

LETTER

Variation between individuals fosters regional species coexistence

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Abstract

Although individual-level variation (IV) is ubiquitous in nature, it is not clear how it influences species coexistence. Theory predicts that IV will hinder coexistence but empirical studies have shown that it can facilitate, inhibit, or have a neutral effect. We use a theoretical model to explore the consequences of IV on local and regional species coexistence in the context of spatial environmental structure. Our results show that individual variation can have a positive effect on species coexistence and that this effect will critically depend on the spatial structure of such variation. IV facilitates coexistence when a negative, concave-up relationship between individuals' competitive response and population growth rates propagates to a disproportionate advantage for the inferior competitor, provided that each species specialises in a habitat. While greater variation in the preferred habitat generally fosters coexistence, the opposite is true for non-preferred habitats. Our results reconcile theory with empirical findings.

Keywords

Beverton–Holt model, competition, habitat specialisation, interpatch dispersal, intraspecific variability, Jensen's inequality, plasticity, spatial coexistence, spatial structure.

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INTRODUCTION

Despite increasing evidence that intraspecific individual variation (IV) accounts for a substantial portion of total variation in natural communities (Messier *et al.* 2010; Violle *et al.* 2012; Siefert *et al.* 2015; Funk *et al.* 2017), most empirical studies of species coexistence have ignored the role of individual variation (but see Clark 2010; Siefert 2012; Bastias *et al.* 2017). Ignoring IV is justifiable if it has no influence on coexistence, but problematic if IV affects coexistence.

Recent theoretical developments suggest that individual, non-heritable variation in the traits that mediate the response to competition will generally hinder local species coexistence for a number of reasons (Barabas & D'Andrea 2016; Hart *et al.* 2016). First, when the relationships between competition and species performance exhibit nonlinear, negative, concave-up shapes (similar to a negative exponential), as is common (e.g. Pacala & Silander 1990), IV will generally increase the dominance of superior competitors. This is because dominant species derive a greater benefit from IV than inferior competitors (Hart *et al.* 2016). Second, IV tends to reduce the mean intraspecific interaction coefficient more than the mean interspecific interaction coefficient (Hart *et al.* 2016), unless the differences in trait means are small and those between trait variances are large (phenotypic subsidy) (Barabas & D'Andrea 2016). In other words, competition coefficients are strongest among conspecifics if we assume that all individuals have the same niche whereas IV in heterospecifics may increase or decrease the strength of interspecific interactions. Finally, IV exacerbates demographic stochasticity by favouring abundant species over other species recovering from small population sizes (Hart *et al.* 2016).

According to existing theory, IV will only stabilise local species coexistence when there are trade-offs between means and

variances of the response to competition (Lichstein *et al.* 2007; Bolnick *et al.* 2011; Hart *et al.* 2016). That is to say, IV can promote coexistence when species with poor average performance have greater IV than species with superior average performance. Nevertheless, such a tradeoff will only enhance coexistence over a limited range of conditions and as a result, it is unlikely to be important in nature (Lichstein *et al.* 2007; Hart *et al.* 2016).

In contrast to these theoretical predictions, a number of empirical studies have suggested that individual variation fosters coexistence (Fridley *et al.* 2007; Clark 2010; Ehlers *et al.* 2016) although other studies have shown opposite or neutral patterns (reviewed in Turcotte & Levine 2016). Disagreements between empirical and theoretical studies partially reflect the fact that both species and IV in nature are often spatially structured with respect to environmental conditions (Cornwell & Ackerly 2009; Messier *et al.* 2010; Laughlin *et al.* 2012; Siefert *et al.* 2015; Spasojevic *et al.* 2016; Clark *et al.* 2010), whereas theoretical studies of the role of IV on coexistence have generally assumed well-mixed populations.

A large body of theory has examined the role of spatial environmental heterogeneity on species coexistence (Tilman & Kareiva 1997; Amarasekare 2003; Bolker *et al.* 2003; Chesson 2008). The consensus is that coexistence in spatially structured environments emerges from the combined effects of endogenous (e.g. dispersal limitation) or exogenous (e.g. soil nutrients) spatial environmental heterogeneity and density-dependent processes (e.g. competitive interaction) (Chesson 2000; Bolker *et al.* 2003). How IV influences species coexistence in the context of spatial variation in environmental conditions has not been addressed from a theoretical perspective. As a result, we have a very limited understanding of the role IV plays in shaping species

distributions across broad spatial scales (Laughlin *et al.* 2012; Valladares *et al.* 2014).

The magnitude of IV likely varies across environmental gradients or species ranges. On one hand, we might expect IV for a species to be lower in sites that are less environmentally favourable (e.g. at range edges) due to lack of additive genetic variance, small population sizes, and genetic drift or founder effects (Mägi *et al.* 2011). On the other hand, IV may be higher at range edges if these sites experience greater environmental variability (e.g. climate) that confers an advantage to plastic genotypes (Volis *et al.* 1998; Sultan & Spencer 2002; Cavin & Jump 2017). Simulation studies suggest that the spatial structure of IV matters for population persistence (i.e. no competitive exclusion) across a species range (Valladares *et al.* 2014), but empirical evidence for or against these contrasting hypotheses is limited. In sum, we lack a comprehensive picture of how the spatial structure of IV may influence species coexistence and diversity.

