CellPress
REVIEWS

Opinion

Why Functional Traits Do Not Predict Tree Demographic Rates

Jie Yang,[1] Min Cao,[1] and Nathan G. Swenson[2],*

Foundational to trait-based community ecology is the expectation that functional traits determine demographic outcomes. However, trait–demographic rate relationships are frequently weak, particularly in tree communities. The foundation of trait-based tree community ecology may, therefore, appear to be unstable. Here we argue that there are three core reasons why trait–demographic relationships are generally weak in tree communities. Specifically, important contextual information is frequently ignored, there is too much focus on species relative to individuals, and there are dimensions of tree function that are critical for determining tree demographic rates that are not captured by easily measured functional traits. Rather than being evidence that trait-based community ecology is fundamentally flawed, these issues elucidate a pathway towards a more robust research program.

The Demographic Foundation of Functional Trait-Based Community Ecology

Differential demographic performance across individuals and species scales up to determine whole-community structure and dynamics [1]. A grand challenge in community ecology has, therefore, been to identify the drivers of differential performance. Interactions between organisms and their environment determine demographic performance and these interactions are governed by an organism's phenotype [2]. The linkage between phenotypes, differential demography, and communities forms the foundation of **functional trait**-based community ecology (see Glossary). Functional traits are typically defined as morphological, physiological, and phenological traits that determine the performance of an individual given an environmental context [3,4]. These, typically easily measured, traits have become wildly popular in plant ecology where the linkage between traits and demographic performance has been directly investigated or used as an assumption [5–9]. While the popularity of functional traits in community ecology is clear, the relative success of ecologists attempting to link functional traits to demographic performance is questionable, particularly in tree communities. Here, we first briefly highlight the accumulating evidence that functional traits often fail to predict **demographic rates**, thereby apparently demonstrating that there are cracks in the foundation of functional trait-based community ecology. We then suggest three reasons why functional trait–demographic relationships are weak and how alterations of the current research paradigm may improve these relationships and help to solidify the foundation of functional trait-based community ecology.

Apparent Cracks in the Foundation

The composition and dynamics of tree communities arise from the demographic outcomes of interactions between individuals and their environment. Ideally, functional trait information should predict these demographic outcomes. Tree community ecology has turned from producing patterns of trait similarity (e.g. [10–12]) towards quantifying functional trait–demographic rate relationships [5,13–16], but strong trait–rate relationships are more of an exception than a rule. For example, a recent global-scale effort to relate commonly measured functional

[1]Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Kunming 650223, China
[2]Department of Biology, University of Maryland, College Park, MD 20742, USA

*Correspondence:
swenson@umd.edu (N.G. Swenson).

CrossMark

traits to sapling growth found that the traits considered explained ~3% of the variation in growth [5]. Similarly, a detailed study of the trees in the 50-ha forest plot on Barro Colorado Island in Panama found that seed mass and **leaf mass per area** explained less than 8% of the variation in the average relative growth rates of species, with wood density being the strongest correlate (r^2 = 0.19) [6]. Further, none of the traits measured explained more than 6% of the variation in overall mortality rate among tree species. These results are consistent with other extensive studies of tropical tree trait–demography relationships [13–17].

Given the central importance of linking traits to demographic rates to trait-based community ecology, the consistent reporting of weak relationships between the two in the literature is concerning [9], and we argue it has not been considered seriously enough. Simply put, if commonly measured functional traits do not predict demographic performance, inferences drawn and predictions made from these traits are potentially greatly flawed. In the following sections, we discuss reasons why commonly measured functional traits do not predict tree demographic rates and what steps should be taken to confront and overcome these issues (Box 1).

Context Matters

The relationship between a trait and a demographic rate occurs in a particular context and without this context this relationship may be obscured. Here we consider two types of context that require more attention in the trait-based tree community ecology literature: the **phenotypic context** and the environmental and biogeographic context. We begin with the phenotypic context in which a trait and its value exist. One of the most commonly measured traits in tree ecology is leaf mass per unit area (LMA), [the inverse of specific leaf area (SLA)]. Being a key trait in the leaf economics spectrum related to leaf lifespan and photosynthetic rates

Glossary

Anisohydry: plants that do not reduce their stomatal openings under water stress and therefore have wider ranges of leaf water potentials and thus a higher probability of xylem cavitation. This strategy may be more suitable for droughts that are less intense and short in duration.

Demographic rate: the growth, survival, or reproductive rate of an organism.

Isohydry: plants that have a narrow range of leaf water potentials regulated by stomatal behavior in response to water availability. These species will have a lower probability of xylem cavitation during intense or long droughts.

Leaf area ratio: the total leaf area of a plant divided by the total mass of the plant.

Leaf mass fraction: the total leaf mass of a plant divided by the total mass of the plant.

Leaf mass per area: the mass of a dried leaf divided by the area of the same leaf before drying.

Phenotypic context: the overall multivariate phenotype of an individual in which an individual trait is a component.

Functional trait: a physiological or morphological trait that influences the growth, survival, or reproductive rate of an individual plant.

Box 1. Three Core Reasons Why Traits Do Not Predict Demographic Rates

In this work we present three of the core reasons why commonly measured functional traits do not predict tree demographic rates. Here, we aim to distill and briefly explain those reasons.

