# How variation between individuals affects species coexistence

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**Abstract**
Although the effects of variation between individuals within species are traditionally ignored in studies of species coexistence, the magnitude of intraspecific variation in nature is forcing ecologists to reconsider. Compelling intuitive arguments suggest that individual variation may provide a previously unrecognised route to diversity maintenance by blurring species-level competitive differences or substituting for species-level niche differences. These arguments, which are motivating a large body of empirical work, have rarely been evaluated with quantitative theory. Here we incorporate intraspecific variation into a common model of competition and identify three pathways by which this variation affects coexistence: (1) changes in competitive dynamics because of nonlinear averaging, (2) changes in species' mean interaction strengths because of variation in underlying traits (also via nonlinear averaging) and (3) effects on stochastic demography. As a consequence of the first two mechanisms, we find that intraspecific variation in competitive ability increases the dominance of superior competitors, and intraspecific niche variation reduces species-level niche differentiation, both of which make coexistence more difficult. In addition, individual variation can exacerbate the effects of demographic stochasticity, and this further destabilises coexistence. Our work provides a theoretical foundation for emerging empirical interests in the effects of intraspecific variation on species diversity.

**Keywords**
community assembly, competition, demographic heterogeneity, demographic stochasticity, functional traits, genetic diversity, individual variation, intraspecific variation, nonlinear averaging, species coexistence.

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## INTRODUCTION

Population and community dynamics are emergent properties of the demographic rates and interactions of individuals. Consequently, solving important problems in ecology requires understanding how processes operating at the level of individuals translate into population and community dynamics. Nonetheless, attempts to understand one of the central problems in ecology – species coexistence – have traditionally excluded consideration of intraspecific variation, instead relying on average differences between species to explain diversity maintenance. Ecologists are now being forced to reconsider this approach because of growing empirical evidence that a large fraction of the trait variation in nature occurs within, not just between species (Messier *et al.* 2010; Violle *et al.* 2012). Indeed, approximately 25% of the total trait variation within plant communities worldwide is found within species (Siefert *et al.* 2015). This is a striking pattern with unexplored but likely important consequences for species coexistence that deserve greater theoretical attention.

Although a large theoretical literature on character displacement focuses on the evolutionary processes that influence species diversity via selection on individual variation (Slatkin 1980; Taper & Case 1985; Vellend 2006; Pfennig & Pfennig 2012), the implications of this work for the purely ecological consequences of individual variation are rarely considered. More generally, the theoretical foundation for understanding the ecological mechanisms by which individual variation influences species coexistence is limited (Begon & Wall 1987; Lichstein *et al.* 2007). Nevertheless, ecologists have recently argued that individual variation may provide a previously unrecognised route to species coexistence (Bolnick *et al.* 2003, 2011; Hubbell 2005; Fridley & Grime 2009; Clark 2010; Clark *et al.* 2010; Jung *et al.* 2010; Messier *et al.* 2010; Pfennig & Pfennig 2012; Violle *et al.* 2012). This conjecture is motivating a rapid change in focus in field assessments of diversity maintenance away from average differences between species to concentrate on differences between individuals within species (Jung *et al.* 2010; Messier *et al.* 2010; Violle *et al.* 2012; Siefert *et al.* 2015). However, in the absence of general quantitative theory, common expectations that individual variation promotes species coexistence may be premature.

One compelling argument for a positive effect of individual variation on coexistence is that differences in competitive ability between individuals should 'blur' differences in competitive ability between species. Under this scenario, individual variation is expected to break down competitive hierarchies, which should promote coexistence by making competitive exclusion less likely or less rapid (Hubbell 2005; Fridley *et al.* 2007). It has also been suggested that niche variation evident at the individual level is critical to resolving species-level differences, thereby allowing coexistence of seemingly similar species (Clark 2010). These arguments have generated significant recent interest in the potential positive effects of individual

variation on coexistence. In contrast, an opposing prediction emerges from classical niche theory and suggests that niche variation between individuals should increase species-level niche overlap and therefore decrease the likelihood of coexistence in the absence of evolutionary change (Roughgarden 1972; Slatkin 1980; Taper & Case 1985; Doebeli 1996). When taken together, these arguments suggest contrasting expectations for how intraspecific variation should influence diversity maintenance.

Experimental studies on the effects of intraspecific variation for competitive dynamics remain rare, and tend to investigate the consequences of genetic rather than trait diversity (Hughes *et al.* 2008). Results of these studies are equivocal with respect to species coexistence (Booth & Grime 2003; Crutsinger *et al.* 2008; Fridley & Grime 2009), and reconciling these results is difficult because the ecological and/or evolutionary mechanisms underlying the effects are unknown. Thus, theory should be particularly useful to guide expectations for how high levels of intraspecific variation in nature influence species coexistence.

Here, we develop a quantitative framework and general predictions for understanding the ecological effects of individual variation on coexistence. To do this, we incorporate individual variation into a simple model of competition. We focus explicitly on variation in the traits and/or demographic and competitive rates that determine species' competitive ability or niche differentiation, which together determine the outcome of competition. In doing so, three pathways by which individual variation affects coexistence become clear. First, because the dynamics of competing populations are often nonlinearly dependent on the demographic and competitive rates of individuals, variation changes dynamics via nonlinear averaging. Second, because demographic and competitive rates are themselves nonlinearly dependent on underlying traits, intraspecific variation changes the mean strength of competition (also via nonlinear averaging). And third, because individuals are discrete, intraspecific variation combines with demographic stochasticity to cause population fluctuations that change expected population trajectories of competing species. We find that counter to common expectations of beneficial effects of individual variation on coexistence (Clark 2010; Violle *et al.* 2012), these mechanisms cause intraspecific variation to reduce the likelihood of species coexistence.

## MODEL AND APPROACH

We base our analysis on an annual plant competition model (Beverton & Holt 1957; Leslie & Gower 1958) and provide model-independent generalisations in Appendix S1. The model is well studied analytically (Cushing *et al.* 2004), and describes competitive population dynamics in plant communities in the field (Godoy & Levine 2014). In the absence of individual variation, the dynamics of species 1 (and with subscripts reversed, species 2) can be expressed as:

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

where $n_{1,t}$ is the density of seeds of species 1 at time $t$, $g_1$ is the fraction of seeds that germinate and $\lambda_1$ is the per germinant fecundity at low density. The interaction coefficients $\alpha_{11}$

and $\alpha_{12}$ describe *per capita* effects of conspecifics and heterospecifics on seed production respectively. The model assumes that seeds that do not germinate die, although the addition of a seed bank does not qualitatively change the results (Appendix S1).

An advantage of using this model is that we have previously identified the quantities that describe niche differences and differences in competitive ability (average fitness differences) between species (Godoy & Levine 2014; Godoy *et al.* 2014), both of which are central to the leading hypotheses about the effects of individual variation on coexistence. The interaction between species is stabilised when intraspecific effects (e.g. $\alpha_{11}$) are greater than interspecific effects (e.g. $\alpha_{21}$) and the ratio of these effects for both species determines the niche difference. Such niche differences emerge from underlying trait differences that allow species to exploit resources, for example, in different ways.

To isolate the determinants of competitive ability we first remove the possibility for niche differentiation. We do so by assuming that the *per capita* effect of species 2 on species 1, for example, can be expressed as the product of species 2's generic competitive effect $e_2$ on all species and species 1's generic response to competition $r_1$, such that $\alpha_{12} = r_1 e_2$. Competitive ability then becomes a trait of the species independent of the identity of its competitors, as occurs, for example, with competition for a single limiting resource (i.e. R* in Tilman 1982). Previous work shows that competitive ability of species 1 (and with subscripts reversed, species 2) is then defined as (Appendix S4 in Godoy *et al.* 2014):

$$\frac{g_1 \lambda_1 - 1}{r_1} \qquad (2)$$

The demographic and competitive parameters in expression (2) determine the outcome of competition in the absence of niche differentiation; the species with the largest value of expression (2) excludes all other species.

To bound the problem and to focus on the effects of individual variation *per se*, we concentrate on cases where species have the same amount of variation between individuals, and where there is no trade-off between the amount of intraspecific variation in a trait and the mean value of the same or a different trait. This approach is consistent with the focus of the recent literature, which rarely invokes different levels of variation or trade-offs to make predictions for the effects of individual variation on species diversity. However, in specific cases we relax these assumptions to explore a wider range of dynamics. Furthermore, the approaches we develop are general so that one can explore any of the many possible trade-offs or levels of variation that might occur in different species (Appendix S2).

We divide the paper into three sections. In the first section, we assess the effects of individual variation in competitive ability via nonlinear averaging. In the second section, we assess the effects of individual niche variation via changes in both the mean and the variance of the interaction coefficients. In the third section, we assess the effects of individual variation when individuals are discrete and populations' finite. We provide analytic support for our results in Appendices S1 and S6, and compare our analytic and numerical results in

Appendix S3. We provide R code for implementing our methods in Appendix S2.

