Incorporating responses of functional traits to changing climates into species distribution models: A path forward

Shijia Peng[1,2*], Aaron M. Ellison[1,3], Charles C. Davis[1]

1. Department of Organismic and Evolutionary Biology, Harvard University Herbaria, Harvard University, Cambridge, MA 02138, USA.
2. Department of Earth Sciences, University of Oxford, South Parks Road, Oxford, OX1 3AN, United Kingdom.
3. Sound Solutions for Sustainable Science, Boston, MA 02135, USA.

***Authors for correspondence:**

Shijia Peng (shijia.peng1991@gmail.com)

ORCIDs

Shijia Peng: 0000-0002-3510-119X; **Aaron M. Ellison**: 0000-0003-4151-6081; **Charles C. Davis**: 0000-0001-8747-1101

Summary

Conventional species distribution models (SDMs) typically consider only abiotic factors, thus overlooking critical biotic dimensions, including functional traits that play an important role determining species' distributions in changing environments. Process-based models explicitly incorporate functional traits and have been applied to SDMs. However, their parameterization can be complex and require data that are unavailable for most species. Recently developed hierarchical trait-based models use widely available data and facilitate the incorporation of traits into SDMs at broad temporal, spatial, and taxonomic scales. Despite their promise, however, existing hierarchical trait-based models fail to accommodate changing trait spaces under different climate conditions. Here, we provide a new, simplified framework for hierarchical trait-based SDMs that integrate individuals' trait responses into forecasts of species range shifts in response to ongoing climate changes. We further discuss the utility of phylogenetic information for building trait-based SDMs and holistically enhancing our understanding of species responses to global changes. This work will contribute to an improved understanding of how traits affect species distributions along environmental and temporal gradients and facilitate the application of trait-based SDMs across large temporal, spatial and taxonomic scales.

Keywords

Functional traits, species distribution models, climate change, hierarchical models, process-based models, trait evolution, phylogeny, biodiversity.

1. Introduction

The impacts of climatic changes and human activities on species ranges have greatly increased the need to better forecast biodiversity change (Urban, 2015; Pecl *et al.*, 2017). Species distribution models (SDMs) represent arguably the most important and widespread tool for evaluating the consequences of global change on species distributions and biodiversity (e.g., Urban, 2015; Peng *et al.*, 2022; Daru & Rock, 2023; Mi *et al.*, 2023). However, despite more than two decades of using SDMs, it remains unclear whether they can accurately predict the impacts of global change on species distributions and biodiversity (Zurell *et al.*, 2009; Kissling *et al.*, 2012; Santini *et al.*, 2021). In particular, most conventional implementations of SDMs use only abiotic (environmental) factors as predictors (i.e., “conventional” SDMs). Thus, they do not account for the vast number of processes through which organisms interact with one another and the broader biota (e.g., biotic interactions, reviewed by Kissling *et al.*, 2012; species dispersal, reviewed by Bateman *et al.*, 2013; evolution, reviewed by Diamond, 2018; trait-based feedback, reviewed by Benito Garzón *et al.*, 2019).

Theoretical and empirical studies have demonstrated that functional traits play an important role in determining the current and future distributions of species and communities in the face of changing environments (e.g., Grime *et al.*, 2000; Grime, 2006; Gallagher *et al.*, 2013; Lopez-Iglesias *et al.*, 2014; Pacifici *et al.*, 2017; Maharjan *et al.*, 2021). Functional traits are characteristics of organisms that affect individual demography by influencing their growth, survival, and reproduction (Reich *et al.*, 2003; Grime, 2006; Violle *et al.*, 2007). Functional traits have been categorized as morphological (e.g., leaf size, plant height), phenological (e.g., timing of flowering), or physiological (e.g., photosynthesis rate, plant hydrology), all of which reflect adaptation to certain environments and are related to the fitness (i.e., reproduction, survival; Laughlin *et al.*, 2020). Therefore, the limited inclusion or, as in most cases, the complete lack of functional traits in conventional SDMs may hinder their ability to accurately predict the impacts of global change on species distributions (Kearney & Porter, 2009; Pollock *et al.*, 2012; Zurell *et al.*, 2016).

The concept of integrating both functional traits and environmental factors in SDMs was proposed nearly two decades ago (Westoby & Wright, 2006, Benito Garzón *et al.*, 2019). However, the use of such “trait-based” SDMs is uncommon relative to “conventional” SDMs that include only climatic and other environmental variables in defining habitat suitability. The dearth of SDMs that incorporate traits is likely related to the difficulty in selecting and measuring appropriate traits at broad spatiotemporal scales (Pollock *et al.*, 2012).

To bridge this impasse, some recent investigations have developed process-based models that explicitly incorporate links between functional traits of organisms and their environments in trait-based SDMs (Chuine & Beaubien, 2001; Kearney & Porter, 2009; Briscoe *et al.*, 2023). These process-based models improve predictions under novel conditions, but they require detailed mechanistic information about the relationships between traits, environments, and fitness that are unknown or unquantified for most species (Chuine & Beaubien, 2001; Vesk *et al.*, 2021; Peng *et al.*, 2024). Since such process-based models are difficult to parameterize, they have been applied to only a few species and provide limited insight into forecasts of biodiversity change across large spatial, temporal, and taxonomic scales.

Hierarchical trait-based models that incorporate species’ functional traits into conventional SDMs can use much more widely available data and provide a general ecological reference for how traits affect species distributions (Pollock *et al.*, 2012; Carboni *et al.*, 2018; Vesk *et al.*, 2021). Although such models are still based on correlative relationships between species occurrences and local environments, they appear to improve predictive accuracy by adding additional trait information and facilitate the application of a trait-based framework across broad scales (Pollock *et al.*, 2018). However, among trait-based SDMs, hierarchical models are used less frequently than process-based models. Importantly, existing hierarchical SDMs generally ignore intraspecific variations and fail to accommodate climate-driven intraspecific changes in trait expression, both of which may confer resilience and increase individuals’ fitness under different climate conditions.

In this review, we first summarize the development of trait-based SDMs and describe how to better integrate functional traits into SDMs using hierarchical trait-based models. We then provide new insights into how to integrate trait-climate relationships into existing hierarchical trait-based models to incorporate intraspecific changes in the expression of functional traits resulting from spatial and temporal shifts in abiotic conditions (Fig. 1). We also briefly discuss how phylogenetic information that accounts for evolutionary relatedness can be integrated into hierarchical trait-based frameworks. The motivation for our review builds on a recent effort to integrate plant phenological responses to climate into hierarchical SDMs and better forecast biodiversity change at large spatial, temporal, and taxonomic extents (Peng *et al.*, 2024). We made comparisons between predictions from our newly developed hierarchical framework and those from the more traditional hierarchical models proposed by Pollock *et al.* (2012). Unlike the recent review by Benito Garzón *et al.* (2019), who aimed to separate local adaptation from phenotypic plasticity using data from an extensive common-garden network, our review provides a more general direction for ecological inference into how functional traits affect species distributions, and for forecasting them in target regions as a function of changing environmental conditions.

2. An historical account of SDMs: inferring the ecological niche and forecasting biodiversity

The theoretical underpinning of SDMs is rooted in the concept of the "ecological niche." The ecological niche has been defined in many ways; in the context of SDMs, it is described as a hypervolume in multivariate environmental space (*sensu* Grinnell, 1917; Hutchinson, 1957; Grime, 2006). Indeed, SDMs are also called ecological niche models. The implementation of conventional SDMs can be divided into two sequential processes: first, model habitat suitability (based on sparse species occurrence data) that is assumed to reflect a species' environmental niche; second, estimate species' current distribution and forecast their future geographic occurrence of suitable habitats as a function of climate-change (or land-cover change) scenarios, which are then presumed to be occupied by the species in the future (Kearney & Porter, 2009). Thus, what we herein call "conventional"

SDMs use only a species' multi-dimensional environmental (usually climatic, i.e., abiotic) niche.

Conventional SDMs assume that species distributions are in equilibrium with environmental conditions (Guisan & Thuiller, 2005) and that a species will occur whenever and wherever its environmental niche exists at a specific location. In fact, many species distributions are out of equilibrium with environmental conditions, and limited dispersal ability of species or competitive exclusion among species may exacerbate this disequilibrium under future global changes (Loarie *et al.*, 2009; Pagel & Schurr, 2012). Therefore, biotic niche axes (e.g., axes related to competitive interactions or prey size) also may affect species' responses to changing environments and thus contribute to this observed disequilibrium when using abiotic factors alone (e.g., Fordham *et al.*, 2018).