A Trait with Little Context Has Little Predictive Power

The way in which a trait of an individual influences demographic performance is dependent on the environment as well as the other trait values of the individual. For example, trait values associated with elevated drought tolerance will confer differing levels of demographic success dependent on the precipitation of a given growing season. Expecting a consistent trait–rate relationship across environments that spatially and temporally vary is unrealistic. Similarly, the rate of photosynthesis per cm^2 of leaf will tell us little about total resource capture and growth rates without knowing the total leaf area of a plant. Last, those traits most closely linked to demographic performance are likely to change through ontogeny as the environment that an individual experiences changes.

Measuring Individuals Is Challenging, But Advised

A tradition in functional trait ecology has been to average trait and demographic rate values at the species level for downstream analyses. Individuals, however, vary in their trait values as well as the environmental contexts that they occur in on the landscape. Averaging this information will obscure trait–rate relationships that could be elucidated by analyzing individual-level data. Utilizing species mean values measured from populations not in the study system that they are being applied to will further exacerbate the problem.

Unmeasured Dimensions and Dynamics of Functional Diversity

Plant functional ecology has distilled global functional diversity into a few key axes that can be described by easily measured traits. However, the aspects of function that determine demographic rates (survival rates in particular) are not well characterized by the core set of traits that most measure. Furthermore, the dynamic functional responses of individuals to environmental changes are generally not measured. Combined, these factors greatly reduce our ability to predict demographic rates from traits and to predict the future structure and dynamics of forests.

[18], it may be logical to assume that this trait would be strongly related to tree growth rates. However, it is typically very poorly correlated with growth rates, if at all [6,14–16]. There are multiple non-mutually exclusive reasons for this outcome. One might be that LMA is not mechanistically linked to resource acquisition rates. Specifically, the inclusion of mass in LMA and photosynthetic rate variables may drive their correlation rather than a mechanistic link [19] (but see [20]). A second possibility is that LMA must be considered given the whole-plant relative allocation to leaves versus other tissues (Box 2 and Figures 1 and 2). The integration of leaf level traits into a whole-plant allocation context to predict growth has been established in the plant ecology and physiology literature for over a decade [21–24] but has been almost entirely ignored in the functional trait-based community ecology literature, which relies on a foundation of trait–demographic rate linkages. The problem is likely to be of even greater importance in trees, where relative allocation can vary substantially across species and with ontogeny. Additional other work that has placed individual traits into a whole-phenotypic context has shown that similar demographic rates can be arrived at via very different trait combinations such that it may be nearly impossible to find that a single trait predicts demography consistently without information regarding other trait axes [25,26]. Thus, it would seem unreasonable to expect a single trait to predict demographic rates, and trait-based community ecology should continue to progress towards trait–demographic rate studies that consider

---

Box 2. Leaf-Level Traits, Whole-Plant Allocation Context, and Predicting Growth

The functional trait literature frequently finds little to no relationship between leaf traits and tree growth rates (e.g. [5,6,13,17]). To some this is a surprising result devoid of explanation, largely because the leaf traits chosen are believed to be strong indicators of leaf-level life history tradeoffs and resource acquisition strategies. Some researchers have exclaimed that they 'do not know why' these traits fail to predict tree growth [5]. We suggest that there is a clear reason why leaf traits often fail to predict growth. Further, this reason has been discussed in the plant growth literature for decades (e.g. [21–24]), but for unknown reasons this literature has been largely ignored in tree community ecology. Here we briefly describe two constructs demonstrating the relationship between whole-plant allocation, leaf traits, and growth.

Analyses of plant growth rates worldwide [55] have shown that growth rate (G) scales with body mass (M) to the 3/4 power and photosynthetic mass (M_p) scales to non-photosynthetic mass (M_{np}) to the 3/4 power, such that G and M_p scale isometrically:

$$G \propto M^{3/4}. \qquad\qquad [I]$$

$$M_{np}^{3/4} \propto M_p \propto G. \qquad\qquad [II]$$

The M_p of a standard tree (i.e., with no photosynthetic bark or fruits) can itself be assumed to be equal to the total leaf mass of the tree (M_L) and can be estimated as the product of total leaf area (A_T) and the average leaf mass per unit area ($\overline{LMA}$):

$$M_L \approx A_T * \overline{LMA}. \qquad\qquad [III]$$

If A_T scales consistently across species, $\overline{LMA}$ may be expected to be a strong predictor of G. Conversely, if A_T does not scale consistently across species, it must also be considered when attempting to predict growth on the basis of $\overline{LMA}$. Specifically, the product of the two (M_L) must be calculated to predict G. This simple model can be expanded to consider more traits and interspecific scaling difference [24], but even this simple integration of allocation and a leaf-level trait can provide a strong prediction of G.

Classically, before the scaling described above, plant functional biologists have equated G to the product of a unit leaf rate (ULR) (i.e., the photosynthetic rate) and the **leaf area ratio**, which is equal to A_T divided by M [21,22,24]. The leaf area ratio can also be written as the product of the inverse of $\overline{LMA}$ and the **leaf mass fraction** (M_L divided by M).

$$G = ULR * \left(\frac{1}{\overline{LMA}}\right) * \frac{M_L}{M} = ULR * \frac{A_T}{M}. \qquad\qquad [IV]$$

