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Unifying functional and population ecology to test the adaptive value of traits

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ABSTRACT

Plant strategies are phenotypes shaped by natural selection that enable populations to persist in a given environment. Plant strategy theory is essential for understanding the assembly of plant communities, predicting plant responses to climate change, and enhancing the restoration of our degrading biosphere. However, models of plant strategies vary widely and have tended to emphasize either functional traits or life-history traits at the expense of integrating both into a general framework to improve our ecological and evolutionary understanding of plant form and function. Advancing our understanding of plant strategies will require investment in two complementary research agendas that together will unify functional ecology and population ecology. First, we must determine what is phenotypically possible by quantifying the dimensionality of plant traits. This step requires dense taxonomic sampling of traits on species representing the broad diversity of phylogenetic clades, environmental gradients, and geographical regions found across Earth. It is important that we continue to sample traits locally and share data globally to fill biased gaps in trait databases. Second, we must test the power of traits for explaining species distributions, demographic rates, and population growth rates across gradients of resource limitation, disturbance regimes, temperature, vegetation density, and frequencies of other strategies. This step requires thoughtful, theory-driven empiricism. Reciprocal transplant experiments beyond the native range and synthetic demographic modelling are the most powerful methods to determine how trait-by-environment interactions influence fitness. Moving beyond easy-to-measure traits and evaluating the traits that are under the strongest ecological selection within different environmental contexts will improve our understanding of plant adaptations. Plant strategy theory is poised to (*i*) unpack the multiple dimensions of productivity and disturbance gradients and differentiate adaptations to climate and resource limitation from adaptations to disturbance, (*ii*) distinguish between the fundamental and realized niches of phenotypes, and (*iii*) articulate the distinctions and relationships between functional traits and life-history traits.

Key words: demography, life history, population ecology, survival, reproduction, functional traits, convergent evolution, resource limitation, temperature, disturbance regime.

CONTENTS

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"*Our primary concern as plant ecologists is to know why a plant of this species, and not of that, is growing in a given spot*" (Clapham, 1956, p. 1).
"*Tradeoffs [are] intractable evolutionary dilemmas whereby the assumption of traits conferring fitness in one circumstance result inescapably in loss of fitness in another*" (Grime et al., 1997, p. 260).

I. INTRODUCTION TO PLANT STRATEGIES

The likelihood that a seedling successfully establishes from seed and also survives to produce new seedlings itself is often less than one in a million (Chang-Yang *et al.*, 2021; Terborgh *et al.*, 2014; Van Valen, 1975), yet despite these bafflingly low odds for individuals, the likelihood that any hectare on Earth is covered in vegetation approaches near certainty. This is not a paradox of probabilities. Against the odds, vegetation thrives because plants are rolling loaded dice (Shipley, 2010). Plants have inherited phenotypic traits, such as the size of seeds and the density of belowground buds, that have increased their chance of success in a particular habitat, and these traits are indicators of their strategies to establish, survive, and persist. These strategies are "how a species sustains a population" (Westoby, 1998, p. 214) because all successful strategies must yield positive demographic outcomes in the habitats to which they are adapted. Adaptation is not perfection, but it is certainly better than average (Niklas, 1997).

Plant strategies are *phenotypes shaped by natural selection that enable populations to persist in a given environment* (Laughlin, 2023). Few topics have both inspired and riled ecologists more than plant strategies, yet the topic is critical for understanding the assembly of plant communities, predicting plant responses to environmental change, and enhancing the restoration of our biosphere. There are three key features to this definition of plant strategies: (*i*) population persistence; (*ii*) phenotypic traits; and (*iii*) the environment. Illustrating these features in a causal diagram makes the proposed links explicit (Fig. 1). This definition emphasizes populations rather than individuals because "trait variation may influence the fate of populations, [but] luck often governs the lives of individuals" (Snyder & Ellner, 2018, p. E90). In other words, efforts to detect links between traits and fitness will likely be more successful by focusing on population-level persistence, rather than on individuals that only persist, on average, once in every million chances. Population persistence can be measured in many ways but is usefully expressed as the *per-capita* rate of population growth (i.e. fitness), which can be computed directly by integrating measures of growth, survival and reproduction in a structured population model (Ellner, Childs & Rees, 2016; Caswell, 2001).

Phenotypic traits that affect fitness are often called functional traits (Violle *et al.*, 2007), and include the physiological, morphological, or phenological attributes that influence demographic rates (growth, survival, and reproduction). These effects are, however, contingent on the environmental context, which includes abiotic conditions such as temperature, resource

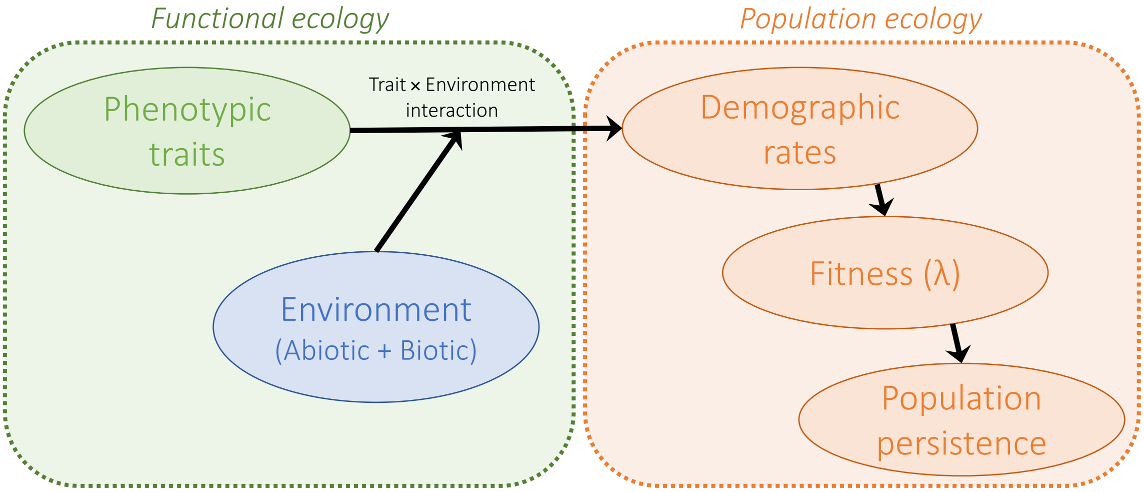


Fig. 1. Plant strategies are phenotypes shaped by natural selection that enable populations to persist in a given environment. Phenotypic traits, by themselves, are not plant strategies until they are shown to enable population persistence in a given abiotic and biotic environment. This definition assumes the following causal architecture: population fitness (λ) is a direct function of demographic rates, and demographic rates are functions of trait-by-environment interactions. The sieve (filter) shown at the intersection of the arrow from environment into the arrow from traits represents a statistical interaction between traits and environments because any effect of traits on demography are contingent on the environmental context.

availability, and disturbance regimes, in addition to biotic conditions such as other species that are present in the competitive milieu (McGill *et al.*, 2006). By considering all factors simultaneously, this definition of plant strategies includes phenotypic adaptations that enable populations to persist in a given set of abiotic conditions and biotic conditions including density and frequency dependence. This definition of plant strategies differs slightly from the evolutionary definition of an adaptation because adaptations, for many evolutionary biologists, are phenotypes that increase the inclusive fitness of the organism regardless of their consequences for long-term population persistence. However, if the trait cannot permit persistence in the presence of neighbours, then it is difficult to see how the trait is adaptive in an ecological context. The causal structure of this definition can be used to build the architecture of a general plant strategy theory (Fig. 1), and the objective of this review is to develop an empirical framework to test the veracity of this theory.

Convergent evolution provides the most intuitive entrance into this vast topic. Consider the most extreme case: phylogenetically unrelated species that occur on different continents that share similar phenotypic traits because they evolved under the same environmental selection pressures (McGhee, 2011). Classic examples include sclerophyllous shrubs in mediterranean chaparral, stem succulents in deserts, and the repeated independent evolution of the C_4 photosynthetic pathway. Indeed, without such global convergence in plant form and function, the whole concept of biomes would never have been conceived. Can we apply the concept of convergent evolution to derive a short list of strategies that describe the vast diversity of plant form and function?

Plant strategy models proposed throughout the 20th century attempted to do just that. These models tended to emphasize either life-history strategies based on demography or functional strategies based on phenotypic traits (Garnier, Navas & Grigulis, 2016; Laughlin, 2023). The disciplinary divide between demography and functional ecology runs deep. Harper (1982, p. 23) criticized descriptive analyses of plants that ignored demography: “The detailed analysis of proximal ecological events is the only means by which we can reasonably hope to inform our guesses about the ultimate causes of the ways in which organisms behave”. In response, Grime (1984, p. 17) wrote “[What is] particularly harmful, in my view, is Harper’s insistence upon the detailed study of proximal events in the field in contemporary populations as the only reliable way to gain a general understanding of vegetation processes. In golfing terms, this is equivalent to ‘putting from the tee’”. Grime used this sport analogy to describe a narrowly focused research program that neglects opportunities for fruitful synthesis between disciplines such as demography and physiology. Fortunately, this disciplinary divide has been breaking down (e.g. Kimball *et al.*, 2012; Kelly *et al.*, 2021; Moles, 2018; Volaire, 2018; Rüger *et al.*, 2018; Bazzaz, 1996; Ackerly *et al.*, 2000), but silos remain. It is only by screening traits (the traditional purview of functional ecologists) and measuring demographic rates (the traditional purview of population ecologists) across multiple species in contrasting environments can we integrate functional ecology and population ecology to conduct robust tests of plant strategy theory.

In this review, I first summarize the traditional approaches to plant strategy theory to define the foundation on which progress must be built. Then I articulate a two-step framework to advance a globally relevant plant ecology. The first objective is to determine what is phenotypically possible by quantifying the dimensionality of plant traits. The second objective is to explain population dynamics as functions of trait-by-environment interactions. Ecologists have made great progress towards achieving the goals in the first step, but we have just begun our journey toward achieving the second.

II. A BRIEF HISTORY OF PLANT STRATEGY MODELS

A legion of models were proposed throughout the 20th century (Laughlin, 2023), but only the most influential are reviewed here. A few plant strategy models were successfully developed to explain plant functional diversity in specific ecosystems, but a general theory became more elusive when the goal broadened to explain global variation in plant form and function.

Many early models classified species into plant functional types. Raunkiaer’s (1934) life form classification system was based on the location of the perennating meristem, and this partially explains species distributions along temperature gradients (Keddy, 2017), but it does not differentiate between plants with the same meristem structure that occur in different environments (Woodward & Kelly, 1997). Box’s (1981) comprehensive life form system grouped species into 77 life forms based on structural types (e.g. tree, shrub, graminoid), plant size, leaf type (i.e. broad, narrow, graminoid, absent), leaf size (i.e. macrophyll, mesophyll, microphyll, nanophyll), leaf structure (i.e. herbaceous, coriaceous, sclerophyll, succulent, ligneous, pubescent), and photosynthetic habit (e.g. evergreen, summer-green, raingreen). This classification is currently under revision and will include even more types (E. Box, personal communication). Classification systems of plant functional types are needed for dynamic global vegetation models to quantify plant–climate feedback (Pavlick *et al.*, 2013). A variety of classifications are in use, but plant ecologists have not yet produced a consensus-based shortlist of plant functional types for modelling vegetation–climate feedback in dynamic global vegetation models (Smith, Shugart & Woodward, 1997).