Another simplifying assumption of conventional SDMs is that all individuals and populations within a species are identical and will respond equivalently to changing environmental conditions. In fact, species' functional traits are neither static nor homogenous in space or time (Bolnick *et al.*, 2011; Violle *et al.*, 2014). It is well documented that all species exhibit important phenotypic differences in phenological, anatomical, morphological, and physiological functional traits among individuals along environmental gradients (i.e., structured variation; Hulshof *et al.*, 2013; Anderegg, 2015), and even within sex, size and age (i.e., unstructured variation). Globally, intraspecific variation accounts for about 25% of the total trait variation within communities and 32% of the total trait variation among communities (Siefert *et al.*, 2015). Intraspecific variation may be the result of heritable differences between individuals (i.e., local adaptation) or phenotypic plasticity in trait values (Donohue *et al.*, 2005; Willis *et al.*, 2008; Valladares *et al.*, 2014; Pritzkow *et al.*, 2020; Cope *et al.*, 2021). Phenotypic plasticity represents the ability of a single genotype to express different phenotypes under different environmental conditions (Nicotra *et al.*, 2010; Gianoli & Valladares, 2012), whereas local adaptation refers to the processes by which a population has heritable traits that lead to a predominance of individuals with high fitness within their local environment (Savolainen *et al.*, 2013). Phenotypic plasticity and local adaptation are ubiquitous and may enable persistence (i.e., avoid migration and local extinction) of individuals in the face of climate change (Valladares *et al.*, 2014; reviewed by Benito Garzón *et al.*, 2019). Thus, the responses of populations to climate change are likely to vary across the geographic and temporal range of a species (Sultan & Spencer, 2002; Benito Garzón *et al.*, 2013; Park *et al.*, 2019; Ramirez-Parada *et al.*, 2024). However, conventional SDMs do not include the potential for evolution of fitness-related traits or plasticity that may accompany strong local environmental variation.

Many recent studies have attempted to integrate intraspecific trait variation into SDMs (Table 1; Chardon *et al.*, 2020). For example, O'Neill *et al.* (2008) suggested that the differential growth responses of *Pinus contorta* associated with genetic differences among populations would redistribute the species' forecasted habitats. Similarly, Benito Garzón *et al.* (2013) integrated intraspecific variation into tree mortality into SDMs, and Oney *et al.* (2013) demonstrated that intraspecific variation could buffer against adverse effects of climatic change. Finally, Chuine & Beaubien (2001) included phenological response to climate in their PHENOFIT model and concluded that phenology is a major determinant of plant species ranges and should be used to assess the consequences of global change on plant distributions.

The trait-based SDMs outlined above are more biologically realistic than conventional ones, and we assert that the former are likely to provide more realistic estimates of species responses to novel climates. However, these trait-based SDMs have two key limitations. First, they still rely only on intraspecific distribution data (e.g., model each of subspecies independently; Oney *et al.*, 2013), not data on phenotypic traits or plasticity itself (Valladares *et al.*, 2014). Second, SDMs that explicitly incorporate functional traits such as climate-dependent phenology (Chuine & Beaubien, 2001; Morin *et al.*, 2009), physiology, or biophysics (Kearney &Warren, 2009; Higgins *et al.*, 2012) are limited in their generality across taxa, space, and a range of traits (Peng *et al.*, 2024). Specifically, parameterizing such trait-based SDMs requires detailed experimental data to calibrate, validate, and understand the underlying casual process among fitness, traits, and environments, and such data are generally not available for most species (Kearney & Warren, 2009; Vesk *et al.*, 2021).

Hierarchical trait-based SDMs could statistically integrate environmental conditions and traits that shape species distributions. Hierarchical trait-based SDMs still include simplified and poorly understood assumptions, but they can use much more widely available data and provide a stronger framework, facilitating the application of trait-based SDMs across broad spatial and taxonomic scales, and deepening our understanding of mechanisms of how traits modulate species' distributions along environmental gradients (Pollock *et al.*, 2012; Vesk *et al.*, 2021). Moreover, hierarchical SDMs overcome the limitations of process-based models that require accurate estimation of plasticity (or adaptation) and well-designed and time-consuming experiments to parameterize them (Kellermann *et al.*, 2012). Although there continues to be a tremendous need for better experimentally-derived estimates of adaptation and plasticity, the species-by-species approach required for such carefully planned experimentation makes scalability a challenge. Thus, better heuristic methods are warranted for more rapid and biologically meaningful forecasts of future species distributions.

3. Hierarchical trait-based framework: expanding conventional SDMs to include functional traits

Hierarchical trait-based SDMs incorporate parameters that account for the responses of multiple species to their environments by sharing statistical strength between species and allowing functional traits to modulate species responses to different environments (Gelfand *et al.*, 2005; Dorrough & Scroggie, 2008). Unlike conventional SDMs that model species separately, hierarchical trait-based models use a single predictive model for species-specific data of many species across communities. For example, generalized linear mixed models (GLMMs; Jamil *et al.*, 2013) can include a hierarchical structure that defines interactions between traits and the environments. Pollock *et al.* (2012) proposed a single coherent framework for trait-based SDMs that integrates a hierarchical structure into a

GLMM to better accomplish the goal of integrating environmental factors and biotically relevant traits.

In general, the single-step hierarchical trait-based model proposed by Pollock *et al.* (2012) (i.e., herein we call "traditional hierarchical SDMs") can be split into two sections. The first is the relationship between species distribution and climate variables. The second links the parameters of species distribution-climate relationships to relevant functional traits (details in Box 1). In this model, trait × environment interactions are treated as fixed effects while species identity is included as a random component to explore species-specific responses. Hierarchical trait-based SDMs typically do not include traits as main-level effects because the hierarchical framework does not expect traits to influence the overall probability of occurrence of species. Rather, the assumption is that traits can modulate species occurrence along different environmental gradients (Fig. 2).

Most studies that used traditional hierarchical SDMs have explored how functional traits influence species distributions along environmental gradients (e.g., Jamil *et al.*, 2013; Brown *et al.*, 2014; Pollock *et al.*, 2018; Miller *et al.*, 2019). Pollock *et al.* (2012), for example, found that species with low specific leaf area (SLA) were more likely to occur in sandy areas with high rock cover, whereas heavier seeded species have a higher probability of occurrence in sandy soils. Similarly, Carboni *et al.* (2018) built a multispecies hierarchical model including the distribution of 10 non-native species in French grasslands and identified that tall non-native species with high SLA were more efficient in resource-rich environments and better at avoiding competition from native species. Such models contain biologically relevant information on links between species and modeled environments and help to establish the role of traits and improve the predictive accuracy of SDMs (Vesk *et al.*, 2021).

Nevertheless, hierarchical trait-based SDMs are rarely used to forecast future species distributions. Moreover, direct comparisons between forecasts from hierarchical trait-based models and those from conventional SDMs under current and future climate scenarios remain scarce (but *see* Peng *et al.*, 2024). This may be attributed to the fact that the trait values of individuals under future conditions are difficult to determine. A major challenge in hierarchical trait-based framework is how to apply SDMs that incorporate traits whose adaptive or plastic responses can be modeled directly as a function of future projected climate change and account for how traits may change through time in a given geographic and environmental context.

Existing SDMs that have incorporated functional traits always assume that individual traits are constant through time (e.g., Gallagher *et al.*, 2013). However, functional traits of individuals should not be considered fixed. Many common fitness-related functional traits, such as plant phenology (Chunie & Beaubien, 2001), seed size (Stanton, 1984), and photosynthetic rates (Athanasiou *et al.*, 2010), are sensitive to environmental fluctuations and can acclimate rapidly or evolve in response to climate change (Benito Garzón *et al.*, 2019; Catullo *et al.*, 2019). Changes in trait space in response to climate change are likely to have significant effects on expected (or modeled) future species distributions. Therefore, the problem of species distributional limits is not only an ecological issue but may also be an evolutionary one, particularly in the context of novel climates (Hoffmann & Blows, 1994; Kearney & Porter, 2009; Colautti & Barrett, 2013). Some mechanistic trait-based SDMs (e.g., Valladares *et al.*, 2014) allow trait values to change as a function of a changing climate based on independently evaluated reaction norms (i.e., the patterns of phenotypic expression of a single genotype across a range of environmental conditions) and geographical variation (i.e., a space for time substitution). The former needs to be better parameterized to encompass the range of variation in populations across a species’ range and to disentangle different sources of trait variation (e.g., adaptative and plastic effects; Benito Garzón *et al.*, 2019). In contrast, it is difficult to split the phenotypic variation of functional traits in the latter model type into the components of phenotypic plasticity and local adaptation. Nevertheless, space-for-time substitutions could implicitly include geographical (i.e., population-level) variations in functional traits and theoretically can include any biological traits associated with species distributions while maintaining the statistical simplicity of hierarchical trait-based SDMs under the premise of not aiming to differentiate trait variation sources.