Here, we use a theoretical model to explore the consequences of IV in the response to competition on local and regional species coexistence in the context of spatial environmental structure. We base our analysis on a non-spatial annual plant competition model for two species because it provides analytical solutions and has already been used to explore the role of IV on species coexistence in a spatially homogeneous context (Hart *et al.* 2016). We consider several scenarios for the spatial structure of species performances and their individual variation and address two distinct but related questions:

- (1) Under what condition does IV facilitate vs. inhibit coexistence in spatially structured environments? We examine coexistence across a range of IV, assuming that species specialize in a particular habitat. As population persistence may depend on dispersal among sites, we also evaluate the effect of dispersal on coexistence.
- (2) How does the spatial structure of IV influence species coexistence? We evaluate the cases where species-specific IV is greater in each species' preferred environment (because larger population sizes in these sites would result in greater additive genetic variation, for example) and conversely, when species-specific IV is lower in each species' non-preferred environment.

MODEL

We base our analyses on a Beverton–Holt model of annual plant competition (Beverton & Holt 1957) because it is well characterised analytically (Cushing *et al.* 2004), describes plant community dynamics in the field (Godoy & Levine 2014) and has been previously used to examine the effects of individual variation on local species coexistence (Hart *et al.* 2016). For a two species model of competition without IV or spatial structure, the dynamics of species 1 are expressed as:

$$n_{1,t+1} = n_{1,t} \frac{g_1 \lambda_1}{1 + \alpha_{11} g_1 n_{1,t} + \alpha_{12} g_2 n_{2,t}} \quad (1)$$

where $n_{1,t}$ is the density of seeds of species 1 at time t , g_1 is the proportion of the seeds that germinate, and λ_1 is the per

germinant fecundity per time step at low density. The coefficients α_{11} and α_{12} describe the per capita effects of conspecifics and heterospecifics on seed production of species 1. Subscripts in eqn 1 are reversed to express the dynamics of species 2.

We further partition the per capita competitive effect of species 2 on species 1 (α_{12}) into the effect of species 2 on all other species (e_2) and the response of species 1 to competition (r_1), such that $\alpha_{12} = r_1 e_2$. The parameter α has units of per seed; we let e have units of per seed and r be unitless. Godoy *et al.* (2014) demonstrated that the competitive ability of species 1 can be expressed as a function of its demographic potential ($g_1 \lambda_1$) and its response to competition (r_1):

$$(g_1 \lambda_1 - 1)/r_1 \quad (2)$$

Godoy *et al.* (2014) demonstrated that in the absence of niche differences or individual variation in any of the three parameters, the species with the largest value of eqn 2 excludes all other species.

In a previous analysis of the effects of individual variation on local coexistence, Hart *et al.* (2016) concluded that individual variation in λ cannot alter the outcome of competition because it relates linearly to per capita seed production, and that g is a population-level, not an individual-level parameter (Bjornstad & Hansen 1994). As a result, their model only considers variation (IV) in r such that the dynamics of species 1 with individual variation become:

$$n_{1,t+1} = n_{1,t} \int \frac{g_1 \lambda_1}{1 + r_1 (e_1 g_1 n_{1,t} + e_2 g_2 n_{2,t})} p_1(r_1) dr_1, \quad (3)$$

where $p_1(r_1)$ is the probability distribution of r_1 . This expression has been used in several previous studies of population dynamics (Bjornstad & Hansen 1994; Hart *et al.* 2016). Under this model, individual variation will favour the superior competitor (i.e. the species with the lower mean r) because the relationship between the variable response to competition (r) and species performance is concave up (Jensen's inequality). This implies that individual variation in r increases population-level seed production and consequently, individuals with lower r contribute more to seed production. Since the mean value of r is lower for the superior competitor, individual variation accelerates competitive exclusion (Hart *et al.* 2016). IV can only foster coexistence when there is greater individual variation in inferior competitors (a mean-variance trade-off in r) (Lichstein *et al.* 2007).

Here, we extend this work to address how individual variation in the response to competition influences coexistence in spatially structured environments. We assume that there are two potential sites or habitats A and B, in which each species has a home advantage (species 1 prefers habitat B, species 2 prefers habitat A). The sites are connected by dispersal (γ , the fraction of seeds that disperse to the other habitat). We assume that seeds that germinate in a given habitat compete in that habitat through adulthood, and then produce L seeds, which are dispersed prior to the next time step. For simplicity, we assume that dispersal is symmetric across species and habitats. The dynamics of species 1 at site A are characterised as follows:

$$n_{1,t+1,A} = (1 - \gamma_{1,A}) L_{1,A,t} + \gamma_{1,B} L_{1,B,t}$$

$$L_{1,A,t} = \int \frac{g_{1,A} \lambda_{1,A} n_{1,t,A}}{1 + r_{1,A} (e_{1,A} g_{1,A} n_{1,t,A} + e_{2,A} g_{2,A} n_{2,t,A})} p_{1,A}(r_{1,A}) dr_{1,A}$$

$$L_{1,B,t} = \int \frac{g_{1,B} \lambda_{1,B} n_{1,t,B}}{1 + r_{1,B} (e_{1,B} g_{1,B} n_{1,t,B} + e_{2,B} g_{2,B} n_{2,t,B})} p_{1,B}(r_{1,B}) dr_{1,B} \quad (4a - c)$$

The equations for other species and sites follow the same form with the appropriate subscripts. For comparison to Hart *et al.* (2016), we represent individual variation in r using a four-parameter beta distribution (characterised by the mean μ_r , the variance σ_r^2 , the maximum, and the minimum, Table S1), which also eases computation compared to gamma-distributed variation. Results derived from a gamma distribution are provided in Appendix S1.