One set of plant strategy models organized species into groups based on their demographic life-history traits. Life-history traits include quantities such as mean longevity and age to reproduction, which are computed directly from demographic rates and are emergent properties of population models (Salguero-Gómez & Gamelon, 2021; Salguero-Gómez *et al.*, 2016; Caswell, 2001). They are conceptually distinct from functional phenotypic traits, yet the boundary between functional and life-history traits is admittedly fuzzy (e.g. seed mass has been considered both a functional trait and a life-history trait). Models based on life-history traits were designed to explain temporal vegetation dynamics in response to disturbances such as grazing, fire, floods, and tree fall. The vital attributes model (Noble & Slatyer, 1980), one of the most highly influential models of temporal dynamics in plant ecology, used life-history traits of species to predict their long-term performance after stand-replacing disturbances. Three key attributes were identified: the method of persistence during and after a disturbance, the ability to establish and grow to maturity, and the time it takes to reach critical stages of life history. This work inspired the development of other models to describe vegetation dynamics in prairie wetlands using life-history traits such as lifespan, seed longevity, and seed establishment requirements (van der Valk, 1981, 1985; van der Valk & Davis, 1978). Similar gap dynamics models were developed in temperate forests (Shugart, 1984), fire-prone shrublands (Bond, 1997), and fire-prone woodlands (Keith *et al.*, 2007; Plumanns-Pouton *et al.*, 2024).

Another set of models emphasized morphological, physiological, and other phenotypic traits, and were more often designed to explain responses to resource limitation. Chapin (1980) distinguished between "competitive/ruderal" and "nutrient-stress tolerant" strategies, where relative growth rates played a central role in distinguishing the strategies. Fast growth was easy to explain in productive sites – the fastest growing phenotypes were able to dominate – but the advantages of slow growth in poor sites proved more difficult to understand. Slow growth came to be associated with slow turnover of tissues, low respiration rates, and allocation of carbon to secondary metabolites (Chapin, Autumn & Pugnaire, 1993; Aerts, Boot & van der Aart, 1991).

Grime's CSR model has become the most widely recognized plant strategy model (Grime, 1977, 1979, 2001). The CSR model assumes that habitat productivity (the availability of limiting resources) and duration (the length of time between disturbances) are the primary agents of natural selection and that three main strategies evolved in response to them: competitors, stress-tolerators, and ruderals. "Competitors" occupy undisturbed and productive habitats by rapidly acquiring resources in crowded vegetation through rapid production of surface area of both leaves and roots. "Stress-tolerators" occupy undisturbed and unproductive habitats by nature of their persistent and long-lived organs and conservation of resources, which enables them to persist and endure in chronically stressful sites. "Ruderals" occupy disturbed and productive habitats by exhibiting short life spans and investing their rapidly acquired capital into reproduction, which enables their populations to persist in the face of frequent disturbance. Grime expanded the *K* end of the *r*–*K* selection gradient into long-lived competitors and stress-tolerators because there was more than one way to be persistent. Grime's most controversial propositions were that no plant could adapt to high stress and high disturbance simultaneously, and that competition is unimportant in stressful sites.

Throughout his writing, Grime often described trade-offs as "evolutionary dilemmas whereby the assumption of traits conferring fitness in one circumstance result inescapably in loss of fitness in another" (Grime *et al.*, 1997, p. 260), yet surprisingly he never described how to measure fitness and link it to traits. The phrase *traits conferring fitness* holds the key to a predictive framework that synthesizes functional and demographic perspectives on plant strategies. The proposition that traits confer fitness is formally illustrated in the causal architecture of Fig. 1. Grime articulated a useful approach to identifying plant strategies through functional traits but, in my opinion, relied too heavily on exploring patterns in trait variation among species (i.e. the first of the two steps described in this review) (Grime *et al.*, 1997), while neglecting tests of whether traits explain population dynamics in different environments (i.e. the second of the two steps described in this review). Perhaps his public disagreements with Harper, a leading plant demographer of his day, prevented him from drawing these necessary connections between functional ecology and population dynamics.

Tilman (1988) developed his plant strategy theory based on species responses to soil nutrients and light. He built his theory on his mathematical model of resource ratios, where species that persist at the lowest resource level (R^*) win in competition (Tilman, 1982). The model is therefore grounded in a demographic model of population dynamics in a community of competitors and can be viewed as an early game theoretic model. In Tilman's theory, light is limited in sites with fertile soil because closed canopies develop in productive sites. This assumption simplified the dimensionality of the environment by collapsing nutrients and light into a single "soil nutrient-to-light ratio". He proposed that species that grew slowly and invested more carbon in roots would be more competitive for nutrients, and species that grew fast and invested more carbon into shoots would be more competitive for light. However, after many experimental tests, these predictions were not supported by empirical data (Craine, 2009). In fact, Tilman's root-to-shoot ratio model never really caught on outside of the USA because coping with low nutrients was not about having large root mass (Berendse & Elberse, 1990; Aerts & van der Peijl, 1993) and coping with shade was not about having large leaf mass (Kitajima, 1994). Despite its overemphasis on root-to-shoot ratios, this model represents an important step forward because it operationalized the causal architecture of Fig. 1 by explicitly modelling population dynamics as functions of trait-by-environment interactions. The models of Grime and Tilman were antithetical, and I refer interested readers to Grace (1990), Goldberg (1990), and Craine (2005) for insightful discussions of the differences between Grime's and Tilman's views of competition.

Given the multidimensionality of trade-offs and environmental gradients in nature, it appeared to many that a triangle could not explain a tesseract. Ecologists began to probe the complexities of environmental gradients and trait variation. Grubb's encyclopaedic understanding of global floras drove him to emphasize the vast corners of trait space and the multiplicity of ways to be stress tolerant. Grubb (1998) expanded the stress-tolerant strategy into low-flexibility, switching, or gearing-down strategies for each limiting resource. Craine (2009) also expanded on stress tolerance and argued that distinct strategies exist for low-nutrient, low-light, low-water, and low-CO_2 environments.

An important shift in the development of plant strategy theory occurred when strategies came to be quantified as single traits that represent spectrums of correlated traits to stimulate global comparisons. Westoby (1998) proposed his "leaf-height-seed" (LHS) model where strategies could be quantified by the location of a species in a trait space defined by specific leaf area (SLA), height at maturity, and seed mass. These traits were chosen because they represent fundamental trade-offs faced by plants. Additional trait axes have been added over time (Westoby *et al.*, 2002), but the true number of dimensions remains an open question (Laughlin, 2014). Westoby (1998) thought that his proposal would be successful if a sufficient proportion of future publications report these three traits to enable global comparisons. His proposal was successful because these traits formed the basis of the largest comparative study ever to have been conducted in the history of plant ecology (Díaz *et al.*, 2016).

This menagerie of models has set the stage for the current search for plant strategies along continuous trait spectra. Most tests of plant strategy models were based on observing species with particular traits in a particular environment and then concluding that those traits confer an advantage in that environment. However, mere observations of a phenotype in a habitat cannot constitute a rigorous test of plant strategies because they cannot determine how suitable or unsuitable the habitat is if there is no information on the dynamics of the population. The most fruitful approach to advance our understanding of plant adaptation will link phenotypes to demographic processes through a two-step framework.

III. THE TWO-STEP FRAMEWORK FOR A GLOBALLY RELEVANT PLANT STRATEGY THEORY

The credibility of plant strategy theory will be judged by its ability to be presented with any phenotype and any environmental context and then successfully predict whether that phenotype can maintain a viable population in that environment (Shipley, 2010). Furthermore, as the environment changes, can the theory predict how populations and communities will respond (Keddy & Laughlin, 2022)?

The framework to advance plant strategy theory is a two-step process (Fig. 2). First, determine what is phenotypically possible by quantifying the dimensionality of plant traits. Second, explain population dynamics as functions of trait-by-environment interactions. The first step has been the focus of a rapidly growing field of research and much progress has been made. The second step, however, is much more difficult and will require coordinated and well-funded campaigns to acquire data that are

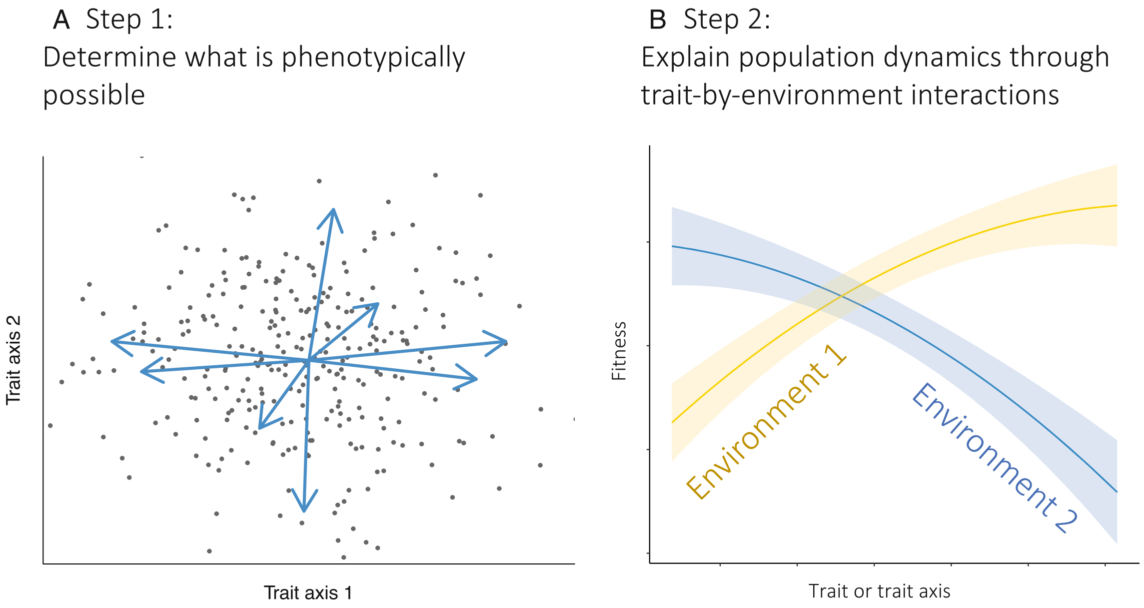


Fig. 2. A two-step framework to advance plant strategy theory. (A) Step 1: quantify the variation and covariation in plant traits among thousands of taxonomically diverse species from all regions of the world. (B) Step 2: fit statistical models of population growth rates (or some other indicator of plant population fitness) as functions of trait-by-environment interactions to test the existence of a plant strategy.

appropriate to quantify the relationship between traits and fitness.

(1) Step 1. Determine what is phenotypically possible

Determining the dimensionality of plant traits involves analysing the variation and covariation of traits among species. Many traits are correlated and redundant, which simplifies our search for the leading dimensions of plant form and function. Previous meta-analyses of plant trait matrices and models of community assembly indicated that the dimensionality of plant traits is likely somewhere between four and eight (Laughlin, 2014) or three and six dimensions (Mouillot *et al.*, 2021). Despite the enormous number of traits that we can measure on plants, there is likely a tractable upper limit to their dimensionality. Our understanding of the dimensionality of functional traits is rapidly growing, but we should consider at least five dimensions to be most important at present: an economics spectrum, a plant size spectrum, a rooting depth spectrum, a spectrum related to collaboration with fungi, and a seed-or-resprout spectrum.

The global community is indebted to the founders of the TRY plant trait database (Kattge *et al.*, 2020), which catapulted plant traits to the global scale. Díaz *et al.* (2016) used this database to analyse covariation in six aboveground traits and concluded that plants span a two-dimensional plane. The first dimension represented variation in plant size and included the following traits: adult height, leaf area, wood density, and seed mass. The second dimension represented variation along the leaf economics spectrum, where leaf nitrogen concentration and SLA described variation along this axis. The leaf economics spectrum has perhaps become the most well-known dimension of plant function, describing a trade-off between leaf lifespan and rate of carbon acquisition (Reich *et al.*, 1999; Reich, Walters & Ellsworth, 1997; Wright *et al.*, 2004), and is the clearest indicator of a plants' location along the continuum from conservative to acquisitive phenotypes.

