LETTER

A predictive model of community assembly that incorporates intraspecific trait variation

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Abstract

Community assembly involves two antagonistic processes that select functional traits in opposite directions. Environmental filtering tends to increase the functional similarity of species within communities leading to trait convergence, whereas competition tends to limit the functional similarity of species within communities leading to trait divergence. Here, we introduce a new hierarchical Bayesian model that incorporates intraspecific trait variation into a predictive framework to unify classic coexistence theory and evolutionary biology with recent trait-based approaches. Model predictions exhibited a significant positive correlation ($r = 0.66$) with observed relative abundances along a 10 °C gradient in mean annual temperature. The model predicted the correct dominant species in half of the plots, and accurately reproduced species' temperature optimums. The framework is generalizable to any ecosystem as it can accommodate any species pool, any set of functional traits and multiple environmental gradients, and it eliminates some of the criticisms associated with recent trait-based community assembly models.

Keywords

Assembly rules, bark thickness, environmental filtering, hierarchical Bayesian model, limiting similarity, maximum entropy, specific leaf area, trait convergence, trait divergence, wood density.

INTRODUCTION

Predicting species abundances is one of the most fundamental pursuits in ecology. The promise of predicting species abundances using physiological principles has generated tremendous interest (Shipley *et al.* 2006), has inspired vigorous debate (Marks & Muller-Landau 2007; Roxburgh & Mokany 2007; Haegeman & Loreau 2008; Shipley 2009) and has been heralded as the Holy Grail of ecology (Lavorel & Garnier 2002). Accurate prediction is crucial given the need to understand the rate and direction of species migrations in a rapidly changing world (Araújo & Rahbek 2006), and predictive models are required to test the rigour of ecological theory (Peters 1991). Ecologists have long observed that phenotypic traits of species influence their abundance and distribution across landscapes (Schimper 1903; Grime 1979), but only recently have mathematical models of trait-based community assembly been developed (Shipley *et al.* 2006), spawning a 'renaissance' in the prediction of species abundances (McGill 2006). However, community assembly is driven by two processes that select functional traits in opposite directions, which makes predicting the outcome of such processes particularly challenging.

Assembly theory proposes that individuals are sorted along environmental gradients because their functional traits (i.e. physiological and morphological properties) influence their fitness and performance (Keddy 1992; McGill *et al.* 2006; Webb *et al.* 2010). Consequently, species with similar functional traits will more likely be found in similar environments, leading to *convergence* of trait values within communities (Shipley 2010). But, there is yet another important process: competition. In opposition to the selective force of the environment, competition for limiting resources tends to limit the functional similarity of co-occurring species, thereby reducing interspecific competition and thus promoting species coexistence (Macarthur & Levins 1967; Silvertown 2004). The general consequence of such limiting similarity is the *divergence* of trait values within communities, although competition can sometimes lead to the exclusion of functionally distinct species as well (Mayfield & Levine 2010). Environmental filtering has been shown to be a stronger force across a range of global plant communities (Freschet *et al.* 2011), but both processes have been simultaneously detected (Kraft *et al.* 2008) and the relative importance of each is likely system dependent. How do we model community assembly when the two dominant processes paradoxically predict trait convergence and divergence?

The first mathematical translation of trait-based community assembly was Shipley's maximum entropy (MaxEnt) model (Shipley *et al.* 2006). This important model focuses on trait convergence by environmental filtering because the species that are predicted to be most likely to occur are those whose mean trait values are closest to the predicted community-weighted mean trait value (Laughlin *et al.* 2011; Shipley *et al.* 2011). This approach ignores intraspecific trait variation, which is an ecologically important source of trait variation in plant communities (Albert *et al.* 2010; Messier *et al.* 2010). Detecting the joint effects of environmental filtering and limiting similarity on community structure is enhanced if this source of variation is incorporated into analyses (Jung *et al.* 2010). Moreover, individuals are the objects responding to environmental gradients, not

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species *per se* (Clark *et al.* 2011), and individual-level variation may be important for species coexistence (Clark 2010). Theoretically, phenotypic variation can promote the fitness of one individual, whereas another individual from the same species with different trait values may be unable to survive. By ignoring intraspecific trait variation, we disregard more than a century of research in evolutionary biology.

The classic theory of limiting similarity proposed that coexistence will be related to the level of niche overlap, which is quantified as the ratio of differences in species niche means to intraspecific niche widths (Macarthur & Levins 1967). Species niches can be quantified by their variation in functional traits because traits reflect the functional adaptations of species (Violle & Jiang 2009). Therefore, we propose that the unification of these antagonistic community assembly processes into a predictive model can be accomplished by incorporating intraspecific trait variation. Indeed, such variation has recently been recognised as being central to understanding community assembly (Violle *et al.* 2012).

Here, we introduce a hierarchical Bayesian modelling framework and evaluate its performance along a 10 °C gradient in mean annual temperature (MAT). We show that incorporating intraspecific trait variation is the key to reconciling antagonistic processes of trait-based community assembly, and that predicting species abundances can be accomplished without knowing or predicting community-weighted mean traits.