If comparing the growth of individuals within species where the differences in ULR may be minimal, G may be simply predicted by the leaf area ratio. If comparing the growth of individuals from different species, incorporation of ULR would be necessary as values can vary substantially across species.
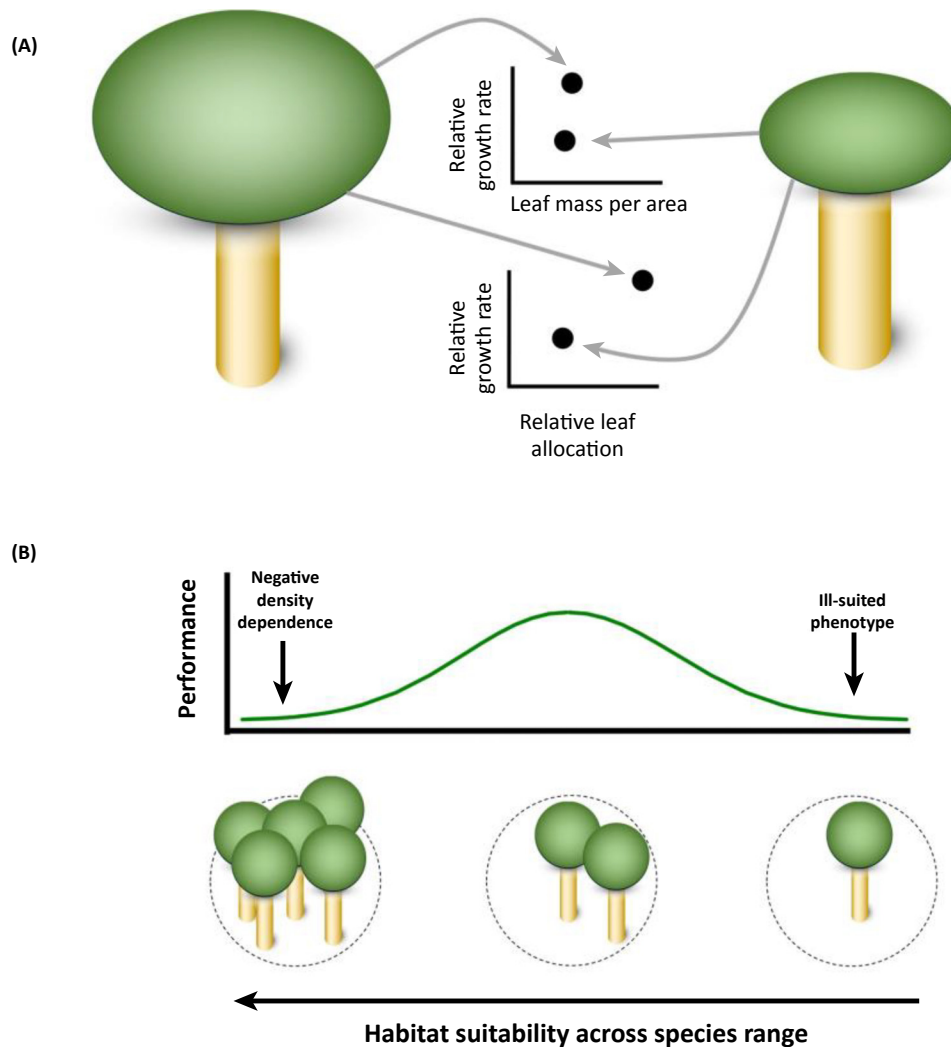
Figure 1. Two Contexts That Are Often Ignored in Trait–Demographic Rate Studies in Tree Community Ecology. (A) A demonstration of where similar values of a commonly measured leaf-level trait (i.e., leaf mass per area) are from species with very dissimilar relative growth rates due to differential allocation to leaves. Organ-level traits will be misleading without a whole-phenotypic context, particularly in large, long-lived organisms like trees. (B) The factors with the greatest impact on demographic rates will vary across habitat suitability gradients and geographic ranges. Here, negative density dependence and intraspecific similarity depress performance in highly suitable habitats where population densities are high while interspecific trait hierarchies and an ill-suited phenotype of the focal species depress its performance in less-suitable habitats. Thus, habitat or geographic range context impact the relationship between traits and demographic rates making general conclusions about the importance of a specific mechanism between populations within species or between species, in a particular community, tenuous.

