BIOLOGICAL FITNESS: A DISCUSSION OF DEFINITIONS AND METRICS
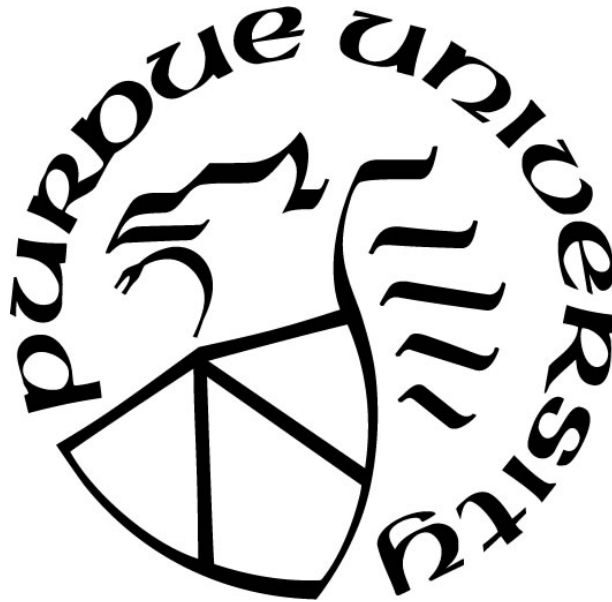
by

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ABSTRACT

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The concept of biological fitness is foundational for our understanding of both ecology and evolution. Fitness is often described vaguely as an organism's contribution to the next generation. The reason this is vague is because researchers define and measure fitness differently across fields. I suggest that the myriad definitions and ways to measure fitness commonly employed have led to debates and, seemingly contradictory results. In order to investigate the use of the concept of fitness, I performed a literature review and asked, (1) How is biological fitness defined and used by researchers? (2) How is fitness actually measured by researchers? To address these questions, I surveyed 478 papers published between 2012 and 2016, that included the word 'fitness' in the title, and were in the Web of Science categories of 'ecology' and 'evolutionary biology'. In my analysis of the journal articles fitness was only defined 33% of the time. Among studies that did explicitly define fitness, I categorized 18 different definitions, though only 7 were found in more than 5% of papers. I also found differences in how fitness was measured. I found 87 measurements that I grouped into 13 categories. In addition to my survey of the literature, I performed an experiment to explore the relationship between different measures of fitness. Vegetative biomass and reproductive biomass are often both used as metrics of fitness by plant ecologists. In this experiment I determined the relationship between two popular measures of plant fitness vegetative biomass and reproductive yield. I found that these two proxies for plant fitness, vegetative biomass and reproduction, were unimodally related, meaning: 1) intermediate sized plants have the greatest reproductive output, and; 2) for any unique amount of reproduction there is both a small and a large plant with identical reproductive output. Two things emerge from the literature review and the experiment: first, given the many definitions that exist, researchers should be clear about which one they are using. Second, one must be clear about the expected relationship between proxy measurements and fitness, as it may be complex, or non-existent.

CHAPTER 1.   INTRODUCTION

1.1   Background

Evolution by natural selection acts upon phenotypes. These phenotypes have genotypes that control them and are inherited (Ayala 2007). Darwin was unaware of any form of genetics, but he did notice changes in phenotypes that were imperfectly passed on to offspring (Darwin 1869). Darwin described the heritable changes in phenotypes he observed as descent with modification. Evolution acts on phenotypes through natural selection, the process where organisms better adapted to their environment are better able to contribute to future generations through survival and reproduction. Fitness is then the currency of natural selection. Therefore, in order to fully understand natural selection, a definition of fitness is absolutely necessary.

Fitness is often described as a measure of an organism's ability to survive and reproduce within an environment (Orr 2009). Most biologists know that Darwin did not originally use the phrase 'survival of the fittest'. Instead, this concept of fitness was coined by philosopher Herbert Spencer after reading Darwin's *On the Origin of Species* (Darwin 1869). The phrase apparently stuck with Darwin, to the point where he edited his 1869 edition of the book to include it as part of the title of chapter 4. Darwin equated survival of the fittest with natural selection and defined them as, "Preservation of favorable individual differences and variations, and the destruction of those which are injurious (Darwin 1869)." Scientists since Darwin have used 'fitness' to describe everything from *Arabidopsis* (Campitelli, Des Marais et al. 2016) to mice (Haanes, Markussen et al. 2013), and from the allele (Jourdan-Pineau, Folly et al. 2012) to the species (Kimball, Gremer et al. 2012). My review of the literature indicates conformity among biologists that an organism's fitness is generally defined as '*its ability to contribute to future generations*'. However, how this contribution is measured or defined greatly differs among scientists. This is not a recent issue. In 1980 S. O. Kimbrough quoted H.J. Muller stating that, "It is unfortunate that Herbert Spencer proposed the expression 'survival of the fittest' for Darwin's term 'natural selection,' and that Spencer's expression was accepted even by Darwin himself (Kimbrough 1980). This tautological form has led people into philosophical muddles and has caused them even to question the validity of the entire concept (Kimbrough 1980)**."** This might be because has been used to describe subtly

difference things (Orr 2009), and also because fitness is a complicated concept as it attempts to condense entire trait functions through time, as well as individual- and population-wide factors into one single number (Grafen 2015).

Another reason fitness is a complicated concept is because it has been applied in many contexts. For example, theoretical ecologists often view fitness as the per capita population growth rate. This allowed it to be used to determine the changes in a population through abundance and success of individuals. There are also various indices of fitness. One index for fitness has become relative fitness, which is defined as the survival or reproduction rate of one genotype in a population compared to that of another. Similarly, inclusive fitness is an index of contribution of an individual's genes to future generations while considering shared genes with close relatives. These are just three examples of uses and indices within the realm of fitness, but they illustrate the variability of the usage of fitness.

The goal of this thesis is to assist, not only in understanding the importance of fitness to the fields of ecology and evolution, but also in understanding that there needs to be increased clarity in defining and measuring fitness. Through both a synthesis of the literature and a series of experiments with plants, my goal is to provide insight into the concept of biological fitness and allow for a clearer path for future researchers to follow.

1.2   Fitness Definitions

In chapter 2 I will examine definitions of fitness used by authors in the literature. Fitness has been used to describe subtly different things (Orr 2009). For example, Fisher was first to use intrinsic rate of natural increase as a way to measure and define fitness (Fisher 1958, Costa 2013). Wright's work led to relative fitness, which has become an index of fitness used to compare two populations (Wright 1937, Costa 2013). Hamilton used inclusive fitness (which includes the success of relatives) to solve problems with altruism found by earlier researchers (Hamilton 1963, Hamilton 1964, Costa 2013). Each of the different descriptions of fitness were all significant findings and all useful for a specific purpose. Because there are so many different definitions of fitness, it can often be difficult to distinguish among implied fitness definitions unless the author explicitly defined the term. In chapter 2 I survey how fitness is defined and measured in current literature. I

show that although the word 'fitness' is frequently used, it is only defined about 1/3 of the time and it is measured in through a wide range of metrics. I end chapter 2 with some suggestions for standardization in future research.

1.3   Fitness Metrics

Evolution is the study of the change in species over time. Evolution is built on the idea that within a species, individuals have different phenotypes. These phenotypes are heritable and affect an organism's fitness. Natural selection requires that different phenotypes and genotypes differ in fitness (Orr 2009)**.** Ecology is the study of how organisms interact with each other and the environment. Ecology assumes that an individual interacts differently with different organisms. These interactions can have positive, negative, or null effect on the individual's fitness (Fordyce 2006)**.** While ecology and evolution are intertwined, and both depend on fitness, they often use fitness to study very different things. These differences are the reason that different fitness measures are needed, however all fitness measures may not be equivalent.

Based on chapter 2, fitness is commonly defined as an organism's ability to contribute to future generations through survival and reproduction. However, in plants, fitness is often estimated as either reproductive output (e.g. seeds) or vegetative mass, and these metrics are frequently equated. In chapter three I explore the correlations between vegetative biomass and reproductive biomass as two metrics of fitness in a greenhouse experiment. This experiment shows that there is a unimodal relationship between plant biomass and reproductive biomass, indicating it would be difficult for both measures to be a useful metric of fitness at all times.

1.4   Discussion

Fitness has become arguably one of the most important concepts in the field of ecology and evolution. This is because the underlying goal of ecology is to understand interactions among organisms and the effect of those interactions on fitness. Similarly, a goal of evolution is to understand the changes in fitness that cause the turnover in traits and species. Although it is well established that fitness is key to many parts of ecology and evolution, there are many definitions of fitness, and many metrics used to estimate fitness. Fitness is such important concept, it is vital

that fitness is well understood and described by those that study ecology and evolution. In chapter four I will summarize the results from chapters two and three in order to show the issue we currently face in ecology and evolutionary biology. Then I provide a prospectus for future research involving the concept of fitness and offer some suggestions for standardizations among researchers.

