

LETTER

The effect of intraspecific variation and heritability on community pattern and robustness

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Abstract

Intraspecific trait variation is widespread in nature, yet its effects on community dynamics are not well understood. Here we explore the consequences of intraspecific trait variation for coexistence in two- and multispecies competitive communities. For two species, the likelihood of coexistence is in general reduced by intraspecific variation, except when the species have almost equal trait means but different trait variances, such that one is a generalist and the other a specialist consumer. In multispecies communities, the only strong effect of non-heritable intraspecific variation is to reduce expected species richness. However, when intraspecific variation is heritable, allowing for the possibility of trait evolution, communities are much more resilient against environmental disturbance and exhibit far more predictable trait patterns. Our results are robust to varying model parameters and relaxing model assumptions.

Keywords

Coevolution, coexistence, community structure, competition, eco-evolutionary dynamics, Lotka-Volterra dynamics, quantitative genetics.

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INTRODUCTION

Despite the persistent (and generally valid) complaint that not enough attention is given to within-species diversity, it is now in fact well established in mainstream ecology that intraspecific trait variation (ITV) can have important ecological consequences (Hughes *et al.* 2008; Clark 2010; Bolnick *et al.* 2011; Violle *et al.* 2012). What is not yet clear is how much ecological insight we actually gain (or lose) by ignoring this variation, looking only at trait means. Do we get the 'basic picture', which is then refined and made more precise by accounting for intraspecific trait variation (Siefert 2012)? Or do we miss certain aspects of the community entirely? In the literature, the importance of intraspecific variation is often equated with its prevalence. A recent study by Siefert *et al.* (2015) estimates that on average 25% of all trait variation in plant communities is intraspecific. The same study gives 'general guidelines for when intraspecific trait variation is likely to be substantial and therefore important to consider in plant community and ecosystem studies' (our emphasis). Similarly, Albert *et al.* (2011) provide a practical guide for when intraspecific trait variation should be included in trait-based studies; their criteria are also based on estimating intraspecific variation prevalence. Our goal here is to study the importance of intraspecific variation for community dynamics and in particular for coexistence, based not on prevalence but impact on species richness, community pattern, and robustness. Critically, once there is individual variation within a species, part of that variation may be heritable. We therefore also consider the possibility of non-zero heritability, leading to the evolution of species traits.

Consequences of intraspecific variation for the dynamics of single populations have been long studied (Metz & Diekmann 1986; Caswell 2001; de Roos & Persson 2013). At the

community level, arguments about the consequences of within-species trait diversity abound. The most common stance is that such variation blurs species boundaries, though authors disagree about whether this would promote coexistence by facilitating ecological equivalence (Hubbell 2005) or hinder it by erasing coexistence-enhancing species differences (Taper & Case 1985).

There are also some deeper theoretical explorations of the community consequences of intraspecific variation. Lichstein *et al.* (2007) looked at the consequences of individual variation in competitive ability, assuming that lower mean performance is accompanied by higher intraspecific variation (mean-variance tradeoff), and find that this enhances coexistence, albeit only slightly so. In addition, community models with explicit life histories have shown strong community consequences of intraspecific age, stage, or physiological structure (Moll & Brown 2008; van Leeuwen *et al.* 2014). Treating every species as a structured population and incorporating interactions between life stages is a very general and powerful way of modelling species with individual variation (see de Roos & Persson 2013; Vindenes & Langanen 2015 for general formalisms), but it can get arbitrarily complicated, depending on the idiosyncrasies of the individual life histories of each species modelled. As such, this approach may not be the most convenient to draw general conclusions from. Another, relatively simple but still explicitly trait-based approach is taken in classic and some more recent studies of character displacement (Roughgarden 1976; Slatkin 1979, 1980; Taper & Case 1985; Vasseur *et al.* 2011). Here trait variation is driven by quantitative genetics and simple interactions defined by those traits. While these studies draw important conclusions about how intraspecific variation shapes competitive communities, they have traditionally focused on the evolutionary and not the ecological aspect of the problem.

All the above approaches consider only two, or at most a handful of species. To our knowledge, only two previous studies have looked at the effects of intraspecific variation on coexistence in multispecies communities. Vellend (2006) simulated communities along a unidimensional trait axis, with clonal reproduction and Lotka–Volterra competitive interactions. He found that within-species trait diversity promotes community-wide coexistence. However, one problematic aspect of this study is that, since all individuals breed true, the distinction between intra- and interspecific variation is purely nominal. It therefore does not yield deep insights into the structure of communities where conspecific individuals can exchange genetic material. Yamauchi & Miki (2009) modified the model to address this problem, incorporating a finite-locus model of genetics following the Shpak–Kondrashov hypergeometric model of inheritance (Shpak & Kondrashov 1999), instead of simple clonal reproduction. They found, in contrast to Vellend (2006), that intraspecific variation only promotes species diversity under a very restricted set of circumstances.

In this work, we aim to give a comprehensive view of the consequences of intraspecific trait variation on coexistence in both two- and multispecies communities. We consider both heritable and non-heritable intraspecific variation in the framework of quantitative genetics (Lande 1976; Slatkin 1979; Bulmer 1980; Falconer 1981), coupled with Lotka–Volterra-style ecological interactions (Roughgarden 1976; Slatkin 1980; Taper & Case 1985; Schreiber *et al.* 2011; Vasseur *et al.* 2011). In contrast to Vellend (2006) and Yamauchi & Miki (2009), we do not focus exclusively on species richness as a measure of whether coexistence is promoted. Rather, we additionally consider community pattern and community robustness against environmental perturbations. We find that the only strong and general consequence of intraspecific variability *per se* is that it reduces species richness, while its effect on trait patterns and community robustness is very small. In contrast, effects are huge when part of the intraspecific variance is heritable. This allows species to evolve their trait values towards local optima, thus alleviating historical constraints and leading to communities that are far more robust and have far more regular trait patterns than corresponding communities with zero heritability. We check and confirm that our results are not sensitive to our particular choice of model parameters and simplifying assumptions such as the infinite-locus model of quantitative genetics.

