A universal coexistence hypothesis resolves the biodiversity paradox: Species differences that generate diverse forests

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Abstract

Ecological theory aims to understand how and why species differences allow competitors to coexist, but explanations remain inconsistent with data. Tightly constrained parameter tradeoffs needed for coexistence in models contrast with evidence that forests can support high diversity and be invaded repeatedly by species that lack specialized tradeoffs. By translating environmental responses to individual covariance, a universal coexistence hypothesis shows i) that species differences lead to a natural tendency to concentrate competition within the species, the common feature needed to promote coexistence in models, and ii) the fingerprint of this effect is available in covariances between individuals that can be observed in nature. The many ways in which species differ make high diversity almost inevitable. This covariance not only provides the evidence for this mechanism; it further provides a new direction for earth surface models that currently cannot sustain diverse communities despite large numbers of evidence-based parameters.

Introduction

Ecology lacks theory that predicts high species diversity from data as an inevitable consequence of the variation that is ubiquitous in nature (fig. 1). The need to understand diverse forests when ecological models can explain only limited coexistence (Tilman, 1985; Falster et al., 2017) has become more than an academic exercise. The earth system models used to anticipate future forest function suffer the same problem, despite dozens to hundreds of parameters that are, to the extent possible, extracted from empirical data or evidence-based theory (Fisher and Koven, 2020). A universal coexistence hypothesis developed here translates the high-dimensional variation that is well-known to ecologists and systematists into its observable effects that generate the diversity needed to study forest change.

A challenge shared by simple, theoretical models of competition (May, 2001; Tilman, 1985; Serván et al., 2018), large stand simulators (Maréchaux and Chave, 2017; Rüger et al., 2020; Courbaud et al., 2022), and dynamic earth system models used to predict global change (Fisher et al., 2018; Longo et al., 2019; Fisher and Koven, 2020; Rollinson et al., 2021) is the problem of predicting the high diversity observed in nature. Ecologists have long recognized that plant populations can be limited by a small number of resources (Tilman, 1985; Nogueira et al., 2018), seemingly utilized in similar ways by many competing species. In closed forests, trees compete for light, in part, through height growth. They procure water and nutrients through expanded root systems. Tree growth and fecundity respond to variation in one to a few resources, but not to dozens of resources (Bloom et al., 1985; Tilman et al., 1998; Qiu et al., 2022). Despite intense density-dependent mortality from competition for apparently few limiting resources (Assmann, 1970; Westoby, 1984; D'Amato et al., 2013; He et al., 2022), diversity can be high, and stands are still frequently invaded by introduced species. Yet the many structural and physiological differences that are parameterized in large models do not lead to coexistence. Instead, maintaining diversity in the absence of parameter values carefully selected for this purpose depends on the assumption that seeds remain available even when the adults that would produce those seeds are not (Pacala et al., 1996; Maréchaux and Chave, 2017; Longo et al., 2019; Rüger et al., 2020).

Models that achieve coexistence of competitors for few resources do so in one of two related ways. The first way is through a narrow specification of parameter values, usually in the form of tradeoffs, to assure that each species wins somewhere. For plant species competing for only two resources, coexistence in the resource-ratio model (Tilman, 1985) requires a strict trade-off in minimum resource requirements for each species. Despite this restrictive tradeoff assumption, coexistence still only occurs if the environment offers the precise supply rates that would make a different species pair stable at each ratio of resource requirements. Higher diversity requires more specifically aligned tradeoffs to allow that every species has the advantage somewhere (MacArthur, 1969; Falster et al., 2017; Detto et al., 2022). Coexistence in models is also achieved with narrowly specified competitive intransitivities to insure that there are enough competitive reversals between species such that each species can win for some combination of interactions (Laird and Schamp, 2006; Bunin, 2017; Serván et al., 2018; Gavina et al., 2018; Laan and de Polavieja, 2018; Amarasekare, 2002).

A second, albeit related (see below), way to predict diversity in models is to build in the assumption that competition is weak. Diverse communities are predicted by the Lotka-Volterra model if there is diagonal dominance in the species-by-species interaction matrix

(Serván et al., 2018; Clark et al., 2020): so long as the diagonal of the interaction matrix is sufficiently negative, there is strong intra-specific competition, and each species limits itself. Diagonal dominance can arise in consumer-resource models when there are more limiting resources than there are species competing for them (MacArthur, 1969; Advani et al., 2018). This self-regulation can operate in models indirectly, as when a species' suffers disproportionately whenever it increases in abundance (Gavina et al., 2018). Relatedly, models can assume that every species is the competitive dominant somewhere on the landscape without addressing the question of how this occurs. Examples include assigning species dominance rankings or the settings in which there is dominance by every species in ways to assure that each wins somewhere (Hurtt and Pacala, 1995; Sears and Chesson, 2007; Mouquet et al., 2002; Fukami and Nakajima, 2011). The two ways to obtain coexistence, through narrow parameter constraints or weak competition, are related in this sense: where restrictive parameter values are required for coexistence, they do so by limiting competition between species.

Models that generate diversity, either by narrowly defined parameter tradeoffs or by assuming that inter-specific competition is too weak to limit diversity, do not address the diversity paradox in forests. On the one hand, if forest diversity depended on narrowly defined tradeoffs, then those precisely aligned tradeoffs should be evident in data, and species invasion would rarely occur. Recent evidence for structure in multivariate trait analyses show a number of weak correlations (Wright et al., 2007), but none approaching the strict tradeoffs that would be needed to achieve coexistence in models (Clark, 2010; Clark et al., 2018). If coexistence depended on strict tradeoffs, then invading species would be limited to those possessing the specific parameter combinations needed to slot in between species already there. However, species invasions are common in forests, and the most diverse communities can be among the most highly invaded (Stohlgren et al., 1999; Lowry et al., 2012). The alternative to parameter tradeoffs, building in as many ways to persist as there are species (e.g., by randomly assigning each species a place to dominate), sidesteps the problem of intense competition for few resources. Even so, proposed remedies in models often admit small diversity increases, not thousands of species, as in hyper-diverse Indonesian and New World Tropical forests. Further limitations include model parameters that cannot be estimated from data (e.g., competitive intransitivies) or that admit only abstract interpretation (e.g., Lotka-Volterra). Models constructed in either of these ways cannot guide further development of the earth system models used to understand climate change, which must build in responses to the key environmental variables that can be measured and tied to plant performance (Fisher et al., 2018; Longo et al., 2019).

At the same time that species compete intensely for a few resources, they also differ in thousands of ways. A single example, leaf shape, highlights species differences that can only evolve if they affect fitness and, thus, demographic rates (fig. 1). Leaf size and shape affect carbon capture and water loss across the range of temperatures, light, and humidity levels that vary within and between habitats. The diversity of responses across these dimensions engage photosynthetic and transpiration rates, water loss, evaporative cooling, and risk of heat and frost damage. The complexity of sizes and shapes encountered within a single inventory plot (fig. 1) are best explained as adaptive responses to the environment (Peppe et al., 2011). [Ecologists do not need to assume that all variation like that in fig. 1 is adaptive in order to recognize that much of it can be.] The many species differences result in individual responses that are most similar to others of the same species. For example, most

species suffer from late frost, but a given frost event may affect only the individuals of those species flowering on that date (Augspurger, 2013; Bigler and Bugmann, 2018). Many species benefit from long growing seasons, yet the growth benefits in a given year vary across species depending on differences in phenology and the day-to-day variation in moisture demand (Way, 2011; Clark et al., 2014*b*; Fu et al., 2018; Montgomery et al., 2020). And while drought affects most species, drought-induced mortality is often concentrated in one or a few species on a given site and drought event (Schwantes et al., 2017; Choat et al., 2018). The striking variation between species may not have tractable effects on their abundances within a community, because the many effects are cumulative, happening at the same times, and combining in complex ways, and they are sampled at much finer scales (typically, small plots) than the scale at which natural selection operates. Because the many species differences recognized by systematists and physiologists can only arise through adaptive evolution if they affect fitness, they have to affect demographic rates. Yet data reveal only vague trait correlations between a relatively small number of trait axes (Wright et al., 2007; Berdanier and Clark, 2016), and not the strict parameter tradeoffs that are required for coexistence in models (e.g., (Tilman, 2011; Clark et al., 2018; Falster et al., 2017)). If models with intense competition for few resources predict that coexistence is hard in the absence of tight tradeoffs that are not evident in data, while nature shows both that high diversity is common and that diverse communities are often invaded (Stohlgren et al., 1999; Simberloff, 2009; Lowry et al., 2012), then models miss a fundamental mechanism.