CHAPTER 2.   THE SURVIVAL OF FITNESS AS A CONCEPT: A LITERATURE REVIEW OF THE DIVERSITY OF FITNESS

2.1   Introduction

Natural selection has been one of the pillars of ecology and evolutionary biology since Darwin described it in *On the Origin of Species*. While Darwin did not yet have an understanding of genetics, he was able to recognize descent with modification (Darwin 1869). Later, the modern synthesis was responsible for bringing together the fields of genetics and evolution and allowed scientist to discover how evolutionary changes occur (Huxley 1942). One of these ways is natural selection, which refers to how genetic adaptations in combination with the environment, shape which organisms or phenotypes survive and contribute to the next generations (Fisher 1958). A key concept for evolution by natural selection is fitness described as the currency of natural selection, such that we would expect natural selection to favor genes that increase fitness, regardless of the definition. Over the years there have been a proliferation of definitions of fitness and metrics used to quantify fitness. I suggest that it has led to debates and, seemingly contradictory results, simply because researchers have used different definitions. These different results generally occur because fitness is investigated through two different analyzation methods, through mathematical methods, such as the population growth rate, and through components that contribute to differences in fitness, such as reproductive ability (Orr 2009). Because of this uncertainty, some scientists have argued that we should stop using the concept of fitness in research and have sought to standardize fitness and understand it better (Thoday 1953, Mills and Beatty 1979, Orr 2009, Costa 2013). Here, I will argue that fitness is an invaluable concept to the field of biology and that this issue could be resolved simply if authors were clear about: (i) the definition used in any particular study, and; (ii) the relationship between the measure of fitness used and the definition. To provide context, I performed a survey of the literature to systematically quantify whether individual studies defined fitness, how it was measured, and collected the various definitions for fitness into one place.

Before beginning, it is useful to define terms, namely, adaptations and natural selection. Here I define adaptations as traits that increase an individual's ability to pass genes to the next generation, and therefore have been shaped by natural selection. Any traits that are not heritable or do not

affect contributions of genes to the next generation are neutral and thus not an adaptation. Natural selection occurs when there are; (i) heritable traits; (ii) variation in traits; (iii) variation in fitness based on the differences in the traits. Fitness is a key concept to quantify the effects of natural selection and shape adaptations. In what follows I seek to accomplish the following objectives: 1) review different definitions of fitness that are used in the literature, 2) review different metrics found in the literature, 3) conclude by offering suggestions going forward.

2.2   Methods

In September 2017, I searched the Web of Science for the word "fitness" constrained to occur in the title of articles published in the five years between 2012 and 2016. From these papers I further constrained the search to papers in the Web of Science categories of "Ecology" and "Evolutionary Biology". I then further narrowed the search to only primary research journal articles (i.e. excluding reviews or opinion style articles). This search method produced 608 papers. This set of 608 papers was further reduced to 478 because some articles were a verbal description of theory, had no online access available, or because they were mislabeled as a research article by Web of Science. I excluded verbal descriptions of theories, because they were descriptions of fitness and were not measuring fitness or using it in research. For each of the 478 papers, the article text was searched for the word 'fitness'. Each sentence that contained the word 'fitness' was read as well as the sentence after. Tables and graphs with the word 'fitness' on them or in their description were also included in this reading. From this sample I collected the following data: (*i*) the type of study categorized as model, empirical, or both; (*ii*) if fitness was defined; (*iii*) if fitness was defined, I recorded the definition(s) of fitness; (*iv*) the usage of different fitness types; (*v*) the Web of Science categories the paper was listed under; (*vi*) the species name and kingdom studied; (*vii*) the measure used to empirically estimate fitness, and; (*viii*) the number of times the word fitness was used in the manuscript. These results were then combined and summarized.

2.3   Results

Of the 126,349 journal articles published in the web of science categories of ecology and evolutionary biology between 2012 and 2016, 608 of them had the word "fitness" in the title. Of these 608 articles, I analyzed 478 for this review. These articles each used the word 'fitness' an

average of 41 times, but it was used as few as 2 and as many as 249 times in an article. Surprisingly, fitness was only defined 33.3% of the time across all articles. However, this varied depending on the type of article. Articles classified as empirical, or data-based, made up 77.8% of all articles, and fitness was defined in these articles 21.2% of the time. Articles classified as theoretical or model-based made up 13.8% of all articles, and defined fitness 86.4% of the time. Articles classified as a combination of empirical and theoretical comprised 8.4% of all articles and defined fitness 57.5% of the time (Figure 2.1). When dividing articles by kingdom of study, researchers that studied plants define fitness the least, just 15.5% of the time, and of those listed as "other", often theoretical articles, define fitness 78.0% of the time (Figure 2.2).
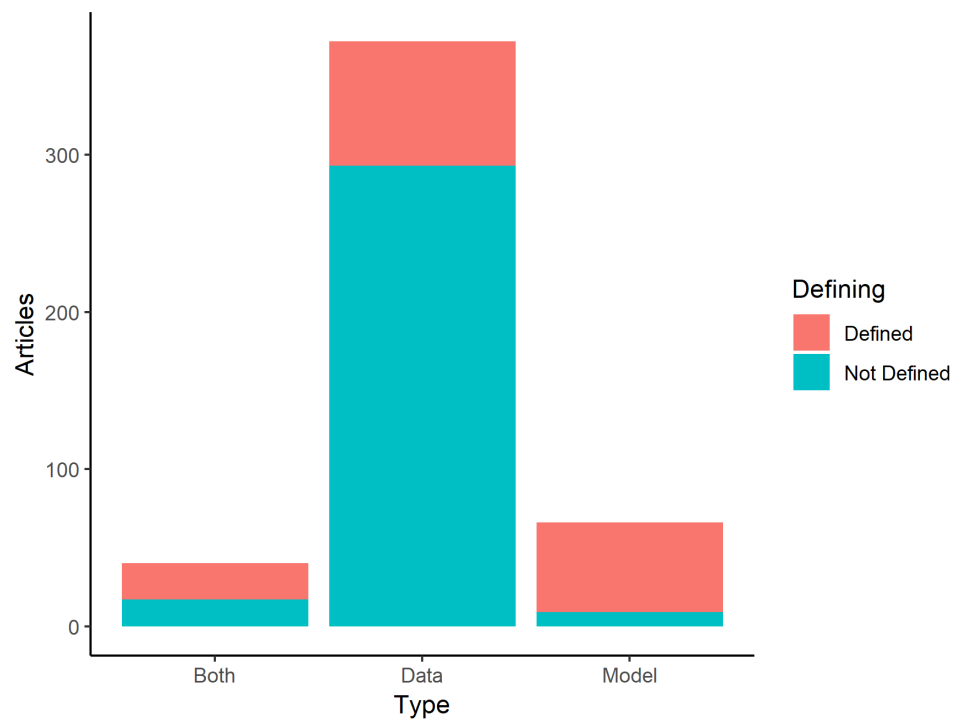
Figure 2.1 Breakdown of how often fitness was defined by type of article. Type of article represents whether the article was empirical (data based), theoretical (model based) or a combination (both). Bar height corresponds with number of articles in category. Red portion corresponds with articles that define fitness while blue corresponds with those that do not.
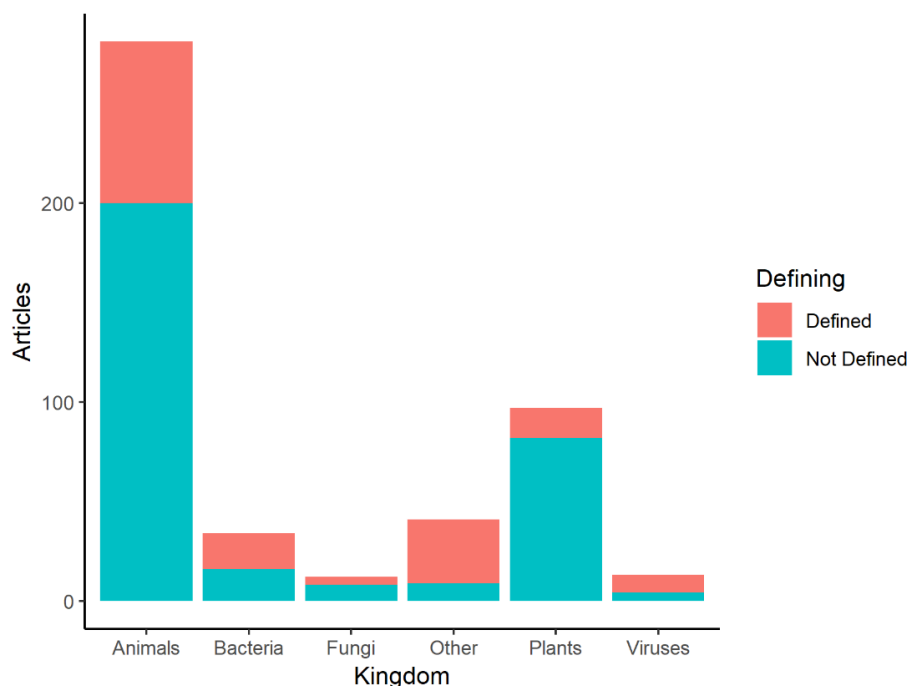
Figure 2.2 Breakdown of how often fitness is defined based on Kingdom of study. Kingdom corresponds with the kingdom or group of origin the study species fell into. Those within other include mostly models as well as a few obscure kingdoms. Bar height corresponds with number of articles in category. Red portion corresponds with articles that define fitness while blue corresponds with those that do not.