THE MODEL

We assume individuals of a species vary along a unidimensional trait of interest. The phenotypic distribution of this trait is considered in the quantitative genetic limit (Lande 1976; Bulmer 1980; Falconer 1981; Schreiber *et al.* 2011; Vasseur *et al.* 2011). In this limit, each of infinitely many loci contributes an infinitesimal additive value to the trait, on top of normally distributed environmental noise. Under these assumptions, the distribution $p_i(z, t)$ of species i 's trait value z at any moment of time t is normal, with a total phenotypic variance σ_i^2 that does not change in response to selection (Supporting Information, Section 1.1):

$$p_i(z, t) = \sqrt{\frac{1}{2\pi\sigma_i^2}} \exp\left(-\frac{(z - \mu_i(t))^2}{2\sigma_i^2}\right) \quad (1)$$

where $\mu_i(t)$ is the mean trait value at time t . The total phenotypic variance is the sum of the additive genetic variance and an independent environmental variance, which we assume is species-specific but does not change in time. The heritability h_i^2 in species i is defined as the ratio of the additive and the total phenotypic variance (Falconer 1981). If species i has total population density $N_i(t)$ at time t , then $N_i(t)p_i(z, t)dz$ is the population density of individuals with phenotype values between z and $z + dz$.

Since the shape and variance of the trait distribution does not change in the quantitative genetic limit, the full distribution $N_i(t)p_i(z, t)$ can be recovered from just tracking the population density and mean trait value of each species in time. These equations read

$$\frac{dN_i(t)}{dt} = N_i(t) \int r_i(\vec{N}, \vec{p}, z, t) p_i(z, t) dz \quad (2)$$

$$\frac{d\mu_i(t)}{dt} = h_i^2 \int (z - \mu_i(t)) r_i(\vec{N}, \vec{p}, z, t) p_i(z, t) dz \quad (3)$$

(Supporting Information, Section 1.2), where $r_i(\vec{N}, \vec{p}, z, t)$ is the per capita growth rate of species i 's phenotype z , defined by the ecological interactions of the community (it is density- and frequency-dependent, therefore written as a function of the vector of abundances \vec{N} and trait distributions \vec{p}). The above equations therefore provide the general framework for the eco-evolutionary dynamics in the presence of intraspecific trait variation that will hold regardless of the ecological details.

Ecological interactions are assumed to depend only on phenotype, not on species identity. We use the Lotka–Volterra model in the quantitative genetic limit (Roughgarden 1976; Slatkin 1979, 1980; Taper & Case 1985; Vasseur *et al.* 2011), where the fitness of any individual with phenotype z depends both on its absolute position and its distance from any other individual along the trait axis, summed over all individuals:

$$r(\vec{N}, \vec{p}, z, t) = b(z) - \sum_{j=1}^S N_j(t) \int a(z, z') p_j(z', t) dz' \quad (4)$$

(Supporting Information, Section 2.1). Here $b(z)$ is the maximum population growth an individual with phenotype z would achieve were it to reproduce clonally, S is the number of species, and $a(z, z')$ is the interaction kernel – the effect of an individual with phenotype z' on the growth rate of another individual with phenotype z . Substituting eqn 4 into the general eqns 2 and 3, we get

$$\frac{dN_i(t)}{dt} = N_i(t) \left(b_i(t) - \sum_{j=1}^S \alpha_{ij}(t) N_j(t) \right) \quad (5)$$

$$\frac{d\mu_i(t)}{dt} = h_i^2 \left(\bar{b}_i(t) - \sum_{j=1}^S \beta_{ij}(t) N_j(t) \right) \quad (6)$$

Here $b_i(t)$ is a species-level intrinsic growth rate, $\alpha_{ij}(t)$ are species-level competition coefficients, $\bar{b}_i(t)$ quantifies the evolutionary pressure on species i caused by growth, and $\beta_{ij}(t)$ quantifies the evolutionary pressure on species i caused by

competition with species j . Given the functions $a(z, z')$ and $b(z)$, these four ingredient functions can be obtained analytically by evaluating appropriate integrals (Supporting Information, Section 2). In our study, the interaction kernel $a(z, z')$ is Gaussian with competition width ω :

$$a(z, z') = \exp\left(-\frac{(z - z')^2}{\omega^2}\right) \quad (7)$$

We assume $b(z)$ is positive on an interval $[-\theta, \theta]$ but zero outside; $\theta > 0$ is therefore the effective half-width of the trait axis. Biologically, this means that any trait value falling outside this region is too extreme to efficiently forage for any of the available resources and thus achieve positive growth. Within the range $[-\theta, \theta]$ however, we consider three alternative forms: $b(z) = 1$ (rectangular), $b(z) = 1 - z^2/\theta^2$ (quadratic), and $b(z) = (z + \theta)/(2\theta)$ (asymmetric triangular).

TWO-SPECIES CASE

A model predicts coexistence if it has an equilibrium where all species abundances are positive (feasibility; Barabás *et al.* 2012; Rohr *et al.* 2014), the equilibrium is dynamically stable (stability), and the equilibrium remains stable and feasible under a sufficiently wide range of environmental conditions (robustness; Barabás *et al.* 2014). The two-species case of the quantitative genetic Lotka–Volterra model is particularly interesting as it gives insight into the coexistence-affecting role played by intraspecific variation. In the two-species version of the model with zero heritability, any feasible equilibrium is always globally stable (Supporting Information, Section 3.1). Therefore, analyses of feasibility and robustness are sufficient to determine whether species coexist.

