

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

James S. Clark^{1,2}, Adam Clark³, Benoit Courbaud², Claire Fortunel⁴,
Camille Girard-Tercieux⁴, Georges Kunstler², Isabelle Maréchaux⁴, Nadja
Rüger^{5,6}, and Ghislain Vieilledent⁴.

¹Nicholas School of the Environment, Duke University, Durham, NC USA 27708

²Université Grenoble Alpes, Institut National de Recherche pour Agriculture, Alimentation et
Environnement (INRAE), 38402 St. Martin-d'Herès, France

³Institute of Biology, Karl-Franzens University of Graz, Graz, Austria

⁴AMAP, Univ. Montpellier, CIRAD, CNRS, INRAE, IRD, Montpellier, France

⁵Department of Economics, University of Leipzig, Leipzig, Germany

⁶German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

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correspondence: jimclark@duke.edu, 919-282-8688

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.

1 Introduction

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

11 A challenge shared by simple, theoretical models of competition (May, 2001; Tilman,
12 1985; Serván et al., 2018), large stand simulators (Maréchaux and Chave, 2017; Rüger et al.,
13 2020; Courbaud et al., 2022), and dynamic earth system models used to predict global change
14 (Fisher et al., 2018; Longo et al., 2019; Fisher and Koven, 2020; Rollinson et al., 2021) is the
15 problem of predicting the high diversity observed in nature. Ecologists have long recognized
16 that plant populations can be limited by a small number of resources (Tilman, 1985; Nogueira
17 et al., 2018), seemingly utilized in similar ways by many competing species. In closed forests,
18 trees compete for light, in part, through height growth. They procure water and nutrients
19 through expanded root systems. Tree growth and fecundity respond to variation in one to a
20 few resources, but not to dozens of resources (Bloom et al., 1985; Tilman et al., 1998; Qiu
21 et al., 2022). Despite intense density-dependent mortality from competition for apparently
22 few limiting resources (Assmann, 1970; Westoby, 1984; D’Amato et al., 2013; He et al.,
23 2022), diversity can be high, and stands are still frequently invaded by introduced species.
24 Yet the many structural and physiological differences that are parameterized in large models
25 do not lead to coexistence. Instead, maintaining diversity in the absence of parameter values
26 carefully selected for this purpose depends on the assumption that seeds remain available
27 even when the adults that would produce those seeds are not (Pacala et al., 1996; Maréchaux
28 and Chave, 2017; Longo et al., 2019; Rüger et al., 2020).

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

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

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

58 Models that generate diversity, either by narrowly defined parameter tradeoffs or by as-
59 suming that inter-specific competition is too weak to limit diversity, do not address the
60 diversity paradox in forests. On the one hand, if forest diversity depended on narrowly de-
61 fined tradeoffs, then those precisely aligned tradeoffs should be evident in data, and species
62 invasion would rarely occur. Recent evidence for structure in multivariate trait analyses
63 show a number of weak correlations (Wright et al., 2007), but none approaching the strict
64 tradeoffs that would be needed to achieve coexistence in models (Clark, 2010; Clark et al.,
65 2018). If coexistence depended on strict tradeoffs, then invading species would be limited
66 to those possessing the specific parameter combinations needed to slot in between species
67 already there. However, species invasions are common in forests, and the most diverse com-
68 munities can be among the most highly invaded (Stohlgren et al., 1999; Lowry et al., 2012).
69 The alternative to parameter tradeoffs, building in as many ways to persist as there are
70 species (e.g., by randomly assigning each species a place to dominate), sidesteps the prob-
71 lem of intense competition for few resources. Even so, proposed remedies in models often
72 admit small diversity increases, not thousands of species, as in hyper-diverse Indonesian and
73 New World Tropical forests. Further limitations include model parameters that cannot be
74 estimated from data (e.g., competitive intransitivities) or that admit only abstract interpreta-
75 tion (e.g., Lotka-Volterra). Models constructed in either of these ways cannot guide further
76 development of the earth system models used to understand climate change, which must
77 build in responses to the key environmental variables that can be measured and tied to plant
78 performance (Fisher et al., 2018; Longo et al., 2019).

