakDeadDensity" output-type "," output-type corr-peak-dead-
density-distance output-print " "
write-csv "CorrRandWalkDeadResults.txt" ( list "Corr Max Dead Distance" corr-max-dead-
distance
"Corr Dead Range" corr-dead-range
"Corr Peak Dead Density" corr-peak-dead-density
"Corr Peak Dead Density Distance" corr-peak-dead-density-distance )
; writes maximum turtle displacement, turtle displacement range, turtle peak density and
distance to peak density to a csv file dubbed CorrRandomWalk, per timestep
; for dead turtles
set-current-plot "CRW Dead Dispersal"
set-current-plot-pen "corr-max-dead-distance"
set-plot-pen-color black ; set plot pen color to black
plot corr-max-dead-distance ; plots the maximum turtle distance covered by the turtles doing
correlated random walk at each timestep or tick
set-current-plot-pen "corr-dead-range"
set-plot-pen-color blue ; set plot pen color to blue
plot corr-dead-range ; plots the range of distances covered by turtles doing correlated random
walk at each timestep or tick
set-current-plot-pen "corr-peak-dead-density-distance"
set-plot-pen-color red ; set plot pen color to yellow
plot corr-peak-dead-density-distance ; plot the distance to peak density of turtles doing
correlated random walk at each timestep or tick
set-current-plot-pen "corr-peak-dead-density"
set-plot-pen-color green ; set the plot pen color to green
plot corr-peak-dead-density ; plot the peak density of turtles doing correlated random walk
at each timestep or tick (per prescribed area)
set-current-plot-pen "dead-count"
set-plot-pen-color grey ; sets the plot pen color for the count of the number of dead turtles to
grey
plot dead-count ; plots the count of the number of dead turtles

```

```

]
]
end ; end of procedure for simulation data and plot generation for dead correlated random walkers

to Correlated-Random-Walk ; the "move" procedure to be executed by turtles performing
correlated random walk
  set move-strat "CRW"
  ask turtles [
    if ( color = yellow ) [
      Pass-Away-Time
      stop
    ]
    if ( color = red ) [
      stop
    ]
  ]
  Corr-Rand-Move ; execute correlated random walk movement strategy for turtles
  settle ; settle by the allocated chance of settlement
  Pass-Away-Time ; call mortality function as needed based on state of interface switch (on, time-
  based or off, space (distance)-based cumulative mortality assessed on constant
  ;per-step hazard rate))
]
  Corr-Export-n-Plot-Live ; outputs and plots results subsidy distribution for living turtles
  executing correlated random walk movement strategy
  Corr-Export-n-Plot-Dead ; outputs and plots results subsidy distribution for dead turtles
  executing correlated random walk movement strategy
  Corr-consp-Export-n-plot
  Find-Corr-Consp-Clusters-n-Plot
  tick ; proceed a timestep
  if ( ticks = duration ) ; queries if the number of timesteps exceeds the assigned duration
  [
    let corr-simfile-label random-float 1.0 ; creates a random number to assign to output file names
    ask turtles with [ color = black ] [ ; plots living CRW dispersers locations and distances
      set-current-plot "CRW Disperser locations"
      set-current-plot-pen "corr-live-location"
      set-plot-pen-color green
      plotxy xcor ycor ; plots x and y location of living CRW dispersers relative to origin of world
      set-current-plot "CRW Disperser Distances"
      set-current-plot-pen "corr-live-distance"
      set-plot-pen-color blue
      plot distance start-patch ; plots distance of living CRW dispersers from start-patch
    ]
    ask turtles with [ color = yellow ] [
      set-current-plot "CRW Disperser locations"
      set-current-plot-pen "consp-corr-location"
      set-plot-pen-color black
    ]
  ]

```

```

    plotxy xcor ycor ; plots x and y locations of living CRW dispersers relative to the origin of the
world
    set-current-plot "CRW Disperser Distances"
    set-current-plot-pen "consp-corr-distance"
    set-plot-pen-color yellow
    plot distance start-patch ; plots the distances of living CRW dispersers from the start-patch
]
ask dead-turt [ ; plots dead CRW dispersers locations and distances
    set-current-plot "CRW Disperser Locations"
    set-current-plot-pen "corr-dead-location"
    set-plot-pen-color brown
    plotxy pxcor pycor ; plots x and y locations of dead CRW dispersers relative to origin of world
    set-current-plot "CRW Disperser Distances"
    set-current-plot-pen "corr-dead-distance"
    set-plot-pen-color red
    plot distance start-patch ; plots distance of dead CRW dispersers from start-patch
]
export-output (word "corr-output" corr-simfile-label ".txt") ; exports output csv file
export-world (word "corr-input" corr-simfile-label ".txt") ; exports world/ parameter
initialization to csv file
export-interface (word "corr-interface" corr-simfile-label ".png") ; exports graphic of interface
as png file
export-all-plots (word "corr-plots " corr-simfile-label ".txt") ; exports plot data to csv file
;setup ; runs initialization setup procedure
stop ; if so, stop the simulation run
]
end ; end Correlated Random Walk turtle procedure

to Levy-Flight-Move ; movement procedure for levy walk
;pen-down ; marks the path travelled by each turtle
set orient turning-angle-range 0 360 ; sets the turning angle orientation or direction of levy walk
for each turtle at the start of each move to a randomly generated
; angle between 0 and 360 degrees
set heading + one-of [-1 1] * orient ; set direction of movement of turtle
set step power-law-dist norm-constant min-move-length scale-exponent ; derives the levy walk
step length from the power law distribution with a normalization constant
; of 0.5, a minimum step length of 0.5 and a scaling exponent of 3
fd step ; moves the turtle forward by the step length described above, as executed in a levy walk
end ; end of movement procedure for Levy Walkers

to Find-Levy-Consp-Clusters-n-Plot
let settle-turtles turtles with [ color = yellow ]
if ( count settle-turtles > 3 ) [
let clusters dbscan:cluster-by-location live-turt 3 percep-range
(foreach clusters range length clusters [ [g i] ->
    foreach g [

```

```

t -> ask t [
  set label i
]
]
])
let levy-num-clusters length clusters
if (levy-num-clusters ) > 1 [
let levy-max-cluster-density max map length clusters
let levy-mean-cluster-density mean map length clusters
let levy-min-cluster-density min map length clusters
let levy-max-cluster-size max map radial-extent clusters
let levy-mean-cluster-size mean map radial-extent clusters
let levy-min-cluster-size min map radial-extent clusters
let levy-mean-dist-interclust-live mean map [ c1 ->
mean map [ c2 ->
  cluster-distance c1 c2
] remove c1 clusters ; Get distance to all other clusters but c1
] clusters
let levy-max-dist-interclust-live max map [ c1 ->
max map [ c2 ->
  cluster-distance c1 c2
] remove c1 clusters ; Get distance to all other clusters but c1
] clusters
let levy-min-dist-interclust-live min map [ c1 ->
min map [ c2 ->
  cluster-distance c1 c2
] remove c1 clusters ; Get distance to all other clusters but c1
] clusters
if ( ticks <= duration ) ; while the number of timesteps is greater than 0 and less than the prescribed
limit (duration at interface) perform the code content in the ensuing
; square brackets
[ ; comma separated output to command center window
output-type "LevyNumberClusters" output-type "," output-type levy-num-clusters output-type
","
output-type "LevyMaxClusterDensity" output-type "," output-type levy-max-cluster-density
output-type ","
output-type "LevyMeanClusterDensity" output-type "," output-type levy-mean-cluster-density
output-type ","
output-type "LevyMinClusterDensity" output-type "," output-type levy-min-cluster-density
output-type ","
output-type "LevyMaxClusterSize" output-type "," output-type levy-max-cluster-size output-
type ","
output-type "LevyMeanClusterSize" output-type "," output-type levy-mean-cluster-size
output-type ","
output-type "LevyMinClusterDensity" output-type "," output-type levy-min-cluster-density
output-type ","

```



```

write-csv "LevyClustRandWalkLiveResults.txt" ( list "NumberClusters" levy-num-clusters
"Levy Max Cluster Density" levy-max-cluster-density
"Levy Mean Cluster Density" levy-mean-cluster-density
"Levy Min Cluster Density" levy-min-cluster-density
"Levy Max Cluster Size" levy-max-cluster-size
"Levy Mean Cluster Size" levy-mean-cluster-size
"Levy Min Cluster Size" levy-min-cluster-size
"Levy Mean interclust-live Distance" levy-mean-dist-interclust-live
"Levy Max interclust-live Distance" levy-max-dist-interclust-live
"Levy Min interclust-live Distance" levy-min-dist-interclust-live)
; writes maximum turtle displacement, turtle displacement range, turtle peak density and
distance to peak density to a csv file dubbed CorrRandomWalk, per timestep
set-current-plot "LW Cluster Density Metrics" ;sets the correlated random walk plot to be
updated with each tick
set-current-plot-pen "levy-num-clusters"
set-plot-pen-color red ; set plot pen color to black
plot levy-num-clusters ; plots the maximum turtle distance covered by the turtles doing
correlated random walk at each timestep or tick
set-current-plot-pen "levy-max-cluster-density"
set-plot-pen-color blue ; set plot pen color to blue
plot levy-max-cluster-density ; plots the range of distances covered by turtles doing
correlated random walk at each timestep or tick
set-current-plot-pen "levy-mean-cluster-density"
set-plot-pen-color yellow ; set plot pen color to yellow
plot levy-mean-cluster-density ; plot the distance to peak density of turtles doing correlated
random walk at each timestep or tick
set-current-plot-pen "levy-min-cluster-density"
set-plot-pen-color grey ; set plot pen color to yellow
plot levy-min-cluster-density ; plot the distance to peak density of turtles doing correlated
random walk at each timestep or tick
set-current-plot "LW Cluster Size Metrics"
set-current-plot-pen "levy-max-clust-size-live"
set-plot-pen-color black ; set the plot pen color to green
plot levy-max-cluster-size ; plot the peak density of turtles doing correlated random walk at
each timestep or tick (per prescribed area)
set-current-plot-pen "levy-mean-cluster-size"
set-plot-pen-color green ; set plot pen color to yellow
plot levy-mean-cluster-size ; plot the distance to peak density of turtles doing correlated
random walk at each timestep or tick
set-current-plot-pen "levy-min-cluster-size"
set-plot-pen-color orange ; set plot pen color to yellow
plot levy-min-cluster-size ; plot the distance to peak density of turtles doing correlated
random walk at each timestep or tick
set-current-plot "LW interclust-live Metrics"
set-current-plot-pen "levy-mean-dist-interclust-live"
set-plot-pen-color black ; set the plot pen color to green

```

```

    plot levy-mean-dist-interclust-live ; plot the peak density of turtles doing correlated random
    walk at each timestep or tick (per prescribed area)
    set-current-plot-pen "levy-max-dist-interclust-live"
    set-plot-pen-color red ; set plot pen color to yellow
    plot levy-max-dist-interclust-live ; plot the distance to peak density of turtles doing
    correlated random walk at each timestep or tick
    set-current-plot-pen "levy-min-dist-interclust-live"
    set-plot-pen-color yellow ; set plot pen color to yellow
    plot levy-min-dist-interclust-live ; plot the distance to peak density of turtles doing
    correlated random walk at each timestep or tick
  ]
]
end ; end of procedure for simulation data and plot generation for living correlated random walkers

```

to Levy-Export-n-Plot-Live ; procedure for simulation data and plot generation for living Levy walkers

```

let live-levy-turtles turtles with [ color != red ]
if ( count live-levy-turtles >= 1 ) [
  let levy-max-distance max [ distance start-patch ] of live-levy-turtles ; calculates the maximum
  turtle distance from the starting patches
  let levy-min-distance min [ distance start-patch ] of live-levy-turtles ; calculates the minimum
  turtle distance from the starting patches
  let levy-range ( levy-max-distance - levy-min-distance ) ; determines range of levy-walk turtles
  let levy-peak-density-turtle max-one-of live-levy-turtles [ count live-levy-turtles with [ distance
  myself < density-area ] ] ; locate turtle with greatest number of surrounding turtles within
  ;prescribed area or region
  let levy-peak-density [ count live-levy-turtles with [ distance myself < density-area ] ] of levy-
  peak-density-turtle ; determines the number of surrounding turtles for the located
  ;turtle with the highest number of turtles around it as the peak subsidy density
  let levy-peak-density-distance [ distance start-patch ] of levy-peak-density-turtle ; determines
  the distance from the origin of the world to the location of the turtle at
  ;the center of peak subsidy density of levy walkers
  if ( ticks <= duration ) ; while the number of timesteps is greater than 0 and less than the
  prescribed limit (duration at interface) perform the code content in the ensuing
  ;square brackets
  [ ; comma separated output to command center window
  output-type "LevyMaxDistance" output-type "," output-type levy-max-distance output-type ","
  output-type "LevyRange" output-type "," output-type levy-range output-type ","
  output-type "LevyPeakDensity" output-type "," output-type levy-peak-density output-type ","
  output-type "LevyDistancetoPeakDensity" output-type "," output-type levy-peak-density-
  distance output-type ","
  write-csv "LevyWalkLiveResults.txt" ( list "Levy Max Distance" levy-max-distance
  "Levy Range" levy-range
  "Levy Peak Density" levy-peak-density
  "Levy Distance to Peak Density" levy-peak-density-distance )

```

```

; writes maximum turtle displacement, turtle displacement range, turtle peak density and
distance to peak density to a csv file dubbed LevyWalk, per timestep
set-current-plot "LW Live Dispersal" ; sets the levy walk plot to be updated with each tick
set-current-plot-pen "levy-max-distance"
set-plot-pen-color black ; sets the plot pen color to black
plot levy-max-distance ; plots the maximum turtle distance covered by the turtles doing levy
walk at each timestep or tick
set-current-plot-pen "levy-range"
set-plot-pen-color blue ; sets the plot pen color to blue
plot levy-range ; plots the range of turtle levy walkers at each timestep or tick
set-current-plot-pen "levy-peak-density-distance"
set-plot-pen-color red ; sets the plot pen color to yellow
plot levy-peak-density-distance ; plots the distance to peak subsidy density of levy walkers at
each timestep
set-current-plot-pen "levy-peak-density"
set-plot-pen-color green ; sets the plot pen color to green
plot levy-peak-density ; plots the peak subsidy density of turtle levy walkers at each timestep
or tick (per prescribed area)
]
]
end ; end of procedure for simulation data and plot generation for living Levy walkers

```

```

to Levy-consp-Export-n-plot
if ( count turtles with [ color = yellow ] ) >= 1 [
let consp-levy-max-distance max [ distance start-patch ] of turtles with [ color = yellow ]
let consp-levy-min-distance min [ distance start-patch ] of turtles with [ color = yellow ]
let consp-levy-range ( consp-levy-max-distance - consp-levy-min-distance )
let consp-levy-peak-density-turtle max-one-of turtles with [ color = yellow ] [ count turtles with
[ distance myself < density-area and ( color = yellow ) ] ]
let consp-levy-peak-density [ count turtles with [ distance myself < density-area and ( color =
yellow ) ] ] of consp-levy-peak-density-turtle
let consp-levy-peak-density-distance [ distance start-patch ] of consp-levy-peak-density-turtle
if ( ticks <= duration ) ; while the number of timesteps is greater than 0 and less than the
prescribed limit (duration at interface) perform the code content in the ensuing
; square brackets
[ ; comma separated output to command center window
output-type "conspLevyMaxDistance" output-type "," output-type consp-levy-max-distance
output-type ","
output-type "conspLevyRange" output-type "," output-type consp-levy-range output-type ","
output-type "conspLevyPeakDensity" output-type "," output-type consp-levy-peak-density
output-type ","
output-type "conspLevyDistancetoPeakDensity" output-type "," output-type consp-levy-peak-
density-distance output-type ","
write-csv "conspLevyRandWalkLiveResults.txt" ( list "consp Levy Max Distance" consp-
levy-max-distance
"consp Levy Range" consp-levy-range

```

```

"consp Levy Peak Density" consp-levy-peak-density
"consp Levy Distance to Peak Density" consp-levy-peak-density-distance )
; writes maximum turtle displacement, turtle displacement range, turtle peak density and
distance to peak density to a csv file dubbed CorrRandomWalk, per timestep
set-current-plot "LW conspecific Subsidies" ;sets the correlated random walk plot to be
updated with each tick
set-current-plot-pen "consp-levy-max-distance"
set-plot-pen-color black ; set plot pen color to black
plot consp-levy-max-distance ; plots the maximum turtle distance covered by the turtles
doing correlated random walk at each timestep or tick
set-current-plot-pen "consp-levy-range"
set-plot-pen-color blue ; set plot pen color to blue
plot consp-levy-range ; plots the range of distances covered by turtles doing correlated
random walk at each timestep or tick
set-current-plot-pen "consp-levy-peak-density-distance"
set-plot-pen-color red ; set plot pen color to yellow
plot consp-levy-peak-density-distance ; plot the distance to peak density of turtles doing
correlated random walk at each timestep or tick
set-current-plot-pen "consp-levy-peak-density"
set-plot-pen-color green ; set the plot pen color to green
plot consp-levy-peak-density ; plot the peak density of turtles doing correlated random walk
at each timestep or tick (per prescribed area)
]
]
end

```

to Levy-Export-n-Plot-Dead ; procedure for simulation data and plot generation for dead Levy walkers

```

set dead-turt turtles with [ color = red ] ; sets patches where turtle deaths occur from green to
yellow
if dead-count >= 1 [ ; asks if the number of locations of turtle deaths is greater than unity
let levy-max-dead-distance max [ distance start-patch ] of dead-turt ; determines the maximum
distance among locations of turtle deaths from the world origin or
; start-patch
let levy-min-dead-distance min [ distance start-patch ] of dead-turt ; determines the minimum
distance among locations of turtle deaths from the world origin or
;start-patch
let levy-dead-range ( levy-max-dead-distance - levy-min-dead-distance ) ; determines the range
(difference between maximum and minimum distances) among locations of turtle
;deaths from world origin or start-patch
let levy-peak-dead-density-patch max-one-of dead-turt [ count dead-turt with [distance myself <
density-area ] ] ; determines the center patch at peak density (by
; density-area parameter) or patches where turtle deaths occur as locale of peak density
let levy-peak-dead-density [count dead-turt with [ distance myself < density-area ] ] of levy-
peak-dead-density-patch ; determines the number of death patches at the
; location of peak death patch density, based on density-area criterion

```

```

let levy-peak-dead-density-distance [ distance start-patch ] of levy-peak-dead-density-patch ;
determines the distance from the start-patch or world origin to the location
; of peak death patch density
if ( ticks <= duration ) ; while timesteps increase but remain beneath prescribed duration limit
[ ; comma separated output to command center window
output-type "LevyMaxDeadDistance" output-type "," output-type levy-max-dead-distance
output-type ","
output-type "LevyDeadRange" output-type "," output-type levy-dead-range output-type ","
output-type "LevyDeadCount" output-type dead-count output-type ","
output-type "LevyPeakDeadDensity" output-type "," output-type levy-peak-dead-density
output-type ","
output-type "LevyDistancetoPeakDeadDensity" output-type "," output-type levy-peak-dead-
density-distance output-print " "
write-csv "LevyWalkDeadResults.txt" (list "Levy Max Dead Distance" levy-max-dead-
distance
"Levy Dead Range" levy-dead-range
"Levy Peak Dead Density" levy-peak-dead-density
"Levy Peak Dead Density Distance" levy-peak-dead-density-distance )
; writes maximum turtle displacement, turtle displacement range, turtle peak density and
distance to peak density to a csv file dubbed CorrRandomWalk, per timestep for
; dead turtles
set-current-plot "LW Dead Dispersal" ; sets the levy walk plot to be updated with each tick
set-current-plot-pen "levy-max-dead-distance"
set-plot-pen-color black ; set plot pen color to black
plot levy-max-dead-distance ; plots the maximum turtle distance covered by the turtles doing
correlated random walk at each timestep or tick
set-current-plot-pen "levy-dead-range"
set-plot-pen-color blue ; set plot pen color to blue
plot levy-dead-range ; plots the range of distances covered by turtles doing correlated random
walk at each timestep or tick
set-current-plot-pen "levy-peak-dead-density-distance"
set-plot-pen-color red ; set plot pen color to yellow
plot levy-peak-dead-density-distance ; plot the distance to peak density of turtles doing
correlated random walk at each timestep or tick
set-current-plot-pen "levy-peak-dead-density"
set-plot-pen-color green ; set the plot pen color to green
plot levy-peak-dead-density ; plot the peak density of turtles doing correlated random walk
at each timestep or tick (per prescribed area)
set-current-plot-pen "dead-count"
set-plot-pen-color grey ; sets the plot pen color for the count of the number of dead turtles to
grey
plot dead-count ; plots the count of the number of dead turtles
]
]
end ; end of procedure for simulation data and plot generation for dead Levy walkers

```