allocation and integrated phenotypes. Importantly, multivariate decomposition of a trait matrix is likely to not be as useful in this regard. Rather, logical and informed piecing together of an integrated plant phenotype should be a preferred approach [21–24]. Specifically, leveraging knowledge from the physiological ecology literature that has elucidated how aspects of plant form and function are interrelated will lead to more progress and mechanistic predictions of plant performance in current and future climates.
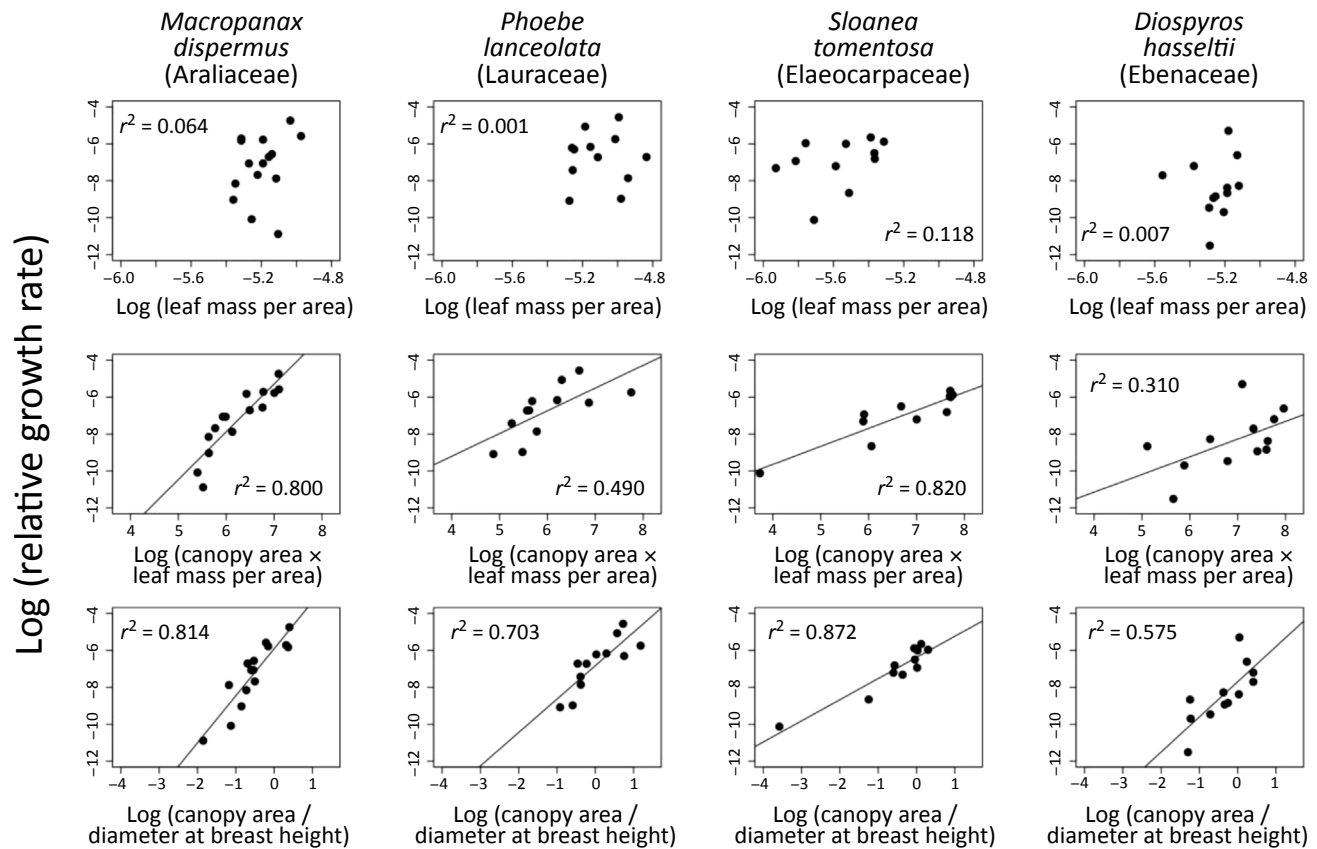
Figure 2. An Empirical Example of How Knowing Allocational Context Improves Trait–Demographic Rate Relationships. Here we show data for four tropical tree species in Xishuangbanna, China where annual mean relative growth rates are plotted on the y-axis. In the top row, we plot relative growth rate against the leaf mass per area (g/cm^2) for individual trees and find little variance explained. In the middle row, we plot relative growth rate against the leaf mass per area multiplied by the canopy area ($\pi \times$ mean canopy radius squared)(m^2) as a rough estimate of relative leaf biomass. In the bottom row, we plot relative growth rate against canopy area divided by trunk diameter at breast height (cm) as a rough estimate of leaf area per unit biomass (i.e., leaf area ratio).

The environmental and biogeographic context in which an individual is observed is also critical for understanding of trait–demography relationships. A consideration of these contexts may seem an obvious necessity, but frequently they are only partially considered in trait-based tree ecology. If the environmental context of an individual is considered, it is with respect to local abiotic gradients (e.g., soil nutrients [27]) or the individual trees immediately surrounding a focal individual [8,28]. This work has successfully shown that these contexts are important, particularly the density of neighboring conspecific individuals reducing survival rates [8]. However, the regional-scale context of the populations being studied is often ignored. Where the observed population falls in the climatic niche or geographic range of the species may have a large impact on its demographic rates directly or through interactions with local-scale environmental contexts and traits. For example, recent work by Zambrano *et al*. [29] has shown that there is an interactive effect between the habitat suitability in which a population is found and the local population density on tree demographic rates such that growth and survival rates are suppressed in very-suitable habitats where the density of conspecifics is high and in less-suitable habitats where conspecific density is low. Thus, knowing the local density of conspecifics alone and not the context of where the population is in the regional-scale habitat range will result in flawed interpretation of the data.

Temporal variation in the environment is additional context that merits more focus in trait–demographic rate research. Specifically, the trait value that optimally fits a location changes as the environment changes through time. Thus, the correlation between a trait and rate may strengthen or even reverse through time dependent on environmental change. There are well-known examples of this in the literature (e.g., Darwin's Finches [30]), perhaps making it all the more surprising that there is an expected consistent relationship between a trait and a demographic rate without knowing the environmental context. This also underscores a problem with correlating rates averaged over many years, and potentially populations, with average trait values.