Feasibility in our model is characterised by pairs of intrinsic growth rates (b_1, b_2) that lead to positive equilibrium densities. Robustness may then be characterised by the fraction of growth rate combinations leading to feasibility, out of all possible combinations. This is the feasibility domain Ξ . We derive a formula for Ξ in the Supporting Information (eqn 3.10):

$$\Xi = \frac{2}{\pi} \left\{ \arctan \left[\exp \left(\frac{(\mu_1 - \mu_2)^2}{2\sigma_1^2 + 2\sigma_2^2 + \omega^2} \right) \sqrt{\frac{2\sigma_1^2 + 2\sigma_2^2 + \omega^2}{4\sigma_2^2 + \omega^2}} \right] - \arctan \left[\exp \left(-\frac{(\mu_1 - \mu_2)^2}{2\sigma_1^2 + 2\sigma_2^2 + \omega^2} \right) \sqrt{\frac{4\sigma_1^2 + \omega^2}{2\sigma_1^2 + 2\sigma_2^2 + \omega^2}} \right] \right\} \quad (8)$$

Note that there are alternative ways of characterising robustness (Supporting Information, Section 3.2); they yield qualitatively identical results.

The predictions of the formula are shown in Fig. 1 as a function of the distance between species' mean traits, for various values of the intraspecific variances (Supporting Information, Section 3.2). There are two main messages. First, unless species' trait means are very close, more intraspecific variation always leads to a smaller feasibility domain, diminishing the chances of coexistence. Second, for very similar mean traits, having sufficiently different trait variances promotes coexistence, and this effect is larger for more substantial differences

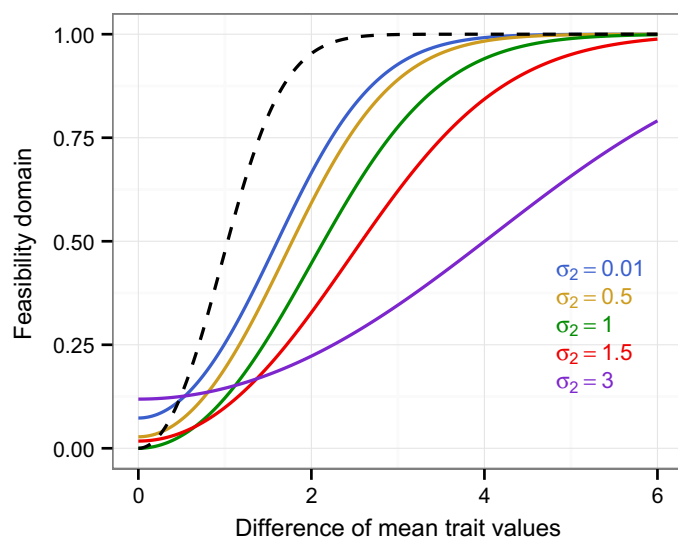


Figure 1 The fraction of intrinsic growth rate combinations out of all possible ones that lead to coexistence (the feasibility domain), as a function of mean trait distance and intraspecific variability. The competition width is $\omega = 1.1$ for all cases. The dashed black line is the reference case with no intraspecific variation: $\sigma_1 = \sigma_2 = 0$. For all solid curves, $\sigma_1 = 1$; colours denote different values of σ_2 (see legend). Except for very small differences in mean trait, the case with no intraspecific variation leads to the largest feasibility domains. For very small mean trait difference, the feasibility domain is larger for bigger differences in σ_1 and σ_2 . Intraspecific variation therefore promotes the coexistence of tightly packed species, but only if their σ s are sufficiently different.

between σ_1 and σ_2 . This can be understood in terms of Fig. 2: the overlap between two species having similar trait means is reduced by a difference in variances (phenotypic subsidy; Bolnick *et al.* 2011). Since eqn 8 is valid for all trait means and variances, it handles these two modes of coexistence in a unified way. Moreover, the formula allows for the direct comparison of coexistence with- and without intraspecific variability (Fig. 1, solid vs. dashed lines).

There is also an evolutionary aspect to this problem. So far we have treated the mean traits of the species as parameters. If heritabilities are non-zero however, these will be subject to change, governed by eqn 6. If the intraspecific variances are sufficiently different, the two species can converge and end up having equal mean trait values (Roughgarden 1976; Slatkin 1979, 1980; Taper & Case 1985; Supporting Information, Section 3.3). Although strictly speaking the evolution of equal trait means is only possible via symmetric intrinsic growth functions $b(z)$, this result is robust to introducing an asymmetry in $b(z)$ in the sense that the difference in mean trait values at the eco-evolutionary equilibrium will be much smaller than either of the intraspecific standard deviations (Supporting Information, Section 3.4). In the parlance of Taper & Case (1985), character displacement will not be substantial.

In summary, a rule of thumb for the effect of intraspecific variation on two-species coexistence is that it is *harmful*, considerably narrowing the range of parameter combinations allowing for coexistence compared with the no-variation scenario. The only exception is when the trait means are very

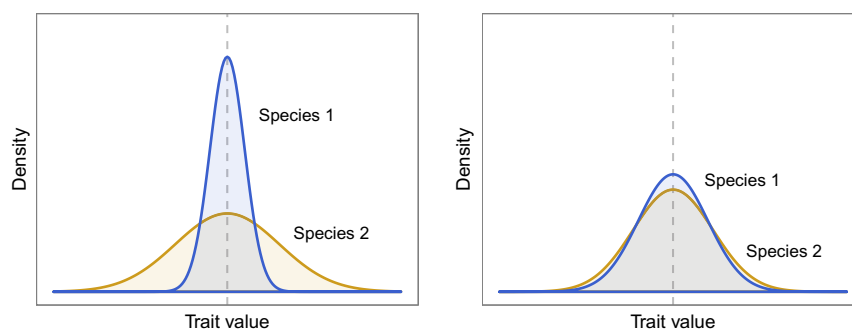


Figure 2 Left: The intensity of interspecific competition between two species with the same mean trait is lowered if their trait variances are different. The reason is that the species with the higher variance has individuals that do not overlap with individuals of the other species. This way those individuals avoid competition by accessing different resources. Right: when two species with the same mean trait have very similar intraspecific variances, the overlap in individuals is not reduced substantially, leading to non-robust coexistence. The dashed grey line indicates the species' mean trait position.

similar and the standard deviations are sufficiently different. Due to this possibility, much tighter species packing may in principle be achieved, provided that one species is a generalist and the other a specialist consumer. Species can either be segregated in their trait means or in their trait variances. Focusing exclusively on the mean trait may lead to the false conclusion that two species are coexisting without niche segregation.