```

to Levy-Walk ; the "move" procedure to be executed by turtles performing the levy walk
  set move-strat "LW"
  ask turtles [
    if ( color = yellow ) [
      Pass-Away-Time
      stop
    ]
    if ( color = red ) [
      stop
    ]
  ]
  Levy-Flight-Move ; execute Levy walk movement strategy for turtles
  settle ; settle by the allocated chance of settlement
  Pass-Away-Time ; call mortality function as needed based on state of interface switch (on,
time-based or off, space (distance)-based cumulative mortality assessed on constant per-step
hazard rate))
]
  Levy-Export-n-Plot-Live ; outputs and plots results of subsidy distribution for living turtles Levy
walk movement strategy
  Levy-Export-n-Plot-Dead ; outputs and plots results of subsidy distribution for living turtles
executing Levy walk movement strategy
  Levy-consp-Export-n-plot
  Find-Levy-Consp-Clusters-n-Plot
  tick ; proceed a timestep
  if ( ticks = duration ) ; queries if the number of timesteps exceeds the assigned duration
  [
    let levy-simfile-label random-float 1.0 ; assigns export output file floating-point number
identifiers
    ask turtles with [ color = black ] [ ; plots locations and distances of living LW dispersers
      set-current-plot "LW Disperser locations"
      set-current-plot-pen "levy-live-location"
      set-plot-pen-color green
      plotxy xcor ycor ; plots x and y locations of living LW dispersers relative to the origin of the
world
      set-current-plot "LW Disperser Distances"
      set-current-plot-pen "levy-live-distance"
      set-plot-pen-color blue
      plot distance start-patch ; plots distances of living LW dispersers from the start-patch
    ]
    ask turtles with [ color = yellow ] [
      set-current-plot "LW Disperser locations"
      set-current-plot-pen "consp-levy-location"
      set-plot-pen-color black
      plotxy xcor ycor ; plots x and y locations of living CRW dispersers relative to the origin of the
world
      set-current-plot "LW Disperser Distances"
      set-current-plot-pen "consp-levy-distance"
    ]
  ]

```

```

set-plot-pen-color yellow
plot distance start-patch ; plots the distances of living CRW dispersers from the start-patch
]
ask dead-turt [ ; plots locations and distances of dead LW dispersers
set-current-plot "LW Disperser Locations"
set-current-plot-pen "levy-dead-location"
set-plot-pen-color brown
plotxy pxcor pycor ; plots x and y locations of dead LW dispersers relative to the origin of the
world
set-current-plot "LW Disperser Distances"
set-current-plot-pen "levy-dead-distance"
set-plot-pen-color red
plot distance start-patch ; plots distances of dead LW dispersers from the start-patch
]
export-output (word "levy-output" levy-simfile-label ".txt") ; exports output to csv file
export-world (word "levy-input" levy-simfile-label ".txt") ; exports world/ initialization
parameters to csv file
export-interface (word "levy-interface" levy-simfile-label ".png") ; exports interface graphic as
png file
export-all-plots (word "levy-plots " levy-simfile-label ".txt") ; exports plot data to csv file
;setup ; runs initialization setup procedure
stop ;if so, stop the simulation run
]
end ; end Levy Walk turtle procedure

```

```

to output ; output procedure for reporting results
if ( ticks <= duration ) [
set live-turt turtles with [ color != red ]
set live-count ( count live-turt )
if ( count live-turt >= 1 ) [
set live-max-dist max [ distance start-patch ] of live-turt ; calculates the maximum turtle distance
from the starting patch
set live-min-dist min [ distance start-patch ] of live-turt ; calculates the minimum turtle distance
from the starting patch
set live-range ( live-max-dist - live-min-dist ) ; calculates range of turtles (difference between
maximum and minimum turtle distance from the starting patch)
set live-mean-dist mean [distance start-patch ] of live-turt ; calculates the mean turtle distance
from the starting patch
set live-peak-dens-entity max-one-of live-turt [ count live-turt with [ distance myself < density-
area ] ] ; locates turtle with maximum number of surrounding turtles by selected
; surrounding radial distance or range
set live-peak-dens [ count live-turt with [ distance myself < density-area ] ] of live-peak-dens-
entity ; counts number of turtles around located peak density turtle as density
; and determines the maximum occurrence as peak subsidy density analogue
set live-peak-dens-dist [ distance start-patch ] of live-peak-dens-entity ; determines distance from
the start-patch (origin of world) to the location of turtle at the center

```

```

; of the area of peak subsidy density of correlated random walkers
]
set dead-turt turtles with [ color = red ]
if ( count dead-turt >= 1 ) [
  set dead-max-dist max [ distance start-patch ] of dead-turt ; calculates the maximum turtle
  distance from the starting patch
  set dead-min-dist min [ distance start-patch ] of dead-turt ; calculates the minimum turtle distance
  from the starting patch
  set dead-range ( dead-max-dist - dead-min-dist ) ; calculates range of turtles (difference between
  maximum and minimum turtle distance from the starting patches)
  set dead-mean-dist mean [distance start-patch ] of dead-turt ; calculates the mean turtle distance
  from the starting patch
  set dead-peak-dens-entity max-one-of dead-turt [ count dead-turt with [ distance myself <
  density-area ] ] ; locates turtle with maximum number of surrounding turtles by
  ; selected surrounding radial distance or range
  set dead-peak-dens [ count dead-turt with [ distance myself < density-area ] ] of dead-peak-dens-
  entity ; counts number of turtles around located peak density turtle as
  ; density and determines the maximum occurrence as peak subsidy density analogue
  set dead-peak-dens-dist [ distance start-patch ] of dead-peak-dens-entity ; determines distance
  from the start-patch (origin of world) to the location of turtle at the center
  ; of the area of peak subsidy density of correlated random walkers
]
set black-turt turtles with [ color = black ]
set non-consp-count ( count black-turt )
set settle-turt turtles with [ color = yellow ]
set consp-count ( count settle-turt )
if ( count settle-turt > 3 ) [
  set db-clusters-live dbscan:cluster-by-location live-turt 3 percep-range
  (foreach db-clusters-live range length db-clusters-live [ [u v] ->
    foreach u [
      w -> ask w [
        set label v
      ]
    ]
  ]
]
)
set cluster-count-live length db-clusters-live
if ( cluster-count-live > 1 ) [
  set max-clust-dens-live max map length db-clusters-live
  set mean-clust-dens-live mean map length db-clusters-live
  set min-clust-dens-live min map length db-clusters-live
  set max-clust-size-live max map radial-extent db-clusters-live
  set mean-clust-size-live mean map radial-extent db-clusters-live
  set min-clust-size-live min map radial-extent db-clusters-live
  ;set consp-max-dist max [ distance start-patch ] of turtles with [ color = yellow ]
  ;set consp-min-dist min [ distance start-patch ] of turtles with [ color = yellow ]
  ;set consp-range ( consp-max-dist - consp-min-dist )

```



```

;set consp-peak-dens-entity max-one-of turtles with [ color = yellow ] [ count turtles with
[ distance myself < density-area and ( color = yellow ) ] ]
;set consp-peak-dens [ count turtles with [ distance myself < density-area and ( color = yellow ) ] ]
of consp-peak-dens-entity
;set consp-peak-dens-dist [ distance start-patch ] of consp-peak-dens-entity
set mean-dist-interclust-live mean map [ 11 ->
mean map [ 12 ->
  cluster-distance 11 12
  ] remove 11 db-clusters-live ; Get distance to all other clusters but c1
] db-clusters-live
set max-dist-interclust-live max map [ 11 ->
max map [ 12 ->
  cluster-distance 11 12
  ] remove 11 db-clusters-live ; Get distance to all other clusters but c1
] db-clusters-live
set min-dist-interclust-live min map [ 11 ->
min map [ 12 ->
  cluster-distance 11 12
  ] remove 11 db-clusters-live ; Get distance to all other clusters but c1
] db-clusters-live
]
]
if ( count dead-turt > 3 ) [
set db-clusters-dead dbscan:cluster-by-location dead-turt 3 percep-range
(foreach db-clusters-dead range length db-clusters-dead [ [n j] ->
  foreach n [
    k -> ask k [
      set label j
    ]
  ]
])
set cluster-count-dead length db-clusters-dead
if (cluster-count-dead > 1 ) [
set max-clust-dens-dead max map length db-clusters-dead
set mean-clust-dens-dead mean map length db-clusters-dead
set min-clust-dens-dead min map length db-clusters-dead
set max-clust-size-dead max map radial-extent db-clusters-dead
set mean-clust-size-dead mean map radial-extent db-clusters-dead
set min-clust-size-dead min map radial-extent db-clusters-dead
;set consp-max-dist max [ distance start-patch ] of turtles with [ color = yellow ]
;set consp-min-dist min [ distance start-patch ] of turtles with [ color = yellow ]
;set consp-range ( consp-max-dist - consp-min-dist )
;set consp-peak-dens-entity max-one-of turtles with [ color = yellow ] [ count turtles with
[ distance myself < density-area and ( color = yellow ) ] ]
;set consp-peak-dens [ count turtles with [ distance myself < density-area and ( color = yellow ) ] ]
of consp-peak-dens-entity

```

```

;set consp-peak-dens-dist [ distance start-patch ] of consp-peak-dens-entity
set mean-dist-interclust-dead mean map [ d1 ->
mean map [ d2 ->
  cluster-distance d1 d2
  ] remove d1 db-clusters-dead ; Get distance to all other clusters but c1
] db-clusters-dead
set max-dist-interclust-dead max map [ d1 ->
max map [ d2 ->
  cluster-distance d1 d2
  ] remove d1 db-clusters-dead ; Get distance to all other clusters but c1
] db-clusters-live
set min-dist-interclust-dead min map [ d1 ->
min map [ d2 ->
  cluster-distance d1 d2
  ] remove d1 db-clusters-dead ; Get distance to all other clusters but c1
] db-clusters-dead
]
]
]
end ; end of results reporting procedure

```

```

to move-turtles ; procedure for batch implementation of both movement strategies in sequence
  if move-strat = "CRW" [ ; checks condition that movement strategy chooser is set to Correlated
Random Walk conditions for simulation
  Corr-Rand-Move ; execute correlated random walk movement strategy for turtles
  ]
  if move-strat = "LW" [ ; Checks condition that movement strategy chooser is set to Levy Walk
conditions for simulation
  Levy-Flight-Move ; calls the simplified levy walk movement strategy procedure for batch
experimentation
  ]
end ; end of sequential batch experimentation implementation of Levy walk procedure

```

```

to go ; procedure performs batch simulations of movement strategies in sequence
  if ticks <= duration [ ; checks the condition that the time passed is less than allotted simulation
duration
  ask turtles [
    if ( color = yellow ) [
      Pass-Away-Time
      stop
    ]
    if ( color = red ) [
      stop
    ]
  ]
  move-turtles ; moves turtles according to different movement strategies for duration in
sequence

```

```

    settle ; settle by the allocated chance of settlement
    Pass-Away-Time ; call mortality function as needed based on state of interface switch (on,
time-based or off, space (distance)-based cumulative mortality assessed on constant
    ; per-step hazard
    ]
    ;output ; outputs values for reporting
    ;consp-output
    ;do-plots ; runs plots of results in sequence
    ;backup-sim-output ; outputs results of simulations to be saved; inputs, processing and output
    tick ; a progression of unit timestep in simulation run
    ]
if ( ( ticks > duration - 3 ) or ( dead-count > duration - 3 ) ) [
    output
]
;backup-sim-output ; outputs results of simulations to be saved; inputs, processing and output
end ; end of batch simulations

```

to do-plots ; procedure that runs plots of results of results in sequence

```

    if move-strat = "CRW" [ ; checks the condition that the current movement strategy choice for
simulation is a Correlated Random walk

```

```

        if ( ticks <= duration ) [

```

```

            Corr-Export-n-Plot-Live ; outputs and plots results subsidy distribution for living turtles
executing correlated random walk movement strategy

```

```

            Corr-Export-n-Plot-Dead ; outputs and plots results subsidy distribution for dead turtles
executing correlated random walk movement strategy

```

```

            Corr-consp-Export-n-Plot

```

```

            Find-Corr-Consp-Clusters-n-Plot

```

```

        ]

```

```

    ]

```

```

    if move-strat = "LW" [ ; checks condition that current movement strategy choice for
simulation is Levy Walk

```

```

        if ( ticks <= duration ) [

```

```

            Levy-Export-n-Plot-Live ; outputs and plots results of subsidy distribution for living turtles
Levy walk movement strategy

```

```

            Levy-Export-n-Plot-Dead ; outputs and plots results of subsidy distribution for living turtles
executing Levy walk movement strategy

```

```

            Levy-consp-Export-n-Plot

```

```

            Find-Levy-Consp-Clusters-n-Plot

```

```

        ]

```

```

    ]

```

```

end ; end of plotting procedure

```

to backup-sim-output ; procedure that backs up all simulation data, including inputs and outputs

```

    if ( ticks = duration or count turtles with [ color = black ] = 0 ) [ ; queries if the number of
timesteps exceeds the assigned duration

```

```

        let simfile-label random-float 1.0 ; creates a random number to assign to output file names

```

```

if move-strat = "CRW"[ ; checks the condition that the current movement strategy choice for
simulation is a Correlated Random walk
  ask turtles with [ color = black ] [ ; plots locations and distances of living CRW dispersers
  set-current-plot "CRW Disperser locations"
  set-current-plot-pen "corr-live-location"
  set-plot-pen-color green
  plotxy xcor ycor ; plots x and y locations of living CRW dispersers relative to the origin of the
world
  set-current-plot "CRW Disperser Distances"
  set-current-plot-pen "corr-live-distance"
  set-plot-pen-color blue
  plot distance start-patch ; plots the distances of living CRW dispersers from the start-patch
]
ask turtles with [ color = yellow ] [
  set-current-plot "CRW Disperser locations"
  set-current-plot-pen "consp-corr-location"
  set-plot-pen-color black
  plotxy xcor ycor ; plots x and y locations of living CRW dispersers relative to the origin of the
world
  set-current-plot "CRW Disperser Distances"
  set-current-plot-pen "consp-corr-distance"
  set-plot-pen-color yellow
  plot distance start-patch ; plots the distances of living CRW dispersers from the start-patch
]
ask dead-turt [ ; plots location and distances of dead CRW dispersers
  set-current-plot "CRW Disperser Locations"
  set-current-plot-pen "corr-dead-location"
  set-plot-pen-color brown
  plotxy pxcor pycor ; plots x and y locations of dead CRW dispersers relative to the origin of
the world
  set-current-plot "CRW Disperser Distances"
  set-current-plot-pen "corr-dead-distance"
  set-plot-pen-color red
  plot distance start-patch ; plots the distances of dead CRW dispersers from the start-patch
]
  export-output (word "corr-output" simfile-label ".txt") ; exports output csv file
  export-world (word "corr-input" simfile-label ".txt") ; exports world/ parameter initialization
to csv file
  export-interface (word "corr-interface" simfile-label ".png") ; exports graphic of interface as
png file
  export-all-plots (word "corr-plots " simfile-label ".txt") ; exports plot data to csv file
]
if move-strat = "LW"[ ; checks the condition that the current movement strategy choice for
simulation is a Correlated Random walk
  ask turtles with [ color = black ] [ ; plots the locations and distances of living LW dispersers
  set-current-plot "LW Disperser locations"

```

```

set-current-plot-pen "levy-live-location"
set-plot-pen-color green
plotxy xcor ycor ; plots the x and y locations of living LW dispersers from the origin of the
world
set-current-plot "LW Disperser Distances"
set-current-plot-pen "levy-live-distance"
set-plot-pen-color blue
plot distance start-patch ; plots the distances of living LW dispersers from the start-patch
]
ask turtles with [ color = yellow ] [
set-current-plot "LW Disperser locations"
set-current-plot-pen "consp-levy-location"
set-plot-pen-color black
plotxy xcor ycor ; plots x and y locations of living CRW dispersers relative to the origin of the
world
set-current-plot "LW Disperser Distances"
set-current-plot-pen "consp-levy-distance"
set-plot-pen-color yellow
plot distance start-patch ; plots the distances of living CRW dispersers from the start-patch
]
ask dead-turt [ ; plots the locations and distances of dead LW dispersers
set-current-plot "LW Disperser Locations"
set-current-plot-pen "levy-dead-location"
set-plot-pen-color brown
plotxy pxcor pycor ; plots the x and y locations of dead LW dispersers relative to the origin of
the world
set-current-plot "LW Disperser Distances"
set-current-plot-pen "levy-dead-distance"
set-plot-pen-color red
plot distance start-patch ; plots the distances of dead LW dispersers from the start-patch
]
export-output (word "levy-output" simfile-label ".txt") ; exports output to csv file
export-world (word "levy-input" simfile-label ".txt") ; exports world/ initialization
parameters to csv file
export-interface (word "levy-interface" simfile-label ".png") ; exports interface graphic as
png file
export-all-plots (word "levy-plots " simfile-label ".txt") ; exports plot data to csv file
]
]
end

to-report output-results ; behaviorspace (batch simulation) report function by movement strategy
subsidy distribution results
set live-turt turtles with [ color != red ]
if ( count live-turt >= 1 ) [

```

```

set live-max-dist max [ distance start-patch ] of live-turt ; calculates the maximum turtle distance
from the starting patch
set live-min-dist min [ distance start-patch ] of live-turt ; calculates the minimum turtle distance
from the starting patch
set live-range ( live-max-dist - live-min-dist ) ; calculates range of turtles (difference between
maximum and minimum turtle distance from the starting patch)
set live-mean-dist mean [distance start-patch ] of live-turt ; calculates the mean turtle distance
from the starting patch
set live-peak-dens-entity max-one-of live-turt [ count live-turt with [ distance myself < density-
area ] ] ; locates turtle with maximum number of surrounding turtles by selected
; surrounding radial distance or range
set live-peak-dens [ count live-turt with [ distance myself < density-area ] ] of live-peak-dens-
entity ; counts number of turtles around located peak density turtle as density
; and determines the maximum occurrence as peak subsidy density analogue
set live-peak-dens-dist [ distance start-patch ] of live-peak-dens-entity ; determines distance from
the start-patch (origin of world) to the location of turtle at the center
; of the area of peak subsidy density of correlated random walkers
]
set dead-turt turtles with [ color = red ]
if ( count dead-turt >= 1 ) [
set dead-max-dist max [ distance start-patch ] of dead-turt ; calculates the maximum turtle
distance from the starting patches
set dead-min-dist min [ distance start-patch ] of dead-turt ; calculates the minimum turtle distance
from the starting patches
set dead-range ( dead-max-dist - dead-min-dist ) ; calculates range of turtles (difference between
maximum and minimum turtle distance from the starting patches)
set dead-peak-dens-entity max-one-of dead-turt [ count dead-turt with [ distance myself <
density-area ] ] ; locates turtle with maximum number of surrounding turtles by
;selected surrounding radial distance or range
set dead-peak-dens [ count dead-turt with [ distance myself < density-area ] ] of dead-peak-dens-
entity ; counts number of turtles around located peak density turtle as
;density and determines the maximum occurrence as peak subsidy density analogue
set dead-peak-dens-dist [ distance start-patch ] of dead-peak-dens-entity ; determines distance
from the start-patch (origin of world) to the location of turtle at the center
; of the area of peak subsidy density of correlated random walkers
if ( count turtles with [ color = yellow ] ) >= 1 [
set consp-max-dist max [ distance start-patch ] of turtles with [ color = yellow ]
set consp-min-dist min [ distance start-patch ] of turtles with [ color = yellow ]
set consp-range ( consp-max-dist - consp-min-dist )
set consp-peak-dens-entity max-one-of turtles with [ color = yellow or color = orange ] [ count
turtles with [ distance myself < density-area and ( color = yellow ) ] ]
set consp-peak-dens [ count turtles with [ distance myself < density-area and ( color = yellow ) ] ]
of consp-peak-dens-entity
set consp-peak-dens-dist [ distance start-patch ] of consp-peak-dens-entity
]
]

```

