Viewpoint

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

Summary

Conventional species distribution models (SDMs) typically consider only abiotic factors, thus overlooking critical biotic dimensions, including traits that play an important role in determining species' distributions in changing environments. Process-based trait SDMs explicitly incorporate 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 SDMs use widely available data and facilitate the incorporation of traits into SDMs at broad temporal, spatial, and taxonomic scales. However, despite their promise, existing hierarchical trait-based SDMs fail to accommodate changing trait spaces under different climate conditions. Here, we provide a new, simplified framework for hierarchical trait-based SDMs that integrates individuals' trait responses into forecasts of species range shifts in response to ongoing climate changes. We further briefly discuss the issue of non-independence among species in hierarchical trait-based SDMs. 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 at large scales under future climate change.

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) are one of the most important and widespread tools 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 (we refer herein to such SDMs as '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 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). 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). They may be 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 fitness (i.e. reproduction, survival; Laughlin *et al.*, 2020). Therefore, the limited inclusion or, as in most cases, the complete lack of 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). We also note that the term 'functional traits' is also used in the literature without distinguishing them from 'traits', so herein we refer to all such ecologically relevant traits simply as 'traits'.

The concept of integrating both traits and environmental factors into SDMs was proposed nearly two decades ago (Westoby & Wright, 2006; Benito Garzón *et al.*, 2019), and several reviews have synthesized the theoretical foundations of such 'trait-based' approaches (e.g. Kearney & Porter, 2009; Laughlin & Laughlin, 2013; Benito Garzón *et al.*, 2019; Vesk *et al.*, 2021; Green *et al.*, 2022). However, empirical applications of 'trait-based SDMs' remain relatively uncommon compared to conventional SDMs that include only climatic and other environmental variables in defining habitat suitability. This gap likely stems from challenges 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 trait SDMs' that explicitly incorporate links between traits of organisms and their environments into trait-based SDMs (Chuine & Beaubien, 2001; Kearney & Porter, 2009; Briscoe *et al.*, 2023). Process-based trait SDMs significantly improve predictions under novel conditions (Higgins *et al.*, 2012), 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). Because process-based trait SDMs are difficult to parameterize, they have been applied to only a few species and have provided limited insight

into forecasts of biodiversity change across large spatial, temporal, and taxonomic scales.

'Hierarchical trait-based SDMs' that incorporate species' traits into conventional SDMs provide a general ecological reference for how traits influence species distributions (Pollock *et al.*, 2012; Carboni *et al.*, 2018; Vesk *et al.*, 2021). Although these models are still based on correlative relationships between species occurrences and local environments, they offer a more biologically informed framework for predicting species distributions and thus may enhance predictive accuracy (Vesk *et al.*, 2021). More importantly, hierarchical trait-based SDMs are statistical rather than mechanistic. Thus, in contrast to process-based trait SDMs that are highly data-intensive, hierarchical trait-based SDMs can leverage much more available data (i.e. species occurrence and trait data) and are more readily applicable across broad spatial and taxonomic scales (Pollock *et al.*, 2018; Peng *et al.*, 2024). However, existing hierarchical trait-based 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 traits into SDMs using hierarchical trait-based SDMs. We then provide new insights into how to integrate trait–climate relationships into existing hierarchical trait-based SDMs to incorporate intraspecific changes in the expression of traits resulting from spatial and temporal shifts in abiotic conditions (Fig. 1). We also briefly discuss the importance of incorporating phylogenetic information, which accounts for evolutionary relatedness, into hierarchical trait-based SDMs. The motivation for our review builds on a recent effort to integrate plant phenological responses to climate into hierarchical trait-based SDMs and better forecast biodiversity change at large spatial, temporal, and taxonomic extents (Peng *et al.*, 2024). We also compare predictions from our newly developed hierarchical framework with those from the hierarchical trait-based SDMs presented by Pollock *et al.* (2012).

A 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; Dallas & Ten Caten, 2025). 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) which 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).

Studies have shown that conventional SDMs are generally reliable in future 'analog' environments (e.g. Higgins *et al.*, 2012). 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 and in 'nonanalog' environments (Loarie *et al.*, 2009; Pagel & Schurr, 2012). 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 disequilibrium when using abiotic factors alone (e.g. Fordham *et al.*, 2018). These elements may overestimate the extent of suitable habitats for a given species in future climates.

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' traits are neither static nor homogeneous 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 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 *c.* 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, 2005; Willis *et al.*, 2008; Valladares *et al.*, 2014; Pritzkow *et al.*, 2020; Cope *et al.*, 2021).

Phenotypic plasticity differs from local adaptation. 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 the evolution of fitness-related traits or plasticity that may accompany strong local environmental variation.

