



Intraspecific variation promotes coexistence under competition for essential resources

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Abstract

Intraspecific variation may be key to coexistence in diverse communities, with some even suggesting it is necessary for large numbers of competitors to coexist. However, theory provides little support for this argument, instead finding that intraspecific variation generally makes it more difficult for species to coexist. Here we present a model of competition where two species compete for two essential resources and individuals within populations vary in their ability to take up different resources. We found a range of cases where intraspecific variation expands the range of conditions under which coexistence can occur, which provides a mechanism that allows the ecologically neutral evolutionary stable strategy (ESS) to become ecologically stable. We demonstrate that this result relies on nonlinearity in the function that describes how traits map onto ecological function. A sigmoid mapping function is necessary in order to model essential resources because it allows for variation in an unbounded trait while maintaining biologically realistic boundaries on uptake rates, and differs from other kinds of nonlinearity, which only unidirectionally increase or decrease ecological function. The sigmoid function's nonlinearity spreads individuals unevenly along the growth function, which allows positive growth contributions from some individuals to compensate for growth losses from others, akin to source-sink dynamics, leading to coexistence. In this way, intraspecific trait variation is able to amplify niche differences, thereby strengthening coexistence. We discuss empirical systems beyond competition for essential resources in which piecewise functions (i.e., thresholds) are important.

Keywords Intraspecific trait variation · Individual variation · Competition · Coexistence · Resource competition · R^* model

Introduction

Intraspecific variation is ubiquitous and, while its role has long been appreciated by evolutionary biologists, there has only recently been an increase in its impact on ecological processes and functions (Bolnick et al. 2011). A focal point of this work has been the study of coexistence of competing species. While many empirical studies have found that intraspecific variation promotes coexistence between competitors (Lankau and Strauss 2007; Clark 2010; Hausch et al. 2018), most theoretical work shows that intraspecific variation makes coexistence more difficult to achieve, except in a few specific contexts (Lichstein et al. 2007; Hart et al. 2016;

Barabás and D'Andrea 2016; Uriarte and Menge 2018). In this paper, we utilize the essential resource competition framework first developed by León and Tumpson (1975) and popularized by Tilman (1980) to demonstrate that intraspecific variation can promote coexistence by allowing some individuals in the population to compensate for other individuals whose traits confer negative growth rates when traits map onto uptake rates through a nonlinear function.

Recent work describing intraspecific variation has stressed its significance in ecological processes (Kichenin et al. 2013; Forsman and Wennersten 2016), including competition and coexistence (Lankau and Strauss 2007; Lankau 2009; Clark et al. 2010; Ehlers et al. 2016; Hausch et al. 2018). Work on “intraspecific trait variation” (ITV) in competitive communities has typically focused on variation in quantitative functional traits related to resource use (Roughgarden 1972, 1974; Bolnick et al. 2003), for example, seed size in the diets of desert granivores (Brown and Lieberman 1973), although variability can occur in any trait. This ITV can have important effects on the ecology of communities independently

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of the effects of selection and eco-evolutionary feedbacks. In part, these effects stem from alterations in their constituent populations' abilities to exploit resources (e.g., niche expansion—Berg and Ellers 2010) and buffer environmental changes (Agashe 2009). In addition, when traits map onto an ecological effect via a nonlinear function, variation can strongly influence the ecological effect due to Jensen's inequality (Ruel and Ayres 1999). Fitness load, the decrease in average population fitness that can occur when traits vary around a peak in the fitness landscape, is a specific example of how trait variation can affect populations through nonlinear averaging (Bolnick 2001; Bolnick et al. 2011).

Most empirical evidence supports the idea that ITV makes it easier for competing species to coexist, and can increase both equalizing mechanisms (Fridley and Grime 2010) and stabilizing mechanisms (Lankau and Strauss 2007). Stabilizing mechanisms are broadly defined as those which increase the invasion growth rate of all species in a competitive community (Chesson 2000). Stabilizing mechanisms (e.g., niche differences) permit the coexistence of species whose average fitness differs. When combined with stabilizing mechanisms, equalizing mechanisms can reduce average fitness differences between competitors, leading to stable coexistence. Without stabilizing mechanisms, it can support unstable coexistence (Chesson 2000).

Long-term data on the individual growth rates of trees shows that random but ecologically important differences between individuals can allow species to coexist via high-dimensional niche partitioning (Clark 2010). Although the high dimensionality of traits in the system makes coupling ITV to species-level niche differentiation difficult (Chase and Myers 2011), it is possible that individual variation ensures that fitness differences among species are small—thus allowing weak stabilizing mechanisms or neutrality to maintain a high diversity of species. Based on these data, Clark (2010) suggests that this ITV is a necessary condition for coexistence among a large number of competing species. In less diverse experimental populations, genetic variation in allelopathic secondary compounds has been shown to create an intransitive competitive hierarchy between the various *Brassica nigra* genotypes and their heterospecific competitors, which leads to mutual invasibility and, thereby, coexistence (Lankau and Strauss 2007). Such experiments are challenging to conduct, because experimental manipulation of ITV while controlling for selection requires careful consideration. ITV has been shown to help coexistence in experimental populations of congeneric bean weevils by increasing the probability that some individuals can exploit a non-overlapping niche during invasion (Hausch et al. 2018). However, demonstrating ITV's importance as fuel during the initial stages of invasion and establishment does not lend support to its importance for coexistence at equilibrium where character displacement is expected to reduce niche

overlap. Unfortunately, it is nearly impossible to increase stabilizing mechanisms (i.e., niche differentiation) without also affecting fitness differences (Song et al. 2019). The key question is therefore best posed: When and how does ITV increase stabilizing mechanisms more rapidly than fitness differences?

Theoretical work has shown that this is indeed a difficult requirement to achieve (reviewed by Stump et al. 2022). Various theoretical approaches have been utilized to investigate the ecological effects of ITV on coexistence, including generalized Lotka-Volterra competition frameworks (Barabás and D'Andrea 2016; Hart et al. 2016; Uriarte and Menge 2018), competition between stage-structured and size-structured populations (Hartvig and Andersen 2013, Miller and Rudolph 2011), and zero-sum models of competition (Maynard et al. 2019), each other their own insights and limitations. These works differ markedly in many respects, but are consistent in their assumption that variation in some trait or character maps smoothly and continuously onto variation in an ecologically relevant parameter (e.g., a competition coefficient, Hart et al. 2016). It is possible for ITV to enhance coexistence if competitors have large niche differences and individuals interact as strongly with conspecifics as they do with heterospecifics. However, ITV tends to weaken intraspecific competition, making this scenario unlikely (Hart et al. 2016). Intraspecific trait variation can also promote coexistence between competitors that experience a specialist-generalist tradeoff (Begon and Wall 1987; Barabás and D'Andrea 2016) because making the dominant competitor a generalist by increasing ITV decreases niche overlap. Uriarte and Menge (2018) found that intraspecific variation can facilitate coexistence if competitors are habitat specialists and the inferior competitor specializes on a habitat with a lower carrying capacity such that competition is less severe. In general, these mechanisms rely on carefully balanced assumptions about ITV itself, making them difficult to apply generally.

The way that quantitative traits map onto ecological function is a key piece in understanding how ITV will affect competitive outcomes. This is because mapping functions dictate how variation in a trait will influence an individual's ecological role and, in turn, how that individual's ecological role will influence stabilizing mechanisms. For example, a snake's jaw morphology will determine the size of prey it can ingest, which, in turn, determines which species it will compete with for prey (Arnold 1983). Empirical evidence has shown that trait mapping functions can take on many different forms (e.g., Barbour et al. 2016). Furthermore, it is often the case that multiple traits control any one metric of function or performance in an individual. For example, roughly a dozen morphological and physiological traits, such as caudal fin size, white muscle volume, and number of vertebrae, can affect burst swimming speed in fishes

(Ghalambor et al. 2003). Here, we are not concerned with reviewing or synthesizing the current understanding of the forms of trait mapping functions. The more relevant question in the context of our study is: what might a trait mapping function need to look like in order for ITV to promote coexistence?

Variation within species is typically small relative to variation between species (Roughgarden 1974; Siefert et al. 2015; Rhoades et al. 2018; Des Roches et al. 2018), though there are exceptions (e.g., Burton et al. 2017). In addition, changes in traits between generations, as a result of selection, mutation, or drift, tend to be relatively small in magnitude. For these reasons, a trait mapping function that allows ITV to contribute positively to stabilizing mechanisms needs to ensure that small differences in traits produce disproportionately large differences in ecological function, thereby creating the opportunity to substantially decrease the intensity of interspecific competition relative to intraspecific competition via small trait differences. One way to achieve this is through Jensen's inequality. In the context of trait mapping functions, Jensen's inequality means that when the mapping function is nonlinear, the ecological function evaluated at an average trait value is not equal to the average ecological function across all values for a variable trait. The direction of this difference depends on the concavity of the nonlinear function. As a result, when traits map onto ecological function via a nonlinear function, variation in the trait can have large effects on the ecological function (Ruel and Ayres 1999). Jensen's inequality has proven to be important in ecology due to the nonlinear nature of many ecological properties (Denny 2017). One mechanism by which nonlinear effects can strengthen coexistence is through relative nonlinearity, which can occur when competitors have different nonlinear responses to competition and the intensity of competition fluctuates temporally or spatially (Chesson 1994). Relative nonlinearity has been shown to promote coexistence in models where resources fluctuate due to endogenous (Armstrong and McGehee 1980) and exogenous (Hsu 1980) factors by providing greater fitness benefits to low abundance species (e.g., invaders) relative to high abundance species (e.g., residents).

Here we use a model of competition between two consumers, in which exploitative competition occurs through shared use of two non-living essential resources (León and Tumpson 1975; Fox and Vasseur 2008). This model is a staple in studies of competition among aquatic autotrophs (e.g., Sommer 1989; Grover 1991; Fujimoto et al. 1997), where abiotic nutrients such as phosphate and nitrite are essential (excess phosphate cannot compensate for a lack of nitrite and vice versa; Rhee 1978). When resources are essential, growth can only be achieved when resources are provided in a fixed ratio (generally assumed to match the organism's stoichiometry). If the intake of resources does not match this

ratio, one resource will be limiting for growth (Droop 1968). However, as resource densities or consumer traits such as uptake preference change, there can be a shift to limitation by the alternative resource. To our knowledge, this is the first model to explore the effects of ITV on competition for essential resources, which represents a biologically plausible scenario in which thresholds can have important effects on ecological function and coexistence. We demonstrate that non-heritable ITV expands the range of conditions under which coexistence is possible. We conclude by discussing the properties of the trait mapping function that allow ITV to promote coexistence and some systems in which functions of this form might be found.