```

;report ( word "live-max-dist," live-max-dist ",live-min-dist," live-min-dist ",live-range," live-
range ",live-peak-dens," live-peak-dens ",live-peak-dens-dist,"
; live-peak-dens-dist "dead-max-dist," dead-max-dist ",dead-min-dist," dead-min-dist ",dead-
range," dead-range ",dead-peak-dens," dead-peak-dens ",dead-peak-dens-dist,"
; dead-peak-dens-dist ",dead-count," dead-count )
report ( list "live-max-dist" live-max-dist "live-min-dist" live-min-dist "live-range" live-range
"live-peak-dens" live-peak-dens "live-peak-dens-dist" live-peak-dens-dist
"dead-max-dist" dead-max-dist "dead-min-dist" dead-min-dist "dead-range" dead-range
"dead-peak-dens" dead-peak-dens "dead-peak-dens-dist" dead-peak-dens-dist
"dead-count" dead-count "consp-count" consp-count "consp-max-dist" consp-max-dist
"consp-min-dist" consp-min-dist
"consp-range" consp-range "consp-peak-dens-entity" consp-peak-dens-entity "consp-peak-
dens" consp-peak-dens "consp-peak-dens-dist" consp-peak-dens-dist) ; reports results
end ; end of results output/ reporter function

```

-Model Use:

-Info Tab in NetLogo

What is it?

AniSocSub is a spatiotemporally explicit individual-based model that simulates the effect of animal sociality (i.e., conspecific interaction) and movement on animal-transported (i.e., active) subsidy distribution. The model simulates animal movement with conspecific interaction and extracts information about emergent spatial distributions. An example system is emergent amphibians emerging from ponds into surrounding landscapes, settling and dying during dispersal. The model computes displacement, density and clustering metrics of spatial patterns for a population of virtual animals moving from a donor ecosystem to a recipient ecosystem.

How it works

Animals are randomly oriented from the central location (donor ecosystem) at the left vertical boundary of the 1000 by 2000 unit-space (i.e. patch) world and move outward and rightward into the adjacent region (recipient ecosystem). Users can simulate movement and conspecific interaction for up to 1000 virtual animals over a period of up to 1000 timesteps. The model also allows the user to choose between correlated random walk (CRW) and Lévy walk (LW) movement patterns and different mortality risk levels. Users can change the straightness of correlated random walk movement patterns by adjusting the correlation coefficient, as well as alter the degree of step length variability of Lévy walk movement patterns by adjusting the scaling exponent over a comprehensive range of options for each movement type. Users can adjust the global mortality probability virtual dispersers. Users can alter the type of conspecific interaction dispersers experience across three levels; attraction, null, (i.e., no interaction) and avoidance. Users can also adjust the perceptual range and settlement probabilities at which each level conspecific interaction is effectuated. Sociality can either enhance (i.e., a positive effect corresponding to a decrease in mortality probability) or attenuate (i.e., a negative effect corresponding to an increase in mortality) dispersers survival. Users can therefore change the effect of conspecific interaction of disperser survival. Users can also vary the strength of conspecific interaction between a multiplicative (i.e., additive function of number of dispersers) and exponential (i.e., exponential function of the number of dispersers) models. The plots show how living and dead subsidy distribution metrics change with each timestep for each movement

type. Dispersers settle as a function of the number of settled dispersers in their perceptual range. In attraction scenarios, a higher number of settled dispersers within a focal disperser's perceptual range increases the settlement probability above baseline (i.e., global model settlement probability). In avoidance scenarios, the settlement probability decreases with a higher number of settled dispersers around a focal disperser and the settlement probability stays at baseline level in the null (i.e., no conspecific interaction/behavior) scenario. Subsidy distribution metrics include the number of dead subsidies, the maximum subsidy deposition distance (i.e., furthest displaced subsidy) and range (i.e., distance between farthest and least displaced subsidy), the peak density (i.e., greatest density of subsidies) and distance to peak density (i.e., distance to the location where the greatest density of subsidies occurs), maximum cluster size (i.e., radial extent of the most spread-out cluster) and density (i.e., subsidy count in the cluster with the greatest number of subsidies), and the maximum inter-cluster distance (i.e. the distance between the furthest and least displaced subsidies).

How to use it

Specify model inputs (adjust corresponding sliders, switches or choosers - in permitted [ranges]): Number of dispersers (number-turtles - [0,1000]), duration (duration - [0,1000]), Sociality (conspecific-behavior - [attraction|avoidance|null]), Settlement probability (settle-prob - [0,1]), Perceptual range (percep-range - [1,10]), Conspecific interaction effect (conspecific-survival - [positive-effect, negative-effect]), Movement strategy (move-strat - [CRW|LW]), correlation coefficient to vary CRW turning angles (corr-eff - [0,1]), scaling exponent to vary LW step lengths (scale-exp - [0,1]), mean step length for CRW (mean-move-length - [1,5]), minimum step length for LW [min-move-length - [0,1]), mortality level/probability (mortality - [0,0.002]), death as a function of space of time (space-death - [on|off]), radius of patches circumscribing area for peak density estimation (density-area - [0,100]), normalization constant to vary LW frequency of longer step length (norm-const - [0,1]). Upon making desired adjustments, click the "CRW" or "LW" button for dispersers to move according to either CRW or LW from donor ecosystem start patch (brown patch) at center of left vertical boundary of world into adjacent recipient ecosystem (green area). Alternatively, click the "Go" button for dispersers to execute both movement patterns one after the other.

Things to notice

First thing to notice on the model interface is the movement of dispersers from the donor ecosystem or patch into the adjacent recipient ecosystem of the world as the simulation progresses. Note that different parameter combinations result in different virtual animal movement and distribution patterns, particularly depending on movement strategy and scaling coefficients. Note that when dispersers return into the world at the opposite edges if or when they reach either horizontal edge of the world but bounce of vertical edges. Note that dead dispersers that die turn red and stop moving. Influenced by conspecific interaction, settled dispersers also turn yellow and stop moving. Notice updating plots CRW ("Corr-"), LW ("Levy-") and/or with Conspecific ("Consp") subsidy distribution metrics: maximum ("-max-"), minimum ("-min-") and mean ("-mean-") dispersal distance ("-max-distance") and range ("-range") as well peak density ("-peak-density") and distance to peak density ("peak-density-distance"), cluster size (cluster-size) and cluster density ("cluster-density"), number of clusters ("num-clusters") and inter-cluster distance ("dist-interclust") for living ("-live-") and dead ("-dead-") subsidies respectively. Also notice plots for the locations ("-location") and total distances traveled (-

distance) by CRW ("Corr-") and LW ("Levy-") for all living ("-live-") and dead ("-dead-") at the end of simulation duration. Also notice the "dead-count" (i.e., number of dead subsidies) and "consp-count" (i.e., number of living subsidies that settled because of conspecific interaction) monitors as the simulation progresses. Observe all trends for above subsidy distribution metrics in plots and monitors. See "CorrRandomWalk" and "LevyWalk" files in working directory for full results of subsidy distribution metrics by CRW and LW respectively.

Things to try

The model is most useful for performing batch simulations in behavior space (Ctrl+Shift+B). Users can edit a comprehensive list of all model variables to include specific levels or range of parameter space for each variable to conduct fully factorial batch simulations with data output to the working directory. Generate different movement patterns by adjusting the scaling coefficient sliders CRW ("corr-eff") and LW ("scale-exp") from left to right (i.e., increasing) or from right to left (i.e., decreasing) and observe how disperser movements (particularly the difference in disperser step sizes between the two types of movement patterns) and subsidy distribution patterns change. Similarly, move mortality slider and observe changes in the number and distribution of dead dispersers (colored red) and dispersers on the move (colored black), as well as the dead-count monitor. Change the type of conspecific interaction, settlement probability and perceptual range sliders in similar ways and observe difference in the emerging spatial patterns of virtual animal settlement (colored yellow). Be sure to observe corresponding plot trends. For LW, switch space-death on or off and observe how the numbers of distribution of dead dispersers changes between the two states. Finally, switch between positive and negative effects of conspecific survival and observe changes in the distribution of dead and settled dispersers between the two states.

Extending the model

Users can use a Weibull distribution to generate dynamic variation in CRW step lengths around mean-move-lengths instead of using constant step lengths. See commented block of corresponding code and remove comment marks (i.e. semi colon) to experiment. Users may also use other step length and turning angle distributions, run simulations and observe how living and dead subsidy distribution patterns respond. Users can also change world-wrapping or torus conditions and observe corresponding changes in subsidy distribution patterns. The same can be done with the size of the world or the respective donor and recipient ecosystem sizes. Change the range of the turning angle range for LW in the code tab, run simulations and observe how resulting subsidy distribution patterns respond. Users can also switch between different models of the strength of conspecific interaction (i.e. multiplicative and exponential). Users may consider changing the survival models for settled conspecifics from a fixed decrement (positive effect) or increment (negative effect) in mortality probability to a density-dependence model (i.e. as a function of the number of settled conspecifics) - Uncomment corresponding sections of code in "Pass-Away-Time" procedure to explore this option.

NETLOGO FEATURES

The backup-sim-output procedure uses the "export" function in NetLogo to export pictures and details of the world and interface as well as all output and plots at the end of the simulation to the user working directory for troubleshooting, error checking and proofing purposes. The dbscan

extension for density-based clustering assessment is a facile tool for performing clustering analysis on spatially auto-correlated points.

Related models

Related models include:

- Wilensky, U. (1999). NetLogo. <http://ccl.northwestern.edu/netlogo/>. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.

Credits and references

-Earl, J. E., & Zollner, P. A. (2017). Advancing research on animal-transported subsidies by integrating animal movement and ecosystem modelling. *Journal of Animal Ecology*, 86(5), 987-997.

-Earl, J. E., & Zollner, P. A. (2014). Effects of animal movement strategies and costs on the distribution of active subsidies across simple landscapes. *Ecological Modelling*, 283, 45-52.

-Stamps, J., McElreath, R., & Eason, P. (2005). Alternative models of conspecific attraction in flies and crabs. *Behavioral Ecology*, 16(6), 974-980.

-Byers, J. A. (2001). Correlated random walk equations of animal dispersal resolved by simulation. *Ecology*, 82(6), 1680-1690.

-Ghaemi, M., Zabihinpour, Z., & Asgari, Y. (2009). Computer simulation study of the Levy flight process. *Physica A: Statistical Mechanics and its Applications*, 388(8), 1509-1514.

-Stamps, Judy A. "Conspecific attraction and aggregation in territorial species." *The American Naturalist* 131.3 (1988): 329-347.

-Kareiva, P. M., & Shigesada, N. (1983). Analyzing insect movement as a correlated random walk. *Oecologia*, 56(2-3), 234-238.

-Bovet, Pierre, and Simon Benhamou. "Spatial analysis of animals' movements using a correlated random walk model." *Journal of theoretical biology* 131.4 (1988): 419-433.

-Bartumeus, F. (2007). Lévy processes in animal movement: an evolutionary hypothesis. *Fractals*, 15(02), 151-162.

Data Processing and Analysis R version 3.5.3

```
##### Daniel Bampoh #####
```

```
##### Data Analysis #####
```

```
### set working drive for analysis code updates and output
setwd("C:/Users/dbamp/Desktop/Ch_2_Retry")
```

```
### install r packages for random forest and classification analysis
```

```
install.packages("randomForest")
install.packages("rpart")
install.packages("rpart.plot")
install.packages("sandwich")
install.packages("party")
install.packages("rattle")
install.packages("ggplot2")
```

```
### load package libraries
```

```
library(randomForest)
library(sandwich)
library(party)
library(rpart)
library(rpart.plot)
library(rattle)
library(RColorBrewer)
library(ggplot2)
```

```
# read in CRW data file
```

```
AniMoveSubDatMainRF <- read.csv("CRWDataSet.txt", header = TRUE, sep = ",")
names(AniMoveSubDatMainRF)[1] <- "scale.coef"
AniMoveSubDatMainRF
  names(AniMoveSubDatMainRF)
  dim(AniMoveSubDatMainRF)
  str(AniMoveSubDatMainRF)
  summary(AniMoveSubDatMainRF)
```

```
# write and ammended and appended CRW,LW tables to single csv file under one header
```

```
write.csv(file= "AniMoveSubDatFin.txt", x=AniMoveSubDatMainRF, row.names = F)
AniMovSubDatRF <- read.csv("AniMoveSubDatFin.txt", header = TRUE, sep = ",")
AniMovSubDatRF
  names(AniMovSubDatRF)
  dim(AniMovSubDatRF)
  str(AniMovSubDatRF)
  summary(AniMovSubDatRF)
```

```
### order factor levels for independent variables
```

```
AniMovSubDatRF[,c("settle.prob")] = factor(AniMovSubDatRF[,c("settle.prob")],
levels=c(0.001, 0.0025, 0.005, 0.0075, 0.01))
AniMovSubDatRF[,c("percep.range")] = factor(AniMovSubDatRF[,c("percep.range")],
levels=c(1, 3, 5, 7, 10))
AniMovSubDatRF[,c("scale.coef")] = factor(AniMovSubDatRF[,c("scale.coef")], levels=c(0.5,
0.8, 0.9, 0.95, 0.99))
AniMovSubDatRF[,c("conspecific.behavior")] =
factor(AniMovSubDatRF[,c("conspecific.behavior")], levels=c("attraction", "null", "avoidance"))
```

```

#### observe final data structure
AniMovSubDatRF
names(AniMovSubDatRF)
dim(AniMovSubDatRF)
str(AniMovSubDatRF)
summary(AniMovSubDatRF)

#### dependent variable assignments
#dvnamesz <- paste(names(subset(AniMovSubDatRF[,c(8:29)]),
dvnamesz <- paste(names(subset(AniMovSubDatRF[,c(5:24)])),
                    # select = -c(live.min.dist, dead.min.dist))),
                    sep = ',')
dvnamesz
str(dvnamesz)

#### independent variables initialization
#ivnamesz0 <- paste(names(subset(AniMovSubDatRF[,c(1:7)]),
ivnamesz0 <- paste(names(subset(AniMovSubDatRF[,c(1:4)])),
                    # select = -c(density.area, norm.constant))),
                    sep = ', ')
ivnamesz0
str(ivnamesz0)

#### boxplots of dependent variables against independent variables
pdf('ConspCRWBoxplots.pdf')
boxplotz.vars <- list()
for (i in dvnamesz) {
  for (j in ivnamesz0) {
    #dev.new()
    boxz.vars <- as.formula(paste(i, "~", j))
    boxplotz.vars[[i]] <- boxplot(boxz.vars, data = AniMovSubDatRF,
                                main = paste(" CRW with Conspecific Interaction - ", i),
                                xlab = j, ylab = i, cex.axis = 0.3525)
                                #xlab = j, ylab = i, cex.axis = 0.75)
  }
}
dev.off()

#### random forest and classification analysis on data addressing space-based mortality effects
attach(AniMovSubDatRF)

# Conducts manova to test for significance of effect of variation in conspecific interaction
sink("DissCh2SimExpManovaResults.txt", append=TRUE, split=TRUE)
manova.results <- manova(cbind(live.count, dead.count, live.max.dist, dead.max.dist, live.range,
dead.range,
```

```

live.peak.dens, dead.peak.dens, live.peak.dens.dist, dead.peak.dens.dist,
consp.count,
non.consp.count, cluster.count.live, max.clust.dens.live, max.clust.size.live,
max.dist.interclust.live, cluster.count.dead, max.clust.dens.dead,
max.clust.size.dead,
max.dist.interclust.dead)~consppecific.behavior, data = AniMovSubDatRF)
summary(manova.results) # shows manova results
summary.aov(manova.results) # shows anova results within manova summary
sink()
#### Conduct TukeyHSD analysis for multiple pairwise comparisons between conspecific
interaction levels
sink("DissCh2SimExpTukeyResults.txt", append=TRUE, split=TRUE)
aov.test <- list()
for (i in dvnamesz) {
  #dev.new()
  aov.list <- as.formula(paste(i, "~consppecific.behavior"))
  aov.test[[i]] <- aov(aov.list, data = AniMovSubDatRF)
}
aov.summary <- lapply(aov.test, summary)
aov.summary
tukey.summary <- lapply(aov.test, TukeyHSD)
tukey.summary
sink()

#### lists for model results
CARTtreemodelsz <- list() # CART
RFtreemodelsz <- list() # random forest

#### independent variable assignments
#ivnamesz <- paste(names(subset(AniMovSubDatRF[,c(1:7)]),
ivnamesz <- paste(names(subset(AniMovSubDatRF[,c(1:4)])),
# select = -c(density.area, norm.constant))),
collapse = ' + ')
ivnamesz
str(ivnamesz)

#### random forest and classification models accounting for the effects of death as a function of
space (z)
for (y in dvnamesz){
  formz <- as.formula(paste(y, "~", ivnamesz))
  CARTtreemodelsz[[y]] <- rpart(formz, data = AniMovSubDatRF, method = "anova",
# control = rpart.control(minsplit = 600, minbucket = 200, cp = 0.001))
control = rpart.control(minsplit = 2000, minbucket = 2000, cp = 0.001))
  RFtreemodelsz[[y]] <- randomForest(formz, data = AniMovSubDatRF,
improve = 0.001, doBest = TRUE, importance = TRUE, ntree = 2000)
}

```

```

#### classification tree results
sink("DissCh3SimCARTResults.txt", append=TRUE, split=TRUE)
CARTtreemodelsz.summary <- lapply(CARTtreemodelsz, summary)
CARTtreemodelsz.results <- lapply(CARTtreemodelsz, print)
sink()

#### random forest results
sink("DissCh3SimRFResults.txt", append=TRUE, split=TRUE)
RFtreemodelsz.results <- lapply(RFtreemodelsz, print)
RFtreemodelsz.imp <- lapply(RFtreemodelsz, randomForest::importance)
RFtreemodelsz.imp
sink()

#### Classification tree plots
pdf('ConspCRWCART.pdf')
for (var in names(CARTtreemodelsz)){
  #dev.new()
  fancyRpartPlot(CARTtreemodelsz[var][[1]], main = var)
}
dev.off()

#### Pruned classification trees
pdf('ConspCRWCARTPruned.pdf')
for (var in names(CARTtreemodelsz)){
  #dev.new()
  fancyRpartPlot(prune(CARTtreemodelsz[var][[1]],
    cp
    CARTtreemodelsz[var][[1]]$cptable[which.min(CARTtreemodelsz[var][[1]]$cptable[, "xerror"]),
    "CP"]),
    main = var)
}
dev.off()

#### variable importance plots
pdf('ConspCRWRandForsVarImp.pdf')
for (var in names(RFtreemodelsz)){
  #dev.new()
  varImpPlot(RFtreemodelsz[var][[1]], main = var)
}
dev.off()

#### conspecific interaction effect plots
pdf('ConspEffectPlots.pdf')
boxplot.ConspCRW <- list()
for (i in dvnamesz) {

```