Many recent studies have attempted to construct conventional SDMs at the subspecies level to reflect intraspecific variation (Oney *et al.*, 2013) or to develop process-based trait SDMs that 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

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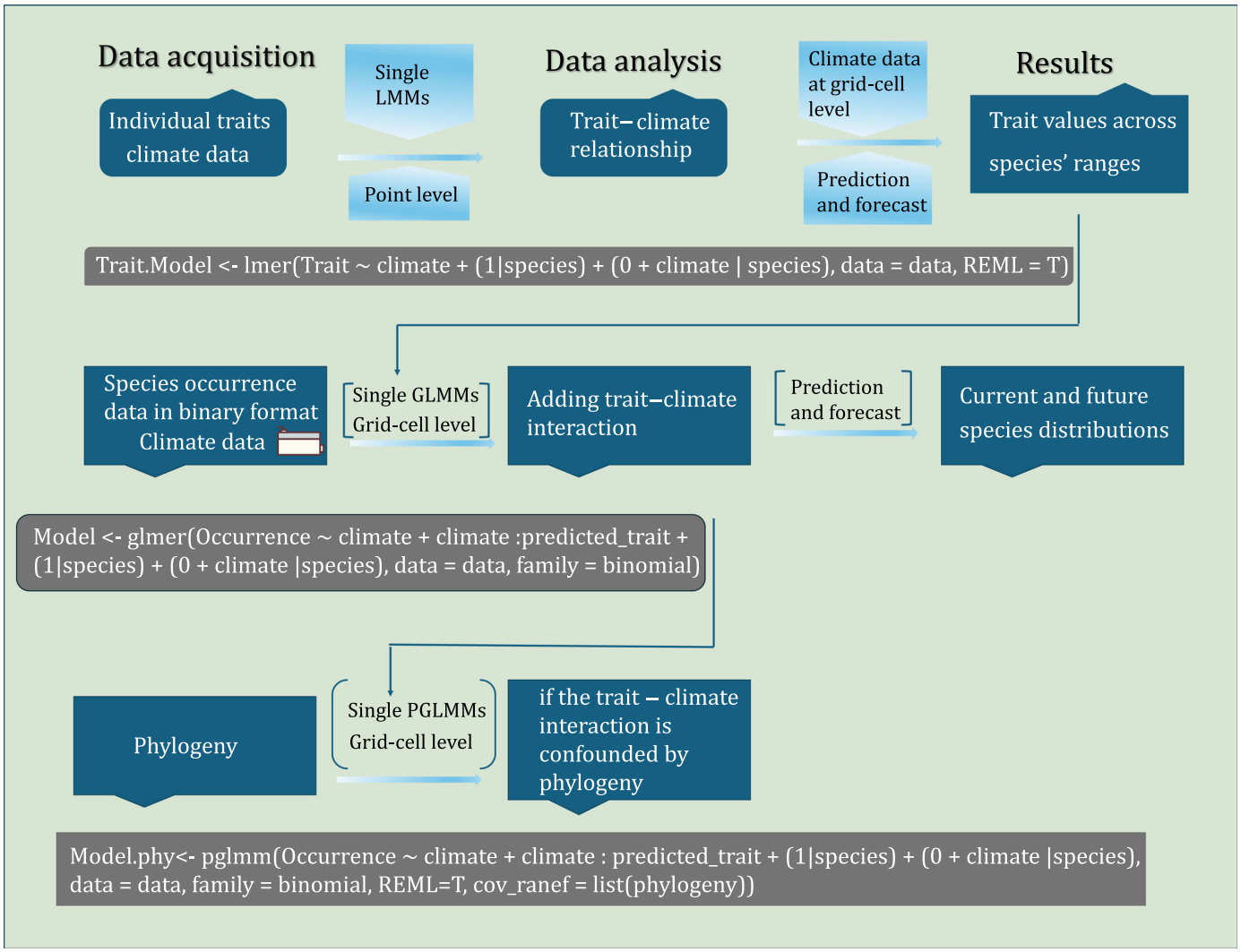

Fig. 1 Flowchart diagram of the next generation hierarchical trait-based species distribution models (SDMs) that integrate trait–climate relationships. *R* code for each model section is also provided. Both individual-specific traits (often at point levels) and local environmental data serve as key initial inputs for constructing trait–climate relationships mainly using linear mixed-effect models (LMMs). These relationships are modeled to generate predicted trait values across species' distribution ranges (often at the grid-cell level) under changing environmental conditions. The predicted trait values are then incorporated into hierarchical trait-based SDMs as interaction terms with climate variables, enabling the prediction and forecasting of individual occurrence probabilities under current and future environmental scenarios. Hierarchical trait-based SDMs use a single predictive model – here, a generalized linear mixed-effect model (GLMM) – to simultaneously model multiple species, with species as random components. Given that the phylogenetic relatedness of unmeasured traits may inflate Type I error rates in regression analyses, phylogenetic generalized linear mixed-effect models (PGLMMs) can be further used to evaluate whether trait–climate interactions are confounded by shared evolutionary history.

