Review

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Why can't we predict traits from the environment?

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Summary

Plant functional traits are powerful ecological tools, but the relationships between plant traits and climate (or environmental variables more broadly) are often remarkably weak. This presents a paradox: Plant traits govern plant interactions with their environment, but the environment does not strongly predict the traits of plants living there. Unpacking this paradox requires differentiating the mechanisms of trait variation and potential confounds of trait–environment relationships at different evolutionary and ecological scales ranging from within species to among communities. It also necessitates a more integrated understanding of physiological and evolutionary equifinality among many traits and plant strategies, and challenges us to understand how supposedly 'functional' traits integrate into a whole-organism phenotype in ways that may be largely orthogonal to environmental tolerances.

I. Introduction

Functional traits are the morphological, phenological, and physiological attributes that mediate a plant's interactions with its environment and are integral to an individual's fitness and to mechanistic vegetation models. Understanding how species attributes determine their presence and abundance has deep roots in ecology (e.g. the 'fourth corner' problem, Legendre *et al.*, 1997). The idea that functional traits themselves can abstract beyond taxonomic identity and species-specific natural history to provide a universal framework for understanding plant interactions with their environment grew out of this early work (Mouillot *et al.*, 2013) and has become central to modern functional, community, and physiological ecology. Fueled in part by the rise of global trait databases, plant functional ecology has realized marked successes in simplifying Earth's dazzling functional diversity into a few axes of ecophysiological strategies represented by trait 'spectra'. For instance, the leaf economic spectrum captures the majority of variation in leaf morphology, stoichiometry, and function with one fast-vs-slow resource use axis (Wright *et al.*, 2004), and another largely orthogonal axis captures differences in organ and whole-plant size (Díaz *et al.*, 2016).

Yet a conundrum persists in plant functional ecology: Many 'functional traits', even those associated with physiological tolerance of abiotic stress, often show remarkably weak relationships with environmental factors such as climate or soil. Conceptually, to be 'functional', a trait must influence some element of plant performance, be it growth, survival, or fecundity (Violle *et al.*, 2007), and show variation among species and/or across environmental gradients. Yet, global analyses of trait–environment

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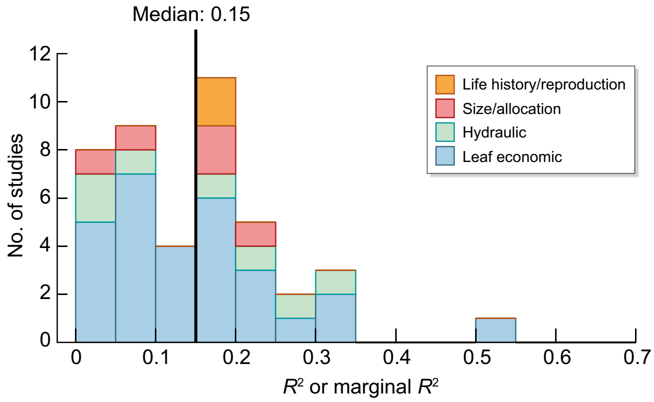

Fig. 1 Trait–climate relationships are typically weak. Histogram of R^2 values (or marginal R^2 for models with random effects) from studies that investigated global trait–environment relationships using compiled trait databases and climate from the site of trait observations and that reported goodness-of-fit statistics for climate or soil predictors. Data and associated citations are in Supporting Information Table S1.

relationships typically explain < 20% or even 10% of total trait variation with climate or soil factors (Fig. 1). Consistently weak trait–environment relationships raise ecological, evolutionary, and methodological questions about our most conceptually powerful and well-measured traits. Here I review the eco-evolutionary processes that drive trait variation at various ecological scales and their implications both for how we look for trait–environment relationships and for how we interpret trait variation.