The analysis by Díaz *et al.* (2016) set a high bar for the number of species that should be compared in functional ecology, but it was also disappointing to many who consider belowground plant organs to be fundamental to plant function. Roots anchor plants in place, provide support for growing stems, acquire water and mineral nutrients from the soil, transport water and minerals to aboveground tissues, and support structures that promote regeneration and clonal movement. Roots perform many complex functions that make life on land possible. Roots were discarded by Díaz *et al.* (2016) for good reason: few data on root traits existed at that time. However, this galvanized root experts to compile fine root trait databases, which led to the conclusion that fine root traits span at least two dimensions (Bergmann *et al.*, 2020; Iversen *et al.*, 2017; Guerrero-Ramírez *et al.*, 2021). The first dimension has been called the "collaboration axis", defined by a trade-off between specific root length and root diameter, where thick-rooted species tend to associate with mycorrhiza and thin-rooted species tend to acquire nutrients by themselves. Root traits also span a second independent dimension called the "conservation axis", where conservative species invest in high root tissue density, and acquisitive species construct more metabolically active tissue with low root tissue density and high root nitrogen concentration (Weemstra *et al.*, 2016; Kramer-Walter *et al.*, 2016; Bergmann *et al.*, 2020). The conservation axis appears to align with the leaf economic spectrum because acquisitive leaves require acquisitive roots to maintain adequate resource supply (Weigelt *et al.*, 2021), although I refer interested readers to an on-going debate about this latter point (Carmona *et al.*, 2021; Weigelt *et al.*, 2023; Bueno *et al.*, 2023).

Fine roots are just one aspect of belowground plant function, and there are at least two other belowground spectrums that belong on this short list of plant strategy dimensions. Weigelt *et al.* (2021) hypothesized that rooting depth would scale with aboveground height, but surprisingly found that these two traits aligned on independent dimensions. Rooting depth is an architectural root system trait that makes it possible to avoid drought by tapping into deep soil water (Fan *et al.*, 2017; Laughlin *et al.*, 2023; Tumber-Dávila *et al.*, 2022) and could be considered as a fourth dimension. Bud banks and clonal growth organs are another set of belowground traits that must be considered. Given the widespread importance of clonality in plants (Klimešová, Martínková & Ottaviani, 2018), the relevance of bud banks to plant survival (Klimešová & Klimeš, 2007), and the well-known trade-off between being a resprouter or a seeder in the context of disturbance regimes (Pausas & Keeley, 2014; Clarke *et al.*, 2013), I suggest that a seeder–resprouter spectrum could be considered a fifth dimension. Five strategy spectrums, or six or seven or eight, will not explain all the variation in plant traits worldwide, but we should seek a low dimensionality that captures the most important variation.

I anticipate that our endeavour to determine the feasible set of all plant phenotypes will take us beyond simple strategy schemes and move us toward sets of traits that are under the strongest selection in the environments for which we aim to make predictions. Linking specific traits to specific agents of selection should yield stronger results. Global analyses of trait variation along climatic gradients often explain low percentages of variation (Bruelheide *et al.*, 2018; Laughlin *et al.*, 2021), so we need to move beyond analyses of the easy-to-measure traits and analyse the traits that matter most to understanding and predicting how species respond to changing environments. If we want to predict how species will respond to drought, our analyses should not only be based on easy-to-measure traits like SLA and wood density (Greenwood *et al.*, 2017), but rather should use physiologically relevant traits like xylem vulnerability to embolism and maximum rooting depth (Laughlin *et al.*, 2023). Physiological traits are not widely measured, given the expertise and resources needed to quantify them accurately, but this situation is slowly improving.

We must continue to measure traits locally and share data globally. Tremendous progress has been made in the last few decades towards advancing the first step of this framework. However, the end is not yet in sight. Ecologists should not become complacent and rely solely on the biased sample of traits that is available in current databases (Cornwell *et al.*, 2019). Not only are trait databases biased towards easy-to-measure traits, many regions of the world and many clades of plants are chronically under sampled. I encourage us to continue to do the hard work of measuring traits from all plant organs, including roots, belowground bud banks, and clonal organs, as well as stems, leaves, and reproductive structures (Laughlin, 2014). I encourage plant ecologists to take these measurements on local plants in local field sites, and then generously contribute to the scientific community by sharing the trait data globally. Determining what is phenotypically possible in plants is not the end game – quantifying the shape of trait space is just the beginning. It is not sufficient to merely observe a phenotype in a habitat and assume it is evolutionarily adapted to those environmental conditions. This assumption needs to be explicitly tested using demographic data.

(2) Step 2. Explain population dynamics through trait-by-environment interactions

In the ecological and evolutionary game of life, the prize for winning is permission to keep playing but the cost of losing is extinction (Vincent & Brown, 2005). All successful plant strategies must exhibit positive demographic outcomes that permit its persistence in a given environment. The mission is to predict the likelihood of persistence of *any phenotype* in *any environment*, an admittedly rather lofty goal. Determining which, where, and when traits matter for explaining population performance is the critical second step for advancing the explanatory power of plant strategies. As has been said twice before, "There is much to be done" (Stearns, 1992, p. 9; Westoby *et al.*, 2002, p. 148).

In many ways, the science of plant strategy theory seeks to understand the distributions of phenotypes, rather than species. It converts a species-based "nomenclatural ecology" into a generalizable "trait-based ecology" (Weiher *et al.*, 1999; McGill *et al.*, 2006). The environmental niche of a phenotype can be distinguished from the niche of a species, because it is circumscribed with respect to traits rather than taxonomic identity. For example, the niche of an acquisitive, deep-rooted phenotype will be the environmental conditions within which all populations that are acquisitive and deep-rooted maintain viable populations. One of the greatest challenges facing ecologists is distinguishing between the density-independent effects that determine the fundamental niche of a phenotype from the density-dependent and frequency-dependent effects that, in combination with density-independent effects, determine the realized niche of the phenotype (Soberón, 2007; Hutchinson, 1957; Chase & Leibold, 2003). It is difficult in practice to separate the effects of the environment from the effects of neighbours, but that is our ultimate quest.

The description of this second step of the framework is organized into two parts. First, I review the key abiotic factors that limit the fundamental niche of phenotypes and describe theoretical approaches that address density and frequency dependence. Second, I review empirical approaches that seek to predict population performance as a function of trait-by-environment interactions that attempt to account for density and frequency dependence, with an emphasis on common garden studies that explicitly test population performance "beyond the range".

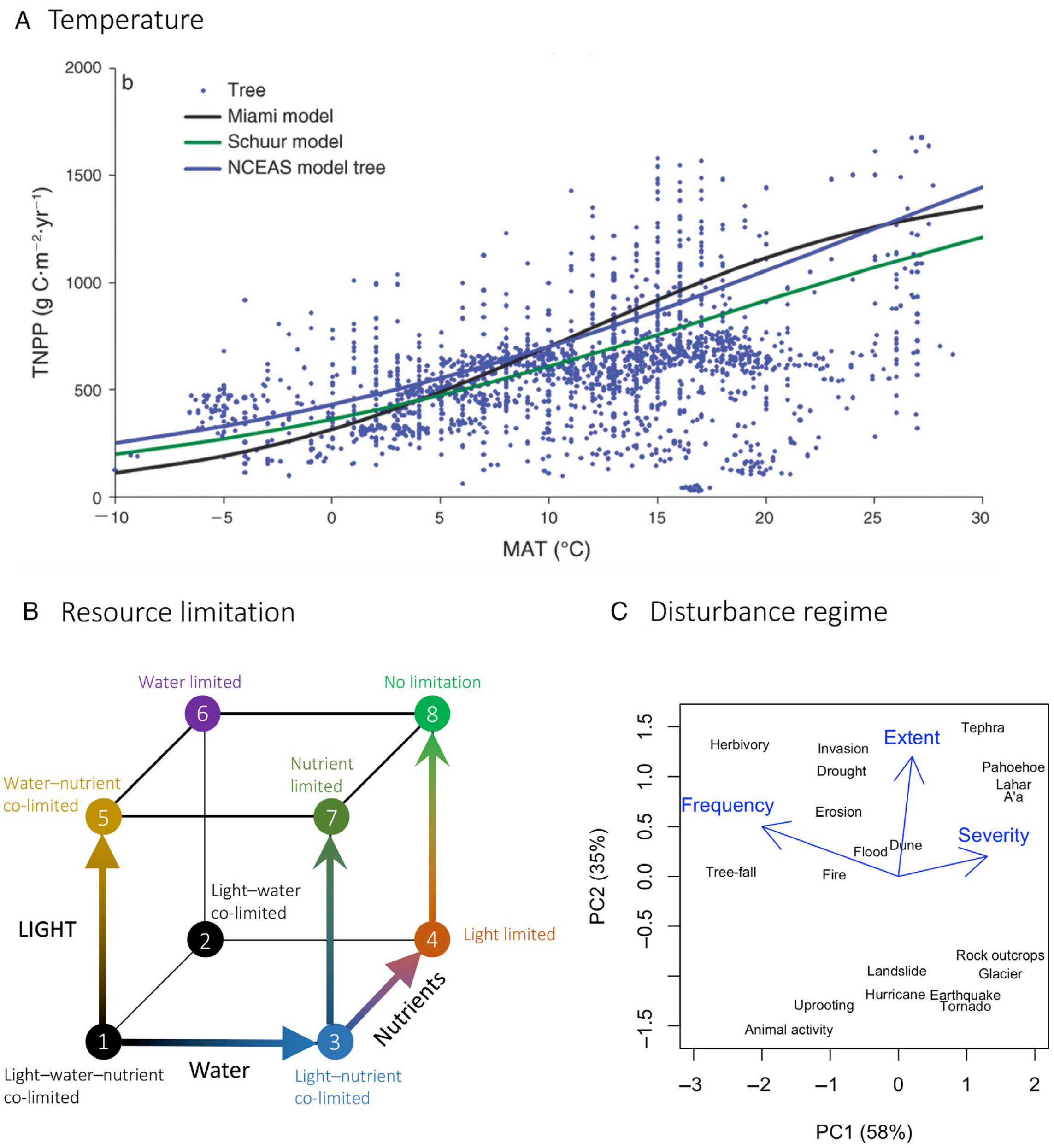
(*a*) *Principal agents of selection in the evolution of plant strategies*

Abiotic density-independent factors have received the most attention in the study of plant strategies. One of the most enduring proposals was that site productivity and disturbance were the two primary drivers of plant strategy evolution (Grime, 1977; Southwood, 1977). However, each of these concepts are multidimensional in nature so it is necessary to unpack them into their component parts.

First, site productivity is largely a function of temperature and resource availability, which together limit biomass production. Temperature is best considered separately from the effects of resources given that temperature cannot be consumed. Temperature is the ultimate regulating factor because it governs non-linear reaction rates for all biological processes (Arroyo *et al.*, 2022). Sites with warm temperatures and longer growing seasons have higher site productivity than cold sites (Fig. 3A) (Del Grosso *et al.*, 2008). Surprisingly, simple traits that explain species distributions along temperature gradients have largely proved elusive (Laughlin, 2023).

The three most important resources that limit biomass production are light, water, and mineral nutrients, and variation in these three resources can be conceptualized as a resource cube (Fig. 3B). The resource cube includes regions where multiple resources co-limit plant growth (Harpole *et al.*, 2011). Microeconomics theory applied to ecophysiology has been used to explore how plants may optimize their growth in the presence of multiple limiting resources (Wright, Reich & Westoby, 2003; Bloom, Chapin & Mooney, 1985). For example, if production is limited by two resources, the least-cost combination of inputs that optimizes production for a given total cost is the location on the equiproduct curve that has the same slope as and is tangential to the equal-cost line. It has also been argued that limitation of each resource selects for different suites of traits, where there exist combinations of traits associated with low-light, low-water, and low-nutrient strategies (Craine, 2009). To my knowledge, there have been no concerted efforts to define all suites of traits that evolved under all possible combinations of co-limitation of these three required resources.

