

A reframing of trait-demographic rate analyses for ecology and evolutionary biology

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Abstract

The relationship between plant functional traits and demographic performance forms the foundation of trait-based ecology. It also serves as the natural linkage between trait-based ecology and much of evolutionary biology. Despite these important aspects, plant trait-demographic performance relationships reported in the literature are typically weak or non-existent and a synthetic picture of how traits are related to ecological and evolutionary patterns remains under-developed. Here, we begin by presenting an overview of the shortcomings in functional trait-demographic performance research and why weak results are more common than trait-based ecologists like to admit. We then discuss why there should be a natural synthesis between trait-based ecology and evolutionary ecology and potential reasons for why this synthesis has yet to emerge. Finally, we present a series of conceptual and empirical foci that should be incorporated into future trait-demographic performance research that will hopefully solidify the foundation of trait-based ecology and catalyze a synthesis with evolutionary ecology. These include: (1) focusing on individuals as the fundamental unit of study instead of relying on population or species mean values for traits and demographic rates; (2) placing more emphasis on phenotypic integration, alternative designs and performance landscapes; (3) coming to terms with the importance of regional- and local-scale context on plant performance; (4) an appreciation of the varied drivers of life stage transitions and what aspects of function should be linked to those transitions; and (5) determining how the drivers of plant mortality act independently and in concert and what aspects of plant function best predict these outcomes. Our goal is to help highlight the shortcomings of trait-demographic performance research as it stands and areas where this research could course correct, ultimately, with the hope of promoting a trait-based research program that speaks to both ecologists and evolutionary biologists.

Overview

The traits of individuals interact with the abiotic and biotic environment and are, therefore, fundamental for understanding ecological and evolutionary dynamics (Arnold 1983; McGill et al. 2006). Specifically, traits dictate ecological interactions, which contribute to the demographic success or failure of an individual. These individual-level successes and failures scale up to determine the structure and dynamics of populations and communities. Thus, establishing how the traits of individuals influence demography is foundational to population and community ecology as well as evolutionary biology.

Plant ecologists have frequently focused their research efforts over the past decade on measuring and analyzing functional traits (Reich et al. 1997; Westoby 1998; Westoby et al. 2002; Chave et al. 2009). Broadly, we can define plant functional traits as traits that should influence plant fitness that can also be measured in a standardized fashion across species, life forms and ecosystems (Reich et al. 2003). The plant functional trait literature is now vast and there have been many studies that successfully demonstrate how functional traits can be used to predict demographic rates (e.g. Enquist et al. 2007), to elucidate non-neutral community structure and dynamics (e.g. Weiher et al. 1998; Swenson and Enquist 2009), to modernize plant geography (e.g. Swenson and Weiser 2010; Swenson et al. 2012; van Bodegom et al. 2014) and to refine dynamic global vegetation models (e.g. Fyllas et al. 2014).

Despite these successes, there are two major weaknesses that need to be confronted. First, while some have found moderately strong or strong relationships between traits and demographic performance, these studies have been the exception and not the rule. Indeed, most studies find surprisingly little variation in demography explained by commonly measured traits (Yang et al 2018; Worthy and Swenson 2019) Second, the empirical failure to routinely and robustly link functional traits to demographic rates and under-appreciated conceptual connections have limited a synthesis between trait-based population and community ecology and evolutionary ecology (McGill et al. 2006).

In this work, we have three major goals. First, we will discuss why the plant trait literature should take a closer look at how well widely-measured traits have predicted demographic rates. Second, we will discuss why a synthesis between trait-based population and community ecology and evolutionary ecology

should be natural and why this synthesis has not taken root. Lastly, we will discuss potential ways forward in plant trait-demography research that may lead to new opportunities and a more solid foundation going forward.

Empirical Shortcomings in Trait-Demography Research

Foundational to most trait-based research in plant ecology and evolutionary biology is that the traits measured mediate ecological interactions and resulting demographic rates. Certainly, many trait-based ecological investigations do not venture to establish the links between traits and demographic rates, but they do rely on this link having been established by others. For example, the definition of what a functional trait is, typically, indicates that the trait is directly or indirectly linked to demographic rates or fitness (Reich et al. 2003; Reich 2014). If this were not the case, then it would be less clear why the trait was being considered for study in the first place. For these reasons, an examination of how well traits predict demographic outcomes is valuable.

Researchers often use correlations between single functional traits or single principal component (PC) axes derived from decomposing matrices of multiple traits and demographic rates to infer the functional drivers of differential demography (e.g. Poorter et al. 2008; Kraft et al. 2010; Enquist et al. 2015; Jager et al. 2015; Paine et al. 2015). These methods often utilize species mean trait and demographic rate values and seek to uncover new or confirm expected global trait-rate relationships.