MATERIAL AND METHODS

Traitspace: a new trait-based model of community assembly

Our new framework explicitly combines trait convergence and divergence into the prediction of species' relative abundances. Rather than relying on trait means (Shipley *et al.* 2006), we incorporate the full distribution of observed trait values. This approach allows species to overlap in trait space and allows individuals within species to differ. This is based on the premise that the traits that exist at a site were filtered by the environment, and that the relative abundance of each species is a function of its trait value distribution (Fig. 1). Mathematically, this hierarchical dependence structure can be represented using a directed acyclic graph: $E \rightarrow T \rightarrow S$ (Fig. 1), where E represents m-dimensional environmental gradients, T represents n-dimensional functional traits and S is a vector of the relative abundances of s unknown species $S_1, \ldots, S_s$. Our objective is to estimate the relative abundance of the ith species in a given environment $P(S_i | E)$, by incorporating information about individual-level functional traits.

Our Traitspace model consists of two stages: a *calibration* stage and an *inference* stage (see Fig. 2 for a step-by-step guide). The calibration stage involves the following two steps. Step 1a: Characterise the size and shape of the environmental filter using a Generalised Linear Model to fit $T = f(E)$. This calibrates the conditional distributions of individual-level plant traits given the environmental conditions $\phi_{T|E}$. This approach differs from MaxEnt because it models variation in individual-level traits, not variation in community-weighted mean traits (Laughlin *et al.* 2011). This step can easily accommodate multiple environmental gradients by incorporating more than one environmental variable into a multiple regression model. We limited our study to a single climate variable because mean annual precipitation was highly collinear with MAT. Other
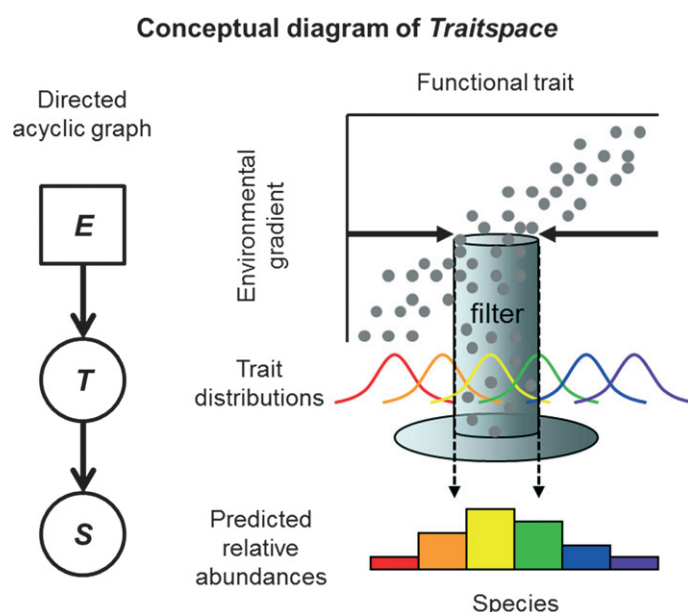
environmental gradients (soil properties, disturbance history) would have improved our ability to model trait distributions, but such data were unavailable. In our application, we used Generalised Linear Models with a *log* link function and polynomial regression equations using the 'lm' function in R (version 2.13.1, R Core Development Team 2012) to determine the relationship between individual-level plant trait values and MAT. While the use of the *log* link function ensured that the simulated trait values were always positive, the polynomial regression equations were used to account for the inherent non-linearity in the trait values. Specific leaf area (SLA) exhibited a distinctly bimodal distribution because of the strong differences between conifers and angiosperms. This also caused increasing variance in SLA along the temperature gradient. To accommodate this bimodality, the regression equation was fit separately to the SLA values corresponding to the two classes of species; this is a standard statistical approach for accommodating bimodal distributions. The models used for each of the trait values are as described below. In these models, t denotes the MAT, and the error ε is assumed to follow a Gaussian distribution with mean zero and a constant variance. For SLA (fit separately to the two classes of species), the model was $\log(SLA) = \alpha + \beta_1 t + \beta_2 t^2 + \varepsilon$. For wood density, the model was $\log(\text{wood density}) = \alpha + \beta_1 t + \beta_2 t^2 + \beta_3 t^3 + \varepsilon$. For Bark thickness, the model was $\log(\text{bark thickness}) = \alpha + \beta_1 t + \beta_2 t^2 + \varepsilon$. These models define the size and shape of the environmental filters. Each trait value was weighted equally in the model (i.e. we did not weight trait observations by species relative abundance).
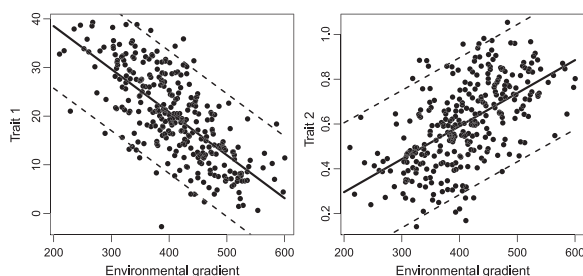
Step 1b: Characterise the location and dispersion of species in trait space using semi-parametric Gaussian mixture models with the