Disturbance is the second key evolutionary driver of plant strategies, and its principal effect is the destruction of plant biomass. Adaptations have evolved in plants to either persist through a disturbance or recover from them after they occur. Disturbance regimes can be characterized by their type, frequency, magnitude, and extent (Walker & del Moral, 2003; Walker & Willig, 1999). Disturbance types vary along a trade-off between frequency and severity, where more



A Temperature

B Resource limitation

C Disturbance regime

Fig. 3. Site productivity and disturbance are the two general factors that have driven the evolution of plant strategies, but these are multidimensional concepts that must be unpacked into their component parts. (A) Total net primary productivity (TNPP) for tree-dominated systems is a function of mean annual temperature (MAT) in the Miami, Schuur, and NCEAS models; reproduced from Del Grosso *et al.* (2008). (B) The resource cube and multiple combinations of resource limitation and co-limitation, reproduced from Laughlin (2023). (C) Disturbance severity and frequency are negatively correlated among disturbance types, and disturbance extent is orthogonal to the frequency–severity axis. For the Principal Components (PC) axes, ordinal scores were estimated using expert opinion and provided to the author by Lars Walker, with thanks (Walker & Willig, 1999; Walker & del Moral, 2003); reproduced from Laughlin (2023). All figures reproduced with permission under the STM opt-out agreement for Wiley and Oxford University Press.

frequent disturbances tend to be less intense and less severe (Fig. 3C). Individual disturbance types, such as fire regimes, also vary in their frequency and severity. Disturbance extent (i.e. the size of a disturbance) appears to vary independently from the frequency–severity dimension, suggesting that disturbance regimes are inherently two-dimensional. A variety of traits have evolved under selection by disturbance regimes. For example, fire has selected for resprouting and thick bark (Pausas, 2015; Pausas & Keeley, 2014) and herbivory has selected for spines, divaricate growth forms, and leaf toxins (Dantas & Pausas, 2020; Agrawal & Fishbein, 2006).

Before describing empirical approaches that quantify the niche of a phenotype, it is important to consider the theoretical developments that probe density and frequency dependence. When the success of a strategy depends on what others in the community are doing, then evolutionary game theory provides tools for assessing the conditions under which a phenotype can maintain a viable population in the presence of other strategies. The evolutionarily stable strategy (ESS) is a strategy that resists invaders with a different strategy that are introduced at low density (McGill & Brown, 2007; McNickle & Dybzinski, 2013). Fitness landscapes include peaks of high fitness and valleys of low fitness where the coordinates of the landscape are defined by continuous traits, and dynamic fitness landscapes illustrate how these landscapes shift along environmental gradients (Laughlin & Messier, 2015). The ESS is a peak on a fitness landscape, where alternative strategies have lower fitness and are therefore unsuccessful at invading from low densities.

In evolutionary game theory, there are players, strategies, and payoffs (Vincent & Brown, 2005). Players are individual organisms, strategies are heritable phenotypes (traits), and the payoff is fitness expressed as the *per-capita* growth rate of a strategy in a given abiotic and biotic environment. Once the demographic parameters of a population model become functions of the focal population's trait values (u_i), the traits in the community ($\boldsymbol{u}$), the densities of those that possess those trait values in the community ($\boldsymbol{x}$), and the environmental conditions of the site including resource availability ($\boldsymbol{r}$), disturbance regime ($\boldsymbol{d}$), and temperature (T), then the population model becomes a game theoretic model. In anticipation of a mathematical formalism, the general structure of the arguments that should be included in an empirical fitness-function F can be written as follows, using the general notation of Vincent & Brown (2005):

$$F = f(u_i, \boldsymbol{u}, \boldsymbol{x}, \boldsymbol{r}, \boldsymbol{d}, T),\ i = 1, \ldots, S \tag{1}$$

where S is the number of strategies. If the effects of traits ($\boldsymbol{u}$) and densities ($\boldsymbol{x}$) are manifested through their local-scale influence on resources ($\boldsymbol{r}$), disturbances ($\boldsymbol{d}$), and temperature (T), then this could simplify to $F = f(u_i, \boldsymbol{r}, \boldsymbol{d}, T)$.

Game theoretical models have come to an important general conclusion about the traits of plants: plants produce more leaves, stems, and roots than what is optimal for the most efficient harvesting of resources because excess tissue production provides a competitive advantage by pre-empting the resources before others get to them (Dybzinski, Farrior & Pacala, 2015; Farrior *et al.*, 2013; McNickle *et al.*, 2016). These insights have demonstrated that our understanding of plant traits cannot be viewed solely as a function of the abiotic environment because the evolution of traits has occurred within a competitive milieu.

Game theoretical models are important for exploring various assumptions about density and frequency dependence, but they are notoriously challenging to test empirically with data collected in the field (McGill & Brown, 2007). Empirical models of long-term observational data can be leveraged to understand fitness better as functions of the focal plant's traits, the surrounding neighbourhood's traits, and the abiotic environmental conditions (Laughlin *et al.*, 2020; Siefert & Laughlin, 2023; Kunstler *et al.*, 2016). A combination of empirical and game theoretical approaches will be the most promising pathway towards the maturation of plant strategy theory. In this spirit, let us now turn to empirical approaches that can be applied by field ecologists to test for the existence of plant strategies to distinguish between fundamental and realized niches of phenotypes.

(*b*) *Empirically demonstrating that traits affect fitness*

The key feature of the two-step framework is the empirical demonstration that traits affect population persistence. Demographic models require repeated sampling of individuals, which is a time-intensive endeavour and likely a logistical limitation to operationalizing this approach. Critically, demographic data sets must include observations of both successes (i.e. persistence) and failures (i.e. local extinction), but this is not always the case. Indeed, observational demographic data sets often lack measurements of population declines outside their natural range precisely because the species do not live in those conditions. Observing failed introductions into unsuitable habitats is just as important as observing successful introductions into suitable habitats when the goal is to map the complex contours of fitness landscapes.

Experiments will no doubt be the most powerful tool to identify the environments in which populations fail by forcing the environmental filtering process to occur. A variety of approaches have been proposed to leverage the variety of data sources at our disposal to advance this agenda, including observational monitoring data sets (Laughlin *et al.*, 2020). Here I focus on common garden studies as they are the gold standard. Common garden studies that plant the same set of species in each site including sites beyond their native geographic and environmental ranges are so persuasive because they can experimentally control environmental conditions and also the density of competitors (Westoby, 2022). They are also the most effective techniques to observe reduced performance and demographic failures (Lee-Yaw *et al.*, 2016; Hargreaves, Samis & Eckert, 2014). For example, in a reciprocal transplant experiment, *Mimulus lewisii* fitness collapsed when grown at low elevation and *Mimulus cardinalis* fitness collapsed when grown at high elevation, a clear demonstration of demographic failures outside the fundamental niches of the species (Angert & Schemske, 2005). The mechanisms of demographic failures differed for each species: *M. cardinalis* failed at high elevations because of reduced growth and reproduction at high elevations, whereas *M. lewisii* failed at low elevations because of increased mortality. An important lesson from synthetic analyses of transplant experiments is that integrative measures of fitness that combine survival and reproduction are superior to single demographic rates at detecting reductions in performance beyond species ranges (Hargreaves *et al.*, 2014).

Most transplant experiments have focused on one or a small set of species because evaluating genotypic and phenotypic variation within ecologically important foundation species has been an important research agenda. Such common garden studies have informed conservation efforts by testing the adaptive capacity of different phenotypes within species in a changing climate (Whitham *et al*., 2020*a*,*b*; Grady *et al*., 2015, 2013). Provenance trials led by the US Forest Service have demonstrated that intraspecific variation within species can influence individual growth and survival across climate gradients (Park & Rodgers, 2023). Such studies emphasize the important variation within species that can buffer species responses to a changing climate. However, we also need common garden arrays that scale up to include multiple species if we hope to answer broader questions about the evolution of plant strategies.

Reciprocal transplant experiments that involve large sets of species that represent a range of different phenotypes are needed to push the limits of plant strategy theory (Westoby, 2022; Laughlin *et al*., 2020). If we want to identify the adaptive value of traits, we need to test how different traits and trait combinations perform across environments, and the only way to disentangle species-specific effects from pure trait effects is to replicate the study using dozens of species. A hypothetical application of common gardens using multiple species is described in Section IV.2. Identifying traits that influence establishment success in response to different environmental conditions will be useful to inform species selection to optimize restoration outcomes (Balazs *et al*., 2020, 2022; Zirbel & Brudvig, 2020; Laughlin *et al*., 2017, 2018; Fiedler *et al*., 2021; Zirbel *et al*., 2017) and management strategies (Butt & Gallagher, 2018; Gallagher *et al*., 2021; Crockett & Hurteau, 2023; Lalor *et al*., 2023). Experimental tests of assisted migration, that is the intentional translocation of a species outside their current range to facilitate natural range expansion into a more suitable environment (Tíscar, Lucas-Borja & Candel-Pérez, 2018; Wang *et al*., 2019; Hewitt *et al*., 2011; Vitt *et al*., 2010), will perhaps constitute the strongest tests of plant strategy theory.

While experiments will be fundamental to advancing this research agenda, any observational data set that is sufficiently large to capture demographic failures will also be useful for modelling trait-based fitness differences across species and environments. For example, Siefert & Laughlin (2023) applied forest inventory data to develop an integral projection model that models demographic rates across all species to estimate the population growth rate of any phenotype in any environment. This study demonstrated that even forest-monitoring data sets capture a range of population performance spanning positive to negative population growth rates across environmental gradients, which is a prerequisite for using such data for this purpose. The analytical framework described by Siefert & Laughlin (2023) can be applied to both observational and experimental data to map the contours of fitness landscapes to understand better "why a plant of this species, and not of that, is growing in a given spot" (Clapham, 1956, p. 1).

IV. FERTILE GROUND FOR ADVANCING PLANT STRATEGY THEORY

There are several unresolved problems to which plant strategy theory can be applied to make new conceptual advances. Future research can address the following three objectives that contain fertile ground for both theory and empiricism: (*i*) unpack the multiple dimensions of productivity and disturbance gradients and differentiate adaptations to climate and resource limitation from adaptations to disturbance; (*ii*) distinguish between the fundamental and realized niches of phenotypes; and (*iii*) articulate the distinctions and unresolved causal relationships between functional traits and life-history traits.

(1) Unpacking the multidimensional habitat templet

Most ecologists would agree that site productivity and disturbance, the original components of Southwood's (1977) "habitat templet" and Grime's (1979) CSR model, are the most general drivers of plant strategy evolution (Huston, 1994; Westoby, 1998; Keddy, 2017), but each of these concepts are complex and multidimensional (Craine, 2009; Grubb, 1998; Walker, 1999; Walker & Willig, 1999). Grime's CSR model treats all factors that limit productivity (i.e. "stresses") equally, and also does not distinguish between the great variety of disturbance regimes that certainly select for different traits. This level of abstraction was an important attempt towards achieving generality, but now we need clearly to acknowledge that different factors impose distinct selective pressures on trait evolution (Craine, 2009).