Of the 478 articles that contained fitness in the title, only 159 articles defined fitness. From these articles I identified 18 unique definitions (Table 5.1). However, only 7 definitions were found in more than 5% of papers. Because there was a general consensus that fitness was defined as only within the current environment and also accounted for contribution to future generations, I omitted this from each definition for ease of evaluation (Table 2.1).

Table 2.1 Fitness definitions found in more than 5% of articles. The percent is the percent of the 159 articles that defined fitness that the definition was used in. 20% of articles used relative fitness, but to calculate fitness they needed to use one of the definitions below, and thus relative fitness is not included in the Table below. All definitions found can be seen in Table 5.1.

Definitions	Percent of Articles
Survival & Reproduction	25.79%
Per capita population growth rate/intrinsic rate of increase	18.87%
Reproduction	15.09%
Function of traits/phenotype	9.43%
Gene transmission/expression/contribution to future	6.92%
Survival	5.66%
Frequency in population	5.03%

Along with the low number of articles that defined fitness, I also found a wide range of measurements of fitness used across the fields of ecology and evolution. There were over 87 different measurements of fitness found in just 478 articles. All different measures were counted in each article, meaning they could measure fitness in more than one way and each were counted individually. I was able to categorize the 87 measurements into 13 groups, 7 of which were used in more than 5% of articles (Table 2.2). The remainder are shown in Table 5.2.

Table 2.2 Fitness measures found in 95% of articles. The proportion is the proportion of the 478 articles that used each metric. All metrics found can be seen in Table 5.2.

Metric	Number	Proportion	Example units	Number	Proportion
Reproduction measures	232	0.26	Count of Offspring	57	0.12
			Reproduction	48	0.10
			Count of Seeds	38	0.08
			Count of Fruit	28	0.06
			Fecundity	26	0.05
			Lifetime reproduction	26	0.05
			Eggs laid	22	0.05
			Count of Flowers	12	0.03
			Reproductive output	11	0.02
			Reproductive opportunities/partners	5	0.01
			Fertility	4	<0.01
			Spore load	3	<0.01
			Production of daughters	3	<0.01
			Female fecundity	3	<0.01
			Fruit biomass	2	<0.01
			Twinning rate	1	<0.01
Survival measures	139	0.15	Survival, adult and juvenile	72	0.15
			Offspring Survival	31	0.06
			Age, longevity	22	0.05
			Death	9	0.02
			Male survival	3	<0.01
			Female survival	2	<0.01
Trait measures	92	0.10	Behavior, performance	11	0.02
			Plant height	9	0.02
			Seed mass	9	0.02
			Pollen, pollination	9	0.02
			Body length	6	0.01
			Damage, susceptibility	6	0.01
			Flower traits	7	0.01
			Basal metabolic rate/energy	4	<0.01

Metric	Number	Proportion	Example units	Number	Proportion
			Feeding success/Diet	4	<0.01
			Horn/antler growth	3	<0.01
			Sperm quality/count	3	<0.01
			Phenotype	3	<0.01
			Egg size	3	<0.01
			Dominance rank	3	<0.01
			Morphology	2	<0.01
			Gonad weight/size	2	<0.01
			Fruit ripening/attraction of vertebrate frugivores	2	<0.01
			Jaw size	1	<0.01
			Invasiveness	1	<0.01
			Birth time	1	<0.01
			Spleen weight	1	<0.01
			Secondary sexual trait expression	1	<0.01
			Pectoral muscle volume	1	<0.01
Body size or condition measures	86	0.10	Body mass	39	0.08
			Size of offspring, condition	18	0.04
			Body condition	14	0.03
			Body size	8	0.02
			Count of Stems	5	0.01
			Leaf number/length	2	<0.01
Population characteristics	64	0.07	Population Growth Rate	54	0.11
			Population size	7	0.01
			Colonies	2	<0.01
			Replacement rate	1	<0.01
Recruitment measures	53	0.06	Reproductive recruitment	20	0.04
			Seed germination, viability	19	0.04
			Hatching success	10	0.02
			Incubation success	2	<0.01
			Seed dormancy	1	<0.01
			Nest success	1	<0.01
Growth measures	44	0.05	Growth	15	0.03
			Offspring growth/development	10	0.02
			Age to Breeding/time to develop	10	0.02
			Reproductive Lifespan, timing, rate, Phenology	9	0.02

2.4   Discussion

My survey of current ecology and evolution literature focused on fitness revealed several findings about the concept of fitness and natural selection. Firstly, few studies actually clearly defined fitness. Only 33.3% of all studies gave an explicit definition of 'fitness'. While theoretical articles defined fitness 86% of the time, empirical ones only defined fitness 21% of the time likely because modelers commonly describe fitness as the per capita population growth rate while experimental studies have more variability in their fitness measures and definitions.

The most common definition of fitness used survival and reproduction as an organism's contribution to future generations. Closely linked to this definition are those that use just survival or just reproduction. This definition is popular among greenhouse and laboratory studies as it is useful when there is just one generation (e.g. Rutter, Roles et al. 2012, De Jong, Wong et al. 2014). The next most common definition of fitness was per capita population growth rate. This definition is useful in field experiments and mathematical models where multiple generations are being studied (e.g. Tanaka and Tatsuta 2013, Kher, Dosdall et al. 2016, Lehmann, Mullon et al. 2016). The frequency of phenotypes in a population is closely connected to the population growth rate as it looks at the per capita population growth rate of just part of the population (e.g. Kher, Dosdall et al. 2016). Fitness defined as a function of traits or phenotypes is most often used in models, due to the fact that traits can be easily broken down and combined to account for fitness (e.g. Hackett and Bonsall 2016). Fitness defined as gene transmission or expression can commonly be used at any level as long as the focus is on the alleles or genes (e.g. Aarssen 2015).

There was also a lack of articles defining fitness within the plant kingdom. Plant scientists defined fitness just 15% of the time, the least of all kingdoms investigated, while those that study microorganisms (e.g. bacteria, fungi, viruses; Figure 2.2) defined fitness over 50% of the time. This is likely due to use of per capita population growth rate as an easy way to describe fitness within microorganisms, as well as the lack of individual phenotypic measurements. The wide range of fitness metrics found not only across kingdoms, but also within the same kingdom, and even sometimes within a species was also shocking. While different metrics are not necessarily as a problem when describing fitness because of the complexity of the concept, a proportion of articles were unclear about how they measured fitness, 8%. These unclear articles are an issue, which can

cause confusion as what they are measuring may not be related to fitness and the reader is unable to make that judgement for themselves (Table 5.2).

It is also important to note that my survey was not all inclusive of fitness literature. There are many studies that use fitness, but do not use it in the title of their article. I focused on articles that had fitness in the title, as they should be the most centered on the concept of fitness. This assumption could possibly skew my results as article that study fitness but do not include the word fitness in their title could define or measure it differently than those that use fitness in the title.

My purpose here is not to advocate for a single definition of fitness, or even to critique any individual definitions. Fitness clearly is a concept that might need different definitions in different studies and contexts. However, to minimize confusion and unnecessary debate, I suggest the following:

1) If researchers are not studying evolution, adaptations, natural selection, or other concepts where fitness is specifically needed, they should avoid using the word 'fitness'. This should reduce any overuse or misuse of the term.

2) Researchers should explicitly state the definition of fitness that they are using in each study (see Table 2.1 for suggestions). This will allow readers to better understand the study's research objectives.

3) Researchers should state the measure used to represent fitness and further discuss how and why their metric was effective for estimating fitness. This would undoubtedly require preliminary pilot studies to connect a metric of fitness to the definition of fitness. This will create accountability for fitness measures, reducing confounding results across studies.

CHAPTER 3.   VEGETATIVE GROWTH IS NOT FITNESS: A UNIMODAL RELATIONSHIP BETWEEN VEGETATIVE TRAITS AND REPRODUCTIVE OUTPUT IN PISUM SATIVUM

3.1   Introduction

In plant sciences, fitness is generally defined as a plant's contribution to future generations. The vagueness of this definition often complicates determining the correct metric. Chapter two showed that within plant sciences, metrics of fitness include biomass, seed count, seed mass, longevity, flowers, leaves, seed viability, and many more (Table 5.2). The wide array of metrics suggests correlation with each other and fitness. However, if relationships change based on environmental changes this correlation does not exist. Chapter two also demonstrated that plant scientists define fitness in their research papers the least (Fig 2.2). For this chapter, I will focus on the two most commonly used metrics of plant fitness discovered in chapter two: vegetative biomass and total seed production.