## EFFECTS OF INDIVIDUAL VARIATION IN COMPETITIVE ABILITY ON COMPETITIVE EXCLUSION

Superior competitive ability is conferred by high demographic potential (high $g$ and high $\lambda$) and low sensitivity to competition (low [non-negative] $r$; eqn (2)). Therefore, if the intuition that individual variation in competitive ability promotes coexistence is correct, then it is variation in these determinants of competitive ability that must mediate the effect. Furthermore, because differences in competitive ability promote exclusion, if individual variation is to promote coexistence the effects of variation must benefit weak competitors more than strong competitors so that any species-level competitive disadvantage can be overcome.

In general, individual variation will influence dynamics when that variation changes the mean *per capita* offspring production and therefore the realised population growth rate (Bjørnstad & Hansen 1994). According to Jensen's inequality (Jensen 1906), these changes will occur when *per capita* offspring production depends nonlinearly on the demographic rate that is varying (Bjørnstad & Hansen 1994). Following these principles we can rule out any effects of individual variation in germination ($g$) or low-density fecundity ($\lambda$) on dynamics because both of these demographic rates are linearly related to *per capita* seed production (Fig. 1a). Note that the germination term, $g$, in the denominator of eqn (1) is not in itself an individual-level trait. Rather, it determines only the total number of germinants competing in a population, which does not vary between individuals.

In contrast to $g$ and $\lambda$, *per capita* seed production is nonlinearly dependent on competitive sensitivity (Fig. 1b). Therefore, to quantify the effects of individual variation in competitive sensitivity we extend the no-variation model (eqn (1)) to include individual variation in $r$. We include variation between individuals in competitive sensitivity by allowing $r$ to be described by a distribution of values. When individuals of species 1 vary in competitive sensitivity according to a distribution $p_1(r_1)$, dynamics become:

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

This expression is simply eqn (1) with interaction coefficients ($\alpha_{11}$, $\alpha_{12}$) replaced by the products of the generic competitive sensitivity of species 1 ($r_1$) and the species' generic competitive effects ($e_1$, $e_2$), and with competitive sensitivity following a distribution of values describing individual variation. Thus, annual population growth is the integrated seed production of all individuals (differing in competitive sensitivity) in the population. The form of eqn (3) follows approaches previously used in studies of variation on population dynamics (e.g. Hassell *et al.* 1991; Bjørnstad & Hansen 1994; Schreiber *et al.* 2011).

We explore the effects of individual variation on competitive dynamics with numerical simulations of eqn (3). To determine if variation can promote coexistence by assisting weaker
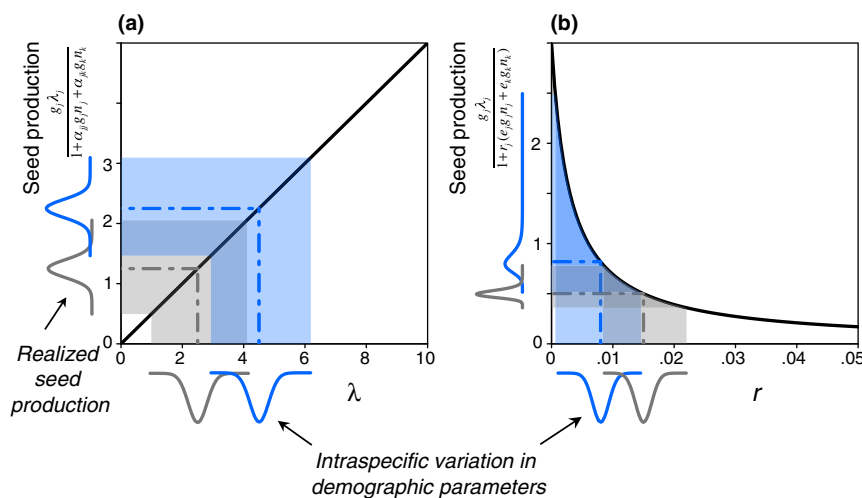


**Figure 1** Illustration of the influence of linear and nonlinear relationships on seed production when individuals within species vary in their demographic rates. The normal distributions below the *x*-axes of each panel represent variation within a 'blue' species and a 'grey' species in (a) low-density seed production, $\lambda$, and (b) competitive sensitivity, $r$. Distributions to the left of the *y*-axes of each panel were generated numerically using the annual plant model and show realised seed production after accounting for the effects of a fixed density of competitors. Linear relationships (a) mean that the higher seed production of superior individuals is offset by the lower seed production of inferior individuals such that individual variation causes no net change in species-level seed production. In contrast, nonlinear, concave-up relationships (b) cause the gains in seed production from low-sensitivity individuals to more than outweigh the losses in seed production from high-sensitivity individuals – notice positive skew of both distributions left of the *y*-axis in (b). 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 $r$ (the on-average competitively superior blue species has greater positive skew than the on-average competitively inferior grey species). The heights of the distributions on the *y*-axis in (b) have been rescaled for clarity. Parameters in (a) where b = blue species and g = grey species: germination = 1, $\overline{\lambda_b} = 4.5$, $\overline{\lambda_g} = 2.5$, $\sigma^2_{\lambda_b} = \sigma^2_{\lambda_g} = 0.09$, $N_b = N_g = 50$, $\alpha_{bb} = \alpha_{gg} = 0.012$, $\alpha_{bg} = \alpha_{gb} = 0.006$ (b): $\overline{\lambda_b} = \overline{\lambda_g} = 3$, $N_b = N_g = 165$, $e_b = e_g = 1$, $\overline{r_b} = 0.008$, $\overline{r_g} = 0.015$, $\sigma^2_{r_b} = \sigma^2_{r_g} = 1.7e-6$.

competitors to overcome their competitive disadvantage, we compete an on-average inferior competitor (higher mean $r$) with an on-average superior competitor (lower mean $r$), keeping all other demographic rates equal between species. Initially we assume that inferior and superior species have the same amount of intraspecific variation, and we relax this assumption in a subsequent analysis. We describe individual variation in competitive sensitivity with symmetric, four-parameter beta distributions, which allows us to define reasonable positive minimum and maximum values for $r$ (Appendix S3). Our qualitative results are robust to the type of distribution used to describe individual variation (Appendices S1, S3).

We quantify the effects of intraspecific variation on competitive outcomes by estimating the growth rate of a low-density invader in the presence of a resident species at its single-species equilibrium density. The winner in competition will have a positive invasion growth rate and the loser in competition will have a negative invasion growth rate. We quantify the invasion growth rate of the species that loses in competition, where a less negative growth rate indicates a smaller difference between species in competitive ability. This metric quantifies competitive dominance in a way that follows from the 'average fitness difference' of Chesson (2000).

To provide general, analytic support for our results, we develop small-variance approximations to describe the effects of variation for a range of different competition models (Appendix S1). We compare our numerical simulations and analytic approximations in Appendix S3. Importantly, the value of the second-order term of the Taylor approximations, which describes the concavity of the *per capita* growth rates with respect to the varying parameter ($r$, in this case), can be used to determine the effect of individual variation on population growth (positive, zero or negative depending on the sign of the second derivative). When this value is compared between species it can be used to quantify whether the effect of variation differentially impacts inferior or superior competitors. We use this feature of the second term of the Taylor approximation to interpret our simulation results.

### Effects of individual variation in competitive ability: Results

Two of the three determinants of competitive ability – germination probability and low-density fecundity – are linearly related to *per capita* seed production, such that individual variation in these demographic rates has no effect on dynamics via nonlinear averaging (Fig. 1a). Individual variation in the third determinant of competitive ability – sensitivity to competition – strengthens the competitive superiority of the dominant competitor, making coexistence more difficult (Fig. 2a, 2b). The magnitude of this effect increases at an increasing rate as variation between individuals increases (Fig. 2c).

The key to understanding the influence of individual variation in competitive sensitivity is to understand how nonlinear relationships between individual-level and population-level demographic rates influence dynamics via Jensen's inequality (Fig. 1). The relationship between competitive sensitivity ($r$) and *per capita* seed production is concave up (positive second derivative; Fig. 1b). By Jensen's inequality, this nonlinear

relationship implies that individual variation in competitive sensitivity increases population-level *per capita* seed production. To see why, consider a single species – the blue (or grey) species in Fig. 1b. Individuals that are less sensitive to competition ($r$ lower than the mean) contribute more to total seed production and individuals that are more sensitive to competition ($r$ higher than the mean) contribute less to total seed production. The key point, however, is that due to the nonlinearity the higher seed production of competitively superior (less sensitive) individuals within a species exceeds the losses of competitively inferior (more sensitive) individuals.