Methods

The base model

We model resource competition among two consumers which differ in their stoichiometric requirements for growth using the formalism described in León and Tumpson (1975). The system is described by the following set of ordinary differential equations:

$$\frac{dR_i}{dt} = D(S_i - R_i) - \sum_j \frac{N_j g_j(R_1, R_2)}{y_{ij}} \quad (1)$$

$$\frac{dN_j}{dt} = N_j(g_j(R_1, R_2) - d_j) \quad (2)$$

where $i, j \in \{1, 2\}$. The first term of Eq. 1 describes the dynamics of resources in the absence of consumers, where R_i is the abundance of the i th resource, S_i is the inflow concentration, and D is the flow rate. The second term describes resource uptake by consumers, where N_j is the abundance of the j th consumer, $g_j(R_1, R_2)$ is the effect of resource consumption, and y_{ij} is a yield coefficient describing the units of consumer j that can be produced with one unit of resource i . For Eq. 2, the rate of change in consumer abundance N_j is determined by the effect of resource consumption $g_j(R_1, R_2)$ minus a constant background death rate of d_j .

In the model without variation (Droop 1968; León and Tumpson 1975; Tilman 1982, 1988; Fox and Vasseur 2008), the effect of resource consumption $g_j(R_1, R_2)$ is determined by whichever resource is limiting and calculated as the lesser of the yield from intake of R_1 and yield from intake of R_2 :

$$g_j(R_1, R_2) = \min[y_{1j}u_jR_1, y_{2j}(1 - u_j)R_2] \quad (3)$$

where u_j is the uptake preference for resource 1 (R_1) and the uptake of R_2 , $(1 - u_j)$, is subject to a strict tradeoff. Each consumer has a different fixed stoichiometric ratio (y_{1j}/y_{2j}),

which ensures that species rely differently on the essential resources. Consumers maintain their stoichiometry by taking up resources in a fixed ratio according to the tradeoff between uptake preference for R_1 and R_2 . We assume that excess resources are excreted in a non-usable form at no cost to the consumer (Vasseur and Fox 2011).

The trait mapping function

We include ITV in consumer uptake preferences by assuming that individuals express differences in a quantitative trait ϕ that determines their uptake rates u_j , according to the sigmoid function:

$$u_j(\phi) = 0.5 + \pi^{-1} \text{ArcTan}(h\phi) \tag{4}$$

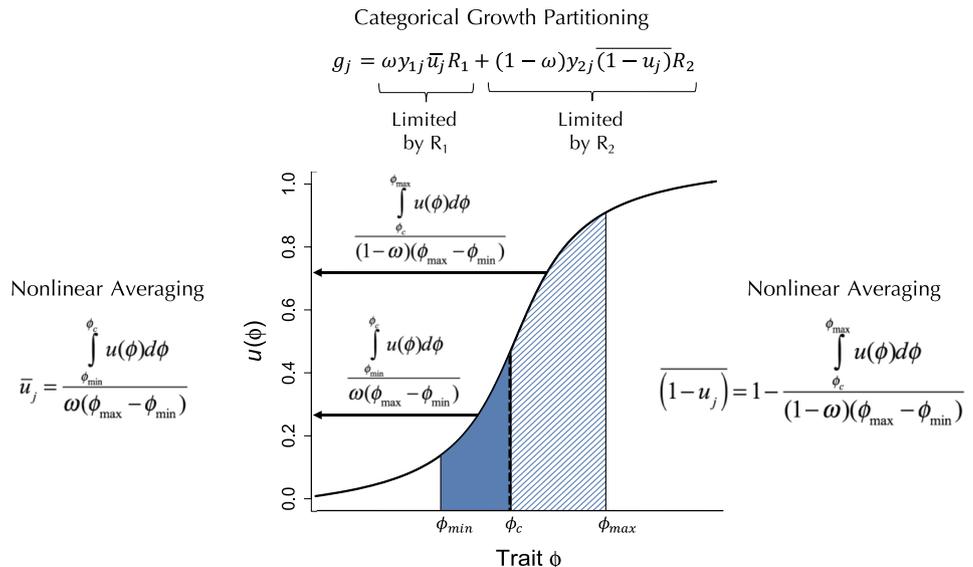
This sigmoid function, which provides a clear mapping of traits onto ecological function, is what generates the potential for ITV to promote coexistence. There are two properties of sigmoid functions that make them an appealing option for exploring the potential for ITV to promote coexistence. First, it is a nonlinear function that is concave up below the inflection point and concave down above it (Fig. 1). As previously stated, one way to ensure that small differences in traits have sufficiently large enough effects on interspecific niche differences to promote coexistence is through Jensen’s inequality, which requires that traits map onto ecological function via a nonlinear function (Ruel and Ayres 1999). The concavity of the nonlinearity determines the direction of this effect. For concave downward functions, the nonlinear average ecological function is less than what is expected based on the average trait value, while for concave upward functions the nonlinear average will be greater than expected based on the average trait. This generates a useful feature of sigmoid

functions: Adding trait variation around the inflection point means that average ecological function on either side will become increasingly different, thereby increasing niche differences and contributing to stabilizing mechanisms.

Second, sigmoid function allows for unconstrained trait variation while enforcing appropriate boundaries on the response. In the case of our model, uptake preference for resource R_1 represents the proportion of an individual’s diet that is composed of R_1 where the remainder of the diet is composed of R_2 . As such, uptake preference must be bound between 0 and 1. However, there are no such constraints on the quantitative trait, ϕ , which maps onto uptake preference, meaning ϕ is free to vary between $-\infty$ and ∞ . The sigmoid function allows us to explore an unbounded trait space (i.e., ϕ has the range $(-\infty, \infty)$) while constraining u_j to the plausible range (0,1). The constant h determines the steepness of the tradeoff and therefore shapes how variation in ϕ translates into differences in u_j . Without loss of generality, we assume $h = 1$ and explore the effect of variation in ϕ . All of the properties discussed here are not exclusive to the particular sigmoid function used here, and our results are qualitatively the same for other sigmoid functions (Appendix 6. Other functional forms).

We focus on variation in uptake rate for two reasons. First, uptake rate has been empirically shown to vary within populations (Hughes et al. 2009; Abbott et al. 2018; Brandenburg et al. 2018), while other traits in the model, such as resource requirement ratios, are typically fixed within taxa (Rhee and Gotham 1980; Boersma and Elser 2006; Behmer and Joern 2008; Götlich and Oschlies 2012; Atkinson et al. 2020). Second, previous theoretical work (Fox and Vasseur 2008) has provided a biologically intuitive, well-behaved function that maps traits onto uptake rates (Eq. 4). Equation 4 is a continuous

Fig. 1 We categorically partition the population into the fraction limited by R_1 (ω ; solid region) and the fraction limited by R_2 ($1 - \omega$; hatched region); these are separated by the trait value at which an individual is co-limited (ϕ_c). Within each group, we calculate the nonlinear average uptake rate given the trait range and the function $u(\phi)$ which describes a sigmoid mapping of traits onto uptake



approximation of the partial derivative of consumer per capita growth rates with respect to uptake rates. Other work has shown that larger values of h and the use of other sigmoid functions do not change competitive outcomes (Fox and Vasseur 2008). Equations 1 and 3 can be used to accurately predict empirical competitive outcomes for populations that compete for essential resources without (Grover 1991) and with ITV (Appendix 5. Competition between *Asterionella formosa* and *Cyclotella meneghiniana*). There is no biological motivation for constraining other parameters, like yield coefficients y_{ij} , which would instead continually evolve higher yields. More biological motivation is required before variation in other parameters like y_{ij} can be reasonably modeled.

The modeling details

The colimitation point for a single consumer is the uptake rate which satisfies the equivalence of both terms inside the minimization function in Eq. 3:

$$u_c = \frac{R_2 y_{2j}}{R_1 y_{1j} + R_2 y_{2j}} \tag{5}$$

(Fox and Vasseur 2008). Rearrangement of Eq. 5 then gives the value of the trait which coincides with colimitation, ϕ_c as:

$$\phi_c = \text{Cot} \left(\frac{\pi R_1 y_{1j}}{R_1 y_{1j} + R_2 y_{2j}} \right) \tag{6}$$

In the presence of ITV, it is possible that some individuals are limited by R_1 while others are limited by R_2 . We achieve this distinction by introducing the parameter ω_j , along with a pair of nonlinear averages into a new equation for the effect of resource consumption:

$$g_j(R_1, R_2) = \omega_j y_{1j} \bar{u}_j R_1 + (1 - \omega_j) y_{2j} \overline{(1 - u_j)} R_2 \tag{7}$$

where ω_j is the fraction of the population that is limited by R_1 and \bar{u}_j and $\overline{(1 - u_j)}$ represent the average uptake rates exhibited by each fraction of the population (Fig. 1).

We determine the weighting parameter ω_j by calculating the fraction of individuals of population j whose trait value causes them to be limited by R_1 , given the densities of R_1 and R_2 . For mathematical tractability, we assume that ITV in a trait ϕ is described by a uniform distribution with a maximum ϕ_{\max} and minimum ϕ_{\min} ; however, our results are robust to other trait distributions (Appendix 4. Other trait distributions). We further assume that this distribution is continually recreated via phenotypic variation (i.e., that variation is not heritable). In this instance, the

fraction of the population that falls below the colimitation threshold, and is therefore limited by R_1 , is:

$$\omega_j = \begin{cases} 1 & \text{if } \phi_c < \phi_{\min} \\ \frac{\text{Cot} \left(\frac{\pi R_1 y_{1j}}{R_1 y_{1j} + R_2 y_{2j}} \right) - \phi_{\min}}{\phi_{\max} - \phi_{\min}} & \text{if } \phi_{\min} < \phi_c < \phi_{\max} \\ 0 & \text{if } \phi_c > \phi_{\max} \end{cases} \tag{8}$$

We determine the average uptake rates for each population fraction as:

$$\bar{u}_j = \omega_j^{-1} (\phi_{\max} - \phi_{\min})^{-1} \int_{\phi_{\min}}^{\phi_{\min} + \omega_j (\phi_{\max} - \phi_{\min})} u(\phi) d\phi \tag{9}$$

$$\overline{(1 - u_j)} = 1 - (1 - \omega_j)^{-1} (\phi_{\max} - \phi_{\min})^{-1} \int_{\phi_{\max}}^{\phi_{\max} - (1 - \omega_j) (\phi_{\max} - \phi_{\min})} u(\phi) d\phi \tag{10}$$

In order to contrast the model with and without trait variation, and to look at behavior across the range of possible uptake rates, we use the following equations to determine the minimum and maximum trait values in the population:

$$\phi_{\min} = -\text{Tan} \left(\frac{\pi}{2 - \pi u_{\text{mid}}} \right) - \delta \tag{11}$$

$$\phi_{\max} = -\text{Tan} \left(\frac{\pi}{2 - \pi u_{\text{mid}}} \right) + \delta \tag{12}$$

where u_{mid} represents the uptake rate at the midpoint of the trait range and δ is half of the range. In this way, we create u_1, u_2 combinations with expected coexistence outcomes based on Fox and Vasseur (2008), and introduce different amounts of variation in one or both consumers to test the effect of variation on those outcomes. Importantly, the models with and without variation are nested because Eq. 7 converges upon Eq. 3 as the extent of ITV approaches 0 (see Appendix 1. Model details).