II. Questions of scale and sampling

The mechanisms by which environmental variation drives trait variation fundamentally differ depending on the ecological scale (Ackerly *et al.*, 2002). Within a species, trait plasticity and micro-evolution (i.e. ecotypic variation) shape phenotypes. Among species, trait variation is driven by macro-evolutionary processes. Among communities, all the drivers of trait variation are integrated through the ecological processes of community assembly, and community-average or community-weighted mean (CWM) trait variation results from within-species variation, abundance shifts, and/or species turnover (Fig. 2, see Cornwell & Ackerly, 2009). The majority of regional or global trait–environment studies (e.g. those in Fig. 1) rely on individual observations drawn from many different studies, by many different investigators. While an expedient first pass for synthesizing decades of work across many systems, such analyses combine multiple ecological and evolutionary processes and numerous biases. As a result, perhaps it is no surprise that the most well-studied leaf traits are rarely strongly related to the climate of the site of the trait observations. Even for traits more strongly linked to stress tolerance, such as plant hydraulic traits, climate explains strikingly little of the variation in large-scale trait databases (Fig. 1, Sanchez Martinez *et al.*, 2020).

If it is indeed the haphazard nature of global trait databases causing weak trait–environment relationships, we might predict that untangling acclimation-driven, ecological, and evolutionary sources of trait variation via explicit analyses of within-species, among-species, and among-community trait–environment relationships could clarify trait–climate patterns. However, this does not necessarily seem to be the case.

Within-species variation

Within-species, a growing literature highlights how divergent the magnitude, strength, and sign of trait–environment relationships can be for different traits and different species (Schulze *et al.*, 1998; Albert *et al.*, 2010; Vilà-Cabrera *et al.*, 2015; Rosas *et al.*, 2019). For instance, in an exhaustive study of variation in specific leaf area in Western Australia, relationships with environmental predictors were only significant for 61 of 85 herbaceous species, < 30% of sampled species showed significant responses to any individual environmental predictor, and the average explained variance was low (Dwyer *et al.*, 2014). Indeed, within-species trait–climate relationships in leaf economic traits are usually considerably weaker than among-species and among-community relationships (Cornwell & Ackerly, 2009; Anderegg *et al.*, 2018).

Several culprits may explain inconsistent and weak trait–climate relationships (see Table 1). Within-species analyses limit the influence of differing life-history or ecological strategies that might confound our functional interpretation of trait variation. However, they simultaneously maximize the potential effects of nonadaptive trait variation that can weaken or occasionally reverse the sign of within-species vs among-species or among-community trait–environment relationships (Fig. 2b; Ackerly *et al.*, 2002). Notably, 'negative' or nonadaptive plasticity (i.e. phenotypic consequences of stress that decrease fitness) can produce trait–climate relationships through space and time that are contrary to predictions (Kerr *et al.*, 2022). Microenvironmental effects can also radically decouple the environment experienced by a plant from macroclimate predictors such as gridded climate data. For example, groundwater subsidies explained geographic patterns of hydraulic traits in trembling aspen that initially appeared maladaptive (Love *et al.*, 2019). Finally, the difficulty in disentangling confounding stress gradients complicates the detection of intraspecific trait–environment relationships. In particular, the confounding increase in cold stress and decrease in drought stress across temperate elevational and latitudinal gradients (where the vast majority of within-species studies have been performed) may be particularly troublesome. This could explain why leaf mass per area (LMA), which is known to increase in response to both experimental drought and cold stress (Poorter *et al.*, 2009), shows no within-species patterns with water availability in six temperate trees in Spain (Rosas *et al.*, 2019) but shows consistent patterns in eight noncold-stressed Australian tree species (Anderegg *et al.*, 2021).