Most importantly, the effect of nonlinear averaging is not equal for species with different mean competitive sensitivities (Fig. 1b). This is because the magnitude of this effect depends on the strength of the nonlinearity (the degree of curvature) around the mean demographic rate. In our model, the degree of curvature decreases with increasing values of competitive sensitivity (i.e. the third derivative with respect to $r$ is negative for all competitor densities; Fig. 1b; Appendix S1). Consequently, individual variation in competitive sensitivity causes larger increases in *per capita* seed production in the species with lower mean sensitivity to competition – in other words, the better competitor (Fig. 1b and 2b). As the better competitor receives the greater fitness benefit from individual variation, it competitively excludes the inferior species more rapidly (Fig. 2a). More generally, the invasion growth rate of the inferior species becomes more negative due to the negative effect of higher heterospecific densities exceeding the positive effect of nonlinear averaging on its own *per capita* seed production. Higher levels of individual variation thereby increase the dominance of the superior competitor, as indicated by the increasingly negative invasion growth rates of the inferior competitor as variation increases (Fig. 2c). Only when inferior competitors have substantially more individual variation than superior competitors can individual variation weaken or reverse a competitive hierarchy (Fig. 2d).

Our analytical approximations in Appendix S1 support these results by demonstrating that these effects are general across parameter values and different models. Indeed, similar results emerge in other common models of competition (e.g. Ricker, Hassell-May; Appendix S1) because species' performance naturally tends to decline monotonically and approach an asymptote with increasing competitive sensitivity (as in Fig. 1b).

### EFFECTS OF INDIVIDUAL NICHE VARIATION ON COEXISTENCE

In two-species systems niche differences arise when individuals within species limit the performance of conspecifics more than they limit heterospecifics (i.e. $\alpha_{11} > \alpha_{21}$). This could occur, for example, if species differ in the soil depth at which they access resources. Implicit in most formulations of species-level niche differentiation is that individuals of the same species share the same niche and so compete equally, but this need not be the case. For example, a relatively deep-rooted individual of a shallow-rooted species will be less sensitive to intraspecific competition than will the other conspecifics on average. Meanwhile, the same individual will, on average, be more
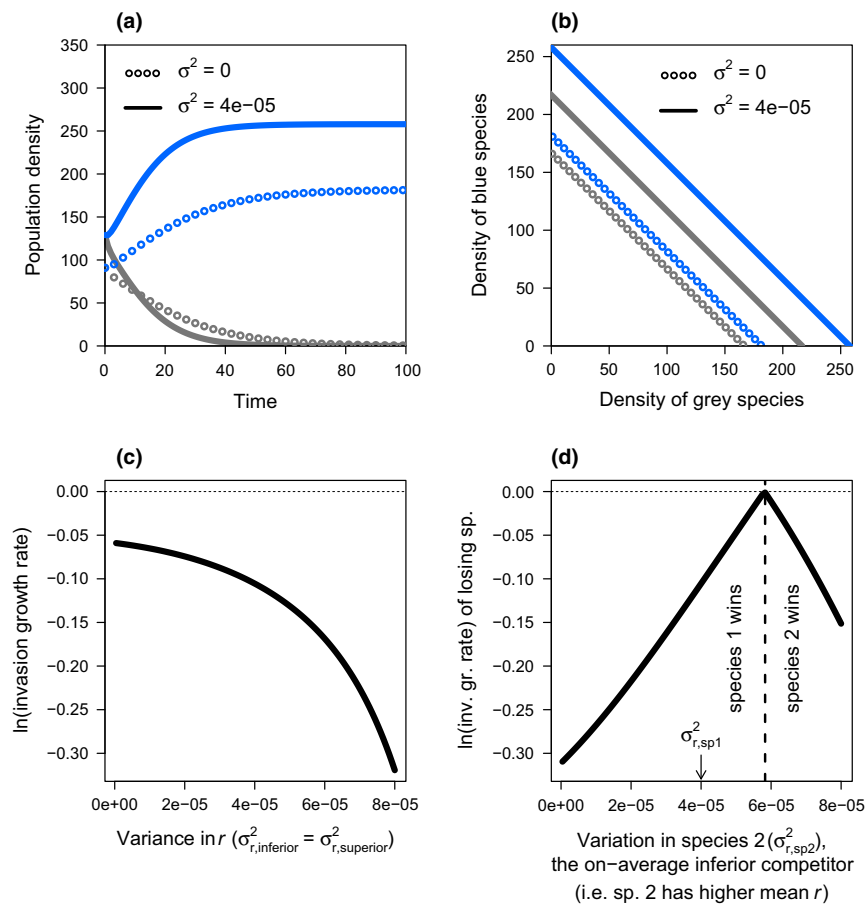
**Figure 2** The effect of individual variation in sensitivity to competition on coexistence. (a) Representative dynamics of two competing species (blue and grey) with (solid lines) and without (circles) individual variation in competitive sensitivity. Because variation in $r$ increases the single-species equilibrium densities of both species, initial population sizes are set at half the equilibrium single-species density of the species with the lowest mean competitive sensitivity (blue species); initial conditions do not change the outcome of competition. (b) Zero-net-growth isoclines for a two-species system with and without individual variation. Isoclines were generated by numerically solving eqn (3) for zero growth of a focal species across a range of densities of its competitor. After the inclusion of individual variation, the isoclines remain perfectly parallel but the distance between them increases, which indicates that individual variation causes a larger difference in average fitness between the two species. (c) Effect of increasing variance in competitive sensitivity on the invasion growth rate of the species with the lower mean competitive sensitivity. The increasingly negative invasion growth rates of the on-average inferior species indicate increasing differences in competitive ability between species as individual variation increases; (d) Effect of unequal variance on invasion growth rates. As intraspecific variation in the species that is the on-average poorer competitor (species 2, which has higher mean $r$) increases relative to its competitor, it reduces and eventually reverses the difference in competitive ability between species. Individual variation was described using four-parameter beta distributions. Parameter values for all plots, where b = blue species and g = grey species: germination = 1, $\lambda_b = \lambda_g = 3$, $\bar{r}_{b(superior)} = 0.011$, $\bar{r}_{g(inferior)} = 0.012$, max/min values for beta distributions: $\bar{r}_b \pm 0.0109$, $\bar{r}_g \pm 0.0109$.

sensitive to interspecific competition from a deep-rooted species. This example implies that niche variation between individuals causes individuals within species to vary in their intra- and interspecific interaction coefficients, and causes these interaction coefficients to be correlated as emerges in models of character displacement (Slatkin 1980; Vasseur *et al.* 2011). We assess the effects of variation in the interaction coefficients in the first part of our analysis of individual niche variation on coexistence.

Niche variation is also expected to affect the mean value of the interaction coefficients. This is most obvious when considering intraspecific interaction coefficients, which are maximised when all individuals interact with the environment (e.g. use resources) in exactly the same way. Intraspecific niche variation should therefore reduce the mean species-level

intraspecific interaction coefficient, and for similar reasons, also affect the mean interspecific interaction coefficient. We address the simultaneous effects of individual niche variation on both the mean and variance of the interaction coefficients in a biologically justified manner using an underlying niche model. This forms the second part of our analysis.

**Part 1: Effects of variation in the interaction coefficients**

We first ask: how does variation between individuals in their response to intra- and interspecific competition affect the dynamics of species that are niche differentiated on average? Even though this question only addresses part of the effects of niche variation on coexistence, answering it is important for interpreting the effects of empirically observed individual

variation in interactions. To explore these effects, we add variation in $\alpha_{11}$ and $\alpha_{22}$ and in $\alpha_{21}$ and $\alpha_{12}$, to the no-variation model by allowing each of these parameters to follow a distribution. Dynamics of species 1 (and, with subscripts reversed, species 2) can then be expressed as:

$$n_{1,t+1} = n_{1,t} \iint \frac{g_1 \lambda_1}{1 + \alpha_{11} g_1 n_{1,t} + \alpha_{12} g_2 n_{2,t}} p(\alpha_{11}, \alpha_{12}) d\alpha_{11} d\alpha_{12} \quad (4)$$

where $p(\alpha_{11}, \alpha_{12})$ describes the joint distribution of individual variation in the intra- and interspecific interaction coefficients. The joint distribution is necessary to account for the correlated nature of the interaction coefficients that emerge in Part 2. In Part 1, we assume the interaction coefficients are uncorrelated to concentrate on the effects of variance *per se*. The population growth of each species is the integrated seed production of all individuals, accounting for their different responses to intra- and interspecific competition.