Given the assumptions above, Eq. 7 can be used to analytically solve the invasion growth rate when a resident consumer does not have ITV (see Appendix 1. Invasion analyses). We leverage this solution, and previous work on this framework (Fox and Vasseur 2008; León and Tumpson 1975) to demonstrate how ITV in an invader alters the potential for invasion across the full range of u_1, u_2 parameter space. We complement the analytical solutions with numerical simulations to determine the outcome of competition (using a pair-wise invasion approach) and extend this to a scenario where just the resident and both the invader and resident have ITV (Appendix 2. Resident variation).

Results

Our model framework allows us to assess coexistence most effectively using an invasion analysis, where one consumer’s (invader) growth rate is measured in an equilibrium community of its competitor (resident). Figure 2b shows the expanded domain of coexistence when an invader has an optimal amount of ITV (i.e., the amount of ITV that maximizes population growth for a given u_1, u_2 combination; see Eq. 14 and Appendix 1. Invasion analyses). When the invader has an optimal amount of ITV, conditions where the resident would otherwise outcompete the invader shift to form a larger contiguous coexistence

region (Fig. 2b) relative to the case without ITV (Fig. 2a). The range of conditions supporting coexistence is also expanded when both the invader and resident have a fixed amount of ITV ($\delta_1 = \delta_2 = 1$) and when the resident has a fixed amount of variation ($\delta_2 = 1$), although the expanded coexistence region is shifted and expanded slightly to accommodate the effects of fixed variation on the resident community at equilibrium in the latter case (Appendix 2. Resident variation, Fig. 5).

The aforementioned shift in resource limitation plays a supporting role in driving these patterns. Competition for essential resources results in stable coexistence when consumers (i) are limited by different resources and (ii)

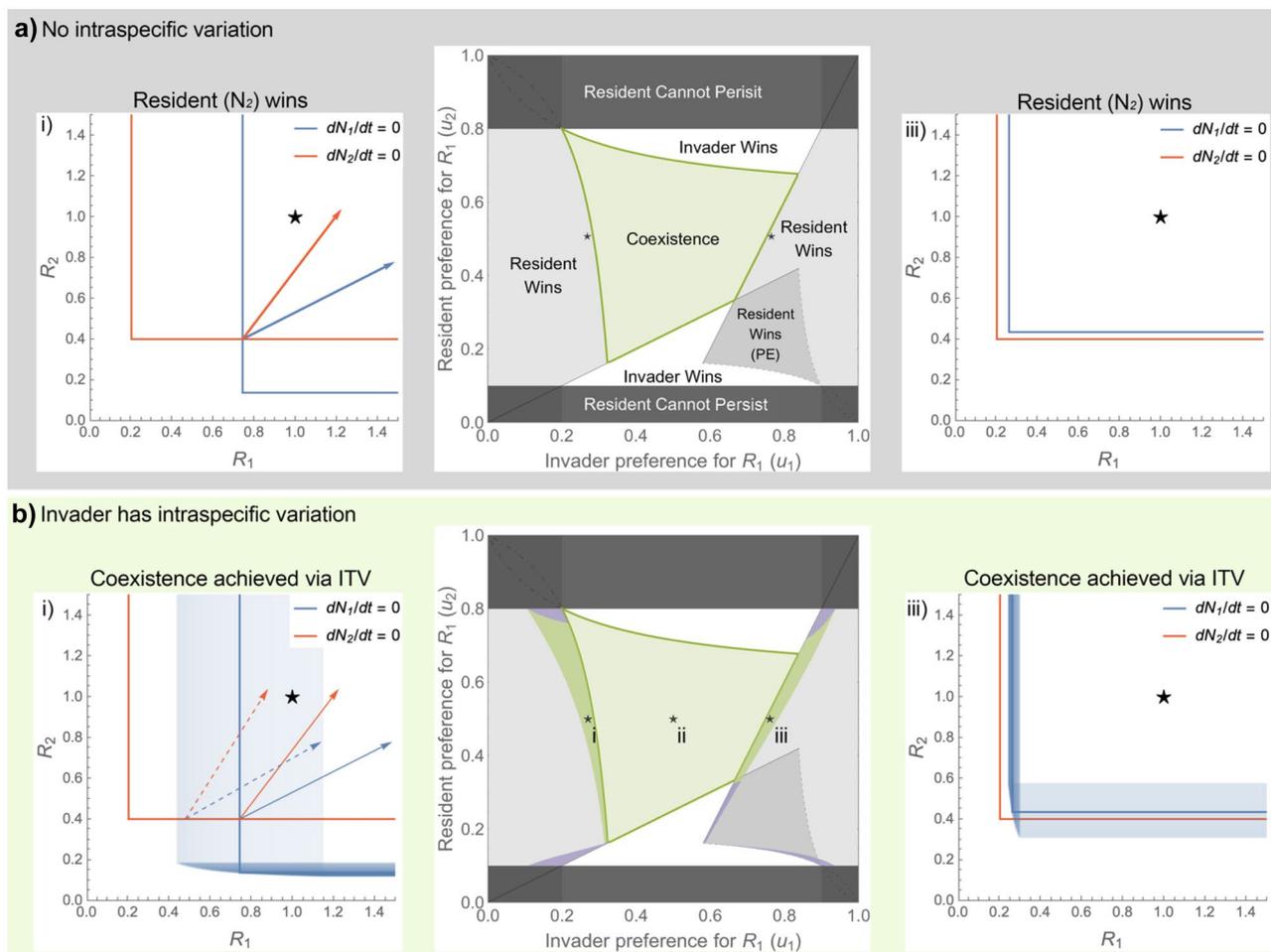


Fig. 2 The outcome of competition across the domain of uptake preferences (u_{mid}) for resident and invading consumers **a** with no ITV and **b** when the invader has an optimal amount of ITV (that which maximizes its growth rate). The lines dividing outcome domains are adapted from Fox and Vasseur (2008) for the case without ITV and are shown in all panels for contrast. Adding ITV to the invader **b** increases the domain of coexistence (darker green) and the domain where the invader excludes the resident (violet). In panel **b**, the extended regions show the outcome of competition for the extent of ITV (δ) which maximized the invasion growth rate (see Appendix 3.

Sufficient amounts of intraspecific variation for details on how much variation is necessary). Also shown are zero-net growth isoclines (lines), resource supply points (stars) and consumption vectors are shown for parameter sets (i) where variation ($\delta=0.5$) in uptake rate alters the consumption vector of the blue species (N_1) such that stable coexistence occurs and (iii) where variation ($\delta=0.5$) in uptake rate u_j alters the zero-net growth isocline of the invader (blue) such that coexistence occurs where it would not be possible without variation. Additional parameter values are given by $S_1=S_2=1, y_{11}=y_{22}=0.5, y_{12}=y_{21}=1, D=d=0.1$

consume a larger fraction of the resource that is most limiting for their growth (León and Tumpson 1975). These conditions together generate the four boundaries defining the diamond-shaped coexistence region in Fig. 2a (where no ITV is incorporated). Outside those boundaries, coexistence is not possible when all individuals are identical. However, in the presence of ITV, some individuals can have uptake rates (u) that span the shift in resource limitation and place them inside the coexistence region (while the mean remains outside).

We visualize this mechanism using an extension of classic graphical technique (Tilman 1980), whereby a continuum of individual strategies can be plotted as a set of zero-net-growth isoclines (ZNGIs) that follow a boundary (Meszéna and Metz 1999) or geometric envelope (Koffel et al. 2016) along axes of resource densities (Fig. 2). Here the coexistence conditions are realized by the existence of an intersection between consumer ZNGIs and a correct orientation of consumption vectors with respect to the resource supply point. It is not sufficient to merely consider the average values for R_1^* and R_2^* . Instead, we consider the joint distributions of R_1^* and R_2^* , which more accurately reflects interactions between individuals whose traits are bound by a strict tradeoff (Eqs. 3 and 4). Intraspecific variation has effects on both the ZNGIs and, by association, on the consumption vectors (Fig. 2b). However, which effect drives coexistence depends on the location in parameter space. Along the curved persistence boundaries (left and top boundaries in Fig. 1), the condition requiring that consumers have greater impact on the resource limiting their growth is violated (Fig. 2a). Here, the distribution of consumption vectors generated by ITV leads to some individuals that achieve this requirement and some that do not (Fig. 2b). Along the linear coexistence boundaries (right and bottom boundaries in Fig. 1), the condition requiring an intersection among the ZNGIs is violated (Fig. 2b). In this case, the distribution of ZNGIs generated by ITV leads again to some individuals with traits that achieve the required intersection and some that do not (Fig. 2b).

