SYNTHESIS

American Journal of
Botany

A trait-based approach to determining principles of plant biogeography

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Abstract

Lineage-specific traits determine how plants interact with their surrounding environment. Unrelated species may evolve similar phenotypic characteristics to tolerate, persist in, and invade environments with certain characteristics, resulting in some traits becoming relatively more common in certain types of habitats. Analyses of these general patterns of geographical trait distribution have led to the proposal of general principles to explain how plants diversify in space over time. Trait–environment correlation analyses quantify to what extent unrelated lineages have similar evolutionary responses to a given type of habitat. In this synthesis, I give a short historical overview on trait–environment correlation analyses, from some key observations from classic naturalists to modern approaches using trait evolution models, large phylogenies, and massive data sets of traits and distributions. I discuss some limitations of modern approaches, including the need for more realistic models, the lack of data from tropical areas, and the necessary focus on trait scoring that goes beyond macromorphology. Overcoming these limitations will allow the field to explore new questions related to trait lability and niche evolution and to better identify generalities and exceptions in how plants diversify in space over time.

KEYWORDS

environmental variables, functional biogeography, phylogenetic comparative methods, trait evolution, tropical botany

INTRODUCTION: LINEAGE-SPECIFIC TRAITS AS DETERMINANTS OF PLANT DISTRIBUTION

Plant biogeographers are generally interested in understanding how and why certain plant lineages are found in some places but not in others. Lineage-specific traits (i.e., inheritable traits; henceforward "traits") control how plants interact with the surrounding environment and can modulate their geographical distribution in at least three ways. First, they allow plant lineages to survive in environments that, due to physiological constraints, they would not be able to tolerate otherwise (Good, 1931). For example, species native to closed canopy biomes tend to have larger leaf areas (Givnish, 1988) and larger seeds to store nutrients for germination (Foster and Janson, 1985) due to photosynthetic limitations in shady habitats. Second, traits can facilitate lineages to persist and reproduce in certain environments by allowing them to better compete for resources or survive against natural enemies. For instance, spines tend to be more common on plants in open habitats where grazing herbivores are numerous (Charles-Dominique et al., 2016), and chemical compounds are more diverse in plants in tropical rainforests due to constant pressure from pathogens (Kursar et al., 2009). Third, traits may increase chances of invasions of new environments by facilitating movement through geographical barriers and the establishment of new populations from just a few individuals. Such traits include, for instance, capacity for self-fertilization (Pannel et al., 2015) and certain types of seed dispersal strategies that increase lineage vagility over evolutionary time (Onstein et al., 2019; Vasconcelos et al., 2023).

The crucial role that traits play in modulating plant distribution may lead some traits to become more common in certain types of habitats because many species evolve similar phenotypic characteristics to tolerate, persist in, and invade environments with certain characteristics (Figure 1A). Understanding how plant traits become more
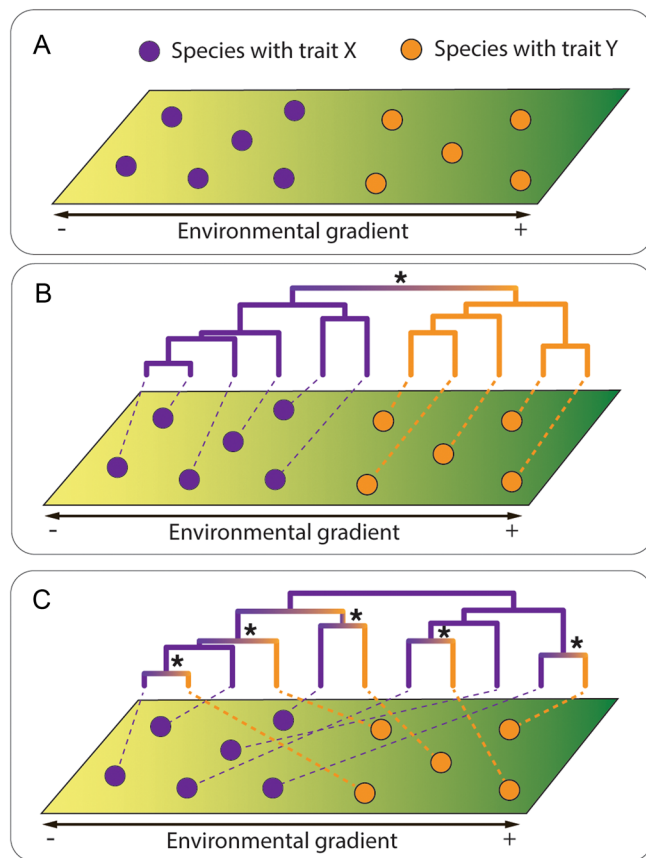
FIGURE 1 (A) Schematic representation of the geographical distribution of 11 species that have trait X or Y across an environmental gradient (– to +). Each trait is more common in one of the extremes of the environmental gradient. Over evolutionary time, this pattern can be formed through (B) common descent of sympatric species or (C) convergent evolutionary responses in unrelated lineages. The second scenario (C) provides significantly more robust evidence for trait–environment correlation in an explicit evolutionary framework due to the larger number of independent empirical replicates (marked with an asterisk).

