Beyond variance: simple random distributions are not a good proxy for intraspecific variability in systems with environmental structure

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Abstract

The role of intraspecific variability (IV) in shaping community dynamics has been intensively discussed over the past decade and modeling studies have played an important role in that respect. However, a major, but often implicit, assumption typically made by these studies, that IV can be represented by independent random draws around species-specific mean parameters, has largely remained undiscussed. A great part of observed IV is however structured in space or time, in particular when resulting from environmental dimensions that influence individual performance but are imperfectly characterized or unobserved in the field. To test this assumption, we designed a simulation experiment where we varied the level of knowledge of the environment in virtual communities, resulting in different relative importance of explained *vs.* unexplained individual variation in performance. We used a community dynamics simulator to generate communities where the unexplained individual variation is, or is not, added as an unstructured random noise. Communities simulated with unstructured IV never reached the community diversity and composition of those where all the variation is explained and structured (full knowledge model). This highlights that incorporating unstructured IV (*i.e.* a random noise) to account for unexplained (but structured) variation can be misleading. Also, comparing communities simulated with the same level of knowledge of the environment, but adding unstructured IV or not, we found that the effects of incorporating unstructured IV depended on the relative importance of structured versus unstructured IV. In particular, increasing the proportion of unstructured IV into the model moved from a positive to a negative effect on community

diversity and similarity in composition with the full knowledge model. This suggests that it is crucial to account for the sources and structure of observed IV in real communities to better understand its effect on community assembly and properly include it in community dynamics models.

Keywords—community dynamics, community model, ecological niche, environmental filtering, high-dimensional environment, individual variation, species coexistence

Introduction

The role of intraspecific variability (IV) in shaping community dynamics has been intensively discussed over the past decade (Bolnick et al. 2011; Albert et al. 2011; Violle et al. 2012). Observed IV, *i.e.* the variability among measured individual attributes (functional or demographic traits, or any proxy of individual performance) within a species has indeed been reported to be large within communities (Siefert et al. 2015; Poorter et al. 2018). Modeling studies have played an important role to decipher the effect of IV on species coexistence (*e.g.* Lichstein et al. 2007; Vieilledent et al. 2010; Courbaud et al. 2012; Hart et al. 2016; Uriarte and Menge 2018; Crawford et al. 2019), offering opportunities of virtual experiments out of the scope of empirical approaches. These studies have led to contrasting results however, letting the debate unresolved: IV could either (i) blur species differences, thus promoting transient or unstable coexistence (Vieilledent et al. 2010; Crawford et al. 2019), (ii) disproportionately advantage the strongest competitor, thus hindering coexistence (Courbaud et al. 2012; Hart et al. 2016), or (iii) promote coexistence in specific spatial configurations (Uriarte and Menge 2018). While a unifying framework differentiating whether IV affects niche traits or hierarchical traits has been recently proposed to explain these discrepancies (Stump et al. 2021), a major assumption usually made in modeling studies, namely that IV is unstructured in space or time and can be represented by independent random draws around species-specific mean parameters, remains largely undiscussed (Girard-Tercieux et al. 2022).

The IV observed on individual attributes can, however, emerge from various genetically- and environmentally-driven processes (Violle et al. 2012; Moran et al. 2016). Most of these processes are unlikely to generate unstructured IV in the form of a normal noise. Instead, IV can be highly structured in space or time. In particular, high-dimensional (and often unobserved) variation of the environment can lead to large observed IV. For instance, in a highly controlled clonal experiment, IV in tree growth within clones was larger than genetically-driven IV between clones (Girard-Tercieux et al. 2022). Differences in attributes among conspecific individuals can result from differences in unobserved environmental dimensions, and do not necessarily mean that conspecific individuals substantially differ in their response to the environment. While it is widely accepted that environmentally-driven structured IV (sIV) is ubiquitous in natural communities (Nicotra et al. 2010), the consequences of its substitution by unstructured IV (uIV) on species coexistence and community dynamics remain to be thoroughly tested in models (Clark 2010; Girard-Tercieux et al. 2022).

Here, we explore the effect of considering IV either as structured by environmental dimensions (sIV) or as an unstructured random noise (uIV), using a simulator of community dynamics. To do so, we created a virtual plant community, where individual performance is fully determined by species-level responses to 15 environmental dimensions (*Perfect knowledge model*, Fig. 1A). We then considered imperfect knowledge models, where this 15-dimensional individual performance is estimated using 0 to 15 supposedly "observed" environmental dimensions, while the remaining IV (or unexplained variation) resulting from effect of "unobserved" environmental dimensions, is ignored (*Imperfect knowledge models without uIV*) or is included as random unstructured IV (*Imperfect knowledge models with uIV*, Fig. 1B). These three performance models are used to run a community dynamics simulator and assess their effects on species coexistence and community dynamics.

Specifically, we are asking two questions: First, how well does random unstructured IV (uIV) mimic the effect of environmentally-driven structured IV (sIV) on diversity and community composition? To answer this question, we compare communities simulated under the *Perfect knowledge model* and under *Imperfect knowledge models with uIV*. These models share the same amount of total variation, but partitioned differently between sIV and uIV, depending on the amount of knowledge of the environment we consider (Fig. 1C, arrow 1). Second, how does the effect of adding

uIV on diversity and community composition (Fig. 1C, arrow B) vary with the knowledge of the environment (Fig. 1C, arrow C), *i.e.* with the relative importance of sIV and uIV in our model? To answer this question, we compare pairs of models with the same amount of sIV, *i.e.* with the same knowledge of the environment, but including or excluding uIV. This latter comparison corresponds to the approaches proposed in previous studies testing the effects of IV on coexistence (Vieilledent et al. 2010; Courbaud et al. 2012; Hart et al. 2016).