4. Functional traits in a changing world: the application of next-generation hierarchical trait-based SDMs that integrate trait-climate relationships

As climate changes, populations can i.) persist *in situ* via phenotypic plasticity and local adaptation, ii.) track climate by migrating, or iii.) become locally extinct (Brito-Morales *et al.*, 2018). Plasticity and adaptation allow species to persist *in situ* because this may allow them to expand their climatic tolerance beyond their present realized niches (Valladares *et al.*, 2014; Des Roches *et al.*, 2018), although phenotypic plasticity also can delay evolutionary adaptation to new environments in the long term (Wund, 2012). Because of plasticity and adaptation, trait values observed under current conditions may not be fully representative of those that will occur in the future. Ignoring continuous trait variation in models may lead to incorrect assessments of species' responses to climate. A better understanding of the extent to which traits vary within species and across environmental gradients will improve our ability to anticipate how these processes will affect species performances as a function of future climatic change.

4.1 Modeling trait-climate relationships under different climate space

Geographic patterns in plant functional traits and their relationships with the environment is a central topic in plant ecology (Reich *et al.*, 2003; Grime, 2006; Bruelheide *et al.*, 2018). It is abundantly clear that environmental factors are essential in determining the distribution of individuals' functional traits and provide essential information necessary to infer trait values in regions with no available data. Numerous observational studies have documented quantitative relationships between functional traits and climate (Werger & Ellenbroek, 1978; Wright *et al.*, 2004; Cornwell & Ackerly, 2009). For example, Wright *et al.* (2017) characterized global patterns in leaf size and supported the well-known natural-history lore that large-leaved species dominate sunny, wet, and hot environments, whereas small-leaved species dominate in arid areas. Li *et al.* (2016) mapped the patterns of leaf-margin traits in China and suggested that the relationships between the percentage of various leaf-margin types and temperature were significantly enhanced with increasing precipitation.

Many algorithms based on the geographic variation of traits can be used to quantify trait-climate relationships. These algorithms include community abundance-weighted means (CWMs), linear models (LMs), generalized linear models (GLMs) and generalized additive models (GAMs), linear/generalized linear mixed effect models (LMMs/GLMMs), and machine-learning approaches. CWMs are only applicable at the community level, but others also can be applied at the individual level. LMs and GLMs are the simplest ones, but GLMs allow for non-normal distribution of model errors. GAMs are more flexible and allow for non-linear relationships using smoothing functions. Machine-learning approaches are more flexible and offer powerful tools for modeling complex and non-linear relationships between traits and climate variables (Cutler *et al.*, 2007; Sandel *et al.*, 2021). They can incorporate large datasets and many predictors. However, machine-learning models have not been used as widely as other familiar statistical models. Generalized linear mixed-effect models (GLMMs) are the most widely used because of their flexibility and ability to account for both fixed and random effects (i.e., parameters associated with specific groups such as species). The general form of a GLMM describing the relationship between traits and environmental drivers is:

$$T_1 = a_0 + b_1 x_1 + b_2 x_2 + b_3 x_3 + \cdots + b_n x_n + \beta + \delta + \varepsilon \qquad (1)$$

where T_1 is the individual's value for a certain functional trait, a_0 represents the intercept, $b_1, b_2, b_3, \dots, b_n$ are coefficients of the regression, $x_1, x_2, x_3, \dots, x_n$ represent the fixed variables (and their interactions) that may affect trait variations (e.g., climatic variables, life forms), β refers to a matrix of covariates that should be included if needed, δ is the (matrix of) random effect(s), and ε is the model error. Equation 1 allows us to incorporate many species simultaneously and to quantify trait variation across time and space.

Trait-climate relationships can be then used to generate spatial projections of trait variation under current and future climate scenarios. Many studies have suggested that the functional compositions of plants would change considerably under rapid climate change (e.g., Post *et al.*, 2009). For example, long-term monitoring has demonstrated an increase in plant height in response to climate warming in the tundra over a 30-year period (Bjorkman *et al.*, 2018). Climate warming also may lead to an increase in leaf size if sufficient moisture and nutrients are available (Bjorkman *et al.*, 2018). However, projections based on microclimate may differ from those based on coarse-resolution macroclimatic and soil data. For instance, soil moisture can decrease the variability of local temperatures (Aalto *et al.*, 2018), which may be one of the mechanisms by which soil moisture affects the direction and strength of trait-temperature relationships. Because the resolution of existing databases (e.g., WorldClim) used for future climate projections is relatively coarse (e.g., at least 1 km), studies using macroclimatic data are likely to project only a relatively small proportion of the variation in functional traits. As more trait data become available through global databases (e.g., TRY; Kattge *et al.*, 2011), there is an urgent need to better quantify and model microclimate to greatly improve assessments of trait-climate relationships and enable more accurate projections of individuals' traits across different biomes (Lembrechts *et al.*, 2019).

4.2 Constructing hierarchical trait-based SDMs using predicted trait values to predict current species distributions and forecast them into the future

Trait values estimated under different climate spaces are substituted into the hierarchical SDMs (Equations A1-A4 in Box1) to predict and forecast the probability of occurrence of individuals under current and future environmental conditions. Incorporating trait-climate relationships into traditional hierarchical trait-based model may improve model predictions and forecasts. However, it is normally not possible to assess model forecasts because the scenarios being projected have not yet occurred (Arau´jo & Guisan, 2006). Alternatives such as backward projections (i.e., hind-casting) can be used for model validation. This approach encourages us to predict trait values and resulting species distributions under past climate scenarios and compare them with historical records and fossil occurrences (Peng *et al.*, 2024).

Traditional hierarchical SDMs also assume linearity and may ignore niche concepts that assume unimodality (Hutchinson, 1957). Adding polynomial terms to a hierarchical model would allow for curvilinear responses and better reflect real ecological phenomena, yet such models are less general and require more data (Austin & Meyers, 1996). GLMMs remain useful and are applicable to various types of datasets. Moreover, since statistical models of trait-climate relationships based solely on geographical variation in functional traits cannot differentiate between phenotypic plasticity and local adaptation, disentangling the contributions of different sources of trait variation to species distributions using hierarchical framework is still challenging. Large common-garden and reciprocal-transplant experiments established along broad environmental gradients are needed to provide new insights into assessing changes in the distributional range of individuals due to climate change (Rehfeldt *et al.*, 1999; Robson *et al.*, 2018; Benito Garzón *et al.*, 2019).

5. A comparison between newly developed and traditional hierarchical trait-based SDMs: A case study of plant reproductive phenology

Using over 120,000 herbarium specimens, Peng *et al.* (2024) developed a novel framework that considers both intraspecific variability in a functional trait and its dynamic responses under different climate space. They compared the predictions and forecasts of traditional hierarchical trait-based SDMs proposed by Pollock *et al.* (2012) with those of the hierarchical trait-based framework that integrates trait-climate relationships as a function of current and future climate scenarios (Shared Socio-economic Pathway 5-8.5 [SSP 5-8.5]) for 360 species in the eastern United States. Plant phenology was adopted as an example of a climate-sensitive trait that is also an important component of fitness (Reekie & Bazzaz, 1987; Kozlowski, 1992) and may contribute to changes in species distribution and abundance (Primack, 1980; O’Neil, 1997; Chuine & Beaubien, 2001; Willis *et al.*, 2008).

Peng *et al.* (2024) explored how plant phenology (e.g., the day of year of peak flowering time) mediates observed species geographic distributions along environmental gradients and affects regional biodiversity patterns under future climatic change scenarios. The results demonstrated that traditional and newer hierarchical trait-based SDMs yielded similar estimates of current ranges but significantly different estimates of future ones. Specifically, hierarchical trait-based SDMs that consider trait evolution under changing climates forecast a higher probability of occurrence in areas within the current range and a lower probability of occurrence in areas located outside their current range than did traditional hierarchical SDMs (Fig. 3). The differences between forecasts of traditional versus newly developed hierarchical trait-based SDMs can be interpreted either as resulting from strong phenotypic plasticity or local adaptation (Richardson *et al.*, 2017; Ramirez-Parada *et al.*, 2024), both of which could enable species to adjust their climatic niche and to persist *in situ*. Importantly, this example illustrates that trait-based SDMs, which accommodate changing trait spaces under different climate conditions, may provide more conservative predictions and less alarming results about the influences of future climate change on species range loss.