We use eqn (4) to simulate competitive dynamics between species with variation in their interaction coefficients. We are interested in the effects of individual variation on species-level niche differentiation and so we assess the case where species are symmetric (i.e. parameters of the two species are equal) and niche differentiated on average (i.e. $\overline{\alpha_{11}} = \overline{\alpha_{22}} > \overline{\alpha_{12}} = \overline{\alpha_{21}}$), and have equal levels of individual variation. We investigate departures from these conditions in Appendix S4. To assess the effects of variation on coexistence we quantify the ability of a rare species, which experiences only interspecific competition, to increase from low density in the presence of a resident, which experiences only intraspecific competition. In these analyses we assume that the invader is at low density, but with large enough population size to ensure deviations from deterministic dynamics are inconsequential (an assumption we relax in our assessment of individual variation in the context of stochastic dynamics, below). In our simulations we describe individual variation in interaction coefficients using symmetric,

four-parameter beta distributions, although the choice of distribution does not change our results (Appendices S1, S3). Analytic, small-variance approximations of the invasion dynamics support our results for a larger class of models (Appendix S1).

**Part 1: Results**

When species are niche differentiated on average and the variance in the intra- and interspecific interaction coefficients is equal, variation between individuals in their response to intra- and interspecific competition strengthens stabilised coexistence by increasing the ability of species to recover from low density (Fig. 3).

The effect is again driven by Jensen's inequality, and in particular, the different effects of nonlinear averaging on the growth rates of common vs. rare species. Population growth is a nonlinear function of the interaction coefficients with positive second derivative (concave-up relationship; Fig. 3a). Therefore, variation between individuals in their response to intra- or interspecific competition as expressed in the interaction coefficients increases the mean *per capita* seed production of both species at any given density of competitors. The net effect on coexistence again depends on the strength of the nonlinearity (degree of curvature) of the growth function around the mean interaction coefficient experienced by each competitor. In our model, curvature decreases as the magnitude of the interaction coefficients increase (i.e. the third derivative is negative; Fig. 3a, Appendix S1). When the variance in both interaction coefficients is equal, the positive effect of variation on seed production is larger for the species experiencing the smaller of the two interaction coefficients. When species are niche differentiated on average (i.e. $\overline{\alpha_{11}} > \overline{\alpha_{21}}, \overline{\alpha_{22}} > \overline{\alpha_{12}}$), the invader experiences the smaller of the two interaction coefficients because it experiences only
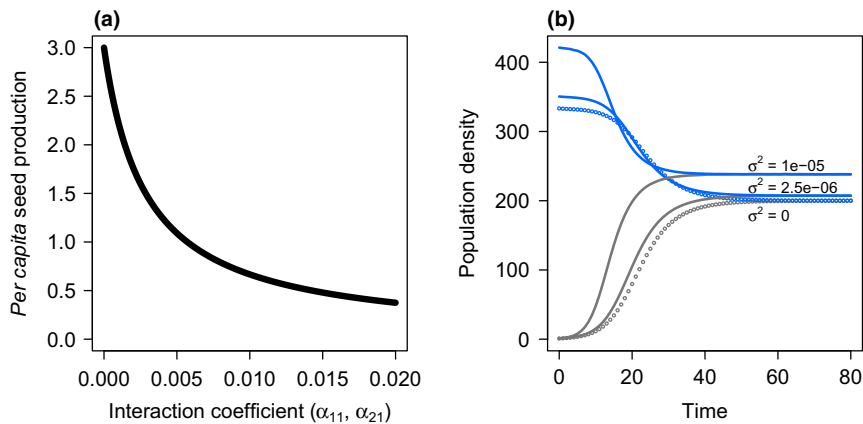
**Figure 3** Effect of variation between individuals in their intra- and interspecific competition coefficients. (a) The relationship between the magnitude of a competition coefficient and *per capita* seed production is nonlinear, with positive second derivative and negative third derivative such that variation results in a larger increase in *per capita* seed production in the species experiencing the smaller average competition coefficient. (b) Dynamics when individuals vary in their intra- and interspecific interaction coefficients. Individual variation increases *per capita* seed production of both species, which results in higher equilibrium densities of the resident (blue species) and a higher invasion growth rate of the invader that more than compensates for the higher level of competition it experiences from the resident, thus strengthening coexistence. Individual variation was described using four-parameter beta distributions. Parameter values: (a) $\lambda = 3$, germination = 1, total density = 350; (b), where b = blue species and g = grey species: germination =1, $\lambda_b = \lambda_g = 3$, $\overline{\alpha}_{bb} = \overline{\alpha}_{gg} = 0.006$, $\overline{\alpha}_{gb} = \overline{\alpha}_{bg} = 0.004$, max/min values for beta distributions: mean interaction coefficient $\pm 0.0039$.

interspecific competition. Consequently, an invader's higher *per capita* growth more than offsets the higher competition exerted by a more abundant resident (Fig. 3b). In this case, coexistence is strengthened by variation between individuals in their response to competition. Importantly, this effect on coexistence does not arise because individual variation favours one competitor over another, but instead emerges because the magnitude of the effect of individual variation is different for species at high vs. low density.

### Part 2: Effects of niche variation between individuals on coexistence

Niche variation involves more than variation in interaction coefficients; it also involves changes in the mean values of those interaction coefficients. To determine how niche variation between individuals affects coexistence, we need to understand how this variation translates into intra- and interspecific interaction coefficients in a biologically justified manner. To do this we rely on classic models of individual-level niche variation based on resource-utilisation functions traditionally used to explore evolutionary character displacement (Roughgarden 1972; Slatkin 1980; Taper & Case 1985; Doebeli 1996). These models begin with the premise that the strength of the interaction between two individuals is negatively related to their distance along a niche axis, such as the soil depth at which plants access resources. Following classic evolutionary models we formalise this thinking with the expression:

$$\alpha(z, z') = \alpha_0 e^{\frac{-(z-z')^2}{2\sigma_\alpha^2}} \qquad (5)$$

where $\alpha(z, z')$ describes the strength of the interaction between individuals at locations $z$ and $z'$ along the niche axis. The interaction takes its maximum value, $\alpha_0$, when two individuals have zero niche difference (i.e. when $z - z' = 0$), and the strength of the interaction declines monotonically with increasing distance between individuals along the niche axis following a Gaussian function with variance $\sigma_\alpha^2$.

The individual-to-individual interactions described in eqn (5) can be used to calculate an intraspecific and interspecific interaction coefficient for each individual in the population (Appendix S5). The total intraspecific competition experienced by a focal individual is the sum of each of its interactions with all conspecific individuals. Because individual-to-individual interactions are additive, an individual's intraspecific interaction coefficient is equal to the mean of its conspecific interactions. The interspecific interaction coefficient for each individual is determined the same way, but this time averaging interactions with all heterospecific individuals. Repeating for all individuals generates a distribution of intraspecific and interspecific interaction coefficients that reflect underlying niche differentiation between individuals.

To evaluate the effects of niche variation on coexistence, we simulated an invasion scenario using eqn (4), but with numerically generated (and correlated) distributions of the interaction coefficients following from the niche model (eqn (5), Appendix S2, S5). In these simulations, we describe niche variation between individuals within species along a one-dimensional niche axis using Gaussian distributions (i.e. for

species 1: $Z_1 \sim \mathcal{N}(\mu_{Z_1}, \sigma_{Z_1}^2)$), assuming that species are niche differentiated on average (i.e. $\mu_{Z_1} \neq \mu_{Z_2}$), have the same amount of niche variation between individuals (i.e. $\sigma_{Z_1}^2 = \sigma_{Z_2}^2$) and are equal in all other parameters. Our simulations incorporate the influence of niche variation on the mean, variance and covariance of species' interaction coefficients. In Appendix S1 we provide analytic support for our numerical results.

### Part 2: Results

Niche variation between individuals in our model weakens stabilised coexistence by reducing the ability of species to increase from low density in the presence of a competitor (Fig. 4a). The negative effect on coexistence is largely driven by reductions in the mean intraspecific competition coefficient with increasing niche variation (Fig. 4b). This reduction occurs because intraspecific interactions are strongest when all individuals have the same niche, and thus niche variation necessarily reduces the mean intraspecific interaction coefficient (Fig. 4b). Lower intraspecific competition increases the equilibrium density of the resident species (Fig. 4a), which reduces growth of the low-density invader. In our model, mean interspecific interaction coefficients can increase or decrease because of niche variation (explained in more detail in Appendices S1, S5), but in either case, the mean interspecific interaction coefficient is not reduced to the same extent as the mean intraspecific interaction coefficient (Fig. 4b). Thus, the ratio of mean intraspecific to mean interspecific effects declines with individual niche variation, causing coexistence to be less stabilised.

The negative effects of changes in the mean values of the interaction coefficients on invasion growth rates overwhelm any positive effects that arise because of variation in the interaction coefficients (the effects demonstrated in Part 1; Fig. 4c). Nevertheless, variance in the interaction coefficients as a consequence of niche variation still influences dynamics. For example, the negative consequences of changes in the mean values of the interaction coefficients on invasion growth rates are partially offset by the positive effects of variance in the interaction coefficients that occur via nonlinear averaging (Fig. 4c). This result emerges in part because individual niche variation causes more variation in interspecific than intraspecific interaction coefficients in our model (Appendices S1, S5).