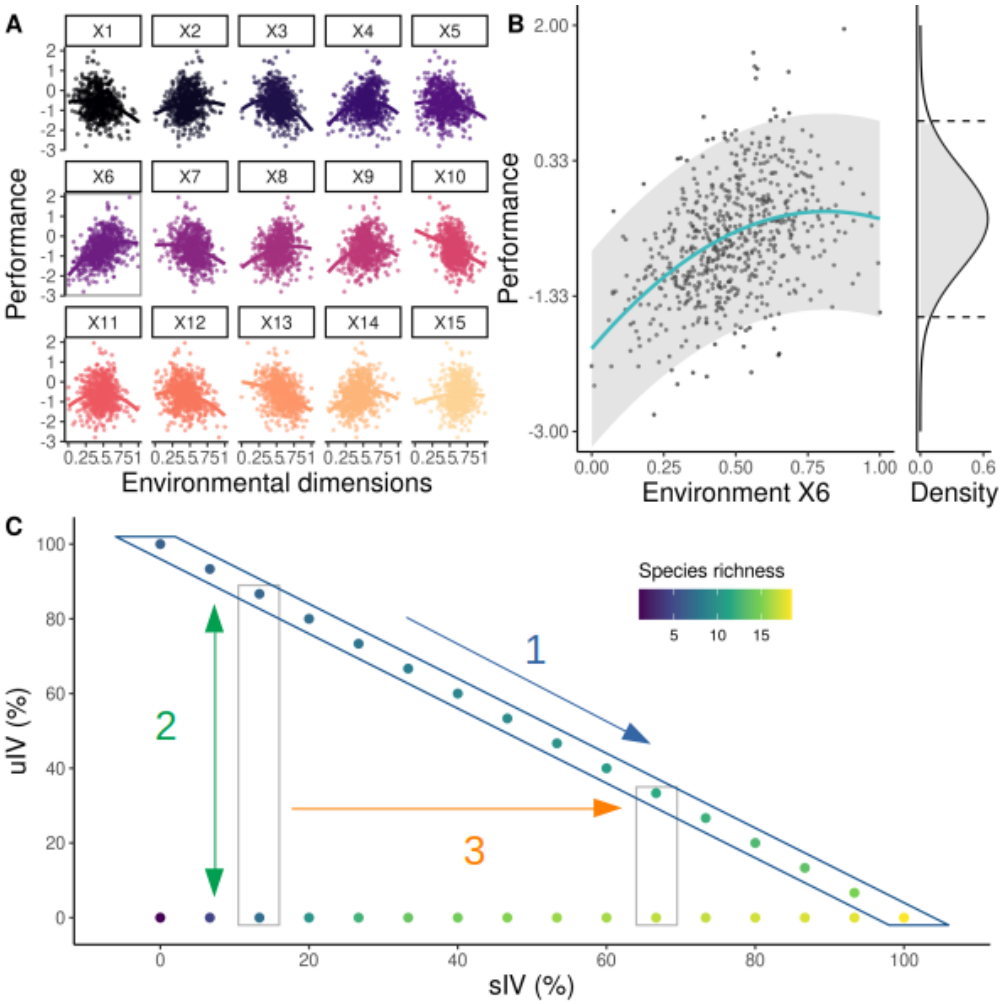

Figure 1: Conceptual framework. Consider an environment that is varying in many dimensions, X1 to X15. Each dimension influences individual performance in a species-specific way, as illustrated in A for one species. In practice, several of these environmental dimensions are actually unobserved in the field. The effect of unobserved environmental dimensions on individual performance results in an observed intraspecific variability (IV) in the species response to observed dimensions (*e.g.* X6 in B). This variability is often represented as a probability distribution, with individual random draws that are independent and unstructured in space and time (B). We propose a framework to assess the consequences of representing the variation resulting from unobserved environmental dimensions, which has an inherent structure, by such unstructured IV (uIV) on community dynamics, and how these consequences vary with the level of knowledge of the environment (C). To do so, we varied from 0 to 15 the number of dimensions that are observed and used for estimating the 15-dimensional performance. By increasing the number of observed dimensions, we thus increased the proportion of structured IV (sIV) that is accounted for in estimating individual performance (C, horizontal axis; see also Fig. 2). For a given number of observed dimensions, or % of sIV, the variation resulting from unobserved dimensions can be either added as uIV or not (C, vertical axis). For each way to estimate performance (with uIV or not, and with different numbers of observed dimensions), we simulated community dynamics using the same simulator. We then compared the simulated communities in terms of diversity and composition (*e.g.* species richness in colored points in C). By comparing communities simulated with uIV with the one with 100 % sIV (arrow 1) we tested the effect of substituting sIV with uIV on community dynamics. By comparing communities simulated with and without uIV, for a given % of sIV (arrow 2), we mimicked the approach of previous modeling studies testing the effect of intraspecific variability on community dynamics and species coexistence. By comparing this difference between communities simulated with and without uIV across different % of sIV (arrow 3), we tested whether the results of previous studies can be influenced by the level of knowledge of the environment.

Materials and methods

Environmental variables

We consider a grid of $25 \times 25 = 625$ sites. Each site i is characterized by a multidimensional environment defined by 15 environmental variables $x_1, \ldots, x_{15}$. Each environmental variable is spatially auto-correlated and independently derived from a conditional autoregressive model, with a normal distribution centered on 0 and of variance 1. Therefore, environmental variables are not uniformly distributed, some habitats ($x_1, \ldots, x_{15}$ values) being more frequent than others. Environmental variables are then scaled to $[0, 1]$.

Individual performance

We consider 20 species, whose individual performance is computed in three alternative ways, as follows.

The *Perfect knowledge model*

We first consider a simple model representing the "real" functioning of a plant community, *i.e.* where all determinants of individual performance are known. We consider that the environment is multidimensional and partitioned among species. To this end, in this *Perfect knowledge model*, the performance of individuals of species j is maximal at one point in the multidimensional environmental space, denoted $x^*_j = (x^*_{1,j}, \ldots, x^*_{15,j})$. For an environmental axis k, $x^*_{k,j}$ is drawn in a uniform distribution in $[0, 1]$. Then, the performance of an individual of species j on site i, p_{ij}, is computed as the additive inverse of the normalized Euclidean distance between x^*_j and the local environment at the site where the individual thrives, $x_i = (x_{1,i}, \ldots, x_{15,i})$ (Eq.1).

Therefore, at each site one species outperforms all others. The number of sites where each species has the highest performance varies between species, since the environmental variables are not uniformly distributed. For some species, there is no site where they are the most competitive. Importantly, all individuals of a given species j respond in the same way to the environment, the performance of conspecifics differing only because they thrive in a different environment. Individual variation is thus fully environmentally-driven and structured in space (0% uIV and 100% sIV in Fig. 1C).

$$\begin{aligned} p_{ij} &= -(d_{ij} - \mu_d)/\sigma_d \\ d_{ij} &= \sqrt{(x^*_{1,j} - x_{1,i})^2 + \cdots + (x^*_{15,j} - x_{15,i})^2} \end{aligned} \tag{Eq.1}$$

where μ_d and σ_d are the mean and variance of $d_{i,j}$ across all sites i and species j respectively.

The *Imperfect knowledge models*

Just like a field ecologist is typically not able to fully characterize all dimensions of environmental variation, we then assumed that only $n_{obs} < 15$ environmental variables were monitored and accounted for when estimating individual performance. These performances are thus estimated from a statistical model fitting the individual performance provided by the *Perfect knowledge model* $p_{i,j}$ (Eq.1, representing what actually happens in the field and is measured, assuming no measurement error) against the n_{obs} observed environmental variables (Fig. 1). We consider the simple case where ecologists assume a quadratic relationship between performance and each observed environmental

variable, thus approaching the triangular shape of the actual relationship of the *Perfect knowledge model* (Eq.2).

$$\begin{aligned} p_{ij} &= \beta_{0,j} + \beta_{1,j}x_{1,i} + \beta_{2,j}x_{1,i}^2 + \cdots + \beta_{2n_{obs}-1,j}x_{n_{obs},i} + \beta_{2n_{obs},j}x_{n_{obs},i}^2 + \varepsilon_{ij} \\ \varepsilon_{ij} &\sim Normal(0, V) \end{aligned} \tag{Eq.2}$$

This statistical model was fitted using the lm function of the stats R package. Species parameters $\beta_j = [\beta_{0,j}, \ldots, \beta_{2n_{obs},j}]$ and residuals (ε_{ij}) were retrieved. In this model, we considered that the ε_{ij} represented an unstructured IV. The observed IV was thus estimated as the variance of the ε_{ij} for each species j, V_j. This variability emerges from the spatial variation in environmental variables that were not monitored and accounted for, namely $[x_{n_{obs}+1}, \ldots, x_{15}]$.

In order to answer our second question (Fig. 1C, arrows 2 and 3), we varied the level of knowledge of the environment, *i.e.* varied n_{obs} from 0 to 15. ε_{ij} thus accounted for the $15 - n_{obs}$ unobserved environmental variables, respectively. In the *Imperfect models without uIV*, the residual variation, ε_{ij}, was neglected (Eq.3), while in the *Imperfect knowledge models with uIV*, it was included as a random noise $\hat{\varepsilon_{ij}}$ estimated from independent individual draw in a normal distribution of variance V_j (Eq.4).

Therefore, in the *Imperfect knowledge models without uIV*, conspecific individuals respond similarly to the environment as in the *Perfect knowledge model* for the observed environmental dimensions, but lacking information on the other environmental dimensions (0% uIV in Fig. 1C). In contrast to the *Perfect knowledge model* and the *Imperfect knowledge models without uIV*, in the *Imperfect knowledge models with uIV*, conspecific individuals can perform differently in the same environment (0 to 100% uIV in Fig. 1C).

$$\hat{p_{ij}} = \beta_{0,j} + \beta_{1,j}x_{1,i} + \beta_{2,j}x_{1,i}^2 + \cdots + \beta_{2n_{obs}-1,j}x_{n_{obs},i} + \beta_{2n_{obs},j}x_{n_{obs},i}^2 \tag{Eq.3}$$

$$\hat{p_{ij}} = \beta_{0,j} + \beta_{1,j}x_{1,i} + \beta_{2,j}x_{1,i}^2 + \cdots + \beta_{2n_{obs}-1,j}x_{n_{obs},i} + \beta_{2n_{obs},j}x_{n_{obs},i}^2 + \hat{\varepsilon_{ij}} \tag{Eq.4}$$

The three types of performance models (Eq.1, Eq.3, Eq.4) were then implemented in a simulator of community dynamics, in order to disentangle the effects of random, unstructured IV and of the imperfect characterization of the environment on community dynamics and species coexistence.