6. Phylogenetic species distribution models

Three ecological factors determine which species can occur within communities: the dispersal ability of species to enter the community, their environmental tolerance, and their biological interactions with other species. These three factors depend on functional traits that reflect evolutionary history and biogeographic processes (Warren *et al.*, 2014; Gerhold *et al.*, 2018). Phylogenetic niche conservatism refers to the tendency of closely related species to be more similar to one another in terms of their ecological niches (Prinzing, 2001; Wiens & Donoghue, 2004; Wiens & Graham, 2005), and phylogenetically related species normally have similar trait values (e.g., *see* Davis *et al.*, 2010a; Davis *et al.*, 2010b; Li *et al.*, 2016; Li *et al.*, 2020). Therefore, incorporating phylogeny into SDMs should be fully considered, for both biological and statistical reasons.

Biologically, owing to the varying phylogenetic history of different clades, some groups may be able to easily shift out of their niche space in the face of anthropogenetic climate change whereas others may not (Davis *et al.*, 2010a; Davis *et al.*, 2010b). If losses are not randomly distributed across the Tree of Life, climate change may lead to a disproportionate loss of evolutionary history (Nee & May, 1997; Heard & Mooers, 2000; Ceballos & Ehrlich, 2023); examples include the loss of species in various flowering plant clades in New England, USA (Willis *et al.*, 2008), the reduction of *Rhododendron* from the Himalaya-Hengduan Mountain (Kumar, 2012), and the loss of Dipterocarpaceae from southeastern Asian forests (Shukla *et al.*, 2013). Accordingly, any SDM, but especially trait-based SDMs, should fully incorporate phylogenetic information to examine whether responses to climate change or probabilities of occurrence as a function of climate change differ among clades. For example, if functional traits are shared by species within a specific clade that also inhabits a particular habitat or climatic space (e.g., shifts in staggered pollination among Dipterocarpaceae in Southeast Asian wet forests [Ashton *et al.*, 1988]), climate change could affect the entire clade similarly.

Statistically, if multiple functional traits affect species occurrence (or abundance), the unmeasured traits with significant phylogenetical signals (Harvey & Pagel, 1991; Blomberg *et al.*, 2003) would result in covariance of unexplained residual variations, leading to inaccurate estimation and inflated Type-I errors when testing the significance of regression coefficients (Garland *et al.*, 2005; Revell, 2010). Existing trait-based SDMs (including both process-based SDMs and hierarchical SDMs) generally ignore the evolutionary history of species and we should seek to better specify independent variables in hierarchical models to improve the predictions of species distributions while reducing the amount of unexplained variance in the model.

Despite the well-known importance of incorporating phylogeny into SDMs, analyses applying phylogenetic generalized linear mixed models (PGLMMs) only use a phylogenetic “correction” (Ives & Helmus, 2011; Gallinat & Pearse, 2021). Compared to common linear model, PGLMMs also include a phylogenetic matrix as a random component (details in Box 2). Although PGLMMs reduce overfitting and bring the Type-I error rate to an acceptable level, they do not help us identify which clade(s) may respond similarly to climate and climatic change. How to do this effectively within the PGLMM framework remains an open question for future research.

7. Summary

Functional traits in large part determine species distributions. Compared to conventional SDMs, trait-based SDMs can better reveal how functional traits mediate geographic distributions of species along environmental gradients and how the resulting regional biodiversity patterns will change as the climate continues to change. Hierarchical trait-based SDMs overcome limitations of process-based models that require fine-scale, species-by-species parameterization of plasticity or adaptation determined empirically and experimentally. Hierarchical trait-based SDMs also can extend the use of trait-based SDMs across very large spatial, temporal, and taxonomic extents.

There are two critical points that need to be accounted for when using hierarchical trait-based SDMs, and that motivated this review. First, individual traits are not fixed parameters. Rather, they change through time and space as populations acclimate and adapt to changing environmental conditions. Therefore, trait variation must be modelled explicitly for different climatic spaces using trait-environment regressions whose parameters are then incorporated in trait-based SDMs. Second, functional traits are likely to be shared among related species, but these traits may not have been measured for all related taxa. Such unmeasured traits strongly affect the covariation of residuals, which may in turn affect the estimation and tests of the significance of regression coefficients. Therefore, hierarchical trait-based SDMs must, at a minimum, explicitly incorporate phylogenetic relationships among species as a random component, minimally to avoid overfitting and inflated Type-I error rates. Phylogenetic generalized linear mixed models are useful for assessing whether the results are affected by phylogeny, but they do not yet allow us to identify clade-specific patterns. Future models should be developed to better identify specific clades, and ultimately the biomes that harbor them, at particular risk of being imperiled.

Finally, whether process-based or hierarchical, trait-based SDMs so far have used only a small number of functional traits. More fitness-related traits should be measured and incorporated in future SDMs. International efforts to establish and promote interoperable trait databases will, if successful, enable us to examine long-term changes by multiple species traits and the resulting changes in biodiversity pattern at large spatial and taxonomic scales.

Author Contributions

SP proposed the initial idea for the study with subsequent development by CCD and AME. SP drafted the first version of the manuscript, and all authors contributed significantly to subsequent revisions.

Conflict of interest statement

The authors do not have any conflict of interest to report.

Acknowledgements

This study was supported by National Science Foundation grants DEB2105903 and DEB1754584.

References

Aalto J, Karjalainen O, Hjort J, Luoto M. 2018. Statistical Forecasting of Current and Future Circum-Arctic Ground Temperatures and Active Layer Thickness. *Geophysical Research Letters* **45**: 4889-4898.

Anderegg WRL. 2015. Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. *New Phytologist* **205**: 10081014.

Araújo MB, Guisan A. 2006. Five (or so) challenges for species distribution modelling. *Journal of Biogeography* **33**: 1677-1688.

Ashton PS, Givnish YJ, Appanah S. 1988. Staggered floweringin the Dipterocarpaceae: New insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *American Naturalist* **132**: 44-46.

Athanasiou K, Dyson BC, Webster RE, Johnson GN. 2010. Dynamic Acclimation of Photosynthesis Increases Plant Fitness in Changing Environments. *Plant Physiology* **152**: 366-373.

Austin MP, Meyers JA. 1996. Current approach to modelling the environmental niche of eucalypts: implication for management of forecast biodiversity. *Forest Ecology and Management* **85**: 95-106.

Bateman BL, Murphy HT, Reside AE, Mokany K, VanDerWal J. 2013. Appropriateness of full-, partial- and no-dispersal scenarios in climate change impact modelling. *Diversity and Distributions* **19**: 1224-1234.

Benito-Garzón M, Ruiz-Benito P, Zavala, MA. 2013. Interspecific differences in tree growth and mortality responses to environmental drivers determine potential species distributional limits in Iberian forests. *Global Ecology and Biogeography* **22**: 1141-1151.

Benito Garzón M, Robson TM, Hampe A. 2019. ΔTraitSDMs: species distribution models that account for local adaptation and phenotypic plasticity. *New Phytologist* **222**: 1757-1765.

Bjorkman AD, Myers-Smith IH, Elmendorf SC, Rüger N, Beck PSA, Blach-Overgaard A, Blok

D, Cornelissen JHC, Forbes BC, Georges D *et al*. 2018. Plant functional trait change across a warming tundra biome. *Nature* **562**: 57-62.

Blomberg SP, Garland Jr T, Ives AR. 2003. Testing for phylogenetic signal in comparative data:behavioral traits are more labile. Evolution **57**: 717-745.

Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM, Novak M, Rudolf VHW, Schreiber SJ, Urban MC, Vasseur DA. 2011. Why intraspecific trait variation matters in community ecology? *Trends in Ecology and Evolution* **26**: 183-192.

Briscoe NJ, Morris SD, Mathewson PD, Buckley LB, Jusup M, Levy O, Maclean IMD, Princebourde S, Riddell EA, Robert JA *et al*. 2023. Mechanistic forecasts of species responses to climate change: The promise of biophysical ecology. *Global Change Biology* **29**: 1451-1470.

Brito-Morales I, García Molinos J, Schoeman DS, Burrows MT, Poloczanska ES, Brown CJ, Ferrier S, Harwood TD, Klein CJ, McDonald-Madden E *et al*. 2018. Climate Velocity Can Inform Conservation in a Warming World. *Trends in Ecology and Evolution* **33**: 441-457.

Brown AM, Warton DI, Andrew NR, Binns M, Cassis G, Gibb H. 2014. The fourth-corner solution – using predictive models to understand how species traits interact with the environment. *Methods in Ecology and Evolution* **5**: 344-352.

Bruelheide H, Dengler J, Purschke O, Lenoir J, Jiménez-Alfaro B, Hennekens SM, Botta-Dukát Z, Chytrý M, Field R, Jansen F *et al*. 2018. Global trait–environment relationships of plant communities. *Nature Ecology and Evolution* **2**: 1906-1917.