MULTISPECIES CASE

Motivating examples

Figure 3 shows nine communities at equilibrium: without intraspecific variation (left column), with non-heritable variation (centre column), and heritable variation (right column; $h^2 = 0.1$ for all species). The σ_i in the centre and right columns are identical in each row and are uniformly drawn from [0.1, 0.3] (top row), [0.01, 0.05] (middle row), and [0.01, 0.3] (bottom row). Rows differ in the form of $b(z)$ (top: rectangular; middle: quadratic; bottom: triangular). Otherwise, all panels have the same parameters and initial conditions. In each row, the number of persisting species is highest in the absence and intermediate in the presence of non-heritable intraspecific variation, and lowest in the presence of heritable variation. In addition to reduced species richness, positive heritability leads to much more regular spacing between surviving species, with no two species very closely packed along the trait axis.

These observations outline the questions pertinent to the effects of intraspecific variation and heritability on multi-species coexistence. How does intraspecific variation affect species richness, and is the effect different for zero and non-zero heritability? Are species more evenly spaced in the case of non-zero heritability? Do we ever observe trait convergence in multispecies communities? How does intraspecific variation affect our ability to detect the signature of competition in field-collected trait data? And what is the effect of intraspecific variation and heritability on the community's ability to withstand environmental perturbations?

The simulation scheme

To address these questions, we use data generated by the quantitative genetic Lotka–Volterra model described in

Section 'The model'. Our simulations are organised into sets. Within each set there are 90 simulations, each with a different choice of parameters but the same initial conditions. All simulations start with $S = 51$ species, $\theta = 1/2$, and initial abundances equal to one. The initial trait means $\mu_i(0)$ are uniformly sampled from the interval $[-\theta, \theta]$. Then, the set is generated by varying the following parameters independently:

- Heritability: all species share the same $h_i^2 \equiv h^2$, equal to either 0, 0.1, or 0.5.
- Shape of $b(z)$: either rectangular, quadratic, or triangular (Section 'The model').
- Competition width ω : either 0.1, 0.15, or 0.2.
- Degree of intraspecific variability: species' intraspecific standard deviations σ_i are uniformly sampled from either [0, 0] (no variation), [0.01, 0.05] (low levels of variation), [0.01, 0.3] (mixed levels of variation), or [0.1, 0.3] (high levels of variation).

Combinations with zero intraspecific variability ($\sigma_i = 0$) but non-zero heritability are discarded, since species cannot evolve without intraspecific variation. This results in (three heritabilities) \times (three intrinsic growth functions) \times (three competition widths) \times (four intraspecific variability levels) = 108 different simulations within a set, minus the 18 cases with non-zero heritabilities but zero intraspecific variation, for a total of 90 different combinations. A total of 100 such sets are generated altogether, each determined by the set of initial trait means.

Note that both the initial trait positions $\mu_i(0)$ and the intraspecific standard deviations for each of the three non-zero cases (low, mixed, and high levels) are pre-generated for each set prior to simulations and so are kept the same within each set. This way we can disentangle the effects of initial conditions from those of the parameters. Each simulation ran for 10^{10} time units, more than enough in every case to reach eco-evolutionary equilibrium. Species with final density lower than an extinction threshold of $N_{\text{ext}} = 10^{-3}$ were removed from the community.

Species richness

Figure 4 shows species richness results across all our sets. Compared to the $\sigma_i = 0$ case (top left subplot), introducing intraspecific variation with zero heritability lowers the