We offer an alternative explanation for coexistence that is universal, in the sense that it emerges from a ubiquitous property of communities: individuals tend to respond to environmental variation most like others of the same species (Clark, 2010). In forests, where mortality increases in step with growth, this tendency can concentrate competition within the species, the common feature needed to promote coexistence in models. Two attractive features of this universal coexistence hypothesis include A) the potential to explain high diversity, not by narrow specification of species tradeoffs, but rather through the ubiquitous tendency for individuals to respond more like others of the same species, and B) the fingerprint of this mechanism is observable, in the covariances between individual trees. Importantly, this covariance relationship could hold even where individuals of all species tend toward positive correlation, as expected if responses include some widely-shared resources. The tendency for intra- to dominate inter-specific correlation between individuals emerges for both fecundity and growth across networks of forest stands in the southeastern US (Clark, 2010), but the connection between observation and theory has not been demonstrated quantitatively. Here we demonstrate the quantitative link from A to B. This long-standing missing connection between observation and theory provides a way forward for models that exploit both the observable differences between species and the individual correlation needed to maintain species diversity.

A simple demonstration

Universal coexistence can be demonstrated using a model with as few as three elements: i) species responses that covary between individuals of the same and different species, ii) local competition that drives mortality, regardless of species identity, and iii) dis-

persal (fig. 1B, Supplement). Individuals compete within a landscape where the environment varies over sites $k = 1, \ldots, K$. The environment determines individual capacity to reproduce. Reproduction increases abundance locally and contributes to dispersal. Mortality increases with local crowding, but without underlying assumptions that a species mortality rate increases simply because that species is abundant–individuals of all species suffer equally from crowding. This competition that results from local population growth and the crowding that transfers to accelerated mortality is a ubiquitous feature of forests. The connection is so tight in even-aged stands that the proportionate mortality rate is precisely equal to the proportionate rate of increase in individual crown area (Clark, 1990). In uneven-aged stands, the relationship between growth and mortality can vary widely. But it is still constrained by the fact that growth must translate to mortality, because biomass does not accumulate indefinitely. The growth-mortality relationship is embodied in forest yield tables that predict how mortality rate increases along with site fertility, through its effects on growth, and it informs selective thinning practice (Assmann, 1970). Based on these three elements, the only way to promote diversity in the model is through the tendency for individuals that respond similarly to the environment to compete most intensely.

The multitude of structures and functions that differentiate species (e.g., fig. 1) can affect responses to the environment. Consider E ways for S species to differ across the K locations. E is the number of environmental predictors that might affect individual response, but only a small subset of these effects could be observed and measured. E is not the number of resources, but rather the number of dimensions the environment offers for responses to differ (Chesson, 2000; Letten and Stouffer, 2019). E can be large, including climate variables and resources such as moisture, light, and nutrients. A given environmental variable can affect responses in multiple ways, such as climate norms (averages for a location), seasonality, and extremes. It can include non-linearities and interactions between variables. Landscape variation in these effects is held in a $K \times E$ matrix $\mathbf{E}$. Species responses to these variables are held in a $E \times S$ matrix $\mathbf{S}$. We exploit the transparency of mean responses and covariance matrices available from Gaussian distribution theory, as used for demographic estimates (Aakala et al., 2013; Sonti et al., 2019; Qiu et al., 2022), ecological theory, such as generalized Lotka-Volterra (Clark et al., 2020), and covariances among individuals (Clark, 2010).

We demonstrate coexistence and why it occurs by comparing three ways of organizing individual variation. A joint distribution of S species responses at a site k can be summarized by a multivariate distribution,

$$\mathbf{h}_k \sim MVN_S(\mathbf{b} + \mathbf{S}'\mathbf{E}_k, \tau^2\mathbf{I}_S) \tag{SK}$$

where vector $\mathbf{h}_k$ holds the S responses, one for each species, centered on mean responses $\mathbf{b} = \mathbf{1}_S b$. [For simplicity, all species have the same value $b_s = b$.] To simplify comparison with models that follow, and without loss of generality, we assume that the variables in $\mathbf{E}$ are centered on zero, a common centering used when models are fitted to data. We refer to this as the structured-known (SK) model, because it requires full knowledge of environmental effects on all species. $\mathbf{E}_k$ is the kth row of matrix $\mathbf{E}$, τ^2 is residual (non-environmental) variation, and $\mathbf{I}_S$ is the identity matrix. Of course, species responses in eq. SK depend on their mean differences in the vector $\mathbf{S}'\mathbf{E}_k$. They are otherwise independent, because covariance matrix $\tau^2\mathbf{I}_S$ has zeros everywhere except along the diagonal. Eq. SK is written as a multivariate

distribution to highlight the connection between known sources of variation in $\mathbf{E}$ and the case that follows, where causes and effects are unknown.

The knowledge of all E dimensions at each of K locations that affect each of S species is never available. However, environmental effects that cannot be accommodated in the mean of eq. (SK), i.e., those that cannot be observed and measured, contribute variation through the covariance,

$$\begin{aligned} \mathbf{h}_k &\sim MVN_S(\mathbf{b}, \mathbf{C}) \\ \mathbf{C} &= \mathbf{S}'\mathbf{V}_\mathbf{E}\mathbf{S} + \tau^2\mathbf{I}_S \end{aligned} \tag{SU}$$

This structured-unknown (SU) model includes $\mathbf{V}_\mathbf{E} = cov(\mathbf{E})$, the covariance in unobserved environmental variables. Its effect on the first term of the species covariance matrix $\mathbf{C}$ combines environmental complexity with species responses and translates them into species covariance. For example, two species that respond similarly (similar columns in response matrix $\mathbf{S}$) to variables with meaningful variation across the landscape (large diagonal elements in $\mathbf{V}_\mathbf{E}$) have positive covariance in $\mathbf{C}$. Although one version of the model expresses species differences as mean values (SK) and the other as a covariance matrix (SU), eq. (SK) and eq. (SU) make the same assumptions about the relationship between species. The only difference between them is knowledge about the underlying basis for those relationships. We return to this mean-covariance connection after introducing individuals into the model.

The most direct translation from species in eqs. SK and SU to individuals comes from expanding the mean and covariance. If there are n_{sk} individuals of species s at location k, then there are $n_k = \sum_s n_{sk}$ individuals at k. The matrix of individual means is obtained by repeating n_{sk} times the column in $\mathbf{S}$ assigned to species s. This expansion results in the $E \times n_k$ matrix of individual mean responses $\tilde{\mathbf{S}}_k$. There is a k subscript only because the numbers and species identities of individuals at each site differ; we retain the assumption that individuals share the same species-level responses to the environment, regardless of where they occur. With this shift from species to individuals, response $\mathbf{h}_k$ in eq. (SK) is now a length-n_k vector.

There is an equivalent translation for the covariance model in eq. (SU), from $S \times S$ species covariance $\mathbf{C}$ to $n_k \times n_k$ individual covariance $\tilde{\mathbf{C}}_k$ (Appendix S1 in Supporting Information). This individual covariance matrix has a block structure, where each block holds the covariance $\mathbf{C}_{ss'}$ between two species s and s' within a $n_{sk} \times n_{s'k}$ submatrix. Again, $\tilde{\mathbf{C}}_k$ has a location subscript only because the numbers of individuals of each species vary by location. As before, covariances between individuals of any two species depend on species identity, regardless of where those individuals occur.

Both ways of organizing environmental responses are needed to understand the relationship between coexistence and the individual covariances that can be observed in field data. The structured-known (eq. SK) model describes species differences in terms of their responses to the environment. The SK model describes *why* competition is concentrated within the species. By shifting the mean differences to the covariance between indviduals, the structured-unknown (eq. SU) representation exposes the fingerprint of this process. This translation to observable variation suggests models that can generate diversity: everything about species responses to the environment that affect competition is contained in the covariance between individuals. For completeness, the unstructured-unknown (eq. (UU)) variation

is included as a link to literature that considers effects of adding noise to a mean parameter value for a species s (held in a vector $\mathbf{s}$) contributes to coexistence (Courbaud et al., 2012; Hart et al., 2016; Uriarte and Menge, 2018; Crawford et al., 2019),

$$h_{isk} \sim N(b_s, c_k + \tau^2) \tag{UU}$$

The variance term c_k is included to assure that the SU and UU models are compared for the same overall variance levels. The three models are used with the same assumptions about local, crowding-driven mortality and dispersal between sites (Appendix S1 in Supporting Information).