```
#dev.new()
ConspCRW <- as.formula(paste(i, "~conspecific.behavior"))
boxplot.ConspCRW[[i]] <- boxplot(ConspCRW, data = AniMovSubDatRF,
                                main = paste("conspecific Interaction Effects - ", i),
                                xlab = "Conspecific Interaction", ylab = i,
                                cex.axis = 0.5)
}
dev.off()
detach(AniMovSubDatRF)
```

APPENDIX C. SUPPLEMENTARY INFORMATION (SI): THE EFFECT OF LANDSCAPE HETEROGENEITY ON ACTIVE SUBSIDY DISTRIBUTION

-Section S: Supplementary Results

- ❖ Classification and Regression Trees (CARTs) of subsidy deposition distribution metrics (Displacement (maximum distance, range and distance to peak density)), Density (peak density) for experiment 1 (i.e., homogeneous landscape: open, partial or closed canopy habitat) and experiment 2 (i.e., heterogeneous landscapes: open, partial and closed canopy), with leaves containing mean response values, number (n) and percentage (%) of data points resulting from predictor splits.

-Section T: Random Forest and CART Error Analysis

- ❖ Subsidy distribution metrics by % IncMSE, IncNodePurity (RSS), % variance explained and misclassification rate for:
 - Forest type, Mean Step Length, Mean Vector Length, Settlement probability, Mortality Probability, Movement probability
- ❖ Descriptive statistics for predictor landscape metrics
- ❖ Statistical significance tests for subsidy distribution metrics with
 - Juvenile wood frog MSL and MVL (See table 1 in Manuscript Mean and CI: [High, Low])
 - Canopy closure
- ❖ Descriptive statistics:
 - Egg mass surveys
 - Pond surveys
 - HEE canopy type proportional composition

Section U: Model Construction

- ❖ Model Overview, Design Concepts, Details (ODD) description:
 - Overview: Purpose, State variables and scale, Process overview and scheduling
 - Design concepts: Emergence, Sensing, Interaction, Stochasticity, Observation
 - Details: Initialization, Inputs, Sub-models

-Section V: Code

- ❖ Code:
 - Model construction: NetLogo Version 6.0.4 Code
 - NetLogo Model description and function
 - Data processing and analysis: R version 3.5.1

-CART Response Variable Notation

Number of dead subsidies: *dead.count*, maximum living subsidy deposition distance: *live.max.dist*, maximum dead subsidy deposition distance: *dead.max.dist*, maximum living subsidy range: *live.range*, maximum dead subsidy range: *dead.range*. peak living subsidy deposition density:

live.peak.dens, peak dead subsidy deposition density: *dead.peak.dens*, distance to peak living subsidy deposition density: *live.peak.dens.dist*, distance to peak dead subsidy deposition density: *dead.peak.dens.dist*, number of living subsidies: *live.count*,

Section S: Supplementary Results

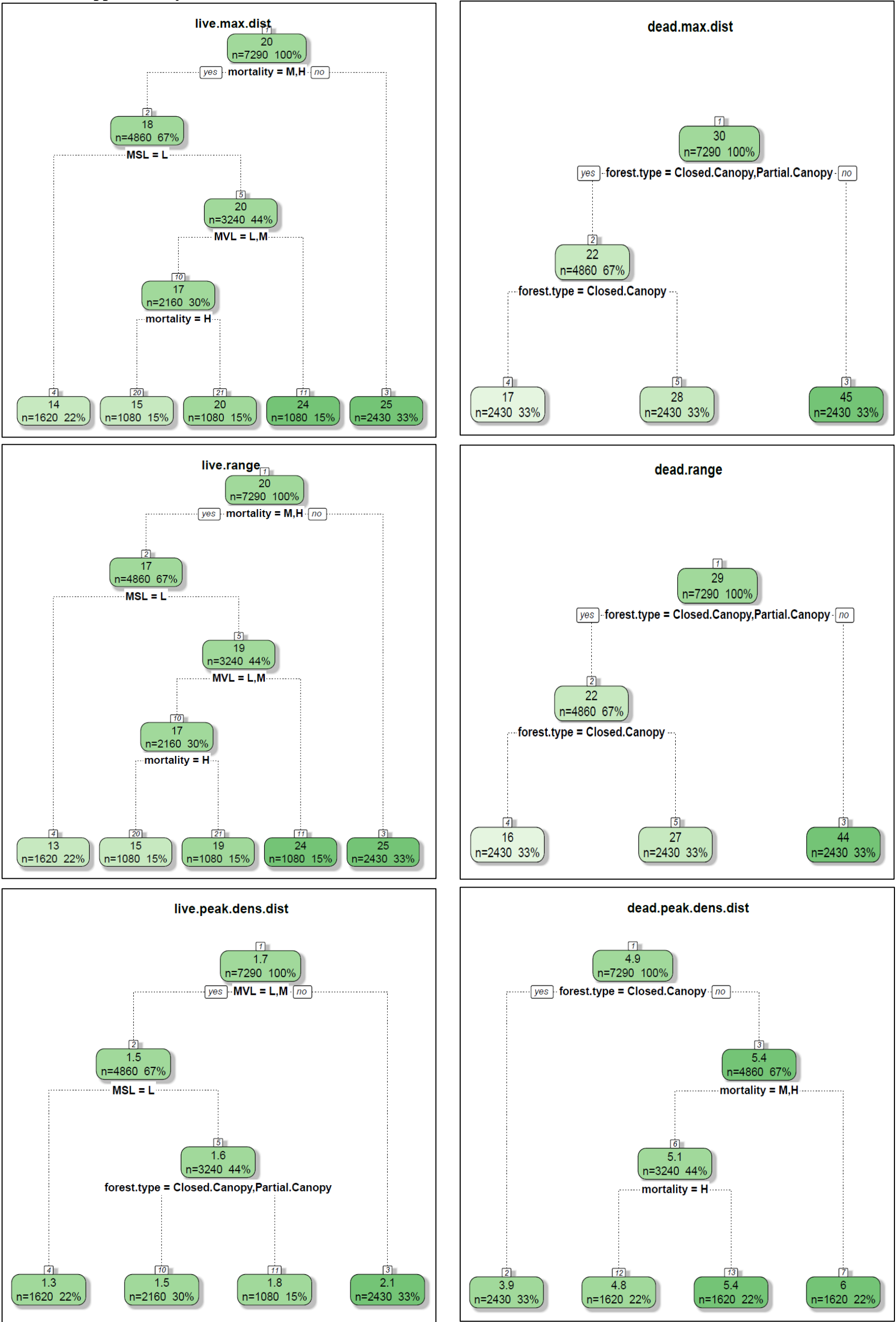


Figure 33 Subsidy displacement trends in homogeneous landscapes. Open canopy cover resulted in the furthest displaced dead subsidies and closed canopy cover limited dead subsidy displacement. Lower mortality results and straighter movements with greater step lengths displace subsidies farthest, particularly for living subsidies. Given high and intermediate mortality levels, more sinuous movements with smaller steps constrained subsidy displacement in recipient ecosystem.

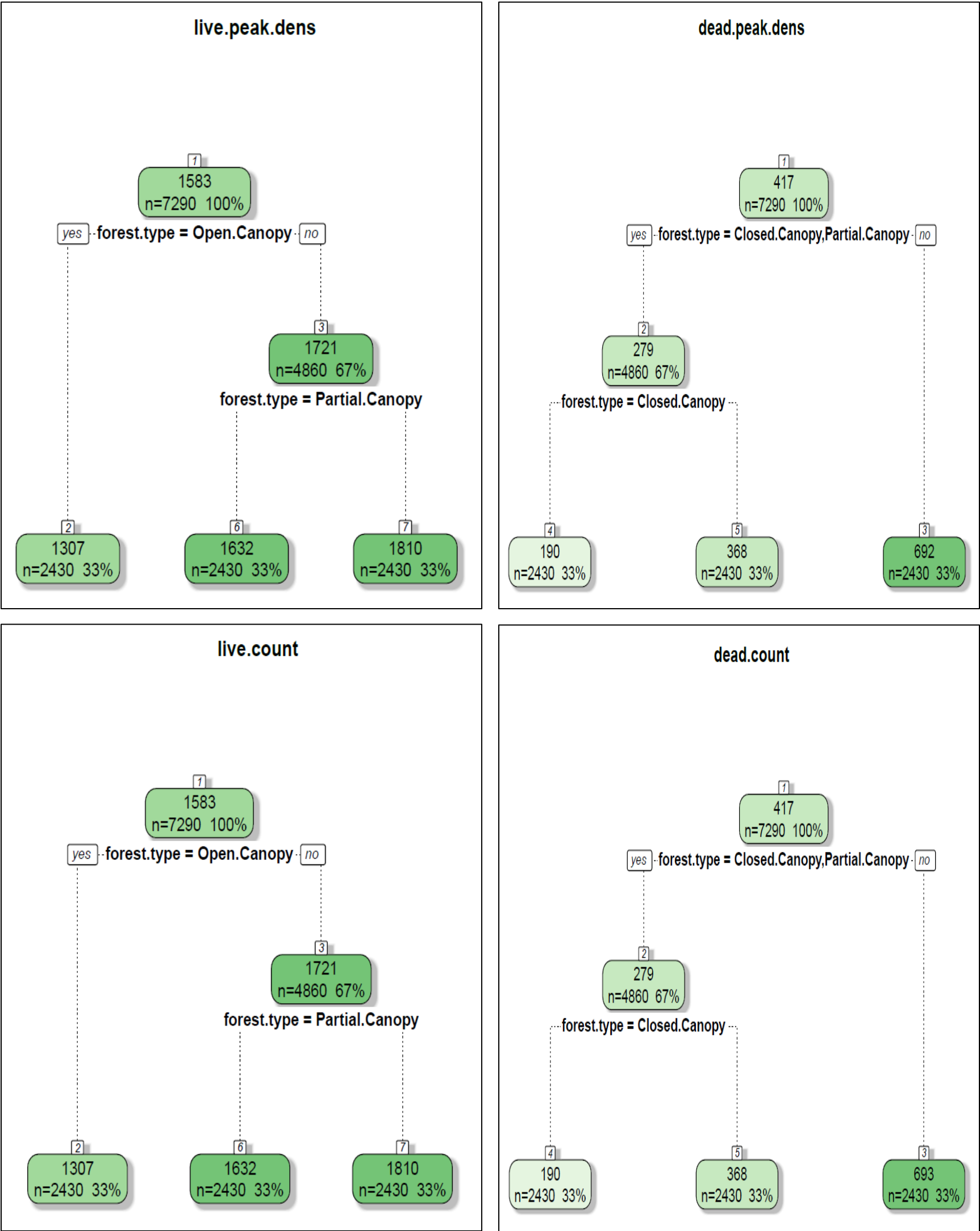


Figure 34 Subsidy density trends in homogeneous landscapes. The density and quantity of living subsidies increased with closed canopy cover and the density of dead subsidies is greatest for open canopy cover.

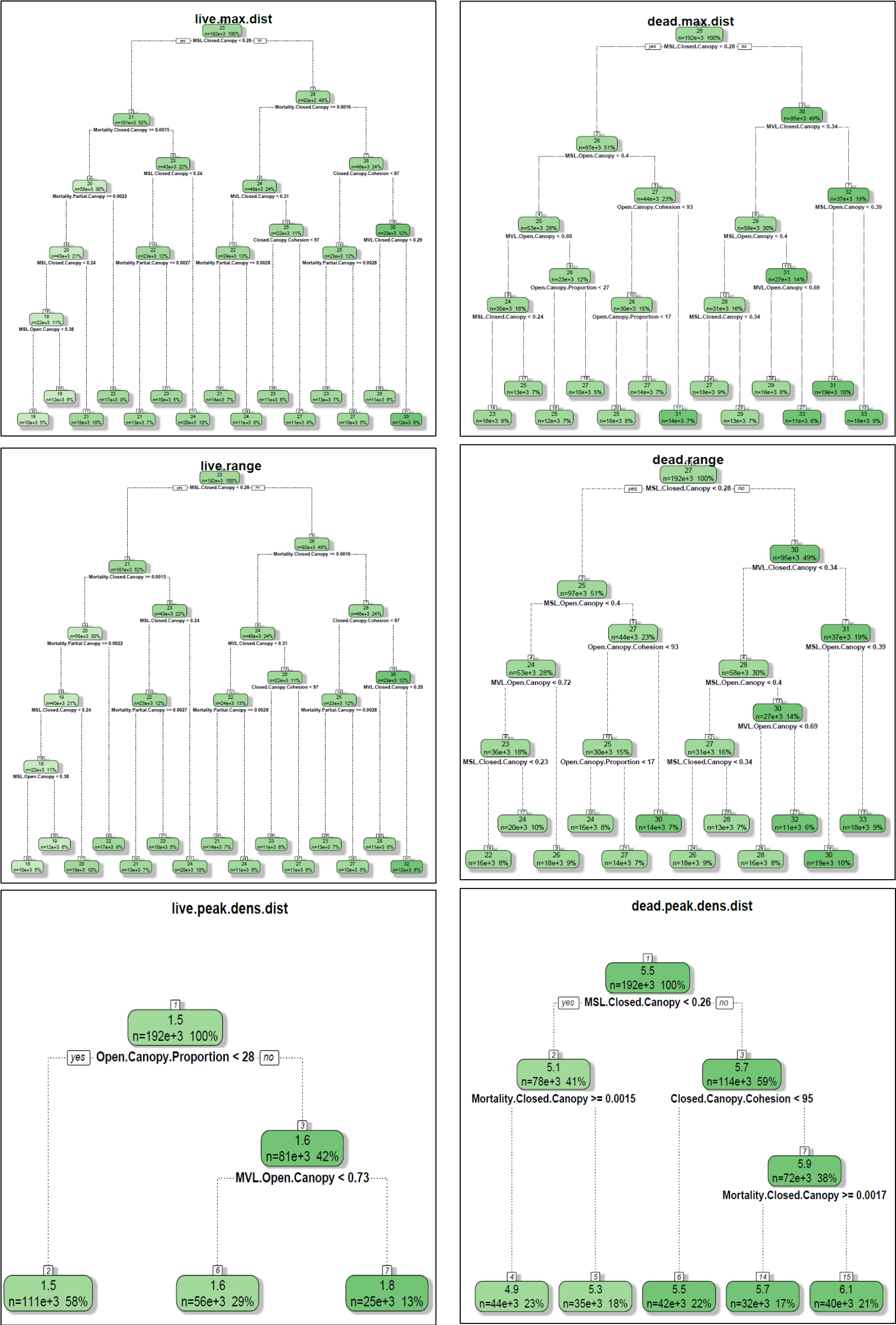


Figure 35 Subsidy displacement trends in heterogeneous landscapes. Given lower mortality and straighter movements with greater step lengths in heterogeneous forests, greater cohesion of closed canopy habitat resulted in greater subsidy displacement. Lower mortality in partial canopy habitat generated intermediate subsidy displacement. Straighter movement in open canopy cover displaced subsidies farther into recipient ecosystems, particularly for dead subsidies.

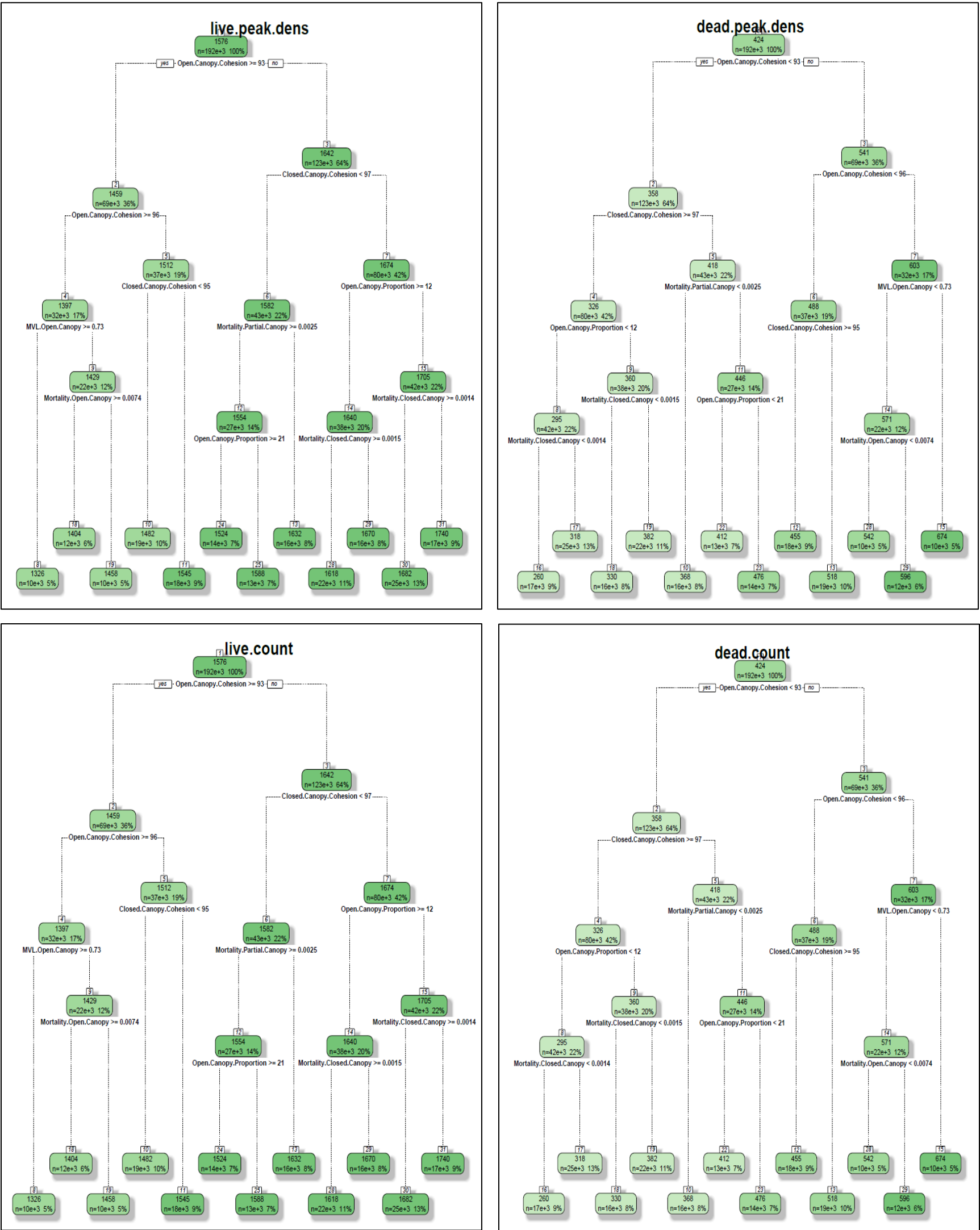


Figure 36 Subsidy density trends in heterogeneous landscapes. Given lower mortality and greater cohesion in closed canopy cover in heterogeneous forests, lower cohesion and proportion of open canopy habitat generated the greatest subsidy deposition densities. Lower mortality in partial canopy forest resulted in intermediate subsidy deposition densities, particularly for living subsidies. More sinuous movement and higher mortality in closed canopy habitat resulted in greater subsidy deposition density, particularly for dead subsidies.

Section T: Random Forest and CART Error Analysis

Table 10 *Increase in percentage means square prediction error (%IncMSE) for metrics of living (consumer) and dead (nutrient) juvenile wood frog subsidy distribution in homogeneous landscapes (i.e., experiment 1).* Values indicate the relative importance as prediction strength of each state variable to subsidy distribution metrics. Larger values indicate greater predictor importance.

| <i>Percentage increase in mean square error of subsidy deposition distribution metric by state variable</i> | | | | | | |
|---|----------------------|------------------------------------|---------------------------------|---|--------------------------------|----------------------------|
| <i>State Variable</i> | <i>Subsidy State</i> | Maximum deposition distance | Maximum deposition range | Peak deposition density distance | Peak deposition density | Number of subsidies |
| <i>Forest Type</i> | <i>Living</i> | 57.71 | 54.58 | 39.34 | 61.79 | 65.18 |
| | <i>Dead</i> | 58.09 | 59.84 | 61.64 | 64.53 | 65.93 |
| <i>Mean Vector Length (m)</i> | <i>Living</i> | 65.81 | 62.74 | 55.36 | 35.33 | 35.19 |
| | <i>Dead</i> | 48.06 | 47.51 | 43.53 | 35.84 | 37.92 |
| <i>Mean Step Length (m)</i> | <i>Living</i> | 62.84 | 61.78 | 40.33 | 14.08 | 16.10 |
| | <i>Dead</i> | 50.92 | 51.49 | 48.02 | 16.75 | 14.78 |
| <i>Mortality Probability</i> | <i>Living</i> | 54.06 | 54.68 | 17.48 | 63.75 | 61.66 |
| | <i>Dead</i> | 43.47 | 41.81 | 50.61 | 62.60 | 64.96 |
| <i>Settlement Probability</i> | <i>Living</i> | 23.14 | 24.08 | 0.27 | 19.22 | 18.96 |
| | <i>Dead</i> | 19.63 | 19.79 | 14.34 | 19.32 | 20.95 |
| <i>Movement Probability</i> | <i>Living</i> | 28.63 | 19.96 | 17.44 | 23.20 | 13.56 |
| | <i>Dead</i> | 12.44 | 17.46 | 16.23 | 19.83 | 15.92 |

Table 11 *Increase in node purity (residual sum of squares) (IncNodePurity (RSS)) for metrics of living (consumer) and dead (nutrient) juvenile wood frog subsidy distribution in homogeneous landscapes (i.e., Experiment 1). Values indicate the relative importance as prediction accuracy of each state variable. Larger values indicate greater predictor precision.*

| <i>Increase in node purity of subsidy deposition distribution metric by state variable</i> | | | | | | |
|--|----------------------|------------------------------------|---------------------------------|---|--------------------------------|----------------------------|
| <i>State Variable</i> | <i>Subsidy State</i> | Maximum deposition distance | Maximum deposition range | Peak deposition density distance | Peak deposition density | Number of subsidies |
| <i>Forest Type</i> | <i>Living</i> | 6.52E+04 | 6.23E+04 | 1.91E+02 | 1.83E+08 | 1.89E+08 |
| | <i>Dead</i> | 5.84E+05 | 5.91E+05 | 2.86E+03 | 1.89E+08 | 1.92E+08 |
| <i>Mean Vector Length (m)</i> | <i>Living</i> | 4.98E+04 | 4.84E+04 | 4.14E+02 | 1.67E+07 | 1.69E+07 |
| | <i>Dead</i> | 1.71E+05 | 1.73E+05 | 6.95E+02 | 1.67E+07 | 1.75E+07 |
| <i>Mean Step Length (m)</i> | <i>Living</i> | 5.84E+04 | 6.01E+04 | 1.85E+02 | 1.05E+06 | 1.08E+06 |
| | <i>Dead</i> | 1.99E+05 | 1.96E+05 | 1.16E+03 | 1.08E+06 | 1.06E+06 |
| <i>Mortality Probability</i> | <i>Living</i> | 7.84E+04 | 7.92E+04 | 8.43E+01 | 3.14E+07 | 3.08E+07 |
| | <i>Dead</i> | 5.65E+04 | 5.38E+04 | 1.13E+03 | 3.08E+07 | 3.16E+07 |
| <i>Settlement Probability</i> | <i>Living</i> | 2.60E+03 | 1.18E+04 | 4.59E+01 | 1.94E+06 | 1.88E+06 |
| | <i>Dead</i> | 1.17E+04 | 2.68E+03 | 2.85E+02 | 1.93E+06 | 1.95E+06 |
| <i>Movement Probability</i> | <i>Living</i> | 3.99E+03 | 5.55E+03 | 7.19E+02 | 4.34E+04 | 1.90E+04 |
| | <i>Dead</i> | 2.16E+03 | 1.99E+03 | 2.12E+03 | 4.57E+03 | 2.15E+04 |

Table 12 Predictor importance measured as increase in percentage mean square prediction error (%IncMSE) for metrics of living (consumer) and dead (nutrient) juvenile wood frog subsidy distribution in heterogeneous landscapes (i.e., experiment 2). Values indicate the relative importance as prediction accuracy of each state variable. Lower values indicate greater predictor precision.

| <i>Percentage increase in mean square error of subsidy deposition distribution metric by state variable</i> | | | | | | |
|---|----------------------|------------------------------------|---------------------------------|---|--------------------------------|----------------------------|
| <i>State Variable</i> | <i>Subsidy State</i> | Maximum deposition distance | Maximum deposition range | Peak deposition density distance | Peak deposition density | Number of subsidies |
| <i>Open Canopy Proportion</i> | <i>Living</i> | 2.56 | 2.64 | 1.74 | 5.09 | 5.00 |
| | <i>Dead</i> | 2.97 | 3.16 | 0.81 | 5.14 | 5.22 |
| <i>Open Canopy Clumpiness</i> | <i>Living</i> | 0.66 | 0.38 | 0.61 | 2.65 | 2.67 |
| | <i>Dead</i> | 1.07 | 0.87 | 0.11 | 2.56 | 2.44 |
| <i>Open Canopy Cohesion</i> | <i>Living</i> | 2.98 | 2.86 | 1.27 | 5.79 | 5.77 |
| | <i>Dead</i> | 3.49 | 3.44 | 1.44 | 5.90 | 5.77 |
| <i>Partial Canopy Proportion</i> | <i>Living</i> | 1.03 | 1.24 | 0.24 | 2.25 | 1.94 |
| | <i>Dead</i> | 1.28 | 1.26 | 1.44 | 2.10 | 2.14 |
| <i>Partial Canopy Clumpiness</i> | <i>Living</i> | 0.48 | 0.55 | 0.27 | 1.08 | 0.71 |
| | <i>Dead</i> | 0.42 | 0.36 | 0.18 | 0.92 | 0.90 |
| <i>Partial Canopy Cohesion</i> | <i>Living</i> | 1.35 | 1.30 | 0.29 | 2.03 | 2.17 |
| | <i>Dead</i> | 1.45 | 1.53 | 1.84 | 2.03 | 2.05 |
| <i>Closed Canopy Proportion</i> | <i>Living</i> | 2.78 | 2.72 | 0.60 | 3.62 | 3.74 |
| | <i>Dead</i> | 1.76 | 2.00 | 2.98 | 3.72 | 3.72 |
| <i>Closed Canopy Clumpiness</i> | <i>Living</i> | 0.39 | 0.40 | 0.40 | 1.60 | 1.65 |
| | <i>Dead</i> | 0.00 | 0.40 | 0.02 | 1.43 | 1.61 |
| <i>Closed Canopy Cohesion</i> | <i>Living</i> | 3.47 | 3.54 | 0.59 | 4.52 | 4.31 |
| | <i>Dead</i> | 1.91 | 2.28 | 2.17 | 4.18 | 4.42 |
| <i>Landscape Contagion</i> | <i>Living</i> | 1.67 | 1.65 | 1.50 | 3.57 | 3.88 |
| | <i>Dead</i> | 1.37 | 1.26 | 1.55 | 3.46 | 3.25 |
| <i>Landscape Contiguity</i> | <i>Living</i> | 0.00 | 0.00 | 0.39 | 0.68 | 0.78 |
| | <i>Dead</i> | 0.23 | 0.23 | 0.59 | 0.82 | 0.81 |
| <i>Landscape Interspersion</i> | <i>Living</i> | 1.05 | 0.94 | 0.62 | 2.89 | 2.75 |
| | <i>Dead</i> | 1.02 | 0.92 | 0.66 | 3.02 | 3.15 |
| <i>MSL in Closed Canopy</i> | <i>Living</i> | 6.26 | 6.29 | 3.82 | 0.74 | 0.83 |
| | <i>Dead</i> | 6.77 | 6.74 | 6.09 | 0.99 | 0.67 |
| <i>MSL in Partial Canopy</i> | <i>Living</i> | 1.31 | 1.53 | 0.17 | 0.23 | 0.00 |
| | <i>Dead</i> | 1.88 | 1.97 | 1.70 | 0.00 | 0.00 |
| <i>MSL in Open Canopy</i> | <i>Living</i> | 3.60 | 3.59 | 3.02 | 0.00 | 0.00 |
| | <i>Dead</i> | 5.82 | 5.36 | 5.00 | 0.00 | 0.23 |
| <i>MVL in Closed Canopy</i> | <i>Living</i> | 4.69 | 4.85 | 3.68 | 0.31 | 0.32 |
| | <i>Dead</i> | 5.06 | 5.02 | 3.50 | 0.46 | 0.43 |
| <i>MVL in Partial Canopy</i> | <i>Living</i> | 2.14 | 2.05 | 2.69 | 0.31 | 0.44 |
| | <i>Dead</i> | 2.53 | 2.42 | 2.35 | 0.17 | 0.17 |
| <i>MVL in Open Canopy</i> | <i>Living</i> | 3.28 | 3.03 | 5.16 | 2.59 | 2.73 |
| | <i>Dead</i> | 4.88 | 5.00 | 3.66 | 2.73 | 2.68 |
| <i>Mortality in Closed Canopy</i> | <i>Living</i> | 5.91 | 5.64 | 2.52 | 2.49 | 2.39 |
| | <i>Dead</i> | 2.82 | 2.76 | 5.46 | 2.30 | 2.34 |
| <i>Mortality in Partial Canopy</i> | <i>Living</i> | 5.11 | 4.98 | 1.40 | 2.56 | 2.61 |
| | <i>Dead</i> | 3.47 | 3.13 | 4.73 | 2.74 | 2.60 |
| <i>Mortality in Open Canopy</i> | <i>Living</i> | 1.66 | 1.92 | 1.43 | 1.33 | 1.51 |
| | <i>Dead</i> | 2.65 | 2.78 | 1.35 | 1.28 | 1.35 |

Table 13 *Predictor precision measured as Increase in node purity (residual sum of squares) (IncNodePurity (RSS)) for metrics of living (consumer) and dead (nutrient) juvenile wood frog subsidy distribution in heterogeneous landscapes (i.e., experiment 2). Values indicate the relative importance as prediction accuracy of each state variable. Lower values indicate greater predictor precision.*

| <i>Increase in node purity for subsidy deposition distribution metric by state variable</i> | | | | | | |
|---|----------------------|------------------------------------|---------------------------------|---|--------------------------------|----------------------------|
| <i>State Variable</i> | <i>Subsidy State</i> | Maximum deposition distance | Maximum deposition range | Peak deposition density distance | Peak deposition density | Number of subsidies |
| <i>Open Canopy Proportion</i> | <i>Living</i> | 1.79E+04 | 1.85E+04 | 2.75E+02 | 3.74E+08 | 3.75E+08 |
| | <i>Dead</i> | 2.58E+04 | 3.07E+04 | 1.36E+02 | 3.97E+08 | 4.05E+08 |
| <i>Open Canopy Clumpiness</i> | <i>Living</i> | 2.77E+02 | 1.21E+02 | 1.17E+01 | 2.64E+07 | 2.72E+07 |
| | <i>Dead</i> | 1.00E+03 | 5.74E+02 | 3.77E+00 | 2.59E+07 | 2.20E+07 |
| <i>Open Canopy Cohesion</i> | <i>Living</i> | 2.30E+04 | 2.17E+04 | 2.61E+02 | 4.72E+08 | 4.81E+08 |
| | <i>Dead</i> | 3.64E+04 | 3.47E+04 | 1.72E+02 | 4.88E+08 | 4.82E+08 |
| <i>Partial Canopy Proportion</i> | <i>Living</i> | 1.83E+03 | 2.15E+03 | 1.07E+01 | 1.02E+07 | 7.38E+06 |
| | <i>Dead</i> | 1.42E+03 | 1.45E+03 | 1.15E+02 | 9.65E+06 | 9.87E+06 |
| <i>Partial Canopy Clumpiness</i> | <i>Living</i> | 4.42E+01 | 6.83E+01 | 1.14E+00 | 7.86E+05 | 4.30E+05 |
| | <i>Dead</i> | 4.01E+01 | 2.39E+01 | 1.94E+00 | 6.17E+05 | 5.04E+05 |
| <i>Partial Canopy Cohesion</i> | <i>Living</i> | 2.25E+03 | 1.90E+03 | 1.18E+01 | 1.11E+07 | 1.13E+07 |
| | <i>Dead</i> | 2.16E+03 | 2.48E+03 | 1.54E+02 | 1.11E+07 | 1.10E+07 |
| <i>Closed Canopy Proportion</i> | <i>Living</i> | 2.90E+04 | 2.87E+04 | 2.18E+02 | 1.74E+08 | 1.82E+08 |
| | <i>Dead</i> | 6.78E+03 | 9.02E+03 | 5.59E+02 | 1.82E+08 | 1.78E+08 |
| <i>Closed Canopy Clumpiness</i> | <i>Living</i> | 1.73E+01 | 4.87E+01 | 3.84E+00 | 1.68E+06 | 2.10E+06 |
| | <i>Dead</i> | 0.00E+00 | 6.43E+00 | 1.69E+00 | 1.98E+06 | 2.29E+06 |
| <i>Closed Canopy Cohesion</i> | <i>Living</i> | 4.50E+04 | 4.74E+04 | 2.56E+02 | 2.74E+08 | 2.35E+08 |
| | <i>Dead</i> | 9.01E+03 | 1.11E+04 | 5.53E+02 | 2.20E+08 | 2.56E+08 |
| <i>Landscape Contagion</i> | <i>Living</i> | 7.96E+03 | 7.86E+03 | 9.12E+01 | 9.52E+07 | 1.10E+08 |
| | <i>Dead</i> | 3.42E+03 | 3.16E+03 | 1.40E+02 | 8.82E+07 | 7.62E+07 |
| <i>Landscape Contiguity</i> | <i>Living</i> | 0.00E+00 | 0.00E+00 | 4.21E+00 | 2.35E+05 | 3.01E+05 |
| | <i>Dead</i> | 1.61E+00 | 4.89E-01 | 1.12E+01 | 2.71E+05 | 3.61E+05 |
| <i>Landscape Interspersion</i> | <i>Living</i> | 1.60E+03 | 1.28E+03 | 1.92E+01 | 3.35E+07 | 3.17E+07 |
| | <i>Dead</i> | 8.87E+02 | 7.97E+02 | 2.65E+01 | 3.85E+07 | 4.02E+07 |
| <i>MSL in Closed Canopy</i> | <i>Living</i> | 3.29E+05 | 3.40E+05 | 9.54E+01 | 2.19E+05 | 1.70E+05 |
| | <i>Dead</i> | 3.69E+05 | 3.72E+05 | 8.17E+03 | 2.37E+05 | 2.11E+05 |
| <i>MSL in Partial Canopy</i> | <i>Living</i> | 9.28E+02 | 1.30E+03 | 4.75E+00 | 2.78E+03 | 0.00E+00 |
| | <i>Dead</i> | 2.32E+03 | 2.38E+03 | 8.35E+01 | 0.00E+00 | 0.00E+00 |
| <i>MSL in Open Canopy</i> | <i>Living</i> | 2.50E+04 | 2.73E+04 | 7.16E+01 | 0.00E+00 | 0.00E+00 |
| | <i>Dead</i> | 1.41E+05 | 1.23E+05 | 1.49E+03 | 0.00E+00 | 3.43E+03 |
| <i>MVL in Closed Canopy</i> | <i>Living</i> | 7.70E+04 | 8.13E+04 | 1.00E+02 | 2.40E+04 | 7.92E+03 |
| | <i>Dead</i> | 7.92E+04 | 7.99E+04 | 5.87E+02 | 3.54E+04 | 2.19E+04 |
| <i>MVL in Partial Canopy</i> | <i>Living</i> | 3.21E+03 | 3.36E+03 | 3.17E+01 | 1.41E+04 | 1.59E+04 |