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

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

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

128 A simple demonstration

129 **U**niversal coexistence can be demonstrated using a model with as few as three ele-
130 ments: i) species responses that covary between individuals of the same and different
131 species, ii) local competition that drives mortality, regardless of species identity, and iii) dis-

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

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

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

$$\mathbf{h}_k \sim MVN_S(\mathbf{b} + \mathbf{S}^\theta \mathbf{E}_k; \mathbf{I}_S) \quad (\text{SK})$$

165 where vector \mathbf{h}_k holds the S responses, one for each species, centered on mean responses
 166 $\mathbf{b} = \mathbf{1}_S b$. [For simplicity, all species have the same value $b_s = b$.] To simplify comparison
 167 with models that follow, and without loss of generality, we assume that the variables in \mathbf{E} are
 168 centered on zero, a common centering used when models are fitted to data. We refer to this as
 169 the structured-known (SK) model, because it requires full knowledge of environmental effects
 170 on all species. \mathbf{E}_k is the k^{th} row of matrix \mathbf{E} , ϵ^2 is residual (non-environmental) variation,
 171 and \mathbf{I}_S is the identity matrix. Of course, species responses in eq. SK depend on their mean
 172 differences in the vector $\mathbf{S}^\theta \mathbf{E}_k$. They are otherwise independent, because covariance matrix
 173 \mathbf{I}_S has zeros everywhere except along the diagonal. Eq. SK is written as a multivariate

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

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

$$\begin{aligned} \mathbf{h}_k & \sim MVN_S(\mathbf{b}; \mathbf{C}) \\ \mathbf{C} & = \mathbf{S}^T \mathbf{V}_E \mathbf{S} + \sigma^2 \mathbf{I}_S \end{aligned} \quad (\text{SU})$$

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

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

199 There is an equivalent translation for the covariance model in eq. (SU), from $S \times S$ species
 200 covariance \mathbf{C} to $n_k \times n_k$ individual covariance $\tilde{\mathbf{C}}_k$ (Appendix S1 in Supporting Information).
 201 This individual covariance matrix has a block structure, where each block holds the covariance
 202 $\mathbf{C}_{ss'}$ between two species s and s' within a $n_{sk} \times n_{s'k}$ submatrix. Again, $\tilde{\mathbf{C}}_k$ has a location
 203 subscript only because the numbers of individuals of each species vary by location. As before,
 204 covariances between individuals of any two species depend on species identity, regardless of
 205 where those individuals occur.

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

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

$$h_{isk} \sim N(b_s; c_k + \sigma^2) \quad (\text{UU})$$

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

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

231 How and why?

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

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

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

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

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

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

283 Process to data

284 If high-dimensional variation between species, a tiny fraction of which is repre-
285 sented by leaf shape (fig. 1), evolves by natural selection (not all of it does), then this
286 variation has to affect demographic rates in ways that affect fitness. If this has to be true,
287 how does natural selection act on the variation that is rarely evident in estimated demo-
288 graphic rates? Demographic studies commonly find few significant predictors in noisy data
289 and broad overlap between species parameters (Clark et al., 2014a; Kunstler et al., 2021).
290 The typical sample size for demographic estimates can range from tens to thousands of in-
291 dividuals of a given species. Most include a small number of sample dates (Mantgem et al.,
292 2009; Stanke et al., 2021; Qiu et al., 2021; Kunstler et al., 2021). Finding significant relation-
293 ships in noisy data from limited sites and few time intervals is challenging (Tang et al., in
294 review). By contrast, natural selection can operate every year over generations on variation
295 across individuals spanning entire regions, especially where pollen and/or seed dispersal is

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

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

306 Hybrid solution to model diversity

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

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

$$\mathbf{h}_k \sim MVN(\mathbf{b} + \tilde{\mathbf{S}}^l \mathbf{E}_k; \tilde{\mathbf{C}}_k + \mathbf{I}_{n_k}) \quad (\text{HY})$$

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

330 Universal application

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

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

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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 modeling 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 $C = S^0 V_E S + \sigma^2 I_S$. 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 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 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 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

$$[y_s; \sigma_s^2] / \prod_{i,j} N(g_{s;i;j;k} | x_k^0; \sigma_s^2) \quad (1)$$

for predictors in the vector x_k , responses for species s in coefficient vector g_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, $(\hat{\sigma}_s; \hat{\sigma}_s^2)$ are estimates from the fitted model (eq. (1)):