Individuals versus Species

A comparison of the functional trait-based community ecology literature and evolutionary ecology literature will lead to the realization that there is a substantial schism between the two in how they conceptualize and analyze trait–performance relationships [31]. The functional trait-based community ecology literature has largely utilized mean trait values to characterize all individuals of a species [32]. Additionally, a substantial fraction of that literature also uses mean demographic rates for species. Conversely, evolutionary ecology has often, but not always, focused on individuals as the fundamental unit of study, where traits of individuals are related to individual performance and ultimately fitness (Figure 3). This framework, furthermore, has often incorporated trait covariation as well, thereby addressing the issue of phenotypic context discussed in the previous section [2]. The averaging of traits and demographic rates could itself substantially obscure our understanding of how the two are related. Recent work by Liu *et al.* [33] that measured a battery of easily measured functional traits along with less-easily measured traits (e.g., hydraulic conductance) demonstrated that species' mean trait values were more weakly correlated with tree growth than individual-level data. There are additional conceptual and empirical reasons that should promote conversion to an individual-centric approach over a species-mean approach. For example, there is tremendous interest in coexistence theory in the trait literature, with one of the fundamentally important considerations being the relative strength of intra- and interspecific interactions (i.e., niche differences) [34]. It is, therefore, perhaps surprising that intraspecific trait variation is frequently ignored even when great pains are taken to measure competition coefficients (e.g. [7]). In other words, the literature is now accumulating correlative studies of niche differences and species average trait values that do not measure the relative variation in traits within and among species and how this variation is associated with competition coefficients. Such studies would be logistically challenging, which is why they are not commonplace, but would be of greater use when trying to determine how traits may or may not align with coexistence theory. Similarly, intraspecific negative density dependence is now widely documented in tree communities [8,35] and it should, therefore, be a major promoter of species co-occurrence. We are not aware of studies that have clearly linked intraspecific functional variation to these patterns, but there is evidence that the genetic relatedness of neighboring conspecifics is correlated with demographic success [36]. Thus, the challenge is to determine the functional mechanisms underlying these patterns. Last, a stronger focus on intraspecific variation as it relates to demography will facilitate a clearer integration of evolutionary and community ecology where researchers would be able to genotype and phenotype individuals to address the relative importance of local adaptation and phenotypic plasticity and how these will influence the future composition and dynamics of forests.

The Under-Studied Dimensions of Plant Function and Dynamic Functional Responses

The distillation of the diversity in plant function into a few major axes of variation has been a major goal in functional ecology [4,37–39]. This distillation has broadened the community of
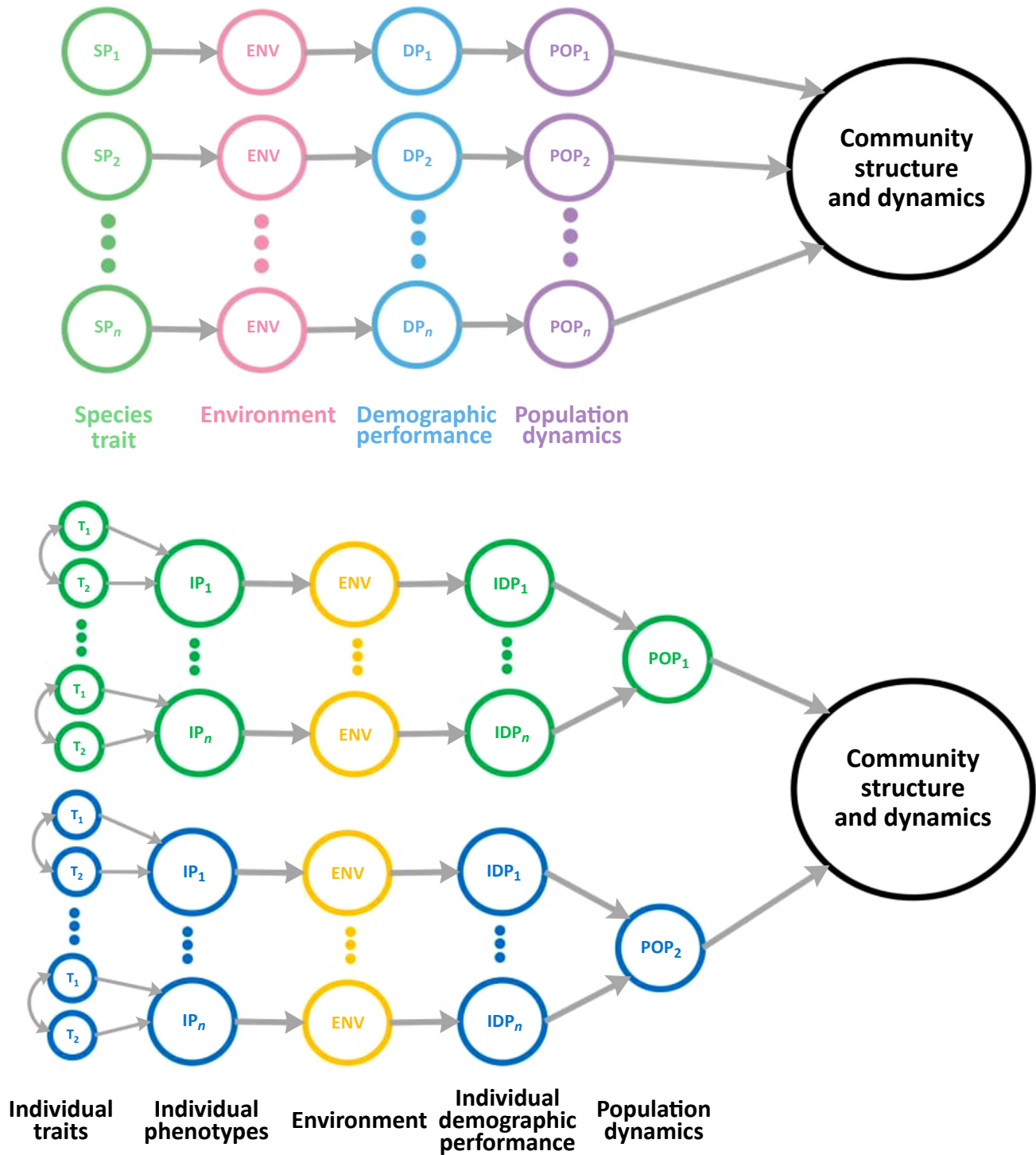
Figure 3. Two Approaches for Relating Traits to Demographic Performance. Top: A species-centric univariate approach when species mean trait values (SP_x) are taken in the context of the environment (ENV) to understand mean species mean demographic rates (DP_x) with the ultimate goal of establishing a connection to population (POP_x) and community structure and dynamics. Bottom: An individual-centric multivariate approach here showing only two species in a community where