Conceptual diagram of *Traitspace*

Figure 1 Conceptual illustration of the Traitspace model illustrating the directed acyclic graph on the left (E = environmental gradients, T = traits, S = species), and trait selection through environmental filters on the right. Grey dots represent hypothetical observed individual-level functional trait values, and the size of the environmental filter (indicated by the arrows at a specific point on the gradient) determines the range of trait values in a given environment. The trait distributions of six hypothetical species indicate that the yellow and green species should be the most likely to occur in that environment because their trait values occur within the range of the filter.
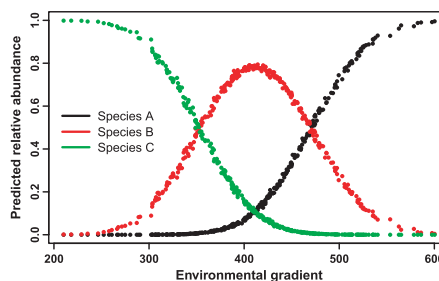
Figure 2 Step-by-step guide to Traitspace using simulated data to illustrate the general framework. This example can be followed and explored further using the R code for implementing Traitspace in Appendix S1. E = environmental gradients; T = traits; S = species relative abundances.

'Mclust' function in the 'mclust' library of R (Fraley & Raftery 2009). This calibrates the conditional distributions of traits given species $\phi_{T|Si}$ (Fig. 2). This function fits a series of mixture models with different number of components and also with various covariance structures using the Expectation Maximisation algorithm (Fraley & Raftery 2009) and then selects the best model using the Bayesian Information Criterion. This method provides a flexible approach for locating species in trait space because it can handle complex, multivariate, non-normal distributions.

The inference stage involves the following four steps (Fig. 2). Step 2a: Simulate community assembly stochastically by sampling a large number (e.g. $N = 1000$) of traits from the distributions $\phi_{T|E}$ at every value along the environmental gradient(s). This simulation is the critical step in resolving the antagonistic processes because it emulates environmental filtering by centring the samples on the expected mean trait values (leading to trait convergence), but also incorporates limiting similarity by representing the full range of trait values that are possible within a given environment (leading to trait divergence). In other words, it maximises trait dispersion within the boundaries of the empirical filter. In our application, the temperature values (i.e. E) were taken from locations at which community structure had been measured to assess model fit. Note that this step can also be expanded to include multiple environmental filters if the data are available. In the case of SLA, two-thirds of the samples were drawn from the lower distribution and one-third was drawn from the higher distribution because these reflect the proportions of each class in the dataset. Samples were drawn from within the boundaries of their range.

Step 2b: For every trait sampled in step 2a, compute the likelihood $P(T|S_i)$ using the conditional distributions $\phi_{T|Si}$. Step 2c: for every trait, compute the posterior distribution of species conditioned on both the trait data and the environmental conditions $P(S_i|T,E)$ using Bayes theorem (McCarthy 2007):

$$P(S_i|T, E) = \frac{P(T|S_i)P(S_i)}{\sum_{i=1}^{S} P(T|S_i)P(S_i)}. \tag{1}$$

$P(S_i)$ denotes a flat (uniform) prior on the species. This choice of prior reflects that all species are assumed equally likely to occur prior to the analysis. If certain species are more likely to occur (e.g. dispersal may be limited for uncommon species), then more informative priors could be used (Shipley *et al.* 2012). The numerator in Equation 1 is the product of the likelihood and the prior, and the denominator is a normalizing term so that the probabilities sum to one. Note that Equation 1 is valid because we have $P(S_i|T, E) = P(S_i|T)$, which is an implication of the directed acyclic graph model. Step 2d: Integrate out the traits to obtain the relative abundances of species given the environmental conditions

$$P(S_i|E) = \int P(S_i|T, E)P(T|E)dT. \tag{2}$$

Using Monte Carlo integration, the desired conditional distribution is thus approximated as

$$P(S_i|E) \cong \frac{1}{N}\sum_{k=1}^{N} P(S_i|T_k, E)P(T_k|E). \tag{3}$$

Importantly, Traitspace develops predictions of relative abundances that do not rely on community-weighted mean traits, which removes the necessity of measuring species abundances to quantify trait–environment relationships (Shipley *et al.* 2006; Marks & Muller-Landau 2007; Roxburgh & Mokany 2007). Traitspace was implemented using widely available statistical packages in R, and we have made our program code available (see Appendix S1 in the Supporting Information).