Community dynamics simulation

Our simulator of community dynamics was inspired by Hurtt and Pacala (1995). However, several of our modeling choices differed. First, we explicitly used several environmental dimensions to account for niche multidimensionality, while they used a summary environmental index. Second, we randomly drew species optima, therefore leading to various sizes of the environmental space where each species outperforms all the others, while they used equally wide ecological niches across species. This allowed us to test several configurations of niche partitioning. Finally, mortality and recruitment were stochastic in their model, while we chose a deterministic process to stabilize coexistence and limit the sources of uncertainty to the effect of IV, although we also tested a stochastic alternative (see details below).

For a given simulation of community dynamics, the simulated community was initialized with ten individuals of each of the 20 species, located randomly in the landscape. The performance of these individuals was computed using either the *Perfect knowledge model* (Eq.1), an *Imperfect knowledge model without uIV* (Eq.3), or an *Imperfect knowledge model with uIV* (Eq.4). Mortality events result in vacant sites for which species then compete for recruitment. To test the robustness

of our results to the choices made in building the community dynamics simulator, we implemented alternative ways to simulate mortality and fecundity. For mortality, we explored the three following approaches: (i) the one percent less performing individuals in the landscape die at each timestep, henceforth denoted *deterministic mortality*; (ii) one percent of the individuals die at each timestep, and the probability of each individual to die is proportional to its performance, henceforth denoted *stochastic mortality*; (iii) the probability θ_{ij} of each individual j to die is computed as a function of its performance, $\theta_{ij} = \text{logit}^{-1}(\text{logit}(0.01) - 0.5 \times p_{ij})$, henceforth denoted *logistic stochastic mortality*. Death events are then drawn in a binomial distribution $B(n_s, \theta)$ with θ the vector of all θ_{ij}. For fecundity, we explored the two following approaches: (i) the number of propagules $prop_{j,t}$ depends on species abundance $A_{j,t}$: $prop_{j,t} = round(0.5 \times A_{j,t})$, henceforth denoted the *abundance-dependent fecundity*; or (ii) each species present in the community produces ten offspring per timestep, henceforth denoted the *fixed fecundity*. In both cases, propagules are then randomly distributed among all vacant sites (*i.e.* there is no limited dispersal). If several propagules land on the same vacant site, the propagule with the highest individual performance outcompetes the others and wins the site. Hence a species that is not the best at a site can win "by forfeit". When individual performance is computed using the *Perfect knowledge model*, the colonization of a vacant site only depends on the species optima. When individual performance is computed using an *Imperfect knowledge model without uIV*, this colonization depends on the estimated species parameters (the β_j), and, for an *Imperfect knowledge model with uIV*, also on a random individual variation (the $\hat{\varepsilon_{ij}}$), that enables potential inversions of competition hierarchy locally.

Overall, multidimensional niche partitioning and environmental filtering are the main coexistence mechanisms within the simulated communities: mortality and recruitment are controlled by performance, which depends on the local environment in a species-specific way. Therefore, individuals that are maintained and recruited on a site are filtered by the environment, and performance on each site increases rapidly. When using the performance models without uIV (*i.e.* *Perfect knowledge* and *Imperfect knowledge models without uIV*), each species rapidly occupies a preferred habitat defined by its optima (perfectly or imperfectly estimated) in many environmental dimensions. It should be noted that species favorable habitats are not equally frequent across species, thus intrinsically defining rare and dominant species in the landscape. Few species that have a rare favorable habitat and whose initial individuals randomly land on unfavorable sites, can be excluded from the community.

As most results remained qualitatively unchanged across the different alternatives for simulating mortality and fecundity, we present below the results for the *deterministic mortality* and the *abundance-dependent fecundity* only, and refer the reader to Appendix 1 for the other alternatives.

Experimental setup and analyses

For each model of individual performance and number of observed environmental dimensions, we used ten different Environment $\times$ Species optima ($E \times S$) configurations, each prescribed randomly. Within each $E \times S$ configurations, ten simulations differing only in their initial conditions (location of the initial individuals) were run. Each simulation of community dynamics was run for 10,000 generations (Table 1). The ten $E \times S$ configurations were the same across models of individual performance and number of observed environmental dimensions and the ten initial conditions were the same across $E \times S$ configurations. In total, this leads to 3300 simulations.

Table 1: Experimental setup.

Experimental setting	Number	Comments
Model of individual performance	3	*Perfect knowledge*, *Imperfect knowledge without uIV*, *Imperfect knowledge with uIV*
Number of observed environmental dimensions n_{obs}	0 to 15	Except for the *Perfect knowledge model*
$E \times S$ configuration	10	The same configurations are used across the models of individual performance and number of observed environmental dimensions
Initial conditions	10	Determined by the locations of the 10 individuals per species within the landscape
Generations	10000	Sufficiently long so that changes in the community are very slow

In order to compare simulation outputs, we studied several aspects of final communities: (1) community diversity, (2) the similarity in community composition between simulations, and (3) site sorting. Community diversity was estimated using species richness and the Hill-Shannon diversity index (Roswell et al. 2021). Similarity in community composition was estimated as the pairwise percentage similarity of final species abundances between pairs of simulations. For two vectors of species abundances $A = (a_1, \ldots, a_i, \ldots, a_S)$ and $B = (b_1, \ldots, b_i, \ldots, b_S)$, the percentage similarity was computed as

$$PS = \frac{2 \times \sum_{i=1}^{S} min(a_i, b_i)}{\sum a_i + \sum b_i} \quad \text{(Eq.5)}$$

To quantify site sorting, we computed for each simulation the final community mean performance as the performance obtained with the *Perfect knowledge model*, averaged across all individuals at the end of the simulation. This community mean performance thus corresponds to the strength of the environmental filtering in community assembly, *i.e.* the site sorting: the higher the mean performance, the stronger the effect of the environment on community assembly.

Results

Final community diversity

Final community diversity, both in terms of species richness and Hill-Shannon index, was lower with unstructured IV than with the *Perfect knowledge model* whatever the number of observed environmental dimensions *i.e.* relative importance of structured and unstructured IV (Fig. 3A and B). This

diversity increased with the number of observed dimensions. In most cases, adding unstructured IV reduced the species diversity with respect to the corresponding *Imperfect knowledge model without uIV* (Fig. 3C and D). However, this effect varied with the number of observed dimensions (but see in case of alternative mortality implementation, Appendix 1): below 50% of explained variance (*i.e.* up to three observed environmental dimensions, Fig. 2), adding unstructured IV resulted in a higher or similar diversity than with the *Imperfect knowledge models without uIV*. This difference first decreased and then increased as the number of observed dimensions increased, while staying negative from 3 to 15 observed dimensions.