Carboni M, Calderon-Sanou I, Pollock L, Violle C, DivGrass C, Thuiller W. 2018. Functional traits modulate the response of alien plants along abiotic and biotic gradients. *Global Ecology and Biogeography* **27**: 1173-1185.

Catullo RA, Llewelyn J, Phillips BL, Moritz CC. 2019. The potential for rapid evolution under anthropogenic climate change. *Current Biology* **29**: R996-R1007.

Ceballos G, Ehrlich PR. 2023. Mutilation of the tree of life via mass extinction of animal genera. *Proceedings of the National Academy of Sciences, USA* **120**: e2306987120.

Chardon NI, Pironon S, Peterson ML, Doak DF. 2020. Incorporating intraspecific variation into species distribution models improves distribution predictions, but cannot predict species traits for a wide-spread plant species. *Ecography* **43**: 60-74.

Chuine I, Beaubien EG. 2001. Phenology is a major determinant of tree species range. *Ecology Letters* **4**: 500-510.

Colautti R, Barrett SCH. 2013. Rapid adaptation to climate facilitates range expansion of an invasive plant. *Science* **342**: 364-366.

Cope OL, Lindroth RL, Helm A, Keefover-Ring K, Kruger EL. 2021. Trait plasticity and trade-offs shape intra-specific variation in competitive response in a foundation tree species. *New Phytologist* **230**: 710-719.

Cornwell WK, Ackerly DD. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. *Ecological Monograph* **79**: 109-126.

Culter DR, Edwards Jr TC, Beard KH, Cutler A, Hess KT, Gibson J, Lawler JJ. 2007. Random forests for classification in ecology. *Ecology* **88**: 2783-2792.

Daru BH, Rock BM. 2023. Reorganization of seagrass communities in a changing climate. – *Nature Plants* **9**: 1034-1043.

Davis CC, Edwards EJ, Donoghue MJ. 2010. A clade-eye view of global climate change. In M. A. Bell, D. J. Futuyma, W. F. Eanes & J. S. Levinton (Eds.), Evolution since Darwin: The first 150 years (pp. 623-627). Sunderland, Massachusetts: Sinauer.

Davis CC, Willis CG, Primack RB, Miller-Rushing AJ. 2010. The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**: 3201-3213.

Des Roches S, Post DM, Turley NE, Bailey JK, Hendry AP, Kinnison MT, Schweitzer JA, Palkovacs EP. 2018. The ecological importance of intraspecific variation. *Nature Ecology and Evolution* **2**: 57-64.

Diamond SE. 2018. Contemporary climate-driven range shifts: Putting evolution back on the table. *Functional Ecology* **32**: 1652-1665.

Donohue K. 2005. Niche construction through phenological plasticity: life history dynamics and ecological consequences. *New Phytologist* **166**: 83-92.

Dorrough J, Scroggie MP. 2008. Plant responses to agricultural intensification. *Journal of Applied Ecology* **45**: 1274-1283.

Fordham DA, Bertelsmeier C, Brook BW, Early R, Neto D, Brown SC, Ollier S, Araújo MB. 2018. How complex should models be? Comparing correlative and mechanistic range dynamics models. *Global Change Biology* **24**: 1357-1370.

Gallagher RV, Hughes L, Leishman MR. 2013. Species loss and gain in communities under future climate change: consequences for functional diversity. *Ecography* **36**: 531-540.

Gallinat AS, Pearse WD. 2021. Phylogenetic generalized linear mixed modeling presents novel opportunities for eco-evolutionary synthesis. *Oikos* **130**: 669-679.

Garland T, Bennett AF, Rezende EL. 2005. Phylogenetic approaches in comparative physiology. *Journal of Experimental Biology* **208**: 3015-3035.

Gelfand AE, Schmidt AM, Wu S, Silander Jr JA, Latimer A, Rebelo AG. 2005. Modelling Species Diversity Through Species Level Hierarchical Modelling. *Journal of the Royal Statistical Society: Series C (Applied Statistics)* **54**: 1-20.

Gerhold P, Carlucci MB, Procheş Ş, Prinzing A. 2018. The Deep Past Controls the Phylogenetic Structure of Present, Local Communities. *Annual Review of Ecology, Evolution, and Systematics* **49**: 477-497.

Gianoli E, Valladares F. 2012. Studying phenotypic plasticity: the advantages of a broad approach. *Biological Journal of the Linnean Society* **105**: 1-7.

Grime JP, Brown VK, Thompson K, Masters GJ, Hillier SH, Clarke IP, Askew AP, Corker D, Kielty JP. 2000. The response of two contrasting limestone grasslands to simulated climate change. *Science* **289**: 762-765.

Grime JP. 2006. Plant strategies, vegetation processes, and ecosystem properties. John Wiley & Sons, New York, NY.

Grinnell J. 1917. The niche-relationships of the California Thrasher. *The Auk* **34**: 427-433.

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* **8**: 993-1009.

Harvey PH, Pagel MD. 1991. The comparative method in evolutionary biology. Oxford University Press Oxford.

Heard SB, Mooers AØ. 2000. Phylogenetically patterned speciation rates and extinction risks change the loss of evolutionary history during extinctions. *Proceedings of the*

Royal Society B: Biological Sciences **267**: 613-620.

Higgins SI, O'Hara RB, Bykova O, Cramer MD, Chuine I, Gerstner EM, Hickler T, Morin X, Kearney MR, Midgley GF *et al*. 2012. A physiological analogy of the niche for projecting the potential distribution of plants. *Journal of Biogeography* **39**: 2132-2145.

Hoffmann AA, Blows MW. 1994. Species borders: ecological and evolutionary perspectives. *Trends in Ecology and Evolution* **9**: 223-227.

Hulshof CM, Violle C, Spasojevic MJ, McGill B, Damschen E, Harrison S, Enquist BJ. 2013. Intra-specific and inter-specific variation in specific leaf area reveal the importance of abiotic and biotic drivers of species diversity across elevation and latitude. *Journal of Vegetation Sciences* **24**: 921-931.

Hutchinson GE. 1957. Population studies-animal ecology and demography-Concluding remarks. *Cold Spring Harbor Lab Press* **22**: 415-427.

Ives AR, Helmus MR. 2011. Generalized linear mixed models for phylogenetic analyses of community structure. *Ecological Monographs* **81**: 511-525.

Jamil T, Ozinga WA, Kleyer M, ter Braak CJF. 2013. Selecting traits that explain species–environment relationships: a generalized linear mixed model approach. *Journal of Vegetation Science* **24**: 988-1000.

Kattge J, DÍaz S, Lavorel S, Prentice IC, Leadley P, BÖnisch G, Garnier E, Westoby M, Reich PB, Wright IJ *et al.* 2011. TRY – a global database of plant traits. *Global Change Biology* **17**: 2905-2935.

Kearney M, Porter W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* **12**: 334-350.

Kellermann V, Overgaard J, Hoffmann AA, Fløjgaard C, Svenning JC, Loeschcke V. 2012. Upper thermal limits of Drosophila are linked to species distributions and strongly constrained phylogenetically. *Proceedings of the National Academy of Sciences, USA* **109**: 16228-16233.

Kissling WD, Dormann CF, Groeneveld J, Hickler T, Kühn I, McInerny GJ, Montoya JM, Römermann C, Schiffers K, Schurr FM *et al*. 2012. Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents.

Journal of Biogeography **39**: 2163-2178.

Kozłowski J. 1992. Optimal allocation of resources to growth and reproduction: Implications for age and size at maturity. *Trends in Ecology and Evolution* **7**: 15-19.

Kumar P. 2012. Assessment of impact of climate change on Rhododendrons in Sikkim Himalayas using Maxent modelling: limitations and challenges. *Biodiversity and Conservation* **21**: 1251-1266.

Laughlin DC, Gremer JR, Adler PB, Mitchell RM, Moore MM. 2020. The net effect of functional traits on fitness. *Trends in Ecology and Evolution* **35**: 1037-1047.

Lembrechts JJ, Nijs I, Lenoir J. 2019. Incorporating microclimate into species distribution models. *Ecography* **42**: 1267-1279.

Li Y, Wang Z, Xu X, Han W, Wang Q, Zou, D. 2016. Leaf margin analysis of Chinese woody plants and the constraints on its application to palaeoclimatic reconstruction. *Global Ecology and Biogeography* **25**: 1401-1415.

Li Y, Zou D, Shrestha N, Xu X, Wang Q, Jia W, Wang, Z. 2020. Spatiotemporal variation in leaf size and shape in response to climate. *Journal of Plant Ecology* **13**: 87-96.