Among-species variation

At larger phylogenetic scales, we see more promising trait–climate relationships. Indeed, comparative analysis of climatically contrasting species within lineages has been the go-to method for understanding the adaptive significance of traits for decades (Felsenstein, 1985). At this phylogenetic scale, the total variation in life history, body plan, physiological strategy, and ecological

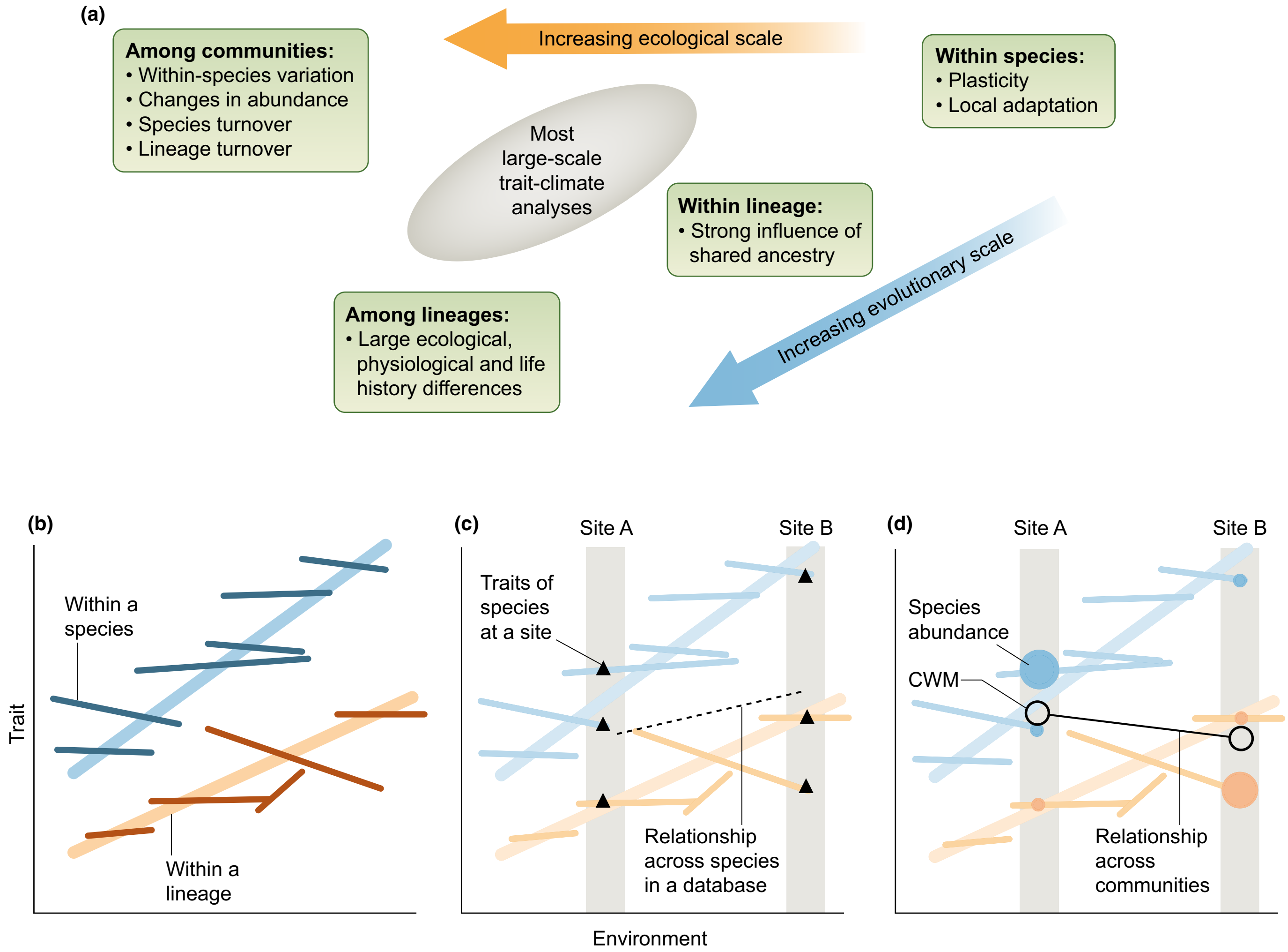

Fig. 2 Combination of processes at different evolutionary and ecological scales can drastically complicate trait–environment patterns (a) Different evolutionary and ecological processes drive trait changes across scales. Most phylogenetically naïve trait–climate analyses that use site-of-measurement climate values haphazardly and likely nonrandomly sample these various ecological and evolutionary processes. (b) Trait variation within individual species (dark lines) vs among species of a lineage (lighter lines). Differences in evolutionary history and life-history strategies lead to a large trait offset between the two lineages, but the among-species trait–climate relationship is consistent within each lineage. (c) A classic trait study that compiles observations from two different sites (Sites A and B, gray boxes) would find a nonsignificant trait–environment relationship due to the haphazard combination of within-species, within-linage, and among-lineage trait variation. (d) Weighting the same species by their abundance to create 'community-weighted mean' (CWM) trait values reveals yet a different trait–environment relationship, largely driven in this case by changes in abundance between the two lineages.

niche remains partially constrained, increasing the probability of a single trait being implicated as an adaptive response to an environmental gradient. For example, xylem resistance to embolism is a key trait for drought survival (Anderegg *et al*., 2016) and shows strong relationships with the aridity niche inhabited by congeneric oaks (Skelton *et al*., 2021) and conifers in the Cupressaceae family (Pittermann *et al*., 2012). Yet, across all land plants, embolism resistance has only a weak relationship with climate (Choat *et al*., 2012). The greater the evolutionary distance considered, the more likely that variation in other traits complicates the functional importance of any individual trait. In the case of embolism resistance, a major evolutionary divergence in how conifers regulate stomatal closure leads to a strong embolism resistance–aridity relationship within Cupressaceae but no relationship within other conifer families (Brodribb *et al*., 2014). The evolution of deciduousness also seems to drive consistent trait patterns within lineage but contrasting patterns among lineages due to the development of divergent physiological strategies (Mitchell *et al*., 2015; Anderegg *et al*., 2022).