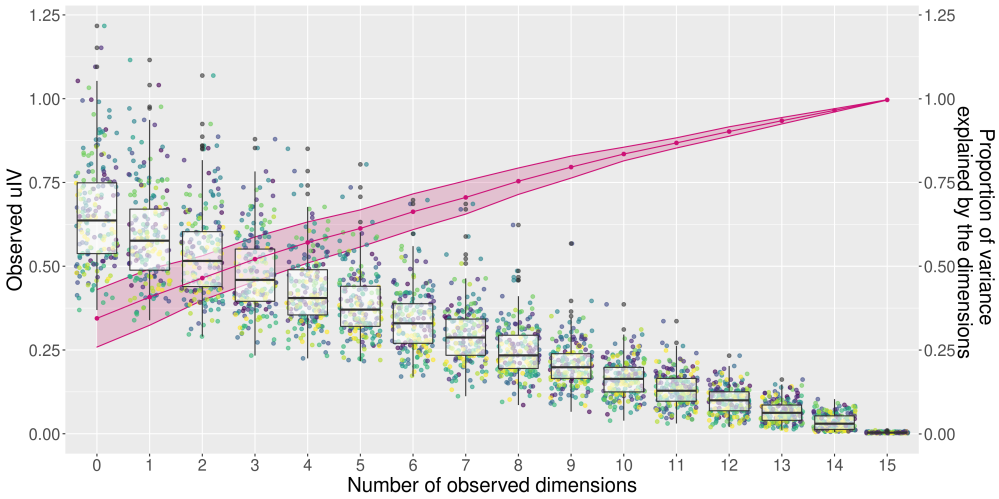

Figure 2: Observed IV depending on the level of knowledge of the environment. Each point represents the unstructured IV inferred for one species, and each color represents an configuration (twenty points per color for the twenty species). Unstructured IV was inferred using a statistical model (Eq.2) taking 0 to 15, out of 15, dimensions into account to fit the performance provided by the *Perfect knowledge model*; the pink points, curve and ribbon correspond to the mean and standard deviation of the R2 of these statistical models (computed over the ten different configurations for each number of observed dimensions). As expected, observed unstructured IV decreases with the number of observed dimensions, *i.e.* with the level of knowledge of the environment.

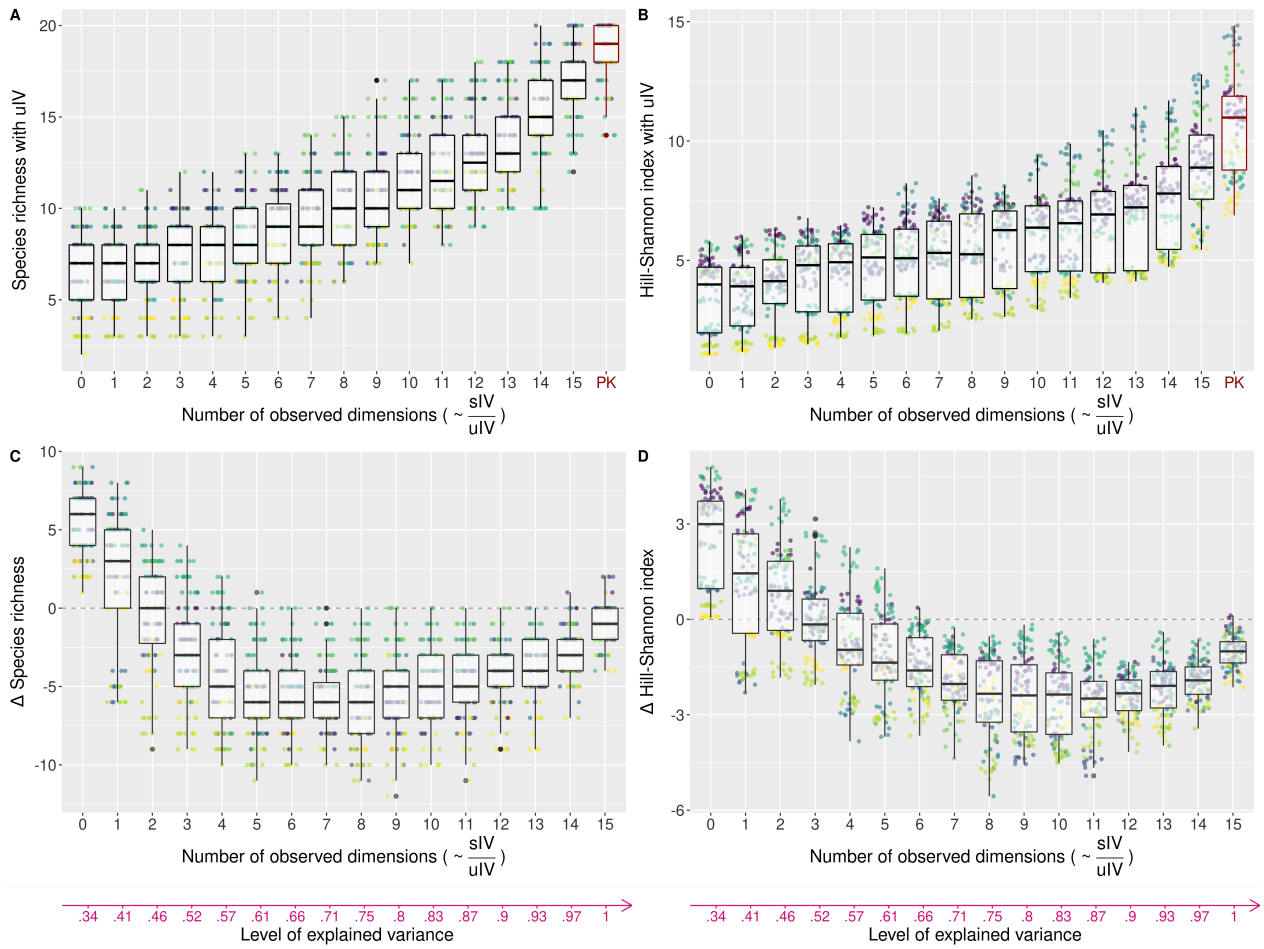

Figure 3: Effect of the structure of individual variation on community diversity. Each point represents the diversity, either computed as the species richness – left panels – or the Hill-Shannon diversity index – right panels – of a final simulated community. Each color represents an $E \times S$ configuration (ten points per color, for the ten initial conditions). The horizontal axis corresponds to the number of observed environmental dimensions, which is proportional to the ratio of structured and unstructured IV in the performance models. Each number of observed dimensions corresponds to a level of explained variance in individual performance (see Fig. 2) depicted with the pink arrow at the bottom. The top panels show the final community diversity obtained with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). This is useful to examine our first question (Fig. 1C, arrow 1). The bottom panels show the difference in the final community diversity obtained with the *Imperfect knowledge models with* and *without uIV*. Points that are above zero (horizontal dashed line) correspond to a higher diversity when adding unstructured IV. This is useful to examine our second question (Fig. 1C, arrows 2 and 3), by comparing the effect of adding unstructured IV at different levels of knowledge of the environment. The *Imperfect knowledge models with uIV* never reach the diversity obtained with the *Perfect knowledge model* (A and B). Moreover, adding unstructured IV as a random noise has an effect on community diversity that varies with the number of observed environmental dimensions (C and D). Results shown here were obtained with a *deterministic mortality* and an *abundance-dependent fecundity* (see main text).

Final community composition

Similarity (as measured by PS, Eq.5) of the *Imperfect knowledge models with uIV* with the *Perfect knowledge model* was low when few environmental dimensions were observed, *i.e.* the relative

importance of structured *vs.* unstructured IV was low. This similarity increased with the number of observed dimensions (from 0.55 to 0.9, Fig. 4A). Adding unstructured IV increased the similarity with the *Perfect knowledge model* at low numbers of observed dimensions (from 0 to 2 dimensions, *i.e.* below 50% explained variance) but decreased it at higher numbers of observed dimensions, with respect to the corresponding *Imperfect knowledge model without uIV* (Fig. 4C, but see in case of alternative mortality implementation, Appendix 1). This negative effect became stronger (from 3 to 8 observed dimensions) before becoming weaker (from 9 to 15 observed dimensions). See Appendix 2 for the similarity within models.