Data collection

To evaluate this new model's performance, we calibrated Traitspace using three functional traits measured on nine tree species in the southwest USA. We tested Traitspace predictions using independent observations of tree species abundances measured on 196 plots within forests that have been relatively undisturbed by humans on the North Rim of Grand Canyon National Park (lat 36.342, long −112.355) and in the Kachina Peaks Wilderness Area on the San Francisco Peaks (lat 35.320, long −111.672) in Arizona, USA. These sites spanned upland vegetation between 2200 and 3600 m altitude, corresponding to a 10 °C range in MAT. These sites included ponderosa pine–Gambel oak, mixed conifer, and subalpine forests. Plots were 0.1 ha in size (i.e. 20 × 50 m). On each plot tree species and diameter at breast height (dbh; 1.37 m) were recorded for all trees >15 cm dbh on the whole plot, and on all trees between 2.5 and 15 cm on a 250 m² subplot. A total of nine tree species was encountered in these upland forests. Bayesian inference yields predictions of probability, and since the probabilities across all species sum to one we interpret them as relative abundances. Therefore, we calculated the relative abundances of each of the nine species as the proportional basal area at breast height of each of the species divided by the total basal area of the plot. These plots were only used to test the predictive power of the model, and were not used in the Traitspace model calibration.

We measured SLA, wood density, and bark thickness on individuals of each species. These traits were chosen to represent key spectrums of plant strategies (Vines 1968; Wright *et al.* 2004; Chave *et al.* 2009). Previous studies have shown that SLA and wood density vary along climatic gradients and that bark thickness varies along climatically induced fire regimes (Laughlin *et al.* 2011). These traits are also useful in that they are not strongly correlated and therefore provide non-redundant information about an individual plant. Samples were obtained along the full climatic range of each species to maximise the variance observed in each trait. Traits were measured at locations that were separate from the sites used to assess model fit, ensuring independence between model calibration and inference. We measured traits on robust individuals growing in well-lit environments or canopy gaps in the summers of 2009 and 2010. For seven species, we sampled all three traits simultaneously on between 58 and 89 individuals per species. For *Quercus* and *Robinia* we were only able to sample 22 and 21 individuals, respectively. This lower sample size for these two species did not affect the ability to discriminate these species in trait space since they were very strongly separated from other species and from each other. We note that the observed trait variation in this study does not distinguish between the three sources of trait variation (i.e. genetic, environmental, or genetic × environmental variation).

The SLA is the ratio of leaf area to dry weight expressed as mm² mg⁻¹. We non-randomly selected one fully expanded, healthy leaf from each individual for this measurement. Leaves were immediately sealed in plastic bags and one-sided leaf area was measured using WinFolia (Regent Instruments, Inc.) within 5 h of harvesting.

Leaves were oven-dried for at least 72 h at 55 °C prior to obtaining dry weights.

Wood density is the dry mass to fresh volume ratio of woody material. We used increment borers to extract two cores at breast height from different sides of each individual tree. Wood density for the individual was calculated as the mean density of the two subsamples. Fresh volume of the core was estimated using the formula of a cylinder: $V = \pi r^2 l$, where r is the radius of the core (2.54 mm), and l is the length of the core sample. Wood was oven-dried for at least 2 weeks at 55 °C prior to obtaining dry weights.

Bark thickness is an important trait of woody species in fire-prone ecosystems because it protects the cambium from external damage. On each of the core samples extracted for measuring wood density, we measured the thickness of the outer bark (i.e. we did not include the spongy phloem). Bark thickness varies substantially in species with ridged bark, such as ponderosa pine. Therefore, the borers were inserted in a furrow and in a ridge to obtain a mean bark thickness per individual tree, which implicitly assumes equal ratios of ridges to furrows around the surface of the stem. This produces a conservative estimate of bark thickness since ridges generally comprise >50% of the tree surface area for species with ridged bark. In addition, we standardised bark thickness by expressing it as mean thickness divided by dbh (cm cm^{-1}) because bark thickness tends to increase as a function of the age or size of the tree.

Maximum entropy model

Shipley *et al.*'s (2006) maximum entropy model of community assembly proposes that the vector of species relative abundances at a site (p_i) can be estimated by developing a system of linear constraint equations of the general form $\sum_{i=1}^{S} t_i p_i = \overline{T}$. This equation states that the linear combination of species traits (t_i) and unknown species relative abundances (p_i) is equal to the constraint $\overline{T}$, where $\overline{T}$ is the trait value of an average unit of biomass in a community. MaxEnt selects the solution with maximum entropy, i.e., the distribution that maximises the entropy function, $H' = -\sum_{i=1}^{S} p_i \ln p_i$. We obtained the maximum entropy predictions using the 'maxent' function in the 'FD' library of R with a tolerance level of 1×10^{-8}. We used independent cross-validation to evaluate model predictions from sites where trait constraints were predicted from environmental conditions (Laughlin *et al.* 2011).