Following Hart *et al.* (2016), we consider individual variation in the parameter r , the response to competition. In addition to assuming that species 1 specialises in habitat B and species 2 in habitat A, we also assume that competition is more severe in habitat A (the site has a lower carrying capacity, due to lower soil fertility or some other resource). These assumptions are formalised by the inequality:

$$\mu_{r_{1,A}} > \mu_{r_{2,A}} > \mu_{r_{2,B}} > \mu_{r_{1,B}} \quad (5)$$

To make our results comparable to Hart *et al.* (2016), we also assume that species 2 has a greater competitive ability when averaging across habitats, with the same values they used (i.e. $\mu_{r_1} = 0.012$, $\mu_{r_2} = 0.011$).

To explore the effects of IV, we focus on the variance of r , σ_r^2 (listed on figure axes as 'variance in r '). The case of no IV corresponds to $\sigma_r^2 = 0$, whereas cases of IV correspond to a range of values where $\sigma_r^2 > 0$. We consider a number of scenarios and examine the consequences of IV for local (within each habitat) and regional (across both habitats) coexistence.

Results are divided into two sections. First, we explore the effects of IV on coexistence when there is habitat specialisation. In this case, we assume that variation in r (σ_r^2) is the same for both species and habitats (which we relax in Case 2),

$$\sigma_{r_{1,A}}^2 = \sigma_{r_{1,B}}^2 = \sigma_{r_{2,A}}^2 = \sigma_{r_{2,B}}^2, \quad (6)$$

but that it ranges jointly across species and habitats (values ranging from 0 to 7×10^{-5}). In this first case, we also consider how dispersal influences competitive outcomes, by allowing γ to range from 0 (no dispersal) to 0.5 (equal dispersal to each patch).

Assuming the conditions specified in eqns 5–6, we evaluate the effect of IV in r , the parameter for the response to competition, on coexistence, following Hart *et al.* (2016). In our second case, we consider cases where IV varies across species and habitats. We examine scenarios where IV is greater in species' preferred habitats than in their non-preferred habitats ($\sigma_{r_{1,B}}^2 \geq \sigma_{r_{1,A}}^2 = \sigma_{r_{2,B}}^2$ and $\sigma_{r_{2,A}}^2 \geq \sigma_{r_{1,A}}^2 = \sigma_{r_{2,B}}^2$) and varies across species in their preferred habitats ($\sigma_{r_{1,B}}^2$ and $\sigma_{r_{2,A}}^2$ vary), where IV is greater in species' non-preferred habitats ($\sigma_{r_{1,A}}^2 \geq \sigma_{r_{1,B}}^2 = \sigma_{r_{2,A}}^2$ and $\sigma_{r_{2,B}}^2 \geq \sigma_{r_{1,B}}^2 = \sigma_{r_{2,A}}^2$) and varies across species in their non-preferred habitats ($\sigma_{r_{1,A}}^2$ and $\sigma_{r_{2,B}}^2$ vary), and where IV varies across preferred vs. non-preferred habitats but

not across species ($\sigma_{r_{1,B}}^2 = \sigma_{r_{2,A}}^2$ but both vary concurrently, and $\sigma_{r_{1,A}}^2 = \sigma_{r_{2,B}}^2$ but both vary concurrently).

We determined coexistence by simulating mutual invisibility (Chesson 1994): Each species increased its population size when starting at low population density while the competitor started at its numerical equilibrium. For display purposes, however, we show results of simulations where each species in each habitat starts at an intermediate density. Given that our model has spatial structure, coexistence could be local, where both species coexist in a given habitat, or regional, where both species coexist across habitats. We examine both local and regional coexistence, although there is a trivial case for regional coexistence when there is no dispersal. All analyses were conducted in R (R Core Development Team 2017).

RESULTS

Case 1: Habitat specialisation

Without intraspecific variation, species 2, the superior average competitor, excludes species 1 (Figs 1a and 2) in our base parameter set (Table S1). With intraspecific variation, however, the two species can coexist (Fig. 1b). Over a wide range of variation in r (σ_r^2), IV fosters coexistence. Below that range, the better average competitor-species 2-wins while above it, the worse average competitor (species 1) wins (Figs 1c and 2).