forecasted suitable habitats. Similarly, Higgins *et al.* (2012) inferred a plant niche model based on physiological mechanisms to support species distribution predictions. 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 SDMs accounting for intraspecific variations 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 SDMs have two key limitations. First, they rely only on intraspecific distribution data (e.g. model each of the subspecies independently; Oney *et al.*, 2013), not data on phenotypic traits or plasticity itself (Valladares *et al.*, 2014). Nevertheless, subspecies-level distribution data are often sparse or unavailable. Therefore, our ability to understand the mechanisms underlying species' responses to climate change will be limited, as distribution patterns alone may not capture functional differences or the adaptive potential among individuals or populations. Second, process-based trait SDMs that explicitly incorporate traits such as climate-dependent phenology (Chuine & Beaubien, 2001; Morin *et al.*, 2009), physiology, or biophysics (Kearney & Porter, 2009; Higgins *et al.*, 2012) require well-designed and time-consuming experiments to

Table 1 Summary of representative plant studies using trait-based species distribution models (SDMs).

Model type	Trait	Spatial extent	Conclusions	References
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 account for local adaptation and trait plasticity of a species to its local climate.	Morin *et al*. (2008)
	Phenology	North America	Climate limits species distributions mainly through its 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 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 (SLA) 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	Non-native 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)
	Phenology	Eastern United States	The dynamic phenological responses of species may help them adjust their ecological niches and persist in their habitats as the climate changes.	Peng *et al*. (2024)

calibrate, validate, and understand the underlying causal relationships among fitness, traits, and environments. These relationships are species-specific, and such data are generally not available for most species (Kearney & Porter, 2009; Vesk *et al*., 2021). 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.

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

Hierarchical trait-based SDMs incorporate parameters that account for the responses of multiple species to their environments and allow traits to modulate species responses to different environments (Gelfand *et al*., 2005; Dorrough & Scroggie, 2008). Similar to conventional SDMs, hierarchical trait-based SDMs also include simplifying assumptions (e.g. assuming equilibrium distributions, ignoring dispersal limitation, Vesk *et al*., 2021). However, compared to process-based trait SDMs, hierarchical trait-based SDMs rely only on the statistical relationships (e.g. typically linear) between traits, environment, and species occurrences. Moreover, by assuming commonality of species responses and sharing statistical strength among species, hierarchical trait-based SDMs use a single predictive model to simultaneously model multiple species (Pollock *et al*., 2012). For example, generalized linear mixed models (GLMMs; Jamil *et al*., 2013) can include a hierarchical structure that defines interactions between traits and environments. Such a framework enables the use of more widely available data and allows even species with limited occurrence records to be incorporated. Therefore, hierarchical trait-based SDMs can facilitate the application of trait-based SDMs across broad taxonomic scales and deepen our understanding of mechanisms of how traits modulate species' distributions along large environmental gradients (Pollock *et al*., 2012; Vesk *et al*., 2021).

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 SDMs proposed by Pollock *et al*. (2012) 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

Box 1. Description of a standard hierarchical trait-based species distribution model (SDM) (Pollock *et al*., 2012)

The standard hierarchical trait-based SDMs can be described with the following four equations:

$$\Pr(Y_{ij}=1)=\text{logit}^{-1}(a_{[i]}+S_{k[i]}\times E) \quad \text{Eqn B1}$$

in which the response data Y_{ij} are observed presences or absences of species i in location j. In Eqn B1, the logit probability that species i occurs at the j^{th} 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, columns k representing the number of environmental variables, and a vector of coefficients, one for each of the environmental variables ($S_{k[i]}$) (see Eqn B3). The parameters $a_{[i]}$ and $S_{k[i]}$ are modeled parameters that vary by species:

$$a_{[i]}\sim \text{Normal}_{(\mu,\sigma)} \quad \text{Eqn B2}$$

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 coefficients (slopes) that indicate the response of a given species to the relevant environmental variables. The sub-model for $S_{k[i]}$ is:

$$S_{k[i]}=B_{k[i]}+C_{kn}\times \text{Traits}_{n[i]} \quad \text{Eqn B3}$$

in which 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 $n=1, 2\ldots, n$ traits ($\text{Traits}_{n[i]}$). The elements C_{kn} are partial trait contributions to each species' partial responses to each environmental variable, which describe how the trait matrix C_{kn} of n traits in k environments modulates responses to environmental conditions across species. The intercept $B_{k[i]}$ is modeled as:

$$B_{k[i]}\sim \text{Normal}(U_{[k]},\tau_{[k]}) \quad \text{Eqn B4}$$

where $U_{[k]}$ indicates the average response of species to environmental variables, $\tau_{[k]}$ is its variation, and $B_{k[i]}$ indicates how much each species differs from the overall expected responses to each environmental variable, given the species' set of traits. The output of hierarchical trait-based SDMs involves dimensionless estimates of habitat suitability or probability of occurrence.