MaxEnt can potentially incorporate instraspecific trait variation by changing the mean value of a trait given the MAT if there was a significant relationship between intraspecific trait variation and temperature. For most traits and species, these relationships were weak (most $R^2 < 0.2$), but some were significant (see Appendix S2). We report MaxEnt results using the traditional static mean trait method as well as the method that attempts to incorporate intraspecific trait variation. Incorporation of higher moments (community weighted mean trait variance) to account for trait dispersion (Shipley 2010) did not change MaxEnt model fits.

Model evaluation

Model predictions were compared with observed relative abundances using Procrustes r statistic (Peres-Neto & Jackson 2001), which is a measure of correlation between two matrices. This procedure uses a series of matrix translations, reflections, rigid rotations and dilations of the model-predicted matrix of relative abundances in order to minimise the sum-of-squared deviations between it and the observed matrix of relative abundances. The *P*-values are derived by comparing the observed statistic to statistics obtained after 1000 permutations of entire rows within matrices.

The ability of Traitspace to identify the correct dominant species was compared. We calculated the proportion of times that Traitspace correctly identified the most dominant species in the community defined as the species with the highest relative abundance. We also evaluated the correlation between observed and predicted temperature optimums among species by comparing the MATs at which each species was observed and predicted to obtain their highest relative abundance.

RESULTS

The mean and variance of SLA tended to increase with increasing temperature (Fig. 3A). Wood density was lowest at intermediate temperatures, highest in the hottest and driest environments, and also high in the coldest environments where precipitation was high but where unfrozen water availability was low (Fig. 3B). Bark thickness increased non-linearly with increasing temperatures (Fig. 3C). The three traits varied greatly within and among species (Fig. 4). Across all individuals, SLA ranged from 2.2 to 32.6 mm^2 mg^{-1}, wood density ranged from 0.26 to 0.76 mg mm^{-3}, and bark thickness ranged from 0.001 to 0.082 cm cm^{-1}.

How well do the individual-level trait-environment relationships translate into predictions of relative abundance using the Traitspace framework? Traitspace predictions were positively correlated with observed relative abundances and were significantly better than expected by chance ($r = 0.66$, $P = 0.001$). In comparison, MaxEnt predictions using static mean traits yielded a correlation of 0.74 ($P = 0.001$), and predictions that incorporated intraspecific trait variation yielded a correlation of 0.73 ($P = 0.001$).

Traitspace accurately identified the most abundant species 51% of the time, and mismatches were often associated with species that had similar trait values and were therefore functionally redundant. Traitspace tended to underestimate the abundances of dominant species: the mean ± SE of predicted relative abundances of species with at least 50% of the observed relative abundance was 0.269 ± 0.011. Traitspace usually predicted low abundances of absent species: the mean ± SE of predicted relative abundances of species absent from a plot was 0.074 ± 0.002.

Comparison of observed and predicted relative abundances illustrates that in most cases Traitspace correctly located species along the temperature gradient (Fig. 5a–j). All correlations between observed and predicted relative abundances for each species were significant ($P < 0.05$). There was a strong linear correlation between observed and predicted MAT optimums among species (Fig. 5j).

DISCUSSION

Predicting species abundances based on the selection of functional traits along environmental gradients is a central goal in community ecology. Our new approach provides a flexible and general framework that unifies classic coexistence theory and evolutionary biology with recent trait-based approaches. Our results have several implications.
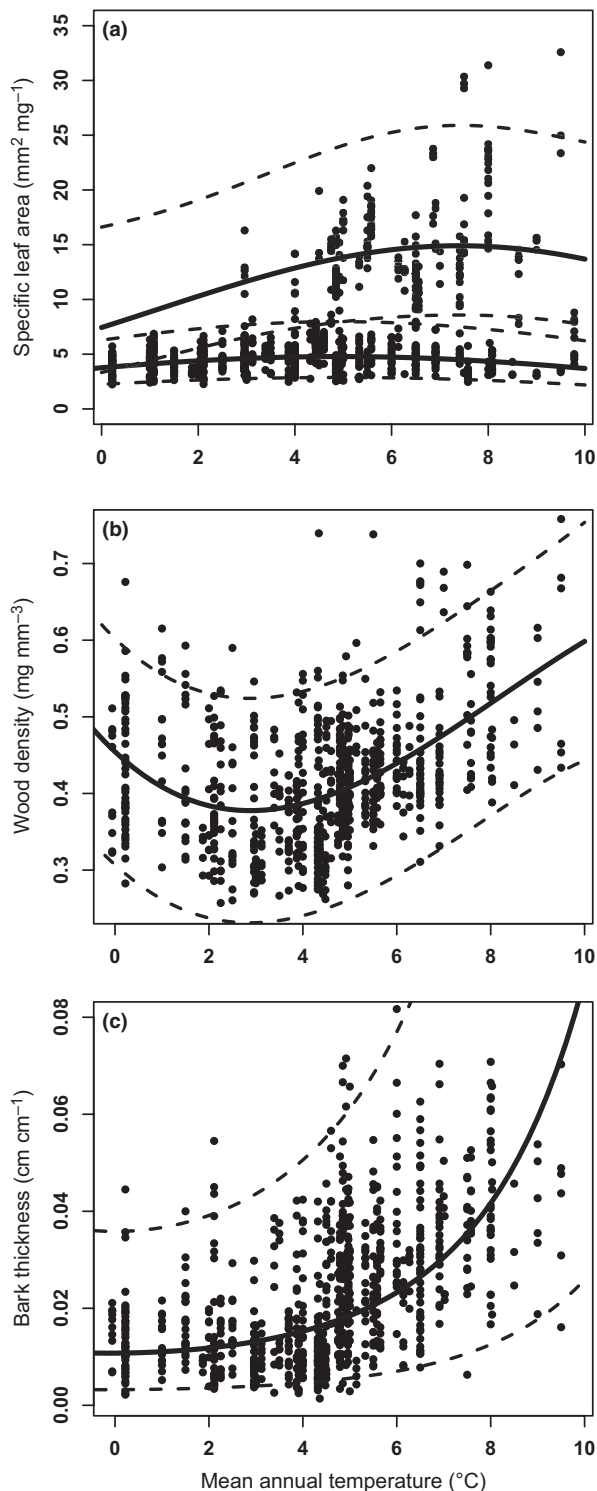
Figure 3 Relationships between mean annual temperature and (A) specific leaf area (SLA), (B) wood density and (C) bark thickness. Traits were measured on individual plants and do not represent community-weighted means. These significant ($P < 0.05$) relationships were quantified in Step 1a of model calibration. Solid lines indicate the expected values. Dashed lines represent the 95% prediction intervals, which approximate the size of the environmental filter and the boundaries from which to randomly sample trait values at each temperature to simulate the assembly process. The SLA was modelled using two classes to account for the bimodal distribution of SLA between conifers (lower curve) and angiosperms (upper curve).