Here, IV facilitates coexistence in a spatially structured environment for the same reason it inhibits coexistence in a spatially homogeneous environment: The nonlinear, concave up relationship between the response to competition (r) and per capita seed production (eqn 4b–c, Fig. 2). In a spatially homogeneous environment (as in Hart *et al.* 2016), the concave-up relationship favours the superior competitor (species 2), accelerating exclusion (Fig. 2b vs. Fig. 2a). In a spatially structured environment, however, the effect can be reversed. When there is little or no IV, habitat specialisation favours species 2, the superior competitor, because the mapping of r to *per capita* seed production is fairly close to an arithmetic mean for the mean r values themselves ($\mu_{r_1} = 0.012$, $\mu_{r_2} = 0.011$; Fig. 2c). However, as variation in r goes up, individuals on the lower edges of the r distribution (i.e. individuals of species 1 in site B) contribute disproportionately to overall seed production. As long as species 1 disperses from habitat B to A, species 1's advantage in habitat B compensates for and ultimately overwhelms species 2's advantage in habitat A (Fig. 2d). Therefore, at a fixed density of competitors, *per capita* seed production is greater with individual variation, and the effect is stronger for species with lower mean r at any one site.

This result also implies a mean-variance tradeoff at the regional level, though not at the local level. If the local variance in response to competition is the same across habitats and species as in eqn 6 ($\sigma_{r_{1,A}}^2 = \sigma_{r_{1,B}}^2 = \sigma_{r_{2,A}}^2 = \sigma_{r_{2,B}}^2$) but the means are arranged as they are in eqn 5 ($\mu_{r_{1,A}} > \mu_{r_{2,A}} > \mu_{r_{2,B}} > \mu_{r_{1,B}}$), the regional (cross-habitat) individual variation for each species is necessarily higher for species 1 than for species 2, which translates to higher seed production at low r because of the nonlinear averaging effect. In

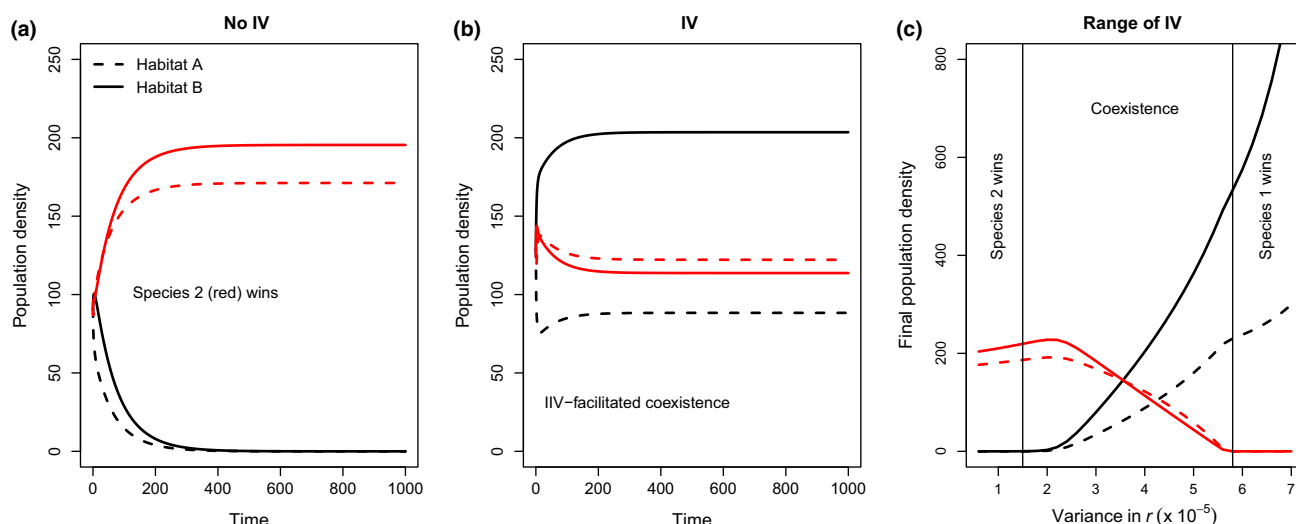


Figure 1 Individual variation (IV) can facilitate coexistence in a spatially structured community. Temporal population dynamics are shown for (a) no IV and (b) IV (variance in $r = 4 \times 10^{-5}$), for two species in two habitats. The final outcome of competition (population density at 1000 time steps) is also shown across a range of IV (c). Black and red show species 1 and 2, and dashed and solid lines show habitats A and B. In all figures, we assume that the mean trait values in each habitat are $\mu_{r1,A} = 0.0145 > \mu_{r2,A} = 0.012 > \mu_{r2,B} = 0.010 > \mu_{r1,B} = 0.0095$. These values satisfy the inequalities in eqn 5, and also retain the feature that each species' mean r across habitats is the same as it was in Hart *et al.* 2016 ($\mu_{r1} = 0.012$, $\mu_{r2} = 0.011$). The variance in r is the same across species and habitats. Dispersal is 0.1 for all species and habitats (see Fig. 3).

sum, when species specialize in different habitats, IV can facilitate coexistence and, if variance is high enough, shift competitive hierarchies. The positive effects of IV on coexistence, however, only occur when the inferior average competitor specialises on the more fertile habitat (Fig. S1c). The underlying mechanism can be thought of either as nonlinear averaging or as a mean-variance tradeoff at the regional level.