or less common in the flora of a region provides key information on how large-scale biogeographical patterns are formed. Similar phenotypic solutions may arise from common descent, when closely related species inherit a similar suite of beneficial traits to exist in a given type of habitat (Figure 1B). For instance, most species of montane lupines (*Lupinus*, Fabaceae) are perennial and belong to a clade that invaded the Andes and diversified in situ, meaning that there are few events of elevational transition linked to the evolution of a perennial life-history strategy in that group (Drummond et al., 2012). However, similar phenotypic solutions can also arise in distantly related species through parallelisms and convergences (Figure 1C; e.g., Donoghue et al., 2022). For instance, we often delineate biomes based on traits that are commonly found across several unrelated lineages that occur under similar climatic conditions. The biome classification of "broadleaf rain-forests", for example, refers to a plant trait ("broadleaves") that is common in warmer forests that receive a lot of rain

throughout the year. Similarly, "shrublands" indicate drier or cooler areas that are dominated by a particular life form ("shrubs"). In this case, independent events of environmental transitions may appear correlated with the acquisition of a similar phenotypic characteristic through the evolution of independent lineages, even if that biome has a disjunct distribution around the world (e.g., savannas and rainforests; Pennington and Hughes, 2014; Eiserhardt et al., 2017).

Distantly related lineages having similar evolutionary responses to survive and persist in similar environmental conditions (such as climate, soil, and topography) or developing similar solutions to overcome physical barriers (such as the oceans in events of transoceanic long-distance dispersal) indicate that general principles may explain how plants diversify in space over time. With modern tools to analyze trait–environment correlations, the extent that unrelated lineages have similar evolutionary responses to a given abiotic environment can be quantified and the applicability of these general principles assessed. In this synthesis, I give a brief overview of how trait–environment correlations have been historically quantified and discuss avenues for future research based on limitations of modern approaches.

HISTORICAL OVERVIEW ON TRAIT-BASED APPROACHES TO PLANT BIOGEOGRAPHY

Before the evolutionary theory was proposed, plant trait distributions were observed to be correlated with aspects of the abiotic environment. In their day, Von Humboldt and Bonpland (1807) provided arguably the most popular account of how vegetative traits respond to environmental temperature by observing that alpine plants in tropical mountains have vegetative characteristics similar to those found in the temperate zones of Europe. These observations were later mentioned by Darwin (1859, Origin of Species, Chapter XI) to support his theory of natural selection, as evidence that unrelated plant lineages (e.g., species of different genera and families) may acquire similar forms when faced with similar environmental challenges, no matter where they are on the planet. In the first half of the 20th century, further key contributions to these observations came from the works of Arber (1920), who described similar anatomical patterns in roots and stems of aquatic plants for different families of flowering plants, and Raunkiaer (1934), who categorized life forms in plants in relation to how growing buds are protected during unfavorable seasons. In the second half of the 20th century, the contributions of Baker (1955) and Stebbins (1950, 1974) were remarkable for linking features of the abiotic environment not only to the convergent evolution of vegetative traits, but also reproductive traits such as flowers and fruits. The first provided a seminal hypothesis for how breeding systems impact chances of long-distance dispersal and invasion of new areas (reviewed by Pannell et al., 2015).

