Discovering the rules of plant biogeography using a trait-based approach

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Abstract

Lineage-specific traits determine how plants interact with their surrounding environment. As different species may find similar phenotypic solutions through evolution to tolerate, persist in and invade environments with certain characteristics, some traits may become more common in certain types of habitats. These general patterns of geographical trait distribution point towards the existence of some rules in how plants diversify in space over time. Trait-environment correlation analyses are ways to discover general rules in plant biogeography by quantifying 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 datasets 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 macro-morphology. Overcoming these limitations will allow the field to explore new questions related to trait lability and niche evolution and to better set apart rules and exceptions in how plants diversify in space over time.

Key words: environmental variables, phylogenetic comparative methods, trait evolution

Introduction: lineage specific trait as determinants of plant distribution

Lineage-specific traits control how plants interact with their physical environment and can modulate their geographical distribution in at least three different ways. First, they can allow plant lineages to survive in an environment 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 & Janson, 1985) due to photosynthesis limitations in shady habitats. Second, lineage-specific 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 in open habitats where grassing herbivores are numerous (Charles-Dominique et al., 2016) and higher diversity of chemical compounds is observed in tropical rainforests where plants are under constant pressure from pathogens (Kursar et al., 2009). Third, lineage-specific traits can increase chances of lineages to invade new environments by facilitating events of long-distance dispersal 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., 2021).

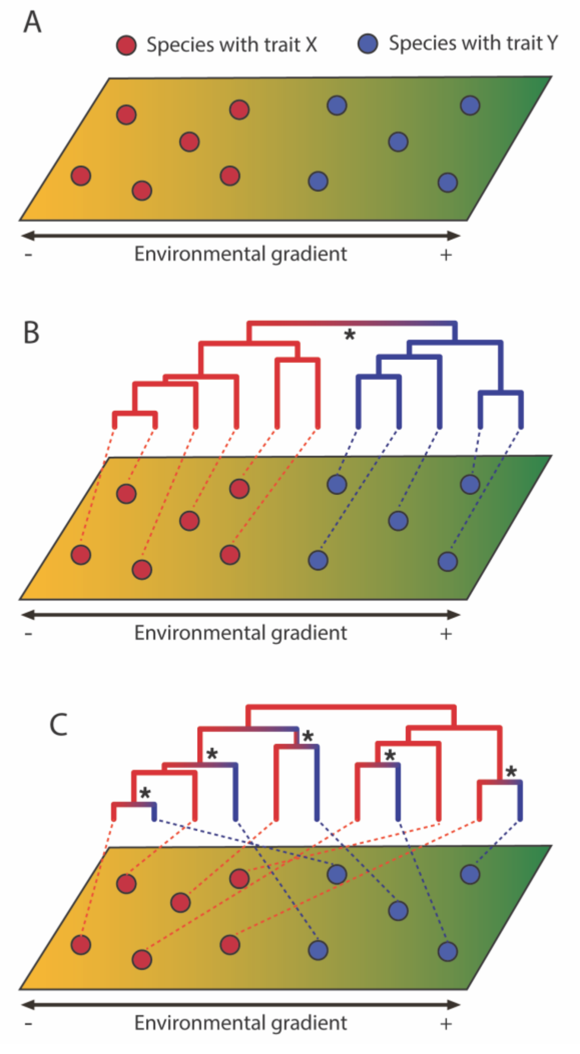

Figure 1. (A) Schematic representation of the geographical distribution of eleven species across an environmental gradient (- to +) and which present two different traits (X and Y). Each trait is more common in one of the extremes of the environmental gradient. Over evolutionary time, this pattern can be formed through: (B) common descendance of sympatric species; or (C) convergent evolutionary responses of 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 empirical replicates (marked with asterisk).

The crucial role that traits play in modulating plant distribution may lead some traits to become more common in certain types of habitats, as many different species find similar phenotypic solutions through their evolution to tolerate, persist in and invade environments with certain characteristics (Figure 1A). Similar phenotypic solutions may arise from common descent, when closely related species inherit a similar suite of beneficial traits to exist in one 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 elevation transition linked to the evolution of 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, the way in which we recognize biomes often refer to traits that are commonly found across several unrelated lineages that occur under a similar temperature and precipitation. The biome classification of “broadleaf rainforests”, for example, refer to a plant trait (“broadleaves”) that is common in warmer forests that receive a lot of rain throughout the year, and “shrublands” indicate drier or cooler areas that are dominated by a particular life form (“shrubs”). In this case, independent events of environment 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 the same component of the physical environment (such as climate, soil, and topography) point towards the existence of some general rules in how plants diversify in space over time. With modern tools, it is possible to quantify to what extent unrelated lineages have similar evolutionary responses to a given physical environment, and thus how general these general rules are, through analyses of trait-environment correlations. In this synthesis, I give a brief overview of how trait-environment correlations have been historically noted and quantified and discuss some avenues for future research based on current limitations of modern approaches.