Given the fact that regional coexistence under a habitat specialisation scenario requires interpatch connectivity (i.e. dispersal), we also evaluated the joint effects of γ , the dispersal parameter (eqn 4), and σ_r^2 , the IV parameter, on the outcome of competition. At zero dispersal, each species wins in its preferred habitat (1 in B, 2 in A), so there is regional but not local coexistence, the trivial case (Fig. 3). At low but non-zero dispersal the advantages in each habitat spill over into the other habitats and they coexist locally and regionally via a rescue effect, regardless of IV. Eventually there is so much dispersal that the best average competitor (species 2) wins. This progression of dynamics happens both without (Fig. 3a) and with (Fig. 3b) IV, but the range of coexistence is much wider with IV (up to $\gamma = 0.2$ for our base parameter set) than without (up to $\gamma = 0.06$).

We also explored how dispersal and variation in r influence the outcome of competition in conjunction. When dispersal is low (less than about 0.07), each species' advantage in its preferred habitat is sufficient to guarantee coexistence, regardless of IV (lower grey region in Fig. 3c). The effects of IV are strongest right at the dispersal threshold around 0.07, where small to moderate amounts of IV facilitate coexistence (green region in Fig. 3c) and large amounts of IV lead to species 1 excluding species 2 (yellow region in Fig. 3c). As dispersal increases (moving upward on Fig. 3c), only higher levels of IV facilitative coexistence (encroachment of upper left grey

region on the green region), and when dispersal = 0.5, even the highest levels of IV have no effect. In other words, some dispersal between habitats is required for IV to facilitate coexistence when species are specialised in different habitats, but too much dispersal negates this effect.

Case 2: Spatially structured IV

Next, we evaluated the cases where species-specific IV is greater vs. lower in a more favourable environment. Greater IV in preferred habitats than in non-preferred habitats tends to facilitate coexistence or, if it is extreme, switch which species is dominant (Fig. 4a,c). The exact effect, however, depends on the relative magnitudes of IV in each species' preferred habitat (Fig. 4a) and the relative magnitude of IV in the non-preferred habitat (Fig. 4c). As before, the mechanisms behind these results stem from the nonlinear, concave up relationship between the response to competition (r) and per capita seed production, which is now modulated by differences in IV among species and habitats. If both species have the same variance in their preferred habitats and lower variance in their non-preferred habitats ($\sigma_{r1,B}^2 = \sigma_{r2,A}^2 > \sigma_{r1,A}^2 = \sigma_{r2,B}^2$, along the 1 : 1 line in Fig. 4a), the situation is analogous to Fig. 2d but with wider solid grey (species 1 in habitat B) and dashed red (species 2 in habitat A) IV distributions and narrower solid red and dashed grey IV distributions. Because of the concave-up relationship, the width of the solid grey distribution has the greatest effect on seed production. As variation in r goes up for species 1 more than for species 2 (below the 1 : 1 line in Fig. 4a), individuals in the lower edges of the r distribution (i.e. individuals of species 1 in site B) contribute disproportionately to overall seed production and species 1