The standard trait-demographic rate research approach implicitly assumes or expects a consistent relationship between a trait and a rate (i.e. a single global optimum trait value). This may sound like an unfair characterization of functional trait-demographic rate research in ecology. However, we argue that conducting analyses of global scale datasets where a single trait is related to a demographic rate (e.g. mortality or growth rate) using a linear regression model estimated using maximum likelihood or Bayes implicitly assumes that there should be a global optimum trait value. For example, one may be expecting that higher wood densities leads to lower mortality rates in forests worldwide (e.g. Kraft et al. 2010) or higher specific leaf area will lead to faster sapling height growth in tropical forests worldwide (e.g.

Poorter et al. 2008; Paine et al. 2015). We do not believe that those conducting global scale analyses truly believe there is always a single global optimum trait, but the analytical approaches largely used to date in trait-based ecology are designed to search for their existence. An alternative viewpoint, that is more attractive to ecologists is that multiple trait optima occur and that the location of those local optima is contingent upon the values of other traits that constitute the phenotype (e.g. Marks and Lechowicz 2006; Enquist et al. 2007; Liu et al. 2016) as well as the local and regional biotic and abiotic contexts (e.g. Liu et al. 2016; Zambrano et al. 2017). This literature regarding multiple phenotypic optima and the importance of context aligns nicely with the study of fitness surfaces and phenotypic adaptive landscapes in evolutionary biology (Conner and Hartl 2004), which provides one of the clearest examples of where a synthesis of trait-based population and community ecology and evolutionary ecology should naturally occur (Figure 1).

The Conceptual Shortcoming - A Missing Trait-Based Eco-Evo Synthesis

An attractive conceptual property of trait-based ecology is that a plant biologist may measure a series of traits that indicate life-history and functional trade-off axes (Westoby 1998; Westoby et al. 2002). The position of an individual or species along these axes and the environmental conditions should be the primary determinants of the demographic rates that determine population, community and ecosystem structure and dynamics.

If this is demonstrated empirically, trait-based approaches in ecology would be extremely powerful. However, this is not the extent of what should be motivating the analysis of traits from populations to ecosystems. The linkage of traits to demographic outcomes at the scale of individuals provides a clear conceptual and empirical connection to evolutionary ecology. Therefore, traits and demography are at the nexus of a synthesis between ecology and evolutionary biology. Despite this importance, trait-based plant ecologists, the authors of this article included, have struggled to conceptually and empirically link their work to evolutionary biology and have, thus far, missed on the opportunity to provide a synthetic framework under which the two fields can operate and inform the work

of one another. In this section, we highlight areas where there should be a clear conceptual linkage between trait-based plant ecology and evolutionary biology and potential reasons why the linkage has not been made.

We begin with traits as indicators of demographic performance. An ecologist incorporates the relationship between traits and demographic performance, generally, in one of two ways. The first would be directly focusing on whether traits predict demographic performance in a given environment. This approach sets the foundation for trait-based studies. Ideally, such work would be conducted at the scale of individuals, but this is often not the case and species-level trait means are correlated with species- or individual-level demographic rates. The second approach is to assume that a trait is predictive of demographic performance so that the traits of interest may be utilized for other research foci such as inferring mechanisms of community assembly or predicting the distribution and abundance of species. This second approach relies upon and leverages the work of those taking the first approach. In other words, an ecologist taking the first approach asks *do* traits predict demographic performance whereas an ecologist taking the second approach states *because* traits predict demographic performance.

An evolutionary ecologist may be primarily interested in the differential performance of an individual phenotype relative to the other individuals in a population. In other words, does a trait or a combination of traits covary with the relative fitness of an individual in a population (i.e. analyses of phenotypic selection and correlational selection)(Lande 1979; Lande and Arnold 1983; Arnold and Wade 1984; Wade and Kalisz 1990; Brodie 1992; Conner and Hartl 2004). Furthermore, how is this correlation related to the environmental context in which the population exists, is of interest. Thus, while trait-based population and community ecologist and evolutionary ecologist may operate in very different spheres academically they share a major shared goal of linking trait differences to demographic performance.

So why has a shared interest in traits and demographic performance in plant ecology and evolution not lead to a stronger unification of the two spheres of research? The first reason is that much of trait-based ecology does not focus on individuals. Rather, it aggregates trait and, often, demographic data to the population- or species-level, which weakens empirical analyses, as discussed above, and reduces

the number of clear pathways for communication and synthesis with evolutionary ecology. Stated differently, trait-based ecology cannot easily speak to evolutionary ecologists with the language of species means. In most cases, population- or species-level means are the most pragmatic approach for an ecologist to take, but this work will not lead to a general unification of the two fields as the use of mean traits or demographic rates, itself, precludes the ability to link to relative fitness or performance and trait differences. In other words, a core interest in phenotypic selection cannot be satisfied using the species mean trait approach used by most ecologists. There are, however, some areas where mean values can still lead to cross communication. Specifically, population mean trait values and placing them into the context of phenotypic adaptive landscapes where changes in population mean traits and performance can be compared through space or time, which leads us to our second reason for a delayed synthesis.