Generating the appropriate conditions for coexistence in a subset of individuals is not sufficient for changing the outcome of coexistence unless that subset's rate of population growth is sufficient to compensate for losses in the remaining fraction. Given that we assume a symmetric distribution of ITV, if the mean trait lies outside the coexistence region, so too will more than half of the population. Thus, those individuals whose traits would allow for a positive invasion growth rate and coexistence must have a disproportionate positive effect on the population growth rate. Hart et al. (2016) demonstrated that nonlinear mapping of parameters onto per capita growth rates is one mechanism by which ITV can affect coexistence. This is achieved through Jensen's inequality, generated by the nonlinearity of the

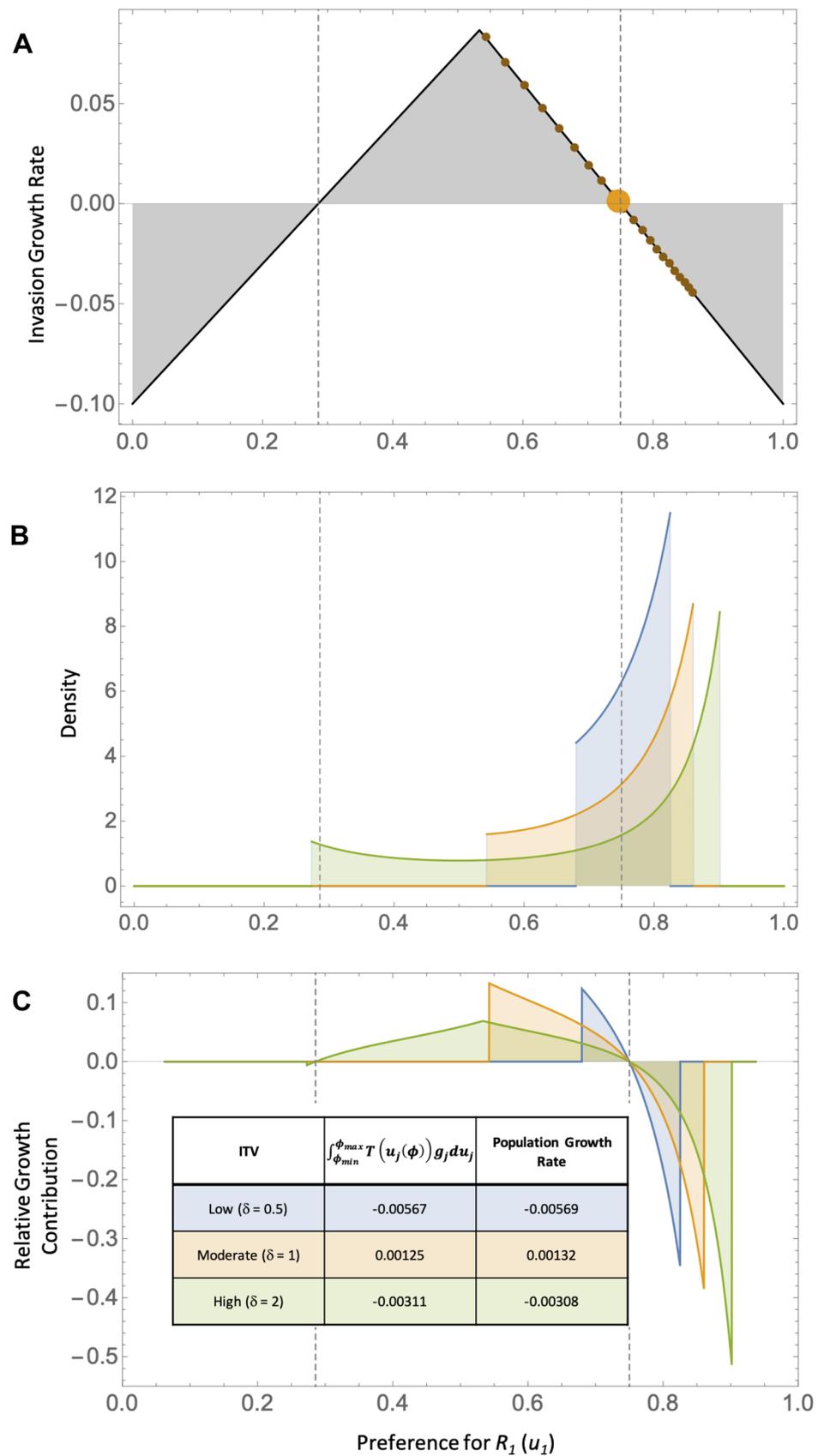
trait mapping function, which allows a subset of individuals with positive growth rates to have a disproportionately large effect on the total population growth rate. Nonlinear mapping of traits onto parameters is a second mechanism by which ITV can affect coexistence (Hart et al. 2016). First, note that resource uptake (u_1) maps linearly onto invasion growth rates (Fig. 3a). If a population's average u_1 falls outside of the coexistence region and variation spreads individuals evenly in both directions along the growth function, it is not possible for ITV to promote coexistence because crossing the peak of this function will only lead to lower average population growth rates. However, because of the nonlinearity of the sigmoid trait mapping function, ITV does not spread individuals evenly in both directions. Instead, the distribution spreads more rapidly into the middle of the function and slowly at the extremes (Fig. 3a). A transformed distribution T represents the distribution of an expression $expr$ given a distribution $dist$ of a random variable x . We used the transformed distribution T of $u_j(\phi)$ (Eq. 4), assuming ϕ is uniformly distributed, to show that individuals within the coexistence region are less densely packed than those at extreme u_1 values outside of the coexistence region (Fig. 3b). However, those individuals within the coexistence region can contribute enough to the total population growth rate to allow for coexistence at an intermediate amount of ITV (Fig. 3c). Whether or not these individuals contribute enough to the total population growth rate to compensate for individuals outside of the coexistence region can be determined by calculating:

$$\int_{\phi_{\min}}^{\phi_{\max}} T(u_j(\phi))g_j(R_1, R_2)du_j \quad (13)$$

Note that if ITV becomes too large, this value becomes negative again and coexistence is no longer possible (Fig. 3c).

In our model, ITV does not promote coexistence simply by causing the expected value of u_1 to fall within the coexistence region. For example, incorporating a large amount of ITV resulted in a negative invasion growth rate even when $E[u_j(\phi)]$ falls within the coexistence region for cases where u_{mid} was within the coexistence region and just outside of the coexistence region (Fig. 4). This is, again, because nonlinearity in the sigmoid function does not spread individuals evenly across the uptake rate parameter space (Fig. 3a) such that $E[u_j(\phi)]$ is not representative of the conditions that most individuals in the population are experiencing. It is also interesting to note that there are cases where a population's u_i distribution can expand outside of both the coexistence and persistence boundaries and still maintain a positive invasion growth rate (e.g., case ii, Fig. 4). Consumer and resource densities following invasion show that coexistence is able to occur because as N_1 invades, it reduces the abundance of R_1 (the resource that is most limiting to

Fig. 3 **a** The relationship between the invasion growth rate and the invader’s resource preference (u_1). This relationship is piecewise continuous. When the invader population has ITV in the trait ϕ , individuals spread along this curve according to the mapping of the trait onto resource preference $u_1(\phi)$ (orange dots). The large dark orange point is $E[u_j(\phi)]$ given $u_{mid} = 0.77$. **b** The transformed distribution of u_1 for three values of ITV $\delta = \{0.5(\text{blue}), 1(\text{orange}), 2(\text{green})\}$ for $u_{mid} = 0.77$. **c** The contribution to population growth across the transformed distribution of u_1 values with corresponding values of the mean invasion growth rate $\int_{\phi_{min}}^{\phi_{max}} T(u_j(\phi))g_j du_j$



its own growth) but not R_2 (the resource most limiting to its competitor's growth) (Fig. 4). This fulfills both conditions necessary for stable coexistence under competition for essential resources: (i) that competitors are limited by different resources and (ii) that each consumes a larger fraction of the resource that is most limiting for their growth (León and Tumpson 1975).

Discussion

Previous work linking ITV to coexistence has produced conflicting results (Stump et al. 2022), with some finding that ITV is beneficial while others find that it is detrimental to coexistence. Those that do find support for the benefits of ITV for coexistence are typically constrained to cases where there are strict assumptions about the form of ITV itself. Here we ask which features of a trait mapping function would allow ITV to be beneficial. We found that nonlinearity is critical for determining how ITV will affect coexistence. Nonlinearity allows for the growth of individuals with beneficial traits to compensate for the losses generated by the rest of the population. The piecewise shift in resource limitation (Fig. 3a) is a double-edged sword in the sense that it can reduce niche overlap by allowing individuals with very similar trait values to have a vastly different ecological role, but it also places an upper limit on the amount of ITV that can be beneficial. The overall effect allows ITV to strengthen coexistence by amplifying resource partitioning between competitors.

The sigmoidal trait mapping function (Fig. 1, Eq. 4) is critical to the observed outcomes in our model because of two specific components of the function. First, the piecewise shift in resource limitation (i.e., individuals are either limited by R_1 or R_2 depending on a continuous trait value) allows individuals with similar trait values to be functionally different. These types of systems, in which smooth changes in a variable of interest produce abrupt changes in behavior when a threshold is traversed, are commonly known as piecewise smooth systems (PWS) and are used to describe the behavior of many biological systems (May 1977; Dercole et al. 2007). Although we draw our conclusions from a model of competition for essential resources, this mechanism could easily be generalized to other systems of competition, including systems where prey switching occurs, in populations that undergo shifts in life history traits, and in size-structured populations. For example, damselfly naiads show frequency-dependent preferences for sessile *Simocephalus* or motile *Daphnia* prey. Naiads utilize two different foraging behaviors—walking and ambush—which influence their encounter rate of *Simocephalus* and *Daphnia* (Akre and Johnson 1979). Since naiads can use either foraging behavior, the proportion of time spent walking versus ambushing prey is a continuous behavioral

trait that varies between individuals. Difference in this continuous trait alters an individual's encounter rate with prey species and drives the observed prey switching. In quantitative genetic threshold models, the underlying continuous trait is sometimes called the “liability” (Roff et al. 1997), which maps onto a response with a threshold, above which individuals have one trait and below a different trait. Liability traits in salmonid fishes, such as body size, influence behavior in migratory tactics (smolting versus freshwater residency, Dodson et al. 2013), which can strongly affect dietary preferences (Rikardsen et al. 2000) and competitive interactions. Dietary overlap in three-spined sticklebacks decreases when individuals differ in gape width (Bolnick and Paull 2009). In this system, ITV in gape width could allow individuals on either side of some threshold gape width to access prey items that heterospecific and conspecific competitors cannot. Interestingly, a continuous trait like gape width could have multiple thresholds (ontogenetic shifts) at which individuals would be able to access novel prey, which creates even more opportunity for niche differentiation to promote coexistence. These kinds of shifts in ecological function along a continuous range of trait variation have the potential to contribute to stabilizing mechanisms in the same way ITV does in our model.