The ability to predict how organisms and systems will behave is an important part of any science field (Evans, Norris et al. 2012). This is becoming especially important in the fields of ecology and evolution as climate change has intensified changes in the environment and organisms (Holt 1990). Predictive models have become useful in plants because they allow predictions of an individual's traits to the world net primary productivity (Mcnickle, Gonzalez-Meler et al. 2016). The predictions of most models of plant production, emerge from the assumed relationship between vegetative production and fitness (Parker and Maynard Smith 1990). Based on definitions presented in chapter 2, this approach defined fitness as a function of traits (Table 2.1). Fitness defined as function of traits means that there are a variety of components that contribute to fitness and they must be taken together to fully understand fitness. For example, if a set of n traits can be expressed as $v_1, v_2 \dots v_n$, then fitness as a function of these traits would be some function, $G(v_1, v_2 \dots v_n)$, where G is fitness (Figure 3.1). Generally, this relationship is broken down into two basic parts: benefits and costs. For example, leaves benefit the plant in the form of photosynthetic products they produce, and leaves have costs in terms of construction and respiration. Benefits and costs can also be indirect. For example, if competition is incorporated into game theoretic models, leaves also have indirect benefits from shading neighbors and

suppressing the growth of competitors. Roots can be conceptualized in the same way in terms of the benefits of nutrient and water uptake, with indirect benefits of pre-empting the supply of neighbors thus suppressing their growth and the costs of construction and maintenance of root tissue. Equipped with mathematical functions for these costs and benefits (Parker and Maynard Smith 1990), it is straightforward to solve for the level of vegetative tissue production that maximizes benefits while minimizing costs. Indeed, variants of such models are the core of the vegetation component of most crop, ecosystem, climate, and earth system models (Fisher, Koven et al. 2017). Importantly, there is a mathematical constraint on such models, that the net benefit equation (i.e. benefits minus costs), which is equated with biological fitness, is unimodal and concave down when plotted against the trait being modeled (Figure 3.1). This means intermediate sized plants would have the largest fitness. If the relationship between vegetative traits like leaf or root production is not unimodal concave down, then two issues arise: 1) there is no global optimum for production, only a series of local optima, or; 2) optimal production is infinite. The first of these options would indicate that vegetative production would be very difficult to predict, and the second is clearly impossible due to the laws of thermodynamics.
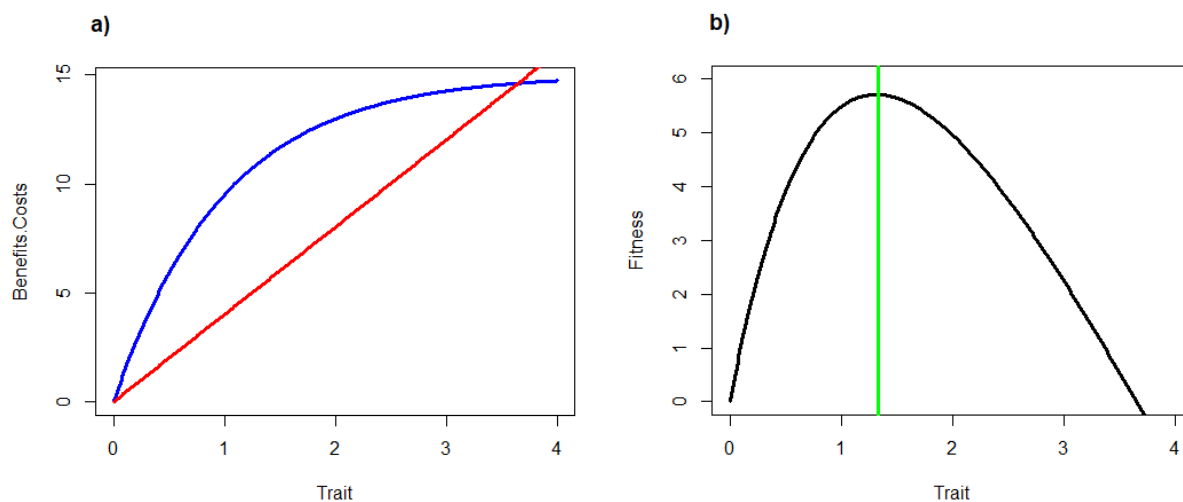
Figure 3.1 The benefits (blue line) and subsequent costs (red line) found to produce any given continuous trait (a). The fitness effects of the costs and benefits to produce a trait (b).

Competition is important for our understanding of ecology (Welden and Slauson 1986). It occurs when both organisms are negatively affected by their interaction. Competition can be found across kingdoms and between the same species or between different species. Understanding competition

allows us to better understand community structure, as it shapes how and where plants germinate and grow (Tilman 1982, Tilman 1986). This is because plants compete for all of their resources; water, space, nutrients, and light (Grime 1979, Tilman 1982, Wilson 1988, Casper and Jackson 1997). The intensity of the competition can drastically change plant phenotypes. These productivity changes can be predicted using plant production models, including game theoretic models.

The use of evolutionary game theory allows researchers to evaluate biological interactions such as competition, benefits, costs and indirect benefits. Evolutionary game theory is the usage of game theory, the study of the interactions between decision makers, in living organisms to evaluate interactions and responses in different ecological situations. Tragedy of the commons is one of these ecological responses. Tragedy of the commons occurs when individuals are in a shared-resource system and use it for their own best interest, regardless of what is best for the community (Gersani, Brown et al. 2001, Falster and Westoby 2003). Starting in the 1980s evolutionary game theory was been developed to study plant-plant competition (Givnish 1982, Givnish 1995), and recently this has been developed to understand plant growth in a more global context (Dybzinski, Farrior et al. 2011, Mcnickle, Gonzalez-Meler et al. 2016). Game theoretic models of plant production predict that vegetative structures like leaves, stems, and roots should be over-produced to maximize competitive ability leading to a tragedy of the commons in terms of community-wide fitness (King 1990, Zhang, Sun et al. 1999, Gersani, Brown et al. 2001, Craine 2006, O'brien, Brown et al. 2007, O'brien and Brown 2008, Dybzinski, Farrior et al. 2011). These game theoretic responses are supported by well-known growth responses and empirical results, For example, when most plants sense a shift in red to far-red light caused by shade by other plants, many plants elongate their internodes, petioles, and leaf laminas (Ballaré, Scopel et al. 1991, Dudley and Schmitt 1996, Murphy and Dudley 2007). When there is a below ground neighbor, some plants behave similarly and produce more lateral roots and root hairs and increase their overall root biomass (Maina, Brown et al. 2002, Mommer, Van Ruijven et al. 2010, Semchenko, Zobel et al. 2010). The mechanism is not as clear below ground, but there is growing evidence that root exudates are part of the cue sensed by plants (Semchenko, Saar et al. 2014). As a result of this over-production of vegetative structures, plants then allocate less biomass to reproduction, a phenomenon that has been described as a "tragedy of the commons" (Gersani, Brown et al. 2001) .

Here, I investigated root and shoot over-production in common pea (*Pisum sativum* L. var little marvel). This variety was chosen because it will over-produce roots in the presence of competitors (Falik, Reides et al. 2003, O'brien, Gersani et al. 2005, Meier, Angert et al. 2013), as well as in the presence of strings in the soil, an inorganic representation of roots (Falik, Reides et al. 2005). I completed four separate experiments, each had the same treatments, which included a full factorial combination of: no neighbor, a below ground neighbor, an above ground neighbor, and both an above- and below ground neighbor. However, each experiment was done using a different soil environment, and experiments were performed at different times. I addressed the following questions:

1) Does a Tragedy of the Commons occur above- or below ground, and how do above- and below ground responses interact? I tested three different hypotheses related to this question: (*i*) I hypothesized that over-proliferation, or over production of tissues, would occur both above- and below ground, when neighbor presence cues were found in each environment. Therefore, I predicted more vegetative biomass when a neighbor was present either above- or belowground. (*ii*) Further, I hypothesized that above- and below-ground responses were intertwined and therefore predicted that below ground competition would not happen without the presence of above-ground competition cues (i.e. shade). (*iii*) I hypothesized that, increasing competition would have a negative correlation with reproduction, which I will estimate as pod mass mediated by allocation to over-proliferation. Specifically, that the order of the treatments by pod mass would be no neighbor > a below ground neighbor > an above ground neighbor > both above- and below ground.

2) What is the relationship between leaf, stem and root biomass and allocation and reproductive output across four different soil and nutrient regimes? I hypothesized that biomass was not linearly related to reproductive output, but rather I predicted a unimodal relationship where the largest and the smallest plants had the lowest lifetime fitness (Parker and Maynard Smith 1990).

3.2   Methods

Plant material:

Common pea (*Pisum sativum* L. var little marvel) is an annual legume commonly used in tragedy of the commons experiments due to its growth rate (maturity at about 60 days) and demonstration of tragedy of the commons growth behavior (O'brien, Gersani et al. 2005). For example, in an experiment involving split pots and split roots, peas were found to over-produce both roots and shoots in response to competition at the expense of their pods (O'brien, Gersani et al. 2005). Another experiment found that *Pisum sativum* is actually able to avoid nylon strings (similarly sized to plant roots) by altering the length of lateral roots, as well as withering those approaching the string (Falik, Reides et al. 2005).