A second reason why a synthesis has not been generated relates to time and whether traits are treated as static or dynamic data. Both ecologists and evolutionary biologists are interested in population changes through time. However, trait-based ecologists may seek to predict population changes from traits and changes in the environment. This approach may explicitly or implicitly treat trait data as static. That is, an ecologist may predict the dynamics of a population as the environment changes from a static mean trait value for that population or species. This is a semi-dynamic approach to trait-based studies. A fully-dynamic approach would be to study how the size and trait distribution of a population changes through time in a given environmental setting. This fully-dynamic approach should be of major interest to ecologists and evolutionary biologists, but it is not common in trait-based ecology. One hurdle to such research is the potential for high amounts of trait variation in populations, which makes distinguishing similar mean trait values (i.e. those expected in a population of trees between two time points) exceedingly difficult. For example, Hulshof and Swenson (2010) have shown that distinguishing mean leaf trait values between species can require greater than 50 individuals being sampled in order to have 80% power. Rarely do trait ecologists quantify traits for that many individuals. In sum, a synthesis has been delayed by too few studies examining trait distributions through time and too few studies that demonstrate how differential demographic rates at the scale of an individual drives changes in trait

distributions. That is, long-term observations of individual performance and resulting changes in trait distributions in populations and communities would naturally bridge the gap between trait-based ecology and evolutionary ecology.

A final issue delaying a trait-based synthesis is omitted context. This issue runs in both directions. First, detailed and controlled studies of how traits relate to demographic performance are foundational. Naturally, this often requires greenhouse and common garden studies and model species. The importance of this work by evolutionary biologists cannot be questioned. However, a great deal of ecological context is missing from such work. For example, shared enemies and intra- and inter-specific competitive effects can be challenging to include in such work despite the importance of these drivers in natural populations. Similarly, model systems are invaluable for elucidating mechanisms, but the degree to which these results translate broadly will always be questioned by some. Thus, one may argue that field ecologists studying natural populations and communities are capturing all of the important context that will elude those doing controlled experiments. This may be true, but we argue that these researchers are also missing a great deal of important context that is well-understood to be important by evolutionary biologists. For example, rarely does the field ecologist studying traits in natural populations consider the genetic variation in the populations they study. They may be studying two co-occurring species, but the populations under study may occur in very different parts of the range of the species (i.e. one species may be on the edge of its range while the other may be in the center), which is likely related to the genetic diversity in that population (Hewitt 2000). Arguably, this contextual information would be as, or more, important than other contextual information (e.g. soil texture) a field ecologist routinely measures. Furthermore, evolutionary ecologists embrace the context-dependency of trait-demographic performance relationships (Wade and Kalisz 1990). As we described in the previous section, a trait-based ecologist will routinely conceptualize and analyze their data with the notion that traits and demographic rates are globally related. Many would recognize that this is a flawed assumption and that the optimal trait value varies through space and time as the environment changes. In sum, both sides of the synthesis are missing contextual information that the other side considers critical for any analyses and understanding of the system.

A Reframing for the Future

In the previous sections, we have outlined two existing issues in trait-based ecology relating to trait-demographic rate relationships that require renewed attention. Wholly or partially resolving these issues would solidify the foundation of trait-based ecology and catalyze a meaningful synthesis between this field and evolutionary biology. The first of these issues is a lower than expected capacity of widely measured traits to predict demographic outcomes (Yang et al. 2018). The second is a failure to connect trait-based population and community ecology with evolutionary ecology, which has helped to prevent the compelling synthesis of the ecology and evolution of plant traits that was a stated goal of many over 15 years ago in a landmark special issue in this journal (Ackerly and Monson 2003). In this section, we hope to provide a partial roadmap for future research that seeks to link plant traits to the ecological interactions and demographic rates that underlie ecological and micro-evolutionary dynamics. This roadmap is incomplete and imperfect. Our hope in providing this incomplete and imperfect roadmap is that it will provoke research that will refine, overturn and improve upon it.

Individuals as the Fundamental Unit of Study

We begin by stating that individuals should be the primary unit of study in trait-demography research. Our goal here is simple, broad and designed to take on larger issues in the trait-based ecology literature that must be solved prior to tackling more refined issues (e.g. levels of selection). As we have shown in the previous sections, there is a strong tradition in trait-based ecology of measuring trait data on a few individuals and aggregating these data into a species-level mean that is used in downstream analyses. The aggregation of these data to the species-level may be perceived by a reader of the trait-based ecology literature on a spectrum from fine to worrying to perplexing. When it comes to establishing trait-demographic relationships, the aggregating of trait and demographic rate data to the population- or species-level, should at least be worrying. There is wide variation among individuals in their traits, demographic outcomes and their environmental contexts. Thus, weak relationships between aggregated

trait and rate data should not be surprising (Yang et al. 2018). In support of this argument, there is evidence that shows that stronger relationships arise when traits and demographic rates are analyzed at the individual-level (Liu et al. 2016). Little progress will be made in the realm of trait-demography rate research if the field continues to fixate primarily on data aggregated above the individual-level.