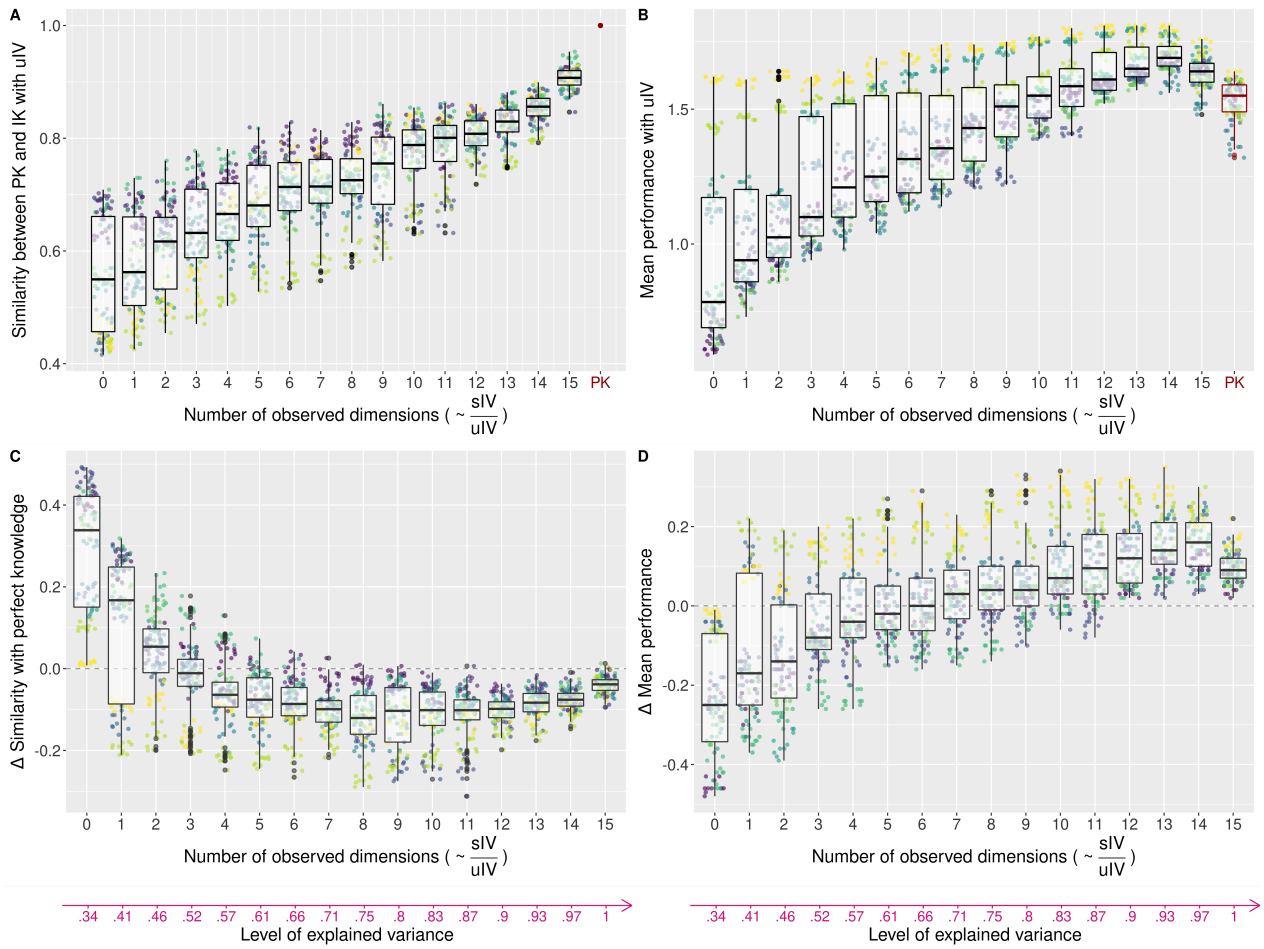

Figure 4: Effect of individual variation on the similarity in final species abundances between models and on the site sorting. Each color represents an $E \times S$ configuration. For the similarity - left panels -, each point represents the pairwise percentage similarity (PS) in the final species abundances between two simulations with the same $E \times S$ configuration and the same initial conditions (ten points per color), but obtained using the *Perfect knowledge model* one the one hand and one of the *Imperfect knowledge models* on the other hand. For the site sorting - right panels -, each point represents the community mean performance of the final communities. This mean performance was calculated with the *Perfect knowledge model* and averaged across all individuals at the end of the simulation. The top panels show these two metrics for communities simulated with the *Imperfect knowledge models with uIV* (0 to 15 observed dimensions) and with the *Perfect knowledge model* (PK, red, far right). The bottom panels show the difference in these metrics for communities obtained with the *Imperfect knowledge models with* and *without unstructured IV*. Points that are above zero (horizontal dashed line) correspond to a higher similarity or mean performance when adding unstructured IV, respectively.The similarity between the *Perfect knowledge model* and the *Imperfect knowledge models with uIV* is low with few observed dimensions and increases with the number of observed dimensions (A). The effect of adding unstructured IV to *Imperfect knowledge models* on the similarity with the *Perfect knowledge model* varies with the number of observed environmental dimensions (C). The mean performance obtained for communities simulated with the *Imperfect knowledge models with uIV* as well as its difference with the *Imperfect knowledge models without uIV* vary with the number of observed dimensions (B, D). Results shown here were obtained with a *deterministic mortality* and an *abundance-dependent fecundity* (see main text).

The mean performance of communities simulated with the *Imperfect knowledge models with uIV* increased with the number of observed dimensions (except between 14 and 15 observed dimensions),

i.e. the relative importance of structured and unstructured IV (Fig. 4B). Below ten observed dimensions, it remained lower than that of the communities simulated with the *Perfect knowledge model*, but was higher above ten observed dimensions. Adding unstructured IV decreased the mean performance of the final species community from zero to six observed dimensions but increased it at higher numbers of observed dimensions, with respect to the corresponding *Imperfect knowledge model without uIV* (Fig. 4D). This difference increased with the number of observed dimensions, except between 14 and 15 observed dimensions.

Discussion

Substituting structured with random unstructured individual variability lowers community diversity and generates unrealistic communities

Ecologists have only access to an imperfect characterization of all the dimensions that actually lead to individual variation. This lack of knowledge results in an observed but unexplained intraspecific variability. To cope with it, it has often been (implicitly) assumed that some unstructured variation could be added to the explained part of variation to reach the actual observed total variation. To test this assumption, in our simulation experiment, we varied the level of knowledge of the environment and incorporated the remaining (unaccounted) variability in individual performance as unstructured noise, thus varying the ratio of structured and unstructured IV. We showed that this difference in the nature of IV has strong consequences on community structure and composition.

Compared to the communities simulated with a 15-dimensional individual performance (*Perfect knowledge model*), the communities simulated with a performance estimated with fewer dimensions and to which the remaining variance was added as a random noise (*Imperfect knowledge models with uIV*) were less diverse (Fig. 3A and B; see also Appendix 3 for further explanation on simulated species richness). Beyond the community diversity *per se*, community composition was unrealistic when the number of observed dimensions was low, *i.e.* when the relative importance of structured *vs.* unstructured IV was low: the strength of environmental filtering in shaping community assembly was too low to generate species abundances similar to the one of the *Perfect knowledge model*. As the relative importance of structured IV increased, both the strength of environmental filtering and the similarity of the final species abundances with the ones obtained with the *Perfect knowledge model* increased (Fig. 4A and B).

Finally, random intraspecific variability is not a good substitute for species response to unobserved environmental dimensions for studying community dynamics. Moreover, interpreting observed IV as unstructured differences in conspecifics' response to the environment can lead to misinterpretations regarding the ecological mechanisms driving the community dynamics: it would mistake the response of species to environmental variation (a niche mechanism) with random variability (a neutral mechanism), and present IV as a coexistence mechanism *per se* independently of the differences in species response it can actually result from. Hence, maintaining the variance observed among individuals is not sufficient to capture the community dynamics, the structure and nature of this individual variability is also critical.

The effect of adding a random IV depends on the relative importance of structured *vs.* unstructured individual variability

Previous studies that typically explored the role of IV on community dynamics actually did not even maintain the total level of variance among individuals. Such studies typically compared communities with and without additional random variability, for a same level of explained individual variation (*Imperfect knowledge model without uIV vs. Imperfect knowledge model with uIV*). Our results showed that the effect of adding a random IV depends on the level of explained variance, *i.e.* in our case on the number of observed dimensions (Fig. 3C and D, Fig. 4C and D).