Experimental design

I performed four separate greenhouse experiment. Each experiment included four treatments: 1) aboveground neighbor only; 2) below ground neighbor only; 3) no neighbor, and; 4) both above- and below ground neighbor. This experiment was replicated four times in total using different growing media, and nutrient applications each time to gain a better understanding of how soil environments might shape growth responses.

The experiments were performed in the Purdue University Lilly greenhouse complex, in West Lafayette, Indiana, USA (40°42'26.0"N, 86°91'88.2"W). The greenhouse was set to 25±2°C and was on an 18 hours light/6 hours dark schedule for all four experiments. In each case, pots were 40 cm deep and 15 cm square at the top (Pot TP616, Stuewe & Sons Inc, Tanget, Oregon, USA). The planting media varied across the four experiments as described below (Table 3.1). To hold plants upright, 92 cm tall bamboo stakes were added for each plant (i.e. two per pot because there were two plants per pot).

To impose the competition treatments, I added dividers either above- or below ground. Above ground, dividers that were 45 cm tall and 15 cm across with 4 cm flaps to attach to the pot were constructed and placed across the middle of each pot (Figure 3.2). All pots received above ground dividers as a control, and the placement of plants was adjusted such that both plants were on the

same side of the divider if interaction above ground was to be permitted, or plants were on opposite sides of the divider if competition was to be blocked. The pots of the no competition treatments were placed in a 5-gallon bucket next to the pots of the other three treatments, which were placed in a 30 cm^2 pot together. The no competition treatments were placed in a bucket to help decrease the amount of leaf overlap between treatments. Each of these groupings created a block. To minimize the effects of shading caused by the above-ground dividers, all pots were turned one-quarter turn every day. Below ground, dividers were constructed by cutting pots in half, and nesting them together. This created a situation where, as above, either belowground interaction was permitted, or not. Pots were arranged in a randomized block design with 15 replicates for all four experiments.
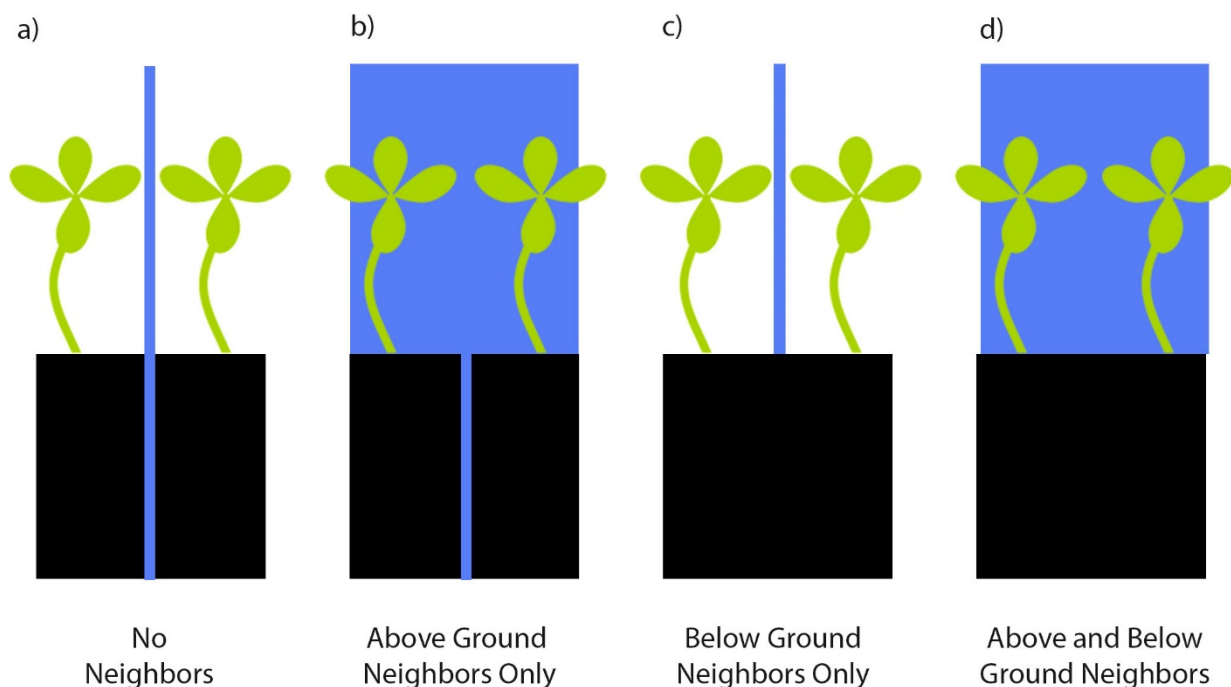
Figure 3.2 shows the layout of each of the treatments. The blue represents the location of the dividers. The black represents the pots.

Two seeds were placed in each pot, in the locations noted above dependent on treatment. At sowing, the soil was saturated with water, and then freely watered each day until germination. Subsequent to germination, each full-sized pot received exactly 1 liter of reverse osmosis water per watering to control below ground resource availability. Watering schedule varied by experiment. In some

experiments (see below), the plants were fertigated with either liquid fertilizer instead or just water. Fertilizer, when applied, was water soluble 24-8-16 of NPK solution (Miracle-Gro All Purpose Plant Food, The Scotts Miracle-Gro Company, Marysville, Ohio, USA). The concentration and application of fertilizer varied by experiment as described below.

In each experiment, after 10 weeks of growth the peas were harvested. The leaves, shoots, pods, and roots were collected separately. Tissues were dried at 60°C to constant mass, and then weighed. Below I detail any deviations in methods among the four experiments. Differences are also summarized in Table 3.1.

Experiment 1:
Experiment one was performed between February 18, 2016-April 28, 2016. The planting media was pure potting soil (propagation mix soil, Sungro Company, Agawam, Massachusetts, USA). The plants were watered every other week except they were fertigated with 1L of nutrient solution with a 0.25 g/L concentration during weeks 3 and 6 in place of water. All other experimental details were as above.

Experiment 2:
Experiment two was performed between September 5, 2016-November 14, 2016. Adjustments were made to reduce nutrient levels because of the results of Experiment 1. The planting media was a 1:1 mixture of potting soil and calcined clay gravel. Because the gravel has no nutrients, this diluted the nutrients available by 50%. Plants appeared to tip away from each other above ground in this experiment, and so bird netting (1.9 cm mesh, Bird Barricade, DeWitt Company, Sikeston, Missouri, USA) was wrapped around the above ground portion of the experiment to keep plants within the vertical space above the pots. The netting was very fine and has undetectable effects on light levels (data not shown). No fertilizer was applied. All other experimental details were as above.

Experiment 3:
Experiment three was performed between December 6, 2017-February 14, 2017. Again, based on the results of experiment 1 and 2, the soil environment was changed again. The planting media

was pure calcined clay gravel (Turface Athletics MVP, PROFILE Products LLC, Buffalo Grove, Illinois, USA). As gravel has no nutrients, all nutrients were supplied by liquid fertilizer. These plants were either watered or fertigated every other week with 1L of either water or nutrient solution. The fertilizer concentration was 0.5 g/L, and supplied during weeks 3, 5, 7, and 9 of growth. All other experimental details were as above.

Experiment 4:

Experiment four was performed between September 6, 2018-November 15, 2018 fall 2018. Again, the potting material was changed. In experiment 4, the planting media was pure vermiculite (Coarse Vermiculite, Perlite Vermiculite Packaging Industries, Inc., North Bloomfield, Ohio, USA), which contains no nutrients. Thus, again all nutrients were supplied by liquid fertilizer as in experiment 3. All other experimental details were the same as experiment 3, or as above.

Table 3.1 The differences in environmental conditions between each of the experimental runs.

	Experiment 1	**Experiment 2**	**Experiment 3**	**Experiment 4**
Media type	100% Soil	50% soil 50% calcined clay	100% calcined clay	100% Vermiculite
Stem support	Stakes	Bird netting + stakes	Ties to stake	Ties to stake
Watering Schedule	Every other week	Every other week	Weekly	Weekly
Nutrient Application	¼ g/L nutrients twice	None	½ g/L nutrients four times	½ g/L nutrients four times

Statistical analyses:

All analyses were performed in the R statistical environment (v 3.3.2, R-Development-Core-Team 2009). First, we investigated over-production using Generalized Linear Mixed Models (GLMM) from the lme4, and lmerTest packages (Bates 2007, Bates 2007, Fox and Weisberg 2010). Each GLMM used a Gaussian distribution. I performed seven GLMMs in total: four on absolute stem, leaf, root and pod mass, and three more on the fraction of vegetative biomass allocated to stem (fStem), leaf (fLeaf), and root (fRoot). The fractional allocation data were arcsine square root transformed for continuity, and the absolute data were not transformed. Model fit was assessed by inspecting residuals. Second, we investigated fitness trait correlations with non-linear

regression, and we selected the most parsimonious model using Akaike information criterion (AIC). We only compared linear and unimodal (i.e. a parabola) models.