This review has started the process of unpacking the multiple dimensions of productivity and disturbance (Section III.2.*a*), but more can be done. Productivity gradients have been divided into non-consumable (direct) gradients, including temperature, soil pH, salinity, etc., and consumable (resource) gradients, including mineral nutrients, water, and light (Austin & Smith, 1989). All of these drivers of productivity can also vary over time within a single site depending on the species present and the stage of vegetation development (Grubb, 1980). Disturbance is another catch-all concept that can be continuous or periodic, it can include different types (e.g. grazing *versus* fire), and can vary in frequency, severity, and extent (Walker & Willig, 1999). More frequent and low-intensity disturbances likely have a stronger influence on trait evolution than infrequent and intense disturbances (Harper, 1982). A general plant strategy theory will decompose these two factors into their component parts. Doing so increases the complexity of the theory, yet not doing so oversimplifies the problem.

Differentiating trait adaptations to spatial gradients in climate and resources from adaptations to temporal gradients in disturbance is another related empirical challenge. There can be nearly as much variation in traits within a habitat as there is across habitats (Reich *et al.*, 2003). For example, consider SLA, the leaf area per unit dry mass, which is an important leaf trait that varies across global climate gradients yet can also vary broadly within a single ecosystem type (Poorter *et al.*, 2009; Butler *et al.*, 2017; Boonman *et al.*, 2020). In forested ecosystems, fast-growing pioneers with high SLA colonize vacant patches created by disturbances and are eventually replaced by slower-growing, shade-tolerant species with low SLA after decades of vegetation development (Falster *et al.*, 2017). In open ecosystems, however, slow-growing, shade-intolerant plants with low SLA are dominant because they are adapted to chronic consumption by herbivory and fire; they are not fast-growing pioneers (Bond, 2019). The variation in traits across the planet that is not explained by climate or soil could possibly be explained by local disturbances (Bruelheide *et al.*, 2018), but decomposing this variation in traits into spatial and temporal drivers will require data that are collected at high spatial and temporal resolution. Current analyses of traits, often measured on individual plants or averaged at the species level, and environmental conditions measured at broader scales such as 1-km grids for climate normals and soil properties, may not be at the correct resolution to solve this problem.

To resolve these issues of scale, it is likely that new data and theory are required. Coupling traits measured at the plot scale with microclimate data that are also measured at the plot scale using on-site weather stations and sensors, rather than relying solely on broad-scale climate grids, will sharpen our understanding of trait relationships to climate (Zellweger *et al.*, 2020). Furthermore, if these measurements can then be replicated over time to account for the vegetation dynamics that occur within sites, then we can possibly distinguish between the variation driven by exogenous factors such as climate and the variation driven by endogenous factors such as species interactions. Coming to terms with the internal dynamics requires new theory through which to interpret the variation (Falster *et al.*, 2017). Species interactions certainly play a role in driving within-community trait variation, but negative competitive interactions alone are not the only drivers of such patterns.

(2) Fundamental and realized niches of phenotypes

Distinguishing between the fundamental and realized niche of species has been a long-standing goal in ecology (Hutchinson, 1957; Soberón, 2007), but little progress has been made in quantifying the fundamental niches of even the most common species (Colwell & Fuentes, 1975; Wisheu, 1998). So, in addition to the importance of reviving this age-old objective at the species-level (Colwell & Rangel, 2009), we can extend this foundational concept to phenotypes more generally and perhaps address both problems simultaneously.

The fundamental niche represents the complete set of environmental conditions in which a species can survive and reproduce (Hutchinson, 1957), but estimating it has proved challenging because negative species interactions and dispersal limitation obscure its true breadth (McGill *et al.*, 2006). These abiotic limits change in the presence of neighbours (Soberón & Arroyo-Peña, 2017), and these new limits define the realized niche of the species, i.e. where the species is found and can persist in nature.

When we shift focus from species (nomenclatural categories) to phenotypic traits (continuous variables), then our interest is in quantifying the fundamental and realized niches of continuous vectors of multiple traits. The model of interest is not how the fitness of a species changes along an environmental gradient, but rather how the fitness of a phenotypic trait changes along an environmental gradient. The fitness of a phenotype depends not only on its own traits in a given abiotic environment, but also on the traits of others in the interaction milieu. Distinguishing the effects of neighbours from the effects of the abiotic environment has been a long-standing challenge in community ecology (McGill & Brown, 2007), but one which plant strategy theory is poised to resolve by combining the theoretical insights of game theory with the empirical insights of reciprocal transplant common garden experiments.

Common garden experiments are needed to test foundational ecological theories about fundamental niches and the organization of ecological communities (Fig. 4). Theory predicts that a competition–tolerance trade-off could generate distinct realized niches along a gradient even if all species share a common preferred environment and have overlapping fundamental niches (Fig. 4A) (Wisheu, 1998; Wisheu & Keddy, 1992; Colwell & Fuentes, 1975; Rosenzweig & Abramsky, 1986). This theory is difficult to test with observational data alone because species interactions and dispersal limitation obscure the true breadth of fundamental niches in nature. Therefore, reciprocal transplant common garden experiments that plant a large set of species across an environmental gradient in the presence and absence of competitors (Fig. 4B) could be used to make robust tests of these unresolved theories. Moreover, measuring demographic rates across all life stages (Fig. 4C) will enhance the value of these experiments because survival rates of mature trees could differ from survival rates of juveniles or seedlings (Jackson *et al.*, 2009), and tracking survival and reproduction simultaneously is needed to estimate integrated measures of fitness (Hargreaves *et al.*, 2014).

(3) Causal relationships between functional and life-history traits

Plant strategy theory must also resolve the distinctions and causal relationships between functional traits and life-history traits (Fig. 1). Earlier in this review, functional traits were defined as heritable morphological, physiological, or phenological attributes that indirectly influence fitness by affecting demographic rates contingent on the environment. By contrast, life-history traits (e.g. longevity, generation time, degree of semelparity, age to reproduction) are attributes of populations that are computed directly from the demographic rates and are emergent properties of population models (Salguero-Gómez &

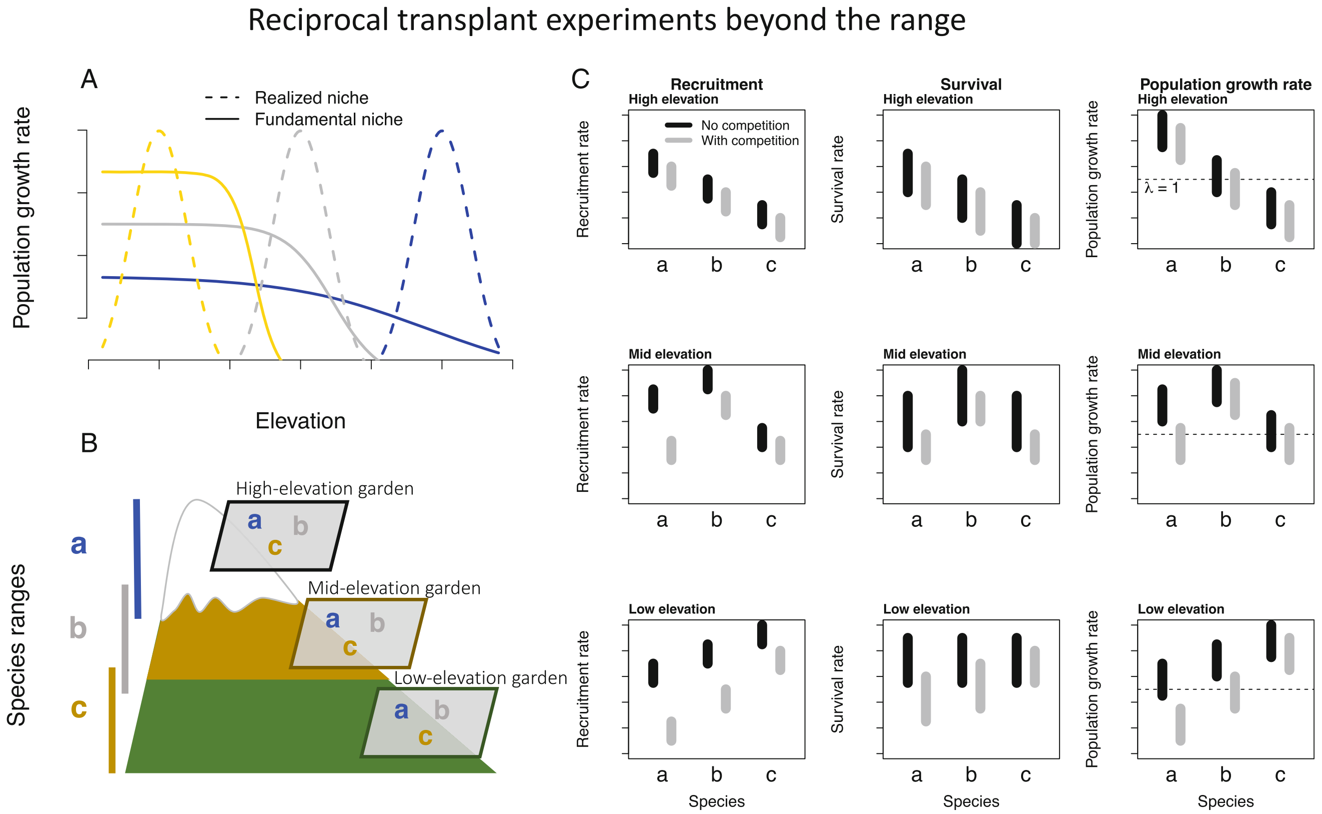


Fig. 4. Use of reciprocal transplant common garden experiments beyond the native range to test ecological theories. (A) In this example, let us assume that three hypothetical species niches (different coloured lines) follow the shared preferences model of community organization (Colwell & Fuentes, 1975; Wisheu, 1998), where all species prefer productive low-elevation sites, but realized niches are constrained to distinct locations along the elevation gradient driven by a competition–tolerance trade-off. (B) Establishing reciprocal transplant common garden sites at locations representative of the elevation gradient is a powerful method for testing the adaptive value of traits. Note that each species in this example occurs in distinct elevation zones, and all three species are planted in each common garden site along the elevation gradient. (C) The most powerful experiments will quantify multiple demographic rates (germination, establishment, growth, survival, seed production, etc.), and will control densities of competitors. At a minimum, measuring recruitment rates of seedlings and survival of mature individuals will permit a calculation of population fitness of each species in each garden. These are hypothetical results if the community was organized according to the shared preference model of fundamental niches.

Gamelon, 2021; Salguero-Gómez *et al.*, 2016). This review has emphasized the importance of functional traits to plant strategies but de-emphasized the importance of life-history traits for one important reason: the distinction and relationships between functional and life-history traits is far from resolved.

One study modelled life-history traits as products of interactions between functional traits and environments and showed, for example, that slow life histories (later age to reproduction, longer generation times, and longer mature lifespans) can be achieved both by short-statured plants in extremely cold and seasonal climates and also by tall-statured plants in warm and aseasonal climates (Kelly *et al.*, 2021). One question lingers: do life-history traits have direct effects on fitness in addition to functional traits? Can we simply swap life-history traits into the spot occupied by phenotypic traits in Fig. 1 and then use interactions between environments and life-history traits as predictors of fitness? At first glance, this may appear reasonable. For example, precocity (early reproduction) is thought to increase the fitness of pines in frequent-fire regimes (Guiote & Pausas, 2023). However, upon deeper inspection, life-history traits do not determine demographic rates and fitness, but rather, they are themselves determined by demographic rates for they are calculated directly from the rates themselves or through algebraic analyses of a projection matrix. This question has consequences for both empirical models of fitness, as well our theoretical understanding of how phenotypes evolve. If fitness can be modelled as a function of both functional and life-history traits, then we need to resolve the causal relationships between functional and life-history traits.

V. CONCLUSIONS

(1) Plant strategies are phenotypes shaped by natural selection that enable populations to persist in a given environment. The strength of plant strategy theory will be judged by its ability to be presented with any phenotype and any abiotic

and biotic context and then successfully predict whether that phenotype can persist in that environment.