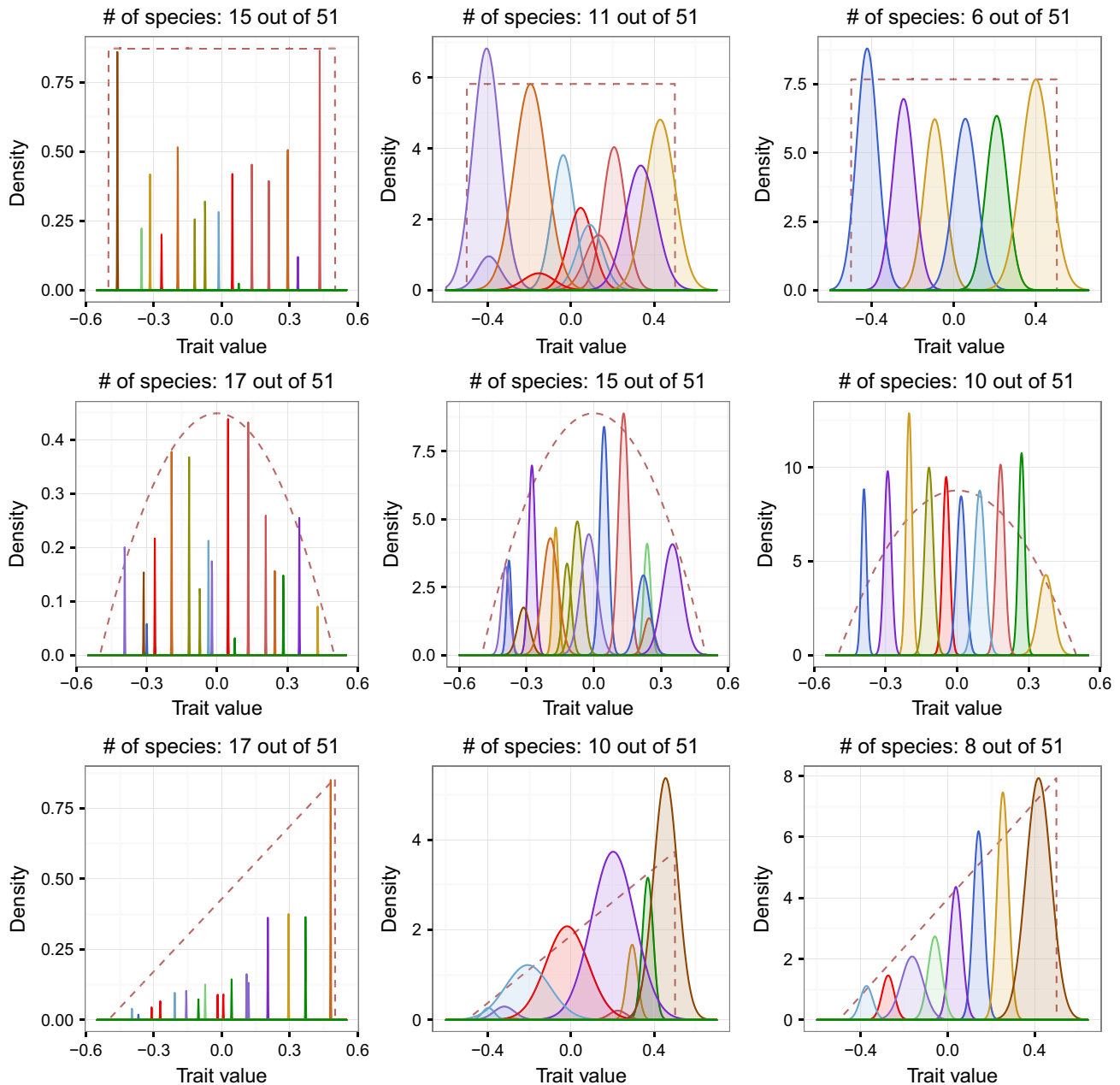


Figure 3 Equilibrium state of simulated communities. Columns correspond to no intraspecific variability (left), non-heritable variability (middle), and heritable variation (right). Rows correspond to different shapes of $b(z)$ (red dashed lines; not to scale): rectangular (top), quadratic (middle), and triangular (bottom). In all panels, $\theta = 0.5$, $\omega = 0.1$, initial mean trait positions are uniformly sampled from $[-\theta, \theta]$, and the initial species richness is $S = 51$. Parameters and initial conditions are identical between middle and right columns, except for heritability. The left column is exactly as the middle column except all σ s are zero. Plot headers show the number of surviving species. Ordinates show actual population density in left column; in the centre and right columns, the area under the species trait distributions yields the densities. When heritability is non-zero (right), species space themselves out more evenly than when they cannot change their initial mean trait positions.

expected diversity (top row). With positive heritability, the equilibrium number of species further decreases, and becomes more predictable. Comparing the panels of Fig. 3 reveals that species become more evenly spaced if they are allowed to evolve, which also results in more predictable species counts (see also Section ‘Trait patterns and detectability’).

Notice that, while there is an important distinction between zero and non-zero heritability, the precise value of h^2 does not

matter much. This can be understood from the general eqns 2 and 3: heritability multiplies the whole right hand side of eqn 3, therefore as long as $h_i^2 \equiv h^2$ for all species, its role is simply to change the timescale of evolution.

Our simulation results are supported by an analytical derivation in the special case of $h^2 = 0$ and $\sigma_i = \sigma$ for all species. In this case, the ratio of species richnesses with- and without intraspecific variation is shown to be

$$\frac{\text{species richness with } \sigma_i = \sigma}{\text{species richness with } \sigma_i = 0} = \frac{1}{\sqrt{4(\sigma/\omega)^2 + 1}} \quad (9)$$

(Supporting Information, Section 4.1), predicting a monotonic decline of diversity with increasing phenotypic

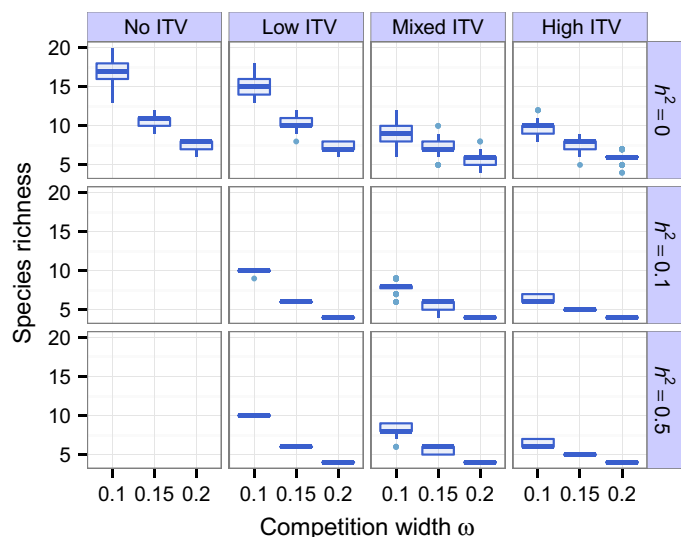


Figure 4 The effect of intraspecific variation and heritability on species richness. Rows of subplots show different heritability values; columns show different levels of intraspecific trait variability (ITV). The ordinate of each subplot is the number of extant species at equilibrium, out of the initial 51. Within each subplot, the three box plots correspond to different values of ω , as shown on the abscissa: they summarize the simulation results across all sets. Only results parameterised with a quadratic intrinsic growth function $b(z)$ are shown; see Supporting Information, Section 4.3 for results with a rectangular and triangular $b(z)$, yielding qualitatively the same results. Box plot guide: median (lines), 25% to 75% quartiles (boxes), ranges (whiskers), outliers (points; defined as falling outside 1.5 times the interquartile range of the box).