Intraspecific trait variation was central to reconciling the antagonistic processes of trait-based community assembly. Traitspace operationalises trait convergence by centring traits on their expected values during the simulation of community assembly, yet simultaneously maximises trait dispersion by drawing samples from the entire range of the probability distributions. The unification of these antagonistic processes is made possible by embracing the phenotypic trait variation within species that has been a central focus of both evolutionary biology (Hallgrimsson & Hall 2005) and the classic theory of limiting similarity (Macarthur & Levins 1967). Furthermore, because large global trait databases (Kattge *et al.* 2011) are including data on intraspecific trait variation collected at specific places with known (or modelled) climatic conditions, it is possible to incorporate global trait datasets into our modelling framework.

There was clear selection of traits along the climatic gradient. The Traitspace framework permits the quantification of the size and shape of the environmental filters because individual trait values (not community-weighted means) are used in model calibration. Individuals with low SLA were preferentially selected in the coldest environments. Low SLA is generally associated with long-lived, dense leaves that continually fix carbon even in cold environments and will promote higher fitness in cold environments. Individuals with less dense wood were preferentially selected in the intermediate temperatures where water availability was highest. Individuals with thick bark were preferentially selected in the warmest environments where fires were most frequent. At the same time, the variance of traits at a given temperature was high, indicating that environmental filtering, at least by MAT, was relatively weak (Fig. 3). For example, the range of values of wood density at any temperature was *c.* 0.3 mg mm^{-3}, which is 60% of the entire range of wood densities observed. Such large trait variance within each site along the temperature gradient may imply that limiting similarity can be a relatively strong force relative to environmental filtering, though the relative importance of each process likely differs among systems. Alternatively, temperature was not the only environmental factor operating along the elevation gradient, but data limitations precluded the incorporation of additional predictors, which might have improved trait–environment relationships.

Traitspace predictions fit the observations nearly as well as MaxEnt without the use of community-weighted mean traits as model constraints. The reliance on community-weighted means in a model requires independent observations of community structure in order to predict them in other sites (Laughlin *et al.* 2011). This might explain MaxEnt's better model fit once such additional information is available to constrain the model.

Traitspace tends to underestimate the abundance of dominant species and overestimates the abundance of absent species. This is a technical issue found in MaxEnt as well because every species is assigned a non-zero probability (Sonnier *et al.* 2010). Positive prediction errors (i.e. higher predicted than observed relative abundances) for absent species accumulate and lead to negative prediction errors for dominant species. Two options for dealing with this problem include using more informative priors, or changing the size of the species pool to include only those species that have some probability of establishing at the site.