The second suggested that the abiotic environment may often cause an indirect effect on the spatial distribution of plant traits that depend on animal behavior because the distribution of animals themselves (e.g., pollinators and dispersers) are also impacted by characteristics of the abiotic environment.

It is important to note that most of the hypotheses on trait–environment correlations developed during this period were mainly based on morphological descriptions, natural history observations, or simple statistics and did not account for common ancestry among species. Though most patterns were described in the context of evolutionary theory, at that time there were no tools available to quantify how specific or general these patterns were across many lineages and within an explicit evolutionary framework— that is, when considering common ancestry among lineages in statistical analyses (Felsenstein, 1985).

The end of the 20th century brought the popularization of computers, global positioning systems, and molecular sequencing techniques. With these new technologies, trait–environment correlations could be quantified using more accurate accounts of species geographical distributions (Colli-Silva et al., 2020) and the impact of shared descent on trait evolution could be considered using DNA-based phylogenies (Felsenstein, 1988; Webb and Donoghue, 2005; Webb et al., 2008) and phylogenetic comparative methods (Felsenstein, 1985; Donoghue, 1989). Some noteworthy findings of these early stages of quantitative trait–environment correlations using comparative methods include a latitudinal gradient of seed size due to a correlation with vegetation type (Moles et al., 2007), the correlation between seed and seedling morphology and degree of canopy opening (Zanne et al., 2005), and the evolution of defense traits in relation to soil variables (Fine et al., 2004). Studies of this period have typically used simple trait evolution models (Pagel 1994) or regressions of phylogenetic independent contrasts (Felsenstein, 1985) to quantify trait–environment correlations.

MODERN APPROACHES TO UNDERSTAND TRAIT–ENVIRONMENT CORRELATIONS

The use of more realistic approaches to measure trait–environment correlations were generally hampered by the lack of global data sets and new models that only became widely available and used in the last 15 years. Existing databases of DNA sequences (e.g., NCBI, 2022) and occurrence points (e.g., GBIF, 2022), newly available environmental layers (Karger et al., 2017; Brown et al., 2018), and collaborative initiatives to score massive trait data sets (e.g., Wright et al., 2004; Kattge et al., 2011; Díaz et al., 2016) have enabled the testing of many trait–environment correlation hypotheses at a global scale and in an explicitly evolutionary framework (e.g., Bruelheide et al., 2018; Moles 2018; Sinnott-Armstrong et al., 2021).

The use of data sets that are broader in taxonomic and geographic scope is important because defining principles requires generalizations that work for as many lineages as possible, and quantifying generalizations is only possible when data from many plant groups are combined in a single analytical framework. Inferences can be dubious when derived from single events (Maddison and FitzJohn, 2015), so multiple natural replicates of the same type of event are needed to understand which patterns are general and which are exceptions in plant biogeography (Figure 1C) (e.g., replicated radiations; Donoghue et al., 2022). By reconstructing large phylogenies (e.g., Zanne et al., 2014, 2018; Beaulieu and O'Meara, 2018) or using multiple phylogenies that present the same pattern of interest (e.g., Simon et al., 2009, Vasconcelos et al., 2020, 2023), a larger number of independent evolutionary transitions of the same type (e.g., multiple habitat shifts and/or multiple trait transitions) can be detected more easily.

With the need for increasing the number of independent replicates of a certain trait–environment association also comes the need for more realistic trait evolution models that can incorporate the heterogeneity of evolutionary processes across the tree of life. For example, new extensions of hidden-Markov models allow transition rates between states of a discrete trait to vary across a phylogeny (Boyko and Beaulieu, 2021, 2022), as expected when the dynamics of trait evolution differ among clades, a compelling assumption especially in larger phylogenies (Beaulieu et al., 2013). Phylogenetic regression methods that allow the error term to be modeled according to different assumptions of how continuous traits evolve (Ho and Ané, 2014) and shift detection methods that allow the parameters of continuous trait evolution models to vary across the phylogeny (Uyeda and Harmon, 2014; Khabbazian et al., 2016) also allowed for more biologically realistic pictures of continuous trait evolution. Models that jointly estimate discrete and continuous trait evolution (Tribble et al., 2021; Boyko et al., 2022) allow for traits and environmental variables to influence one another throughout evolution in cases where they are correlated. Similarly, trait-dependent biogeographical models that jointly estimate trait and range evolution (Sukumaran and Knowles, 2018; Quintero and Landis, 2020) allow dispersal parameter estimates to be conditioned on the presence of a certain trait.