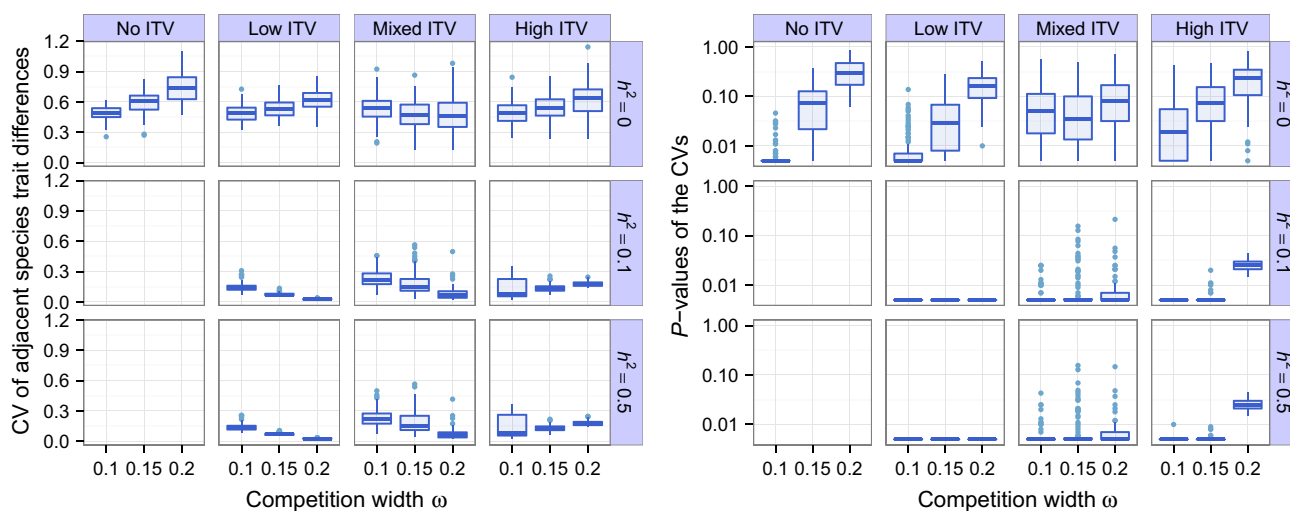


Figure 5 Left: as Fig. 4, except the ordinate shows the evenness of the distribution of mean trait values along the trait axis, as measured by the coefficient of variation of nearest neighbour distances. The CV is not changed much by non-heritable intraspecific variation, but drops significantly when heritability is non-zero. This means that the mean traits in communities where species can evolve are much more evenly spaced than in corresponding communities without the possibility of trait evolution. Right: As on the left, except the ordinate shows the probability that the degree of even spacing a given community ends up with is produced by chance (P -value). For lower values of intraspecific variability (second and third columns), heritable variation results in far lower P -values. For high levels of intraspecific variation and ω large, the effect of heritable variation on the P -values is smaller.

variance. This is consistent with the results in the first row of Fig. 4.

Trait patterns and detectability

Lotka–Volterra models supported the principle that coexisting species cannot be arbitrarily similar to one another (limiting similarity; MacArthur & Levins 1967). Subsequent investigations rigorously demonstrated that the likelihood of coexistence decreases with increasing species similarity (Gyllenberg & Meszéna 2005; Barabás *et al.* 2012), and simulation results generally support the idea that species are distributed more evenly along the trait axis than expected by chance, though this claim is not strictly proven. Here we ask how intraspecific variation affects this tendency towards even spacing.

To assess whether species' mean traits are more evenly distributed than expected by chance alone, we use the coefficient of variation (CV) of distances between the trait means of adjacent species on the trait axis; lower values indicate more even spacing. Figure 5 (left panel) shows the distribution of CVs in our simulations. Compared with the case without intraspecific variation, communities with variation tend to have lower CVs, suggesting that species are more evenly spaced when intraspecific variation occurs. However, the trend towards lower CVs with intraspecific variation is weak when heritability is zero, as can be seen by comparing the subplots of the top row. In contrast, the drop in CV is dramatic when heritability is non-zero. This suggests that when heritability is zero, even spacing is limited by the trait values available in the species pool, but this constraint is alleviated when species can evolve and thus change their initial – possibly unfavourable – trait positions.

One may wonder whether the possibility of trait convergence described in Section 'Two-species case' is realised in multispecies communities with $h^2 > 0$, and whether this would have an impact on community pattern. As it happens,

such convergence is indeed observed, but too sporadically to have an appreciable impact on community structure overall (Supporting Information, Section 4.4).

Statistically significant overdispersion is commonly taken as evidence of competition structuring the community (Kraft *et al.* 2008; Kraft & Ackerly 2010; Baraloto *et al.* 2012; Vergnon *et al.* 2013). While one must be careful with overly simplistic applications of this idea (see, e.g., Mayfield & Levine 2010; D'Andrea & Ostling in press), it is nevertheless meaningful to ask whether the CVs we obtained are indeed lower than expected by chance. To examine the statistical significance of the overdispersion shown in the left panel of Fig. 5, we used a null model consisting of communities whose species' trait values are randomly drawn from a uniform distribution. Our null CV is independent of trait range, but depends on the number of species, so each community in our data is compared to null communities of matching species richness. We compare each community in our data to a set of 1000 corresponding null communities, and obtain a P -value by tallying the proportion of null CVs that were lower than the CV in the data community. Low P -values mean the community is more evenly spaced than expected by chance. The distribution of P -values is shown in the right panel of Fig. 5.

We see that significance in the cases without intraspecific variation may be high or low depending on the competition width ω . Intraspecific variation without heritability either does not substantially alter P -values ($\omega = 0.15, 0.2$), or else increases them ($\omega = 0.1$). Again, positive heritability is the real game changer, substantially lowering P -values. Overall, spacing is more even than expected by chance when species are allowed to evolve, and intraspecific variability and ω are not too large. However, these higher P -values are actually related to the fact that higher levels of variation and larger values of ω result in lower species richness (compare Figs 4 and 5), reducing statistical power. Thus P -values are increased despite

the fact that spacing is more even than in corresponding cases without intraspecific variability.

We conclude that intraspecific variation by itself does not fundamentally change the original tendency for even spacing, but that this even spacing is greatly enhanced when intraspecific variation is heritable. This also greatly increases our ability to detect such spacing, except possibly when species richness is very low. This has implications for pattern detection in field studies: in communities with heritable intraspecific variation and enough species to justify pattern-based tests in the first place, species' mean traits should be significantly more evenly spaced than expected by chance.