When structured IV accounted for less than 50% of the total individual variation, the addition of a random unstructured variation increased community diversity (Fig. 3, but see in case of alternative mortality implementation, Appendix 1). This positive effect was due to the inversions in competitive hierarchy produced by adding a random variation to individual performance; it allowed more species to be maintained in the community although there were few theoretical winners (*i.e.* species that are the best performing somewhere in the landscape) because of the projection of their niches on few environmental dimensions. Similarly to species diversity, when the proportion of structured IV was low, adding unstructured IV increased the similarity of the final species abundances between the *Imperfect knowledge model* and the *Perfect knowledge model* (Fig. 4C). This increase in similarity was however only due to the higher number of species reached when adding unstructured IV (Fig. 3) (the higher number of zero abundances with the *Imperfect knowledge models without uIV* decreases the estimated similarity with the abundances obtained with the *Perfect knowledge model*).

When the proportion of structured IV increased, this positive effect of adding random IV on community diversity vanished (Fig. 3, but see in case of alternative mortality implementation, Appendix 1), because the destabilization of the niche partitioning between species due to unstructured IV decreased. Indeed, as expected, the lower unstructured IV was, the greater community mean performance (*i.e.* site sorting) was in comparison to the communities simulated without unstructured IV (see Appendix 3 for further explanation on the absolute differences in community mean performance). This negative effect first increased but then decreased with the number of observed environmental dimensions, because the magnitude of the added unstructured IV became lower (Fig. 2).

Finally, adding unstructured IV in models is most likely to move simulated community composition away from reality (here represented by the *Perfect knowledge model*), because this type of variation blurs the species properties that are (although imperfectly) captured with the observed dimensions. In other words, adding randomness never compensates for lack of knowledge and can even blur the limited knowledge obtained from field data, although this is not the case at a very low level of knowledge of the environment.

Previous studies testing the effect of adding intraspecific variability on species coexistence provided contrasting results (Lichstein et al. 2007; Vieilledent et al. 2010; Courbaud et al. 2012; Hart et al. 2016; Uriarte and Menge 2018; Crawford et al. 2019). Stump et al. (2021) proposed a framework to explain part of these discrepancies, by differentiating the nature of the traits - niche *vs.* hierarchical traits – on which variation was added. While our virtual experiment only considered additional variability in a hierarchical trait (performance) *sensu* Stump et al. (2021), our results here evidenced an additional source of discrepancies when testing the effect of adding a random variability on community dynamics: the relative importance of explained and structured *vs.* unexplained and unstructured individual variance. Future studies should thus pay great attention to the nature and structure of the observed variability when testing its effect on communities and move away from the systematic approach of adding an unstructured noise.

Accounting for a high-dimensional environment in community dynamics models

Most previous studies have modeled IV as a random noise around species means (Lichstein et al. 2007; Vieilledent et al. 2010; Courbaud et al. 2012; Hart et al. 2016; Uriarte and Menge 2018; Crawford et al. 2019), and did not represent environmental variations that generate individual variation (*e.g.* Lichstein et al. 2007; Courbaud et al. 2012), or did so in a way that does not mirror multi-dimensional variation: Uriarte and Menge (2018) provided two different habitats, Vieilledent et al. (2010) used site effects at a much larger scale than individuals, Crawford et al. (2019) represented biotic interactions with resources that are constant through space and time, and while Banitz (2019) is the first to test the consequences of IV resulting from a spatially-structured environmental index, coexistence relied on trade-offs and random disturbances in a one-dimensional environment. Our results showed that, when the level of knowledge of the environment that generates individual variation is high enough (Fig. 3C, D and Fig. 4C), adding unstructured IV, instead of improving the realism of the simulated communities, can actually move them away from the actual communities (*i.e.* the ones simulated with the *Perfect knowledge model* of individual performance). Thus using independent random draws is not a relevant approach to represent intraspecific variability that is often environmentally-driven (Girard-Tercieux et al. 2022), and progress must be made to take into account the environment-species interactions in models.

Improving the knowledge of the environment: a costly but worthy endeavor

The environment can vary in many ways, even if the number of resources is limited, as it is likely the case (Craine 2009). Indeed, many other biotic and abiotic variables can influence individual performance (soil microbiome and texture, micro-climate, pathogens, Fortunel et al. 2018; Averill et al. 2022). Moreover, species can partition the same environmental dimension (*e.g.* light) by responding non-linearly to it (*e.g.* with different light-performance slopes at different light levels), further increasing the dimensionality of their responses to environmental variation in space and time. As monitoring environmental variables and species responses at fine spatio-temporal scales is difficult and costly, most of the environmental variation that actually influences individuals' attributes is not properly monitored in ecological studies.

Our results suggest that improving the characterization of environmental variation by monitoring additional independent environmental variables (*i.e.* to moving to the right in Fig. 2, 3, and 4) is a worthy endeavor. Using one dimension out of 15, 41% of the variation in individual performance is accounted for. The corresponding simulated communities, in absence of any additional random variation, reached less than half the species richness of the communities simulated with the actual 15-dimensional individual performance (median of 4 *vs.* 18, Fig. S4.1) with relatively dissimilar community composition (median of similarity in abundance of 0.43 *vs.* 0.95, median of mean performance of 1.15 *vs.* 1.54, Fig. S4.2). Adding a second dimension allowed to increase the proportion of explained variance in individual performance to 46%, and simulated species richness to a median of 7, with more realistic communities (median of similarity in abundances of 0.59 and median of mean performance of 1.19). The identification of the most influential environmental variables or dimensions in species responses using ecological knowledge (Rüger et al. 2009; Bartlett et al. 2016; Soong et al. 2020) is of course valuable to optimize and prioritize these efforts in the field.

Another way to improve the characterization of the environment could be to better capture the spatio-temporal structure of the already monitored variables, *i.e.* to monitor them at finer scales in space and time. In our simulation, the scale of the environmental variation was the same as the

individual (prescribed by the grid mesh size) across all models of individual performance. Testing the effect of degrading the resolution of the observed environmental variation in the case of an imperfect characterization of the environment could be explored in the future. Finally, improving the characterization of species responses to a few major environmental variables can also enable to better reveal the realized niche partitioning operating within communities. While niche partitioning is more easily achieved with a high number of environmental dimensions, high level of coexistence can also be reached with only one axis if it is well partitioned among species (*e.g.* Hurtt and Pacala 1995; Detto et al. 2022), thus building a high-dimensional space where each species can perform better somewhere. This is in agreement with several studies that showed significant improvement in the realism of simulated communities by only adding a second dimension to species responses in community models (Falster et al. 2017; Rüger et al. 2020).

While efforts to improve our characterization of environmental variation and species responses are, and need to be, continuously pursued (Tymen et al. 2017; Estes et al. 2018; Zellweger et al. 2019), making a better use of the ecological information contained in existing datasets should also be attempted in parallel.

Structuring variation: a first step towards accurate representation of multidimensionality

Our virtual experiment corresponds to an extreme case in which conspecific individuals have exactly the same response to environmental variation, which is unlikely to be the case under the joint effect of environmental and genetic variation in the field. However, while the intraspecific variation that is added as a noise around species means is not structured in space and time, IV, whether it is environmentally- or genetically-driven or both, is actually highly likely to be structured in space and time (Girard-Tercieux et al. 2022). This structure could appear when IV results from spatially-structured environmental variables or from limited dispersion or local adaptation (Marrot et al. 2021; Schmitt et al. 2021; Westerband et al. 2021). As shown here, this has profound consequences on the properties of the simulated community. Importantly, the spatio-temporal structure of individual variation is an emergent property of conspecific individuals responding more similarly to the environment than heterospecifics (Clark 2010; Girard-Tercieux et al. 2022), an important condition for stable species coexistence (Chesson 2000).

Observed or inferred IV, whatever its source (genetic, environmental or an interaction of both, Westerband et al. 2021), can be structured at the individual scale ("individual variability") using individual effects when one individual is repeatedly observed at one site. While such individual effects are then typically randomly attributed to individuals in the landscape (*e.g.* Clark et al. 2003), which is almost equivalent to adding a random noise, the structure in these inferred individual effects can be conserved when injected in a community dynamics model. In doing so, a part of observed IV is spatially structured. Pioneer studies have started using this approach to structure IV (Purves and Vanderwel 2014; Uriarte and Menge 2018; Banitz 2019), and future work should further explore this direction to generalize its use in community dynamics models. Another source of environmental variation that was not tackled in this study is temporal variation. This variation is often structured, at different temporal scales (seasons, years, El Niño/La Niña events, *etc.*) and this structure should be accounted for in models by expliciting those temporal scales after detection in the data.