A focus on individuals also provides the most obvious and logical road for a synthesis between trait-based ecology and evolutionary ecology. While the study of population-level mean trait values through time is valuable and can be linked via phenotypic adaptive landscapes and long-term trait and demographic data, individual-level data are even more critical for a synthesis to occur. However, simply measuring traits on many individuals in ecological studies will not suffice. We will therefore offer a series of considerations or approaches for future work with a greater focus on ecological studies. First, as we will discuss below in more detail, the large variation in demographic performance between individuals cannot be understood without individual-level contextual information. Thus, while projections can and will be made on aggregated demographic and trait information in the future, such work will provide limited mechanistic insight. Second, analyses of population-level trait mean shifts cannot attribute a mechanism without coincident measures of the genetic composition of the population. Without these pieces of information, we will fail to make reasonable population projections and to understand the interplay of ecological and evolutionary outcomes.

Nothing Makes Sense Without Some Context

A large role for context-dependence in trait-demography relationships complicates the projection of population and community structure and dynamics. Conversely, the variation introduced by context-dependency could be relatively small and ignored for adequate predictions to be made. While gathering infinite knowledge regarding the context of every individual is not possible, we must confront the reality that there are multiple important pieces of contextual information that have large effects and that are frequently ignored in trait-based ecology. These include phenotypic context or integration, regional scale contexts relating to climate and the geographic range position of a population, and climatic variation.

Ecologists should be more skeptical of analyses that simply correlate a trait with a demographic rate or life-stage transition probability and that also ignore these contexts. Here, we briefly expand on the importance of these contexts and how they may be incorporated into future trait-demography research.

We encourage trait-based ecologists to make stronger links between traits and demographic rates or plant performance by collecting individual level traits. Ideally, this work would be informed by work on phenotypic selection, correlational selection and fitness surfaces in evolutionary ecology. Ecologists should aim to quantify the relative performance of individuals in a population relative to their standardized trait values. This would align with phenotypic selection analyses and would be distinct from correlating species mean traits with species mean or individual demographic rates. It would also be similar too, but distinct from, analyses of individual-level performance and trait data across all species. Rather, we advocate that the performance of an individual must be considered in the light of the population and not the community *per se*.

Next, the measurement of multiple traits on individuals will allow ecologists to consider so-called “alternative designs” in phenotypic space that should promote functional diversity within and between communities (e.g. Marks and Lechowicz 2006; Laughlin and Messier 2015; Dwyer and Laughlin 2017b; Laughlin et al. 2018). Some work in this realm has been conducted by investigating community mean trait values along environmental gradients (e.g. Laughlin et al. 2018), which would be closer to phenotypic adaptive landscapes that focus on communities rather than populations. However, we would advocate direct analogs of fitness surfaces that consider correlational selection and focus on individual-level traits rather than mean trait values. That is, multi-variate trait combinations that lead to multiple performance peaks within and across environments. Such work could begin by considering populations, but additional work of more interest to a community ecologist could place all individuals of all species onto the same surface with the performance relativized to the population from which each individual belongs. This would serve to form a bridge between trait-based ecology and evolutionary ecology and it would also push trait-based ecologists to move beyond univariate trait-performance regressions and

towards a consideration of how traits interact with each other and the environment to determine plant performance (Figure 1).

While the benefits of fitness surfaces or performance landscapes are obvious, statistical support for interactions between multiple traits and the environment on demographic rates is more complicated. Before any mathematics are involved, large samples sizes of individual-level functional traits and demographic rates are needed along with measurements of environmental gradients of interest (Yang et al. 2018). Few studies to date have access to this vast amount of data due to extensive field work that it entails, but databases are being compiled to make this type of data more available (Knevel et al. 2003; Kattge et al. 2011; Salguero-Gómez et al. 2015; Klimešová et al. 2017). Current research incorporating these types of data has used a variety of statistical methods including both frequentist and Bayesian mixed-models, path analysis, or simulations when empirical data are absent (Marks and Lechowicz 2006; Clark et al. 2007; Clark 2010; Martínez-Vilalta et al. 2010; Blonder et al. 2018; Laughlin et al. 2018; Borges et al. 2019).

Despite the advances that incorporating performance landscapes will bring to trait-based ecology, they are not without challenges. For example, performance landscapes, to date, typically only consider one demographic aspect at a time. Hence, if data are displayed on growth performance landscapes, the influence of survival rate, recruitment, and reproductive output are, generally, ignored which could have unknown effects on the growth performance peaks seen on the landscapes (Laughlin et al. 2018). Also, to date, aspects of regional scale and climatic variation have yet to be included in a performance landscape framework leaving out crucial contexts that influence trait-demographic rate relationships.