Taking plant phenology as a simple example, the basic R code of a hierarchical trait-based SDM is as follows:

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

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 applied hierarchical trait-based SDMs have explored how 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 had a higher probability of occurring in sandy soils. Similarly, Carboni *et al*. (2018) built a multispecies hierarchical trait-based SDM, including the distribution of 10 nonnative 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 ability of SDMs to predict the current distributions of species (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 SDMs and those from conventional SDMs under current and future climate scenarios remain scarce (but see Peng *et al*., 2024). This lack 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 frameworks is how to apply SDMs that incorporate traits whose adaptive or plastic responses can be

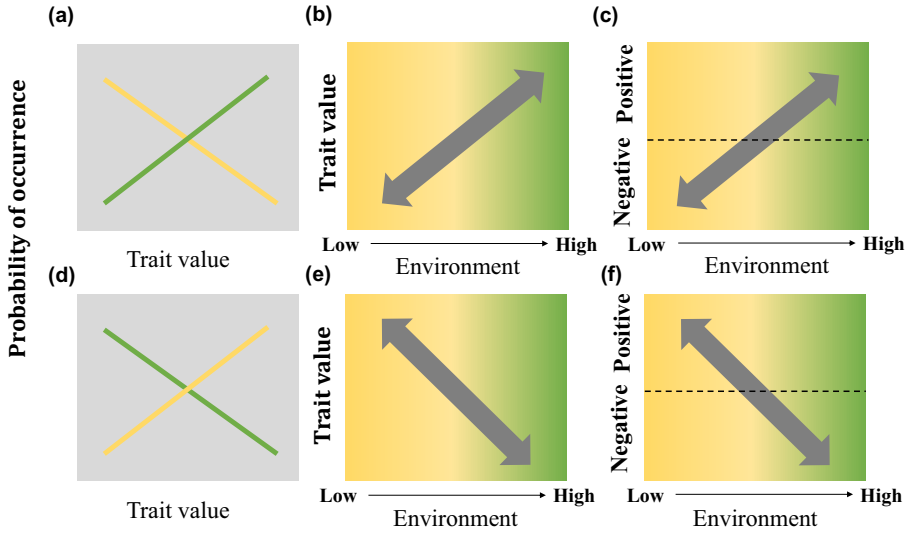

Fig. 2 Conceptual diagram illustrating how trait–environment interactions drive species distributions. The upper row (a–c) represents a positive trait × environment interaction, while the lower row (d–f) represents a negative interaction. Yellow indicates the low end of the environmental gradient, and green indicates the high end. In the case of a positive interaction (a–c), the probability of species occurrence increases with trait values under high environmental conditions (a, green line). That is, high trait values are beneficial to the species' probability of occurrence at the upper end of the environmental gradient (b). By contrast, under low environmental conditions, the positive effect of the trait weakens, and in extreme cases, the relationship may even reverse (yellow line in a), such that lower trait values become more advantageous to species occurrence (b). This pattern implies a trait effect on species occurrence that switches sign along the environmental gradient, being negative at the low end and positive at the high end (c). In the case of a negative interaction (d–f), the probability of species occurrence increases with trait values under low environmental conditions (d, yellow line). That is, high trait values are beneficial to the species' probability of occurrence at the lower end of the environmental gradient (e). On the contrary, under high environmental conditions, the positive effect of the trait weakens, and in extreme cases, the relationship may even reverse (green line in d), such that lower trait values become more advantageous to species occurrence (e). This suggests a trait effect on species occurrence that switches sign along the environmental gradient, being positive at the low end and negative at the high end (f).

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 traits always assume that individual traits are constant through time (e.g. Gallagher *et al.*, 2013). However, the traits of individuals should not be considered fixed. Many common fitness-related traits, such as plant phenology (Chuine & 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 may allow populations to expand their climatic tolerance beyond their present realized niches (Valladares *et al.*, 2014; Des Roches *et al.*, 2018), thereby reducing or even preventing the loss of their geographic ranges. Because of phenotypic plasticity and adaptation, trait values observed under current conditions cannot be fully representative of those that will occur in the future. 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 process-based trait 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. adaptive and plastic effects; Benito Garzón *et al.*, 2019). By contrast, it is difficult to split the phenotypic variation of 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 traits related to environmental variables, and theoretically, they 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.