ADDRESSING LIMITATIONS OF CURRENT APPROACHES

With the development of more realistic models and increasing availability of trait, distribution, and phylogenetic data sets, there are exciting ways in which trait–environment correlations can be used to understand plant biogeography. These advances were also responsible for changing the field of trait-based plant biogeography from a pure exercise of natural history to the core of modern quantitative research programs (e.g., NSF's Rules of Life initiative). However, there are many limitations in current approaches that must be tackled by

future studies that aim to quantify trait–environment correlations as the field moves forward. I highlight three of these limitations below.

First, we need to continue developing more realistic models. For instance, models that simultaneously account for the differential dynamics of speciation and extinction rates, as well as trait and environment evolution, would be more realistic because all these processes affect how traits become common in one type of environment over time (Vasconcelos et al., 2022). A key challenge in bringing realism to model development is that more realistic models tend also to be more complex—that is, with more parameters to be estimated— and then face identifiability problems (i.e., when endless parameter estimates of a model fit the data equally well; Louca and Pennell, 2020), power issues (Davis et al., 2013), and computational limitations (Maliet and Morlon, 2022). Another issue with current modeling approaches is that they frequently require data transformations that may not always be appropriate (e.g., the discretization of traits and environmental variables that are clearly continuous in nature) or the incorrect use of multivariate traits in phylogenetic comparative methods (Uyeda et al., 2015). Biology is complex, but finding the balance between reasonable questions and necessary simplifications is likely to guide best practices for both users and developers of the models.