The regional scale context in which an individual and population reside is important for quantifying trait-demography relationships for multiple reasons (Zambrano et al. 2017), but it is often ignored (Yang et al. 2018). We begin with the importance of regional scale climate and will focus our discussion on trees. Tree species ranges often contain a large range of climates that vary in their suitability to the species. Stated another way, populations of a species are not always found in favorable environments. In these less favorable environments, individuals may grow, survive and reproduce at

lower rates and the populations may be maintained primarily through immigration. Conversely, more favorable climatic conditions in the geographic range of a species may have individuals with higher growth, survival and reproductive rates. This will, however, come with the cost of increased neighborhood crowding and competition (Brown 1984). Negative density dependence has been described as an important force shaping tree communities in tropical and temperate regions by imposing constraints on the performance of an individual (Wills et al 1997, Harms et al 2000, HilleRisLambers et al 2002, Johnson et al 2012, Comita et al 2014). Individuals growing in more dense areas are expected to experience an increase in competition for resources with close neighbors leading to important trade-offs between survival and growth (Janzen 1970, Connell 1971). Increased neighborhood crowding might lead to asymmetric or hierarchical competition where individuals with more suitable traits may experience weaker negative density dependent effects (e.g. Kunstler et al 2012, 2016). Thus, we may expect an interaction to arise between regional scale climatic suitability and local scale population density when modeling individual-level tree demographic performance. Indeed, in a recent study, Zambrano et al. (2017) found a strong interaction between the local neighborhood and regional climate affecting the survival and growth in tree communities in the northeast United States and in Puerto Rico. Specifically, species sensitivity to local neighborhood crowding varied with regional scale climatic suitability and strong density dependence promoted the co-occurrence of functionally similar species in the northeastern United States while the opposite was found in Puerto Rico. Thus, we argue that future studies need to consider the interaction between regional and local scale contexts to gain a better understanding of the drivers shaping plant communities. A clear limitation to including continental and regional scale contexts is obtaining demographic and trait data at these large scales. As we have mentioned above, long-term vegetation monitoring plots are ideal for overcoming these limitations, but simply merging such data with mean trait values taken from a few individuals potentially from a very different parts of the geographic range and very different climates is not advised.

A second and related way in which regional scale context may influence trait-demographic rate studies is the range position as it relates to genetic diversity. For example, historical range contractions

and expansions will lead to dissimilar levels of population genetic diversity at range margins (Hewitt 2000). Populations at the leading edge of a range expansion may have lower genetic diversity relative to populations at the center or trailing margin of the range (Eckert et al. 2008). This has several potentially interesting implications. First, it would be important to know the degree to which intra-specific trait diversity mirrors intra-specific genetic diversity across the range particularly with respect to non-neutral loci. Second, one may assume based on published evidence that negative density dependence will be stronger on the leading edge of a range expansion due to lower-intra-specific genetic diversity (e.g. Shao et al. 2018). However, leading edge populations may be “chasing” favorable environments such that these populations thrive despite their susceptibility to negative density dependence due to lower intra-specific diversity and/or these populations may be so small that the realized impact of negative density dependence is minimal. In either case, knowing the genetic diversity of the populations and the historical biogeography and historical demography of the species and populations would greatly improve our understanding of how traits relate to demographic rates and further link trait-based ecologist and evolutionary ecology.

A final context that we believe should be considered in trait-demographic rate relationships is inter-annual climatic variation and extreme events. It is surprising how often these contexts are ignored. We can start with a non-botanical example, which nicely illustrates these contexts. Perhaps the most detailed and important studies of trait and demographic outcomes come from Darwin’s finches. This work has elucidated that the relationship between demographic performance and trait values (i.e. beak dimensions) changes signs due to precipitation levels (Grant 1999) and that extreme events (i.e. ENSO) can have major and long-lasting impacts on the trait structure of populations (Grant and Grant 1993). Plants are no different. We should expect *a priori* that the relationships between traits and demographic outcomes in plants are dependent on the climatic context and that that context varies between years and that extreme events can have lasting impacts on the structure and dynamics of populations (Gutschick 2003; Kimball et al. 2012; Siepielski et al. 2017). Thus, ecologists studying trait-demographic rate relationships need to more explicitly model trait-climate interactive effects in their models of

demography. Furthermore, longer-term research is needed to sift out the importance of extreme events that cannot be captured in short-term and many experimental studies.

Analyses Across the Life Cycle

The trait-demography literature frequently analyses the relationship at a single life stage (e.g. Paine et al. 2015). In other cases, multiple life stages are considered, but demographic rates are known to vary dramatically through ontogeny as do traits (e.g. Iida et al. 2014a, b, 2016). Rarely are the strengths and signs of the relationships between traits and demographic rates considered to vary across life stages in trait-based ecology (e.g. Wright et al. 2010; Visser et al. 2016). We argue that the drivers and traits underlying plant performance vary across the life cycle and studying the relationship between traits and life stage transitions offers a logical pathway forward (Figure 2)(Arnold and Wade 1984). Here, we focus briefly on four key tree life stages and transitions between those stages and how trait-based studies may be reframed going forward. There is a substantial theoretical and empirical literature that considers these individual transitions. We begin by considering the transition from the seed stage to the established seedling stage. A successful transition between these stages requires a site with abiotic conditions suitable to the individual and one where negative biotic interactions (e.g. pathogen attack, resource competition) are minimized. Theoretical frameworks highlighting the importance of a tolerance-fecundity tradeoff (e.g. Muller-Landau 2010) and shared enemies (Janzen 1970; Connell 1971) during this transition provide a series of clear predictions. Tolerance-fecundity tradeoff-based theory argues that large seeded species with low fecundity are expected to be favored in low resource (e.g. shaded) environments, whereas small seeded species with high fecundity should be competitively superior in high resource (e.g. gap) environments. Thus, the probability of establishment is an outcome of site conditions and the competitive fit of the functional strategy of a species to those conditions. Similarly, the Janzen-Connell model (Janzen 1970; Connell 1971) argues for negative biotic interactions leading to conspecific negative density dependence. Though, in the classic Janzen-Connell case, the negative biotic interactions are intra-specific and mediated by shared enemies rather than inter-specific resource competition. Combined, these bodies