Simulation demonstrates that structured variation of either type (eqns. SK, SU) allows for diverse communities, provided that the environment offers many ways for species to differ (large E in fig. 2a, b). Large E means that not only is there high dimensional variation in the environment, but also that species are capable of responding to it. As E increases, both diversity and richness increase (fig. 2a, b). Despite identical distributions for individual differences on the continuous scale, simulated diversity in the SK and SU cases is not precisely the same due to discretization of birth, survival, and dispersal on small plots where one model responds to the local environment (SK) and the other does not (SU) (Appendix S1 in Supporting Information).

How and why?

How does the model generate diversity and, more paradoxically, how do the differences in SK translate to the SU model, where competition is solely regulated by individual covariance? The SK outcomes can be examined on a suitability map constructed from the known environment and species responses $\mathbf{K} = \mathbf{ES}$ (shading in fig. 2e). In simulation, the dominant individuals are expected to belong to the species having the highest performance for that site. Indeed, these are the dominant species, shown as outlined cells in fig. 2e, with one highlighted cell per row (per site). There is not only alignment of these dominant site-species combinations; there is also positive correlation between species local responses (elements of matrix $\mathbf{K}$) and species abundance in simulation, termed "site sorting" in fig. 2c. This site-sorting is actually stronger than it appears due to the fact that the correlations are degraded in fig. 2c by the zeros for all local extinctions in simulation.

The SU model confirms that coexistence comes from concentrating competition within species, and, less intuitively, why it only happens if there is high dimensional variation in the environment. Demonstrating that coexistence occurs when every species is allowed to dominate somewhere is not new. However, the mechanism here differs from previous models, being based on high-dimensional species differences that incrementally increase overlap between similar individuals, while offering ways to incrementally diverge from dissimilar individuals. When E is large, the most similar individuals tend to be those of the same species. The mechanism does not involve parameter tradeoffs.

By analogy with Lotka-Volterra, which requires diagonal dominance in the interaction matrix, coexistence here comes with diagonal dominance in $\mathbf{C}$, which confers the tendency of individuals to respond more like others of the same species. When the environment is

simple ($E = 2$ in fig. 2f), there is no tendency for diagonal dominance–the covariances between individuals of the same species are rarely the largest pairwise covariances. A low-dimensional environment imposes weak covariance held in a matrix where the most similar responses, and thus, the strongest competition, often comes between individuals belonging to different species. A simple environment offers few ways in which species can differ and, thus, cannot focus competition within the species.

Diagonal dominance in $\mathbf{C}$ emerges as the environment becomes complex. This is an inevitable result of the many ways that an individual can respond to variation, increasing the dimensions in which it aligns with others of the same species and differs from individuals of other species. With E as small as 20, the shift toward diagonal dominance is already apparent (fig. 2g). In the SK model, species differences come through their similar mean responses (matrix $\mathbf{S}$). In the SU model, these differences are transferred to the covariance (matrix $\mathbf{C}$). Either way, the covariances between individuals are the same, in both cases induced by $\mathbf{ES}$. The cumulative increase in confrontation between individuals of similar species occurs on sites where they are favored (SK model). Or it occurs without any reference to the site conditions, but it is observable in the covariances between individual responses (SU model). The species covariance $\mathbf{C}$ becomes a substitute, albeit degraded, for the information held in $\mathbf{ES}$ that cannot be observed. These similarities are the basis for competition, i.e., niche overlap. The important role of the SU model is the link it provides to variation that can be observed in data, the matrix $\tilde{\mathbf{C}}$.

Without variable responses to a variable environmental ($E = 1$), diversity in the UU model reduces to the species that dominates on average (UU in fig. 2a, b). Variation of the UU model type can have effects that depend on specific model assumptions (Courbaud et al., 2012; Hart et al., 2016; Uriarte and Menge, 2018; Crawford et al., 2019). Models that increase variance with the introduction of noise to an individual demographic rate increase the tendency to "drift", as randomly assigning advantages and disadvantages to each individual (and, thus, species) amounts to guaranteeing that members of each species can win somewhere. Our model does not confound individual variation with total variation, because we use c_k to equalize total variation in eq. UU (Appendix S1 in Supporting Information).

Process to data

If high-dimensional variation between species, a tiny fraction of which is represented by leaf shape (fig. 1), evolves by natural selection (not all of it does), then this variation has to affect demographic rates in ways that affect fitness. If this has to be true, how does natural selection act on the variation that is rarely evident in estimated demographic rates? Demographic studies commonly find few significant predictors in noisy data and broad overlap between species parameters (Clark et al., 2014*a*; Kunstler et al., 2021). The typical sample size for demographic estimates can range from tens to thousands of individuals of a given species. Most include a small number of sample dates (Mantgem et al., 2009; Stanke et al., 2021; Qiu et al., 2021; Kunstler et al., 2021). Finding significant relationships in noisy data from limited sites and few time intervals is challenging (Tang et al., in review). By contrast, natural selection can operate every year over generations on variation across individuals spanning entire regions, especially where pollen and/or seed dispersal is

high (Ashley, 2010; Smith et al., 2020; Kling and Ackerly, 2021; Dering et al., 2021).

The high-dimensional variation that promotes coexistence in this study makes noisy demographic rates inevitable. To see this, consider that species covariance $\mathbf{C}$ scales with environmental dimension E. As a transparent illustration, consider the case where both the columns in $\mathbf{E}$ and the rows in $\mathbf{S}$ are centered, and columns in $\mathbf{E}$ are standardized to unit variance. This centered, standardized version of the model exposes the direct scaling between residual covariance and environmental complexity, with $\mathbf{C}$ tending to $E \times Cov(\mathbf{S})$ with increasing E. A typical demographic study might benefit from up to 10 predictors, while responses occur in hundreds of dimensions. Where coexistence depends on large E, demographic rates will necessarily be poorly explained by the variables that can be measured.

Hybrid solution to model diversity

Demonstrating that covariance structure observed in nature can stand in for the species differences that regulate diversity offers a new direction for development of models for global change. Earth system models for this purpose must continue to strive for the relationships that describe real-world responses, without biases that might be imposed simply to guarantee coexistence (e.g., tradeoffs that are not found in data or unrestricted seed availability). The need to incorporate what is known in the mean structure of a model with new understanding of how observed covariance can stabilize coexistence in such models suggests a hybrid approach.

Rather than an omnibus algorithm, the universal coexistence hypothesis offers a strategy for model development that is adaptable. Stand simulators and earth surface models include parameters that describe responses from xylem architecture, chloroplasts, and stomata to leaves to individual birth and death to canopies. The covariance important for coexistence in a model depends on the level at which competition occurs, which can be individuals, species, cohorts, or functional types. The ways in which parameters at one scale induce covariance at another will likewise vary between models. A hybrid strategy for the model used here (individual trees that covary in demographic rates like (Clark, 2010)) integrates the estimates of observable effects together with residual variance (eq. SK),

$$\mathbf{h}_k \sim MVN(\mathbf{b} + \tilde{\mathbf{S}}'\mathbf{E}_k, \tilde{\mathbf{C}}_k + \tau^2 \mathbf{I}_{n_k}) \tag{HY}$$

The residual covariance in eq. HY allows for the unmeasurable variables that contribute to species differences, beyond those that enter through measured variables. In this hybrid, rows in $\tilde{\mathbf{S}}$ only include variables that can be observed, while $\tilde{\mathbf{C}}$ includes the unobservable sources of covariance. This hybrid remains fully consistent with both the SK and SU models, but it exploits information that can be observed for both mean and covariance. Options for this implementation include an approach summarized in Box 1.