Loarie SR, Duffy PB, Hamilton H, Asner GP, Field CB, Ackerly DD. 2009. The velocity of climate change. *Nature* **462:** 1052-1055.

Lopez-Iglesias B, Villar R, Poorter L. 2014. Functional traits predict drought performance and distribution of Mediterranean woody species. *Acta Oecologia* **56**: 10-18.

Maharjan SK, Sterck FJ, Dhakal BP, Makri M, Poorter L. 2021. Functional traits shape tree species distribution in the Himalayas. *Journal of Ecology* **109**: 3818-3834.

Mi C, Ma L, Yang M, Li X, Meiri S, Roll U, Oskyrko O, Pincheira-Donoso D, Harvey LP, Jablonski D *et al.* 2023. Global Protected Areas as refuges for amphibians and reptiles under climate change. *Nature Communications* **14**: 1389.

Miller JED, Damschen EI, Ives AR. 2019. Functional traits and community composition: A comparison among community-weighted means, weighted correlations, and multilevel models. *Methods in Ecology and Evolution* **10**: 415-425.

Morin X, Lechowicz MJ, Augspurger C, O'Keefe J, Viner D, Chuine I. 2009. Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biology* **15**: 961-975.

Nee S, May RM. 1997. Extinction and the Loss of Evolutionary History. *Science* **278**: 692-694.

Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F *et al*. 2010. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* **15**: 684-692.

O'Neil P. 1997. Natural Selection on Genetically Correlated Phenological Characters in *Lythrum salicaria L*. (Lythraceae). *Evolution* **51**: 267-274.

O’Neill GA, Hamann A, Wang T. 2008. Accounting for population variation improves estimates of the impact of climate change on species’ growth and distribution. *Journal of Applied Ecology* **45**: 1040-1049.

Oney B, Reineking B, O'Neill G, Kreyling J. 2013. Intraspecific variation buffers projected climate change impacts on *Pinus contorta*. *Ecology and Evolution* **3**: 437-449.

Pacifici M, Visconti P, Butchart SHM, Watson JEM, Cassola FM, Rondinini C. 2017. Species’ traits influenced their response to recent climate change. *Nature Climate Change* **7**: 205-208.

Pagel J, Schurr FM. 2012. Forecasting species ranges by statistical estimation of ecological niches and spatial population dynamics. *Global Ecology and Biogeography* **21**: 293-304.

Park DS, Breckheimer I, Williams AC, Law E, Ellison AM, Davis CC. 2019. Herbarium specimens reveal substantial and unexpected variation in phenological sensitivity across the eastern United States. *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**: 20170394.

Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen IC, Clark TD, Colwell RK, Danielsen F, Evengård B *et al*. 2017. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* **355**: eaai9214.

Peng S, Zhang J, Zhang X, Li Y, Liu Y, Wang Z. 2022. Conservation of woody species in China under future climate and land-cover changes. *Journal of Applied Ecology* **59**: 141-152.

Peng S, Ramirez-Parada TH, Mazer SJ, Record S, Park I, Ellison AM, Davis CC. 2024. Incorporating plant phenological responses into species distribution models reduces estimates of future species loss and turnover. *New Phytologist* **242**: 2338-2352.

Pollock LJ, Kelly LT, Thomas FM, Soe P, Morris WK, White M, Vesk PA. 2018. Combining functional traits, the environment and multiple surveys to understand semi-arid tree distributions. *Journal of Vegetation Science* **29**: 967-977.

Pollock LJ, Morris WK, Vesk PA. 2012. The role of functional traits in species distributions revealed through a hierarchical model. *Ecography* **35**: 716-725.

Post, E, Forchhammer MC, Bret-Harte MS, Callaghan TV, Christensen TR, Elberling B, Fox AD, Gilg O, Hik DS, Hoye TT *et al.* 2009. Ecological Dynamics Across the Arctic Associated with Recent Climate Change. *Science* **325**: 1355-1358.

Primack RB. 1980. Variation in the Phenology of Natural Populations of Montane Shrubs in New Zealand. *Journal of Ecology* **68**: 849-862.

Prinzing A, Durka W, Klotz S, Brandl R. 2001. The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society B: Biological Sciences* **268**: 2383-2389.

Pritzkow C, Williamson V, Szota C, Trouvé R, Arndt SK. 2020. Phenotypic plasticity and genetic adaptation of functional traits influences intra-specific variation in hydraulic efficiency and safety. *Tree Physiology* **40**: 215-229.

Ramirez-Parada T, Park I, Record S, Davis CC, Ellison AE, Mazer SJ. 2024. Plasticity and not adaptation is the primary source of temperature-mediated variation in flowering phenology in North America. *Nature Ecology and Evolution* **8**: 467-476.

Reekie EG, Bazzaz FA. 1987. Reproductive Effort in Plants. 3. Effect of Reproduction on Vegetative Activity. *American Naturalist* **129**: 907-919.

Rehfeldt GE, Ying CC, Spittlehouse DL, Hamilton Jr DA. 1999. Genetic responses to climate in Pinus contorta: niche breadth, climate change, and reforestation. *Ecological Monograph* **69**: 375-407.

Reich PB, Wright IJ, Cavender-Bares J, Craine JM, Oleksyn J, Westoby M, Walters MB. 2003. The Evolution of Plant Functional Variation: Traits, Spectra, and Strategies. *International Journal of Plant Sciences* **164**: S143-S164.

Revell LJ. 2010. Phylogenetic signal and linear regression on species data. *Methods in*

Ecology and Evolution **1**: 319-329.

Richardson BA, Chaney L, Shaw NL, Still SM. 2017. Will phenotypic plasticity affecting flowering phenology keep pace with climate change? *Global Change Biology* **23**: 2499-2508.

Robson TM, Garzón MB, BeechCOSTe52 database consortium. 2018. Phenotypic trait variation measured on European genetic trials of *Fagus sylvatica L*. *Scientific Data* **5**: 180149.

Sandel B, Pavelka C, Hayashi T, Charles L, Funk J, Halliday FW, Kandlikar GS, Kleinhesselink AR, Kraft NJB, Larios L *et al.* 2021. Predicting intraspecific trait variation among California's grasses. *Journal of Ecology* **109**: 2662-2677.

Santini L, Benítez-López A, Maiorano L, Čengić M, Huijbregts MAJ. 2021. Assessing the reliability of species distribution projections in climate change research. *Diversity and Distributions* **27**: 1035-1050.

Savolainen O, Lascoux M, Merilä J. 2013. Ecological genomics of local adaptation. *Nature Reviews Genetics* **14**: 807-820.

Siefert A, Violle C, Chalmandrier L, Albert CH, Taudiere A, Fajardo A, Aarssen LW, Baraloto C, Carlucci MB, Cianciaruso MV *et al.* 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters* **18**: 1406-1419.

Shukla A, Mehrotra RC, Guleria JS. 2013. Emergence and extinction of Dipterocarpaceae in western India with reference to climate change: Fossil wood evidences. *Journal of Earth System Science* **122**: 1373-1386.

Sultan SE, Spencer HG. 2002. Metapopulation Structure Favors Plasticity over Local Adaptation. *American Naturalist* **160**: 271-283.

Urban MC. 2015. Accelerating extinction risk from climate change. *Science* **348**: 571-573.

Valladares F, Matesanz S, Guilhaumon F, Araújo MB, Balaguer L, Benito-Garzón M, Cornwell W, Gianoli E, van Kleunen M, Naya DE *et al.* 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters* **17**: 1351-1364.

Vesk PA, Morris WK, Neal WC, Mokany K, Pollock LJ. 2021. Transferability of trait-based species distribution models. *Ecography* **44**: 134-147.

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! *Oikos* **116**: 882-892.

Violle C, Reich PB, Pacala SW, Enquist BJ, Kattge J. 2014. The emergence and promise of functional biogeography. *Proceedings of the National Academy of Sciences, USA* **111**: 13690-13696.

Warren DL, Cardillo M, Rosauer DF, Bolnick DI. 2014. Mistaking geography for biology: inferring processes from species distributions. *Trends in Ecology and Evolution* **29**: 572-580.

Werger MJA, Ellenbroek GA. 1978. Leaf size and leaf consistence of a riverine forest formation along a climatic gradient. *Oecologia* **34**: 297-308.

Westoby M, Wright IJ. 2006. Land-plant ecology on the basis of functional traits. *Trends in Ecology and Evolution* **21**: 261-268.

Wiens JJ, Donoghue MJ. 2004. Historical biogeography, ecology, and species richness. *Trends in Ecology and Evolution* **19**: 639-644.