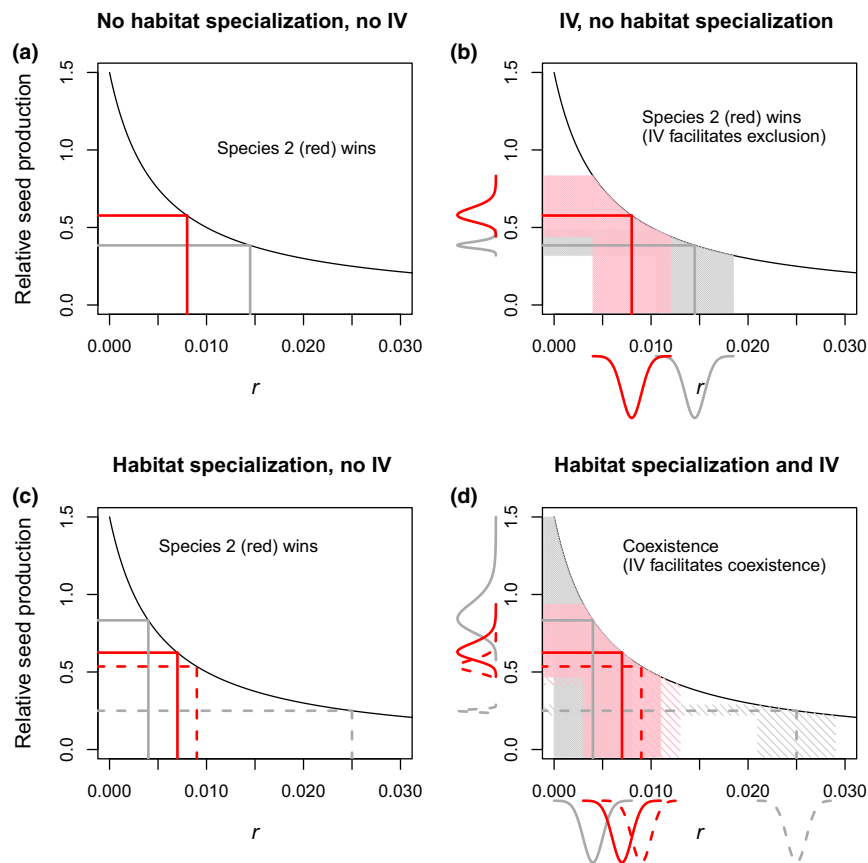


Figure 2 Effects of habitat specialisation and individual variation in r on species coexistence. We assume that variance in r is the same across species and habitats. With no habitat specialisation (a, b), IV accelerates competitive exclusion because the nonlinear translation of r to seed production benefits the superior competitor (species 2) more than the inferior competitor (species 1). With habitat specialisation (c, d), IV can facilitate coexistence or switch dominance (species 1 wins) because the gain in seed production from low-sensitivity individuals is more than enough to outweigh the losses in seed production from high-sensitivity individuals (Notice positive skew of both distributions left of the y -axis). For ease of visualisation, results are illustrated using truncated normal distributions for r and with means of r further spread out than in our simulations, as in Hart *et al.* (2016). Habitat A (dashed line), habitat B (solid line).

excludes species 2. Conversely, at low values of IV for species 1 relative to species 2, species 2 dominates (Fig. 4a,c).

By contrast, greater IV in non-preferred habitats does not facilitate coexistence in most of the parameter space (Fig. 4b, c). This is because greater IV of species 2 in their non-preferred habitat negates the regional mean-variance tradeoff in IV that allowed regional persistence of species 1, the inferior competitor. In other words, as variation in r in non-preferred habitats goes up, individuals of species 2 in the lower edges of the r distribution also contribute to overall seed production. Only when IV of species 2 in non-preferred habitats is relatively low can species 2 persist.

In sum, when species' variances differ across habitats, IV can facilitate coexistence and if variance is high enough, shift competitive hierarchies, particularly when IV is higher in the preferred habitat or for the inferior competitor. Greater variance in non-preferred habitats can only foster coexistence if the variances are high, particularly for the inferior competitor.

DISCUSSION

Our work demonstrates that spatial structure in the environment fundamentally alters how individual-level variation

affects competitive interactions. Although, a spatially homogeneous model suggests that IV inhibits coexistence (Hart *et al.* 2016), our two-patch version of the same underlying model suggests that IV can facilitate both local and regional coexistence. The underlying mechanism is the same in both cases: A negative, concave-up relationship between individuals' response to competition and population growth rates propagates to a disproportionate advantage for certain individuals and populations. Without spatial heterogeneity, the species that is on average a superior competitor benefits more. With spatial heterogeneity, however, the species that is on average the inferior competitor benefits more, as long as the inferior competitor specialises in the more fertile habitat. Thus, the incorporation of spatial heterogeneity reconciles theoretical predictions with empirical situations where IV facilitates coexistence, inhibits it, or has a neutral effect (reviewed in Turcotte & Levine 2016).

According to our model, the three key requirements for IV to facilitate coexistence are (1) differences across habitats in resource availability, (2) the inferior average competitor specialises on the more fertile habitat and vice versa, (3) a nonlinear, concave up relationship between individual competitive response and per-capita growth rates. Additionally,

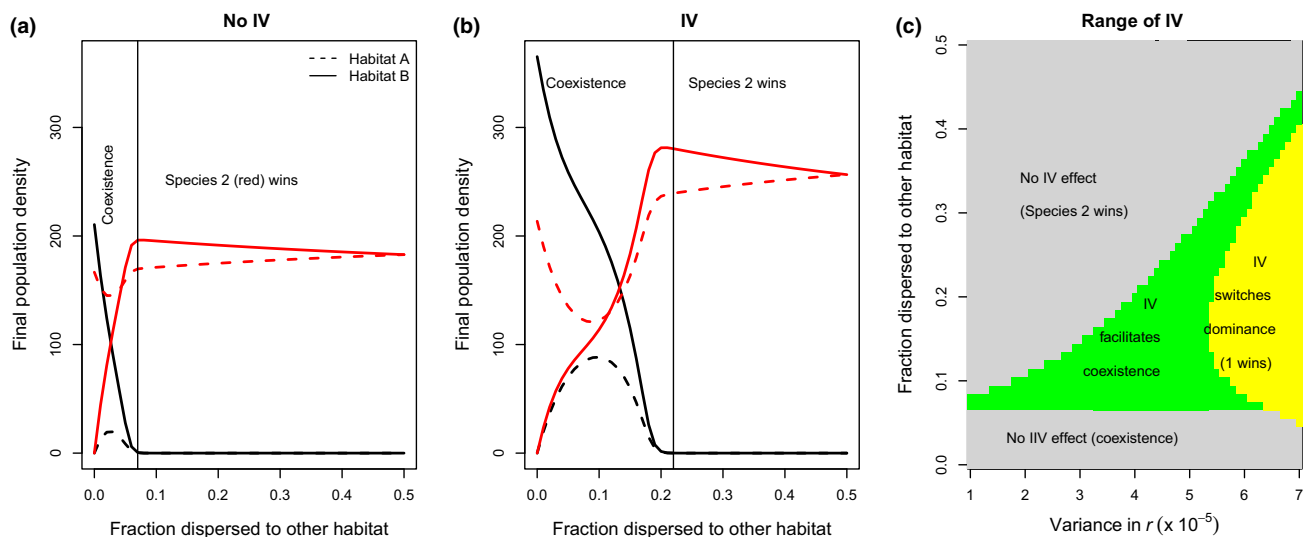


Figure 3 Joint effects of IV and dispersal on the outcome of competition. The effect of dispersal is shown (a) without IV, (b) with IV and (c) across a range of IV. When dispersal is 0, each species wins in its preferred habitat. When dispersal is 0.5, the results are the same as in Hart *et al.* (2016): Species 2 wins. When dispersal is low but not zero, each species is sufficiently productive in its preferred habitat that dispersal maintains regional coexistence. Intermediate levels of IV extend the range of dispersal that facilitates coexistence and high levels of IV can switch which competitor dominates, both because of the mechanism shown in Fig. 2. Variance in r in (b) is 4×10^{-5} . Note that when dispersal is 0.1, these panels correspond to the analogous panels in Fig. 1.