Traits in a changing world: the application of next-generation hierarchical trait-based SDMs that integrate trait–climate relationships

The aims of next-generation hierarchical trait-based SDMs include understanding how traits shape species' current occurrences and examining how spatiotemporal variation in traits may mediate species' responses to future climate change. Characterizing trait–climate relationships is an essential step towards integrating spatiotemporal trait variations into hierarchical trait-based SDMs. This process is motivated by the logic of *space-for-time substitution*, whereby limited available trait values of individuals are first used to establish trait–climate relationships using statistical algorithms

Box 2. Next-generation hierarchical trait-based species distribution models (SDMs) that integrate trait–climate relationships

Standard hierarchical trait-based SDMs (Box 1) assume that individual traits are constant through time and measured uniformly across species' ranges. However, traits should not be considered fixed and often exhibit strong intraspecific variation. Empirical trait data are typically spatially sparse. To integrate the trait–climate relationship into hierarchical trait-based SDMs, a trait–climate relationship is first constructed using these spatially sparse trait data and the environment variables at each observed location (often measured at a point locality). Trait values across species' range (usually in a grid cell (raster)) are then predicted under both current and future climate scenarios.

Trait–environment modeling

Trait values observed at specific locations (e.g. points) are modeled as a function of environmental predictors, including both fixed and random effects to account for species, phylogeny, and so on

$$\text{Trait}_{[v,j]} = a_0 + \sum_n b_m x_{[m,j]} + \beta + \delta + \varepsilon \qquad \text{Eqn B5}$$

where $\text{Trait}_{[v,j]}$ is the trait value of individual v at location j, $x_{[m,j]}$ is the value of the environmental covariate m at location j, b_m is the regression coefficient of environmental covariate m, β are optional covariates, δ are random components, and ε is an error term with a known (or defined) distribution.

Integrating predicted trait values into hierarchical trait-based SDMs

The fitted model (B5) is used to predict trait values across the species' ranges under both current and future climates.

The original model (Eqns B1 and B3 in Box 1) is modified to be:

$$\Pr(Y_{ig} = 1) = \text{logit}^{-1}(a_{[i]} + S_{k[i]} \times E) \qquad \text{Eqn B6}$$

$$S_{k[i]} = B_{k[i]} + C_{kn} \times \text{Traits\_pred}_{n[i,g]} \qquad \text{Eqn B7}$$

where the response data Y_{ig} are observed presences or absences of species i at the grid cell g and $\text{Traits\_pred}_{n[i,g]}$ represent predicted trait values in a matrix with $n = 1, 2 \ldots, n$ traits of species i at the grid cell g. When there are multiple traits, $n > 1$. The explanation of other parameters is as described in Box 1.

Based on the estimated parameters in Eqns B6 and B7, we substitute the predicted trait values and climate variables under future climate scenarios into the model to forecast species' probabilities of occurrence under future environmental conditions.

such as generalized linear mixed-effect models, which are then used to generate trait predictions across species' distribution ranges and through time. These spatially explicit trait predictions serve as key inputs for hierarchical trait-based SDMs, enabling the integration of trait variation into hierarchical trait-based SDMs and thereby capturing species−specific responses across different time periods (details in Box 2).

Modeling trait–climate relationships under different climate spaces

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

$$T_1 = a_0 + b_1 x_1 + b_2 x_2 + b_3 x_3 + \ldots + b_n x_n + \beta + \delta + \varepsilon \qquad \text{Eqn 1}$$

where T_1 is the individual's value for a certain trait, a_0 represents the intercept, $b_1, b_2, b_3, \ldots, b_n$ are the coefficients of the regression, $x_1, x_2, x_3, \ldots, x_n$ 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, δ is the (matrix of) random effect(s), and ε is the model error. Eqn 1 allows us to incorporate many species simultaneously and to quantify trait variation across time and space.

Trait data often are spatially sparse and derived from scattered field observations, herbarium specimens, or global trait databases such as TRY (Kattge *et al.*, 2011). However, when combined with spatially continuous environmental variables, these data could support robust models for predicting trait variation across species' distribution ranges (e.g. grid cell level) under both current and future climate scenarios, even in regions where direct trait measurements are unavailable. These predicted trait values are then incorporated into a hierarchical structure by enabling species' responses to environmental gradients to vary as a function of their traits, thereby exploring how traits mediate species' responses to environmental change.