The shift also creates a downturn in the u_1 -growth rate mapping function (Fig. 3) that generates an upper limit on the positive effects that ITV can have on coexistence. In other words, we found that an intermediate amount of ITV maximizes invasion growth rates (Fig. 4). Without any such limit, ITV can increase without bounds, which would diminish niche differences which, without the assumption that ITV is much greater in the inferior competitor, would favor the superior competitor (Hart et al. 2016). Others overcome this by assuming that population variance trades off with mean performance (Lichstein et al. 2007). However, this assumption is restrictive and it is challenging to find mean–variance tradeoffs in empirical systems (Courbaud et al. 2012). In contrast, biological systems that show shifts in function are fairly common in nature and may provide one alternative mechanism that limits the fitness advantages conferred by ITV. Future work should explore the factors that limit the extent and benefits of ITV and how this might contribute to our understanding of when ITV will and will not promote coexistence between competitors.

Second, the nonlinearity of the sigmoid function, and more specifically the way that concavity changes across the nonlinearity, means that a small difference in trait values has a disproportionately large effect on the ecological function of individuals via Jensen's inequality. Jensen's inequality is common in many biological systems, where variability is often the rule rather than the exception, and has proven to be useful in explaining many biological phenomena (Denny 2017). The difference in concavity above (concave downward) and below (concave upward) the inflection point in the sigmoid function

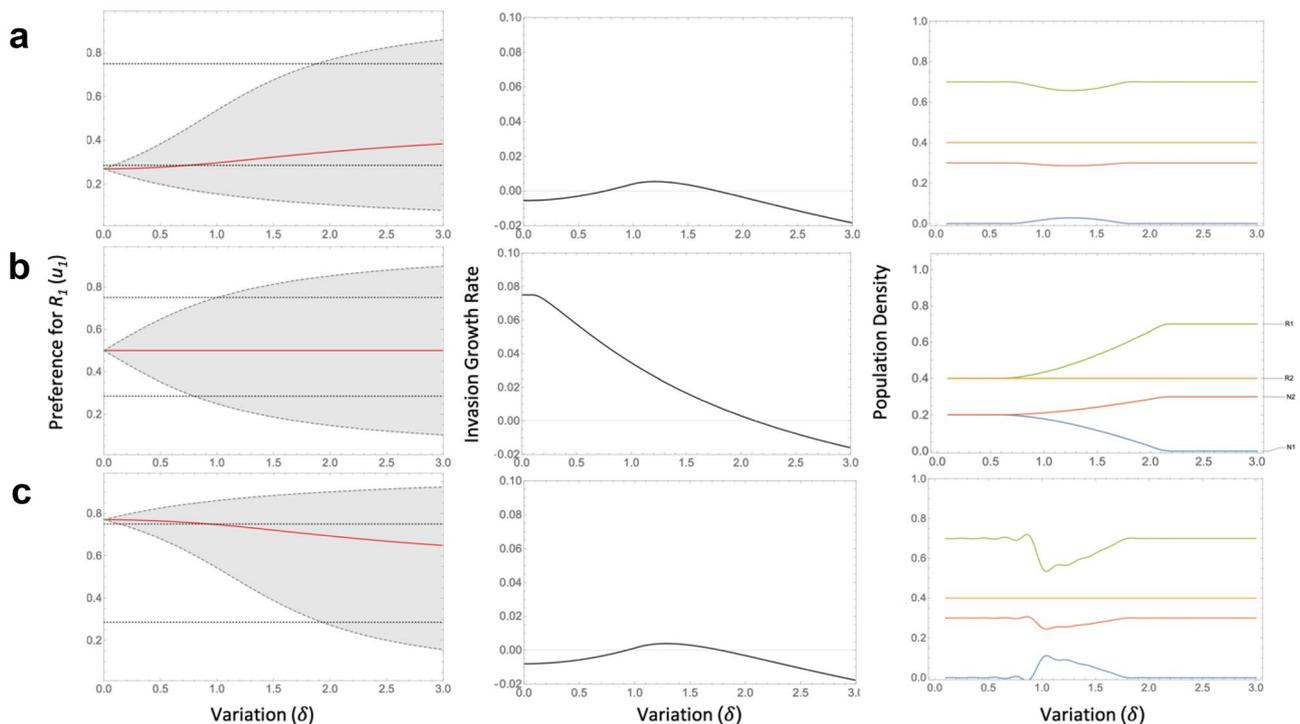


Fig. 4 The maximum and minimum preference for R_1 (u_1) (black dotted lines) and expected value (red lines), corresponding growth rates for invaders (solid black lines), and post-invasion equilibrium population densities (N_1 =blue, N_2 =red, R_1 =green, R_2 =yellow) as a

function of invader variation (δ_1) for **a** $u_{1,mid}$ outside of the persistence boundary ($=0.27$), **b** $u_{1,mid}$ inside the coexistence region ($=0.5$), and **c** $u_{1,mid}$ outside of the coexistence boundary ($=0.77$). For all cases, $u_2=0.5$ and we assume the resident has no ITV

(Fig. 1) creates a different kind of nonlinearity than what has been found to promote coexistence in other models where nonlinearity has a unidirectional effect that either increases or decreases the response (e.g., Hart et al. 2016; Uriarte and Menge 2018). This form of nonlinearity spreads individuals unevenly across the uptake rate parameter space (Fig. 3a) and highlights the necessity of carefully considering how to incorporate ITV into ecological frameworks. Consider a case where ITV is extremely large such that the majority of individuals in the population have an uptake rate of nearly 0 or 1 (e.g., Fig. 8). Although the $E[u_j(\phi)]$ and average ZNGIs will be within the coexistence region, the majority of individuals will not be able to satisfy their stoichiometric requirements, resulting in negative population growth.

Another key component of our model is that a proportion of individuals in the population must grow fast enough to compensate for the proportion of individuals that are limited by the same resource as their competitor (Eq. 10, Fig. 4). Broadly, this can be seen as a source-sink problem where the growth of the proportion of the population that is differentially resource limited (the “source”) can compensate for the growth of the proportion that is limited by the same resource as the heterospecific competitor (the “sink”). It is possible for emigration from a source population with positive growth rates to compensate for negative growth in

a sink (i.e., “the rescue effect” Brown and Kodric-Brown 1977, Pulliam 1988, Gyllenberg and Hanski 1997), the genetic or developmental equivalent of which is phenotypic subsidy (Doebeli 1996, Bolnick et al. 2011). When populations or phenotypes vary in fitness but have sufficient rates of exchange between different subgroups, these processes can alter ecological interactions by decoupling a population or phenotype’s growth rate from its fitness (Bolnick et al. 2011). Meta-community models have shown that competitively inferior populations can be rescued from competitive exclusion when immigration from a competitively dominant source population is sufficiently high (Moquet and Loreau 2003). Similar ideas have been proposed in models of structured populations, where one stage acts as a “refuge” by overcompensating for high mortality in another stage (Miller and Rudolph 2011). Further support comes from empirical work on genetic load in plant populations. It is often assumed that high genetic load is deleterious and should, therefore, be “purged” from the population by selection. However, meta-analyses have found no evidence of purging in plant populations and instead find that populations maintain suboptimal trait variation (Byers and Waller 1999; Byers 2005) in spite of the fact that theory suggests selection should eliminate such variation (Falconer and Mackay 1996).

Relative nonlinearity is a fluctuation-based coexistence mechanism that occurs when (1) populations have different nonlinear responses to competition and (2) competition intensity fluctuates spatially or temporally (Chesson 1994). Fluctuations can occur as a result of resource cycles that are endogenous to the system (Armstrong and McGehee 1980), exogenous fluctuations in resource supply (Hsu 1980), and other environmental fluctuations that lead to variation in competition intensity or resource availability (Descamps-Julien and Gonzalez 2005). Intraspecific trait variation is another mechanism that allows the intensity of competition to fluctuate, since individuals of one population will experience different degrees of competition intensity based on their own traits and those of individuals in the competitor population. This is consistent with our intuition that species traits, combined with their biotic interactions, determine their realized niche and functional role within a community (McGill et al. 2006). We emphasize that the ways in which traits map onto ecological function are a key component to predicting persistence and coexistence. More work is needed in order to understand the many different forms of these functions (e.g., Barbour et al. 2016).

The functional forms and parameter sets we chose allow us to place our model in the context of previous work (Fox and Vasseur 2008). Competition for essential resources is common in nature among plants and phytoplankton (Salisbury and Ross 1992; Rhee 1978) and is theoretically well studied (León and Tumpson 1975; Tilman 1977; Abrams 1987; Huisman and Weissing 2001; Fox and Vasseur 2008). However, different parameter sets or functional forms might result in a larger effect size. Heterotrophs are more likely to compete for nutritionally complementary resources which would show less abrupt threshold behavior, and models such as this have been adapted to include these kinds of utilization functions (Vasseur and Fox 2011). The parameter set we chose assumes that competition is symmetric in that the internal stoichiometry of each species (y_{ij}) is symmetric. However, asymmetric competition is common in plants and can alter competitive outcomes (Weiner 1990). Similarly, we assume that trait variation is symmetric and follows a uniform distribution. Though it does not qualitatively change our results (see Appendix 4. Other trait distributions), different trait distributions have the potential to increase the observed effect size. Finally, because the model presented here is deterministic, it does not allow for any effect of ITV via demographic stochasticity. However, it is important to note that others have demonstrated that demographic stochasticity is another mechanism by which ITV can affect coexistence (Hart et al. 2016).

To isolate the ecological effects of ITV, the trait distributions in our model are externally imposed and held constant while ecological interactions occur. We assume that the distribution is maintained regardless of population size,

and the effects of selection. An eco-evolutionary analysis of this model previously showed that the evolutionary stable strategy (ESS) exists at the intersection of the linear boundaries of the coexistence region (Fox and Vasseur 2008). This point is directly adjacent to parameter regions where ITV can override competitive exclusion and yield coexistence. Thus, competitors which have evolved in sympatry may benefit from a “coexistence buffer” that is provided by ITV if a perturbation were to push the system outside the coexistence region. By expanding the coexistence region, ITV provides a mechanism by which the ecologically neutral ESS can become ecologically stable. Future work is needed to provide insight into how selection on the distribution of traits in the population is (i) shaped by ecological and evolutionary forces and (ii) changes the impact of ITV on coexistence.

We utilize the standard practice of assessing competitive outcomes using the invasion criterion, but recognize that this is precisely the scenario under which the assumption of trait variation makes the least sense (Tsutsui et al. 2000; Sakai et al. 2001; Allendorf and Lundquist 2003). Our intent is not to imply that an invading individual must possess an impossible diversity of traits in order to be successful; rather, we use this technique to measure the change in strength of coexistence mechanisms in the presence of ITV. Others have demonstrated that trait variation can be important during invasion because it increases the probability that some individual will have traits that promote growth (Hausch et al. 2018). Under such a scenario, selection acts as a filter for traits, but ITV itself does not have an effect, *sensu stricto*, on the invasion growth rate. Our work focuses on the ecological mechanisms through which ITV alters competitive outcomes, while previous work has focused on the evolutionary effects of ITV as the fuel on which selection acts.