of theory lead to the empirical expectation that the seed-to-seedling transition should be maximized in resource rich environments for smaller seeded species and in resource poor environments for large seeded species and that the probability of individual establishment should be depressed when the neighborhood density of conspecific individuals increases, which itself should be related to plant defense similarity.

Next, we consider the mechanisms influencing the transitions from a seedling to a sapling and from a sapling to an adult. We will consider these transitions simultaneously as similar mechanisms have been proposed to explain both. The majority of the mortality that occurs during this long phase in a tree life-cycle happens during the seedling stage. For example, approximately 65% of established (i.e. ~10cm tall) seedlings survive annually in a tropical forest (Green et al. 2014). This is compared to a ~95% annual survival rate for saplings with 1cm stem diameter and a ~98% survival rate in adults (J. Needham and S. McMahon *pers comm.*). As with the seed-to-seedling transition, the Janzen-Connell model is often invoked as a key driver of seedling performance and transitioning to the sapling stage. Theory also predicts that asymmetric resource competition should be important during the transitioning from seedling-to-sapling-to-adult. Kohyama's original forest architecture hypothesis, his derived theory (Kohyama 1993; Kohyama and Takada 2009, 2012) and additional frameworks (e.g. Coomes et al. 2011) highlight the important role of neighborhood crowding and competition for light in tree communities. Specifically, the demographic performance of an individual tree is influenced by the degree to which its canopy is covered by neighboring individuals and this effect is potentially independent of the species identity or functional similarity of the overlapping individuals.

Finally, we consider the transition from the adult stage to the seed stage. We can begin with a zero-sum allocation expectation where allocation to adult growth will come at the expense of allocation to reproduction leading to a growth - reproduction tradeoff (Roff 1992; Charnov 1997, 2005). For example, work in Costa Rica on *Bursera simaruba* (Burseraceae) has shown that the annual diameter growth for an individual in this species is negatively correlated with reproductive output (Hulshof et al. 2012). Interestingly, this tradeoff weakens in years with low precipitation. The functional reasons why the tradeoff weakens and how the strength of this tradeoff varies among species with different functional

strategies remain open questions. Future research should pursue these questions with a specific focus on whether acquisitive versus conservative functional strategies in trees strengthen or weaken the tradeoff and whether where species fall on this functional spectrum dictates their sensitivity to inter-annual climatic variation.

Importantly, the drivers of life stage transitions, including those we have not mentioned in the above, are very likely to be context dependent. This is clear in the case of *B. simaruba* with respect to climatic variability. Furthermore, population densities and genetic diversity will also play important roles governing processes like the Janzen-Connell mechanism at the seed, seedling and sapling stages (Shao et al. 2018). Similarly, inter-annual climatic variation and extreme events can play a large and non-uniform role in driving plant mortality across life stages (e.g. Shenkin et al. 2018). Thus, a key challenge going forward is to study life stage transitions, ideally with individual-level trait, demography and genetic data, while taking into account regional and local scale contexts.

Balance the Focus on Death and Reproduction with that Given to Growth

The final area of study that we would like to encourage in trait-demography research is elucidating the drivers of mortality. Many of the traits that are commonly measured in trait-based ecology are related to resource acquisition, which should lead to strong predictions of recruitment, growth and reproduction. Evidence of growth-survival tradeoffs can be quickly found in the literature (e.g. Wright et al. 2010). This may indicate that the traits that predict growth should also predict mortality. However, the exact causes of mortality remain unknown, making predictions of future population and community structure and dynamics less robust. Thus, we need to answer the simple questions of what kills plants and what traits predict that outcome? We suggest there are two obvious starting points. The first is mortality related to drought and the second is mortality related to pests and pathogens. We will discuss both briefly with a primary focus on trees.

Drought events have been reported to affect plant communities worldwide, ranging from humid tropical forest to arid desert grasslands (Milton and Dean 2000) or high latitude boreal forests (Peng et al

2011). Drought effects on plant communities can cause an increase in mortality rates on local and regional scales. For example seedling mortality in a seasonal tropical forest can increase from 89% in the wet season to 96% during the dry season (Marod et al. 2002) with evident regional-scale forest die-off due to drought (Allen et al 2010). Drought-induced mortality appears to be site- (Zuleta et al 2017), species- (Engelbrecht et al. 2005, 2007), and age class-specific (Bennett et al. 2015, Esquivel-Muelbert et al. 2017), which makes predictions of mortality challenging (McDowell et al. 2008).