Finally, the fact that all species respond to the same environmental variation, and that conspecifics tend to respond more similarly to it, can influence the structure of the covariance matrix of species abundances (Clark 2010). Exploring the structure of this covariance matrix could therefore be a way to improve community dynamics models while waiting for new environmental data and species knowledge.

Overall, our results suggest that it is crucial to explore the structure of observed IV in real communities to better understand its impact on diversity and community dynamics.

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Supplementary information and code access

Appendix 1: Alternative implementations of mortality and fecundity
Appendix 2: Stability of the simulations
Appendix 3: Role of suboptimal species depending on the implementation of mortality and fecundity
Appendix 4: Comparisons between communities simulated with the *Imperfect knowledge models without uIV* and with the *Perfect knowledge model*

The code used for this study is available in a GitHub repository (https://github.com/camillegirardtercieux/coexist) and has been permanently archived on Zenodo (https://doi.org/10.5281/zenodo.6929042).

Statements of author roles

CGT, IM and GV conceived the initial ideas and coordinated the INTRACO working group. All authors contributed to the study design and ideas within the INTRACO working group. CGT led the analyses. CGT, IM and GV wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

Declaration of Interests

All authors declare that they have no conflict of interest.

References

C. H. Albert, F. Grassein, F. M. Schurr, G. Vieilledent, and C. Violle. When and how should intraspecific variability be considered in trait-based plant ecology? *Perspectives in Plant Ecology, Evolution and Systematics*, 13(3):217–225, Sept. 2011. ISSN 14338319. doi: 10.1016/j.ppees.2011.04.003. URL https://linkinghub.elsevier.com/retrieve/pii/S143383191100028X.

C. Averill, C. Fortunel, D. S. Maynard, J. van den Hoogen, M. C. Dietze, J. M. Bhatnagar, and T. W. Crowther. Alternative stable states of the forest mycobiome are maintained through positive feedbacks. *Nature Ecology & Evolution*, 6(4):375–382, Apr. 2022. ISSN 2397-334X. doi: 10.1038/s41559-022-01663-9. URL https://www.nature.com/articles/s41559-022-01663-9.

T. Banitz. Spatially structured intraspecific trait variation can foster biodiversity in disturbed, heterogeneous environments. *Oikos*, 128(10):1478–1491, 2019. doi: 10.1111/oik.05787. URL https://onlinelibrary.wiley.com/doi/10.1111/oik.05787.

M. K. Bartlett, Y. Zhang, J. Yang, N. Kreidler, S. Sun, L. Lin, Y. Hu, K. Cao, and L. Sack. Drought tolerance as a driver of tropical forest assembly: resolving spatial signatures for multiple processes. *Ecology*, 97(2):503–514, Feb. 2016. ISSN 0012-9658, 1939-9170. doi: 10.1890/15-0468.1. URL https://onlinelibrary.wiley.com/doi/10.1890/15-0468.1.

D. I. Bolnick, P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26(4):183–192, Apr. 2011. ISSN 01695347. doi: 10.1016/j.tree.2011.01.009. URL https://linkinghub.elsevier.com/retrieve/pii/S0169534711000243.

P. Chesson. Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics*, 31(1):343–366, Nov. 2000. ISSN 0066-4162. doi: 10.1146/annurev.ecolsys.31.1.343. URL http://www.annualreviews.org/doi/10.1146/annurev.ecolsys.31.1.343.

J. Clark. Individuals and the variation needed for high species diversity in forest trees. *Science*, 327 (5969):1129–1132, 2010. doi: 10.1126/science.1183506. URL https://www.science.org/doi/10.1126/science.1183506.

J. S. Clark, J. Mohan, M. Dietze, and I. Ibanez. Coexistence : How to indentify trophic trade-offs. *Ecology*, 84(1):17–31, Jan. 2003. ISSN 0012-9658. doi: 10.1890/0012-9658(2003)084[0017:CHTITT]2.0.CO;2. URL http://doi.wiley.com/10.1890/0012-9658(2003)084[0017:CHTITT]2.0.CO;2.

B. Courbaud, G. Vieilledent, and G. Kunstler. Intra-specific variability and the competition–colonisation trade-off: coexistence, abundance and stability patterns. *Theoretical Ecology*, 5(1):61–71, Feb. 2012. ISSN 1874-1738, 1874-1746. doi: 10.1007/s12080-010-0095-8. URL http://link.springer.com/10.1007/s12080-010-0095-8.

J. M. Craine. *Resource Strategies of Wild Plants:*. Princeton University Press, Princeton, Dec. 2009. ISBN 978-1-4008-3064-0. doi: 10.1515/9781400830640. URL https://www.degruyter.com/document/doi/10.1515/9781400830640/html.

M. Crawford, F. Jeltsch, F. May, V. Grimm, and U. E. Schlägel. Intraspecific trait variation increases species diversity in a trait-based grassland model. *Oikos*, 128(3):441–455, 2019. ISSN 1600-0706. doi: 10.1111/oik.05567. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/oik.05567.

M. Detto, J. M. Levine, and S. W. Pacala. Maintenance of high diversity in mechanistic forest dynamics models of competition for light. *Ecological Monographs*, 92(2), May 2022. ISSN 0012-9615, 1557-7015. doi: 10.1002/ecm.1500. URL https://onlinelibrary.wiley.com/doi/10.1002/ecm.1500.

L. Estes, P. R. Elsen, T. Treuer, L. Ahmed, K. Caylor, J. Chang, J. J. Choi, and E. C. Ellis. The spatial and temporal domains of modern ecology. *Nature Ecology & Evolution*, 2(5):819–826, May 2018. ISSN 2397-334X. doi: 10.1038/s41559-018-0524-4. URL http://www.nature.com/articles/s41559-018-0524-4.

D. S. Falster, A. Brännström, M. Westoby, and U. Dieckmann. Multitrait successional forest dynamics enable diverse competitive coexistence. *Proceedings of the National Academy of Sciences*, 114(13):E2719–E2728, Mar. 2017. ISSN 0027-8424, 1091-6490. doi: 10.1073/pnas.1610206114. URL http://www.pnas.org/lookup/doi/10.1073/pnas.1610206114.

C. Fortunel, J. R. Lasky, M. Uriarte, R. Valencia, S. J. Wright, N. C. Garwood, and N. J. B. Kraft. Topography and neighborhood crowding can interact to shape species growth and distribution in a diverse Amazonian forest. *Ecology*, 99(10):2272–2283, Oct. 2018. ISSN 0012-9658, 1939-9170. doi: 10.1002/ecy.2441. URL https://onlinelibrary.wiley.com/doi/10.1002/ecy.2441.

C. Girard-Tercieux, I. Marechaux, A. T. Clark, J. S. Clark, B. Courbaud, C. Fortunel, J. Guillemot, G. Kunstler, G. le Maire, R. Pelissier, N. Rueger, and G. Vieilledent. Rethinking the nature of intraspecific variability and its consequences on species coexistence, Mar. 2022. URL http://biorxiv.org/lookup/doi/10.1101/2022.03.16.484259.

S. Hart, S. Schreiber, and J. Levine. How variation between individuals affects species coexistence. *Ecology letters*, 19(8):825–838, 2016. doi: 10.1111/ele.12618. URL https://onlinelibrary.wiley.com/doi/10.1111/ele.12618.

G. C. Hurtt and S. W. Pacala. The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, 176(1):1–12, Sept. 1995. ISSN 00225193. doi: 10.1006/jtbi.1995.0170. URL https://linkinghub.elsevier.com/retrieve/pii/S0022519385701701.