| | <i>Dead</i> | 5.21E+03 | 4.75E+03 | 1.59E+02 | 1.60E+04 | 9.43E+03 |
| <i>MVL in Open Canopy</i> | <i>Living</i> | 1.86E+04 | 1.51E+04 | 3.77E+02 | 1.25E+07 | 1.29E+07 |
| | <i>Dead</i> | 1.00E+05 | 1.02E+05 | 6.50E+02 | 1.39E+07 | 1.24E+07 |
| <i>Mortality in Closed Canopy</i> | <i>Living</i> | 1.92E+05 | 1.78E+05 | 3.76E+01 | 6.47E+06 | 6.04E+06 |
| | <i>Dead</i> | 7.60E+03 | 7.41E+03 | 2.31E+03 | 5.65E+06 | 5.86E+06 |
| <i>Mortality in Partial Canopy</i> | <i>Living</i> | 7.23E+04 | 7.10E+04 | 9.92E+00 | 7.57E+06 | 7.47E+06 |
| | <i>Dead</i> | 1.18E+04 | 9.85E+03 | 1.35E+03 | 8.55E+06 | 7.99E+06 |
| <i>Mortality in Open Canopy</i> | <i>Living</i> | 2.24E+03 | 3.06E+03 | 1.21E+01 | 1.62E+06 | 1.92E+06 |
| | <i>Dead</i> | 9.25E+03 | 1.01E+04 | 4.86E+01 | 1.65E+06 | 1.85E+06 |

Table 14 % Variance explained and Misclassification error rate for all CARTs. CARTs explained over 30% of the variance with under 30% misclassification error for all dependent variables.

| <i>Predictor</i> | <i>Canopy Cover, MSL, MVL, Mortality probability, Settlement probability</i> | |
|--|--|-------------|
| | <i>Living</i> | <i>Dead</i> |
| <i>% Variance Explained</i> | | |
| <i>maximum subsidy deposition distance</i> | 50.84 | 64.14 |
| <i>subsidy deposition range</i> | 50.49 | 64.58 |
| <i>peak density</i> | 77.28 | 78.37 |
| <i>distance to peak density</i> | 31.72 | 36.89 |
| <i>number of individuals</i> | 78.28 | 79.18 |
| <i>Misclassification error rate (%)</i> | | |
| <i>maximum subsidy deposition distance</i> | 18.04 | 27.03 |
| <i>subsidy deposition range</i> | 18.96 | 26.86 |
| <i>peak density</i> | 24.22 | 23.80 |
| <i>distance to peak density</i> | 17.63 | 15.94 |
| <i>number of individuals</i> | 24.56 | 27.57 |

Table 15 Descriptive statistics from analysis of virtual landscape predictor metrics. Mean and standard deviation of all heterogeneous landscapes

| Landscape Metric | Mean (SD) |
|--------------------------------------|------------------|
| Open.Canopy.Proportion (%) | 25.32 (16.75) |
| Partial.Canopy.Proportion (%) | 26.87 (18.85) |
| Closed.Canopy.Proportion (%) | 48.61 (22.71) |
| Open.Canopy.Cohesion (%) | 86.32 (13.17) |
| Partial.Canopy.Cohesion (%) | 86.73 (13.12) |
| Closed.Canopy.Cohesion (%) | 94.26 (7.23) |
| Open.Canopy.Clumpiness | 0.76 (0.11) |
| Partial.Canopy.Clumpiness | 0.76 (0.11) |
| Closed.Canopy.Clumpiness | 0.76 (0.05) |
| Landscape Contagion (%) | 40.3 (14.27) |
| Landscape Contiguity | 0.45 (0.06) |
| Landscape Interspersion (%) | 76.4 (22.78) |

-Significance testing of Juvenile wood frog movement with canopy cover (Experiment 1):

-Juvenile wood frog mean step (MSL) and vector lengths (MVL) were significantly different across forest types

$$ANOVA: F_{2,10} > 3.84, \quad p < 0.03$$

-Wood frogs took longer, straighter steps in open canopy than partial and closed canopy forests

$$Tukey - HSD: \quad p = 0.03$$

-Significance testing of subsidy distribution metrics with canopy cover (Experiment 1):

-All response variables were significantly different across forest type:

$$MANOVA; F > 30.56, \quad p < 0.001$$

-Individual response variables were also significantly different across forest types:

$$NOVA; F_{2,7278} > 30.55, \quad p < 0.001$$

-Except for distance to peak density between partial and closed canopy habitat for living and dead subsidies (*Tukey - HSD*; $p > 0.0642$), all response variables were significantly different for pairwise comparisons among forest treatments

$$Tukey - HSD; \quad p < 0.001$$

-Egg mass surveys descriptive statistics (Mean (SD)): Egg mass count = 98.45 (43.29), Egg mass volume = 528.24 (152.71) ml, Egg volume = 1.12 (0.27) ml, Premetamorphic survivorship = 0.04 (Bevern 1990).

-Pond surveys descriptive statistics (Mean (SD)): Pond length = 16.67 (6.85) m, Pond width = 14.07 (4.02) m

-HEE landscape proportional composition (Mean (SD)): Open Canopy = 1.90 (1.74), Partial canopy = 10.25 (11.39) Closed Canopy = 87.85 (12.35)

Section U: Model Construction - Overview, Design Concepts, Details (ODD) Protocol

7. Overview

7.1 Purpose

Ecological subsidies are consumer and resource transfers by animal movements across ecosystems and landscapes. This model is an IBM simulation to investigate how landscape heterogeneity with corresponding variations in animal movement patterns, settlement probability and associated mortality costs impact the distribution of active living and dead subsidies. The model quantifies the spatial extents, intensities and clustering of active subsidy distributions from a broad parameter space of animal dispersal and foraging movement patterns in a variety of settlement and mortality scenarios across heterogeneous landscapes consisting of three habitat types (i.e. open, partial and closed canopy habitat). Depending on the cover type, Animals initiate movement from a donor ecosystem (natal habitat) and disperse into a recipient ecosystem with the stochastic chance of settlement and death during movement. Examples of ecological systems with similar dynamics include spatial subsidies from amphibian and aquatic insect dispersal and foraging movements in surrounding heterogeneous landscapes of variable canopy density adjacent to source ponds and streams. Dead individuals provide nutrients, energy, and/or prey to the recipient ecosystems possibly causing bottom-up effects, while living individuals provide a consumer subsidy with potential top-down effects.

7.2 State variables and scales

The model comprises of three hierarchical levels: individual, population and environment. The environment consists of a heterogeneous landscape: donor ecosystem and recipient ecosystem with three distinct cover types at variable proportions in virtual landscapes. Other cover types may be assigned as needed based on available movement, settlement and mortality information for a model species. Individuals are characterized by the state variables which vary as a function of cover type: Mean step lengths (MSL), mean vector lengths (MVL or correlation coefficient), movement probability, settlement probability and mortality probability. Virtual animals disperse using a correlated random walk (CRW). Depending on the cover type and species, different ranges of MSL and MVL can be implemented to change virtual animal movement behavior as a function of landscape structure. Movement, settlement and mortality probabilities can be varied in similar fashion. Confidence intervals for MSL and MVL in each cover type were determined from movement surveys conducted on 30 juvenile wood frogs in central hardwood forests (Hardwood Ecosystem Experiment (HEE) in (Southcentral Indiana). Confidence intervals for juvenile wood frog movement, mortality and settlement probabilities were determined from relevant literature sources (Cline and Hunter, 2016; Funk et al., 2005; Harper et al., 2015; Patrick et al., 2008; Popescu et al., 2012; Popescu and Hunter, 2011; Rittenhouse et al., 2009; Semlitsch et al., 2009, 2008; Todd et al., 2014).

7.3 Process overview and scheduling

Virtual animals select MSLs and MVLs corresponding to the cover type they are in as they move from the donor to the recipient ecosystem where they can settle or die depending on the settlement and mortality probabilities they experience based on the cover type (Figure 1 in Manuscript). 2000 virtual animals (i.e. determined from HEE egg mass surveys) randomly orient in the donor ecosystem at the start of a simulation and navigate. Dispersers select a

random MSL and MVL within a specified range (i.e. confidence intervals) corresponding the cover type and negotiate a move, repeating this procedure at each timestep to generate successive moves and trajectories for over 2000 15-minute timesteps (i.e. 12 hours of activity a day for 42 days of dispersal). During movement, individuals randomly move, settle and die based on movement, settlement and mortality probability corresponding to the cover type that they are in. All individuals either settle or die by the end of the simulation.

8. Design Concepts

8.1 Emergence

Different living and dead subsidy distribution (deposition) patterns emerge from variation in virtual animal movement behavior and paths over the duration of simulations. The model does not explicitly account for adaption and fitness-seeking as the aim is to quantify emergent spatial distribution patterns based on a comprehensive spectrum of ecologically plausible variation in animal movement patterns and mortality scenarios. Implicit adaptation occurs in animals drawing random step lengths and (or) random turning angles to negotiate movement based on different movement strategies and scales that correspond to the cover type that they are in. Implicit fitness-seeking occurs as animals randomly die or live based on movement, settlement and mortality probabilities corresponding to habitat type that they are in. The model also indirectly accounts for fitness seeking with settled dispersers experiencing a decremented movement and mortality probability (i.e., 5% of set rate) based on cover type.

8.2 Sensing

Virtual animals are aware of their surrounding and move, settle or die based on cover type. The model includes the assumption that individual virtual animals can sense the cover type they are moving through and respond by moving settling and dying at rates corresponding to that cover type. Individuals are aware of their state (dead or alive) and know to keep moving as long as they are alive but stop moving when they settle or die by cover type. Based on their perceptual ranges, dispersers can sense members of the cluster groups in which they have either settled or died.

8.3 Interaction

Virtual animals interact with the environment as living or dead subsidies. Individuals are aware of their state (dead or alive) and location (2D-x,y-coordinates) in the recipient ecosystem at any given timestep. The model incorporates a fully factorial combination of movement and mortality parameter levels. Each virtual animal is aware of its neighbors within an area demarcated by a prescribed model radius.

8.4 Stochasticity

Virtual landscapes are generated using a random modified clusters approach. The proportion and spatial aggregation of each cover type in virtual landscapes varies with each landscape. For two of the three cover types, a random number in the interval [0, 0.5] to determine their proportion in the virtual landscape to be generated. The proportion of the third cover type is determined a $[1 - (\text{sum of two predetermined cover type proportions})]$. To move during each simulation run, virtual animals randomly draw MSLs and MVLs, as well as movement, settlement and mortality probabilities from uniform distributions within corresponding confidence intervals based on cover type. Virtual animal movement, settlement and mortality

therefore occur stochastically during each timestep according to cover type. Each virtual animal also has a stochastic chance of settlement or mortality if a random number drawn from respective uniform probability distribution over [0,1] at each timestep is less than the assigned settlement or mortality probability level of the cover type they are moving through.

8.5 Observation

Metrics of active subsidy displacement and density extracted from spatial distributions at the end of each simulation include: maximum subsidy deposition distance and range, the peak density and the distance to peak density. The maximum subsidy deposition distance is the distance from the donor-recipient ecosystem boundary to the furthest displaced subsidy. The maximum subsidy deposition range is the distance between the most and least displaced subsidies. The peak density is the greatest concentration of subsidies in the recipient ecosystem and the distance to peak density is the distance to the focal location where the peak density occurs. The model accounts for the distribution of living and dead subsidies separately. The maximum cluster size is the radial extent of the most spread-out cluster and the maximum cluster density is the number of subsidies in the cluster with the greatest number of subsidies. The maximum inter-cluster distance is the distance between the least and most displaced clusters. The model accounts for the distribution of living and dead subsidies separately.

9. Details:

The model was designed in NetLogo (version 6.0.4) software (Tisue and Wilensky, 2004; Wilensky, 1999)

9.1 Initialization

The environment is a heterogeneous landscape (donor-recipient ecosystem (with three cover types)) that consists of a two-dimensional 600 (vertical) by 600 (horizontal) m world with boundaries that deflect dispersers that reach edges back into the landscape. The donor ecosystem is a 15 by 15 m zone the center of the world. Virtual landscapes with three cover types are generated by the random modified clusters (Sauna and Martinez-Millan 2000) and analyzed to generate Fragstats-based metrics that describe landscape structure (McGarigal 2002). Simulations are initialized with all individuals randomly distributed at the edge of the donor ecosystem. 2000 virtual move outward from the donor ecosystem into the surrounding recipient ecosystem over a duration of 2000 timesteps. Dispersers cannot return to the donor ecosystem once they entered the recipient ecosystem.

9.2 Inputs

Model inputs include the number of virtual animals and simulation duration (set to 2000 individuals and 2000-timesteps). Model inputs also include the confidence intervals for MSL, MVL, as well as movement, settlement and mortality probabilities (Table 1 in Manuscript). The model includes a density-area radius (a) of 60 m (i.e. 10% of total landscape area) that defines the circular area over which subsidy density estimates are extracted.

9.3 Sub-models

Animal movement behavior as CRW consists of representative statistical distributions of step lengths and turning angle orientations. At each timestep, individuals select a random MSL and MVL from respective confidence intervals to navigate from the donor ecosystem into recipient ecosystem using CRW with a wrapped Cauchy distribution of turning angles $\theta(t)$ as:

$$\theta(t) = \theta(t - 1) + 2 \tan^{-1} \left[\left(\frac{1 - \alpha}{1 + \alpha} \right) \tan(\pi\varphi) \right],$$

$$0 \leq \alpha \leq 1$$

$$-0.5 \leq \varphi \leq 0.5$$

$\theta(t - 1)$ is a previous turning angle and φ is drawn from a uniform distribution over a delta distribution range of $[-0.5, 0.5]$ to normalize the initial direction of movement trajectories to a null orientation angle. CRW features a comprehensive range of movement patterns from sinuous to straight movement controlled by MVL or correlation coefficient (α). CRW movement is straighter as $\alpha \rightarrow 1$ and more sinuous as $\alpha \rightarrow 0$. The range of MSL and MVL implemented in our model represents surveyed wood frog movement tracks in each canopy cover type (Table 1 in Manuscript).

To move, die or settle between during movement, dispersers draw a random number from a uniform distribution ($[0, 1]$) at each timestep. Depending on the cover type, dispersers move, settle or die and stop moving if the number drawn is lower than the randomly drawn movement, mortality or settlement probabilities from respectively assigned confidence intervals for the simulation run. Our model uses juvenile wood frog movement, mortality and settlement probabilities based on relevant literature (Cline and Hunter, 2016; Funk et al., 2005; Harper et al., 2015; Patrick et al., 2008; Popescu et al., 2012; Popescu and Hunter, 2011; Rittenhouse et al., 2009; Semlitsch et al., 2009, 2008; Todd et al., 2014).

Section V: Code

-Model Construction - NetLogo Version 6.0.4

-Code Tab in NetLogo