Community robustness

Natural communities are subject to constant perturbations of abundances as well as of the environmental conditions influencing their dynamics. While reaching an eco-evolutionary equilibrium state implies its local stability, one may also ask whether it is robust – i.e., how much the community's ecological stability and feasibility are threatened by changes in the external environment (Section 'Two-species case'). For instance, changes in resource supply or ambient temperature may alter the shape of the growth function $b(z)$. Local stability of the community in the final state is guaranteed if the community matrix has all eigenvalues lying in the left half of the complex plane. In turn, the geometric mean of the magnitudes of the community matrix's eigenvalues is a measure of community robustness (Meszéna *et al.* 2006; Barabás *et al.* 2012; Aufderheide *et al.* 2013; Barabás *et al.* 2014) comparable across communities with different numbers of species (Supporting Information, Section 4.2). This quantity, the 'average community robustness', measures the expected response of a system to perturbing environmental conditions. The left panel of Fig. 6 compares this metric across our simulation

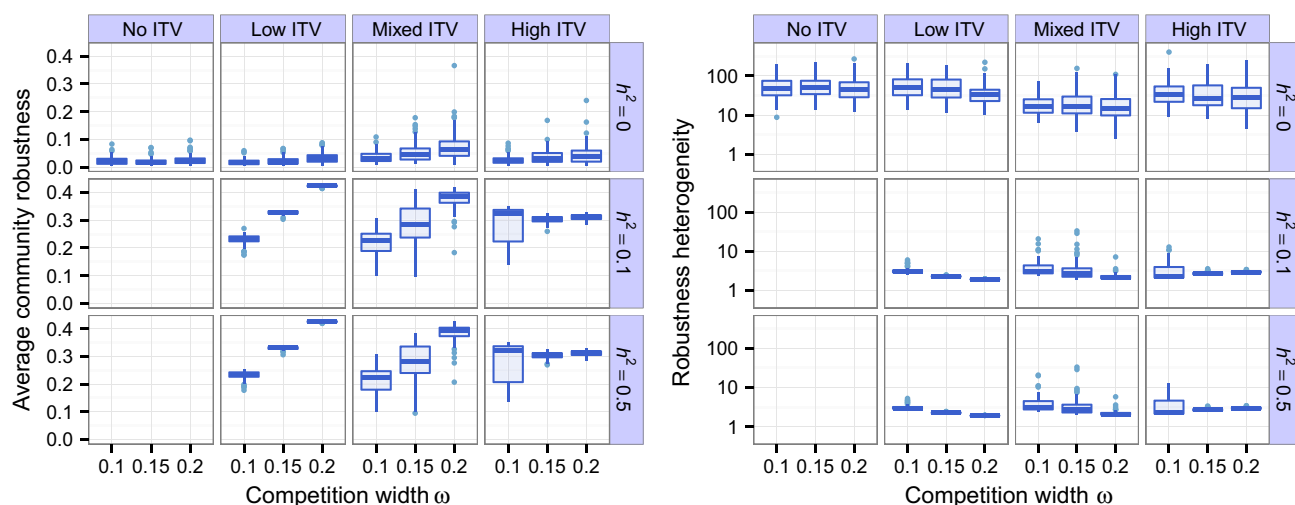


Figure 6 Left: average community robustness of our simulated communities, as measured by the geometric mean of the eigenvalues of the community matrix. Right: robustness heterogeneity of the communities, measured by the geometric standard deviation of the eigenvalues. Otherwise, the plots are organised as in Fig. 4. Intraspecific variation by itself has limited effect on robustness. However, when heritability is non-zero, communities end up with both a larger average community robustness and a reduced robustness heterogeneity. This makes them far more resistant against external perturbations as a whole.

sets. Intraspecific variation, in and of itself, does not influence average community robustness much. However, when heritability is non-zero, there is a strong immediate effect: communities become much more robust than they were in the absence of heritable variation. Note that this effect is not due to heritability *per se*, since two communities with the same trait distributions have equal robustness, regardless of h^2 . Rather, it is a consequence of species evolving their trait means to locations more conducive to robustness (Fig. 3, middle vs. right column).

There is another aspect to robustness. Imagine two systems having identical average community robustness, but suppose the first of these reacts to every environmental perturbation in the same way, while the second one is completely insensitive to perturbing some environmental conditions, but extremely sensitive to perturbing others. It is therefore also of interest to see not just how robust a system is to the average environmental perturbation, but whether it reacts strongly to specific perturbations. This can be measured by the geometric standard deviation of the eigenvalues' magnitudes ('robustness heterogeneity'; Supporting Information, Section 4.2).

As it turns out, not only do communities with heritable variation have a higher average community robustness: their robustness heterogeneity is also much lower (Fig. 6, right panel). As discussed in Section 'Trait patterns and detectability', when species can evolve, they space themselves out far more evenly along the trait axis than expected by chance. When heritability is zero however, communities sometimes end up with species very closely packed along the trait axis, with minimal niche differentiation between them and no ability to change the unfavourable trait positions, making it more likely that any particular change in environmental conditions giving an advantage to just one of those two species will result in the extinction of the other. This in turn leads to increased robustness heterogeneity.

Sensitivity of the results to the assumption of infinitely many loci

Since our model is based on quantitative genetic assumptions of an infinite number of loci contributing to the trait of interest, all trait distributions are normal, and their variances do not change in response to selection (Bulmer 1980). To check the sensitivity of our results to this assumption, we implemented finite-locus genetics using a hypergeometric model of inheritance (Shpak & Kondrashov 1999). In this case, heritabilities themselves evolve, and trait distributions are no longer normal or of constant shape. We found that even with a small number of loci, results from the finite-locus model are not qualitatively different (Supporting Information, Section 5). These assumptions are therefore not restrictive.

DISCUSSION

In this work, we explored the consequences of intraspecific trait variation for the stability, feasibility, and robustness of coexistence in two-species communities, and for species richness, community pattern, and robustness in multispecies communities, where individuals vary in a unidimensional trait of interest. We found that, although intraspecific variation in

principle allows for coexistence between two species with more similar trait means than would be possible in the absence of such variation, species richness decreases with increasing intraspecific variance in the multispecies case. Surprisingly, trait spacing and robustness were not much affected by intraspecific variation alone. Contrary to the idea that large levels of intraspecific variation signal its ecological importance (Albert *et al.* 2011; Siefert *et al.* 2015), this suggests that non-heritable variation within a species may be safely ignored even when it is substantial, at least for the purposes of these two community properties. However, the picture changes drastically when the variation is partially heritable: species in the community become more evenly spaced along the trait axis, and more resistant to environmental perturbations.