Intraspecific variation has an unquestionably important role in ecological processes, but whether it helps or hinders coexistence remains an open question. Here, we present a theoretical model to show that intraspecific variation promotes coexistence of competitors for essential nutrients by allowing a proportion of the population to respond to its environment differently than competitors and to compensate for the growth losses of the rest of the population. We also find that intraspecific variation can allow invaders to displace residents under conditions where they would otherwise not be able to invade. Our approach not only shows how intraspecific variation can promote coexistence between species that compete for essential rather than substitutable resources, but also provides insight into the mechanisms that allow and limit intraspecific variation’s ability to promote coexistence.

Appendix 1. Invasion analyses

To determine the effect of ITV on coexistence, analytically solve the invasion growth rate in a community without ITV (Klausmeier et al. 2007; Fox and Vasseur 2008). We then compare this to an invasion analysis of the model with intraspecific variation in one or both competitors in order to inform our understanding of the importance of ITV for coexistence. The invasion growth rate is proportional to Eq. 4, but where R_1 and R_2 represent the equilibrium resource densities in a community with a single (resident) consumer. Since all other parameters in the model are symmetric or equal ($d_1 = d_2 = 0.1$; $y_{11} = y_{22} = 0.5$; $y_{21} = y_{12} = 1$), the results would be symmetric for scenarios in which N_2 is the invader. We proceed with N_1 as the invader and N_2 as the resident.

The resident equilibrium resource densities R_{11} and R_{21} depend upon which resource is most limiting for the resident’s growth (see Fox and Vasseur 2008) such that:

$$\{R_{11}, R_{21}\} = \left\{ S_1 + \frac{d_1 + S_2(u_2 - 1)y_{22}}{y_{12} - u_2y_{12}}, \frac{d_1}{y_{22}(1 - u_2)} \right\} \tag{14}$$

when R_1 is the limiting resource and

$$\{R_{11}, R_{21}\} = \left\{ \frac{d_1}{y_{12}u_2}, \frac{S_1u_2y_{12} - S_2u_2y_{22} - d_1}{u_2y_{22}} \right\} \tag{15}$$

when R_2 is the limiting resource. The point where resource limitation switches from R_1 to R_2 , as a function of u , can be determined as:

$$u_{c1} = d_1 \left(-2 + \frac{S_1y_{11} + S_2y_{21}}{d_1} + \sqrt{4 + \frac{(-S_1y_{11} + S_2y_{21})^2}{2(-S_1y_{11} + S_2y_{21})}} \right) \tag{16}$$

There is an additional condition that defines the persistence boundary for the resident consumer. When R_1 and R_2 cannot meet or exceed the inflow concentrations of the resources S_1 and S_2 , the consumer cannot persist ($N_2 = 0$) and therefore $R_{11} = S_1$ and/or $R_{21} = S_2$.

Using this set of conditions, we calculate the invasion growth rate of consumer (with ITV) into a resident community (without ITV) as:

$$I_{inv} = \omega_{inv}y_{1inv}\bar{u}_{inv}R_1 + (1 - \omega_{inv})y_{2inv}(1 - u_{inv})R_2 - d_{inv} \tag{17}$$

In cases where both the invading and resident consumer have ITV, Eq. 17 still represents the invasion growth rate. However, R_1 and R_2 will deviate from the analytical values determined in Eqs. 14 and 15 to reflect the effects of ITV. To analyze these cases, we utilize numerical simulation of the resident dynamics to determine the R_1 and R_2 at equilibrium.

We use Eq. 17 to calculate the maximum invasion growth rate for any amount of ITV δ (see Figs. 5 and 7 for details on how much variation is necessary to produce various outcomes).

A different approach is needed to calculate the equilibrium resource values when the resident in allopatry has intraspecific variation. For simplicity, we assume that the resident has a constant amount of variation, $\delta = 1$. To do this, we use the same categorical growth partitioning scheme to calculate the growth of the resident population as we do with the invader,

$$g_{res} = \omega_{res}y_{1res}\bar{u}_{res}R_1 + (1 - \omega_{res})y_{2res}(1 - u_{res})R_2 \tag{18}$$

which is then substituted into the following system of equations:

$$\frac{dR_i}{dt} = D(S_{res} - R_{res}) - \frac{N_{res}g_{res}}{y_{ires}} \tag{19}$$

$$\frac{dN_{res}}{dt} = N_{res}(g_{res} - d_{res}) \tag{20}$$

where $i = \{1, 2\}$. This system of equations can then be numerically solved for R_1 and R_2 at equilibrium. Invasion analyses can then proceed as described in the main text by substituting these solutions into Eq. 17.

Appendix 2. Resident variation

Previous work linking ITV to coexistence has found that the benefits of ITV are typically constrained to cases where there are strict assumptions about the form of ITV itself. For example, Barabás and D’Andrea (2016) found that two species with the same mean trait value (on a single trait axis) could coexist if one had large ITV relative to the other. Here the generalist (large ITV) is successful outside the area of trait overlap while the specialist (small ITV) is dominant within this area. When the mean trait values differ among species, adding ITV in equal amounts to both competitors does not promote coexistence (Hart et al. 2016) but instead increases the niche overlap of species, leading to more intense interspecific competition and a weakening of the stabilizing mechanism. In contrast, we found that, in the case of essential resource competition, equal amounts of ITV in one or both competitors are capable of generating coexistence outside of the range of conditions under which coexistence is possible without ITV.

This is demonstrated in Fig. 5, where in the absence of ITV, the invader has a negative invasion growth rate and both consumers are entirely limited by R_2 . Increasing ITV in the invader leads to coexistence even when only a small fraction of individuals are limited by R_1 , because the contribution of

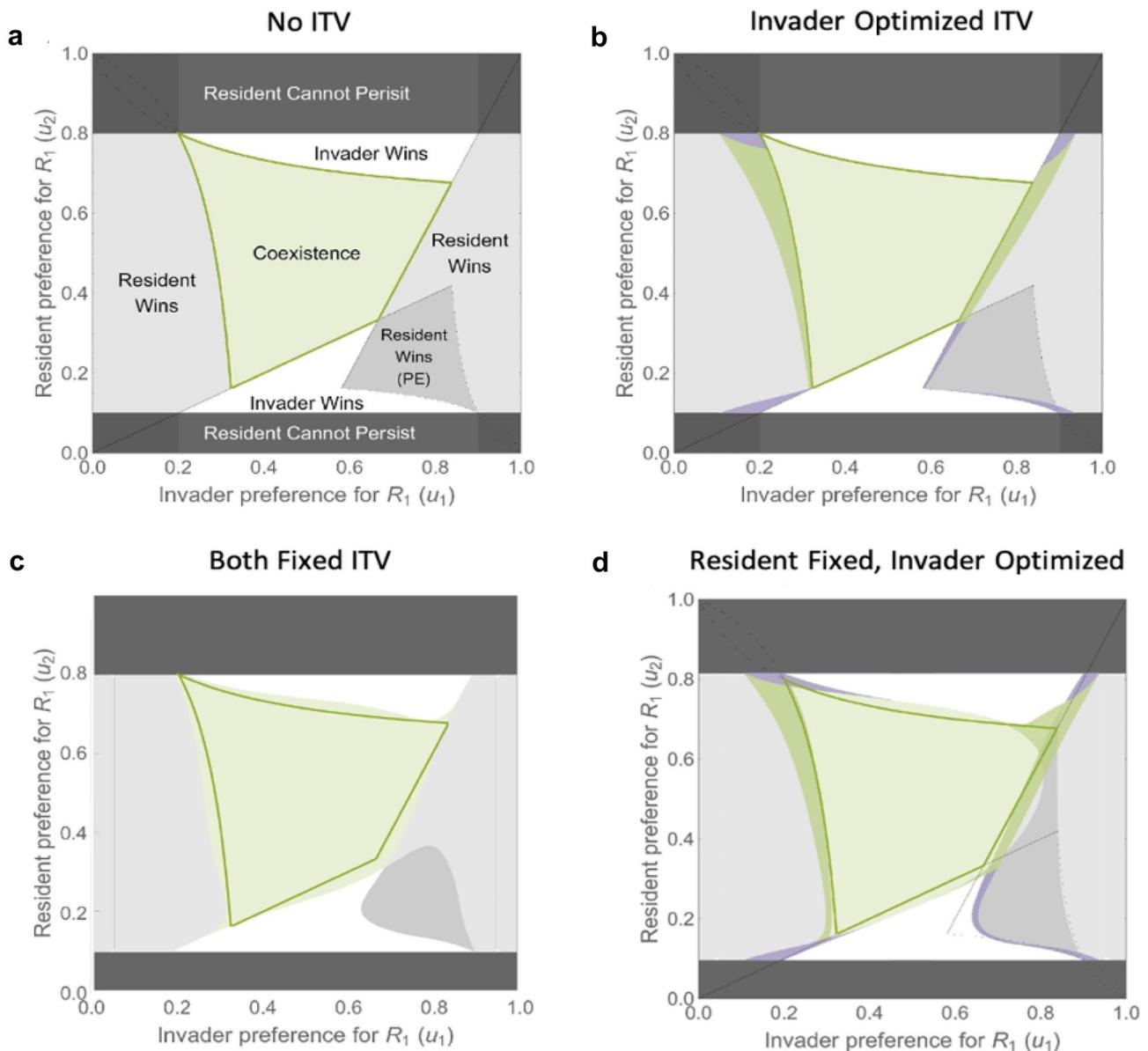


Fig. 5 The outcome of competition across the domain of uptake preferences for resident and invading consumers in for different scenarios incorporating **a** no ITV, **b** optimized ITV in the invader, **c** a fixed amount of ITV in the resident and invader ($\delta_1 = \delta_2 = 1$), and **d** fixed variation in the resident ($\delta_2 = 1$) and optimized variation in the invader. The lines dividing outcome domains are adapted from Fox and Vasseur (2008) for the case without ITV and are shown in all panels for contrast. Adding ITV to the invader **b** increases the domain of coexistence (darker green) and the domain where the

invader excludes the resident (violet). Adding a fixed amount of ITV to the resident and invader **c** shifts the outcome domains and acts in concert with ITV in the invader **d** to further increase the coexistence domain along all four of its boundaries. In panels **b** and **d**, the extended regions show the outcome of competition for the extent of ITV (δ) which maximized the invasion growth rate (see Appendix 3. Sufficient amounts of intraspecific variation for details on how much variation is necessary). Additional parameter values are given by $S_1 = S_2 = 1$, $y_{11} = y_{22} = 0.5$, $y_{12} = y_{21} = 1$, $d = 0.1$

those individuals to the population growth rate is outsized (Fig. 5b). Similarly, when the resident competitor has ITV, coexistence occurs because a large enough fraction of the resident population shifts to limitation by R_1 (Fig. 5c). Even when only a small fraction of the population exists inside of the coexistence region, it can grow quickly enough to result in positive total population growth rates (Fig. 5d).