For each experiment, I analyzed leaf, stem, root, and pod production with individual GLMMs. Thus, there were 16 GLMMs in total. Each model included experiment and competition treatment as a fixed effect, and block as a random effect to control for microclimate differences across the greenhouse bench. Pairwise post-hoc comparisons were made for the competition experiment using the lsmeans function lsmeans library.

3.3   Results

Question 1: Tragedy of the commons

For question 1, I hypothesized that, (*i*) over-proliferation would occur both above- and below ground, when neighbor presence cues were present in each environment. Therefore, I predicted more vegetative biomass when a neighbor was present either above- or belowground. (*ii*) I hypothesized that above- and below-ground responses were intertwined and therefore predicted that below ground competition would not happen without the presence of above-ground competition cues (i.e. shade). (*iii*) I hypothesized that, increasing competition would have a negative correlation with pod mass mediated by allocation to over proliferating tissues. Specifically, that the order of the treatments by pod mass would be no neighbor > a below ground neighbor > an above ground neighbor > both above- and below ground.

I found that in general the soil and vermiculite experiments, tissues were significantly larger than the soil turface mix and the turface experiments (Figure 3.2). I also found few differences between competition treatments. For the fraction allocated to tissues there were no differences in allocation to roots or stems, but in the soil turface mix I found that plants with only above ground neighbors were significantly larger than plants with both above and below ground neighbors and in the pure turface I found that plants with no neighbors were significantly larger than plants with below ground neighbors only (Figure 3.2 a, b, and c). When looking at plant biomass I found no significant difference in pods or in the soil, turface, and vermiculite experiments (Figure 3.2). In the soil turface mix I found that in roots, plants with only above ground neighbors are significantly smaller than plants with neighbors above and below ground and those with no neighbors (Figure

3.2 a). In stems I found that plant with above-ground neighbors only are significantly smaller than those with below-ground neighbors only and in leaves plants with aboveground neighbors are significantly smaller than those with no neighbors (Figure 3.2 b).

Validation of prediction 1a, that above-ground and below-ground neighbors cause over-proliferation of competing tissues, requires significant differences between each of the competition treatments and the no competition treatment. I found no significant differences between any of the treatments. This shows that, in my experiment, tragedy of the commons was not occurring. I needed evidence of tragedy of the commons to evaluate predictions 1b and 1c. Because I found no evidence of it, these predictions were refuted.

Question 2

For question 2, I hypothesized that biomass was not linearly related to reproductive output, but rather I predicted a unimodal relationship where intermediate sized plants have the largest reproductive output (Parker and Maynard Smith 1990). I found when comparing linear to unimodal using AIC in all experiments that each tissues' biomass and fraction allocation is unimodally related to reproduction (pod mass) (Figure 3.4; Table 3.3).

Table 3.2 This is the results of GLM. The convergence default is 0.001 for least squares mean optimum criteria if this was not met we put the value that was met. Tissues with 'f-' represent the fraction of vegetative mass allocated to that tissue, such that fStem+fLeaf+fRoot=1 for any individual plant.

		Experiment			Treatment			Exper:Treat			
	d.f.	Chisq	p	d.f.	Chisq	p	d.f.	Chisq	p	Convergence
fLeaf	3	24.635	**<0.001**	3	1.135	0.769	9	26.215	**0.0019**	
fStem	3	20.238	**0.00015**	3	2.728	0.425	9	12.353	0.194	
fRoots	3	70.224	**<0.001**	3	1.456	0.692	9	26.866	**0.0015**	
Leaf	3	122.87	**<0.001**	3	1.270	0.689	9	26.645	**0.0016**	0.0144
Stem	3	73.830	**<0.001**	3	3.410	0.294	9	22.690	**0.0069**	0.0182
Roots	3	123.79	**<0.001**	3	1.030	0.794	9	21.272	**0.0115**	0.0319
Pods	3	57.031	**<0.001**	3	2.866	0.413	9	17.420	**0.0425**	

31
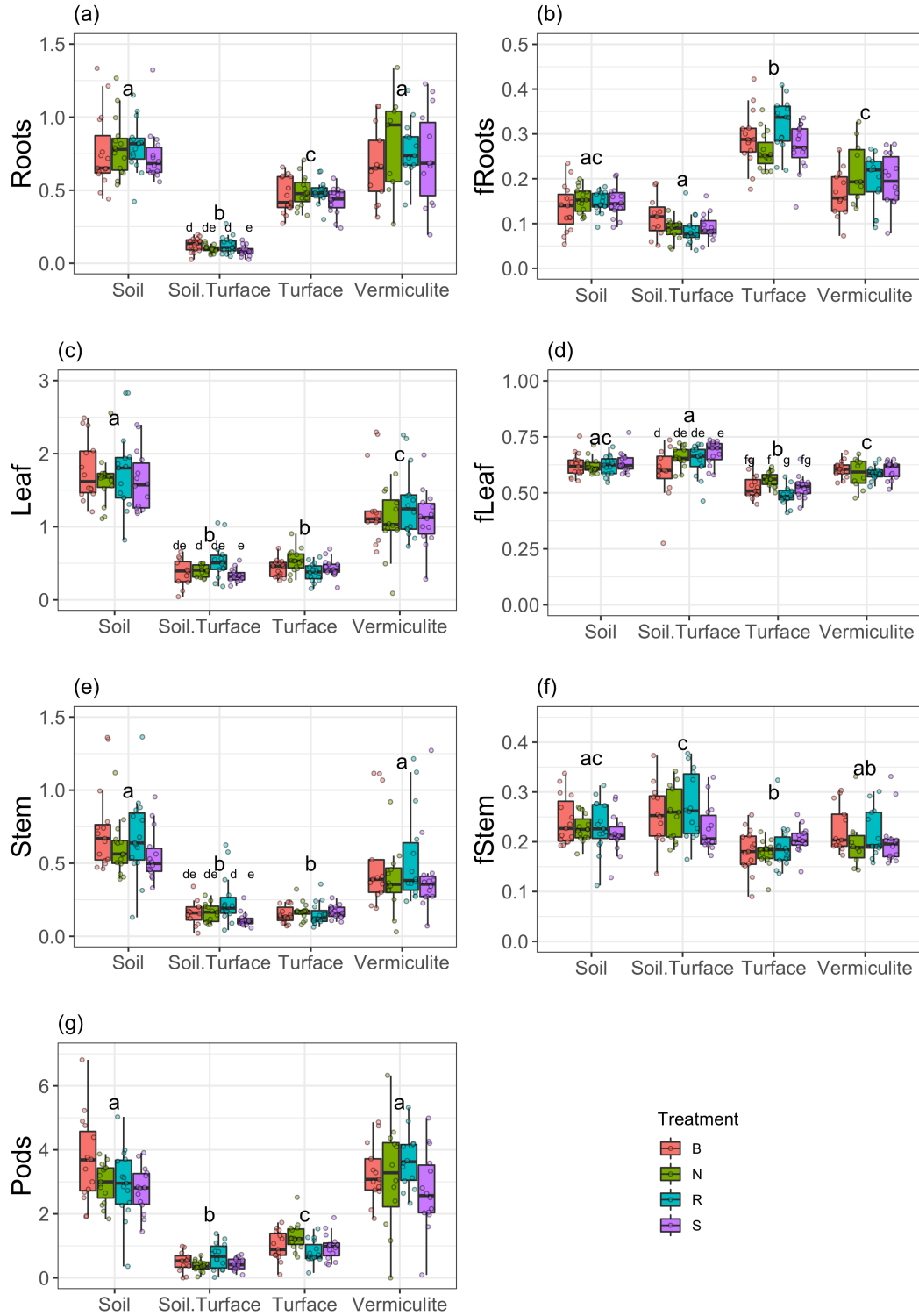
Figure 3.3 Production of (a) roots, (b) stem, (c) leaf, (d) pod, (e) fraction of root, (f) fraction of stem, and (g) fraction of leaf in response to treatment and experiment. The orange bars represent both above and below ground neighbors (B), green is no neighbors (N), blue is root neighbors only (R), and purple is shoot neighbors only (S).

(a) $y = -47.61x^2 + 48.84x - 10.17$

(b) $y = -0.95x^2 + 4.16x - 0.73$

(c) $y = -83.95x^2 + 39.17x - 2.2$

(d) $y = -3.69x^2 + 8.17x - 0.21$

(e) $y = -27.48x^2 + 16.31x - 0.04$

(f) $y = -0.57x^2 + 2.91x - 0.25$

Figure 3.4 The response of reproduction to changes in allocation. Production of pods across (a) fraction of leaf, (b) fraction of stem, (c) fraction of root, (d) leaf, (e) stem, and (f) roots production. Plant reproduction based on allocation and experiment (g). The blue line represents the best fitting model based on AIC.