### EFFECT ON COEXISTENCE OF VARIATION BETWEEN DISCRETE INDIVIDUALS

As with most deterministic models of species interactions, our analyses thus far assume that competition occurs on well-mixed landscapes of infinite size. Therefore, while species densities can fluctuate, population sizes are infinite. However, important dynamical effects of individual variation emerge explicitly because individuals are discrete and populations are finite. Because individuals are discrete, births and deaths are probabilistic events such that individuals that are otherwise identical to each other can differ by chance in their realised fecundity or survival. Such demographic stochasticity causes
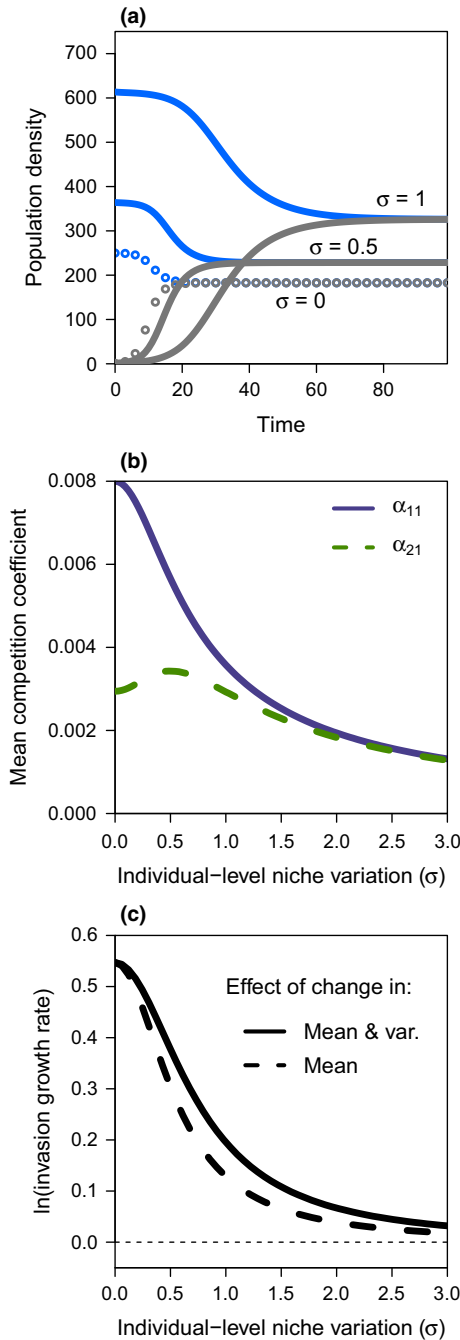
**(a)**



**(b)**



**(c)**



**Figure 4** The effect of intraspecific niche variation on coexistence. (a) Dynamics of two competing species (blue and grey) with (solid lines) and without (circles) individual niche variation. Niche variation reduces the recovery rate of an invader in the presence of a resident at its single-species equilibrium density. (b) Effect of niche variation on the mean strength of the intra- and interspecific interaction coefficients. (c) Partitioning the effects of intraspecific niche variation on coexistence via changes in the means and variances of the interaction coefficients on the invasion growth rate. The dashed line shows effects that arise as a consequence of changes in the mean values of the interaction coefficients, while the solid line shows the combined effects of the changes in the means and the variances. The difference between the lines represents the positive effects of variance in the interaction coefficients on invasion growth rates. The invasion growth rates for the dashed line were calculated with eqn (1) using the mean values of the distributions of the interaction coefficients after accounting for intraspecific niche variation, but ignoring the variance of those distributions. Invasion growth rates for the solid line were calculated using eqn (4), which accounts for changes in both means and variances. Individual variation was described using Gaussian distributions. Parameter values: a) where $b$ = blue species and $g$ = grey species, germination = 1, $\lambda_g = \lambda_b = 3$, $\alpha_0 = 0.008$, $|\overline{z_b} - \overline{z_g}| = 1$, $\sigma_\alpha^2 = 0.5$; b) and c) $\alpha_0 = 0.008$, $|\overline{z_1} - \overline{z_2}| = 1$, $\sigma_\alpha^2 = 0.5$.

single model is a two-step process. The first step determines how many seeds germinate at the beginning of the year, and therefore how many discrete plants compete and produce seeds. The second step determines the discrete number of seeds produced by each plant at the end of the year. While most implementations of stochastic competitive dynamics assume that all individuals within species have the same expected demographic rates, we allow individuals to vary continuously in their expected germination probability and low-density fecundity. We concentrate on variation in these traits to determine how the discrete nature of individuals mediates the effects of individual variation, independent of the effects of nonlinear averaging demonstrated in the sections above.

The stochastic model describing dynamics on finite landscapes of discrete individuals that vary in their expected demographic rates can be expressed as:

$$G_1 = \sum_{i=1}^{N_{1,t}} \text{Bernoulli}(X_{1,i}) \qquad (6a)$$

$$N_{1,t+1} = \sum_{i=1}^{G_1} \text{Poisson}\left(\frac{Y_{1,i}}{1 + \frac{\alpha_{11}G_1}{S} + \frac{\alpha_{12}G_2}{S}}\right) \qquad (6b)$$

where $i$ represents an individual, $G_1$ describes the number of successfully germinating seeds of species 1 and $N_{1,t}$ is the number of discrete individuals of species 1 at time $t$. In eqn (6a), $X_{1,i}$ is a germination probability independently drawn from a fixed distribution ($X_1$) that describes continuous variation between individuals in expected germination probabilities. The Bernoulli process then ensures each seed either germinates or does not. In eqn (6b), total seed production ($N_{1,t+1}$) is the sum of the Poisson distributed seed production of each individual. $Y_{1,i}$ is a single value of expected low-density fecundity drawn from a distribution $Y_1$ of expected low-density fecundities. $S$ describes landscape size and consequently $\frac{G_1}{S}$ is the density of germinants in the landscape. In the limit of landscapes of infinite size there are essentially an infinite number of invading individuals (though at density approaching zero) and the dynamics of the stochastic model

annual growth rates of finite populations to vary between years, which reduces expected population growth rates for single species (Lande 1998). Importantly, individual variation in expected demographic rates – or demographic heterogeneity – may modify this effect (Kendall & Fox 2003). However, the effects of demographic heterogeneity on the stochastic dynamics of competing populations have received little attention. To study these effects, we analyse a stochastic version of the annual plant model that admits continuous variation in expected demographic rates between discrete individuals.

There are two sources of demographic stochasticity for an annual plant whose life cycle is described in eqn (1): germination and seed production. Incorporating both sources into a

(6) converge on the dynamics of the mean-field model (eqn (3); Kurtz 1981; Faure & Schreiber 2014). A second set of equations with species subscripts reversed describes dynamics of species 2.

Because germination probabilities are chosen randomly and independently for each individual, the probability of a seed germinating is the expected value $\overline{X}_1$ of $X_1$, and therefore the number of germinating seeds is a binomial distribution, i.e. $G_1 \sim \text{Binomial}(N_{1,t}, \overline{X}_1)$. Because the number of germinating seeds in this expression depends only on the mean germination rate $\overline{X}_1$ across all individuals, individual variation in expected germination probabilities has no effect on dynamics (see Kendall & Fox 2003 for detailed discussion). In contrast, with stochasticity in individual-level seed production described by a Poisson distribution, individual variation in expected fecundity increases the total variance in realised fecundity (Kendall & Fox 2003; Melbourne & Hastings 2008).

### Analytical approximation of invasion growth rates

To derive an analytical approximation of the stochastic growth rate of a rare invader we assume the landscape is sufficiently large ($S \gg 1$) that resident dynamics tend to remain near the deterministic single-species equilibrium density of the mean-field model (Faure & Schreiber 2014). Residents are thus affected by variation between individuals in their expected demographic rates (as in the deterministic models in the sections above), but are negligibly influenced by dynamics that emerge as a consequence of the discrete nature of individuals in populations of small size. With the density of the resident species (species 2, for example) fixed at its equilibrium, we can describe the stochastic dynamics of an invading species (species 1), assuming the system is not so large that the invader itself is immune to the effects of demographic stochasticity.