The range of conditions that support coexistence expands more evenly along both axes if both the resident and the invader have fixed variation (Fig. 5c). Fixed variation in both populations does not have any conditions under which the invader displaces the resident (Fig. 5c), which can occur when the invader's variation is optimized for maximum invasion growth rate (Fig. 5d).

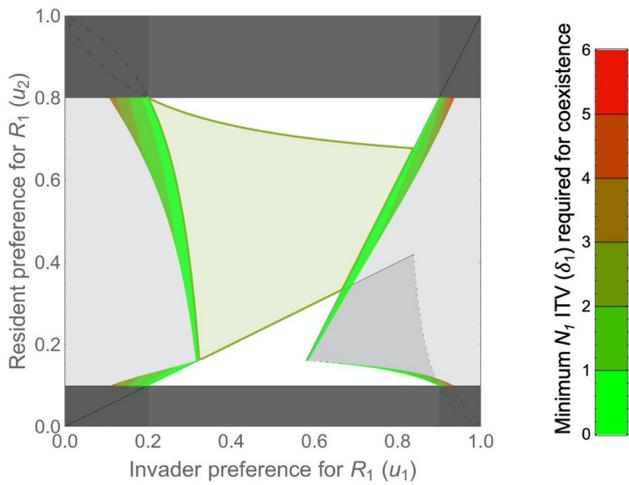


Fig. 6 Phase plane of the u_1, u_2 surface showing the minimum amount of variation δ needed to produce a positive invasion growth rate I_{inv}

Appendix 3. Sufficient amounts of intraspecific variation

Throughout the main text, we discuss competition outcomes with intraspecific variation. Here, we describe how much variation is necessary for these outcomes to occur. Relatively modest amounts of variation ($\delta < 1$) can result in positive invasion growth rates and coexistence where it would otherwise not be possible (Fig. 6), particularly when the resident’s preferences for R_1 and R_2 are close to symmetrical (i.e., $u_2 = \sim 0.5$).

Larger amounts of variation are necessary to produce positive invasion growth rates when the resident’s resource preferences become strongly skewed in either direction (Fig. 6), which roughly corresponds to the regions where intraspecific variation leads to displacement of the resident by the invader rather than coexistence (see Fig. 2b in the main text).

In some cases, when variation increases beyond a certain point (i.e., becomes “too large”), it is no longer beneficial for invasion. We demonstrate this by calculating invasion growth rates for a range of δ from 0 to 10 for three fixed u_1, u_2 combinations just outside of the coexistence boundary (Fig. 7). If variation spreads the trait distribution in such a way that a large proportion of the population has an uptake ratio that skews heavily toward being limited by the same resource as its competitor, the proportion that is limited by the opposite resource is unable to compensate for the high degree of niche overlap experienced by the rest of the population (Fig. 7). As a result, overall population growth rates will be negative.

Since ITV’s effect on coexistence is the product of non-linearity in the uptake function $u(\phi)$ (Eq. 4), it is useful to consider how different values of δ change the distribution of uptake rates in the population becomes increasingly bimodal (Fig. 8), consistent with the conclusion that continuous change in the trait ϕ mapped onto the sigmoid uptake function $u(\phi)$ results in individuals being spread unevenly across the uptake rate parameter space. The steepness of the nonlinearity in the function depends on the shaping parameter h (Eq. 4), which we assume is

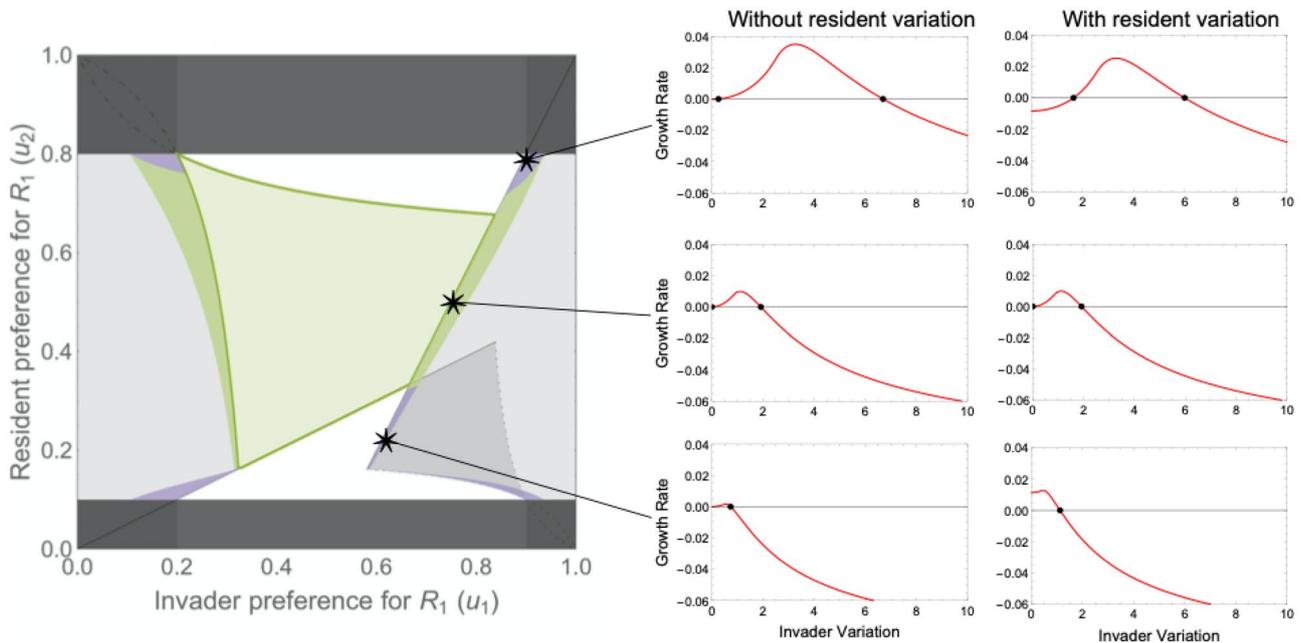


Fig. 7 Invasion growth rates I_{inv} over a range of intraspecific variation values δ at three points along the coexistence boundary, with and without resident variation

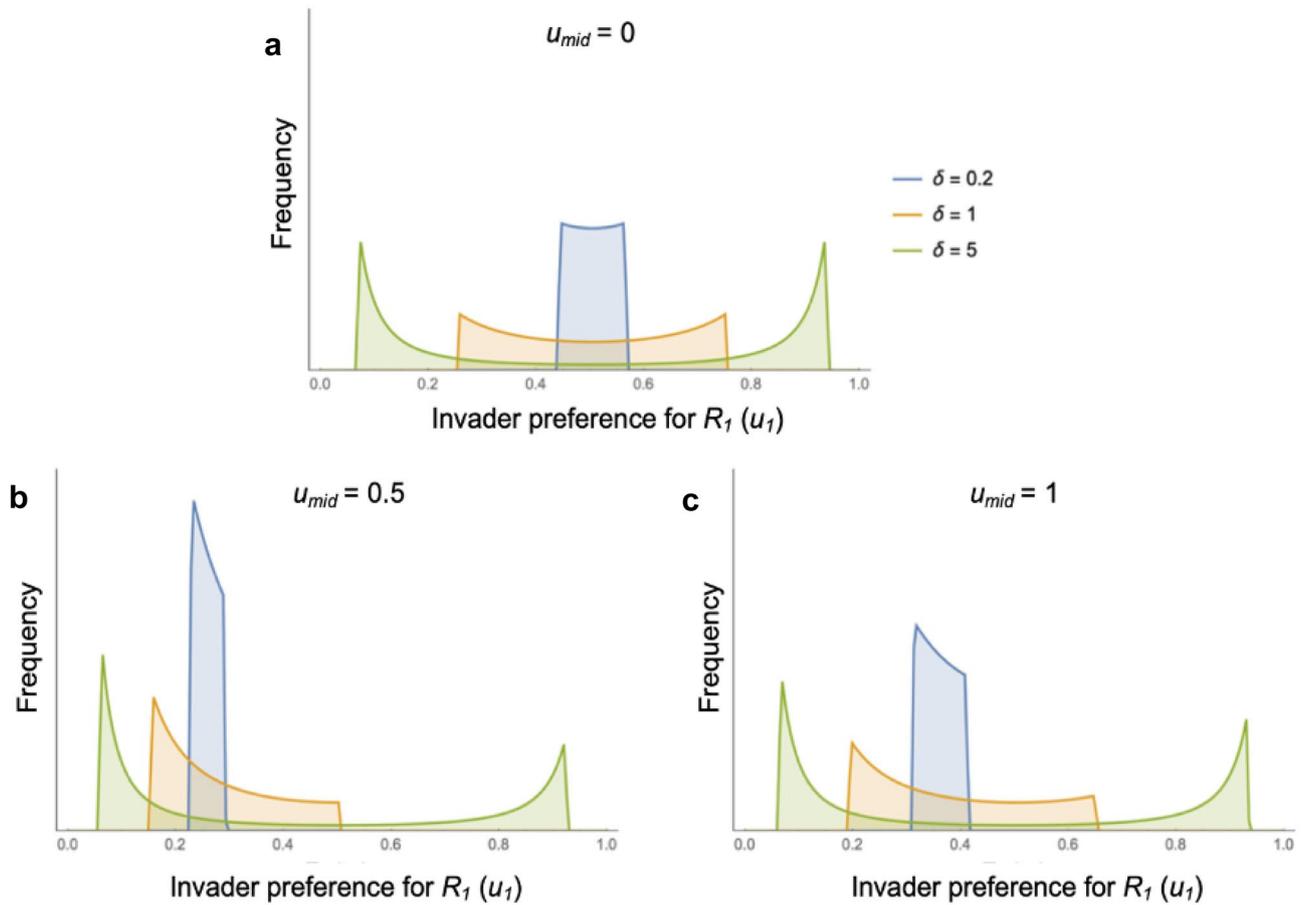


Fig. 8 As the magnitude of variation (δ) increases, populations show an increasingly bimodal distribution of uptake rates (u_1). Shown here are distributions of uptake rates for populations with mid-uptake rate values (u_{mid}) of **a** 0, **b** 0.5, and **c** 1 for $\delta=0.2, 1$, and 5 (blue, yellow,

and green curved respectively). Note that the distribution of uptake rates converges upon the same distribution regardless of u_{mid} as δ increases

equal to 1 throughout our analyses. Larger amounts of ITV would be necessary for individuals to shift their limiting resource for values of $h < 1$. However, our results remain qualitatively the same.

where Φ is the cumulative distribution function of a normal distribution with a mean μ and a standard deviation σ , and ϕ_c is the colimiting trait value, we show that variation in uptake rates still allows for positive invasion growth rates outside of the region where they are possible without variation (Fig. 9).