Table 3.3 AIC values comparing linear and quadratic models for the correlation between each vegetative variable and pod production.

	Linear AIC	Quadratic AIC
fLeaf	796.99	763.45
fStem	792.18	782.97
fRoots	794.38	766.31
Leaf	579.33	512.44
Stem	596.40	549.19
Roots	656.92	640.80

3.4   Discussion

By exposing peas to scenarios where they experienced different combinations of competition from neighbors and different soil environments, I was able to evaluate a competition-wide range of vegetative and reproductive combinations. One of the responses found previously is tragedy of the commons, which occurs when individuals are in a shared-resource system and use it for their own best interest, regardless of what is best for the community (Falster and Westoby 2003, O'brien, Gersani et al. 2005). The range of environments also allowed me to evaluate the relationship between changes in the environment and changes in tissue allocation.

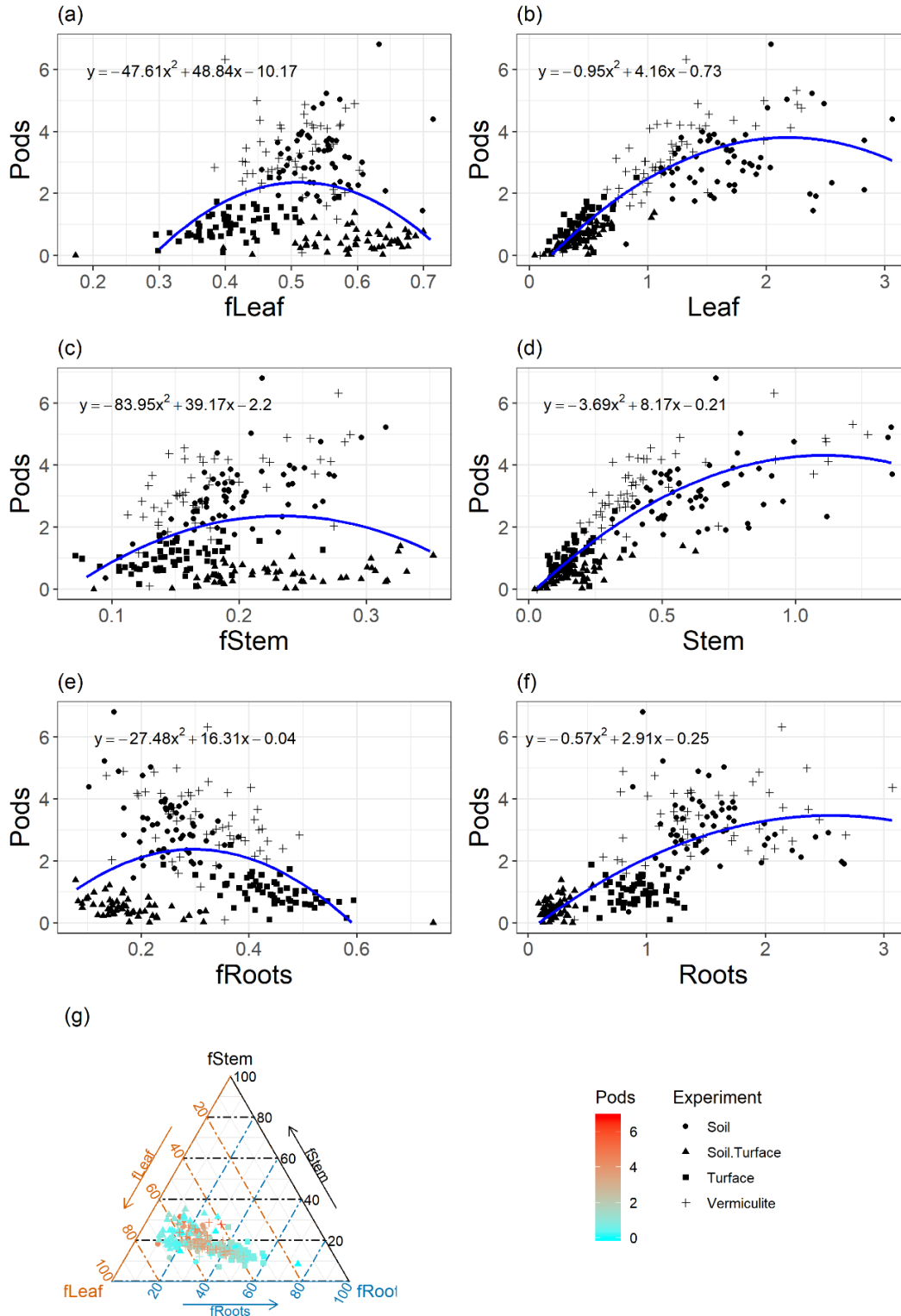It has been shown numerous times that little marvel responds to competition (O'brien, Gersani et al. 2005). However, I repeated the same experiment four times varying the soil environment each time and found that little marvel did not respond to competition under any of the environments I used. This raises questions not only to the reproducibility of past studies, but also the conditions under which the tragedy of the commons response can be seen. Many prior studies that found changes in competitive growth used just the both above- and below ground neighbor and no neighbor treatments, as well as planted peas in vermiculite (O'brien, Gersani et al. 2005, O'brien, Brown et al. 2007). These past studies, in addition to this one, suggest that competition responses are different in sterile, artificial greenhouse conditions as compared to field conditions. In order to

answer this question, field experiments will need to be used to evaluate above-ground and below-ground neighbor effects.

There is a debate in the literature about the cause of increased root growth in competition experiments associated with the tragedy of the commons. This is because it is nearly impossible to fully control neighbor addition, pot volume and nutrient concentration of soil, and total nutrients per plant, all of which can have an effect on plant root growth (Hess and De Kroon 2007). One idea is that when plants are grown in smaller pots, they will reduce their growth not only due to the change in nutrient amount, but also due to the limited space of changing pot volume, which I will call the half pot hypothesis (Hess and De Kroon 2007). This restricted rooting volume would then give the appearance of over-proliferation in response to a neighbor, but for the wrong reason. My belowground root dividers effectively change pot volume by cutting it in half (Fig 3.2), and it is possible that the limited pot volume caused a reduction in growth independent of changes in nutrient status attributable to competition. In the soil-turface mix experiment, I found evidence of the half pot theory because the plants in the above ground competition and no neighbor treatments (i.e. the ones with their roots in half-pots) were consistently smaller than those in the belowground competition and both neighbor treatments (i.e. the ones with their roots in full pots). This likely is due to the roots encountering the sides of the pots more often and having to change their course of growth, thus stunting their growth, and therefore is consistent with the half pot hypothesis (Hess and De Kroon 2007).

When comparing the results of the different soil condition experiments, I found that the media the plant is grown in and the nutrient holding capabilities has a large effect on the plants' size and growth pattern. In experiment 1 the media was propagation soil and in experiment 4 the media was vermiculite. The potting soil and vermiculite have a higher cation exchange capacity than the turface, which means they are able to hold onto nutrients longer (Alexiades and Jackson 1965).

Question 2 asked, what is the relationship between allocation or biomass and reproductive output? I hypothesized that biomass was not linearly related to reproductive output, but rather I predicted a unimodal relationship where the largest and the smallest plants had the lowest lifetime fitness (Parker and Maynard Smith 1990). A unimodal relationship is commonly assumed in mathematical

models, but it appears as though many empirical articles equate biomass and reproduction, as seen in Chapter 2. By covering a large variety of planting media and nutrient gradients, as well as neighbor effects I was able to see a fuller picture of this relationship, validating the assumption found in models. I found that for all tissues, as the biomass and as the fraction of allocation increase, the pod production first increased then decreased in a unimodal relationship. This discovery calls into question the widespread use of vegetative biomass and reproduction as measures of plant fitness. Reevaluation of prior studies may yield new interesting results based on new interpretation of the relationship between vegetative biomass, reproduction, and fitness. The relationship between reproduction and biomass is important for our understanding of basic plant functioning and responses. My data suggest that they are not monotonically related and the relationship between vegetative biomass and reproduction is complicated (Fig 3.2). This means biomass and reproduction cannot both be a simple representation of fitness at all times, unless an equation is used to translate vegetative biomass into reproduction and survival. For example, in each case a I found a quadratic equation that can translate vegetative biomass into reproductive yield (Fig 3.2). This point is complicated because vegetative biomass and reproduction are positively correlated sometimes, and prior experiments have shown this. For example, in a review of measurements of plant fitness Younginger et al found that 46% of experiments found a positive correlation between reproduction and vegetative biomass (Younginger, Sirová et al. 2017). If plant fitness and vegetative biomass are positively correlated less than half of the time, then I suggest plant biologists should more carefully determine the relationship between proxy variables and fitness as I have done here.