There is compelling evidence that herbivores and pathogens, through negative density dependence, play a major role in shaping the structure and dynamics of plant communities, particularly in tropical ecosystems (Comita et al. 2014). Nonetheless, the majority of studies are limited to indirectly studying the impacts of herbivores and pathogens by assessing performance at the sapling and/or seedling stages which typically cannot identify the causal mechanism of individual mortality. These shortcomings are expected because studying the effects of natural enemies in any system, much less the tropics, is challenging due to the high diversity of pests and pathogens and the potential for extreme host-enemy specialization (Coley and Barone 1996).

Lastly, a consideration of compounding effects and how they drive mortality is needed in trait-based ecology. For example, individuals likely die due to a confluence of factors where a weakening of an individual due to a poor fit to the abiotic environment or exposure to a pathogen results in a susceptibility to death due to a pathogen or drought, respectively. That is, the ultimate cause of death is not the same as the proximate and the functional mechanism underlying each will not be the same (Raffa et al. 2008; Anderegg et al. 2015).

Conclusions

Here, we have highlighted two major weaknesses in the current framework of trait-based plant ecology and emphasized the main areas where improvements are needed and forthcoming. While we understand that incorporating all of these contexts into a single study may not be currently feasible, we do hope that trait-based ecologists will now consider the high-dimensionality of data needed to address important

questions at the foundation of trait-based ecology when gathering and analyzing data in future projects. Using the incomplete and imperfect roadmap we have proposed, we may begin to finally link individuals, functional traits, and demography, which will allow research integration across scales, from populations, to communities, to ecosystem, and between this trait-based ecology and that of evolutionary ecology. However, despite the many theoretical and technological advances we have made since the original special issue (Ackerly and Monson 2003), many aspects regarding the evolution of plant function and how these are related to ecological interactions are still “sleeping”. Unfortunately, a generally consensus gathered here is that individual-level, long-term, functional, demographic and genetic data are going to be needed to fully “wake” the giant that is the evolution of functional traits in plants. We believe that the combination of contexts and frameworks outlined here will propel the field of trait-based plant ecology into an advanced realm of eco-evolutionary studies that will solidify the foundation of trait-based ecology and its connection with evolutionary biology.