(See figure legend on the bottom of the next page.)

researchers measuring plant function by focusing on relatively easily measured traits that do not require expensive equipment and extensive facilities. The success of this approach should not be discounted. An unintended consequence of these successes, however, may be the impression that one need measure only a handful of easily measured traits in their system. The diversity in plant function, however, is greater than that captured by these few traits [40]. Those dimensions that are not well characterized by commonly measured functional traits may prove to be critically important in determining tree demography.

Commonly measured plant functional traits typically relate in some manner to resource capture rates. They therefore should be strong predictors of growth rates, particularly if they are placed into the whole-phenotypic context. Growth and survival rates are expected to be negatively correlated and we might therefore expect that those traits that predict growth also predict survival. However, it is common to observe results where traits do not predict growth and survival equally well (e.g. [6,13]). This may occur for several reasons, including that growth and survival rates do not perfectly trade off across individuals and species. More importantly, such results beg for a stronger focus in tree community ecology on what processes lead to tree mortality.

For example, as noted above, negative-density-dependent mortality is widespread in tree communities. Shared pests and pathogens are likely to be major drivers of these patterns [41]. The constitutive and induced defenses of plants, however, are typically unmeasured in trait-based community ecology due to taxon-specific methodologies and potentially cumbersome laboratory protocols (particularly in the tropics). As a result, when trait-based ecologists do consider plant defense they will often use relatively crude indicators (e.g., leaf toughness [42]) with limited success. Recent work has sought to leverage emerging technologies such as transcriptomics [43] and metabolomics [44] to quantify plant defense across a broad spectrum of co-occurring species. We expect that such assays of plant defense will become more commonplace in the near future and will greatly improve our understanding of the drivers of mortality due to shared enemies.

Extreme climatic events are major drivers of tree mortality and forest ecologists have spent considerable time focusing on how these events alter ecosystem fluxes and what aspects of tree function best predict mortality. This literature, and the advances made therein, has been largely disjunct from the trait-based tree community ecology literature. For example, drought is a major driver of tree mortality and overall forest ecosystem dynamics [45–48]. The physiological and ecosystem ecology literature has had a rich debate in recent years regarding the ways in which drought causes tree mortality (e.g., hydraulic failure versus carbon starvation) [49–51] and the physiological traits that best capture this diversity of drought responses [52]. Recent work has begun to go beyond easily measured traits and shown that more detailed measurements of drought-related traits [53] and gene expression response to drought [54] can provide stronger insights into the drivers of community structure and dynamics than easily measured functional traits. This work points to another important issue that merits more focus in trait-based tree community ecology and may help resolve trait–rate relationships: dynamic environments, dynamic functional responses, and long lifespans.

The dynamic functional response of species to dynamic environments is critical for projections of their demographic outcomes. In a previous section, we have discussed the importance of

covariation between traits (T_x) within an individual's phenotype (IP_x) is considered, as are the impacts of these traits on demographic rates of individuals (IDP_x) and population and community structure and dynamics. The first approach is more common in current trait-based community ecology while the second approach is central to evolutionary ecology [2]. Here we argue that transitioning towards applying the second, individual- and multivariate-based approach across the species in a community will lead to a more compelling trait-based community ecology and synthesis between evolutionary and community ecology.

dynamic environments, but dynamic functional responses to dynamic environments are also important and frequently ignored in trait-based community ecology. For example, the range of ways in which a species could be drought tolerant (e.g., where it falls on the continuum from **aniso-** to **isohydry** [56,57]) will dictate its differential demographic responses to drought dependent on the duration, intensity, and frequency of drought events. These different dynamic functional responses among individuals, populations, and species are difficult, if not impossible, to gauge from the measurement of a static trait value in a non-stressful environment. Thus, if trait-based community ecology wishes to predict demographic rates in dynamic environments in long-lived species, additional focus must be placed on the dynamic functional responses of individuals, populations, and species to changing environments.

Concluding Remarks: Moving Forwards

Trait-based tree community ecology needs to come to terms with the evidence that frequently measured functional traits do not predict a substantial amount of the variation in demographic rates [5,13–17]. We have presented three reasons why we believe trait–rate relationships are weak (Box 1). Our opinion on these matters is that functional trait-based community ecology should not be abandoned, but it can be moved forwards substantially by considering why traits do not predict rates. In this section we venture to briefly outline this pathway forwards with the realization that it is neither simple nor comprehensive.

A core issue is that the expectation that a single trait can predict a demographic rate – both often averaged across individuals – without any contextual information is unrealistic. The relationship between a trait and a rate is contingent on both the environmental and the phenotypic context. In addition, the environmental and phenotypic contexts of a trait are temporally dynamic. Thus, in moving forwards, trait-based community ecology will have to focus more on modeling demographic performance as a function of trait–trait and trait–environment interactions and environmental changes in space or time (e.g. [58,59]). Ideally, this work will not blindly search for statistical interactions and it will build models informed by the existing literature on plant phenotypic integration as it relates to the environment [21–24].