Wiens JJ, Graham CH. 2005. Niche Conservatism: Integrating Evolution, Ecology, and Conservation Biology. *Annual Review of Ecology, Evolution, and Systematics* **36**: 519-539.

Willis CG, Ruhfer B, Primack RB, Miller-Rushing AJ, Davis CC. 2008. Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. *Proceedings of the National Academy of Sciences, USA* **105**: 17029-17033.

Wright IJ, Dong N, Maire V, Prentice IC, Westoby M, Díaz S, Gallagher RV, Jacobs BF, Kooyman R, Law EA *et al*. 2017. Global climatic drivers of leaf size. *Science* **357**: 917-921.

Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004. The worldwide leaf economics spectrum. *Nature* **428**: 821-827.

Wund MA. 2012. Assessing the Impacts of Phenotypic Plasticity on Evolution. *Integrative and Comparative Biology* **52**: 5-15.

Zurell D, Jeltsch F, Dormann CF, Schröder B. 2009. Static species distribution models in dynamically changing systems: how good can predictions really be? *Ecography* **32**: 733-744.

Zurell D, Zimmermann NE, Sattler T, Nobis MP, Schröder B. 2016. Effects of functional traits on the prediction accuracy of species richness models. *Diversity and Distributions* **22**: 905-917.

Box1 Description of traditional hierarchical trait-based framework (Pollock *et al.*,2012)

The traditional hierarchical models can be described using the following four formulas:

$$\Pr(Y_{ij} = 1) = logit^{-1}\left(a_{[i]} + S_{k[i]} \times E\right) \qquad (A1)$$

The response data Y_{ij} are observed presences or absences of species i in location j. In this base model (Equation A1), the logit probability that species i occurs at the jth location is equal to an intercept term $a_{[i]}$ plus the product of a matrix of environmental variables (E), which has rows j representing the number of locations and columns k representing the number of environmental variables, and a vector of coefficients, one for each of the environmental variables ($S_{k[i]}$) (see Equation A3). The parameters $a_{[i]}$ and $S_{k[i]}$ are modeled parameters that vary by species.

$$a_{[i]} \sim Normal_{(\mu,\sigma)} \qquad (A2)$$

The submodel for $a_{[i]}$ includes the parameter μ, which represents the average probability of occurrence (on a logit scale) among species, and the parameter σ, which is the degree to which a given species departs from its average probability of occurrence. $S_{k[i]}$ are the partial regression slopes that indicate the response of a given species to the relevant environmental variables. The sub-model for the $S_{k[i]}$ is as follows:

$$S_{k[i]} = B_{k[i]} + C_{kn} \times Traits_{n[i]} \qquad (A3)$$

The estimate of $S_{k[i]}$ is calculated as the intercept $B_{k[i]}$ plus the coefficient matrix C_{kn} and trait value matrix for the n = 1, 2 ..., n traits ($Traits_{n[i]}$). The elements C_{kn} are partial trait contributions to species partial responses to each environmental variable, which describes how the trait matrix C_{kn} of n traits in k environments modulate responses to environmental conditions across species. The intercept $B_{k[i]}$ is modeled as:

$$B_{k[i]} \sim Normal(U_{[k]}, \tau_{[k]}) \qquad (A4)$$

where $U_{[k]}$ indicates the average response of species to environmental variables and $\tau_{[k]}$ reflects the degree of variation degree in species departures. The term $B_{k[i]}$ indicates how species depart from expected responses to each environmental variable given the species' set of traits. The output of hierarchical SDMs involve dimensionless estimates of habitat suitability or probability of occurrence.

Taking plant phenology as a simple example, the basic R code of a hierarchical model is as follows:

```
#library(lme4)
#Full model <- lmer (occurrence ~ temperature + precipitation + climate seasonality
                    # Climatic factors that affect
                + temperature*phenology + precipitation*phenology + climate seasonality*phenology #
                Connection to phenology
                + (1+ temperature + precipitation + climate seasonality | species),
                # Responses to climatic factors vary among species
                      data = data, family = binomial)
```

Box 2 Description of phylogenetic trait-based species distribution models

Phylogenetic trait-based species distribution models (PGLMMs) provide a unique framework to include the evolutionary history of species (i.e., phylogeny) into analyses of species occurrences to explore how the shared biogeographic history of related species shape their distribution patterns. Some readily available tools, including the R packages "*pez*" and "*phyr*" can be used for phylogenetic correction. The basic form of PGLMMs is:

$$\Pr\,(Y_{ij}=1)=a_{[i]}+(\alpha_{[i]}^{p}+\alpha_{i})+(\beta_{1}+C_{[i]}+C_{[i]}^{p})env_{j}+\ \beta_{2}trait_{ij}+\beta_{3}env_{j}\times trait_{ij}+\ e_{ij}$$

where $\Pr\,(Y_{ij}=1)$ represents the logit probability that species i occurs at the *j*th site, which is equal to the intercept term $a_{[i]}$ plus the fixed effects of environmental conditions at site *j* $(env_j;\ \beta_1 \neq 0)$, trait values of species i at the *j*th site $(trait_{ij};\ \beta_2 \neq 0)$, and their interactions $(env_j \times trait_{ij};\ \beta_3 \neq 0)$; and random effects $\alpha_i,\ \alpha_i^p,\ C_i$, and C_i^p. Random effect α_i allows different species to have different overall probabilities of occurrence, and α_i^p models how closely related species have similar overall probabilities of occurrence. Random effect C_i allows different species to have different responses to environments, and C_i^p models how closely related species have similar responses to environments to capture the interactive effects of traits and environment for traits that have significant association with phylogeny.

For exploring species distributions, the dependent variable is a binary (Bernoulli) which takes values of 0 or 1. However, PGLMMs could use other data distributions such as Gaussian, binomial or Poisson. For example, PGLMM can be used in models of trait-environment relationships, in which the dependent variable is the trait value, and the independent variables are different environmental variables. Species enter the model as random effect term and the phylogenetic covariance matrix accounts for known phylogenetic relationships.

Table 1 Summary of representative plant studies using trait-based framework.

Model type	**Trait**	**Spatial extent**	**Conclusions**	**Reference**
Process-based	Phenology	North America	Phenology is a major determinant of plant species range and can be used to assess the impacts of global warming on plant distributions.	Chuine & Beaubien, 2001
	Phenology	North America	Loss of species' habitat would be mitigated since predictions take into account the local adaptation and trait plasticity to climate of a species.	Morin *et al.*, 2008
	Phenology	North America	Climate limits species distributions mainly through their impact on phenological processes.	Morin *et al.*, 2007
	Physiological characteristics	Europe	Physiological models can be used to derive physiological niche dimensions from species distribution data.	Higgins *et al.*, 2012
Correlative	Specific leaf area (thickness) Root C, N content Specific root length Leaf C: N Leaf dry matter content Leaf area Seed mass	Russia	Plant functional traits could be used as predictors for forecasting changes in plant communities, and their associated ecosystem services, in response to global change.	Soudzilovskaia *et al.*, 2013
	Biomass Plant height Leaf width	Central United States	The assumption that species always respond homogenously to climate change is untenable	Smith *et al.*, 2017
	Specific leaf area Seed mass Plant height	Australia	SLA strongly modulates species response to rocky areas. Tall plants are competitive in high light and high rainfall conditions. Seed mass modulates species responses to soil texture.	Pollock *et al.*, 2012

	Specific leaf area Seed mass Plant height	France	Nonnative plants with exploitative traits are less dependent on human pressure, more efficient in resource rich environments and better at avoiding competition from natives.	Carboni *et al*., 2018

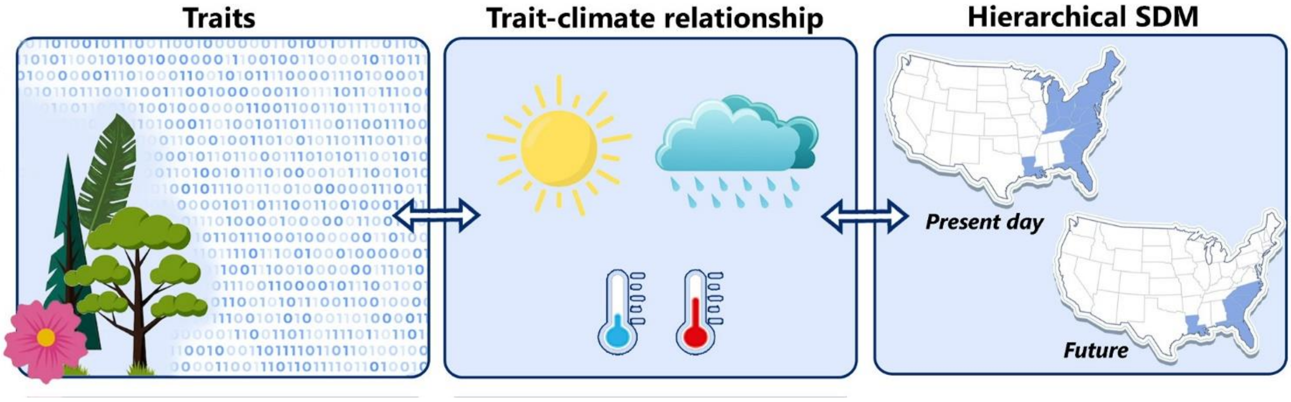

Fig. 1 Conceptual diagram of newly developed hierarchical trait-based species distribution models (SDMs) that integrate trait-climate relationships. Both individual-specific functional traits and local environmental data are key initial inputs for hierarchical trait-based SDMs. Trait-climate relationships are also modeled to generate predicted trait values in a changing environment. These trait values are then substituted into the hierarchical SDMs to predict and forecast the probability of occurrence of individuals under the current and future environmental conditions.