J. Lichstein, J. Dushoff, S. Levin, and S. Pacala. Intraspecific variation and species coexistence. *American Naturalist*, 170(6):807–818, 2007. doi: 10.1086/522937. URL https://www.journals.uchicago.edu/doi/10.1086/522937.

P. Marrot, M. Latutrie, J. Piquet, and B. Pujol. Natural selection fluctuates at an extremely fine spatial scale inside a wild population of snapdragon plants. *Evolution*, page evo.14359, Oct. 2021. ISSN 0014-3820, 1558-5646. doi: 10.1111/evo.14359. URL https://onlinelibrary.wiley.com/doi/10.1111/evo.14359.

E. V. Moran, F. Hartig, and D. M. Bell. Intraspecific trait variation across scales: implications for understanding global change responses. *Global Change Biology*, 22(1):137–150, Jan. 2016. ISSN 13541013. doi: 10.1111/gcb.13000. URL https://onlinelibrary.wiley.com/doi/10.1111/gcb.13000.

A. B. Nicotra, O. K. Atkin, S. P. Bonser, A. M. Davidson, E. J. Finnegan, U. Mathesius, P. Poot, M. D. Purugganan, C. L. Richards, F. Valladares, and M. van Kleunen. Plant phenotypic plasticity in a changing climate. *Trends in Plant Science*, 15(12):684–692, Dec. 2010. ISSN 1360-1385. doi: 10.1016/j.tplants.2010.09.008. URL https://www.sciencedirect.com/science/article/pii/S1360138510001986.

L. Poorter, C. V. Castilho, J. Schietti, R. S. Oliveira, and F. R. C. Costa. Can traits predict individual growth performance? A test in a hyperdiverse tropical forest. *New Phytologist*, 219(1): 109–121, July 2018. ISSN 0028646X. doi: 10.1111/nph.15206. URL http://doi.wiley.com/10.1111/nph.15206.

D. W. Purves and M. C. Vanderwel. Traits States and Rates: Understanding Coexistence in Forests. In *Forests and Global Change*. Cambridge University Press, british ecological society edition, Feb. 2014. ISBN 978-1-107-04185-1. Google-Books-ID: FU9kAgAAQBAJ.

M. Roswell, J. Dushoff, and R. Winfree. A conceptual guide to measuring species diversity. *Oikos*, 130(3):321–338, Mar. 2021. ISSN 0030-1299, 1600-0706. doi: 10.1111/oik.07202. URL https://onlinelibrary.wiley.com/doi/10.1111/oik.07202.

N. Rüger, A. Huth, S. P. Hubbell, and R. Condit. Response of recruitment to light availability across a tropical lowland rain forest community. *Journal of Ecology*, 97(6):1360–1368, Nov. 2009. ISSN 00220477, 13652745. doi: 10.1111/j.1365-2745.2009.01552.x. URL http://doi.wiley.com/10.1111/j.1365-2745.2009.01552.x.

N. Rüger, R. Condit, D. H. Dent, S. J. DeWalt, S. P. Hubbell, J. W. Lichstein, O. R. Lopez, C. Wirth, and C. E. Farrior. Demographic trade-offs predict tropical forest dynamics. *Science*, 368(6487):165–168, Apr. 2020. ISSN 0036-8075, 1095-9203. doi: 10.1126/science.aaz4797. URL https://www.sciencemag.org/lookup/doi/10.1126/science.aaz4797.

S. Schmitt, N. Tysklind, B. Hérault, and M. Heuertz. Topography drives microgeographic adaptations of closely related species in two tropical tree species complexes. *Molecular Ecology*, 30(20):5080–5093, Oct. 2021. ISSN 0962-1083, 1365-294X. doi: 10.1111/mec.16116. URL https://onlinelibrary.wiley.com/doi/10.1111/mec.16116.

A. Siefert, C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, L. W. Aarssen, C. Baraloto, M. B. Carlucci, M. V. Cianciaruso, V. d. L. Dantas, F. d. Bello, L. D. S. Duarte, C. R. Fonseca, G. T. Freschet, S. Gaucherand, N. Gross, K. Hikosaka, B. Jackson, V. Jung, C. Kamiyama, M. Katabuchi, S. W. Kembel, E. Kichenin, N. J. B. Kraft, A. Lagerström, Y. L. Bagousse-Pinguet, Y. Li, N. Mason, J. Messier, T. Nakashizuka, J. M. Overton, D. A. Peltzer, I. M. Pérez-Ramos, V. D. Pillar, H. C. Prentice, S. Richardson, T. Sasaki, B. S. Schamp, C. Schöb, B. Shipley, M. Sundqvist, M. T. Sykes, M. Vandewalle, and D. A. Wardle. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecology Letters*, 18 (12):1406–1419, 2015. ISSN 1461-0248. doi: 10.1111/ele.12508. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ele.12508.

J. L. Soong, I. A. Janssens, O. Grau, O. Margalef, C. Stahl, L. Van Langenhove, I. Urbina, J. Chave, A. Dourdain, B. Ferry, V. Freycon, B. Herault, J. Sardans, J. Peñuelas, and E. Verbruggen. Soil properties explain tree growth and mortality, but not biomass, across phosphorus-depleted tropical forests. *Scientific Reports*, 10(1):2302, Dec. 2020. ISSN 2045-2322. doi: 10.1038/s41598-020-58913-8. URL http://www.nature.com/articles/s41598-020-58913-8.

S. M. Stump, C. Song, S. Saavedra, J. M. Levine, and D. A. Vasseur. Synthesizing the effects of individual-level variation on coexistence. *Ecological Monographs*, Dec. 2021. ISSN 0012-9615, 1557-7015. doi: 10.1002/ecm.1493. URL https://onlinelibrary.wiley.com/doi/10.1002/ecm.1493.

B. Tymen, G. Vincent, E. A. Courtois, J. Heurtebize, J. Dauzat, I. Marechaux, and J. Chave. Quantifying micro-environmental variation in tropical rainforest understory at landscape scale by combining airborne LiDAR scanning and a sensor network. *Annals of Forest Science*, 74 (2):32, June 2017. ISSN 1286-4560, 1297-966X. doi: 10.1007/s13595-017-0628-z. URL http://link.springer.com/10.1007/s13595-017-0628-z.

M. Uriarte and D. Menge. Variation between individuals fosters regional species coexistence. *Ecology Letters*, 21(10):1496–1504, 2018. doi: 10.1111/ele.13130. URL https://onlinelibrary.wiley.com/doi/10.1111/ele.13130.

G. Vieilledent, B. Courbaud, G. Kunstler, J.-F. Dhôte, and J. S. Clark. Individual variability in tree allometry determines light resource allocation in forest ecosystems: a hierarchical Bayesian approach. *Oecologia*, 163(3):759–773, July 2010. ISSN 0029-8549, 1432-1939. doi: 10.1007/s00442-010-1581-9. URL http://link.springer.com/10.1007/s00442-010-1581-9.

C. Violle, B. Enquist, B. McGill, L. Jiang, C. Albert, C. Hulshof, V. Jung, and J. Messier. The return of the variance: Intraspecific variability in community ecology. *Trends in Ecology and Evolution*, 27(4):244–252, 2012. doi: 10.1016/j.tree.2011.11.014. URL https://linkinghub.elsevier.com/retrieve/pii/S0169534711003375.

A. C. Westerband, J. L. Funk, and K. E. Barton. Intraspecific trait variation in plants: a renewed focus on its role in ecological processes. *Annals of Botany*, 127(4):397–410, Mar. 2021. ISSN 0305-7364, 1095-8290. doi: 10.1093/aob/mcab011. URL https://academic.oup.com/aob/article/127/4/397/6122550.

F. Zellweger, P. De Frenne, J. Lenoir, D. Rocchini, and D. Coomes. Advances in Microclimate Ecology Arising from Remote Sensing. *Trends in Ecology & Evolution*, 34(4):327–341, Apr. 2019. ISSN 01695347. doi: 10.1016/j.tree.2018.12.012. URL https://linkinghub.elsevier.com/retrieve/pii/S0169534718303045.