```
; Daniel Bampoh
; Simulation Experimentation Code
; April 12 , 2019
```

; The following simulation experimentation code implementation explores how active subsidy distributions respond to landscape heterogeneity as function of variation in the proportion and spatial aggregation of three different habitat quality types that result in different animal movements, as well as settlement and mortality probabilities. ; The world requires the user to build in buttons, sliders and monitors ; in the NetLogo interface to support ; functionality of procedures – The model requires behaviorspace mode to conduct batch simulations - see submission attachments for code with interactive interface and model use details.

```
extensions [ r gis dbscan csv]
```

```
globals [ step-length-unharvested step-length-shelterwood step-length-clearcut corre-coeff-
unharvested corre-coeff-clearcut corre-coeff-shelterwood live-max-dist dead-max-dist live-min-
dist dead-min-dist live-range dead-range live-peak-dens-entity
```

```
    dead-peak-dens-entity dead-turt settle-turt live-count live-peak-dens dead-peak-dens live-
peak-dens-dist dead-peak-dens-dist black-turt live-turt dead-count non-consp-count cluster-
count-live max-clust-dens-live max-clust-size-live
```

```
    mortality-p-clearcut mortality-p-shelterwood mortality-p-unharvested max-dist-interclust-
live db-clusters-live db-clusters-dead cluster-count-dead max-clust-dens-dead max-clust-size-
dead max-dist-interclust-dead min-dist-interclust-dead consp-count ]
```

```
; global variable
```

```
; settings, including (from right to left) the starting patch for turtles, the number of dead turtles,
the maximum distance for live and dead turtles, the minimum distance for
; live and dead turtles, the range for live and dead turtles, the peak density for live and dead
turtles, and the distance to peak density for live and dead turtles respectively
```

```
turtles-own [
  orient
  reorient
  start-patch
]
```

```
patches-own [
  cluster-id
  landcover
]
```

```
to setup
```

```

ca

generate-landscape

create-central-square

spawn-central-turtles

initialize-behavior-rules

reset-ticks
end

to initialize-behavior-rules
  set corre-coeff-clearcut ( 0.52 + random-float 0.3 )
  set step-length-clearcut ( 0.26 + random-float 0.26 )
  set mortality-p-clearcut ( 0.005 + random-float 0.005 )
  set corre-coeff-shelterwood ( 0.41 + random-float 0.22 )
  set step-length-shelterwood ( 0.23 + random-float 0.08 )
  set mortality-p-shelterwood ( 0.001 + random-float 0.004 )
  set corre-coeff-unharvested ( 0.14 + random-float 0.32 )
  set step-length-unharvested ( 0.18 + random-float 0.20 )
  set mortality-p-unharvested ( 0.00075 + random-float 0.00175 )
end

to generate-landscape
  ask patches [
    if ( forest-type = "homoscape-unharvested" ) [
      set pcolor green
      set landcover 3
    ]
    if ( forest-type = "homoscape-shelterwood" ) [
      set pcolor orange
      set landcover 2
    ]
    if ( forest-type = "homoscape-clearcut" ) [
      set pcolor brown
      set landcover 1
    ]
  ]
  if ( forest-type = "heteroscape" ) [
    create-and-save-raster
    load-raster-and-apply
  ]
end

```

```

; Pick central patch and those within 7 patches xy to turn blue
to create-central-square
  let center round ( world-width / 2 )
  let max_ center + 7
  let min_ center - 7
  ask patches with [
    ( pxcor <= max_ and pxcor >= min_ ) and
    ( pycor <= max_ and pycor >= min_ )
  ] [
    set pcolor blue
    set landcover 0
  ]
end

to create-and-save-raster
  ;; Daniel- comment this next line out- it's necessary for me
  ;; due to my library location changes
  r:eval ".libPaths('/:path to R library')"
  ;-----

; If the 'use-seed?' switch is off, randomize the seed for parallel implementation
;if not use-seed? [
;  set r_seed_value random 100000
;]

; Use the current r_seed_value (random or input) for parallel implementation
;r:eval ( word "set.seed(" r_seed_value ")" )

; Generate ai values in r
r:eval "a <- runif(1, min = 0, max = 0.5)"
r:eval "b <- runif(1, min = 0, max = 0.5)"
r:eval "c <- 1 - (a + b)"
r:eval "ai_ <- c(a,b,c)"

; According to the chooser, generate the appropriate landscape
;-----
if landscape-type = "Modified Random Clusters" [
  print "Generating Modified Random Cluster Landscape..."
  r:eval "recmat <- rbind(c(-0.5, 1/3, 1), c(1/3, 2/3, 2), c(2/3, 1, 3))"
  r:eval "x <- NLMR::nlm_randomcluster(40,40, p = 0.5, ai = ai_)"
  r:eval "x <- raster::reclassify(x, recmat)"

; Run the code below when no longer testing
;  r:eval "x <- raster::disaggregate(x, fact = 600/40)"

```

```

]

if landscape-type = "Midpoint Displacement" [
  print "Generating MidPoint Displacement Landscape..."
  ; change the landscape size below when no longer testing
  r:eval "x <- NLMR::nlm_mpd(40, 40, roughness = 0.5)"
  r:eval "x <- landscapetools::util_classify(x, weighting = ai_)"
]

if landscape-type = "Fractal Dimension Brownian Motion" [
  print "Generating Fractal Dimension Brownian Motion Landscape..."
  ; change the landscape size below when no longer testing
  r:eval "x <- NLMR::nlm_fbm(40, 40, fract_dim = 1)"
  r:eval "x <- landscapetools::util_classify(x, weighting = ai_)"
]
; -----

; Calculate stats and assign to interface widgets
; -----

set class_stats_name_order ""
set class_stats_as_string ""
set landscape_stats_name_order ""
set landscape_stats_as_string ""

if metrics-level-generated = "class-only" or metrics-level-generated = "landscape-and-class" [
  r:eval "metrics.class <- landscapemetrics::calculate_lsm(x, level = 'class')"
  r:eval "metrics.class$class <- paste('class.', metrics.class$class, sep = '')"
  r:eval "united.class <- tidyr::unite(metrics.class[, c(3,5,6)], class, class, metric, sep = '.')"
  r:eval "spread.vals.class <- tidyr::spread(united.class, class, value)"
  r:eval "class.names <- paste(names(spread.vals.class), collapse = ', ')"
  r:eval "class.values <- paste(spread.vals.class[1,], collapse = ', ')"
  set class_stats_name_order r:get "class.names"
  set class_stats_as_string r:get "class.values"
]

if metrics-level-generated = "landscape-only" or metrics-level-generated = "landscape-and-
class" [
  r:eval "metrics.landscape <- landscapemetrics::calculate_lsm(x, level = 'landscape',
classes_max = 3)"
  r:eval "united.landscape <- tidyr::unite(metrics.landscape[, c(2,5,6)], level, level, metric, sep =
'.')"
  r:eval "spread.vals.landscape <- tidyr::spread(united.landscape, level, value)"
  r:eval "landscape.names <- paste(names(spread.vals.landscape), collapse = ', ')"

```

```

r:eval "landscape.values <- paste(spread.vals.landscape[1,], collapse = ', ')"
set landscape_stats_name_order r:get "landscape.names"
set landscape_stats_as_string r:get "landscape.values"
]

; Write the raster to a temporary file ('tempraster')
;
; Daniel - for now, change the filepath below to the folder you want to use
; to store the temporary raster for landscape generation
r:eval "raster::writeRaster(x, ':/path to temp raster', format = 'ascii', overwrite = TRUE)"
end

to load-raster-and-apply
  resize-world 0 600 0 600
  set-patch-size 1
  ; Load the landscape that was generated in 'create-and-save-raster'
  ;
  ; Daniel - Change the filepath below to the same filepath that you used in 'create-and-save-raster'
  let landscape gis:load-dataset ":/path to temp raster"
  gis:set-world-envelope gis:envelope-of landscape
  gis:apply-raster landscape landcover
  let lbound min [ landcover ] of patches
  let ubound max [ landcover ] of patches
  ask patches [
    ifelse landcover = 3 [
      set pcolor green
    ] [
      ifelse landcover = 2 [
        set pcolor orange
      ] [
        set pcolor brown
      ]
    ]
  ]
end

; Create some test turtles and put them on the central border patches
; facing out into the generated landscape
to spawn-central-turtles
  let landcover-list n-values ( length remove-duplicates [ landcover ] of patches ) [ 0 ]
  crt number-turtles [
    move-to one-of patches with [
      landcover = 0 and
      any? neighbors with [ landcover != 0 ]
    ]
  ]
end

```

```

]
set start-patch patch-here
face one-of neighbors with [ landcover != 0 ]
set color black
set size 1
fd 1
]
end

```

to-report turning-angles-dist [#correlation] ; wrapped Cauchy turning distribution function for correlated random walk with correlation coefficient as input

```

let turning-angle ( ( 1 - #correlation ) * tan ( 180 * ( random-float 1 - 0.5 ) ) ) / ( 1 +
#correlation ) ; wrapped Cauchy distribution formula
report 180 - ( 2 * atan 1 turning-angle ) ; orientation randomizer
end ; end of correlated random walk wrapped Cauchy distribution function

```

to write-csv [#filename #items] ; function that allows that creates a csv file for writing data to using filename and items (list entry) as variables

```

if is-list? #items and not empty? #items ; #items is a list of the data (or headers!) to write
[ file-open #filename ; opens file for output export into file as input by given filename
set #items map quote #items ; quote non-numeric items
ifelse length #items = 1 [ file-print first #items ] ; print the items
[file-print reduce [ [?1 ?2] -> (word ?1 "," ?2) ] #items] ; if only one item, print it
file-close ; close file once output export is complete (when code stops running)
]

```

end ; end of procedure for exporting essential simulation output to comma-separated-value file

to-report xcor-mean [xcors] ; reports mean x-coordinate location of a patch or turtle set relative to edges of the world

```

let angles map [ x -> 360 * ( x - (min-pxcor - 0.5)) / world-width ] xcors ; maps out the mean x-
coordinate location

```

```

let mean-x mean map cos angles ; determines the cosine of mean x-coordinate location to
determine position relative to horizontal edge

```

```

let mean-y mean map sin angles ; determines the sine of mean x-coordinate location to
determine position relative to vertical edge

```

```

report (atan mean-y mean-x) / 360 * world-width + (min-pxcor - 0.5) ; determines mean x-
position relative to edges of world

```

end ; end of mean x-position calculation function

to-report ycor-mean [ycors] ; reports mean y-coordinate location of a patch or turtle set relative to edges of the world

```

let angles map [ y -> 360 * ( y - (min-pycor - 0.5)) / world-height ] ycors ; maps out the mean y-
coordinate location

```

```

let mean-x mean map cos angles ; determines the cosine of mean y-coordinate location to
determine position relative to horizontal axis

```

```

let mean-y mean map sin angles ; determines the sine of mean y-coordinate location to
determine position relative to vertical axis
report (atan mean-y mean-x) / 360 * world-height + (min-pycor - 0.5) ; determines mean x-
position relative to edges of world
end ; end of mean x-position calculation function

```

```

to-report cluster-distance [ cluster1 cluster2 ] ; reports location or distance of conspecific clusters
relative to each other in world
let x1 xcor-mean [ xcor ] of turtle-set cluster1 ; determines x-coordinate location of first cluster
let y1 ycor-mean [ ycor ] of turtle-set cluster1 ; determines y-coordinate location of first cluster
let x2 xcor-mean [ xcor ] of turtle-set cluster2 ; determines x-coordinate location of second
cluster
let y2 ycor-mean [ ycor ] of turtle-set cluster2 ; determines y-coordinate location of second
cluster
report sqrt ((x1 - x2) ^ 2 + (y1 - y2) ^ 2) ; determines distance between first and second cluster
end ; end of interclust-live distance function

```

```

to-report quote [ #thing ] ; function that allows for string formatted entries to be included in
inverted commas as listable items in the csv file so that row/column headings,
;as well as no-value numbers may be added
ifelse is-number? #thing ; queries whether reported entry is a number
[ report #thing ] ; reports number if entry is a number
[ report (word "\"" #thing "\"") ] ; reports text in quotes if entry is text so that it can be
recognized as a string
end ; end of entry formatting procedure for simulation output export to csv

```