Universal application

Recent evidence that intra-specific competition in forests may be stronger than inter-specific competition (Harms et al., 2000; Wills et al., 2006; Bagchi et al., 2014; Zhu et al., 2015; LaManna et al., 2017; Hülsmann and Hartig, 2018) is expected from the universal coexistence hypothesis, but it is attributed in the literature to a different cause. The Janzen-Connell (JC) effect (Janzen, 1970; Connell, 1970) requires that any abundant species will suffer increased losses to host-specific natural enemies, disproportionate to its less abundant neighbors. While this effect would certainly contribute to diversity, the requirement for as many host-specific enemies as there are competing host species may not be widely applicable (Novotny et al., 2006). As with efforts to achieve coexistence in competition models by imposing tight tradeoffs, the many host-specific natural enemies need for JC lacks the empirical support that already exists for the universal coexistence hypothesis (Clark 2010), which has the further advantage that it does not depend on assumptions that may lack generality.

Continuing efforts to understand coexistence and anticipate biodiversity loss have to start by resolving what has become a 50-year impasse: how to generate diversity in models of intense competition for apparently few limiting resources. The ubiquitous requirement for tradeoffs in models (Tilman, 2011) must confront the long (and still growing) legacy of demographic studies that do not support the existence of these tradeoffs (Clark 2010, A. Clark et al., 2018). From the earliest stand simulators (reviewed in (Shugart, 1984)) through recent efforts (Rüger et al., 2020), models using estimates that find support in field data have resorted to immigration from elsewhere to stave off the extinction of all but a few species. The universal coexistence hypothesis resolves the paradox of widely appreciated species differences that must contribution to biodiversity, while having few observable effects on demographic data. Coexistence of competitors need not appeal to carefully specified tradeoffs for the same reason that real communities are invaded repeatedly–if many variables contribute to population success, then universal coexistence is nearly automatic; individuals typically respond more like other individuals of the same species, thus concentrating competition within the species. Individual differences observable as covariance structure can guide future modeling efforts needed to maintain realistic diversity without abandoning realistic assumptions or the evidence in data.

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References

Aakala, T., S. Fraver, A. W. D'Amato, and B. J. Palik. 2013. Influence of competition and age on tree growth in structurally complex old-growth forests in northern Minnesota, USA. Forest Ecology and Management **308**:128–135. URL https://www.sciencedirect.com/science/article/pii/S037811271300515X.

Advani, M., G. Bunin, and P. Mehta. 2018. Statistical physics of community ecology: A cavity solution to MacArthur's consumer resource model. Journal of Statistical Mechanics: Theory and Experiment **2018**:033406.

Amarasekare, P. 2002. Interference competition and species coexistence. Proceedings of the Royal Society of London. Series B: Biological Sciences **269**:2541–2550. URL https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2002.2181.

Ashley, M. V. 2010. Plant Parentage, Pollination, and Dispersal: How DNA Microsatellites Have Altered the Landscape. Critical Reviews in Plant Sciences **29**:148–161. URL https://doi.org/10.1080/07352689.2010.481167.

Assmann, E. 1970. The Principles of Forest Yield Study. Pergamon.

Augspurger, C. K. 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: Spring damage risk is increasing. Ecology **94**:41–50. URL http://www.jstor.org/stable/23435667.

Bagchi, R., R. E. Gallery, S. Gripenberg, S. J. Gurr, L. Narayan, C. E. Addis, R. P. Freckleton, and O. T. Lewis. 2014. Pathogens and insect herbivores drive rainforest plant diversity and composition. Nature **506**:85–88. URL https://doi.org/10.1038/nature12911.

Berdanier, A. B., and J. S. Clark. 2016. Divergent reproductive allocation trade-offs with canopy exposure across tree species in temperate forests. Ecosphere **7**:e01313–n/a. URL http://dx.doi.org/10.1002/ecs2.1313.

Bigler, C., and H. Bugmann. 2018. Climate-induced shifts in leaf unfolding and frost risk of European trees and shrubs. Scientific Reports **8**:9865. URL https://doi.org/10.1038/s41598-018-27893-1.

Bloom, A., F. Chapin, III, and H. Mooney. 1985. Resource Limitation in Plants-An Economic Analogy. Annual Review of Ecology and Systematics **16**:363–392. URL https://www.annualreviews.org/doi/abs/10.1146/annurev.es.16.110185.002051.

Bunin, G. 2017. Ecological communities with Lotka-Volterra dynamics. Physical Review E **95**. URL <GotoISI>://WOS:000400239600006.

Chesson, P. 2000. Mechanisms of Maintenance of Species Diversity. Annual Review of Ecology and Systematics **31**:343–366. URL https://www.annualreviews.org/doi/abs/10.1146/annurev.ecolsys.31.1.343.

Choat, B., T. J. Brodribb, C. R. Brodersen, R. A. Duursma, R. López, and B. E. Medlyn. 2018. Triggers of tree mortality under drought. Nature **558**:531–539. URL https://doi.org/10.1038/s41586-018-0240-x.

Clark, A., C. Lehman, and D. Tilman. 2018. Identifying mechanisms that structure ecological communities by snapping model parameters to empirically observed tradeoffs. Ecology Letters **21**:494–505. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12910.

Clark, J. S. 1990. Integration of Ecological Levels: Individual Plant Growth, Population Mortality and Ecosystem Processes. Journal of Ecology **78**:275–299. URL http://www.jstor.org/stable/2261112.

Clark, J. S. 2010. Individuals and the variation needed for high species diversity in forest trees. Science **327**:1129–32. URL https://www.ncbi.nlm.nih.gov/pubmed/20185724.

Clark, J. S., D. M. Bell, M. C. Kwit, and K. Zhu. 2014*a*. Competition-interaction landscapes for the joint response of forests to climate change. Glob Chang Biol **20**:1979–91. URL https://www.ncbi.nlm.nih.gov/pubmed/24932467.

Clark, J. S., J. Melillo, J. Mohan, and C. Salk. 2014*b*. The seasonal timing of warming that controls onset of the growing season. Global Change Biology **20**:1136–1145. URL http://dx.doi.org/10.1111/gcb.12420.

Clark, J. S., C. L. Scher, and M. Swift. 2020. The emergent interactions that govern biodiversity change. Proceedings of the National Academy of Sciences page 202003852. URL https://www.pnas.org/content/pnas/early/2020/07/02/2003852117.full.pdf.

Connell, J., 1970. Herbivores and the Number of Tree Species in Tropical Forests, Page 298–312 . Pudoc, Wageningen.

Courbaud, B., L. Larrieu, D. Kozak, D. Kraus, T. Lachat, S. Ladet, J. Müller, Y. Paillet, K. Sagheb-Talebi, A. Schuck, J. Stillhard, M. Svoboda, and S. Zudin. 2022. Factors influencing the rate of formation of tree-related microhabitats and implications for biodiversity conservation and forest management. Journal of Applied Ecology **59**:492–503. URL https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2664.14068.

Courbaud, B., G. Vieilledent, and G. Kunstler. 2012. Intra-specific variability and the competition–colonisation trade-off: coexistence, abundance and stability patterns. Theoretical Ecology **5**:61–71. URL https://doi.org/10.1007/s12080-010-0095-8.

Crawford, M., F. Jeltsch, F. May, V. Grimm, and U. E. Schlägel. 2019. Intraspecific trait variation increases species diversity in a trait-based grassland model. Oikos **128**:441–455. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/oik.05567.

D'Amato, A. W., J. B. Bradford, S. Fraver, and B. J. Palik. 2013. Effects of thinning on drought vulnerability and climate response in north temperate forest ecosystems. Ecological Applications **23**:1735–1742. URL <GotoISI>://WOS:000328568400001.

Dering, M., M. Baranowska, B. Beridze, I. J. Chybicki, I. Danelia, G. Iszkuło, G. Kvartskhava, P. Kosiński, G. Raczka, P. A. Thomas, D. Tomaszewski, Walas, and K. Sekiewicz. 2021. The evolutionary heritage and ecological uniqueness of Scots pine in the Caucasus ecoregion is at risk of climate changes. Scientific Reports **11**:22845. URL https://doi.org/10.1038/s41598-021-02098-1.

Detto, M., J. M. Levine, and S. W. Pacala. 2022. Maintenance of high diversity in mechanistic forest dynamics models of competition for light. Ecological Monographs **92**:e1500. URL https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecm.1500.

Falster, D. S., Brännström, M. Westoby, and U. Dieckmann. 2017. Multitrait successional forest dynamics enable diverse competitive coexistence. Proceedings of the National Academy of Sciences **114**:E2719–E2728. URL https://www.pnas.org/doi/abs/10.1073/pnas.1610206114.