While realisations of stochastic population trajectories can vary substantially, we are interested in the most likely population trajectory of an invader. When considering population trajectories driven by variable fates of discrete individuals, a square-root transformation of population size tends to produce a more symmetrical distribution of potential population sizes (Lande 1998). This means that the expected population size on the square-root scale describes the change in the median/mode population size. For an invader (species 1) that remains rare, the dynamics of its expected population size on the square-root scale can be expressed (Appendix S6):

$$E\left[\sqrt{N_{1,t+1}}\right] \approx \sqrt{\mu_1 N_{1,t}} - \frac{\sigma_1^2 \mu_1^{-3/2}}{8\sqrt{N_{1,t}}} \qquad (7)$$

where $\mu_1$ is the arithmetic mean individual-level seed production after accounting for competition from the resident and $\sigma_1^2$ describes the total variance in individual-level seed production, including both expected (i.e. innate) and stochastic differences between individuals in their demographic rates. When individuals vary in their low-density fecundity, $\mu_1$ equals $\frac{g_1 \bar{\lambda}_1}{1 + g_2 \hat{N}_2 \alpha_{12}}$, where $\hat{N}_2$ is the equilibrium density of the resident and $\sigma_1^2$ equals $\sigma_{\lambda_1}^2 \left(\frac{g_1}{1 + g_2 \hat{N}_2 \alpha_{12}}\right)^2$, where $\sigma_{\lambda_1}^2$ is the variance between individuals in low-density fecundity.

Equation (7) can be used to evaluate the effects of individual variation in demographic rates between discrete individuals on the expected growth rate of the invader. Crucially, notice that variation between individuals ($\sigma_1^2$) reduces the growth rate of the invading species because the sign of the second term is negative. This effect occurs because growth is a multiplicative process and any factor that causes variation in growth between years – individual variation in this case – will tend to reduce the expected growth rate (Lande *et al.* 2003). The approximation also shows that the negative effect of individual variation is small and declines as population size increases (Fig. 5a). Overall, in systems of competing finite populations composed of discrete individuals, populations will suffer from being reduced to low numbers because individual variation causes fluctuations in annual growth rates that depress expected growth.

### Stochastic simulations of invasion trajectories

Our analytical approximation (7) assumes that variation between individuals is small and that the resident assumes a fixed density in a large landscape and so cannot respond to changes in invader population size, nor fluctuate itself. We are able to relax these assumptions in stochastic simulations using eqn (6). Furthermore, the analytical approximation does not distinguish between the sources of the variation between individuals. Importantly, the total amount of individual variation comes from both expected and stochastic differences between individuals (Kendall & Fox 2003). Because we are explicitly interested in the consequences of individual variation in expected demographic rates and how these effects are mediated by the discrete nature of individuals, we explore this dynamic using simulations.

In our simulations we assess the effect of variation in expected low-density fecundity ($\lambda$) between discrete individuals. We simulate an invasion scenario, which requires first simulating resident dynamics to generate a range of potential (stochastic) resident population sizes. We then initialise each invasion scenario by drawing one value from this resident abundance distribution as the initial resident population size, while the invader begins with two individuals. We then use eqn (6) to project population sizes of both species forward in time. We use the median trajectory of 10 000 runs to compare stochastic invasion dynamics with and without individual variation. We also record the proportion of 100 000 realisations in which the invader reaches half of its equilibrium population size in the two-species system, which should provide a good indication of the likelihood of longer term coexistence (Turelli 1980; Faure & Schreiber 2014). In our analyses the resident and invader have the same mean demographic rates, and the same variance in low-density fecundity, and we set intraspecific competition coefficients greater than interspecific competition coefficients to ensure that deterministic low-density growth rates of the invader are positive. Individual variation in expected low-density fecundity ($\lambda$) is described using gamma distributions. From the first section of the paper it is clear that in the absence of demographic stochasticity individual variation in $\lambda$ has no effect on coexistence because it is linearly related to population growth. Therefore, any effects of variation in expected low-density fecundity in our
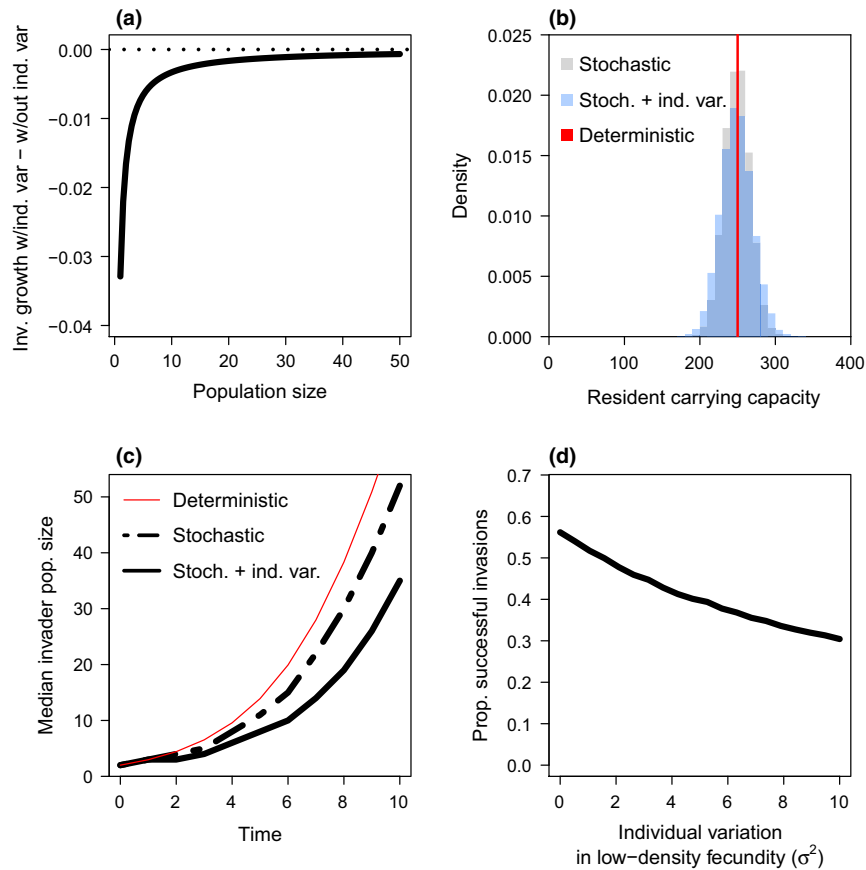
**Figure 5** The effect of individual variation between discrete individuals on coexistence. (a) The effect on the invasion growth rate of variation between discrete individuals from eqn (7). The negative effect of individual variation declines as population size increases. (b) Distributions of stochastic resident carrying capacity with and without individual variation. When the deterministic resident carrying capacity is large, carrying capacity is relatively unaffected by variation between discrete individuals ($n = 100\,000$ simulations). (c) The effect of variation in expected fecundity between discrete individuals on invasion trajectories. The deterministic trajectory (red line) was evaluated using eqn (1). Because $\lambda$ is linearly related to population growth (Fig. 1a) the deterministic trajectory is the same with or without individual variation. Demographic stochasticity has a negative effect on the median trajectory (dashed line), and this effect is exacerbated with variation between individuals in their expected fecundity (solid black line) ($n = 10\,000$ simulations). (d) The effect of individual variation on the proportion of successful invasions of a species at low abundance in the presence of a resident competitor. Higher levels of individual variation reduce the likelihood of the invader reaching half its equilibrium population size ($n = 100\,000$ simulations). Individual variation for the simulations was described using gamma distributions. Parameter values: $\bar{\lambda}_1 = \bar{\lambda}_2 = 3$, $g_1 = g_2 = 1$, $\alpha_{11} = \alpha_{22} = 0.008$, $\alpha_{12} = \alpha_{21} = 0004$; a) $\sigma_\lambda^2 = 0.9$; b & c) $\sigma_{\lambda_1}^2 = \sigma_{\lambda_2}^2 = 5$.

stochastic simulations are mediated by demographic stochasticity arising from the discrete nature of individuals.

**Results of stochastic simulations**

Our simulations support the central result from the analytical approximation – variation between discrete individuals in expected low-density fecundity reduces the median population trajectory of a low-density invader (Fig. 5c). Higher levels of individual variation increase the negative effect on invasion trajectories, which decreases the likelihood of successful invasion (Fig. 5d).

We know from the deterministic model that individual variation in low-density fecundity has no effect on competitive dynamics via nonlinear averaging (Fig. 1a). However, following Lande (1998), when individuals are discrete and populations finite, variation between individuals causes fluctuations between years in annual population growth rates and this reduces likely growth trajectories. Because individual variation

in expected fecundity increases the total amount of variation between discrete individuals in realised fecundity the negative effects on population growth are exacerbated. For an invading species with low numbers of individuals, between-year growth fluctuations reduce population growth and so reduce the most likely invasion trajectory (eqn (7), Fig. 5a and c). In contrast, the resident population is much larger and so suffers little from this effect (Fig. 5b). Individual variation thereby favours resident species with large population size over invading species with small population size. Because these effects induce positive frequency dependence (i.e. favouring species at high abundance over species at low abundance), individual variation in low-density fecundity ($\lambda$) between discrete individuals destabilises coexistence.