```

to-report radial-extent [ cluster ] ; report function for the radial extent of a conspecific cluster
report max map [ ; reports function for cluster
a -> max map [ ; maps the maximum distance of the spread of a conspecific cluster
b -> [
distance a ] of b ; considers the distance of spread across a cluster
]
cluster ; cluster radial extent identifier
]
cluster ; reported cluster radial extent value
end

```

```

to Pass-Away ; procedure for determining incurred turtle (time-based) per time-step as turtles
navigate world regardless of movement strategy (Levy or CRW)
let chances-death random-float 1 ; set the chances of death to a random floating-point number
between 0 and 1
if ( color = black ) [
if (( pcolor = green ) and ( chances-death <= mortality-p-unharvested )) or
(( pcolor = orange ) and ( chances-death <= mortality-p-shelterwood )) or
(( pcolor = brown ) and ( chances-death <= mortality-p-clearcut )) [ ; determine if the chances
of death supersede that of the fixed mortality level

```

```

    set color red ; set turtle color to red to signify dead turtle
  ]
]
if ( color = yellow ) [
  if (( pcolor = green ) and ( chances-death <= mortality-p-unharvested * settlement-adv-
unharvested )) or
    (( pcolor = orange ) and ( chances-death <= mortality-p-shelterwood * settlement-adv-
shelterwood )) or
    (( pcolor = brown ) and ( chances-death <= mortality-p-clearcut * settlement-adv-clearcut )) [
    set color red
  ]
]
end

```

to Settle ; procedure for determining incurred turtle (time-based) per time-step as turtles navigate world regardless of movement strategy (Levy or CRW)

```

  let chances-settlement random-float 1 ; set the chances of death to a random floating-point
number between 0 and 1
  if ( color = black ) [
    if (( pcolor = green ) and ( chances-settlement <= settlement-p-unharvested )) or
      (( pcolor = orange ) and ( chances-settlement <= settlement-p-shelterwood )) or
      (( pcolor = brown ) and ( chances-settlement <= settlement-p-clearcut )) [ ; determine if the
chances of death supersede that of the fixed mortality level
      set color yellow ; set turtle color to red to signify dead turtle
    ]
  ]
  if ( color = yellow ) [
    if (( pcolor = green ) and ( chances-settlement <= settlement-p-unharvested * movement-p-
unharvested )) or
      (( pcolor = orange ) and ( chances-settlement <= settlement-p-shelterwood * movement-p-
shelterwood )) or
      (( pcolor = brown ) and ( chances-settlement <= settlement-p-clearcut * movement-p-
clearcut )) [ ; determine if the chances of death supersede that of the fixed mortality level
      set color black ; set turtle color to red to signify dead turtle
    ]
  ]
end

```

to Corr-Rand-Move ; movement procedure for correlated random walk

```

;pen-down ; marks the path traveled by each turtle while performing correlated random walk
let chances-move random-float 1
if ( color = black ) or ( color = yellow ) [
  if (( pcolor = green ) and ( chances-move <= movement-p-unharvested )) [
    set orient turning-angles-dist corre-coeff-unharvested ; assigns turtle orientation to a random
turning angle from the wrapped Cauchy distribution function based on a correlation
  ]
]

```



```

    set heading heading + one-of [-1 1] * orient ; sets the correlated random walk turtle heading or
orientation to random angle selected from the Cauchy distribution
    fd step-length-unharvested
  ]
  if (( pcolor = orange ) and ( chances-move <= movement-p-shelterwood )) [
    set orient turning-angles-dist corre-coeff-shelterwood ; assigns turtle orientation to a random
turning angle from the wrapped Cauchy distribution function based on a correlation
    set heading heading + one-of [-1 1] * orient ; sets the correlated random walk turtle heading or
orientation to random angle selected from the Cauchy distribution
    fd step-length-shelterwood
  ]
  if (( pcolor = brown ) and ( chances-move <= movement-p-clearcut )) [
    set orient turning-angles-dist corre-coeff-clearcut ; assigns turtle orientation to a random
turning angle from the wrapped Cauchy distribution function based on a correlation
    set heading heading + one-of [-1 1] * orient ; sets the correlated random walk turtle heading or
orientation to random angle selected from the Cauchy distribution
    fd step-length-clearcut
  ]
]
end ; end of movement procedure for correlated random walk

```

```

to output ; output procedure for reporting results
; if ( ticks <= duration ) [
  set live-turt turtles with [ color != red ]
  set live-count ( count live-turt )
  if ( count live-turt >= 1 ) [
    set live-max-dist max [ distance start-patch ] of live-turt ; calculates the maximum turtle
distance from the starting patch
    set live-min-dist min [ distance start-patch ] of live-turt ; calculates the minimum turtle distance
from the starting patch
    set live-range ( live-max-dist - live-min-dist ) ; calculates range of turtles (difference between
maximum and minimum turtle distance from the starting patch)
    set live-peak-dens-entity max-one-of live-turt [ count live-turt with [ distance myself < density-
area ] ] ; locates turtle with maximum number of surrounding turtles by selected
    ; surrounding radial distance or range
    set live-peak-dens [ count live-turt with [ distance myself < density-area ] ] of live-peak-dens-
entity ; counts number of turtles around located peak density turtle as density
    ; and determines the maximum occurrence as peak subsidy density analogue
    set live-peak-dens-dist [ distance start-patch ] of live-peak-dens-entity ; determines distance
from the start-patch (origin of world) to the location of turtle at the center
    ; of the area of peak subsidy density of correlated random walkers
  ]
  set dead-turt turtles with [ color = red ]
  set dead-count count dead-turt
  if ( count dead-turt >= 1 ) [

```

```

    set dead-max-dist max [ distance start-patch ] of dead-turt ; calculates the maximum turtle
distance from the starting patch
    set dead-min-dist min [ distance start-patch ] of dead-turt ; calculates the minimum turtle
distance from the starting patch
    set dead-range ( dead-max-dist - dead-min-dist ) ; calculates range of turtles (difference
between maximum and minimum turtle distance from the starting patches)
    set dead-peak-dens-entity max-one-of dead-turt [ count dead-turt with [ distance myself <
density-area ] ] ; locates turtle with maximum number of surrounding turtles by
    ; selected surrounding radial distance or range
    set dead-peak-dens [ count dead-turt with [ distance myself < density-area ] ] of dead-peak-
dens-entity ; counts number of turtles around located peak density turtle as
    ; density and determines the maximum occurrence as peak subsidy density analogue
    set dead-peak-dens-dist [ distance start-patch ] of dead-peak-dens-entity ; determines distance
from the start-patch (origin of world) to the location of turtle at the center
    ; of the area of peak subsidy density of correlated random walkers
]
set black-turt turtles with [ color = black ]
set non-consp-count ( count black-turt )
set settle-turt turtles with [ color = yellow ]
set consp-count ( count settle-turt )
if ( count settle-turt > 3 ) [
set db-clusters-live dbscan:cluster-by-location live-turt 3 percep-range
(foreach db-clusters-live range length db-clusters-live [ [u v] ->
    foreach u [
        w -> ask w [
            set label v
        ]
    ]
])
set cluster-count-live length db-clusters-live
if ( cluster-count-live > 1 ) [
set max-clust-dens-live max map length db-clusters-live
set max-clust-size-live max map radial-extent db-clusters-live
set max-dist-interclust-live max map [ l1 ->
    max map [ l2 ->
        cluster-distance l1 l2
    ] remove l1 db-clusters-live ; Get distance to all other clusters but c1
] db-clusters-live
]
]
if ( count dead-turt > 3 ) [
set db-clusters-dead dbscan:cluster-by-location dead-turt 3 percep-range
(foreach db-clusters-dead range length db-clusters-dead [ [n j] ->
    foreach n [
        k -> ask k [
            set label j
        ]
    ]
])
]

```

```

    ]
  ]
])
set cluster-count-dead length db-clusters-dead
if (cluster-count-dead > 1 ) [
  set max-clust-dens-dead max map length db-clusters-dead
  set max-clust-size-dead max map radial-extent db-clusters-dead
  set max-dist-interclust-dead max map [ d1 ->
    max map [ d2 ->
      cluster-distance d1 d2
    ] remove d1 db-clusters-dead ; Get distance to all other clusters but c1
  ] db-clusters-live
]
]
];]
end ; end of results reporting procedure

to go ; procedure performs batch simulations of movement strategies in sequence
  if ticks <= duration [ ; checks the condition that the time passed is less than allotted simulation
    duration
    ask turtles [
      if ( color != black ) [
        stop
      ]
      Corr-Rand-Move ; moves turtles according to different movement strategies for duration in
sequence
      settle ; settle by the allocated chance of settlement
      Pass-Away ; call mortality function as needed based on state of interface switch (on, time-
based or off, space (distance)-based cumulative mortality assessed on constant
      ; per-step hazard
    ]
    tick ; a progression of unit time-step in simulation run
  ]
  if ( ticks > duration - 1 ) [
    output
  ]
end ; end of batch simulations

```

-Model Use:
-Info Tab in NetLogo

What is it?

LandHeteroMovSub is a spatiotemporally explicit individual-based model that simulates the effect of animal movement and mortality on animal-transported (active) subsidy distribution. The model simulates spatial subsidy patterns from variation in movement, settlement and mortality probability as a function of cover types in heterogeneous landscapes. The model computes displacement and density metrics of spatial distributions of a population of virtual animals dispersing from a donor ecosystem into a recipient ecosystem of variable proportions and spatial aggregations of three different cover types. The model is based on the movement behavior of juvenile wood frogs emerging from ponds into surrounding heterogeneous landscapes in central hardwood forests at the Hardwood Ecosystem Experiment (HEE) in southern Indiana, USA.

How it works

The world is 600 by 600 m heterogeneous recipient ecosystem of variable proportional compositions and spatial aggregations of open, partial and closed canopy habitat. The world has a 15 by 15 m donor ecosystem (i.e. pond) at the center. The open and partial canopy proportional compositions vary in a [0,0.5] interval and the closed canopy fraction is [1 - (sum of partial and open canopy fractions)]. Animals are randomly oriented from the central location (donor ecosystem) in the middle and move outward and rightward into the surrounding heterogeneous landscape (recipient ecosystem) with three cover types (i.e., open, partial and closed canopy habitat). Users can simulate movement, settlement and mortality for up to 2000 virtual animals over a period of up to 2000 timesteps based on estimated emergence from wood frog egg mass surveys at the HEE, and 42-day dispersal event with 12 hours of activity per day at the HEE (Homan et al. 2014). Dispersers move by correlated random walk (CRW) using Mean Step Lengths (MSL) and Mean Vector Lengths (MVL) (i.e. correlation coefficients) derived from corresponding confidence intervals from movement track surveys of juvenile wood frogs in the three cover types at the HEE. Dispersers also move, settle and die based on confidence intervals juvenile wood frog movement, settlement and mortality probabilities derived from relevant literature (Cline and Hunter, 2016; Funk et al., 2005; Harper et al., 2015; Patrick et al., 2008; Popescu et al., 2012; Popescu and Hunter, 2011; Rittenhouse et al., 2009; Semlitsch et al., 2009, 2008; Todd et al., 2014). Users can change the straightness of correlated random walk movement patterns by altering the confidence intervals for MVL (i.e., correlation coefficient) and MSL for each of the three cover types. Similarly, users can adjust the confidence intervals for movement, settlement and mortality probabilities for each cover type. The model outputs subsidy distribution metrics at the end of simulations, including the number of dead subsidies, the maximum subsidy deposition distance (furthest displaced subsidy) and range (distance between farthest and least displaced subsidy), the peak density (greatest density of subsidies) and distance to peak density (distance to the location where the greatest density of subsidies occurs). The model also outputs the maximum cluster size is the radial extent of the most spread-out cluster and the maximum cluster density is the number of subsidies in the cluster with the greatest number of subsidies. The maximum inter-cluster distance is the distance between the least and most displaced clusters. The model accounts for the distribution of living and dead subsidies separately.

How to use it

Specify model inputs (adjust corresponding sliders, switches or choosers - in permitted [ranges]) in NetLogo Interface and “initialize-behavior-rules” procedure in the code tab. Pertinent inputs include the number of dispersers (number-turtles - [0,2000]), duration (duration - [0,2000]), Forest type (heterogeneous or homogenous open partial or closed canopy cover (forest-type - [heteroscape, | homoscape])), the type of heterogeneous landscape generation method (landscape-type – [Modified Random Clusters | Midpoint Displacement | Fractal Dimension Brownian Motion]), the type of landscape metrics to be extracted from virtual heterogenous landscapes (metrics-level-generated – [landscape-only, class-only, landscape-and-class]), MSL (step-length), MVL (corre-coeff), as well as movement, settlement and mortality probabilities (p) for each cover type. The model also has a perceptual range (percep – [0, 10]) input to determine minimum neighbor distance for density-based (k-means) subsidy cluster pattern analysis. Specify the desired settlement advantage (settlement-adv) for each canopy cover as the decremented mortality rate dispersers experience after settling. Click the “setup”, then “go” buttons upon specifying desired input ranges (i.e. confidence intervals) for corresponding sliders and input boxes (or in the “initialize-behavior-rules” procedure). Specify inputs and run model using behaviorspace tool to output resulting distribution metrics to a file.

Things to notice

First thing to notice is when forest-type is set to heteroscape, a different type of heterogenous landscape is generated each time the set-up button is clicked. When forest-type is set to homoscape, a homogeneous landscape is generated. Homogenous landscape color varies with homoscape settings to indicate the different cover types. Each cover type has different parameter confidence intervals that govern disperser behavior rules (i.e. MSL, MVL, as well as movement, settlement, settlement advantage and mortality probabilities) Observe dispersers orient at outward at the edge of donor ecosystem (blue) when “setup” button is clicked. When “go” button is clicked, observe living dispersers (black) move and settle (turn yellow) or die (turn red) and stop moving in the recipient ecosystem as tick counter paces towards set duration in the top navigation pane. Slow the pace of simulation progression by dragging “ticks” slider to the left and observe the different rates of movement, settlement in death dispersers experience in different cover types in heteroscape setting.

Things to try

The model is most useful for performing batch simulations in behavior space (Ctrl+Shift+B). Users can edit a comprehensive list of all model variables to include specific levels of each for fully factorial batch simulations with data output to the working directory. Do this in conjunction with altering confidence intervals for behavior rules in the “initialize-behavior-rules” procedure code to observe how virtual animal movement, settlement, mortality and subsidy distribution patterns change for different virtual landscape and cover types. When the model is run in behavior space, descriptive metrics for the structure of simulation landscapes can be output to a file in tabular format. The output includes Fragstats-based (McGarigal 2002) metrics about the structure of heterogeneous landscape (e.g., proportion of cover types, clumpiness, cohesion, contagion, interspersions) along with behavior parameters used for each simulation run. Adjust perceptual range to see how density-based clustering analysis changes cluster pattern analysis.

Extending the model

Users can model subsidy distributions of other species by gathering confidence interval inputs for MSL and MVL, as well as movement, settlement and mortality probabilities for the model species in three different spatially concurrent cover types. Users can also alter the size of the world or the respective donor and recipient ecosystem sizes respectively and observe how that affects subsidy distribution metrics. The range of proportional compositions for each cover type can be adjusted in the landscape generation procedure code to change the ratio of cover types virtual landscapes to suit a real-world circumstance. Observe how changing landscape structures affect subsidy distribution patterns on the interface and from running descriptive statistics, statistical models and machine learning algorithms on output data on subsidy distribution metrics, behavior and landscape parameters generated from behaviorspace model runs.

NETLOGO FEATURES

The model makes extensive use of the program R version 3.5.3 in the landscape generation code. It relies on packages NLMR, Landscapemetrics, Landscapetools and raster in program R to generate and analyze virtual landscapes used in simulations.

Related models

Related models include:

- Jackson, HB, Fahrig L. What size is a biologically relevant landscape? *Landscape Ecology*.
- Wilensky, U. (1999). NetLogo. <http://ccl.northwestern.edu/netlogo/>. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL.

Credits and references

- Earl, J. E., & Zollner, P. A. (2017). Advancing research on animal-transported subsidies by integrating animal movement and ecosystem modelling. *Journal of Animal Ecology*, 86(5), 987-997.
- Earl, J. E., & Zollner, P. A. (2014). Effects of animal movement strategies and costs on the distribution of active subsidies across simple landscapes. *Ecological Modelling*, 283, 45-52.
- McGarigal, K., et al. (2002) "FRAGSTATS: spatial pattern analysis program for categorical maps."
- Gardner, Robert H., et al. "Neutral models for the analysis of broad-scale landscape pattern." *Landscape ecology* 1.1 (1987): 19-28.
- Etherington, T. R., et al. (2014). "NLMpy: A Python Software Package for the Creation of Neutral Landscape Models Within a General Numerical Framework." *Methods in Ecology and Evolution* 6 (2): 164–68.
- Palmer, Michael W. (1992). "The Coexistence of Species in Fractal Landscapes." *The American Naturalist* 139 (2): 375–97.
- Sciaini, M., et al. (2018). "NLMR and Landscapetools: An Integrated Environment for Simulating and Modifying Neutral Landscape Models in R." *Methods in Ecology and Evolution* 0 (0).

- Polis, G. A., et al. (1997). "Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs." *Annual review of ecology and systematics* 28.1: 289-316.
- Nathan, R., et al. "A movement ecology paradigm for unifying organismal movement research." *Proceedings of the National Academy of Sciences* 105.49 (2008): 19052-19059.
- Kalb, Rebecca A., and Cortney J. Mycroft. "The hardwood ecosystem experiment: goals, design, and implementation." (2013).
- Lima, S. L., & Patrick A. Z., "Towards a behavioral ecology of ecological landscapes." *Trends in Ecology & Evolution* 11.3 (1996): 131-135.

Data Processing R version 3.5.3

```
##### Daniel Bampoh #####
```

```
##### Analysis code for data from NetLogo batch simulation in behaviorspace #####
```

```
### set working drive for analysis code updates and output  
setwd("/:Working_Directory")
```

```
### install r packages for random forest and classification analysis
```

```
install.packages("randomForest")  
install.packages("rpart")  
install.packages("rpart.plot")  
install.packages("sandwich")  
install.packages("party")  
install.packages("rattle")  
install.packages("ggplot2")  
install.packages("gridExtra")  
install.packages("ggpubr")  
install.packages("data.table")  
install.packages("parallel")  
install.packages("doParallel")  
install.packages("foreach")  
install.packages("ranger")  
install.packages("Hmisc")  
install.packages("dplyr")
```

```
### load package libraries
```

```
library(randomForest)  
library(sandwich)  
library(party)  
library(rpart)  
library(rpart.plot)  
library(RGtk2)  
library(rattle)  
library(RColorBrewer)  
library(ggplot2)  
library(gridExtra)  
library(ggpubr)  
library(data.table)  
library(parallel)  
library(doParallel)  
library(foreach)  
library(ranger)  
library(tidyr)  
library(Hmisc)
```



```

# Split the values and convert to numeric. Note that if NA values were output
# by the LSM stats, that will throw an error but most likely still
# correctly assign the "NA" string to an NA value
vals <- df[[valvar]]
splitvals <- strsplit(x = as.character(vals), split = ", ")
print(length(splitvals))
splitvals <- data.frame(do.call(rbind, lapply(splitvals, as.numeric)))

## Assign the names as pulled from the stats_name_order column
names(splitvals) <- new.headers
return(splitvals)
}

# Pull names for class and landscape, if needed, and join data frames
if (!is.na(df$class_stats_as_string[1])) {
  class.vals.df <- generate_dataframe(df, "class_stats_name_order", "class_stats_as_string")
  df <- data.frame(df, class.vals.df)
}
if (!is.na(df$landscape_stats_as_string[1])) {
  landscape.vals.df <- generate_dataframe(df, "landscape_stats_name_order",
"landscape_stats_as_string")
  df <- data.frame(df, landscape.vals.df)
}

# View dataframe to double check output- note that it can be quite large
df <- df[,c(2:282)]
names(df)
dim(df)
str(df)
summary(df)