It is common to encounter claims in the literature that intraspecific variation promotes coexistence (Hubbell 2005; Vellend 2006; Messier *et al.* 2010; Bolnick *et al.* 2011; Violle *et al.* 2012). Our results make a point of the importance of defining precisely what is meant by 'promote'. Intraspecific variation does not, for example, lead to higher species richness; rather, it always and predictably reduces species richness. On the other hand, it may lead to coexistence that is more resilient to environmental perturbations. Whether it does so depends on whether it is heritable: communities with heritable intraspecific variation evolve to a much more robust state than those without, or with non-heritable variation.

Here we have worked with supersaturated communities where the initial number of species is always substantially greater than in the final state. This means that our methods can be used to study community assembly and response to selective pressure, but are ill-suited for approaching the problem from the other end: starting with low diversity and ending up with species-rich assemblages via adaptive diversification (Geritz *et al.* 1998). Our model does not allow for evolutionary branching because the shape of the trait distribution cannot change in response to selection. Speciation and its effects on community structure are therefore outside our scope.

Our work is relevant for empirical studies detecting the signature of species interactions in functional trait data (Kraft *et al.* 2008; Kraft & Ackerly 2010; Baraloto *et al.* 2012; Vergon *et al.* 2013). Pattern detection in these studies generally proceeds by rejecting appropriate null models assuming no interactions; significant overdispersion in the trait of interest is taken as evidence of competition structuring the community (Kraft & Ackerly 2010) – though, as mentioned before, such evidence must be interpreted with care (D'Andrea & Ostling *in press*; Mayfield & Levine 2010). These studies usually ignore individual variation (but see Siefert 2012). Here we took this variation into account, and also checked the sensitivity of our results to varying parameters and assumptions: different levels of intraspecific variation, shapes of the intrinsic growth function, competition widths, and heritability. The degree of intraspecific variation and the competition width have the strongest influence on species richness; positive heritability greatly enhances even spacing and robustness, and the degree of heritability affects the time scale over which these effects are observed. We also checked that our results are not sensitive to the infinite-locus assumption of quantitative

genetics. All in all, the predicted community pattern is robust and very characteristic (Fig. 3, right column).

Despite this strong prediction, trait data are idiosyncratic, sometimes conforming to these expectations (e.g. Grant *et al.* 1985), but often revealing considerable overlap between species (Clark 2010; Clark *et al.* 2011; Siefert 2012; Vergnon *et al.* 2013; Siefert *et al.* 2015), and no strikingly even spacing even in cases where overdispersion is detected (e.g. Kraft *et al.* 2008). Discrepancy with observations may be due to a number of reasons. First, zero heritability leads to more noisy patterns (Fig. 3, middle column). Second, the Lotka–Volterra model may not be adequate. Third, even if it is, competition between individuals may not be a function of their trait distance or depend on the trait at all. Fourth, immigration from outside sources may lead to persistence of species that would otherwise be extirpated. Fifth, the system could be far from equilibrium. Sixth, more than one trait could be driving community dynamics. Let us consider each of these possibilities in turn.

Studies show that almost all traits imaginable have heritabilities between 0.1 and 0.9 (Mousseau & Roff 1987), and so $h^2 = 0$ does not appear plausible – still, this must be determined empirically on a case-by-case basis. Non-Lotka–Volterra interactions (nonlinear relationships between densities and per capita growth rates) may cause the system to no longer settle on a point equilibrium: eco-evolutionary cycles (as in Vasseur *et al.* 2011; Patel & Schreiber 2016) become possible. When the dynamics do settle on a point equilibrium however, linearisation around the equilibrium will reduce the model to Lotka–Volterra form, and thus we do not expect fundamentally different results. Naturally, in many cases $a(z, z')$ will not be a simple function of distance, as e.g. in systems with competitive hierarchies (Tilman 1994; Muller-Landau 2010). These models may produce patterns in which spacing between species is not homogeneous along the trait axis.

For source-sink systems, sufficiently strong immigration may blur expected pattern. Immigration rates should therefore be estimated (Abadi *et al.* 2010), or the scale of the study extended to make the communities closed to migration. Furthermore, a system far from equilibrium may display transient patterns quite different from those expected at equilibrium (D'Andrea & Ostling in press). There are ways to infer whether transients are indeed dominating. For instance, independent evidence for fast and predictable recovery from disturbance (Clark 2010) would render transients implausible. Slow recovery times make transients more likely, and successional patterns not converging on predictable species compositions may signal ecological equivalence or alternative stable states.

Even in a system with positive heritability, fast and predictable disturbance recovery, and negligible immigration, any pattern may be obscured or even reversed (a phenomenon known as the ‘ecological fallacy’) if niche space is high-dimensional but the data are projected on a single trait axis (Clark 2010; Clark *et al.* 2010, 2011). We conducted a preliminary exploration and found that, although multidimensional interactions lead to the same regular spacing as in Fig. 3, this regularity is lost when the pattern is projected onto just one axis (Supporting Information, Section 6). Multidimensional niche differentiation may be evidenced by whether individual-level responses to environmental changes co-vary more within than

between species (Clark 2010). Studies aimed at detecting trait patterning along a single dimension implicitly assume that the trait in question is of overriding importance in the system at hand.

The utility of our results lie in that, when the model assumptions are met, they provide strong predictions for community structure, and when those assumptions are not met, they narrow down the potential reasons to a handful of testable hypotheses amenable to further empirical investigations. This way, they can facilitate a deeper understanding of the ecology of natural systems.

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AUTHORSHIP

GB and RD conceived of the study and developed the model framework; RD designed tests of trait patterns; GB designed tests of community robustness; GB and RD wrote the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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