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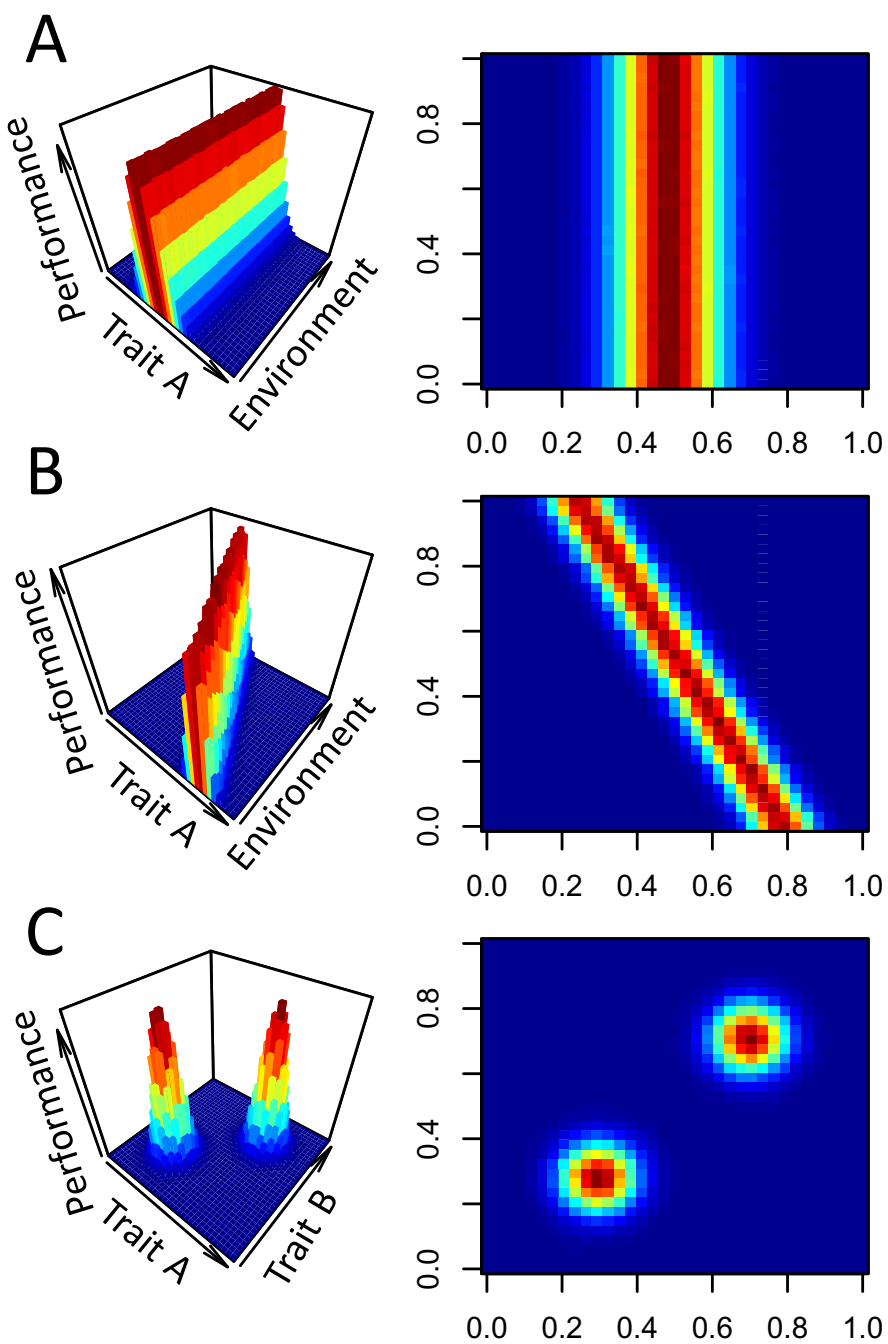
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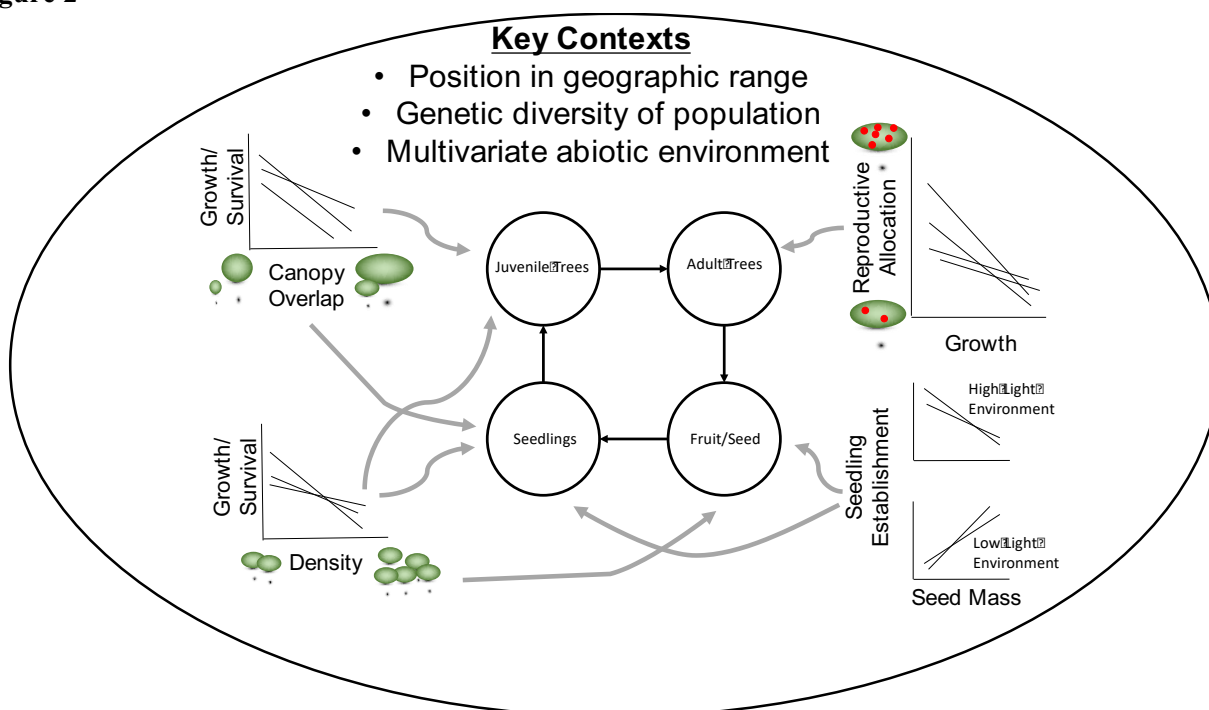
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Figure Legends

Figure 1. Hypothetical relationship between traits, environment and plant demographic performance represented as 3-dimensions (left) and 2-dimensional landscapes (right). (A) Performance is maximized at a single trait value globally (i.e. across environments). This is the standard assumption of trait-demographic rate studies. (B) Performance is maximized at different trait values along an environmental gradient. This is consistent with trait-based ecology analyzing trait means across gradients, but not standard trait-demographic rate studies. (C) Two roughly equivalent performance peaks that are the outcome of two combinations. Importantly, if performance was regressed against one of these traits there would be no correlation. Conversely, a statistical model with an interaction term for the traits would detect how traits relate to performance.

Figure 2. A depiction of the four tree life stages and transitions between those stages. For simplicity, we focus on four main mechanisms that are hypothesized to be important for transitions between stages. Seed-to-seedling transitions are governed by tolerance-fecundity tradeoffs and Janzen-Connell effects. Seedling-to-juvenile-to-adult transitions are governed by asymmetrical resource competition and Janzen-Connell effects. Adult-to-seed transitions are governed by reproduction-growth tradeoffs. Finally, we state contexts that should impact each of these transitions (e.g. the slopes and intercepts of the regressions).

788 **Figure 1**789
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791 **Figure 2**

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