A second pathway that must be forged more vigorously is to broaden our assays of plant function. The ability of tree ecologists to model survival rates is inextricably linked to whether they have information about the factors that kill trees and the associated plant functions. The response of plants to abiotic and biotic stresses should play a large role in this realm. Advances in transcriptomics [54] and metabolomics [44] now mean that ecologists can assay a much broader spectrum of plant function as well as the dynamic response of a plant to a key stressor. In those cases where such approaches are not feasible, trait-based ecologists still should not feel comfortable measuring a small set of traits and relying on the assumption that those traits will indicate the relative success of a plant in a given environment.

The final pathway forwards in trait-based community ecology is to take intraspecific variation more seriously. We are far from the first to make this plea (e.g. [32]) and we recognize that measuring every individual is often impossible. However, if one is seeking to solidify the foundation of trait-based ecology by demonstrating trait–demographic rate relationships, such studies should focus on individual-level data. Importantly, to have the most useful insights individual-level data should be averaged as little as possible. In other words, an average growth rate over a decade still might not be correlated with the most detailed of individual-level trait measurements. In sum, not all trait-based community ecology needs individual-level data, but it becomes useful when the goal is prediction of demographic rates.

Outstanding Questions

Why is so little variation in growth and survival explained by the traits believed to explain the key axes of functional differentiation in plants?

Are we measuring the 'right' traits and just failing to put them into the proper allocational context or are we also failing to measure many other traits of importance?

Why do the traits that predict growth often fail to predict survival?

Do we know what traits we should measure and only fail to measure them due to logistical and financial constraints or are there aspects of plant function of importance that we would never consider measuring?

Should trait-based community ecology abandon univariate trait analyses?

In closing, we hope that this work has served multiple purposes. First, trait–demographic rate relationships are not as strong as often assumed or portrayed. Second, there are clear reasons for these weak relationships. Third, by identifying these issues we can identify a pathway forwards for those studying the relationships between traits and demography and how they influence population and community structure and dynamics.

References

1. McGill, B.J. *et al.* (2006) Rebuilding community ecology from functional traits. *Trends Ecol. Evol.* 21, 178–185
2. Arnold, S.J. (1983) Morphology, performance and fitness. *Am. Zool.* 23, 347–361
3. Violle, C. *et al.* (2007) Let the concept of trait be functional! *Oikos* 116, 882–892
4. Reich, P.B. (2014) The world- wide 'fast–slow' plant economics spectrum: a traits manifesto. *J. Ecol.* 102, 275–301
5. Paine, C.E.T. *et al.* (2015) Globally, functional traits are weak predictors of juvenile tree growth, and we do not know why. *J. Ecol.* 103, 978–989
6. Wright, S.J. *et al.* (2010) Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* 91, 3664–3674
7. Kraft, N.J.B. *et al.* (2015) Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl. Acad. Sci. U. S. A.* 112, 797–802
8. Kunstler, G. *et al.* (2016) Plant functional traits have globally consistent effects on competition. *Nature* 529, 204–207
9. Swenson, N.G. (2013) The assembly of tropical tree communities – the advances and shortcomings of phylogenetic and functional trait analyses. *Ecography* 36, 264–276
10. Weiher, E. *et al.* (1998) Community assembly rules, morphological dispersion, and the coexistence of plant species. *Oikos* 81, 309–322
11. Swenson, N.G. and Enquist, B.J. (2007) Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *Am. J. Bot.* 91, 451–459
12. Kraft, N.J. *et al.* (2008) Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322, 580–582
13. Poorter, L. *et al.* (2008) Are functional traits good predictors of demographic rates? Evidence from five neotropical forests. *Ecology* 89, 1908–1920
14. Iida, Y. *et al.* (2016) Linking leaf veins to growth and mortality rates: an example from a subtropical tree community. *Ecol. Evol.* 6, 6085–6096
15. Iida, Y. *et al.* (2014) Linking functional traits and demographic rates in a subtropical tree community: the importance of size-dependency. *J. Ecol.* 102, 641–650
16. Iida, Y. *et al.* (2014) Linking size-dependent growth and mortality with architectural traits across 145 co-occurring tropical tree species. *Ecology* 95, 353–363
17. Kraft, N.J. *et al.* (2010) The relationship between wood density and mortality in a global tropical forest data set. *New Phytol.* 188, 1124–1136
18. Reich, P.B. *et al.* (1997) From tropics to tundra: global convergence in plant functioning. *Proc. Natl. Acad. Sci. U. S. A.* 94, 13730–13734
19. Osnas, J.L.D. *et al.* (2013) Global leaf trait relationships: mass, area, and the leaf economics spectrum. *Science* 340, 741–744
20. Onoda, Y. *et al.* (2017) Physiological and structural tradeoffs underlying the leaf economics spectrum. *New Phytol.* 214, 1447–1463
21. Poorter, H. (1989) Interspecific variation in relative growth rate: on ecological causes and physiological consequences. In *Causes and Consequences of Variation in Growth Rate and Productivity in Higher Plants* (Lambers, H. *et al.*, eds), pp. 45–68, SPB Academic
22. Hunt, R. (1978) *Plant Growth Analysis,* Edward Arnold
23. Garnier, E. (1991) Resource capture, biomass allocation and growth in herbaceous plants. *Trends Ecol. Evol.* 6, 126–131
24. Enquist, B.J. *et al.* (2007) A general integrative model for scaling plant growth and functional trait spectra. *Nature* 449, 218–222
25. Marks, C.O. and Lechowicz, M.J. (2006) A holistic tree seedling model for the investigation of functional trait diversity. *Ecol. Model.* 193, 141–181
26. Marks, C.O. and Lechowicz, M.J. (2005) Alternative designs and the evolution of functional diversity. *Am. Nat.* 167, 55–66
27. Fortunel, C. *et al.* (2016) Functional trait differences influence neighbourhood interactions in a hyperdiverse Amazonian forest. *Ecol. Lett.* 19, 1062–1070
28. Uriarte, M. *et al.* (2010) Trait similarity, shared ancestry, and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly. *Ecol. Lett.* 13, 1503–1514
29. Zambrano, J. *et al.* (2017) Local neighbourhood and regional climatic contexts interact to explain tree performance. *Proc. Biol. Sci.* 284, 20170523
30. Grant, P.R. and Grant, B.R. (2002) Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296, 707–711
31. Laughlin, D.C. and Messier, J. (2015) Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends Ecol. Evol.* 30, 487–496
32. Violle, C. *et al.* (2012) The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.* 27, 244–252
33. Liu, X. *et al.* (2016) Linking individual-level traits to tree growth in a subtropical forest. *Ecology* 97, 2396–2405
34. Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* 31, 343–366
35. Lamanna, J.A. *et al.* (2017) Plant diversity increase with the strength of negative density dependence at the global scale. *Science* 356, 1389–1392
36. Browne, L. and Karubian, J. (2016) Frequency- dependent selection for rare genotypes promotes genetic diversity of a tropical palm. *Ecol. Lett.* 19, 1439–1447
37. Westoby, M. (1998) A leaf–height–seed (LHS) plant ecology strategy scheme. *Plant Soil* 199, 213–227