A brief historical overview on trait-based approaches to plant biogeography

The history of observation that plant trait distribution correlate with aspects of the physical environment goes back to before the proposition of the evolutionary theory. Von Humboldt and Bonpland (1807) provided arguably the most popular account of his time on how vegetative traits respond to environmental temperature, by observing that alpine plants in tropical mountains have similar vegetative characteristics as 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 globe. In the first half of the 20th century, key further 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 proposed a categorization for life forms in plants in relation to how growing buds are protected during unfavorable seasons. In the second half of the 20th century, Stebbins (1950, 1974) contributions were remarkable for linking the physical environment not only to the convergent evolution of vegetative traits, but also reproductive traits such as flower and fruits. He suggested that the physical 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 physical environment. It is important to note that most of the trait-environment correlation hypotheses developed during this period were based mainly 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 the evolutionary theory, at that time there were no tools available to quantify how specific or general these patterns were across many lineages and in an explicit evolutionary framework – that is, when considering common ancestry among lineages in the analyses (Felsenstein, 1985).

The end of the 20th century brought the popularization of computers, the global positioning system (“GPS”) and molecular sequencing techniques. These new technologies allowed quantifying trait-environment correlations using more accurate accounts of species geographical distributions (see also Colli-Silva et al., 2020) and to consider the impact of shared descendance on trait evolution through molecular-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 measure trait-environment correlations.

Modern approaches to trait-environment correlations

The use of more realistic approaches for measuring trait-environment correlations were generally hampered by the lack of global datasets and new models that only became widely available, or popularized, in the last 15 years. Existing databases of molecular sequences (e.g. NCBI, 2022) and occurrence points (e.g. GBIF, 2022), and newly available environmental layers (Karger et al., 2017; Brown et al., 2018), as well as collaborative initiatives to score massive trait datasets (e.g. Wright et al., 2004; Kattge et al., 2011; Díaz et al., 2016), have allowed many trait-environment correlation hypotheses to be tested at a global scale and in an explicitly evolutionary framework (e.g. Moles 2018; Bruelheide et al., 2018; Sinnott-Armstrong et al., 2021). The use of broader datasets in terms of both taxonomic and geographic scope is important because defining rules requires generalizations that work for as many lineages as possible, and quantifying that 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 to understand which patterns are rules and which are exceptions multiple natural replicates of the same type of event are needed (Figure 1C) (e.g. replicated radiations; Donoghue et al., 2022). The possibility of reconstructing large phylogenies (e.g. Zanne et al., 2014, 2018; Beaulieu and O'Meara, 2018), or using multiple phylogenies that present the pattern of interest (e.g. Simon et al., 2009, Vasconcelos et al., 2020; 2021), means that an adequate number of independent evolutionary transitions of the same type (e.g. multiple habitat shifts and/or multiple transitions between trait states) can be achieved 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), which would be expected if 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 (Khabbazian et al., 2016; Uyeda and Harmon, 2014) also allowed for more biologically realistic pictures of continuous trait evolution. Similarly, models that allow for the joint evolution of discrete and continuous traits (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.

Limitations of current approaches

There are exciting ways in which trait-environment correlations can be used to understand plant biodiversity with the development of more realistic models and increasing availability of trait, distribution, and phylogenetic datasets. However, there are also many limitations in current approaches that must be tackled by future studies aiming at quantifying trait-environment correlations as the field moves forward. I highlight three of these limitations below.

First, we need to keep working on the development of 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, as all these processes affect how traits become common in one type of environment (Vasconcelos et al. 2022). A common problem in model development is that more realistic models tend also to be more complex (i.e., with more parameters to be estimated) and then face identifiability problems (Louca and Pennell, 2020), power issues (Davis et al., 2013), and computational limitations (Maliet and Morlon, 2022). Many of the current available approaches also frequently require data transformations that may not be realistic. For example, the discretization of traits and environmental variables that are clearly continuous in nature (e.g., elevation) and the lack of appropriate ways to simplify multivariate traits in an explicit phylogenetic framework (Uyeda et al., 2015). Solving these limitations will increase our flexibility in asking different types of questions due to the use of more realistic datasets and assumptions related to how correlated evolution works.

Second, we must fill the gaps in datasets 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). The fact that data richness (Collen et al., 2008; Cornwell et al., 2019) and taxonomic accuracy (Freeman and Pennell, 2021) is still skewed towards the poles may lead to biased interpretations of results from large scale analyses. This means that 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 observed in temperate habitats. Global generalities in trait-environment correlations will only be properly documented when data from the whole globe is included in the analyses (Cornwell et al., 2019). Until sampling in the tropics matches the sampling in the 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 that seek to understand these general patterns should seek not only theoretical and methodological advancement, but also in filling this fundamental lack of data from tropical regions.