Thus, the treatment of phylogenetic structure is critical. The majority of the signal in global trait analyses (e.g. Fig. 1) putatively derives from variation among species, yet the weakness of these patterns may be due, at least in part, to the 'phylogenetic noise' of haphazardly sampling distantly related species with diverging strategies, at which point nonmeasured life history or physiological differences alter the functional context and adaptive value of any individual trait. Indeed, the majority of global plant trait variation (except for tissue allometries) is at the family level or higher (Anderegg *et al*., 2022), meaning that co-occurring lineages complicate among-species trait–environment relationships. Consequently, lineage turnover will usually swamp most other sources of trait variation. If the functional interpretation of an absolute trait

Table 1

	Hypotheses for weak trait–environment relationships	Potential workarounds
Within species	Nonadaptive trait variation, such as ‘negative plasticity’ (a stress-induced change in phenotype that decreases fitness) and genetic drift among populations or founder-effects in small range-edge populations (Fig. 2b) Microclimatic or micro-edaphic variation decouples the environment that sampled individuals actually experience from environmental predictors used in analysis Incomplete sampling of species’ environmental niche hides true trait patterns Confounding stress gradients have opposing effects on focal traits but are difficult to disentangle geographically	• Common garden studies to disentangle plasticity and ecotypic variation • Sample more populations to overcome noise • Careful site selection using multiple climate variables
Among species	‘Phylogenetic noise’ of sampling across lineages obscures consistent patterns within lineages (Fig. 2c) Measures of species climate niche are much stronger predictors of relative trait values among species than the site-of-observation climate for any particular trait measurement Equal influence of common species and rare species with outlier trait values obscures trait signal	• Phylogenetically informed analyses • Use metrics of species’ climate from occurrence data as predictors • Calculate CWM traits to account for abundance
Among communities	Lineage turnover among communities complicates the functional significance of an absolute change in trait value (Fig. 2d) Conflicting and countergradient patterns at multiple ecological scales sum to inconclusive community patterns	• Hierarchical analyses to decompose effects of lineage turnover, species turnover, and within-species variation
All levels	Measured traits are ‘functional’ (i.e. they affect fitness) along orthogonal ecological axes to simple climate or soil gradients, and thus only indirectly relate to abiotic environmental variables Unmeasured/underappreciated traits are more important or ‘functional’ than the most easily measured traits Trait integration/equifinality among many trait combinations minimizes univariate relationships with any individual trait even while functional phenotype changes strongly with environment	• Explore the whole-organism or integrated phenotype, including the effects of many traits (e.g. by using mechanistic models to understand trait equifinality and performance landscapes)