Second, we must fill the gaps in data sets of phylogenies, traits, and distributions from poorly known groups, especially in tropical areas. Though large online databases of molecular data, geographical distribution, and traits are exceptional resources for global analyses, they tend to cover a higher proportion of the diversity of temperate regions (Figure 2; see also Collen et al., 2008; Cornwell et al., 2019) compared with other regions. The fact that data richness (Collen et al., 2008; Cornwell et al., 2019) and taxonomic accuracy (Freeman and Pennell, 2021) are still skewed toward the poles may lead to biased interpretations of results from large-scale analyses. Thus, to understand, for example, how plant lineages have moved in space over time or how they adapted to specific habitats, even if we try to include all the available data, results may be weighted for patterns in temperate habitats. Until the sampling proportion in the tropics matches that of temperate regions, efforts on understanding the role of traits on the spatial diversification of plants at a global scale will remain preliminary at best. Future studies should seek not only to advance theory and analytical methods, but also to address this fundamental lack of data. Strengthening collaborative links between researchers based in the global north and global south is likely to provide the most immediate solution for filling gaps in data sets of tropical biodiversity (e.g., BFG, 2022).
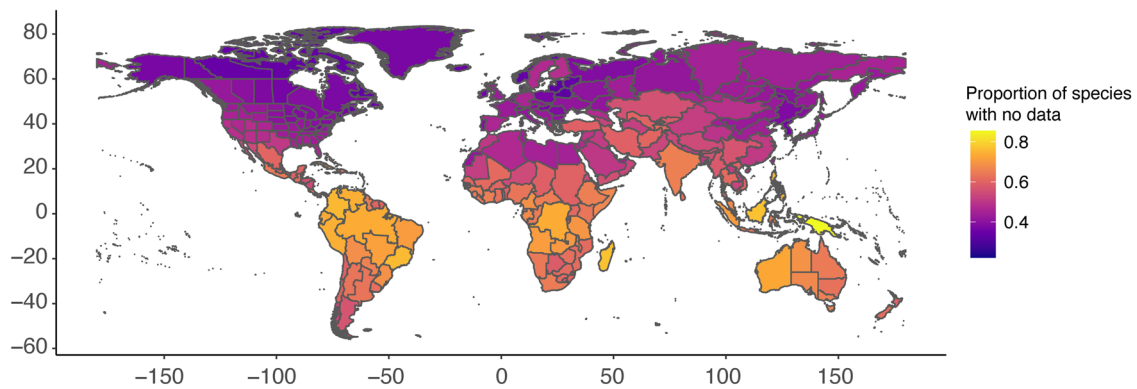
Third, we should focus on improving available data sets of phylogenies, traits, and distributions not only in quantity, but also in quality. Most of the large-scale analyses on trait–environment correlations have so far been focused on macromorphological traits that can be readily scored from herbarium collections and taxonomic descriptions or that are commonly measured from plots of forestry surveys. Though form and function are linked and macromorphology can tell us a lot about plant adaptations to their environment (e.g., Donoghue et al., 2022), traits related to seed germination (e.g., Tudela-Isanta et al., 2018), cytotype (e.g., Rice et al., 2019), belowground organs (e.g., Howard et al., 2019; Tribble et al., 2021), defensive chemicals (e.g., Hahn et al., 2019), phenology (e.g., Staggemeier et al., 2010; Fernandéz-Martínez et al., 2019), and anatomy (e.g., Alcantara et al., 2018) are also crucial to understand spatial diversification of plants, but comprehensive data sets for such traits are still scarce. To understand the role of the abiotic environment on the evolution of traits that are primarily associated with animal interactions, such as pollination or dispersal strategies, we must also have a better understanding of the spatial distributions of the pollinators and dispersers (e.g., Aguiar et al., 2020) and details of these interactions, but these data are also scant for most plant groups (see also Weber and Agrawal, 2012; Dellinger, 2020). The same is true for interactions with pathogens, soil fungi, and other inhabitants of the microbiome that also significantly interact with plants (e.g., Classen et al., 2015) but that are less studied. Much of these data can be only collected through carefully designed experiments or field observations (Sinnott-Armstrong et al., 2022) that can be expensive, risky, and time-consuming. Though often avoided by research groups, focusing on collecting data of this nature is likely to be an endeavor with high risk but high reward.
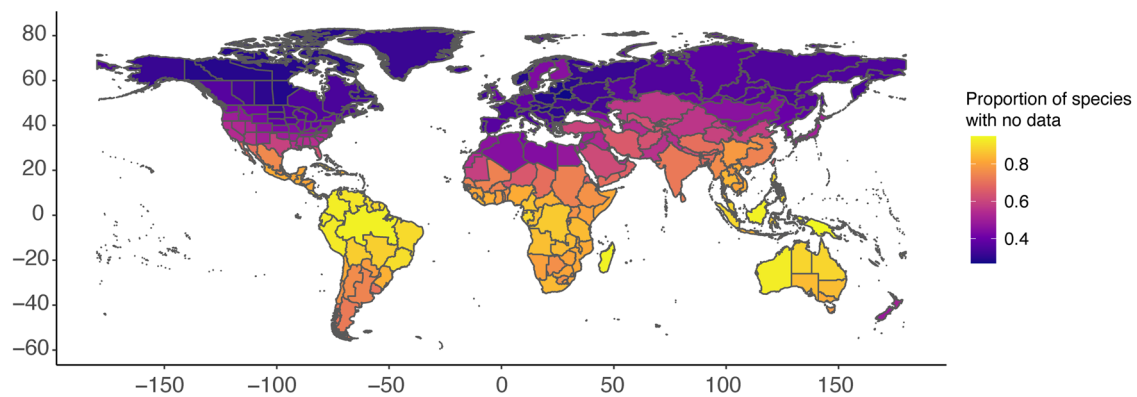
NEW BIOLOGICAL QUESTIONS AND PARADIGM SHIFTS