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

Even in GLMM implementations, hierarchical trait-based SDMs typically assume linear responses. Thus, GLMM implementation extends the approach used in conventional SDMs, which relate binary species occurrence data to environmental variables, by incorporating predicted current trait values – based on the trait–climate relationships across species' distribution ranges – as interaction terms with climate predictors. The hierarchical framework

also includes random intercepts and slopes for species, thereby capturing variations in baseline occurrence and in responses to environmental variables among species (Eqns B1–B4 in Box 1). Next-generation hierarchical trait-based SDMs thereby provide a mechanistic basis for explaining current species distribution patterns from a trait-based perspective and can be used to forecast future probability of occurrence by substituting trait values projected under future climate scenarios across species' ranges.

Despite their flexibility, next-generation hierarchical trait-based SDMs have several limitations. First, like most SDMs, they typically assume linear relationships between species distributions and environmental variables (Pollock *et al.*, 2012; Vesk *et al.*, 2021). This may oversimplify ecological processes since species often exhibit unimodal responses to environmental gradients (Hutchinson, 1957; Austin, 2002; DeLong *et al.*, 2023). Adding polynomial terms to a hierarchical framework would allow for curvilinear responses and better reflect real ecological phenomena, yet such extensions may reduce model generality and require substantially more data (Austin & Meyers, 1996; Jamil & ter Braak, 2013; Anderson *et al.*, 2022). Second, *space-for-time substitutions* assume that spatial variation in traits can be used to infer temporal responses to climate change. For example, species found in warmer, low-latitude regions tend to have larger leaf sizes than those growing in cooler, high-latitude regions (Wright *et al.*, 2017; D. Li *et al.*, 2020; Y. Li *et al.*, 2020). One might expect that leaf size in high-latitude populations will increase to levels comparable to those observed in low-latitude populations, as the former warms to temperatures currently experienced in the latter. However, spatial variations in trait and temporal dynamics in trait response often result from entirely different ecological and evolutionary processes. Trait gradients observed across space typically reflect long-term evolutionary history, species turnover, and biogeographic constraints. By contrast, temporal responses involve rapid trait changes within populations, driven by phenotypic plasticity or genetic variation. Therefore, spatial trait differences may not necessarily imply that a given population will exhibit the same trait changes in response to future climate warming.

To better understand and project temporal trait responses, it is crucial to establish large networks of common-garden and reciprocal-transplant experiments across broad environmental gradients to disentangle the relative contributions of different sources of trait variations (e.g. phenotypic plasticity and local adaptation) to species distributions and provide new insights into assessing changes in the distributional range of individuals due to climate change (Rehfeldt *et al.*, 1999; Robson & Benito Garzón, 2018; Benito Garzón *et al.*, 2019). Despite recent increases in large-scale common-garden and reciprocal-transplant experiments, these efforts are still restricted to a limited set of taxa and geographic regions (Robson & Benito Garzón, 2018). Enhanced collaboration among research institutions and across biogeographic regions will be critical in expanding both the taxonomic scope and environmental representativeness of such experimental frameworks. Importantly, differentiating between phenotypic plasticity and local adaptation and integrating both into hierarchical trait-based SDMs remains challenging, but should be an important goal for future research. Such integration would improve the explanatory power of hierarchical trait-based SDMs and allow for the separation of short-term trait responses driven by phenotypic plasticity from longer-term evolutionary shifts due to local adaptation, thereby enhancing our capacity to predict both the persistence and redistribution of species under climate change.

A comparison between next-generation and standard 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 considered both intraspecific variability in a trait and its dynamic responses in different climates ('next-generation hierarchical trait-based SDMs'). They compared the predictions and forecasts of 'standard' hierarchical trait-based SDMs proposed by Pollock *et al.* (2012) with those of the next-generation hierarchical SDMs that integrate 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; Kozłowski, 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 standard and next-generation hierarchical trait-based SDMs yielded similar estimates of current ranges but significantly different estimates of future ones. Specifically, next-generation hierarchical trait-based SDMs that included trait evolution under changing climates forecasted 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 standard hierarchical trait-based SDMs (Fig. 3). The differences between forecasts of standard and next-generation 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.

Accounting for phylogenetic relationships in hierarchical trait-based SDMs

Even next-generation hierarchical trait-based SDMs, which incorporate both trait–climate relationships and trait–climate interactions, generally ignore phylogenetic relationships among species (Li *et al.*, 2020) and thus may result in biased or misleading inferences about trait–environment associations. Phylogenetic niche conservatism refers to the tendency of closely