value is identical across the tree of life, lineage turnover would create strong trait–environment signals. However, if absolute trait values have different functional consequences for different lineages (e.g. wood density or LMA in gymnosperms vs angiosperms), this instead decreases the trait–environment signal (Fig. 2b, offset between the two lineages).

Successful comparative analyses also typically rely on a species’ environmental niche as a climate predictor, rather than the climate where the traits were actually sampled. Among-species analyses that use site-of-measurement climate jumble observations that represent very different portions of each species’ climate niche (Fig. 2c, gray vertical boxes indicate sampling locations), mixing information from processes driving trait variation within and among species.

Among-community variation

A key assumption underpinning many trait–environment analyses is that there is an ecological or physiological strategy that is favored in certain environments, which should result in a detectible shift in community trait values across environmental gradients. If this is true, we might conclude that large-scale trait–climate analyses are weak because they imperfectly combine sources of trait variation from a smorgasbord of ecological and evolutionary scales without accounting for the changes in abundance and species turnover that cause community-level trait variation. We might also conclude that rare species (which might be rare because their traits are a poor match for the environment) add considerable noise to these analyses because their traits receive the same weight as dominant species. By this logic, we would expect that analyses of CWM traits, which average the trait values of all community members weighted by their dominance (often basal area, leaf area, or biomass), should capture trait–climate relationships more cleanly.

However, CWM trait–environment analyses are generally quite mixed. Across global tundra ecosystems, Bjorkman *et al.* (2018) found strong increases in CWM canopy height, specific leaf area, and leaf size, and decreases in leaf dry matter content with warming summer temperatures, moderated by soil moisture. This pattern was primarily driven by species turnover, but reinforced by cogradient trait patterns within species. However, CWM leaf trait–environment relationships are typically weaker than among-species and in some cases within-species relationships across temperate conifer forests (Anderegg *et al.*, 2018). And globally, CMW values of 17 functional traits show statistically significant but quite weak relationships to climate across 1.1 million vegetation plots ($r^2 < 0.15$ for all traits; Bruelheide *et al.*, 2018). Weak among-community relationships may suggest that issues at lower ecological scales plague higher ecological scales (Table 1). More likely, however, they reveal that issues of ecological and evolutionary scale alone are not sufficient to explain why the environment does not predict traits.

III. Troublesome traits

Another interpretation of weak trait–environment relationships is that we poorly understand the functional significance of traits themselves. Individual traits or trait spectra are clearly useful tools for exploring physiological and even ecological ‘strategies’ (Reich *et al.*, 2003) and illuminating important axes of functional diversity (Wright *et al.*, 2010). However, our understanding of how plant traits fit together to influence which elements of performance (establishment, growth, survival, and reproduction) in which environments is still evolving. We may be focusing on the wrong traits (e.g. chemical defense traits are more important than economic traits for understanding tropical coexistence, Forrister *et al.*, 2019). Expediency often drives trait choice rather than strong ecological or physiological hypotheses (e.g. the globally most measured plant traits are easy-to-measure specific leaf area and plant height (Kattge *et al.*, 2011)). The lack of trait–environment relationships for easily measured traits should inspire us to enumerate new axes of functional diversity that more strongly govern a plant's performance along environmental gradients than classic 'tissue economics' traits.