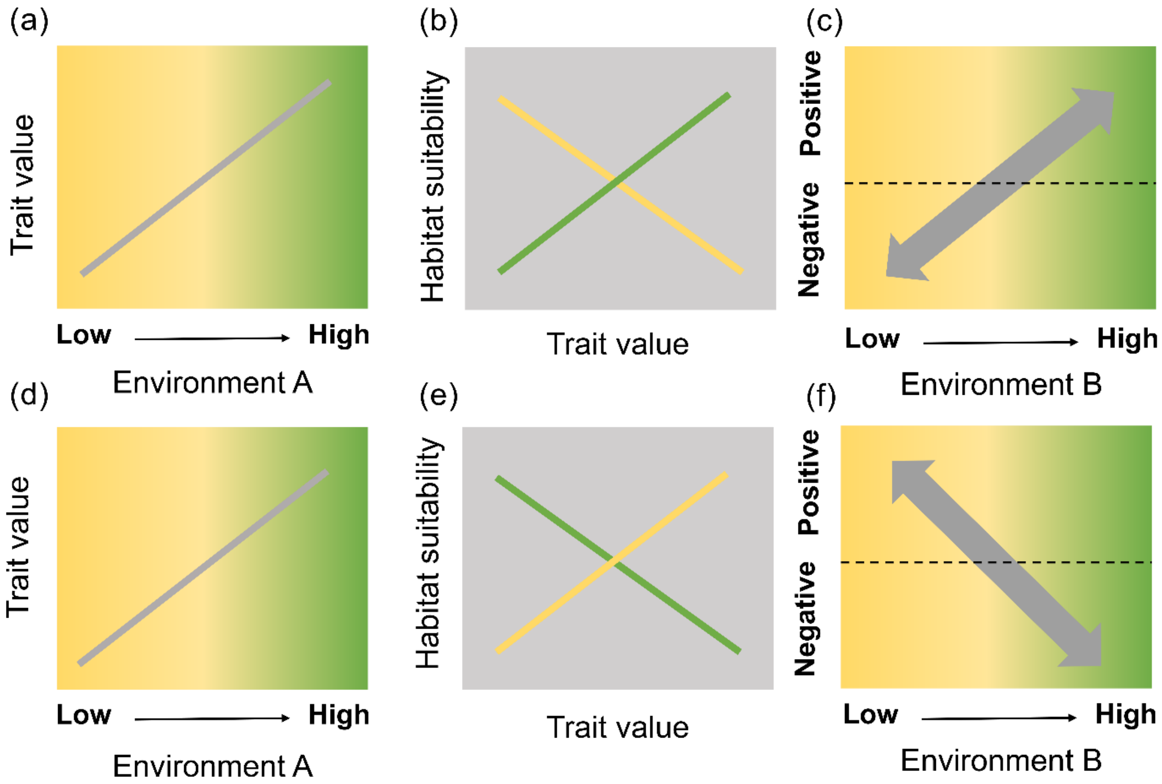

Fig. 2 Conceptual diagram illustrating how functional traits mediate species distributions along environmental gradients. We illustrate examples for both positive (a–c) and negative (d–f) trait-environment interactions driving species occurrences. We assumed: 1) the trait value linearly increases along the environment gradient (a, d); 2) species' probability of occurrence monotonically increases along the environment gradient. Environmental factors affecting trait variation and species distribution are different. We defined environment A as environmental factors that affect trait variations and environment B as environmental factors that affect species occurrences. In the case of a positive interaction between a trait and an environmental gradient, high trait values make the relationship between species occurrence and an environmental variable more positive (b, c). Alternatively, a negative interaction between a trait and an environmental gradient indicates the opposite: high trait value is beneficial at the low end of environmental gradient, and low trait value is beneficial at the high end of environmental gradient (e, f).

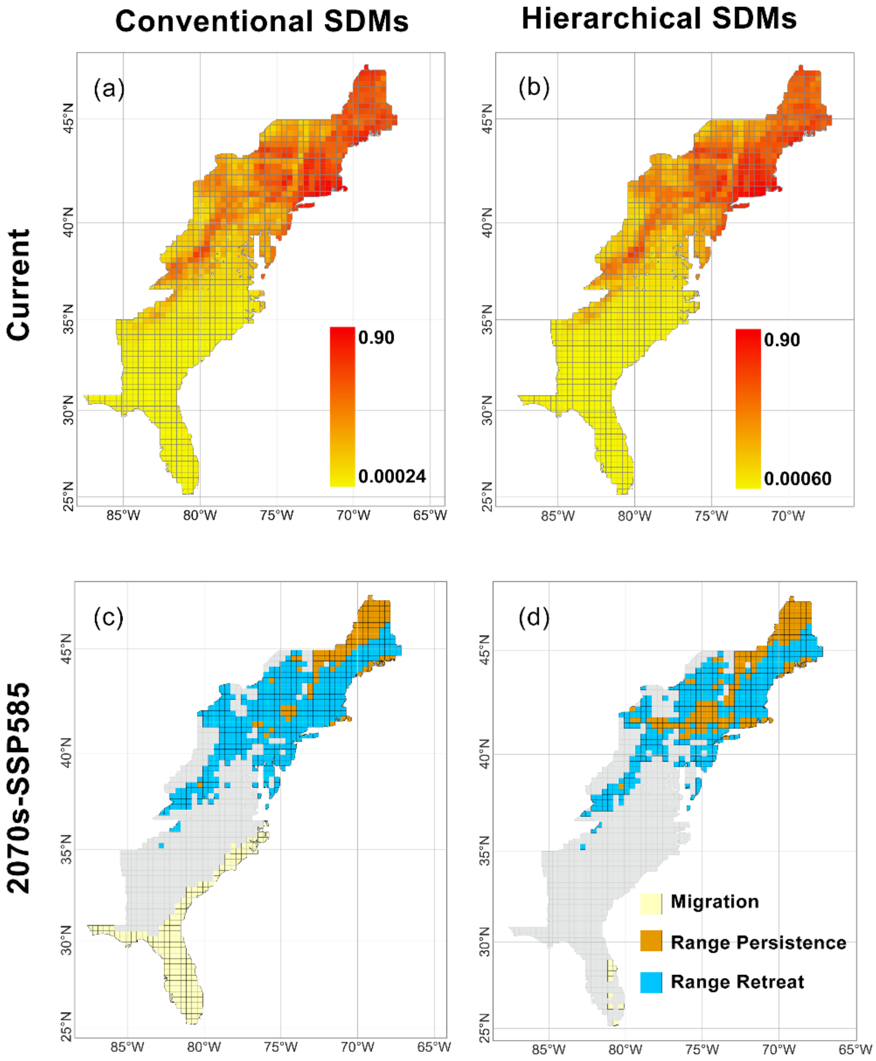

Fig. 3 Changes in species ranges forecasted by conventional (a, c) and hierarchical trait-based SDMs (b, d). The maps compare the current and future distributions (probability of occurrence) of *Trientalis borealis* (Raf.) U.Manns & Anderb. We classified future species distribution ranges into three categories. Orange areas represent regions currently occupied by *T. borealis* that are projected to remain suitable in the future (i.e., range persistence); blue areas represent regions currently occupied by *T. borealis* that are projected to have low suitability in the future (i.e., range retreat); yellow areas represent regions currently unoccupied by *T. borealis* that are projected to have high suitability in the future (i.e., migration; range expansion). Future forecasts are based on Shared Socioeconomic Pathways 5-8.5 (SSP5-8.5) scenario from average estimate of six General Circulation Models (GCMs) in 2070.