**DISCUSSION**

Our work suggests that the purely ecological effects of individual variation do not promote species coexistence. If

anything, intraspecific variation impedes the maintenance of species diversity. Working with a common model of competition we find three important results: (1) variation between individuals in the drivers of competitive ability either has no effect on coexistence or tends to reinforce competitive dominance via the effects of nonlinear averaging (Fig. 2); (2) while individual variation in the response to intra- and interspecific interactions can stabilise coexistence (Fig. 3), niche variation between individuals tends to weaken coexistence by strongly reducing species-level niche differentiation (Fig. 4); and (3) variation between individuals combines with demographic stochasticity to reduce the likelihood of long-term coexistence by favouring abundant competitors over species recovering from small population sizes (Fig. 5). Only when additional conditions are invoked, such as mean–variance trade-offs (e.g. Lichstein *et al.* 2007; Bolnick *et al.* 2011), including higher levels of individual variation in otherwise inferior competitors (Fig. 2d), do we find that individual variation increases the potential for coexistence. In sum, our results suggest that the ecological effects of individual variation create additional hurdles for species to overcome if they are to coexist.

### Individual variation in competitive ability promotes competitive exclusion

When individuals within species vary in competitive ability, differences in competitive ability between species are less obvious (Hubbell 2005; Clark 2010; Messier *et al.* 2010). Intuition might therefore suggest that individual variation in traits that determine competitive ability should reduce differences in competitive ability between species. Our work suggests the opposite is true (Fig. 2). Why doesn't the intuition work?

Addressing this question requires understanding if gains from individuals that are relatively strong competitors offset losses from individuals that are weak competitors, and whether the balance differs between species with different mean competitive abilities. When the relationship between individual-level traits and population growth is linear (as for low-density fecundity and germination), there is no net change in competitive ability at the species level and therefore no effect of variation in these traits on coexistence. But for nonlinear relationships individual variation changes the potential growth rate of both superior and inferior species at any fixed level of competition. When individuals vary in their sensitivity to competition, species gain more (in terms of seed production) from individuals that are stronger competitors than they lose from individuals that are weaker competitors (Fig. 1). To promote coexistence, the effects of individual variation must benefit inferior species more than superior species, but in our model and other common models of competition the opposite occurs. This is because the curvature of the relationship (i.e. the positive effect of the nonlinearity) around the mean trait value is greater for superior than inferior species regardless of the densities of competitors, giving the net competitive advantage to the superior species (Fig. 2). Only when there is more variation between individuals of an on-average inferior species can a competitive disadvantage be overcome (Fig. 2d).

Therefore, in the absence of *a priori* reasons to expect more variation in inferior than superior competitors, individual variation in sensitivity to competition reinforces competitive hierarchies, making coexistence more difficult.

### Individual niche variation tends to weaken coexistence

Individual-level niche variation causes changes in both the mean and the variance of the interaction coefficients that ultimately determine species-level niche differentiation. In our model, while increasing the variance in the interaction coefficients assists in the recovery of species from low density via the effects of nonlinear averaging (Fig. 3), individual variation in niches ultimately weakens coexistence by reducing the mean strength of intraspecific relative to interspecific competition (Fig. 4). This occurs because niche variation can only weaken average *per capita* intraspecific competition, but will increase the strength of interspecific competition in at least some individuals. Consequently, decreases in the strength of intraspecific effects cannot be offset by decreases in interspecific effects. Our result is consistent with those of character displacement models showing that selection favours reductions in trait variation leading to less niche overlap (Pfennig & Pfennig 2012).

Although understanding the effects of niche variation on coexistence requires recognising that the negative effect of changing mean interaction coefficients overwhelms any effects of variation in these coefficients, the latter effect remains empirically relevant. Quantifying niche variation in a theoretically justified manner is difficult (Kraft *et al.* 2015), whereas measuring interaction coefficients and their variation between individuals is feasible. Further empirical approaches are needed to evaluate the effects of individual niche variation *per se*.

### Individual variation between discrete individuals further destabilises coexistence

Variation in expected fecundity between discrete individuals carries a small but unavoidable demographic cost that reduces the likelihood of long-term coexistence (Fig. 5; Turelli 1980). This is because variation between discrete individuals causes fluctuations in population-level demographic rates between years, which reduces average population growth (Lande 1998). Because this effect is disproportionately experienced by rare species, individual variation results in positive frequency-dependent dynamics (abundant species are favoured), impeding coexistence (Fig. 5). The more individual variation, the greater the demographic cost of being rare and the more vulnerable species are to competitive exclusion.

Although variation between discrete individuals incurs a cost, not all demographic rates are equal in this respect. While individual variation in low-density fecundity increases the costs of demographic stochasticity, individual variation in germination success has no effect over and above the negative effects of simple demographic stochasticity (but see Kendall & Fox 2002). Finally, we note that although the effects of individual variation combined with demographic stochasticity are

consistently negative for a population depressed to low numbers, effects tend to be weak and diminish rapidly as population size increases (Fig. 5a). Nevertheless, these effects will increase the demand on the species-level niche differences required for coexistence to occur.

## Limitations and extensions

Much of our work has focused on individual variation in demographic rates and competitive parameters, while most field studies quantify intraspecific variation in species' functional traits, such as wood density or specific leaf area (Messier *et al.* 2010; Jung *et al.* 2014; Siefert *et al.* 2015). Nonlinear relationships between specific functional traits and the demographic rates that we consider will add yet another layer of nonlinear averaging, which can affect the distributions (means, variances and higher moments) of demographic rates in complex ways. Indeed, our niche model provides one such example, where effects on dynamics are influenced by the nonlinear relationship between niche position and the interaction coefficient (eqn (5)), such that the distribution of the underlying niche traits affects the mean species-level interaction strengths (Fig 4b, Appendix S2). Empirically accounting for these additional nonlinearities between traits and demographic rates, which may not simply be concave or convex, is important because they will modify, and can sometimes reverse, the predicted effects of variation (e.g. Drake 2005). Until these relationships are understood, our approach provides a default set of expectations for the effects of individual variation on coexistence.

To resolve the effects of individual variation when individuals are discrete we applied the logic of the invasion condition, developed for infinite systems, to finite systems. Although this condition is not proven in competitive systems with finite numbers of individuals (but see Faure & Schreiber 2014), we believe the underlying logic should still apply. Moreover, empirical studies commonly make this assumption when relying on inference from the fate of small numbers of discrete individuals to understand coexistence (Seabloom *et al.* 2003; Levine & Hille Ris Lambers 2009; Hart & Marshall 2013). One lesson from our results for such studies is that ecologists may need to account for the effects of demographic stochasticity and individual variation on predicted dynamics. Indeed, recent theoretical work formally includes extinction risk as a consequence of stochasticity into assessments of species coexistence, which is more consistent with empirical realities (Turelli 1980; Tilman 2004; Adler & Drake 2008; Gravel *et al.* 2011; Kramer & Drake 2014).

Two important extensions of our work will require understanding how spatial processes and structured variation between individuals mediate the influence of individual variation on multispecies interactions. We have assumed a well-mixed system and while our own preliminary analyses suggest that spatially explicit neighbourhood competition does not change our qualitative results, additional analyses are required. In addition, we assume that individuals within and between generations are independent. However, variation in demographic rates that is correlated between discrete individuals can modify the effects of individual variation for single-species population dynamics (Kendall & Fox 2002), with unknown consequences for coexistence. Finally, we note that our results in no way undermine the central importance of individual variation as the material on which selection can act to promote coexistence (Taper & Case 1985; Doebeli 1996; Vellend 2006).

## Implications for empirical studies

There is currently an unprecedented push to quantify intraspecific trait variation in nature and the majority of this work appears motivated by the potential positive effects of individual variation on species diversity (Violle *et al.* 2012). Arguably, the most prominent recent empirical work on the positive effects of individual variation on coexistence is by Clark and colleagues (e.g. Clark 2010; Clark *et al.* 2011). This work describes analytical techniques that demonstrate that empirical differences between species only become clear when variation between individuals is appropriately accounted for (Clark 2003). However, there is a large difference in aim between using individual-level data to infer species-level differences, and explicitly testing the causal effects of individual variation on species dynamics. Our contribution addresses the latter – the effects of individual variation on dynamics – and suggests that individual variation is more likely to prevent coexistence than promote it, and may often have little or no effect.

Our results have clear implications for future empirical work. First, empirical evidence that intraspecific variation is significant and obscures species-level differences is insufficient for inferring how such variation affects species diversity. Second, our results suggest that moving forward requires not only quantifying the magnitude of intraspecific trait variation, but also defining the potentially nonlinear relationship between the trait of interest and the population growth rates of the competing species. This latter step requires integrating field data into mathematical models of competition, which also allows one to quantify the effects of individual variation on stochastic dynamics. Only when the relationship between traits and demographic parameters is explicitly described can robust hypotheses about the effects of individual variation on competitive outcomes be accurately formulated.