Fisher, R. A., and C. D. Koven. 2020. Perspectives on the Future of Land Surface Models and the Challenges of Representing Complex Terrestrial Systems. Journal of Advances in Modeling Earth Systems **12**:e2018MS001453. URL https://agupubs.onlinelibrary.wiley.com/doi/abs/10.1029/2018MS001453.

Fisher, R. A., C. D. Koven, W. R. L. Anderegg, B. O. Christoffersen, M. C. Dietze, C. E. Farrior, J. A. Holm, G. C. Hurtt, R. G. Knox, P. J. Lawrence, J. W. Lichstein, M. Longo, A. M. Matheny, D. Medvigy, H. C. Muller-Landau, T. L. Powell, S. P. Serbin, H. Sato, J. K. Shuman, B. Smith, A. T. Trugman, T. Viskari, H. Verbeeck, E. Weng, C. Xu, X. Xu, T. Zhang, and P. R. Moorcroft. 2018. Vegetation demographics in Earth System Models: A review of progress and priorities. Global Change Biology **24**:35–54. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.13910.

Fu, Y., S. Piao, N. Delpierre, F. Hao, H. Hänninen, Y. Liu, W. Sun, I. Janssens, and M. Campioli. 2018. Larger temperature response of autumn leaf senescence than spring leaf-out phenology. Global Change Biology **24**.

Fukami, T., and M. Nakajima. 2011. Community assembly: alternative stable states or alternative transient states? Ecology Letters **14**:973–984. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1461-0248.2011.01663.x.

Gavina, M. K. A., T. Tahara, K.-i. Tainaka, H. Ito, S. Morita, G. Ichinose, T. Okabe, T. Togashi, T. Nagatani, and J. Yoshimura. 2018. Multi-species coexistence in Lotka-Volterra competitive systems with crowding effects. Scientific Reports **8**:1198. URL https://doi.org/10.1038/s41598-017-19044-9.

Harms, K. E., S. J. Wright, O. Calderón, A. Hernández, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. Nature **404**:493–495. URL https://doi.org/10.1038/35006630.

Hart, S. P., S. J. Schreiber, and J. M. Levine. 2016. How variation between individuals affects species coexistence. Ecology Letters **19**:825–838. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12618.

He, Y., H. Liu, Q. Yang, Y. Cao, H. Yin, Z. Zhou, Q. Yu, and X. Wang. 2022. Neighborhood Effects on Tree Mortality Depend on Life Stage of Neighbors. Frontiers in Plant Science **13**. URL https://www.frontiersin.org/article/10.3389/fpls.2022.838046.

Hurtt, G. C., and S. W. Pacala. 1995. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. Journal of Theoretical Biology **176**:1–12. URL https://www.sciencedirect.com/science/article/pii/S0022519385701701.

Hülsmann, L., and F. Hartig. 2018. Comment on x201c;Plant diversity increases with the strength of negative density dependence at the global scalex201d. Science **360**:eaar2435. URL https://www.science.org/doi/abs/10.1126/science.aar2435.

Janzen, D. 1970. Herbivores and the Number of Tree Species in Tropical Forests. The American Naturalist **104**:501–528. URL http://www.journals.uchicago.edu/doi/abs/10.1086/282687.

Kling, M. M., and D. D. Ackerly. 2021. Global wind patterns shape genetic differentiation, asymmetric gene flow, and genetic diversity in trees. Proceedings of the National Academy of Sciences **118**:e2017317118. URL https://www.pnas.org/doi/abs/10.1073/pnas.2017317118.

Kunstler, G., A. Guyennon, S. Ratcliffe, N. Rüger, P. Ruiz-Benito, D. Z. Childs, J. Dahlgren, A. Lehtonen, W. Thuiller, C. Wirth, M. A. Zavala, and R. Salguero-Gomez. 2021. Demographic performance of European tree species at their hot and cold climatic edges. Journal of Ecology **109**:1041–1054. URL https://besjournals.onlinelibrary.wiley.com/doi/abs/10.1111/1365-2745.13533.

Laan, A., and G. G. de Polavieja. 2018. Species diversity rises exponentially with the number of available resources in a multi-trait competition model. Proceedings of the Royal Society B: Biological Sciences **285**:20181273. URL https://royalsocietypublishing.org/doi/abs/10.1098/rspb.2018.1273.

Laird, R., and B. Schamp. 2006. Competitive Intransitivity Promotes Species Coexistence. The American Naturalist **168**:182–193. URL https://www.journals.uchicago.edu/doi/abs/10.1086/506259.

LaManna, J. A., S. A. Mangan, A. Alonso, N. A. Bourg, W. Y. Brockelman, S. Bunyavejchewin, L.-W. Chang, J.-M. Chiang, G. B. Chuyong, K. Clay, R. Condit, S. Cordell, S. J. Davies, T. J. Furniss, C. P. Giardina, I. A. U. N. Gunatilleke, C. V. S. Gunatilleke, F. He, R. W. Howe, S. P. Hubbell, C.-F. Hsieh, F. M. Inman-Narahari, D. Janík, D. J. Johnson, D. Kenfack, L. Korte, K. Král, A. J. Larson, J. A. Lutz, S. M. McMahon, W. J. McShea, H. R. Memiaghe, A. Nathalang, V. Novotny, P. S. Ong, D. A. Orwig, R. Ostertag, G. G. Parker, R. P. Phillips, L. Sack, I.-F. Sun, J. S. Tello, D. W. Thomas, B. L. Turner, D. M. Vela Díaz, T. Vrška, G. D. Weiblen, A. Wolf, S. Yap, and J. A. Myers. 2017. Plant diversity increases with the strength of negative density dependence at the global scale. Science **356**:1389–1392. URL https://science.sciencemag.org/content/sci/356/6345/1389.full.pdf.

Letten, A. D., and D. B. Stouffer. 2019. The mechanistic basis for higher-order interactions and non-additivity in competitive communities. Ecology Letters **22**:423–436. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13211.

Longo, M., R. G. Knox, D. M. Medvigy, N. M. Levine, M. C. Dietze, Y. Kim, A. L. S. Swann, K. Zhang, C. R. Rollinson, R. L. Bras, S. C. Wofsy, and P. R. Moorcroft. 2019. The biophysics, ecology, and biogeochemistry of functionally diverse, vertically and horizontally heterogeneous ecosystems: the Ecosystem Demography model, version 2.2 – Part 1: Model description. Geosci. Model Dev. **12**:4309–4346. URL https://gmd.copernicus.org/articles/12/4309/2019/.

Lowry, E., E. J. Rollinson, A. J. Laybourn, T. E. Scott, M. E. Aiello-Lammens, S. M. Gray, J. Mickley, and J. Gurevitch. 2012. Biological invasions: a field synopsis, systematic review, and database of the literature. Ecology and evolution **3**:182–196. URL https://pubmed.ncbi.nlm.nih.gov/23404636https://www.ncbi.nlm.nih.gov/pmc/articles/PMC3568853/.

MacArthur, R. H. 1969. Species packing, and what competition minimizes. Proceedings of the National Academy of Sciences **64**:1369–1371.

Mantgem, P. J. v., N. L. Stephenson, J. C. Byrne, L. D. Daniels, J. F. Franklin, P. Z. Fulé, M. E. Harmon, A. J. Larson, J. M. Smith, A. H. Taylor, and T. T. Veblen. 2009. Widespread Increase of Tree Mortality Rates in the Western United States. Science **323**:521–524. URL https://www.science.org/doi/abs/10.1126/science.1165000.

Maréchaux, I., and J. Chave. 2017. An individual-based forest model to jointly simulate carbon and tree diversity in Amazonia: description and applications. Ecological Monographs **87**:632–664. URL https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1002/ecm.1271.

May, R. 2001. Stability and Complexity in Model Ecosystems. Princeton University Press, Princeton.

Montgomery, R. A., K. E. Rice, A. Stefanski, R. L. Rich, and P. B. Reich. 2020. Phenological responses of temperate and boreal trees to warming depend on ambient spring temperatures, leaf habit, and geographic range. Proceedings of the National Academy of Sciences **117**:10397–10405. URL https://www.pnas.org/doi/abs/10.1073/pnas.1917508117.

Mouquet, N., J. L. Moore, and M. Loreau. 2002. Plant species richness and community productivity: why the mechanism that promotes coexistence matters. Ecology Letters **5**:56–65. URL https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1461-0248.2002.00281.x.