(2) Plant strategy models proposed throughout the 20th century tended to emphasize either life-history strategies based on demography or functional strategies based on phenotypic traits. This disciplinary divide between functional ecology and population ecology has been breaking down, but silos remain. It is only by screening traits (the traditional purview of functional ecologists) and screening demographic rates (the traditional purview of population ecologists) across multiple species in contrasting environments can we integrate functional ecology and population ecology to conduct robust tests of plant strategy theory.

(3) Most tests of plant strategy theory simply observed species with particular traits growing in a particular environment and assumed that those traits confer an advantage in that environment. However, mere observations of a phenotype in a habitat cannot constitute a rigorous test of plant strategies because they cannot determine how suitable or unsuitable the habitat is if there is no information on the dynamics of the population.

(4) The framework described herein consists of two steps. The first objective is to determine what is phenotypically possible by determining the dimensionality of plant traits. Measure traits locally and share data globally. The second objective is to test the power of traits for predicting population growth rates across gradients of resource limitation, disturbance regimes, temperature, vegetation density, and frequencies of other strategies.

(5) To test for the existence of plant strategies, we need to observe both demographic successes (i.e. population persistence) and demographic failures (i.e. local extinction). Observational demographic data sets often lack measurements of population declines outside their natural range precisely because the species do not live in those conditions. Observing failed introductions into unsuitable habitats is just as important as observing successful introductions into suitable habitats. Reciprocal transplant common garden experiments that plant species beyond their natural ranges will generate the most convincing results because they experimentally control environmental conditions and the density of competitors and are the most proximate techniques for observing demographic failures.

(6) There are three timely research objectives that plant strategy theory is poised to resolve: (*i*) unpack the multiple dimensions of productivity and disturbance gradients and differentiate adaptations to climate and resource limitation from adaptations to disturbance; (*ii*) distinguish between the fundamental and realized niches of phenotypes; and (*iii*) articulate the distinctions and causal relationships between functional traits and life-history traits.

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VII. REFERENCES

Ackerly, D. D., Dudley, S. A., Sultan, S. E., Schmitt, J., Coleman, J. S., Linder, C. R., Sandquist, D. R., Gebber, M. A., Evans, A. S., Dawson, T. E. & Lechowicz, M. J. (2000). The evolution of plant ecophysiological traits: recent advances and future directions. *Bioscience* **50**(11), 979–995.

Aerts, R., Boot, R. G. A. & van der Aart, P. J. M. (1991). The relation between above- and belowground biomass allocation patterns and competitive ability. *Oecologia* **87**(4), 551–559.

Aerts, R. & van der Peijl, M. J. (1993). A simple model to explain the dominance of low-productive perennials in nutrient-poor habitats. *Oikos* **66**(1), 144–147.

Agrawal, A. A. & Fishbein, M. (2006). Plant defense syndromes. *Ecology* **87**(sp7), S132–S149.

Angert, A. L. & Schemske, D. W. (2005). The evolution of species' distributions: reciprocal transplants across the elevation ranges of *Mimulus cardinalis* and *M. lewisii*. *Evolution* **59**(8), 1671–1684.

Arroyo, J. I., Díez, B., Kempes, C. P., West, G. B. & Marquet, P. A. (2022). A general theory for temperature dependence in biology. *Proceedings of the National Academy of Sciences* **119**(30), e2119872119.

Austin, M. P. & Smith, T. M. (1989). A new model for the continuum concept. *Vegetatio* **83**, 35–47.

Balazs, K. R., Kramer, A. T., Munson, S. M., Talkington, N., Still, S. & Butterfield, B. J. (2020). The right trait in the right place at the right time: matching traits to environment improves restoration outcomes. *Ecological Applications* **30**(4), e02110.

Balazs, K. R., Munson, S. M., Havrilla, C. A. & Butterfield, B. J. (2022). Directional selection shifts trait distributions of planted species in dryland restoration. *Journal of Ecology* **110**(3), 540–552.

Bazzaz, F. A. (1996). *Plants in Changing Environments: Linking Physiological, Population, and Community Ecology*. Cambridge University Press, Cambridge.

Berendse, F. & Elberse, W. T. (1990). Competition and nutrient availability in heathland and grassland ecosystems. In *Perspectives on Plant Competition* (eds J. B. Grace and D. Tilman), pp. 93–116. Academic Press, Inc, San Diego, CA.

Bergmann, J., Weigelt, A., van der Plas, F., Laughlin, D. C., Kuyper, T. W., Guerrero-Ramirez, N., Valverde-Barrantes, O. J., Bruelheide, H., Freschet, G. T., Iversen, C. M., Kattge, J., McCormack, M. L., Meier, I. C., Rillig, M. C., Roumet, C., *et al.* (2020). The fungal collaboration gradient dominates the root economics space in plants. *Science Advances* **6**(27), eaba3756.

Bloom, A. J., Chapin, F. S. & Mooney, H. A. (1985). Resource limitation in plants - an economic analogy. *Annual Review of Ecology and Systematics* **16**(1), 363–392.

Bond, W. J. (1997). Functional types for predicting changes in biodiversity: a case study of Cape fynbos. In *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change* (eds T. M. Smith, H. H. Shugart and F. I. Woodward), pp. 174–194. Cambridge University Press, Cambridge.

Bond, W. J. (2019). *Open Ecosystems: Ecology and Evolution beyond the Forest Edge*. Oxford University Press, Oxford.

Boonman, C. C. F., Benítez-López, A., Schipper, A. M., Thuiller, W., Anand, M., Cerabolini, B. E. L., Cornelissen, J. H. C., Gonzalez-Melo, A., Hattingh, W. N., Higuchi, P., Laughlin, D. C., Onipchenko, V. G., Peñuelas, J., Poorter, L., Soudzilovskaia, N. A., *et al.* (2020). Assessing the reliability of predicted plant trait distributions at the global scale. *Global Ecology and Biogeography* **29**(6), 1034–1051.

Box, E. O. (1981). *Macroclimate and Plant Forms: An Introduction to Predictive Modeling in Phytogeography*. Springer Science & Business Media, Berlin.

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S. M., Botta-Dukát, Z., Chytrý, M., Field, R., Jansen, F., Kattge, J., Pillar, V. D., Schrodt, F., Mahecha, M. D., Peet, R. K., *et al.* (2018). Global trait–environment relationships of plant communities. *Nature Ecology & Evolution* **2**(12), 1906–1917.

Bueno, C. G., Toussaint, A., Träger, S., Díaz, S., Moora, M., Munson, A. D., Pärtel, M., Zobel, M., Tamme, R. & Carmona, C. P. (2023). Reply to: the importance of trait selection in ecology. *Nature* **618**(7967), E31–E34.

Butler, E. E., Datta, A., Flores-Moreno, H., Chen, M., Wythers, K. R., Fazayeli, F., Banerjee, A., Atkin, O. K., Kattge, J. & Amiaud, B. (2017). Mapping local and global variability in plant trait distributions. *Proceedings of the National Academy of Sciences* **114**(51), E10937–E10946.

Butt, N. & Gallagher, R. (2018). Using species traits to guide conservation actions under climate change. *Climatic Change* **151**(2), 317–332.

Carmona, C. P., Bueno, C. G., Toussaint, A., Träger, S., Díaz, S., Moora, M., Munson, A. D., Pärtel, M., Zobel, M. & Tamme, R. (2021). Fine-root traits in the global spectrum of plant form and function. *Nature* **597**(7878), 683–687.

Caswell, H. (2001). *Matrix Population Models*, 2nd Edition (). Sinauer Associates, Inc, Sunderland, MA.

Chang-Yang, C. H., Needham, J., Lu, C. L., Hsieh, C. F., Sun, I. F. & McMahon, S. M. (2021). Closing the life cycle of forest trees: the difficult dynamics of seedling-to-sapling transitions in a subtropical rainforest. *Journal of Ecology* **109**, 2705–2716.

Chapin, F. S. (1980). The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**, 233–260.

Chapin, F. S., Autumn, K. & Pugnaire, F. (1993). Evolution of suites of traits in response to environmental stress. *The American Naturalist* **142**, S78–S92.

Chase, J. M. & Leibold, M. A. (2003). *Ecological Niches: Linking Classical and Contemporary Approaches*. University of Chicago Press, Chicago.

Clapham, A. (1956). Autecological studies and the biological flora of the British Isles. *Journal of Ecology* **44**(1), 1–11.

Clarke, P. J., Lawes, M. J., Midgley, J. J., Lamont, B. B., Ojeda, F., Burrows, G. E., Enright, N. J. & Knox, K. J. E. (2013). Resprouting as a key functional trait: how buds, protection and resources drive persistence after fire. *New Phytologist* **197**(1), 19–35.

Colwell, R. K. & Fuentes, E. R. (1975). Experimental studies of the niche. *Annual Review of Ecology and Systematics* **6**(1), 281–310.

Colwell, R. K. & Rangel, T. F. (2009). Hutchinson's duality: the once and future niche. *Proceedings of the National Academy of Sciences* **106**(supplement_2), 19651–19658.

Cornwell, W. K., Pearse, W. D., Dalrymple, R. L. & Zanne, A. E. (2019). What we (don't) know about global plant diversity. *Ecography* **42**(11), 1819–1831.

Craine, J. M. (2005). Reconciling plant strategy theories of Grime and Tilman. *Journal of Ecology* **93**(6), 1041–1052.

Craine, J. M. (2009). *Resource Strategies of Wild Plants*. Princeton University Press, Princeton, NJ.

Crockett, J. L. & Hurteau, M. D. (2023). Ability of seedlings to survive heat and drought portends future demographic challenges for five southwestern US conifers. *Tree Physiology* **44**(1), tpad136.

Dantas, V. L. & Pausas, J. G. (2020). Megafauna biogeography explains plant functional trait variability in the tropics. *Global Ecology and Biogeography* **29**(8), 1288–1298.

Del Grosso, S., Parton, W., Stohlgren, T., Zheng, D., Bachelet, D., Prince, S., Hibbard, K. & Olson, R. (2008). Global potential net primary production predicted from vegetation class, precipitation, and temperature. *Ecology* **89**(8), 2117–2126.

Díaz, S., Kattge, J., Cornelissen, J. H. C., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönisch, G., Westoby, M., Poorter, H., Reich, P. B., *et al.* (2016). The global spectrum of plant form and function. *Nature* **529**(7585), 167–171.

Dybzinski, R., Farrior, C. E. & Pacala, S. W. (2015). Increased forest carbon storage with increased atmospheric CO_2 despite nitrogen limitation: a game-theoretic allocation model for trees in competition for nitrogen and light. *Global Change Biology* **21**(3), 1182–1196.

Ellner, S. P., Childs, D. Z. & Rees, M. (2016). *Data-Driven Modelling of Structured Populations: A Practical Guide to the Integral Projection Model*. Springer, Switzerland.

Falster, D. S., Brännström, Å., Westoby, M. & Dieckmann, U. (2017). Multitrait successional forest dynamics enable diverse competitive coexistence. *Proceedings of the National Academy of Sciences* **114**(13), E2719–E2728.

Fan, Y., Miguez-Macho, G., Jobbágy, E. G., Jackson, R. B. & Otero-Casal, C. (2017). Hydrologic regulation of plant rooting depth. *Proceedings of the National Academy of Sciences* **114**(40), 10572–10577.

Farrior, C. E., Dybzinski, R., Levin, S. A. & Pacala, S. W. (2013). Competition for water and light in closed-canopy forests: a tractable model of carbon allocation with implications for carbon sinks. *The American Naturalist* **181**(3), 314–330.

Fiedler, S., Monteiro, J. A. F., Hulvey, K. B., Standish, R. J., Perring, M. P. & Tietjen, B. (2021). Global change shifts trade-offs among ecosystem functions in woodlands restored for multifunctionality. *Journal of Applied Ecology* **58**(8), 1705–1717.