Results suggest that functionally redundant species can be difficult to discriminate. For example, on several occasions the model predicted *Abies lasiocarpa* dominance when *Picea engelmannii* was the
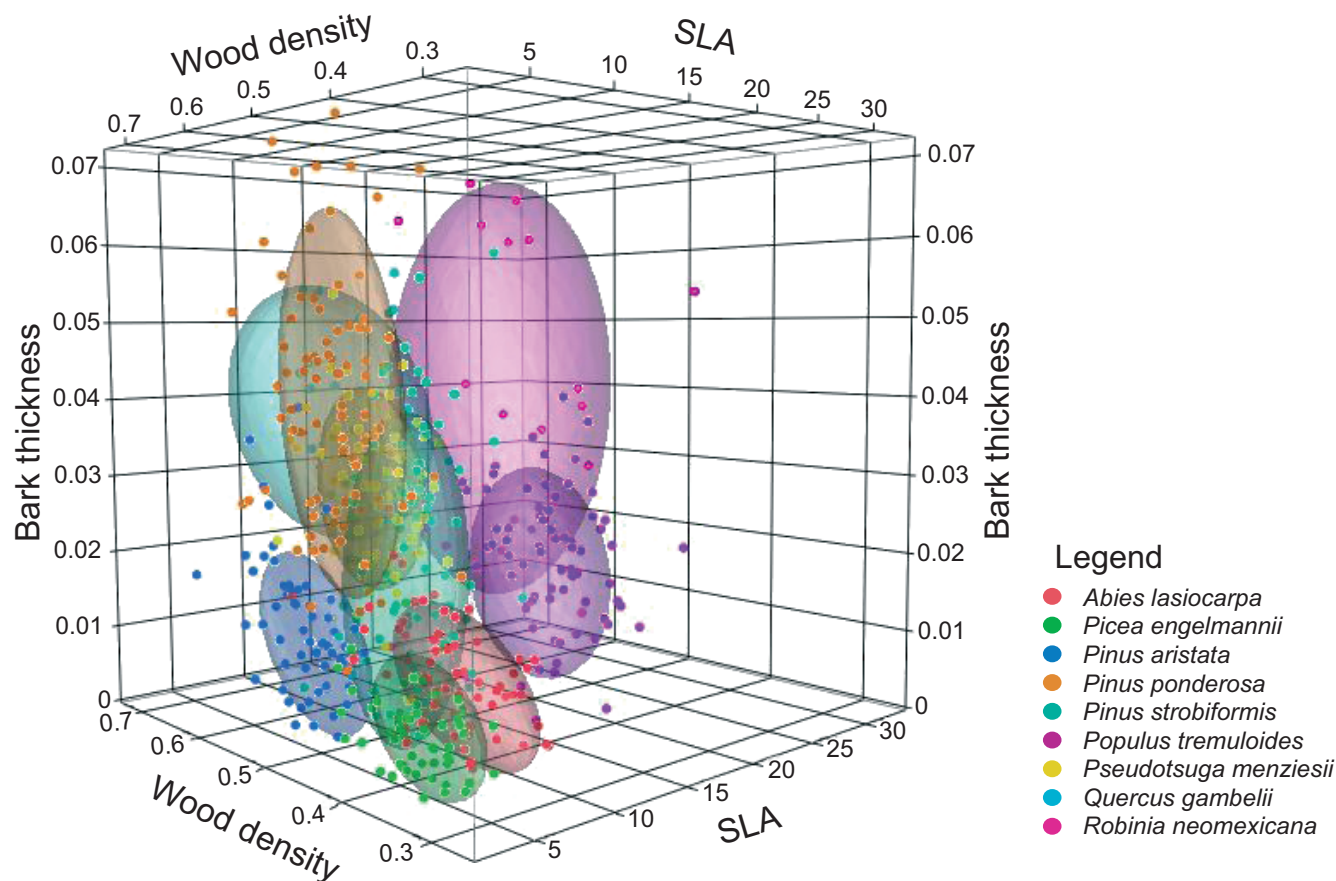
Figure 4 The location and variation of the nine tree species within three-dimensional trait space. These distributions are quantified in Step 1b of model calibration. The density clouds shown here represent the middle 50th percentile of a Gaussian distribution, and are therefore greatly simplified representations of the mixture models.

actual dominant. These two species substantially overlap in three-dimensional trait space (Fig. 4). The species pool of the southwest USA is small compared to other species-rich ecosystems that contain much greater functional redundancy, indicating that this type of error would likely be greater in more diverse systems. Testing this approach in different ecosystems of varying diversity will be important to understand the limitations of the model. As diversity increases, the use of additional traits will make it easier to discriminate between functionally similar species.

Traitspace provides an alternative approach for predicting the relative abundances of every species in the regional pool. There are two notable advantages of Traitspace. First, it provides a natural incorporation of intraspecific trait variation into the modelling framework, and this variation is increasingly recognised as being central to understanding community assembly (Violle *et al.* 2012). Second, it does not require the measurement of community structure and the calculation of community-weighted mean traits at independent sites to predict community structure elsewhere. Traitspace implementation requires adequate replication of traits for every species in the regional pool associated with measurements of environmental conditions. These data requirements can be demanding, but this information is necessary to account for intraspecific trait variability. An advantage of MaxEnt is that species are defined more simply by a vector of trait means, thus requiring less input data to parameterise the model. However, estimates of mean traits require

adequate replication within species as well, and so in practice MaxEnt also requires substantial data. Both models are valuable tools for assessing the importance of niche-based processes in community assembly.