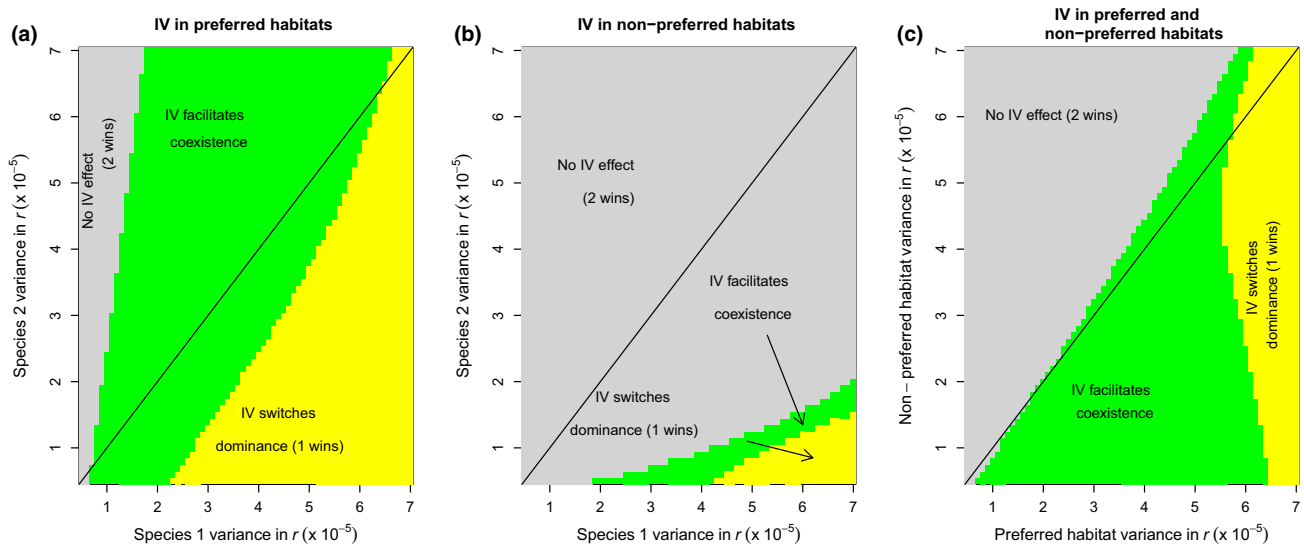


Figure 4 Effects of spatially structured IV on coexistence. (a) IV varies in each species' preferred habitat (each axis) is greater than IV in each species' non-preferred habitat (kept at 0.5×10^{-5}). Above the black 1 : 1 line species 2's IV in its preferred habitat exceeds species 1's IV in its preferred habitat, whereas below the 1 : 1 line, the converse is true. (b) IV varies in each species' non-preferred habitat is greater than IV in each species' preferred habitat (kept at 0.5×10^{-5}). Above the 1 : 1 line, species 2's IV in its non-preferred habitat exceeds species 1's IV in its non-preferred habitat, whereas below the 1 : 1 line, the converse is true. (c) IV varies between preferred and non-preferred habitats, and is the same for each species. On the 1 : 1 line IV is the same in preferred and non-preferred habitats, corresponding to Fig. 1c and to where dispersal = 0.1 in Fig. 3c. Below the 1 : 1 line IV is greater in each species' preferred habitat, whereas above the 1 : 1 line IV is greater in species' non-preferred habitats.

we find that two other conditions modify the degree to which IV facilitates coexistence: (4) The connectivity between patches (dispersal) must not be too large. In the limit, equal dispersal to both (or more generally, all) patches prohibits coexistence. Finally, (5) the spatial structure of individual variation matters for coexistence. While greater variation in preferred habitats generally fosters

coexistence, the opposite is true for non-preferred habitats. In sum, our results suggest that individual variation will generally have a positive effect on regional species coexistence and that this effect will critically depend on the spatial structure of such variation. In the following sections, we examine each of these five conditions and then note some potential future directions.

Habitat specialisation and nonlinear response to competition

A large body of theoretical and empirical work has shown that spatial heterogeneity in resources (e.g. soil moisture, fertility) fosters local and regional species coexistence in plant communities (Tilman & Kareiva 1997; Amarasekare 2003; Bolker *et al.* 2003). Heterogeneity can act by influencing species average performance (equalizing effects) and responses to intra- and interspecific competition (stabilizing effects) (Goldberg *et al.* 1999; Chesson 2008). Although the number of studies testing the effects of individual variation on plant species coexistence is growing rapidly (reviewed in Turcotte & Levine 2016), most of these have focused at local (e.g. neighbourhood) scales (e.g. Kraft *et al.* 2014). Our model demonstrates that individual variation in competitive response can facilitate both local and regional coexistence in a spatially heterogeneous environment.