Gallagher, R. V., Butt, N., Carthey, A. J. R., Tulloch, A., Bland, L., Clulow, S., Newsome, T., Dudaniec, R. Y. & Adams, V. M. (2021). A guide to using species trait data in conservation. *One Earth* **4**(7), 927–936.

Garnier, E., Navas, M.-L. & Grigulis, K. (2016). *Plant Functional Diversity: Organism Traits, Community Structure, and Ecosystem Properties*. Oxford University Press, Oxford.

Goldberg, D. E. (1990). Components of resource competition in plant communities. In *Perspectives on Plant Competition* (eds J. B. Grace and D. Tilman), pp. 27–49. Academic Press, Inc, London.

Grace, J. B. (1990). On the relationship between plant traits and competitive ability. In *Perspectives on Plant Competition* (Volume **2**, eds J. B. Grace and D. Tilman), pp. 51–65. Academic Press, Inc, London.

Grady, K. C., Kolb, T. E., Ikeda, D. H. & Whitham, T. G. (2015). A bridge too far: cold and pathogen constraints to assisted migration of riparian forests. *Restoration Ecology* **23**(6), 811–820.

Grady, K. C., Laughlin, D. C., Ferrier, S. M., Kolb, T. E., Hart, S. C., Allan, G. J. & Whitham, T. G. (2013). Conservative leaf economic traits correlate with fast growth of genotypes of a foundation riparian species near the thermal maximum extent of its geographic range. *Functional Ecology* **27**(2), 428–438.

Greenwood, S., Ruiz-Benito, P., Martínez-Vilalta, J., Lloret, F., Kitzberger, T., Allen, C. D., Fensham, R., Laughlin, D. C., Kattge, J., Bönisch, G., Kraft, N. J. B. & Jump, A. S. (2017). Tree mortality across biomes is promoted by drought intensity, lower wood density and higher specific leaf area. *Ecology Letters* **20**(4), 539–553.

Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist* **111**(982), 1169–1194.

Grime, J. P. (1979). *Plant Strategies and Vegetation Processes*. Wiley, Chichester.

Grime, J. P. (1984). The ecology of species, families and communities of the contemporary British flora. *New Phytologist* **98**(1), 15–33.

Grime, J. P. (2001). *Plant Strategies, Vegetation Processes, and Ecosystem Properties*, 2nd Edition (). John Wiley & Sons, West Sussex.

Grime, J. P., Thompson, K., Hunt, R., Hodgson, J. G., Cornelissen, J. H. C., Rorison, I. H., Hendry, G. A. F., Ashenden, T. W., Askew, A. P., Band, S. R., Booth, R. E., Bossard, C. C., Campbell, B. D., Cooper, J. E. L., Davison, A. W., *et al.* (1997). Integrated screening validates primary axes of specialisation in plants. *Oikos* **79**(2), 259–281.

Grubb, P. J. (1980). Review: plant strategies and vegetation processes by J. P. Grime. *The New Phytologist* **86**(1), 123–124.

Grubb, P. J. (1998). A reassessment of the strategies of plants which cope with shortages of resources. *Perspectives in Plant Ecology, Evolution and Systematics* **1**(1), 3–31.

Guerrero-Ramírez, N. R., Mommer, L., Freschet, G. T., Iversen, C. M., McCormack, M. L., Kattge, J., Poorter, H., van der Plas, F., Bergmann, J., Kuyper, T. W., York, L. M., Bruelheide, H., Laughlin, D. C., Meier, I. C., Roumet, C., *et al.* (2021). Global root traits (GRooT) database. *Global Ecology and Biogeography* **30**, 25–37.

Guiote, C. & Pausas, J. G. (2023). Fire favors sexual precocity in a Mediterranean pine. *Oikos* **2023**(3), e09373.

Hargreaves, A. L., Samis, K. E. & Eckert, C. G. (2014). Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *The American Naturalist* **183**(2), 157–173.

Harper, J. L. (1982). After description. In *The Plant Community as a Working Mechanism. Special Publications Series of the British Ecological Society* (ed. E. I. Newman), pp. 11–25. Blackwell Scientific Publications, Oxford.

Harpole, W. S., Ngai, J. T., Cleland, E. E., Seabloom, E. W., Borer, E. T., Bracken, M. E. S., Elser, J. J., Gruner, D. S., Hillebrand, H., Shurin, J. B. & Smith, J. E. (2011). Nutrient co-limitation of primary producer communities. *Ecology Letters* **14**(9), 852–862.

Hewitt, N., Klenk, N., Smith, A. L., Bazely, D. R., Yan, N., Wood, S., MacLellan, J. I., Lipsig-Mumme, C. & Henriques, I. (2011). Taking stock of the assisted migration debate. *Biological Conservation* **144**(11), 2560–2572.

Huston, M. A. (1994). *Biological Diversity: The Coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.

Hutchinson, G. E. (1957). Concluding remarks. In *Cold Spring Harbor Symposia on Quantitative Biology* (Volume **22**), pp. 415–427. Cold Spring Harbor Laboratory Press, Cold Spring Harbor, NY.

Iversen, C. M., McCormack, M. L., Powell, A. S., Blackwood, C. B., Freschet, G. T., Kattge, J., Roumet, C., Stover, D. B., Soudzilovskaia, N. A., Valverde-Barrantes, O. J., van Bodegom, P. M. & Violle, C. (2017). A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. *New Phytologist* **215**(1), 15–26.

Jackson, S. T., Betancourt, J. L., Booth, R. K. & Gray, S. T. (2009). Ecology and the ratchet of events: climate variability, niche dimensions, and species distributions. *Proceedings of the National Academy of Sciences* **106**(supplement_2), 19685–19692.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., *et al.* (2020). TRY plant trait database – enhanced coverage and open access. *Global Change Biology* **26**(1), 119–188.

Keddy, P. A. (2017). *Plant Ecology*. Cambridge University Press, Cambridge.

Keddy, P. A. & Laughlin, D. C. (2022). *A Framework for Community Ecology: Species Pools, Filters and Traits*. Cambridge University Press, Cambridge.

Keith, D. A., Holman, L., Rodoreda, S., Lemmon, J. & Bedward, M. (2007). Plant functional types can predict decade-scale changes in fire-prone vegetation. *Journal of Ecology* **95**(6), 1324–1337.

Kelly, R., Healy, K., Anand, M., Baudraz, M. E. A., Bahn, M., Cerabolini, B. E. L., Cornelissen, J. H. C., Dwyer, J. M., Jackson, A. L., Kattge, J., Niinemets, Ü., Penuelas, J., Pierce, S., Salguero-Gómez, R. & Buckley, Y. M. (2021). Climatic and evolutionary contexts are required to infer plant life history strategies from functional traits at a global scale. *Ecology Letters* **24**(5), 970–983.

Kimball, S., Gremer, J. R., Angert, A. L., Huxman, T. E. & Venable, D. L. (2012). Fitness and physiology in a variable environment. *Oecologia* **169**(2), 319–329.

Kitajima, K. (1994). Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* **98**(3), 419–428.

Klimešová, J. & Klimeš, L. (2007). Bud banks and their role in vegetative regeneration–a literature review and proposal for simple classification and assessment. *Perspectives in Plant Ecology, Evolution and Systematics* **8**(3), 115–129.

Klimešová, J., Martínková, J. & Ottaviani, G. (2018). Belowground plant functional ecology: towards an integrated perspective. *Functional Ecology* **32**(9), 2115–2126.

Kramer-Walter, K. R., Bellingham, P. J., Millar, T. R., Smissen, R. D., Richardson, S. J. & Laughlin, D. C. (2016). Root traits are multidimensional: specific root length is independent from root tissue density and the plant economic spectrum. *Journal of Ecology* **104**, 1299–1310.

Kunstler, G., Falster, D., Coomes, D. A., Hui, F., Kooyman, R. M., Laughlin, D. C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S. J., Aiba, M., Baraloto, C., Caspersen, J., Cornelissen, J. H. C., Gourlet-Fleury, S., *et al.* (2016). Plant functional traits have globally consistent effects on competition. *Nature* **529**(7585), 204–207.

Lalor, A. R., Law, D. J., Breshears, D. D., Falk, D. A., Field, J. P., Loehman, R. A., Triepke, F. J. & Barron-Gafford, G. A. (2023). Mortality thresholds of juvenile trees to drought and heatwaves: implications for forest regeneration across a landscape gradient. *Frontiers in Forests and Global Change* **6**. https://doi.org/10.3389/ffgc.2023.1198156

Laughlin, D. C. (2014). The intrinsic dimensionality of plant traits and its relevance to community assembly. *Journal of Ecology* **102**(1), 186–193.

Laughlin, D. C. (2023). *Plant Strategies: The Demographic Consequences of Functional Traits in Changing Environments*. Oxford University Press, Oxford.

Laughlin, D. C., Chalmandrier, L., Joshi, C., Renton, M., Dwyer, J. M. & Funk, J. L. (2018). Generating species assemblages for restoration and experimentation: a new method that can simultaneously converge on average trait values and maximize functional diversity. *Methods in Ecology and Evolution* **9**(7), 1764–1771.

Laughlin, D. C., Gremer, J. R., Adler, P. B., Mitchell, R. M. & Moore, M. M. (2020). The net effect of functional traits on fitness. *Trends in Ecology & Evolution* **35**(11), 1037–1047.

Laughlin, D. C. & Messier, J. (2015). Fitness of multidimensional phenotypes in dynamic adaptive landscapes. *Trends in Ecology & Evolution* **30**(8), 487–496.

Laughlin, D. C., Mommer, L., Sabatini, F. M., Bruelheide, H., Kuyper, T. W., McCormack, M. L., Bergmann, J., Freschet, G. T., Guerrero-Ramírez, N. R., Iversen, C. M., Kattge, J., Meier, I. C., Poorter, H., Roumet, C., Semchenko, M., *et al.* (2021). Root traits explain plant species distributions along climatic gradients yet challenge the nature of ecological trade-offs. *Nature Ecology & Evolution* **5**(8), 1123–1134.

Laughlin, D. C., Siefert, A., Fleri, J. R., Tumber-Dávila, S. J., Hammond, W. M., Sabatini, F. M., Damasceno, G., Aubin, I., Field, R., Hatim, M. Z., Jansen, S., Lenoir, J., Lens, F., McCarthy, J. K., Niinemets, Ü., *et al.* (2023). Rooting depth and xylem vulnerability are independent woody plant traits jointly selected by aridity, seasonality, and water table depth. *New Phytologist* **240**, 1774–1787.

Laughlin, D. C., Strahan, R. T., Huffman, D. W. & Sánchez Meador, A. J. (2017). Using trait-based ecology to restore resilient ecosystems: historical conditions and the future of montane forests in western North America. *Restoration Ecology* **25**(S2), S135–S146.

Lee-Yaw, J. A., Kharouba, H. M., Bontrager, M., Mahony, C., Csergő, A. M., Noreen, A. M. E., Li, Q., Schuster, R. & Angert, A. L. (2016). A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecology Letters* **19**(6), 710–722.

McGhee, G. R. (2011). *Convergent Evolution: Limited Forms most Beautiful*. MIT Press, Cambridge.

McGill, B. J. & Brown, J. S. (2007). Evolutionary game theory and adaptive dynamics of continuous traits. *Annual Review of Ecology, Evolution, and Systematics* **38**(1), 403–435.

McGill, B. J., Enquist, B. J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* **21**(4), 178–185.

McNickle, G. G. & Dybzinski, R. (2013). Game theory and plant ecology. *Ecology Letters* **16**(4), 545–555.