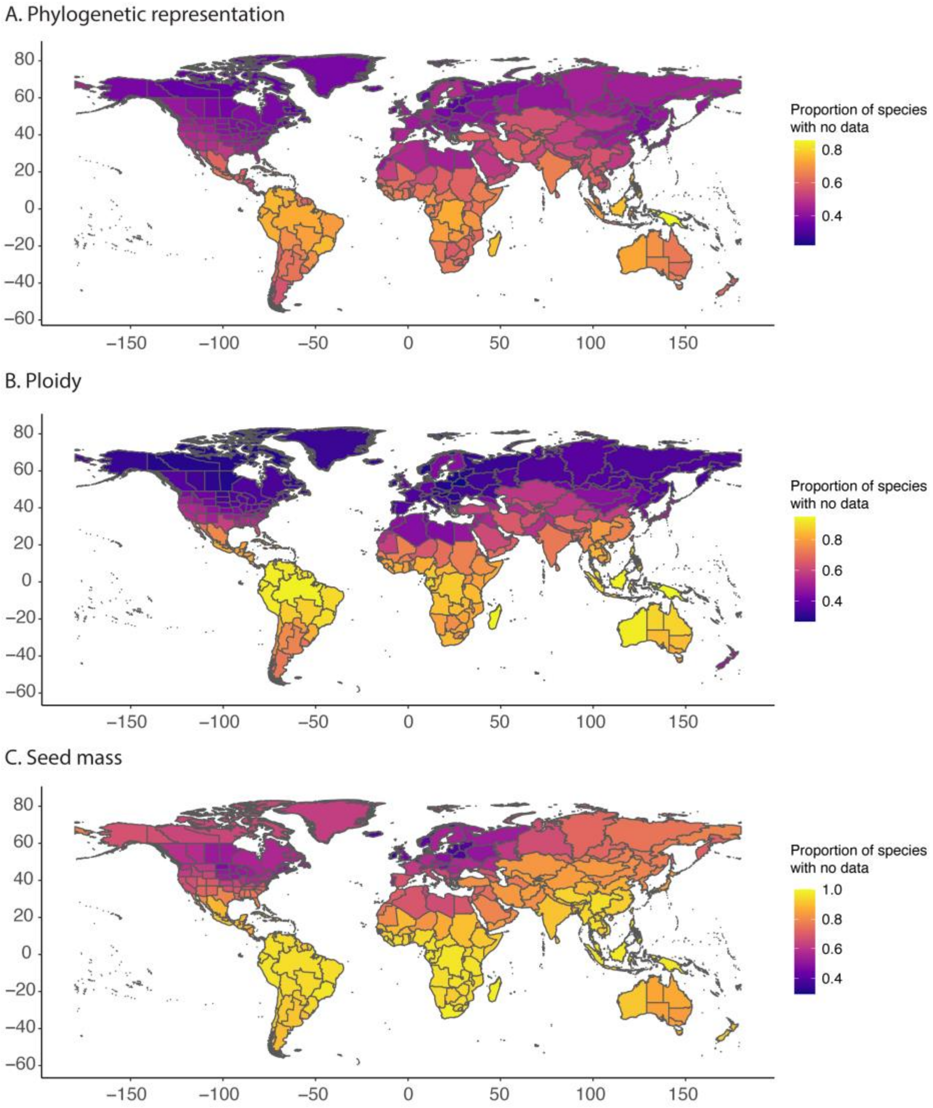

Figure 2. The latitudinal bias in large datasets of phylogenetic representation and traits. (A) Molecular data for phylogenetic reconstruction and (B,C) two traits commonly used in trait-environment correlation analyses: (B) ploidy and (C) seed mass. Distribution data comes from POWO (2022). Other data comes from, respectively, (A) Smith and Brown (2018), (B) Rice et al., (2019), and (C) Maitner et al., (2018). Code and details for plotting maps are available in github.com/tncvasconcelos/synthesis.

Third, we should focus on improving available datasets of phylogenies, traits, and distributions not only in quantity, but also in quality. Much of the large-scale analyses on trait-environment correlations has so far been focused on macro-morphological traits that can be readily scored from herbarium collections, taxonomic descriptions, or that are commonly measured from plots of forestry surveys. Though form and function are linked, and macro-morphology 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., 2020), below ground organs (e.g. Laliberté 2017; Carmona 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, and comprehensive datasets for these are still scarce. To understand the role of the physical 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 pollinator and disperser spatial distributions, as well as details of these interactions, and this data is also scant for most plant groups (see also Weber and Agrawal, 2012; Dellinger, 2020). Much of this 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, and for that reason often avoided by research groups.

New biological questions and shifts in paradigm

It is perhaps worth noting that the progress in the field discussed in here seems to be mostly technical – that is, based on the development of new datasets 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 question of "why plants are where they are and why they look how they look" that existed for centuries. 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 focus on evolutionary rates. Measuring 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 (e.g. Smith & Beaulieu, 2009; López-Jurado et al., 2019; Qiu et al., 2019; Baniaga et al., 2020; Vasconcelos et al., 2021), rather than merely testing if support for a trait-environment correlation exists or not. 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; Vasconcelos et al., 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 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.

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Data Availability Statement

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

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