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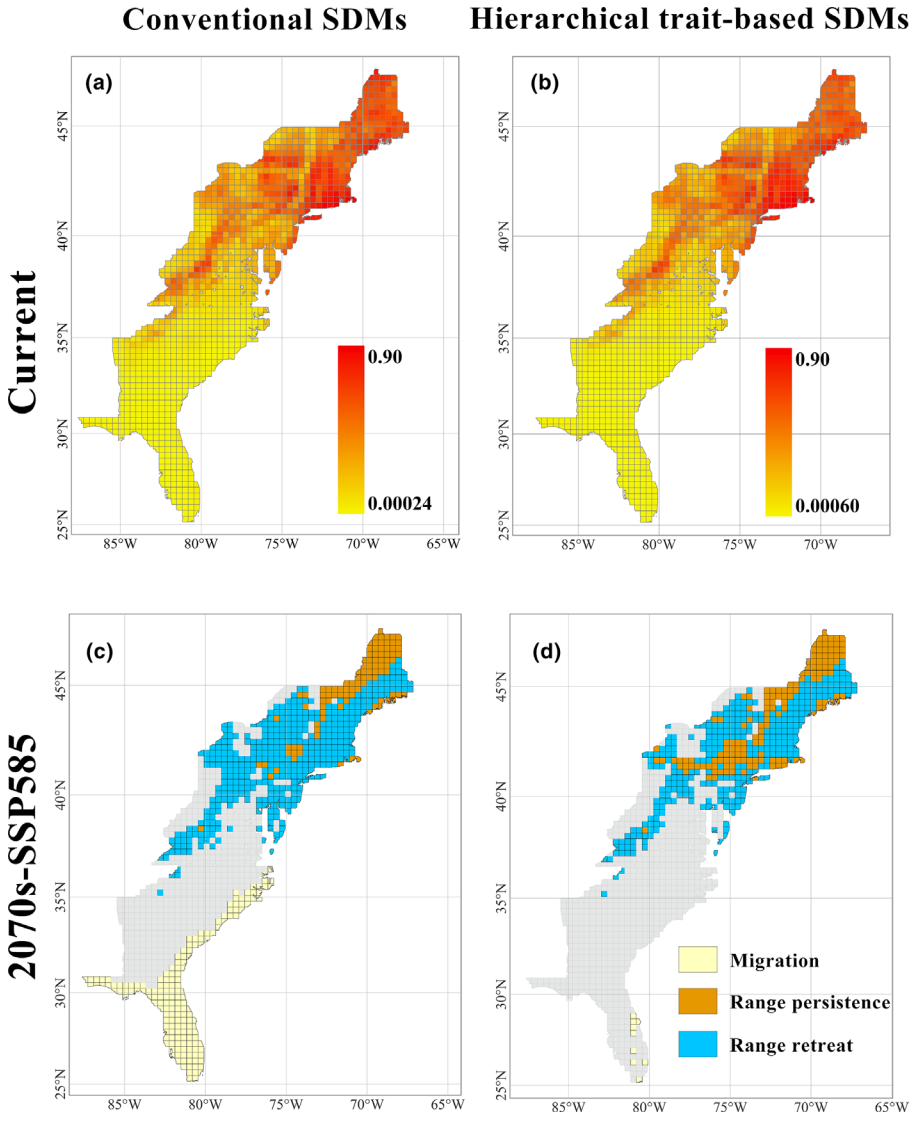

Fig. 3 Changes in species ranges forecasted by conventional species distribution models (SDMs, a, c) and hierarchical trait-based SDMs (b, d). The maps compare the current and future distributions (probability of occurrence) of *Trientalis borealis* (Raf.) U.Manns & Anderb. We classified future species 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); and yellow areas representing 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 Socio-economic Pathways 5–8.5 (SSP5-8.5) scenario from the average estimate of six General Circulation Models (GCMs) in 2070.

related species to be more similar to one another in terms of their ecological niches (Prinzing *et al.*, 2001; Wiens & Donoghue, 2004; Wiens & Graham, 2005), and phylogenetically-related species may have similar trait values (*see* Davis *et al.*, 2010a,b). Statistically, if multiple traits affect species occurrence (or abundance), the unmeasured traits with significant phylogenetic 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).

Li *et al.* (2020) proposed phylogenetic generalized linear mixed models (PGLMMs), which include a phylogenetic matrix, in hierarchical trait-based SDMs to account for the non-independence of species. However, the application of PGLMMs is limited to phylogenetic 'correction' (Gallinat & Pearse, 2021): if a trait shows a significant interaction with climate in a GLMM but loses significance in a PGLMM, this suggests that the trait has limited explanatory power for species distributions beyond phylogenetic constraints. However, existing PGLMM algorithms lack predictive capacity and are not designed to forecast species distributions. Hierarchical trait-based SDMs that do not incorporate phylogenetic information (i.e. the framework we summarized in this paper) thus remain an effective approach for simulating and predicting the influence of trait variation on species distributions under future climate change.

Conclusions

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

trait-based SDMs across very large spatial, temporal, and taxonomic extents.