Nogueira, C., A. Nunes, M. N. Bugalho, C. Branquinho, R. L. McCulley, and M. C. Caldeira. 2018. Nutrient Addition and Drought Interact to Change the Structure and Decrease the Functional Diversity of a Mediterranean Grassland. Frontiers in Ecology and Evolution **6**. URL https://www.frontiersin.org/article/10.3389/fevo.2018.00155.

Novotny, V., P. Drozd, S. E. Miller, M. Kulfan, M. Janda, Y. Basset, and G. D. Weiblen. 2006. Why Are There so Many Species of Herbivorous Insects in Tropical Rainforests? Science **313**:1115–1118. URL http://www.jstor.org/stable/3847084.

Pacala, S. W., C. D. Canham, J. Saponara, J. A. Silander Jr., R. K. Kobe, and E. Ribbens. 1996. Forest Models Defined by Field Measurements: Estimation, Error Analysis and Dynamics. Ecological Monographs **66**:1–43. URL https://esajournals.onlinelibrary.wiley.com/doi/abs/10.2307/2963479.

Peppe, D. J., D. L. Royer, B. Cariglino, S. Y. Oliver, S. Newman, E. Leight, G. Enikolopov, M. Fernandez-Burgos, F. Herrera, J. M. Adams, E. Correa, E. D. Currano, J. M. Erickson, L. F. Hinojosa, J. W. Hoganson, A. Iglesias, C. A. Jaramillo, K. R. Johnson, G. J. Jordan, N. J. B. Kraft, E. C. Lovelock, C. H. Lusk, Niinemets, J. Peñuelas, G. Rapson, S. L. Wing, and I. J. Wright. 2011. Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications. New Phytologist **190**:724–739. URL https://nph.onlinelibrary.wiley.com/doi/abs/10.1111/j.1469-8137.2010.03615.x.

Qiu, T., R. Andrus, M.-C. Aravena, D. Ascoli, Y. Bergeron, R. Berretti, D. Berveiller, M. Bogdziewicz, T. Boivin, R. Bonal, D. C. Bragg, T. Caignard, R. Calama, J. J. Camarero, C.-H. Chang-Yang, N. L. Cleavitt, B. Courbaud, F. Courbet, T. Curt, A. J. Das, E. Daskalakou, H. Davi, N. Delpierre, S. Delzon, M. Dietze, S. D. Calderon, L. Dormont, J. Espelta, T. J. Fahey, W. Farfan-Rios, C. A. Gehring, G. S. Gilbert, G. Gratzer, C. H. Greenberg, Q. Guo, A. Hacket-Pain, A. Hampe, Q. Han, J. Hille Ris Lambers, K. Hoshizaki, I. Ibanez, J. F. Johnstone, V. Journé, D. Kabeya, C. L. Kilner, T. Kitzberger, J. M. H. Knops, R. K. Kobe, G. Kunstler, J. G. A. Lageard, J. M. LaMontagne, M. Ledwon, F. Lefevre, T. Leininger, J.-M. Limousin, J. A. Lutz, D. Macias, E. J. B. McIntire, C. M. Moore, E. Moran, R. Motta, J. A. Myers, T. A. Nagel, K. Noguchi, J.-M. Ourcival, R. Parmenter, I. S. Pearse, I. M. Perez-Ramos, L. Piechnik, J. Poulsen, R. Poulton-Kamakura, M. D. Redmond, C. D. Reid, K. C. Rodman, F. Rodriguez-Sanchez, J. D. Sanguinetti, C. L. Scher, W. H. Schlesinger, H. Schmidt Van Marle, B. Seget, S. Sharma, M. Silman, M. A. Steele, N. L. Stephenson, J. N. Straub, I. F. Sun, S. Sutton, J. J. Swenson, M. Swift, P. A. Thomas, M. Uriarte, G. Vacchiano, T. T. Veblen, A. V. Whipple, T. G. Whitham, A. P. Wion, B. Wright, S. J. Wright, K. Zhu, J. K. Zimmerman, et al. 2022. Limits to reproduction and seed size-number trade-offs that shape forest dominance and future recovery. Nature Communications **13**:2381. URL https://doi.org/10.1038/s41467-022-30037-9.

Qiu, T., S. Sharma, C. W. Woodall, and J. S. Clark. 2021. Niche Shifts From Trees to Fecundity to Recruitment That Determine Species Response to Climate Change. Frontiers in Ecology and Evolution **9**. URL https://www.frontiersin.org/article/10.3389/fevo.2021.719141.

Rollinson, C. R., A. Dawson, A. M. Raiho, J. W. Williams, M. C. Dietze, T. Hickler, S. T. Jackson, J. McLachlan, D. JP Moore, B. Poulter, T. Quaife, J. Steinkamp, and M. Trachsel. 2021. Forest responses to last-millennium hydroclimate variability are governed by spatial variations in ecosystem sensitivity. Ecology Letters **24**:498–508. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13667.

Rüger, N., R. Condit, D. H. Dent, S. J. DeWalt, S. P. Hubbell, J. W. Lichstein, O. R. Lopez, C. Wirth, and C. E. Farrior. 2020. Demographic trade-offs predict tropical forest dynamics. Science **368**:165–168. URL https://science.sciencemag.org/content/sci/368/6487/165.full.pdf.

Schwantes, A. M., J. J. Swenson, M. González-Roglich, D. M. Johnson, J.-C. Domec, and R. B. Jackson. 2017. Measuring canopy loss and climatic thresholds from an extreme drought along a fivefold precipitation gradient across Texas. Global Change Biology **23**:5120–5135. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.13775.

Sears, A. L. W., and P. Chesson. 2007. New methods for quantifying the spatial storage effect: an illustration with desert annuals. Ecology **88**:2240–2247. URL https://esajournals.onlinelibrary.wiley.com/doi/abs/10.1890/06-0645.1.

Serván, C. A., J. A. Capitán, J. Grilli, K. E. Morrison, and S. Allesina. 2018. Coexistence of many species in random ecosystems. Nature Ecology and Evolution **2**:1237–1242. URL https://doi.org/10.1038/s41559-018-0603-6.

Shugart, H. H. 1984. A theory of forest dynamics: The ecological implications of forest succession models. Springer-Verlag, New York, NY, United States. URL https://www.osti.gov/biblio/5642300.

Simberloff, D. 2009. The Role of Propagule Pressure in Biological Invasions. Annual Review of Ecology, Evolution, and Systematics **40**:81–102. URL https://www.annualreviews.org/doi/abs/10.1146/annurev.ecolsys.110308.120304.

Smith, A. L., T. R. Hodkinson, J. Villellas, J. A. Catford, A. M. Csergő, S. P. Blomberg, E. E. Crone, J. Ehrlén, M. B. Garcia, A.-L. Laine, D. A. Roach, R. Salguero-Gómez, G. M. Wardle, D. Z. Childs, B. D. Elderd, A. Finn, S. Munné-Bosch, M. E. A. Baudraz, J. Bódis, F. Q. Brearley, A. Bucharova, C. M. Caruso, R. P. Duncan, J. M. Dwyer, B. Gooden, R. Groenteman, L. N. Hamre, A. Helm, R. Kelly, L. Laanisto, M. Lonati, J. L. Moore, M. Morales, S. L. Olsen, M. Pärtel, W. K. Petry, S. Ramula, P. U. Rasmussen, S. R. Enri, A. Roeder, C. Roscher, M. Saastamoinen, A. J. M. Tack, J. P. Töpper, G. E. Vose, E. M. Wandrag, A. Wingler, and Y. M. Buckley. 2020. Global gene flow releases invasive plants from environmental constraints on genetic diversity. Proceedings of the National Academy of Sciences **117**:4218–4227. URL https://www.pnas.org/doi/abs/10.1073/pnas.1915848117.

Sonti, N. F., R. A. Hallett, K. L. Griffin, and J. H. Sullivan. 2019. White oak and red maple tree ring analysis reveals enhanced productivity in urban forest patches. Forest Ecology and Management **453**:117626. URL https://www.sciencedirect.com/science/article/pii/S0378112719306309.

Stanke, H., A. O. Finley, G. M. Domke, A. S. Weed, and D. W. MacFarlane. 2021. Over half of western United States' most abundant tree species in decline. Nature Communications **12**:451. URL https://doi.org/10.1038/s41467-020-20678-z.

Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. A. Bashkin, and Y. Son. 1999. EXOTIC PLANT SPECIES INVADE HOT SPOTS OF NATIVE PLANT DIVERSITY. Ecological Monographs **69**:25–46.

Tilman, D. 1985. The Resource-Ratio Hypothesis of Plant Succession. The American Naturalist **125**:827–852. URL `http://www.jstor.org/stable/2461449`.

Tilman, D. 2011. Diversification, Biotic Interchange, and the Universal Trade-Off Hypothesis. The American Naturalist **178**:355–371. URL `https://www.journals.uchicago.edu/doi/abs/10.1086/661245`.

Tilman, D., C. L. Lehman, and C. E. Bristow. 1998. Diversity-stability relationships: statistical inevitability or ecological consequence? Am Nat **151**:277–82. URL `https://www.ncbi.nlm.nih.gov/pubmed/18811358`.

Uriarte, M., and D. Menge. 2018. Variation between individuals fosters regional species coexistence. Ecology Letters **21**:1496–1504. URL `https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.13130`.

Way, D. A. 2011. Tree phenology responses to warming: spring forward, fall back? Tree Physiology **31**:469–471. URL `https://doi.org/10.1093/treephys/tpr044`.

Westoby, M., 1984. The Self-Thinning Rule, volume 14, Pages 167–225 . Academic Press. URL `https://www.sciencedirect.com/science/article/pii/S0065250408601713`.

Wills, C., K. E. Harms, R. Condit, D. King, J. Thompson, F. He, H. C. Muller-Landau, P. Ashton, E. Losos, L. Comita, S. Hubbell, J. LaFrankie, S. Bunyavejchewin, H. S. Dattaraja, S. Davies, S. Esufali, R. Foster, N. Gunatilleke, S. Gunatilleke, P. Hall, A. Itoh, R. John, S. Kiratiprayoon, S. L. d. Lao, M. Massa, C. Nath, M. N. S. Noor, A. R. Kassim, R. Sukumar, H. S. Suresh, I.-F. Sun, S. Tan, T. Yamakura, and J. Zimmerman. 2006. Nonrandom Processes Maintain Diversity in Tropical Forests. Science **311**:527–531. URL `https://www.science.org/doi/abs/10.1126/science.1117715`.

Wright, I., D. Ackerly, F. Bongers, K. Harms, G. Ibarra-Manríquez, M. Martinez-Ramos, S. Mazer, H. Muller-Landau, H. Paz, N. Pitman, L. Poorter, M. Silman, C. Vriesendorp, C. Webb, M. Westoby, and S. J. Wright. 2007. Relationships Among Ecologically Important Dimensions of Plant Trait Variation in Seven Neotropical Forests. Annals of botany **99**:1003–15.

Zhu, K., C. W. Woodall, J. V. D. Monteiro, and J. S. Clark. 2015. Prevalence and strength of density-dependent tree recruitment. Ecology **96**:2319–2327. URL `http://dx.doi.org/10.1890/14-1780.1`.

Box 1: Hybrid implementation

THE GOAL of a hybrid model is to permit simulation based on parameters fitted to data, while exploiting residual covariance that promotes diversity. Direct model fitting to individual responses will generally not be feasible, because it requires a positive-definite covariance among individuals. [A positive-definite covariance matrix on 10 individuals would require more than 10 years of measurements.] The species covariance matrix in eq. SU contains two terms, $\mathbf{C} = \mathbf{S}'\mathbf{V_E}\mathbf{S} + \tau^2\mathbf{I}_S$. The first term is positive definite if the inner product E is at least as large as the number of species. This result has direct analogy to MacArthur's analysis of the species interaction matrix (MacArthur, 1969; Advani et al., 2018), where E would represent instead the number of resources. However, matrix $\mathbf{C}$ can be positive-definite even if the first term is not, due to the second term, which acts like the nugget in geospatial models. Either way, we cannot fit (and do not want) the $n(n-1)/2$ coefficients that would be needed to fill a covariance matrix between n individuals. As in Clark (2010), the species covariance matrix here will be built from mean correlations between individuals.

Implementation would differ for each model; here we consider a case where demographic rates (e.g., growth, fecundity) are fitted to j observations on individuals i across monitoring plots k. Fitted estimates constitute the mean structure that will be used to assemble $\tilde{\mathbf{S}}$ in eqn HY. We want to replace the residual (unexplained) variance from this fitted model with a covariance that will have to come from correlation of residual variation between individuals. For a normal or log-normal case, there is a likelihood

$$[\boldsymbol{\beta}_s, \sigma_s^2] \propto \Pi_{i,j} N(g_{s,i,j,k} | \mathbf{x}_k' \boldsymbol{\beta}_s, \sigma_s^2) \tag{1}$$

for predictors in the vector $\mathbf{x}_k$, responses for species s in coefficient vector $\boldsymbol{\beta}_s$, and residual (unstructured) variance σ_s^2. Because the individual covariance is unavailable, we wish to approximate its influence where fitted parameters are used in simulation. In the following steps, $(\hat{\boldsymbol{\beta}}_s, \hat{\sigma}^2)$ are estimates from the fitted model (eq. (1)):

1. Concatenate the $\mathbf{x}_k$ vectors as rows to produce environment $\times$ predictor matrix $\mathbf{E}$ (eq. SK).

2. Concatenate the fitted $\hat{\boldsymbol{\beta}}_s$ coefficient vectors for each species as columns to produce predictor $\times$ species matrix $\mathbf{S}$ (eq. SK).

3. The covariance matrix needed here satisfies $\mathbf{C} = diag(\hat{\boldsymbol{\sigma}})\hat{\mathbf{R}}diag(\hat{\boldsymbol{\sigma}})$, where $\hat{\boldsymbol{\sigma}}$ is a vector of the residual standard deviations from the model fitted to each species (eq. (1)), and $\tilde{\mathbf{R}}$ is the matrix of mean pairwise residual correlations as in (Clark, 2010). Note that this covariance conserves the total variance in the data. This matrix is constructed using the residuals from the fitted model, $r_{i[s,k],j} = g_{i[s,k],j} - \hat{g}_{i[s,k],j}$, which are then correlated between all individual pairs that occur at the same site k, $\rho_{i[s],i'[s'],k} = Cor(r_{i[s,k],j}, r_{i'[s',k],j})$. These correlations are averaged over individual pairs and locations to generate mean correlations

$\bar{r}_{s,s'} = E_{ii',k}\left[\rho_{i[s],i'[s'],k}\right]$ for each species pair. These are the elements of matrix $\hat{\mathbf{R}}$.

4. For simulation, expand species responses $\mathbf{S}$ and covariances $\mathbf{C}$ to individual $\tilde{\mathbf{S}}_k$ and $\tilde{\mathbf{C}}_k$. For example, let $c_{s,s'}$ be an element of $\mathbf{C}$ obtained in the previous step. Upon expansion, covariances between individuals are organized in the $n_{k,t} \times n_{k,t}$ matrix

$$\tilde{\mathbf{C}}_{k,t} = \begin{bmatrix} \mathbf{C}_{1,1} & \dots & \mathbf{C}_{1,S} \\ \vdots & \ddots & \vdots \\ \mathbf{C}_{S,1} & \dots & \mathbf{C}_{S,S} \end{bmatrix} \tag{2}$$

where $\mathbf{C}_{s,s} = c_{s,s} + \tau^2 \mathbf{I}_{n_{ks,t}}$ is the block for individuals of species s, and $\mathbf{C}_{s,s'} = \mathbf{1}_{n_{ks,t}} c_{s,s'} \mathbf{1}'_{n_{ks',t}}$ is the off-diagonal $n_{ks,t} \times n_{ks',t}$ block for individuals of species s and s'. Even with concentration of variance in the diagonal blocks (i.e., within the species), τ^2 is needed to insure that $\tilde{\mathbf{C}}$ is positive definite, because, among other things, the entire diagonal block $\mathbf{C}_{s,s}$ holds the same value $c_{s,s}$.

Although the description here uses the same sites for model fitting as for prediction, $\mathbf{E}$ could also come from other locations. A typical inventory study would have access to pairwise covariances between individuals that can be estimated for time series of limited duration (Clark, 2010).