1. Concatenate the x_k vectors as rows to produce environment predictor matrix E (eq. SK).
2. Concatenate the fitted \hat{g}_s coefficient vectors for each species as columns to produce predictor-species matrix S (eq. SK).
3. The covariance matrix needed here satisfies $C = \text{diag}(\hat{\sigma}_s) R \text{diag}(\hat{\sigma}_s)$, where $\hat{\sigma}_s$ is a vector of the residual standard deviations from the model fitted to each species (eq. (1)), and 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 , $r_{i[s];j}^{q[s^0];k} = \text{Cor}(r_{i[s;k];j}; r_{i[q[s^0];k];j})$. These correlations are averaged over individual pairs and locations to generate mean correlations

$r_{s;s^0} = E_{i[i^0];k \quad i[s];i^0[s^0];k}$ for each species pair. These are the elements of matrix \hat{R} .

4. For simulation, expand species responses and covariances \mathbf{C} to individual \mathbf{S}_k and \mathbf{C}_k . For example, let $c_{s;s^0}$ be an element of \mathbf{C} obtained in the previous step. Upon expansion, covariances between individuals are organized in the $n_{k;t}$ matrix

$$\mathbf{C}_{k;t} = \begin{pmatrix} c_{1;1} & \cdots & c_{1;s} \\ \vdots & \ddots & \vdots \\ c_{s;1} & \cdots & c_{s;s} \end{pmatrix} \quad (2)$$

where $\mathbf{C}_{s;s} = c_{s;s} + \mathbf{I}_{n_{k;t}}$ is the block for individuals of species s , and $\mathbf{C}_{s;s^0} = \mathbf{1}_{n_{k;t}} c_{s;s^0} \mathbf{1}_{n_{k;t}}^0$ is the off-diagonal $n_{k;t} \times n_{k;t}^0$ block for individuals of species s and s^0 . Even with concentration of variance in the diagonal blocks (i.e., within the species), \mathbf{I} is needed to insure that \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 modeling 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).

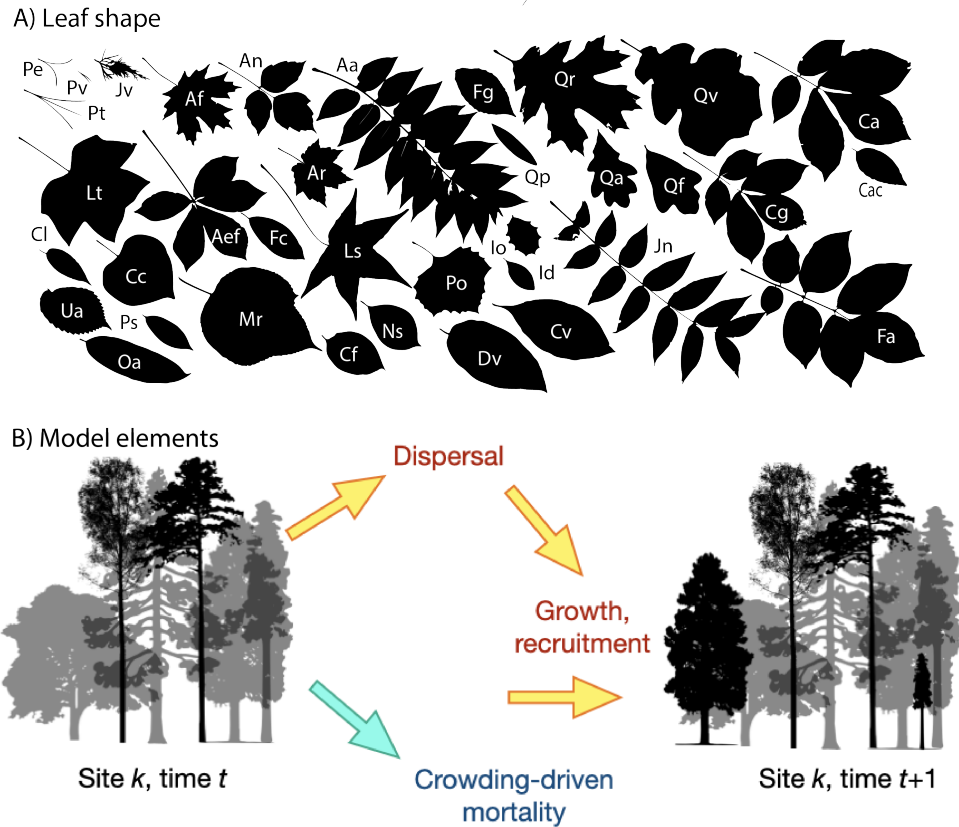


Figure 1: A) Leaf shape is an example trait that varies widely within a single forest [a subset of the variation (34 of 59 tree species) from a temperate forest]. If evolved by natural selection, then this variation must affect fitness and, therefore, demographic rates. B) The model allows for high-dimensional 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.