Positive effects of habitat specialisation on local and regional coexistence in our model, however, are contingent on nonlinear mapping of competitive response to population growth via Jensen's inequality. This contrasts with the findings of Hart *et al.* (2016) that nonlinear mapping of individual-level competitive ability to population growth decreased the potential for local coexistence by exacerbating dominance of superior competitors. In the terminology of Chesson (2000, 2008), our mechanism appears to operate as fitness-density covariance (each species is relatively more abundant in its preferred habitat), which has both stabilizing (IV increases the invader growth rate of both species increases) and equalizing (IV makes the fitnesses of species 1 and species 2 closer to each other) effects (Appendix S2).

Limited dispersal

Dispersal is another critical component for understanding the effects of individual variation on local and regional coexistence. Limited dispersal can handicap a superior competitor or benefit an inferior competitor (Bolker *et al.* 2003). This is a classic form of the competition-colonisation tradeoff (Tilman & Kareiva 1997). However, in our model, coexistence does not result from a competition-colonisation tradeoff although of course, rates of dispersal influence the outcome of competition. At low but non-zero dispersal, the advantages in each habitat spill over into the other habitats and species coexist locally via a rescue effect, regardless of individual variation. At the other extreme, high dispersal benefits the superior competitor. At intermediate levels of dispersal species can coexist but the range of coexistence is much broader when there is individual variation in the competitive responses.

The spatial structure of individual variation

Much of individual variation in nature is spatially structured, often as a result of phenotypic plasticity in response to heterogeneity in environmental conditions or genetically-based local adaptation (Sultan 1987; Cornwell & Ackerly 2009; Albert *et al.* 2010). Whether genetically-based or not, individual variation may occur among individuals from populations distributed across some environmental gradient or within

populations. From a functional trait perspective, patterns of individual variation have been largely investigated in terms of response to environmental gradients (e.g. Reich *et al.* 2003). Much less is known about variation in functional traits within populations and about differences in this variation over larger spatial scales (Albert *et al.* 2010). Plants may show higher individual variation under harsher, unfavourable condition if resources at these sites are more spatially or temporally heterogeneous (e.g. moist soil microsites) conferring an advantage to plastic genotypes (Volis *et al.* 1998; Alpert & Simms 2002; Sultan & Spencer 2002). On the other hand, we may expect greater phenotypic plasticity under more favourable conditions because of higher additive genetic variation or larger population sizes (Lemke *et al.* 2015).

Our results offer several insights into the effects of the spatial structure of individual variation on species coexistence. First, greater phenotypic variability in preferred than non-preferred habitats facilitates species coexistence. Recent empirical studies of plant species across marked climate gradients found greater plasticity in favourable sites (Lemke *et al.* 2015). The authors propose that plants benefit from higher morphological variation in favourable environments because resource competition is stronger under these conditions (e.g. Alpert & Simms 2002). However, a recent study across a large latitudinal gradient did not find greater individual variation with higher species diversity (Bastias *et al.* 2017). Second, we found that higher phenotypic variability in non-preferred habitats can only foster coexistence if the variance of the inferior competitor is high relative to that of the superior competitor, enabling the inferior competitor to persist. This may be the case if inferior competitors that fare poorly under harsh conditions (e.g. dry or low fertility sites) persist in buffered microsites (e.g. moist microsites) (Daws *et al.* 2002).

Implication for empirical studies of coexistence

Our results have clear implications for guiding future empirical work. First, individual variation can foster species coexistence at local and regional scales primarily through nonlinear mapping of competition to population growth rates. Yet this mechanism has received very limited empirical attention. Second, the spatial structure of individual variation matters for coexistence. Although this question has received a considerable amount of consideration in evolutionary research (e.g. Sultan 1987), ecological studies have focused on measuring how the relative magnitude of intraspecific vs. interspecific variability, often with a focus on functional traits, differs across space (e.g. Siefert *et al.* 2015). None of these studies have described the relationship between habitat favourability and individual variation within and across species or considered its implications for coexistence.

Our study provides clear testable hypotheses for when IV is likely to foster, inhibit, or have no effect on co-existence based on the shape of the relationship between competition and population growth, the spatial structure of genetic variation, and interpatch dispersal rates. The challenge of testing our theoretical predictions with long-lived organisms that are not amenable to experimental manipulation (e.g. trees) resides in separating the effects of environment and

competition on fitness or its proxies (e.g. growth, survival). Novel neighbourhood analysis methods (e.g. Clark *et al.* 2017; Lasky *et al.* 2014) and generalised joint attribute models allow us to separate some of these effects at least for tree communities. Coupled with information on dispersal or on the spatial structure of individual variation, these methods can truly advance understanding of community assembly in natural communities.

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AUTHORSHIP

MU conceived the project, MU and DM developed the modelling approach, DM implemented the models, and both authors wrote the manuscript.

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Additional supporting information may be found online in the Supporting Information section at the end of the article.

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