Traitspace incorporates two antagonistic assembly processes that occur across a range of ecosystems into a flexible modelling framework. It can easily be expanded to incorporate the joint effects of multiple environmental factors. Knowledge of dispersal limitation, priority effects and pre-empted trait spaces can also be used to inform the priors and the stochastic sampling of trait values to simulate different conditions in the assembly process. Indeed, future applications should explore the possibility of different trait sampling strategies (in Step 2a of the model inference) to incorporate the fact that the extent of trait divergence changes along environmental gradients. Given that any species pool, any set of functional traits and any environmental gradient can be incorporated into this general framework, it is potentially applicable to any ecosystem and any group of organisms on the planet.
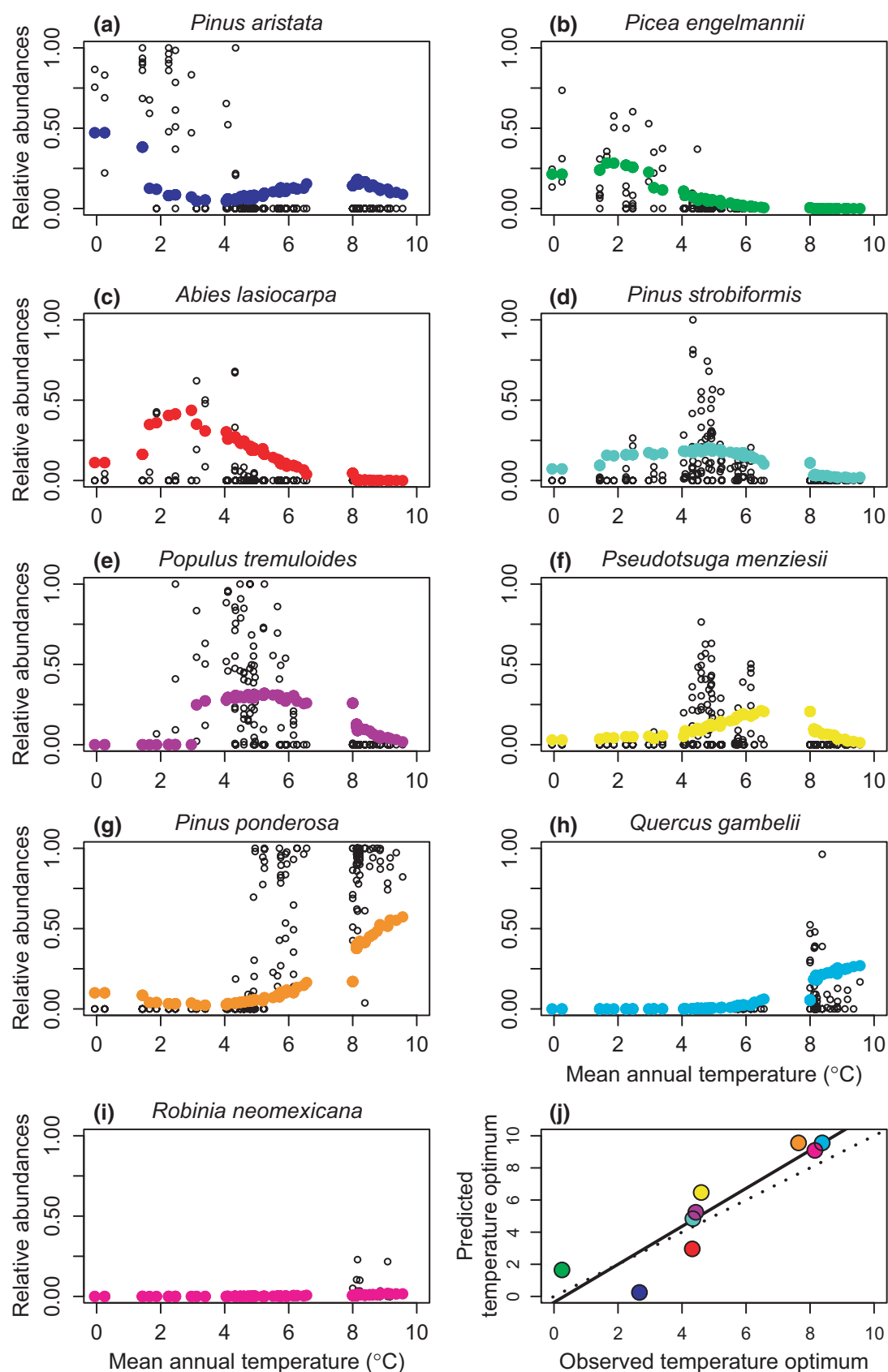
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Figure 5 (a–i) Predicted vs. observed relative abundances displayed separately for each species along the gradient in mean annual temperature. Predicted values are shown as coloured circles and observed values are shown as open white circles. (j) Linear fit between observed and predicted mean annual temperature optimums among species ($r = 0.92$, $P = 0.0005$). Note that species colour coding is the same as shown in panels a through i. The dotted line represents the 1:1 line.

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