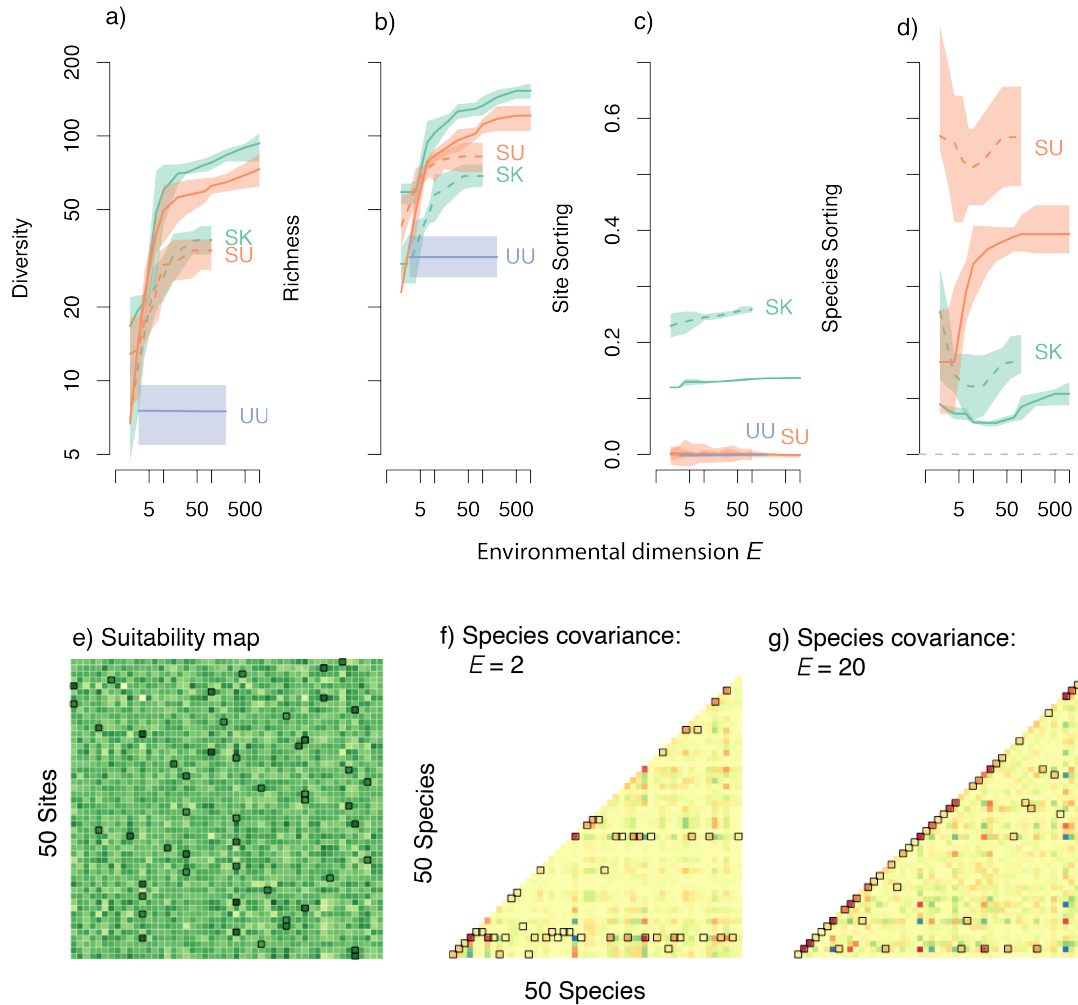


Figure 2: Dimensionality E and coexistence for the structured-known SK, structured-unknown SU, and unstructured UU models. Each model is shown for parameter sets on small (dashed lines, $K = 50$) and a somewhat larger (solid lines, $K = 500$) landscape (Table S2). Species **diversity** (a) and **richness** (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, $\mathbf{K} = \mathbf{E}\mathbf{S}$, 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.