## AUTHORSHIP

SPH and JML conceived the problem; SPH did the research, with JML and SJS providing input; SJS derived the approximations; SPH wrote the manuscript and all authors contributed to revisions.

## REFERENCES

Adler, P.B. & Drake, J.M. (2008). Environmental variation, stochastic extinction and competitive coexistence. *Am. Nat.*, 172, E186–E195.

Begon, M. & Wall, R. (1987). Individual variation and competitor coexistence: a model. *Funct. Ecol.*, 1, 237–241.

Beverton, R.J.H. & Holt, S.J. (1957). *On the Dynamics of Exploited Fish Populations U.K.*. Ministry of Agriculture and Fisheries, London, England.

Bjørnstad, O.N. & Hansen, T.F. (1994). Individual variation and population dynamics. *Oikos*, 69, 167–171.

Bolnick, D.I., Svanback, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D. *et al.* (2003). The ecology of individuals: incidence and implications of individual specialization. *Am. Nat.*, 161, 1–28.

Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M. *et al.* (2011). Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.*, 26, 183–192.

Booth, R.E. & Grime, J.P. (2003). Effects of genetic impoverishment on plant community diversity. *J. Ecol.*, 91, 721–730.

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.

Clark, J.S. (2003). Uncertainty and variability in demography and population growth: a hierarchical approach. *Ecology*, 84, 1370–1381.

Clark, J.S. (2010). Individuals and the variation needed for high species diversity in forest trees. *Science*, 327, 1129–1132.

Clark, J.S., Bell, D., Chu, C.J., Courbaud, B., Dietze, M., Hersh, M. *et al.* (2010). High-dimensional coexistence based on individual variation: a synthesis of evidence. *Ecol. Monogr.*, 80, 569–608.

Clark, J.S., Bell, D.M., Hersh, M.H., Kwit, M.C., Moran, E., Salk, C. *et al.* (2011). Individual-scale variation, species-scale differences: inference needed to understand diversity. *Ecol. Lett.*, 14, 1273–1287.

Crutsinger, G.M., Souza, L. & Sanders, N.J. (2008). Intraspecific diversity and dominant genotypes resist plant invasions. *Ecol. Lett.*, 11, 16–23.

Cushing, J.M., Levarge, S., Chitnis, N. & Henson, S.M. (2004). Some discrete competition models and the competitive exclusion principle. *J. Diff. Equ. Appl.*, 10, 1139–1151.

Doebeli, M. (1996). An explicit genetic model for ecological character displacement. *Ecology*, 77, 510–520.

Drake, J.M. (2005). Population effects of increased climate variation. *Proc. R. Soc. B Biol. Sci.*, 272, 1823–1827.

Faure, M. & Schreiber, S.J. (2014). Quasi-stationary distributions for randomly perturbed dynamical systems. *Ann. Applied Prob.*, 24, 553–598.

Fridley, J.D. & Grime, J.P. (2009). Community and ecosystem effects of intraspecific genetic diversity in grassland microcosms of varying species diversity. *Ecology*, 91, 2272–2283.

Fridley, J.D., Grime, J.P. & Bilton, M. (2007). Genetic identity of interspecific neighbours mediates plant responses to competition and environmental variation in a species-rich grassland. *J. Ecol.*, 95, 908–915.

Godoy, O. & Levine, J.M. (2014). Phenology effects on invasion success: insights from coupling field experiments to coexistence theory. *Ecology*, 95, 726–736.

Godoy, O., Kraft, N.J.B. & Levine, J.M. (2014). Phylogenetic relatedness and the determinants of competitive outcomes. *Ecol. Lett.*, 17, 836–844.

Gravel, D., Guichard, F. & Hochberg, M.E. (2011). Species coexistence in a variable world. *Ecol. Lett.*, 14, 828–839.

Hart, S.P. & Marshall, D.J. (2013). Environmental stress, facilitation, competition, and coexistence. *Ecology*, 94, 2719–2731.

Hassell, M.P., May, R.M., Pacala, S.W. & Chesson, P.L. (1991). The persistence of host-parasitoid associations in patchy environments 1: a general criterion. *Am. Nat.*, 138, 568–583.

Hubbell, S.P. (2005). Neutral theory in community ecology and the hypothesis of functional equivalence. *Funct. Ecol.*, 19, 166–172.

Hughes, A.R., Inouye, B.D., Johnson, M.T.J., Underwood, N. & Vellend, M. (2008). Ecological consequences of genetic diversity. *Ecol. Lett.*, 11, 609–623.

Jensen, J.L. (1906). Sur les fonctions convexes et les inégalités entre les valeurs moyennes. *Acta Math.*, 30, 175–193.

Jung, V., Violle, C., Mondy, C., Hoffmann, L. & Muller, S. (2010). Intraspecific variability and trait-based community assembly. *J. Ecol.*, 98, 1134–1140.

Jung, V., Albert, C.H., Violle, C., Kunstler, G., Loucougaray, G. & Spiegelberger, T. (2014). Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. *J. Ecol.*, 102, 45–53.

Kendall, B.E. & Fox, G.A. (2002). Variation among individuals and reduced demographic stochasticity. *Conserv. Biol.*, 16, 109–116.

Kendall, B.E. & Fox, G.A. (2003). Unstructured individual variation and demographic stochasticity. *Conserv. Biol.*, 17, 1170–1172.

Kraft, N.J.B., Godoy, O. & Levine, J.M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl Acad. Sci.*, 112, 797–802.

Kramer, A.M. & Drake, J.M. (2014). Time to competitive exclusion. *Ecosphere*, 5, art52.

Kurtz, T.G. (1981). *Approximation of population processes*. Society for Industrial and Applied Mathematics (SIAM), Philadelphia.

Lande, R. (1998). Demographic stochasticity and Allee effect on a scale with isotropic noise. *Oikos*, 83, 353–358.

Lande, R., Engen, S. & Saether, B.-E. (2003). *Stochastic Population Dynamics in Ecology and Conservation*. Oxford University Press, Oxford, England.

Leslie, P.H. & Gower, J.C. (1958). The properties of a stochastic model for two competing species. *Biometrika*, 45, 316–330.

Levine, J.M. & Hille Ris Lambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461, 254–257.

Lichstein, J.W., Dushoff, J., Levin, S.A. & Pacala, S.W. (2007). Intraspecific variation and species coexistence. *Am. Nat.*, 170, 807–818.

Melbourne, B.A. & Hastings, A. (2008). Extinction risk depends strongly on factors contributing to stochasticity. *Nature*, 454, 100–103.

Messier, J., McGill, B.J. & Lechowicz, M.J. (2010). How do traits vary across ecological scales? A case for trait-based ecology. *Ecol. Lett.*, 13, 838–848.

Pfennig, D.W. & Pfennig, K.S. (2012). *Evolution's Wedge: Competition and the Origins of Diversity*. University of California Press, Berkeley and Los Angeles, California, USA.

Roughgarden, J. (1972). Evolution of niche width. *Am. Nat.*, 106, 683–718.

Schreiber, S.J., Buerger, R. & Bolnick, D.I. (2011). The community effects of phenotypic and genetic variation within a predator population. *Ecology*, 92, 1582–1593.

Seabloom, E.W., Harpole, W.S., Reichman, O.J. & Tilman, D. (2003). Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proc. Natl Acad. Sci. USA*, 100, 13384–13389.

Siefert, A., Violle, C., Chalmandrier, L., Albert, C.H., Taudiere, A., Fajardo, A. *et al.* (2015). A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. *Ecol. Lett.*, 18, 1406–1419.

Slatkin, M. (1980). Ecological character displacement. *Ecology*, 61, 163–177.

Taper, M.L. & Case, T.J. (1985). Quantitative genetic models for the coevolution of character displacement. *Ecology*, 66, 355–371.

Tilman, D. (1982). *Resource Competition and Community Structure*. Princeton University Press, Princeton, New Jersey.

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *PNAS*, 101, 10854–10861.

Turelli, M. (1980). Niche overlap and invasion of competitors in random environments II. The effects of demographic stochasticity. In: *Biological Growth and Spread: Mathematical Theories and Applications*. (eds Jäger, W., Rost, H. & Tautu, P.). Springer-Verlag, Berlin Heidelberg, pp. 119–129.

Vasseur, D.A., Amarasekare, P., Rudolf, V.H.W. & Levine, J.M. (2011). Eco-evolutionary dynamics enable coexistence via neighbor-dependent selection. *Am. Nat.*, 178, E96–E109.

Vellend, M. (2006). The consequences of genetic diversity in competitive communities. *Ecology*, 87, 304–311.

Violle, C., Enquist, B.J., McGill, B.J., Jiang, L., Albert, C.H., Hulshof, C. *et al.* (2012). The return of the variance: intraspecific variability in community ecology. *Trends Ecol. Evol.*, 27, 244–252.

## SUPPORTING INFORMATION

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