McNickle, G. G., Gonzalez-Meler, M. A., Lynch, D. J., Baltzer, J. L. & Brown, J. S. (2016). The world's biomes and primary production as a triple tragedy of the commons foraging game played among plants. *Proceedings of the Royal Society B: Biological Sciences* **283**(1842), 20161993.

Moles, A. T. (2018). Being John Harper: using evolutionary ideas to improve understanding of global patterns in plant traits. *Journal of Ecology* **106**(1), 1–18.

Mouillot, D., Loiseau, N., Grenié, M., Algar, A. C., Allegra, M., Cadotte, M. W., Casajus, N., Denelle, P., Guéguen, M., Maire, A., Maitner, B., McGill, B. J., McLean, M., Mouquet, N., Munoz, F., *et al.* (2021). The dimensionality and structure of species trait spaces. *Ecology Letters* **24**(9), 1988–2009.

Niklas, K. J. (1997). *The Evolutionary Biology of Plants*. University of Chicago Press, Chicago.

Noble, I. R. & Slatyer, R. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio* **43**(1), 5–21.

Park, A. & Rodgers, J. L. (2023). Provenance trials in the service of forestry assisted migration: a review of North American field trials and experiments. *Forest Ecology and Management* **537**, 120854.

Pausas, J. G. (2015). Bark thickness and fire regime. *Functional Ecology* **29**(3), 315–327.

Pausas, J. G. & Keeley, J. E. (2014). Evolutionary ecology of resprouting and seeding in fire-prone ecosystems. *New Phytologist* **204**(1), 55–65.

Pavlick, R., Drewry, D. T., Bohn, K., Reu, B. & Kleidon, A. (2013). The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs. *Biogeosciences* **10**(6), 4137–4177.

Plumanns-Pouton, E., Swan, M., Penman, T. & Kelly, L. T. (2024). Using plant functional types to predict the influence of fire on species relative abundance. *Biological Conservation* **292**, 110555.

Poorter, H., Niinemets, Ü., Poorter, L., Wright, I. J. & Villar, R. (2009). Causes and consequences of variation in leaf mass per area (LMA): a meta-analysis. *New Phytologist* **182**(3), 565–588.

Raunkiaer, C. (1934). *The Life Forms of Plants and Statistical Plant Geography: Being the Collected Papers of C. Raunkiaer*. Clarendon Press, Oxford.

Reich, P. B., Ellsworth, D. S., Walters, M. B., Vose, J. M., Gresham, C., Volin, J. C. & Bowman, W. D. (1999). Generality of leaf trait relationships: a test across six biomes. *Ecology* **80**(6), 1955–1969.

Reich, P. B., Walters, M. B. & Ellsworth, D. S. (1997). From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences* **94**(25), 13730–13734.

Reich, P. B., Wright, I. J., Cavender-Bares, J., Craine, J. M., Oleksyn, J., Westoby, M. & Walters, M. B. (2003). The evolution of plant functional variation: traits, spectra, and strategies. *International Journal of Plant Sciences* **164**(S3), S143–S164.

Rosenzweig, M. L. & Abramsky, Z. (1986). Centrifugal community organization. *Oikos* **46**(3), 339–348.

Rüger, N., Comita, L. S., Condit, R., Purves, D., Rosenbaum, B., Visser, M. D., Joseph Wright, S. & Wirth, C. (2018). Beyond the fast–slow continuum: demographic dimensions structuring a tropical tree community. *Ecology Letters* **21**(7), 1075–1084.

Salguero-Gómez, R. & Gamelon, M. (2021). *Demographic Methods across the Tree of Life*. Oxford University Press, Oxford.

Salguero-Gómez, R., Jones, O. R., Jongejans, E., Blomberg, S. P., Hodgson, D. J., Mbeau-Ache, C., Zuidema, P. A., de Kroon, H. & Buckley, Y. M. (2016). Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences* **113**(1), 230–235.

Shipley, B. (2010). *From Plant Traits to Vegetation Structure: Chance and Selection in the Assembly of Ecological Communities*. Cambridge University Press, Cambridge.

Shugart, H. H. (1984). *A Theory of Forest Dynamics: The Ecological Implications of Forest Succession Models*. Springer-Verlag, Berlin.

Siefert, A. & Laughlin, D. C. (2023). Estimating the net effect of functional traits on fitness across species and environments. *Methods in Ecology and Evolution* **14**(4), 1035–1048.

Smith, T. M., Shugart, H. H. & Woodward, F. I. (1997). *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*. Cambridge University Press, Cambridge.

Snyder, R. E. & Ellner, S. P. (2018). Pluck or luck: does trait variation or chance drive variation in lifetime reproductive success? *The American Naturalist* **191**(4), E90–E107.

Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* **10**(12), 1115–1123.

Soberón, J. & Arroyo-Peña, B. (2017). Are fundamental niches larger than the realized? Testing a 50-year-old prediction by Hutchinson. *PLoS One* **12**(4), e0175138.

Southwood, T. R. E. (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology* **46**(2), 337–365.

Stearns, S. C. (1992). *The Evolution of Life Histories*. Oxford University Press, Oxford.

Terborgh, J., Zhu, K., Álvarez-Loayza, P. & Cornejo Valverde, F. (2014). How many seeds does it take to make a sapling? *Ecology* **95**(4), 991–999.

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.

Tilman, D. (1988). *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, NJ.

Tíscar, P. A., Lucas-Borja, M. E. & Candel-Pérez, D. (2018). Lack of local adaptation to the establishment conditions limits assisted migration to adapt drought-prone *Pinus nigra* populations to climate change. *Forest Ecology and Management* **409**, 719–728.

Tumber-Dávila, S. J., Schenk, H. J., Du, E. & Jackson, R. B. (2022). Plant sizes and shapes above and belowground and their interactions with climate. *New Phytologist* **235**(3), 1032–1056.

van der Valk, A. G. (1981). Succession in wetlands: a Gleasonian approach. *Ecology* **62**(3), 688–696.

van der Valk, A. G. (1985). Vegetation dynamics of prairie glacial marshes. In *The Population Structure of Vegetation* (ed. J. White), pp. 293–312. Dr W. Junk Publishers, Dordrecht.

van der Valk, A. G. & Davis, C. (1978). The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology* **59**(2), 322–335.

Van Valen, L. (1975). Life, death, and energy of a tree. *Biotropica* **7**(4), 259–269.

Vincent, T. L. & Brown, J. S. (2005). *Evolutionary Game Theory, Natural Selection, and Darwinian Dynamics*. Cambridge University Press, Cambridge.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007). Let the concept of trait be functional! *Oikos* **116**(5), 882–892.

Vitt, P., Havens, K., Kramer, A. T., Sollenberger, D. & Yates, E. (2010). Assisted migration of plants: changes in latitudes, changes in attitudes. *Biological Conservation* **143**(1), 18–27.

Volaire, F. (2018). A unified framework of plant adaptive strategies to drought: crossing scales and disciplines. *Global Change Biology* **24**(7), 2929–2938.

Walker, L. R. (1999). *Ecosystems of Disturbed Ground*. Elsevier, Amsterdam.

Walker, L. R. & del Moral, R. (2003). *Primary Succession and Ecosystem Rehabilitation*. Cambridge University Press, Cambridge.

Walker, L. R. & Willig, M. R. (1999). An introduction to terrestrial disturbances. In *Ecosystems of Disturbed Ground. Ecosystems of the World 16* (ed. L. R. Walker), pp. 1–16. Elsevier, The Netherlands.

Wang, Y., Pedersen, J. L. M., Macdonald, S. E., Nielsen, S. E. & Zhang, J. (2019). Experimental test of assisted migration for conservation of locally range-restricted plants in Alberta, Canada. *Global Ecology and Conservation* **17**, e00572.

Weemstra, M., Mommer, L., Visser, E. J., Ruijven, J., Kuyper, T. W., Mohren, G. M. & Sterck, F. J. (2016). Towards a multidimensional root trait framework: a tree root review. *New Phytologist* **211**, 1159–1169.

Weigelt, A., Mommer, L., Andraczek, K., Iversen, C. M., Bergmann, J., Bruelheide, H., Fan, Y., Freschet, G. T., Guerrero-Ramírez, N. R., Kattge, J., Kuyper, T. W., Laughlin, D. C., Meier, I. C., van der Plas, F., Poorter, H., *et al.* (2021). An integrated framework of plant form and function: the belowground perspective. *New Phytologist* **232**, 42–59.

Weigelt, A., Mommer, L., Andraczek, K., Iversen, C. M., Bergmann, J., Bruelheide, H., Freschet, G. T., Guerrero-Ramírez, N. R., Kattge, J., Kuyper, T. W., Laughlin, D. C., Meier, I. C., van der Plas, F., Poorter, H., Roumet, C., *et al.* (2023). The importance of trait selection in ecology. *Nature* **618**(7967), E29–E30.

Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. (1999). Challenging Theophrastus: a common core list of plant traits for functional ecology. *Journal of Vegetation Science* **10**(5), 609–620.

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* **199**(2), 213–227.

Westoby, M. (2022). Field experiments on mechanisms influencing species boundary movement under climate change. *Plant and Soil* **476**, 527–534.

Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A. & Wright, I. J. (2002). Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* **33**(1), 125–159.

Whitham, T. G., Allan, G. J., Cooper, H. F. & Shuster, S. M. (2020*a*). Intraspecific genetic variation and species interactions contribute to community evolution. *Annual Review of Ecology, Evolution, and Systematics* **51**(1), 587–612.

Whitham, T. G., Gehring, C. A., Bothwell, H. M., Cooper, H. F., Hull, J. B., Allan, G. J., Grady, K. C., Markovchick, L., Shuster, S. M. & Parker, J. (2020b). Using the Southwest Experimental Garden Array to enhance riparian restoration in response to global environmental change: identifying and deploying genotypes and populations for current and future environments [chapter 4]. In *Riparian Research and Management: Past, Present, Future. Volume 2. Gen. Tech. Rep. RMRS-GTR-411* (Volume **411**, eds S. W. Carothers, R. R. Johnson, D. M. Finch, K. J. Kingsley and R. H. Hamre), pp. 63–79. US Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.

Wisheu, I. C. (1998). How organisms partition habitats: different types of community organization can produce identical patterns. *Oikos* **83**(2), 246–258.

Wisheu, I. C. & Keddy, P. A. (1992). Competition and centrifugal organization of plant communities: theory and tests. *Journal of Vegetation Science* **3**(2), 147–156.

Woodward, F. I. & Kelly, C. K. (1997). Plant functional types: towards a definition by environmental constraints. In *Plant Functional Types: Their Relevance to Ecosystem Properties and Global Change*. International Geosphere-Biosphere Programme Book Series (Volume **1**, eds T. M. Smith, H. H. Shugart and F. I. Woodward), pp. 47–65. Cambridge University Press, Cambridge.

Wright, I. J., Reich, P. B. & Westoby, M. (2003). Least-cost input mixtures of water and nitrogen for photosynthesis. *The American Naturalist* **161**(1), 98–111.

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J., Hikosaka, K., *et al.* (2004). The worldwide leaf economics spectrum. *Nature* **428**(6985), 821–827.

Zellweger, F., De Frenne, P., Lenoir, J., Vangansbeke, P., Verheyen, K., Bernhardt-Römermann, M., Baeten, L., Hédl, R., Berki, I., Brunet, J., Van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., *et al.* (2020). Forest microclimate dynamics drive plant responses to warming. *Science* **368**(6492), 772–775.

Zirbel, C. R., Bassett, T., Grman, E. & Brudvig, L. A. (2017). Plant functional traits and environmental conditions shape community assembly and ecosystem functioning during restoration. *Journal of Applied Ecology* **54**(4), 1070–1079.

Zirbel, C. R. & Brudvig, L. A. (2020). Trait–environment interactions affect plant establishment success during restoration. *Ecology* **101**(3), e02971.

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