#### select preferred landscape metrics for analysis and relabel columns intuitively
maindf <- df[,c(100,63,64,155,118,119,210,173,174,229,231,252,23:51)]
names(maindf)[1] <- "Open.Canopy.Proportion"
names(maindf)[2] <- "Open.Canopy.Clumpiness"
names(maindf)[3] <- "Open.Canopy.Cohesion"
names(maindf)[4] <- "Partial.Canopy.Proportion"
names(maindf)[5] <- "Partial.Canopy.Clumpiness"
names(maindf)[6] <- "Partial.Canopy.Cohesion"
names(maindf)[7] <- "Closed.Canopy.Proportion"
names(maindf)[8] <- "Closed.Canopy.Clumpiness"
names(maindf)[9] <- "Closed.Canopy.Cohesion"
names(maindf)[10] <- "Landscape.Contagion"
names(maindf)[11] <- "Landscape.Contiguity"
names(maindf)[12] <- "Landscape.Interspersion"

```

```

maindf
names(maindf)
dim(maindf)
str(maindf)
summary(maindf)

maindf[,c(1:41)] <- lapply(maindf[,c(1:41)], as.character)
maindf[,c(1:41)] <- lapply(maindf[,c(1:41)], as.numeric)

# write prepped dataset to working directory
fwrite(maindf, "AnalysisDataset.txt")

# pull prepped dataset from working directory
maindf <- fread("AnalysisDataset.txt", sep = ",")
maindf
names(maindf)
dim(maindf)
str(maindf)
summary(maindf)

### relabel MSL, MVL and mortality columns as preferred
names(maindf)[13] <- "MSL.Closed.Canopy"
names(maindf)[14] <- "MSL.Partial.Canopy"
names(maindf)[15] <- "MSL.Open.Canopy"
names(maindf)[16] <- "MVL.Closed.Canopy"
names(maindf)[17] <- "MVL.Partial.Canopy"
names(maindf)[18] <- "MVL.Open.Canopy"
names(maindf)[19] <- "Mortality.Closed.Canopy"
names(maindf)[20] <- "Mortality.Partial.Canopy"
names(maindf)[21] <- "Mortality.Open.Canopy"

maindf[,c(1:41)] <- lapply(maindf[,c(1:41)], as.character)
maindf[,c(1:41)] <- lapply(maindf[,c(1:41)], as.numeric)

#maindf[,c(1:10,14:33)] <- round(maindf[,c(1:10,14:33)],1)
#maindf[,c(11:13)] <- round(maindf[,c(11:13)],3)

#maindf <- maindf[ which(maindf$Contagion > 40), ]

### dependent variable assignments
dvnames <- paste(names(maindf[,c(22:41)]), sep = ',')
dvnames
str(dvnames)

ivnames1 <- paste(names(maindf[,c(1:21)]), collapse = '+')
```

```

ivnames1
str(ivnames1)

### Histograms of dependent variables against independent variables
pdf('Ch3Exp2Histograms.pdf')
histplots.vars <- list()
maindf <- as.data.frame(maindf)
for (i in 1:ncol(maindf)) {
  histplots.vars[[i]] <- hist(maindf[,i], main = names(maindf)[i], xlab = names(maindf)[i],
cex.axis = 0.5)
}
dev.off()

#pdf('Ch3Exp2Histograms2.pdf')
#ggplot(gather(maindf), aes(value)) +
# geom_histogram(bins = 10) +
# facet_wrap(~key, scales = 'free_x')
#dev.off()

maindf <- na.omit(maindf)
maindf
names(maindf)
dim(maindf)
str(maindf)
summary(maindf)

### lists for model results
CARTtreemodels <- list() # CART

### random forest and classification models accounting for the effects of death as a function of
space (z)
for (y in dvnames){
  form <- as.formula(paste(y, "~", ivnames1))
  CARTtreemodels[[y]] <- rpart(form, data = maindf, method = "anova",
control = rpart.control(minsplit = 10000, minbucket = 10000, cp = 0.001))
}

#Parallelized Random Forest Model
RFtreemodels <- list()
for (y in dvnames){
  RFcores <- detectCores()/3 + 4
  RFcores
  RFtrees <- 1000/RFcores
  RFtrees
  cl <- makeCluster(RFcores)
  registerDoParallel(cl)

```

```

form <- as.formula(paste(y, "~", ivnames1))
RFtreemodels[[y]] <- foreach(ntree = rep(RFtrees, RFcores), .combine =
randomForest::combine, .multicombine = TRUE, .packages = 'randomForest') %dopar% {
  randomForest(form, data = maindf, mtry = 4,
    keep.forest = FALSE, nodesize = 10000, do.trace = TRUE, maxnodes = 5,
    improve = 0.001, doBest = TRUE, importance = TRUE, ntree = ntree)}
stopCluster(cl)
}

### random forest and classification model summaries
sink("DissCh3SimExp2CARTResults.txt", append=TRUE, split=TRUE)
CARTtreemodels.summary <- lapply(CARTtreemodels, summary)
CARTtreemodels.results <- lapply(CARTtreemodels, print)
sink()

sink("DissCh3SimExp2RFResults.txt", append=TRUE, split=TRUE)
RFtreemodels.results <- lapply(RFtreemodels, print)
RFtreemodels.imp <- lapply(RFtreemodels, randomForest::importance)
RFtreemodels.imp
sink()

### random forest and classification tree plots
pdf('DissCh3Exp2SubsiDistriCART.pdf')
for (var in names(CARTtreemodels)){
  #dev.new()
  fancyRpartPlot(CARTtreemodels[var][[1]], main = var)
}
dev.off()

pdf('DissCh3Exp2SubsiDistriCARTPruned.pdf')
for (var in names(CARTtreemodels)){
  #dev.new()
  fancyRpartPlot(prune(CARTtreemodels[var][[1]],
    cp =
CARTtreemodels[var][[1]]$cptable[which.min(CARTtreemodels[var][[1]]$cptable[, "xerror"]), "
CP"]),
    main = var)
}
dev.off()

pdf('DissCh3Exp2SubsiDistriRFVarImp.pdf')
for (var in names(RFtreemodels)){
  #dev.new()
  varImpPlot(RFtreemodels[var][[1]], main = var)
}
dev.off()

```

Data Processing - Python version 2.7.14 (Unpublished, Benjamin Pauli)

Generating MSL and MVL from step lengths and bearings

```
#install.packages("dplyr")
#install.packages("magrittr")
#library(dplyr)
#library(magrittr)

getwd()

setwd('C:/Users/dbamp/Desktop')
list.files()

WF.mov.dat <- read.table('AniMovDat2.txt', sep = "\t", header = TRUE)
WF.mov.dat

names(WF.mov.dat)
dim(WF.mov.dat)
str(WF.mov.dat)
summary(WF.mov.dat)

New.WF.mov.dat <- WF.mov.dat[c(2, 6:9)]
New.WF.mov.dat

names(New.WF.mov.dat)
dim(New.WF.mov.dat)
str(New.WF.mov.dat)
summary(New.WF.mov.dat)

#NA_Rows <- New.WF.mov.dat %>% filter_all(any_vars(is.na(.)))
#NA_Rows
#is.na(New.WF.mov.dat)
#tail(New.WF.mov.dat, 50)

New.WF.mov.dat[c("Step_Length_X_cm", "Step_Length_Y_cm", "Displacement_Angle_rad",
"Displacement_Angle_deg")] <- 0
New.WF.mov.dat

#attach(New.WF.mov.dat)
#Step_Len_Calc <- function(turn_ang, net_disp){
# Step_Len <- sqrt((((sin(turn_ang))*net_disp)^2) + (((cos(turn_ang))*net_disp)^2))
#}

for (i in 1:nrow(New.WF.mov.dat)){
```

```

# New.WF.mov.dat$Net_Displacement_cm[i] <- New.WF.mov.dat$Net_Displacement_cm[i] /
100
# if (Step_ID[i] == 1)
# {
#   Step_Length_X_cm[i] <- Step_Length_X_cm[i] + Net_Displacement_cm[i]
#   Step_Length_Y_cm[i] <- Step_Length_Y_cm[i] + Net_Displacement_cm[i]
# }
  if ((New.WF.mov.dat$Net_Bearing_o[i] > 0) & (New.WF.mov.dat$Net_Bearing_o[i] < 90)){
    New.WF.mov.dat$Displacement_Angle_rad[i] <-
New.WF.mov.dat$Displacement_Angle_rad[i] + New.WF.mov.dat$Net_Bearing_o[i]*pi/180
    New.WF.mov.dat$Displacement_Angle_deg[i] <-
New.WF.mov.dat$Displacement_Angle_deg[i] +
(New.WF.mov.dat$Displacement_Angle_rad[i])*180/pi
    New.WF.mov.dat$Step_Length_X_cm[i] <- New.WF.mov.dat$Step_Length_X_cm[i] +
((cos(New.WF.mov.dat$Displacement_Angle_rad[i]))*New.WF.mov.dat$Net_Displacement_c
m[i])
    New.WF.mov.dat$Step_Length_Y_cm[i] <- New.WF.mov.dat$Step_Length_Y_cm[i] +
((sin(New.WF.mov.dat$Displacement_Angle_rad[i]))*New.WF.mov.dat$Net_Displacement_cm
[i])
  }
  else if ((New.WF.mov.dat$Net_Bearing_o[i] > 90) & (New.WF.mov.dat$Net_Bearing_o[i] <
180)){
    New.WF.mov.dat$Displacement_Angle_rad[i] <-
New.WF.mov.dat$Displacement_Angle_rad[i] + (New.WF.mov.dat$Net_Bearing_o[i] -
90)*pi/180
    New.WF.mov.dat$Displacement_Angle_deg[i] <-
New.WF.mov.dat$Displacement_Angle_deg[i] +
(New.WF.mov.dat$Displacement_Angle_rad[i])*180/pi
    New.WF.mov.dat$Step_Length_X_cm[i] <- New.WF.mov.dat$Step_Length_X_cm[i] +
((cos(New.WF.mov.dat$Displacement_Angle_rad[i]))*New.WF.mov.dat$Net_Displacement_c
m[i])
    New.WF.mov.dat$Step_Length_Y_cm[i] <- New.WF.mov.dat$Step_Length_Y_cm[i] -
((sin(New.WF.mov.dat$Displacement_Angle_rad[i]))*New.WF.mov.dat$Net_Displacement_cm
[i])
  }
  else if ((New.WF.mov.dat$Net_Bearing_o[i] > 180) & (New.WF.mov.dat$Net_Bearing_o[i] <
270)){
    New.WF.mov.dat$Displacement_Angle_rad[i] <-
New.WF.mov.dat$Displacement_Angle_rad[i] + (New.WF.mov.dat$Net_Bearing_o[i] -
180)*pi/180
    New.WF.mov.dat$Displacement_Angle_deg[i] <-
New.WF.mov.dat$Displacement_Angle_deg[i] +
(New.WF.mov.dat$Displacement_Angle_rad[i])*180/pi
    New.WF.mov.dat$Step_Length_X_cm[i] <- New.WF.mov.dat$Step_Length_X_cm[i] -
((cos(New.WF.mov.dat$Displacement_Angle_rad[i]))*New.WF.mov.dat$Net_Displacement_c
m[i])

```

```

New.WF.mov.dat$Step_Length_Y_cm[i] <- New.WF.mov.dat$Step_Length_Y_cm[i] -
((sin(New.WF.mov.dat$Displacement_Angle_rad[i]))*New.WF.mov.dat$Net_Displacement_cm
[i])
}
else if ((New.WF.mov.dat$Net_Bearing_o[i] > 270) & (New.WF.mov.dat$Net_Bearing_o[i] <
360)){
  New.WF.mov.dat$Displacement_Angle_rad[i] <-
New.WF.mov.dat$Displacement_Angle_rad[i] + (New.WF.mov.dat$Net_Bearing_o[i] -
270)*pi/180
  New.WF.mov.dat$Displacement_Angle_deg[i] <-
New.WF.mov.dat$Displacement_Angle_deg[i] +
(New.WF.mov.dat$Displacement_Angle_rad[i])*180/pi
  New.WF.mov.dat$Step_Length_X_cm[i] <- New.WF.mov.dat$Step_Length_X_cm[i] -
((cos(New.WF.mov.dat$Displacement_Angle_rad[i]))*New.WF.mov.dat$Net_Displacement_c
m[i])
  New.WF.mov.dat$Step_Length_Y_cm[i] <- New.WF.mov.dat$Step_Length_Y_cm[i] +
((sin(New.WF.mov.dat$Displacement_Angle_rad[i]))*New.WF.mov.dat$Net_Displacement_cm
[i])
}
else if ((New.WF.mov.dat$Net_Bearing_o[i] == 0) | (New.WF.mov.dat$Net_Bearing_o[i] ==
360)){
  New.WF.mov.dat$Displacement_Angle_rad[i] <-
New.WF.mov.dat$Displacement_Angle_rad[i] + (New.WF.mov.dat$Net_Bearing_o[i])*pi/180
  New.WF.mov.dat$Displacement_Angle_deg[i] <-
New.WF.mov.dat$Displacement_Angle_deg[i] +
(New.WF.mov.dat$Displacement_Angle_rad[i])*180/pi
  New.WF.mov.dat$Step_Length_X_cm[i] <- New.WF.mov.dat$Step_Length_X_cm[i]
  New.WF.mov.dat$Step_Length_Y_cm[i] <- New.WF.mov.dat$Step_Length_Y_cm[i] +
New.WF.mov.dat$Net_Displacement_cm[i]
}
else if (New.WF.mov.dat$Net_Bearing_o[i] == 90) {
  New.WF.mov.dat$Displacement_Angle_rad[i] <-
New.WF.mov.dat$Displacement_Angle_rad[i] + (New.WF.mov.dat$Net_Bearing_o[i])*pi/180
  New.WF.mov.dat$Displacement_Angle_deg[i] <-
New.WF.mov.dat$Displacement_Angle_deg[i] +
(New.WF.mov.dat$Displacement_Angle_rad[i])*180/pi
  New.WF.mov.dat$Step_Length_X_cm[i] <- New.WF.mov.dat$Step_Length_X_cm[i] +
New.WF.mov.dat$Net_Displacement_cm[i]
  New.WF.mov.dat$Step_Length_Y_cm[i] <- New.WF.mov.dat$Step_Length_Y_cm[i]
}
else if (New.WF.mov.dat$Net_Bearing_o[i] == 180) {
  New.WF.mov.dat$Displacement_Angle_rad[i] <-
New.WF.mov.dat$Displacement_Angle_rad[i] + (New.WF.mov.dat$Net_Bearing_o[i])*pi/180
  New.WF.mov.dat$Displacement_Angle_deg[i] <-
New.WF.mov.dat$Displacement_Angle_deg[i] +
(New.WF.mov.dat$Displacement_Angle_rad[i])*180/pi

```



```

New.WF.mov.dat$Step_Length_X_cm[i] <- New.WF.mov.dat$Step_Length_X_cm[i]
New.WF.mov.dat$Step_Length_Y_cm[i] <- New.WF.mov.dat$Step_Length_Y_cm[i] -
New.WF.mov.dat$Net_Displacement_cm[i]
}
else if (New.WF.mov.dat$Net_Bearing_o[i] == 270) {
  New.WF.mov.dat$Displacement_Angle_rad[i] <-
New.WF.mov.dat$Displacement_Angle_rad[i] + (New.WF.mov.dat$Net_Bearing_o[i])*pi/180
  New.WF.mov.dat$Displacement_Angle_deg[i] <-
New.WF.mov.dat$Displacement_Angle_deg[i] +
(New.WF.mov.dat$Displacement_Angle_rad[i])*180/pi
  New.WF.mov.dat$Step_Length_X_cm[i] <- New.WF.mov.dat$Step_Length_X_cm[i] -
New.WF.mov.dat$Net_Displacement_cm[i]
  New.WF.mov.dat$Step_Length_Y_cm[i] <- New.WF.mov.dat$Step_Length_Y_cm[i]
}
}

```

```

New.WF.mov.dat
names(New.WF.mov.dat)
dim(New.WF.mov.dat)
str(New.WF.mov.dat)
summary(New.WF.mov.dat)

```

```

New.WF.mov.dat[c("Step_Length_cm", "Step_Length_X_m", "Step_Length_Y_m")] <- 0
New.WF.mov.dat

```

```

for (i in 1:nrow(New.WF.mov.dat)) {
  if (New.WF.mov.dat$Step_ID[i] == 1)
  {
    New.WF.mov.dat$Step_Length_cm[i] <- New.WF.mov.dat$Step_Length_cm[i] +
      sqrt((New.WF.mov.dat$Step_Length_X_cm[i])^2 +
(New.WF.mov.dat$Step_Length_Y_cm[i])^2)
  }
  else if (New.WF.mov.dat$Step_ID[i] > 1) {
    New.WF.mov.dat$Step_Length_cm[i] <- New.WF.mov.dat$Step_Length_cm[i] +
      sqrt((New.WF.mov.dat$Step_Length_Y_cm[i] - New.WF.mov.dat$Step_Length_Y_cm[i-
1])^2 + (New.WF.mov.dat$Step_Length_X_cm[i] - New.WF.mov.dat$Step_Length_X_cm[i-
1])^2)
  }
  New.WF.mov.dat$Step_Length_X_m[i] <- New.WF.mov.dat$Step_Length_X_cm[i] +
New.WF.mov.dat$Step_Length_X_cm[i]/100
  New.WF.mov.dat$Step_Length_Y_m[i] <- New.WF.mov.dat$Step_Length_Y_cm[i] +
New.WF.mov.dat$Step_Length_Y_cm[i]/100
}

```

```

New.WF.mov.dat
write.table(New.WF.mov.dat, file = "AniMovDatMain2.txt", sep = "\t")

```

Data Processing - Python version 2.7.14 (Unpublished, Benjamin Pauli)

- HEE Juvenile wood frog Mean Step Length (MSL) and Mean Vector Length (MVL) derivation from turning angels and bearings of movement tracks:

```

from math import *
from string import *

def getangle(line1, line2, line3):
    x1, y1, x2, y2, x3, y3=eval(line3[4]), eval(line3[5]),eval(line2[4]), eval(line2[5]),
    eval(line1[4]), eval(line1[5])
    j=x2-x1
    k=y2-y1
    l=x3-x2
    m=y3-y2
    h=sqrt((k*k)+(j*j))
    i=sqrt((l*l)+(m*m))
    p=2*pi
    if h!=0 and i!=0:
        if (k<0 and j<0):
            a1=-acos(j/h)
        elif k<0:
            a1=asin(k/h)
        else:
            a1=acos(j/h)
        if (m<0 and l<0):
            a2=-acos(l/i)
        elif m<0:
            a2=asin(m/i)
        else:
            a2=acos(l/i)
        ang=a2-a1
        if ang<=-pi:
            ang=ang+p
        elif ang>pi:
            ang=ang-p
        return ang

def mvl(fname):
    c, s, n=0,0,0
    nonecount=0
    como, comZ=[],[]
    cr=180/pi
    habs={'Overall':como}
    infile=open(fname, 'r')
    infile.readline()

```

```

l3=infile.readline()
line3=split(l3, ",")
l2=infile.readline()
line2=split(l2, ",")
for line in infile.readlines():
    line1=split(line, ",")
    angle=getangle(line1, line2, line3)
    if angle!=None:
        como.append(angle)
    else:
        comZ.append(angle)
    line2, line3 = line1, line2
for ww in habs:
    pu=habs[ww]
    hh, n, xr, c, s, xi, yi, r, d, = 0,0,0,0,0,0,0,0,0
    if len(pu)==0:
        print "There are no angles for", ww
        print
    else:
        for hh in range(len(pu)):
            xr=pu[hh]
            c=c+cos(xr)
            s=s+sin(xr)
            n=n+1
        xi=c/n
        yi=s/n
        r=sqrt((yi**2)+(xi**2))
        d=(sqrt(2*(1-r)))*cr
        if (yi==0 and xi==0):
            a="NA"
        elif (yi<0 and xi<0):
            a=-(acos(xi/r)*cr)
        elif yi<0:
            a=(asin(yi/r)*cr)
        else:
            a=acos(xi/r)*cr
        print ww
        print "Number of angles measured is ", n
        print "The preferred angle is ", a
        print "The r value is ", r
        print "The angular deviation is ", d
        print
ff=len(comZ)
print "There were", ff, "unclassified angles."
print

```

```
def main():
    fname=raw_input("Enter filename: ")
    print
    print "ANGLES"
    print "-----"
    mvl(fname)
    raw_input("Press <enter> to exit")

main()
```