There are two critical points that motivated this review and that need to be accounted for when using hierarchical trait-based SDMs. 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 hierarchical trait-based SDMs. Second, 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, to avoid overfitting and inflated Type I error rates, hierarchical trait-based SDMs ideally should explicitly incorporate phylogenetic relationships among species as a random component. PGLMMs are useful for assessing whether results are affected by phylogeny, but they are not yet suited for predicting species distributions.

Finally, whether process-based or hierarchical, trait-based SDMs so far have used only a small number of traits. More fitness-related traits should be measured and incorporated into 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 patterns at large spatial and taxonomic scales.

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Competing interests

None declared.

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.

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References

Anderegg WRL. 2015. Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. *New Phytologist* **205**: 1008–1014.

Anderson MJ, Walsh DCI, Sweatman WL, Punnett AJ. 2022. Non-linear models of species' responses to environmental and spatial gradients. *Ecology Letters* **25**: 2739–2752.

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. 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecological Modelling* **157**: 101–118.

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

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.

Blomberg SP, Garland T Jr, 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 & 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.

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.

Carboni M, Calderon-Sanou I, Pollock L, Violle C, DivGrass C, Thuiller W. 2018. 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.

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.

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

Dallas TA, Ten Caten C. 2025. Linking geographic distribution and niche through estimation of niche density. *Journal of Animal Ecology* **94**: 1221–1230.

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

Davis CC, Edwards EJ, Donoghue MJ. 2010a. A clade-eye view of global climate change. In: Bell MA, Futuyma DJ, Eanes WF, Levinton JS, eds. *Evolution since Darwin: The first 150 years*. Sunderland, MA, USA: Sinauer, 623–627.

Davis CC, Willis CG, Primack RB, Miller-Rushing AJ. 2010b. 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.

DeLong JP, Coblentz KE, Uiterwaal SF, Akwani C, Salsbery ME. 2023. Temperature and predators as interactive drivers of community properties. *Ecology and Evolution* **13**: e10665.

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 & 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 JA Jr, 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.

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

Green SJ, Brookson CB, Hardy NA, Crowder LB. 2022. Trait-based approach to global change ecology: moving from description to prediction. *Proceedings of the Royal Society B: Biological Sciences* **289**: 20220071.

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

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.

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, UK: Oxford University Press.

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 & 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 Science* **24**: 921–931.

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

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.

Jamil T, ter Braak CJF. 2013. Generalized linear mixed models can detect unimodal species-environment relationships. *PeerJ* **1**: e95.

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.

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 & Evolution* **7**: 15–19.

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

Laughlin DC, Laughlin DE. 2013. Advances in modeling trait-based plant community assembly. *Trends in Plant Science* **18**: 584–593.

Li D, Dinnage R, Nell LA, Helmus MR, Ives AR. 2020. PHYR: an R package for phylogenetic species-distribution modelling in ecological communities. *Methods in Ecology and Evolution* **11**: 1455–1463.

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. Traits predict drought performance and distribution of Mediterranean woody species. *Acta Oecologica* **56**: 10–18.

Maharjan SK, Sterck FJ, Dhakal BP, Makri M, Poorter L. 2021. 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. 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, Augspurger C, Chuine I. 2007. Process-based modeling of species' distributions: what limits temperate tree species' range boundaries? *Ecology* **88**: 2280–2291.

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.

Morin X, Viner D, Chuine I. 2008. Tree species range shifts at a continental scale: new predictive insights from a process-based model. *Journal of Ecology* **96**: 784–794.

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, 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.

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.

Pollock LJ, Kelly LT, Thomas FM, Soe P, Morris WK, White M, Vesk PA. 2018. Combining 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 traits in species distributions revealed through a hierarchical model. *Ecography* **35**: 716–725.

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 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 & 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 DA Jr. 1999. Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecological Monographs* **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.

Smith AB, Alsdurf J, Knapp M, Baer SG, Johnson LC. 2017. Phenotypic distribution models corroborate species distribution models: a shift in the role and prevalence of a dominant prairie grass in response to climate change. *Global Change Biology* **23**: 4365–4375.

Soudzilovskaia N, Elumeeva TG, Onipchenko VG, Shidakov II, Salpagarova FS, khubiev AB, Tekeev DK, Cornelissen JHC. 2013. Functional traits predict relationship between plant abundance dynamics and long-term climate warming. *Proceedings of the National Academy of Sciences, USA* **110**: 18180–18184.

Stanton ML. 1984. Seed variation in wild radish: effects of seed size on components of seedling and adult fitness. *Ecology* **65**: 1105–1112.

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.

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

Wiens JJ, Donoghue MJ. 2004. Historical biogeography, ecology, and species richness. *Trends in Ecology & 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, 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.

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 traits on the prediction accuracy of species richness models. *Diversity and Distributions* **22**: 905–917.

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