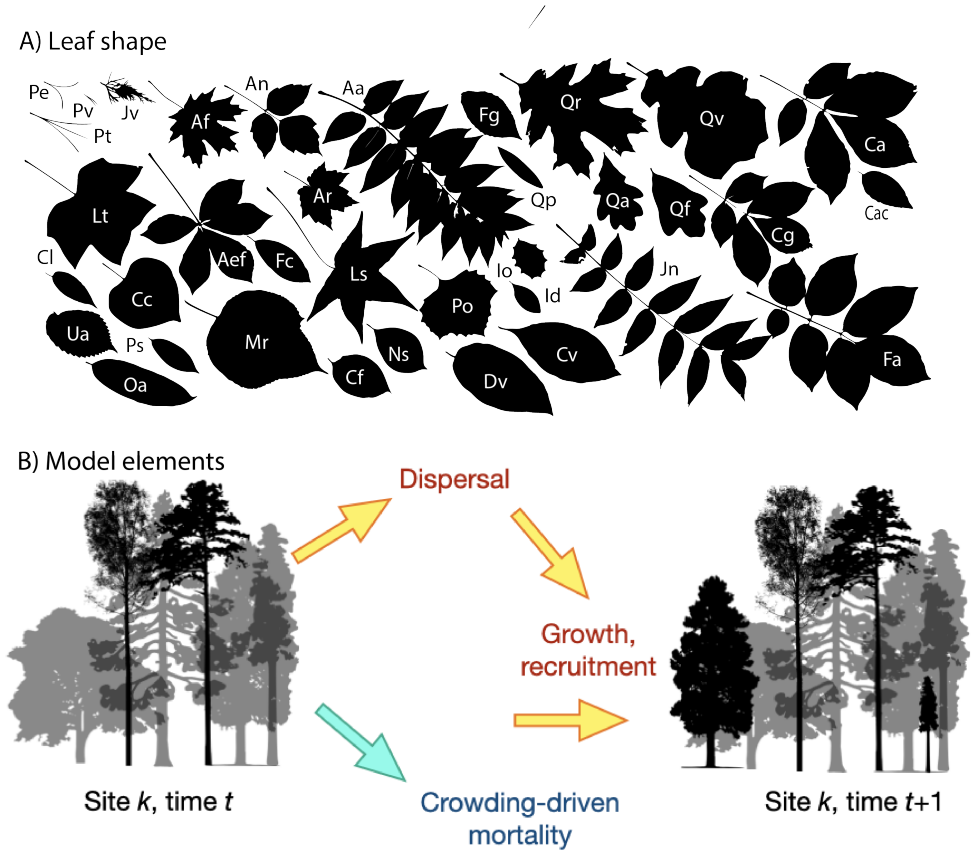

Figure 1: A) Leaf shape is an example trait that varies widely within a single forest [a subset of the variation (34 of 59 tree species) from a temperate forest]. If evolved by natural selection, then this variation must affect fitness and, therefore, demographic rates. B) The model allows for high-dimensional variation in the environment and species responses (see text), partitioned as reproduction, mortality, and dispersal. Acronyms in (A) are for *Acer floridanum, A. negundo, A. rubrum, Aesculus flava, Ailanthus altissima, Carpinus caroliniana, Carya alba, C. glabra, Celtis laevigata, Cercis canadensis, Chionanthus virginiana, Diospyros virginiana, Fagus grandifolia, Frangula caroliniana, Ilex decidua, I. opaca, Juglans nigra, Juniperus virginiana, Liquidambar styraciflua, Liriodendron tulipifera, Morus rubra, Nyssa sylvatica, Oxydendron arboreum, Pinus echinata, P. taeda, P. virginiana, Platanus occidentalis, Prunus serotina, Quercus alba, Q. falcata, Q. phellos, Q. rubrum, Q. velutina, Ulmus americana.* Photos by Samantha Sutton.

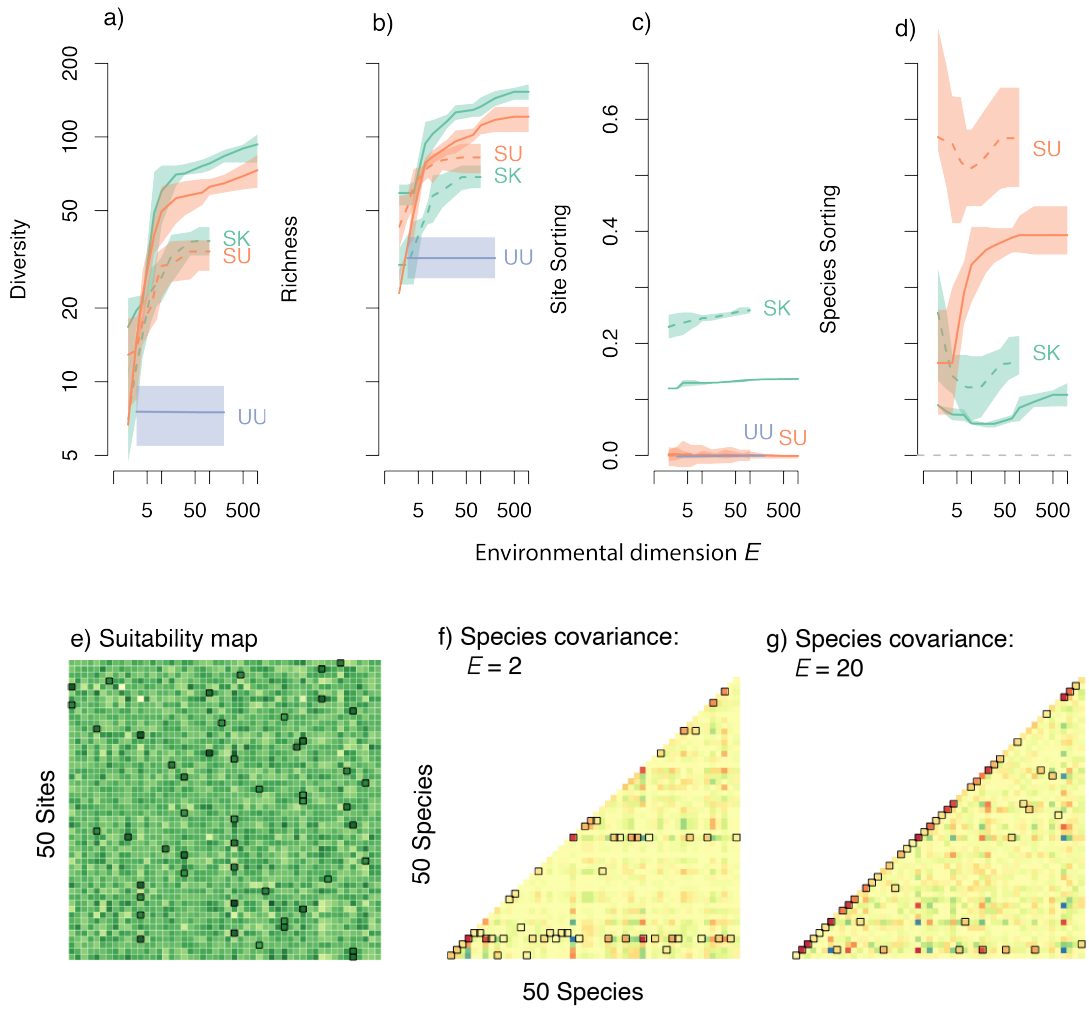

Figure 2: Dimensionality E and coexistence for the structured-known SK, structured-unknown SU, and unstructured UU models. Each model is shown for parameter sets on small (dashed lines, $K = 50$) and a somewhat larger (solid lines, $K = 500$) landscape (Table S2). Species **diversity (a)** and **richness (b)** are Shannon entropy and number of species, respectively. **Site sorting (c)** shows the correlation between species abundance in simulation and the underlying suitability of the landscape, $\mathbf{K} = \mathbf{ES}$, which is shown as a suitability map in **(e)** (dark shading indicates high suitability for a location/species combination). Bounding boxes in **(e)** indicate the dominant species in simulation (one box per row). **Species sorting (d)** is the correlation between species covariances in simulation and the covariance induced by their differing responses in matrix $\mathbf{C}$ **(f, g)**: the largest species covariance pair in each column of **f, g** is highlighted with a bounding box (color ramp from negative blue to positive red). Diversity shifts from **(f)** a simple environment ($E = 2$), where a few species dominate to **(g)** strong diagonal dominance expected where responses depend on a number of variables ($E = 20$). The effect of this shift is the increase in diversity with increasing E in **a, b**. Parameter values are given in Table S2.