Even so, at some level, the existence of functional diversity within plant communities itself indicates a hard limit to univariate trait–climate relationships. Coexistence is a high-dimensional problem (Clark *et al.*, 2010), which we still struggle to understand (Kraft *et al.*, 2015). Yet, the existence of diversity within a community indicates that most 'functional' plant traits must have effects on plant fitness often orthogonal to most simple climate gradients. This is obviously true for leaf economic traits. At least 40% of global trait variation in leaf economics traits is present within individual sites (Wright *et al.*, 2004). This means that most of the global leaf economics spectrum is recapitulated in most communities. Even stress tolerance traits such as embolism resistance show remarkably large diversity within communities (Trugman *et al.*, 2020). This highlights an important truism: There are many successful ways to be a plant in most environments.

IV. Conclusion: a path forward

Ultimately, understanding the paradox of weak trait–environment relationships will require tackling multiple issues. First, an explicit focus on hierarchical analyses of trait variation (*sensu* Cornwell & Ackerly, 2009; Bjorkman *et al.*, 2018) is critical for understanding which ecological and evolutionary mechanisms are dominant drivers of community-level trait variation in which traits and which environments. Though data-intensive (requiring abundance data and locally collected trait data for all species in multiple communities), this multiscale approach is critical for overcoming key limitations identified in Table 1. This focus is particularly critical for understanding (and modeling) the consequences of traits and trait diversity for ecosystem function (Lavorel & Garnier, 2002; van der Plas *et al.*, 2020).

Second, a continued effort to determine the 'function' of specific traits, meaning their context-dependent effects on individual fitness, is necessary to identify missing or underappreciated traits (Forrister *et al.*, 2019) and disentangle direct vs indirect effects of traits on fitness (Sobral, 2021), determine how traits affect biotic interactions orthogonal to abiotic stress (Kunstler *et al.*, 2016), and quantify how context-dependent (i.e. variable through space and time) selection pressures are. While evidence of trait 'function' often comes from among-species studies (Wright *et al.*, 2010), true evolutionary inference requires population or even individual-level trait-performance information. This requires colocation of trait measurements and demographic measurements, as well as experimental methods (such as common gardens or reciprocal transplants) to disentangle genotypic vs phenotypic drivers of variation and interrogate direct vs indirect selection.

Finally, weak univariate trait–climate relationships highlight the paramount importance of the integrated phenotype. This represents an exciting frontier: understanding how many traits integrate to determine whole-plant performance in varying environments. Trait–trait correlations such as the leaf economics spectrum hint at landscapes of evolutionary and physiological equifinality (Falster *et al.*, 2017), where many trait combinations result in similar outcomes. Thus, an integrative understanding of traits could help identify the performance landscape for a given environment and how that landscape shifts in different environments. Often, mechanistic plant models have used empirical trait–trait and trait–environment relationships to constrain functional trade-offs in the model (Pavlick *et al.*, 2013; Scheiter *et al.*, 2013; Sakschewski *et al.*, 2015; Xu *et al.*, 2016). I argue that vegetation models can facilitate inference in the opposite direction. Mechanistic models can provide a 'first guess' about the net effects of trait variation, individually and in concert, on whole-plant performance (Trugman *et al.*, 2019). Trait-constrained modeling could identify surfaces of physiological equifinality and reveal traits with the largest uncertainty and the largest leverage over model outcomes (Dietze *et al.*, 2014). Empirical observations of traits and performance will no doubt identify model shortcomings, but the physiological mechanisms enshrined in vegetation models with coupled assimilation and stomatal conductance, plant hydraulics, and nutrient dynamics represent our current best guess at how components of a plant scale up to whole-organism performance. Compared with mechanistically coarse empirical alternatives such as structural equation modeling, I argue that vegetation models are a useful tool for generating hypotheses about the integrated phenotype, given sufficient cocollected trait, demography, and ecosystem function (e.g. eddy-flux) data. Regardless of the method, exploring the integrated phenotype to understand the whole-organism consequences of trait variation may help realize the broader dream of predictive functional and community ecology.

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Data availability

Model summary statistics compiled from the primary literature for Fig. 1 are available, along with relevant citations, in Table S1 in the Supporting Information.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Table S1 Data and relevant citations for global trait–climate analyses used in Fig. 1.