38. Westoby, M. *et al.* (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annu. Rev. Ecol. Syst.* 33, 125–159

39. Diaz, S. *et al.* (2016) The global spectrum of plant form and function. *Nature* 529, 167–171

40. Swenson, N.G. (2012) The functional ecology and diversity of tropical tree assemblages through space and time: from local to regional and from traits to transcriptomes. *ISRN For.* 2012, 743617

41. Janzen, D.H. (1970) Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104, 501–528

42. Westbrook, J.W. *et al.* (2011) What makes a leaf tough? Patterns of correlated evolution between leaf toughness traits and demographic rates among 197 shade-tolerant woody species in a neotropical forest. *Am. Nat.* 177, 800–811

43. Zambrano, J. *et al.* (2017) Neighborhood defence gene similarity effects on tree performance: a community transcriptomic approach. *J. Ecol.* 105, 616–626

44. Sedio, B.E. (2017) Recent breakthroughs in metabolomics promise to reveal cryptic chemical traits that mediate plant community composition, character evolution and lineage diversification. *New Phytol.* 214, 952–958

45. Anderegg, W.R. *et al.* (2012) Consequences of widespread tree mortality triggered by drought and temperature stress. *Nat. Clim. Change* 3, 30–36

46. Anderegg, W.R. *et al.* (2015) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. *Science* 349, 528–532

47. Adams, H.D. *et al.* (2009) Temperature sensitivity of drought-induced tree mortality portends increased regional die-off under global-change-type drought. *Proc. Natl. Acad. Sci. U. S. A.* 106, 7063–7066

48. Phillips, O.L. *et al.* (2009) Drought sensitivity of the Amazon rainforest. *Science* 323, 1344–1347

49. Rowland, L. *et al.* (2015) Death from drought in tropical forests is triggered by hydraulics not carbon starvation. *Nature* 528, 119–122

50. McDowell, N.G. (2011) Mechanisms linking drought, hydraulics, carbon metabolism, and vegetation mortality. *Plant Physiol.* 155, 1051–1059

51. Sevanto, S. *et al.* (2014) How do trees die? A test of the hydraulic failure and carbon starvation hypotheses. *Plant Cell Environ.* 37, 153–161

52. Anderegg, W.R. *et al.* (2016) Meta-analysis reveals that hydraulic traits explain cross-species patterns of drought-induced tree mortality across the globe. *Proc. Natl. Acad. Sci. U. S. A.* 113, 5024–5029

53. Bartlett, M.K. *et al.* (2016) Drought tolerance as a driver of tropical forest assembly: resolving spatial signatures for multiple processes. *Ecology* 97, 503–514

54. Swenson, N.G. *et al.* (2017) Tree co-occurrence and transcriptomic response to drought. *Nat. Commun.* 8, 1996

55. Niklas, K.J. and Enquist, B.J. (2001) Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proc. Natl. Acad. Sci. U. S. A.* 98, 2922–2927

56. Tyree, M.T. and Sperry, J.S. (1998) Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress? Answers from a model. *Plant Physiol.* 88, 574–580

57. Choat, B. *et al.* (2012) Global convergence in the vulnerability of forests to drought. *Nature* 491, 752–755

58. Laughlin, D.C. *et al.* (2018) Survival rates indicate that correlations between community-weighted mean traits and environments can be unreliable estimates of the adaptive value of traits. *Ecol. Lett.* 21, 411–421

59. Laughlin, D.C. (2017) Rugged fitness landscapes and Darwinian demons in trait-based ecology. *New Phytol.* 217, 501–503