It is perhaps worth noting that the progress in the field discussed here seems to be mostly technical—that is, based on the development of new data sets and methods and not necessarily on a new set of biological questions. A focus on technical progress is not necessarily a bad thing. In a way, trait–environment correlation studies have always aimed to answer the simple centuries-old questions of why plants are where they are and why they look how they look. The advantage of modern approaches is that they allow a more biologically realistic picture of how correlated evolution works, and so can lead to more satisfactory answers to these questions. However, it is also possible to argue that technical developments in studies of trait–environment correlations have allowed for a completely new set of biological questions to be asked. For instance, the parameterization of some evolutionary processes in new extensions of trait evolution models have changed the way in which we investigate trait–environment correlations. One example is the recent focus on rates, that is, the number of evolutionary or biogeographical events happening in a given unit of time. Parametric measurements of rates have opened the possibility to explore questions related to the role of the environment on trait lability (e.g., Lovo et al., 2021) and the role of traits on niche conservatism and niche evolution
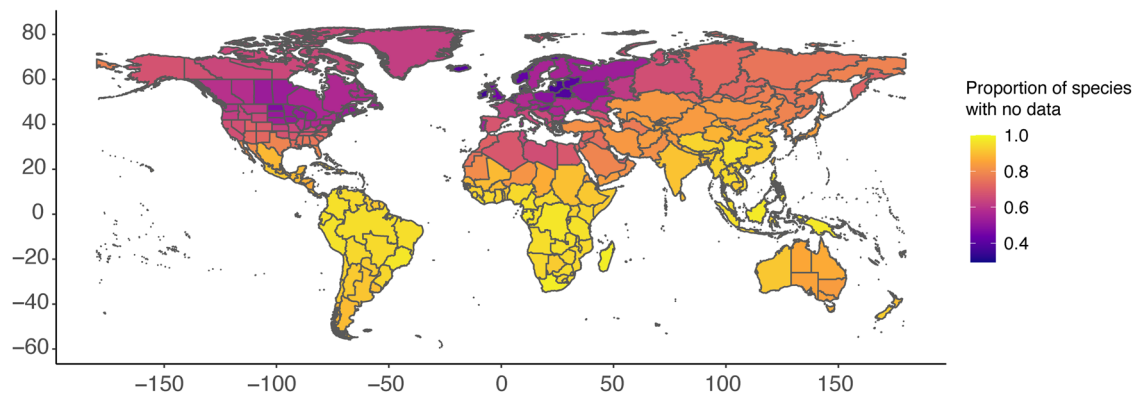
FIGURE 2 Latitudinal bias in large data sets of phylogenetic representation and traits. (A) Molecular data for phylogenetic reconstruction and (B, C) two traits commonly used in trait–environment correlation analyses: (B) ploidy and (C) seed mass. Distribution data comes from POWO (2022). Other data are from (A) Smith and Brown (2018), (B) Rice et al. (2019), and (C) Maitner et al. (2018). Code and details for plotting maps are available at github.com/tncvasconcelos/synthesis.

(e.g., Smith and Beaulieu, 2009; López-Jurado et al., 2019; Qiu et al., 2019; Baniaga et al., 2020; Vasconcelos et al., 2023) rather than merely testing for support of a trait–environment correlation. Previously established generalities are also challenged when old hypotheses are confronted with new data that often come from poorly studied groups and areas (e.g., Vasconcelos et al., 2019, 2020). Increasing the number of empirical replicates may shift paradigms in terms of rules and exceptions of how

plants diversify in space (e.g., Igea and Tanentzap, 2020; Sun et al., 2020). In that way, overcoming current limitations in both data and methods will allow the field to explore new questions and to better set apart rules and exceptions in trait-based approaches to plant biogeography.

AUTHOR CONTRIBUTIONS

T.V. was responsible for conceptualization, analyses, and writing of the manuscript.

ACKNOWLEDGMENTS

DATA AVAILABILITY STATEMENT

Data used for generating the maps in Figure 2 were retrieved from the literature cited in the legend. More details are provided at https://github.com/tncvasconcelos/synthesis.

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How to cite this article: Vasconcelos, T. 2023. A trait-based approach to determining principles of plant biogeography. *American Journal of Botany* e16127. https://doi.org/10.1002/ajb2.16127