In conclusion, the relationship between fitness and its various measures is not always straight forward. I once again suggest that moving forward researchers describe their proxy measures of fitness and note how they determined their measure represents fitness. While the goal of a measure of fitness is to be able estimate fitness across scales and environments, this is not always possible. However, researchers can insure their proxy measures of fitness are accurately representing fitness for their studies. They can test their measures similarly to what I have done through this experiment comparing the relationship of vegetative biomass and reproduction.

CHAPTER 4.   GENERAL DISCUSSION

4.1   Fitness Definitions

Serval previous researchers have discussed the confusion with respect to how to define and measure fitness (Ariew and Lewontin 2004, Krimbas 2004, Orr 2009, Costa 2013). However, to my knowledge, I present the first methodical approach to recognizing the issue with the current usage of fitness through a review of recent articles across the fields of ecology and evolution. I attempt to resolve some of the confusion surround the definition of fitness and offer some suggestions for standardizing vocabulary to avoid confusion in the future. I do however hope I have encouraged more questioning of the definition of fitness. In chapter 2 I use a review of the literature to show that fitness is rarely defined in articles today, especially so in empirical articles. I also found a wide variety of proxy metrics used to estimate fitness. I ended chapter 2 with some suggestions to clarify future studies of fitness.

4.2   Plant vegetative biomass versus reproductive output

I am also not the first to question the validity of common fitness measures, but to the best of my knowledge my study is the first to examine the relationship between vegetative growth and fecundity across multiple soil environments. It is important to note that although metrics can be positively correlated sometimes, in order for them to be a good fitness metric, they would need to be a monotonic relationship. This is because fitness is a complicated concept and it attempts to condense an entire function across all time, as well as to combine individual- and population-wide factors into one single number (Grafen 2015). In chapter 3 I used an experiment to test if biomass and reproduction were both positively correlated with each other and therefor positively correlated with fitness at all environments. I found that the relationship between plant biomass and reproductive biomass was unimodally related. These means both reproduction and biomass cannot be good measures of fitness.

4.3   Concluding Remarks

I do not believe that biology needs a universal definition or metric for fitness, and creating one was not my goal with this thesis. I would argue that the fields of ecology and evolution are doing

themselves and future generations of scientists a disservice by not being clear and purposeful with their use of the concept of fitness. Through this thesis I attempted to acknowledge the confusion about fitness within our fields. It seems that fitness is not only vital to the study of biology, but also is an idea that might need different definitions or metrics in different studies and context. However, to minimize confusion and unnecessary debate, I will repeat the suggestions I made in chapter 2.

1) I suggest that if researchers are not studying evolution, adaptations, natural selection, or other concepts where fitness is specifically needed, then they should avoid using the word "fitness". This should reduce any overuse or misuse and allow the concept to become less muddled.

2) I suggest researchers explicitly state their definition of fitness. Table 2.1 can serve as a menu of options as people consider their research questions. This will allow readers to understand exactly what the researcher is hoping to understand through their study.

3) I suggest that researchers state the measure they are using to represent fitness and further, discuss how and why their metric is a good proxy for estimating fitness in their experiment. This will create accountability for fitness measures, reducing confounding results across studies.

My three suggestions are much easier to say than they are to implement across the field of evolutionary ecology. However, I believe it would be extremely useful for scientists to discuss fitness definitions and test common fitness metrics in their fields. This may allow for some consensus within various fields and create clearer studies in the future. My hope is that this thesis is a starting point for such discussions.

APPENDIX

FULL FITNESS DEFINITION AND PROXY MEASURE TABLES

Table 5.1 shows all the definitions found in review. It is an extension of Table 2.1. 20% of articles used relative fitness, but to calculate fitness they needed to use one of the definitions below, and thus relative fitness is not included in the Table below.

Definitions	Percent of Articles
Survival & Reproduction/fecundity	25.79%
Population growth rate/intrinsic rate of increase	18.87%
Reproduction	15.09%
Function of traits/phenotype,	9.43%
Gene transmission/expression/contribution to future	6.92%
Survival	5.66%
Frequency in population	5.03%
Transmission rate/infection rate	4.40%
Fecundity, development(growth), survivorship	1.89%
Behavior	1.26%
Relatedness of parents	1.26%
Reproduction and performance	0.63%
Currency of Natural Selection	0.63%
Growth and reproduction	0.63%
Protein folding	0.63%
Transcriptional response to different ligands, ability to rescue different phenotypes, and ability to confer resistance to β-lactams	0.63%
Heterozygosity and survivorship	0.63%
Survival, competitiveness, and fecundity	0.63%

Table 5.2 shows all the definitions found in review. It is an extension of Table 2.1. 20% of articles used relative fitness, but to calculate fitness they needed to use one of the definitions below, and thus relative fitness is not included in the Table below.

Metric	Number	Proportion	Example units	Number	Proportion
Reproduction measures	232	0.26	Count of Offspring	57	0.12
			Reproduction	48	0.10
			Count of Seeds	38	0.08
			Count of Fruit	28	0.06
			Fecundity	26	0.05
			Lifetime reproduction	26	0.05
			Eggs laid	22	0.05
			Count of Flowers	12	0.03
			Reproductive output	11	0.02
			Reproductive opportunities/partners	5	0.01
			Fertility	4	<0.01
			Spore load	3	<0.01
			Production of daughters	3	<0.01
			Female fecundity	3	<0.01
			Fruit biomass	2	<0.01
			twinning rate	1	<0.01
Survival measures	139	0.15	Survival, adult and juvenile	72	0.15
			Offspring Survival	31	0.06
			Age, longevity	22	0.05
			Death	9	0.02
			Male survival	3	<0.01
			Female survival	2	<0.01
Trait measures	92	0.10	Behavior, performance	11	0.02
			Plant height	9	0.02
			Seed mass	9	0.02
			Pollen, pollination	9	0.02
			Body length	6	0.01
			Damage, susceptibility	6	0.01
			Flower traits	7	0.01
			Basal metabolic rate/energy	4	<0.01
			feeding success/Diet	4	<0.01
			Horn/antler growth	3	<0.01
			Sperm quality/count	3	<0.01
			Phenotype	3	<0.01
			Egg size	3	<0.01
			Dominance rank	3	<0.01
			Morphology	2	<0.01

Metric	Number	Proportion	Example units	Number	Proportion
			Gonad weight/size	2	<0.01
			Fruit ripening/attraction of vertebrate frugivores	2	<0.01
			Jaw size	1	<0.01
			Invasiveness	1	<0.01
			Birth time	1	<0.01
			Spleen weight (SW)	1	<0.01
			Secondary sexual trait expression	1	<0.01
			Pectoral muscle volume	1	<0.01
Body size or condition measures	86	0.10	Body mass	39	0.08
			Size of offspring, condition	18	0.04
			Body condition	14	0.03
			Body size	8	0.02
			Count of Stems	5	0.01
			Leaf number/length	2	<0.01
Population characteristics	64	0.07	Population Growth Rate	54	0.11
			Population size	7	0.01
			Colonies	2	<0.01
			Replacement rate	1	<0.01
Recruitment measures	53	0.06	Reproductive recruitment	20	0.04
			Seed germination, viability	19	0.04
			Hatching success	10	0.02
			Incubation success	2	<0.01
			Seed dormancy	1	<0.01
			Nest success	1	<0.01
Growth measures	44	0.05	Growth	15	0.03
			Offspring growth/development	10	0.02
			Age to Breeding/time to develop	10	0.02
			Reproductive Lifespan, timing, rate, Phenology	9	0.02
Vague measures	36	0.04			
			Vague or unclear	36	0.08
Genetic measures	26	0.03	DNA/genome	12	0.03
			Mutants/mutations	6	0.01
			Proteins	3	<0.01
			Alleles	3	<0.01
			Codons	2	<0.01
Competitive measures	19	0.02			
			Competition/Competitive assay	19	0.04
Uncategorized	14	0.02	Offspring fitness/reproduction	4	<0.01
			Offspring sex-ratio (male or female Offspring	2	<0.01
			Reactive Oxygen Metabolites	1	<0.01

Metric	Number	Proportion	Example units	Number	Proportion
			Protein folds	1	<0.01
			Fitness parameters	1	<0.01
			Sexual workers	1	<0.01
			Worker brood items	1	<0.01
			Probability of holding nest	1	<0.01
			Plug composition (sexual)	1	<0.01
			Relatedness to partner	1	<0.01
			Glucose uptake rate,	1	<0.01
			Fluctuating asymmetry	1	<0.01
			Opportunity for selection	1	<0.01
			Individual's utility function	1	<0.01
			Cytochrome oxidase activity,	1	<0.01
			Adsorption rate and lysis time	1	<0.01
Environmental conditions	13	0.01	Infection rate/accumulation/Immune Response	15	0.03
			Environment condition Tolerance/response	5	0.01
			Resistance	4	<0.01
			Fecal eggs, condition	2	<0.01
			Leaf damage	1	<0.01
			Coral bleaching	1	<0.01
Dispersal measures	9	0.01	Dispersal	5	0.01
			Arrival to breeding grounds	2	<0.01
			Establishment	1	<0.01
			Habitat selection	1	<0.01

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