Appendix 4. Other trait distributions

Although we assume a uniform distribution for our analyses to aid in mathematical tractability, our results are robust to other trait distributions. For example, if trait variation takes the form of a normal distribution such that ω is calculated as

$$\omega_j = \begin{cases} 1 & \text{if } \phi_c < \mu - 3\sigma \\ \frac{\Phi(\phi_c) - \Phi(-\tan \frac{\pi}{2-\pi(\mu-3\sigma)})}{\Phi(-\tan \frac{\pi}{2-\pi(\mu+3\sigma)}) - \Phi(-\tan \frac{\pi}{2-\pi(\mu-3\sigma)})} & \text{if } \mu - 3\sigma < \phi_c < \mu + 3\sigma \\ 0 & \text{if } \phi_c > \mu + 3\sigma \end{cases} \quad (21)$$

Appendix 5. Competition between asterionella formosa and cyclotella meneghiniana

We show that ITV in uptake rates can alter zero-net growth isoclines and consumption vectors such that coexistence is possible under resource conditions that would otherwise lead to competitive exclusion (Fig. 3 in the main text). Tilman (1977) performed competition experiments with the diatoms *Asterionella formosa* and *Cyclotella meneghiniana* under various resource conditions. Tilman (1982) further shows that the competitive outcomes of these experiments generally

Fig. 9 Invasion growth rates assuming a normal distribution for trait variation in uptake ranging from $\delta=0$ to 1 when the resident preference for R_1 (u_2) = 0.5. The region between the vertical dashed lines is the range of u_1 values over which positive invasion growth rates are possible without variation

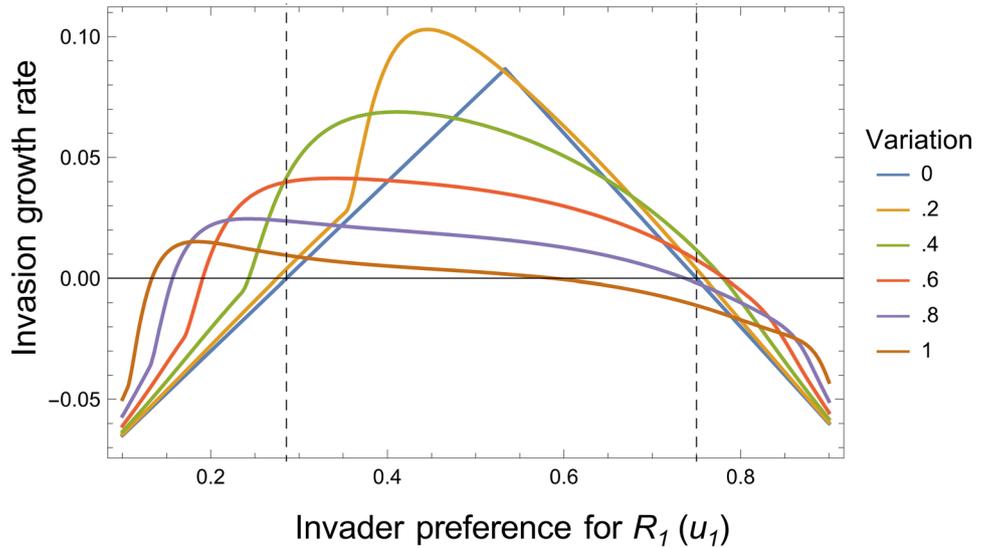


Table 1 Parameter values from Tilman (1977, 1982) used to numerically solve our model for competitive outcomes between *A. formosa* and *C. meneghiniana* with and without ITV in the uptake rates of *A. formosa*

| | y_{SiO_2} | y_{PO_4} | d | $R_{SiO_2}^*$ | $R_{PO_4}^*$ |
|------------------------|--------------------|--------------------|------|---------------|--------------|
| <i>A. formosa</i> | 2.51×10^6 | 2.18×10^8 | 0.25 | 1.9 | 0.01 |
| <i>C. meneghiniana</i> | 4.20×10^6 | 2.59×10^7 | 0.25 | 0.6 | 0.02 |

agree with the graphical predictions based on zero-net growth isoclines and consumption vectors parameterized for these species. However, two data points that fall within the graphical region where *C. meneghiniana* should win resulted in coexistence in the experiments. Using yield and death rate parameters from Tilman (1977) and R^* values from Tilman (1982) (Table 1), we calculated uptake rates of each resource for each species using

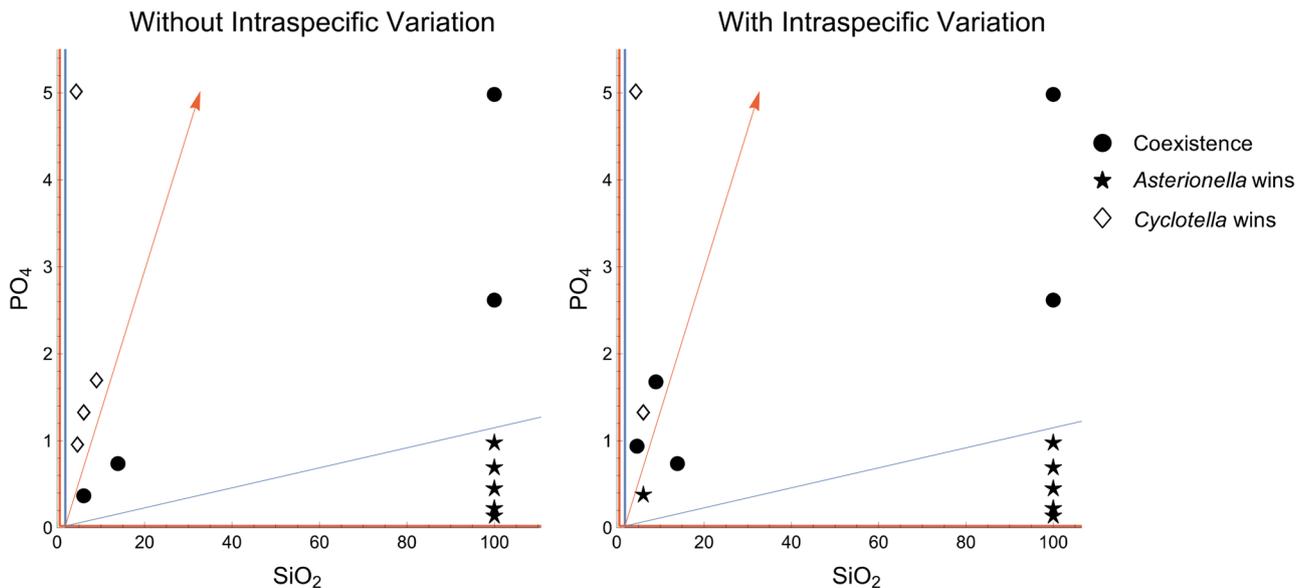


Fig. 10 Intraspecific trait variation can alter zero-net growth isoclines and consumption vectors such that coexistence is possible under resource conditions where it is not possible without ITV. Using parameters from Tilman (1977, 1982), we determined the outcome of competition between diatoms *Asterionella formosa* (blue) and *Cyclotella meneghiniana* (red) with and without ITV in uptake rates

for *A. formosa*. In the original experiments, two data points resulted in coexistence where the model without variation predicts that *C. meneghiniana* should win. The model with ITV in *A. formosa* leads to coexistence in the same two data points, here denoted by the two points that change from diamonds in the left panel to circles in the right panel

Table 2 Summary of functional forms of the trait mapping function considered in Appendix 6: Other functional forms

| Function | Equation($u_j(\phi)$) | Nonlinearity | Piecewise |
|--------------------------|---|--------------|-----------|
| Sigmoid 1 (main text) | $0.5 + \pi^{-1} \text{ArcTan}(h\phi)$ | ✓ | ✓ |
| Sigmoid 2 | $\text{Exp}(\phi) / (1 + \text{Exp}(\phi))$ | ✓ | ✓ |
| Linear | $0.5 + 0.025\phi$ | | |
| Saturating | $0.27 \text{Log}(\phi + 20)$ | ✓ | |
| Exponentially increasing | $0.25(1.2^\phi)$ | ✓ | |

$$u_{ij} = \frac{d_j}{R_{ij}^* y_{ij}} \tag{22}$$

where $i, j = \{1, 2\}$. We then used resource supply values (S_1, S_2) extracted from Tilman (1982) using ImageJ (Schneider et al. 2012) to numerically solve our model for the outcomes of competition with and without ITV in the uptake rates of *A. formosa*. Without ITV, the outcomes are as predicted by the graphical model (Fig. 10). Intraspecific trait variation in the uptake rates of *A. formosa* alters the outcomes

of competition at three data points, including the two that do not align with the prediction in the original data set (Fig. 10). ✓

Appendix 6. Other functional forms

In the main text, we consider what a trait mapping function that would allow ITV to promote coexistence might look like. The sigmoid trait mapping function (Eq. 4) used in our model is the critical component that allows ITV to contribute to stabilizing mechanisms and, thereby, promote competition. In this appendix, we consider other functional forms of trait mapping.

Here we consider four alternatives (Table 2) to the trait mapping function used in the main text (Eq. 4). We consider a sigmoid function that differs in detail from the sigmoid function used in the main text but produces a qualitatively similar function form. Importantly, it retains the two key features of (Eq. 4)—nonlinearity and piecewise shifts. We also consider linear, saturating, and exponentially increasing functions. The latter retain the feature of nonlinearity,

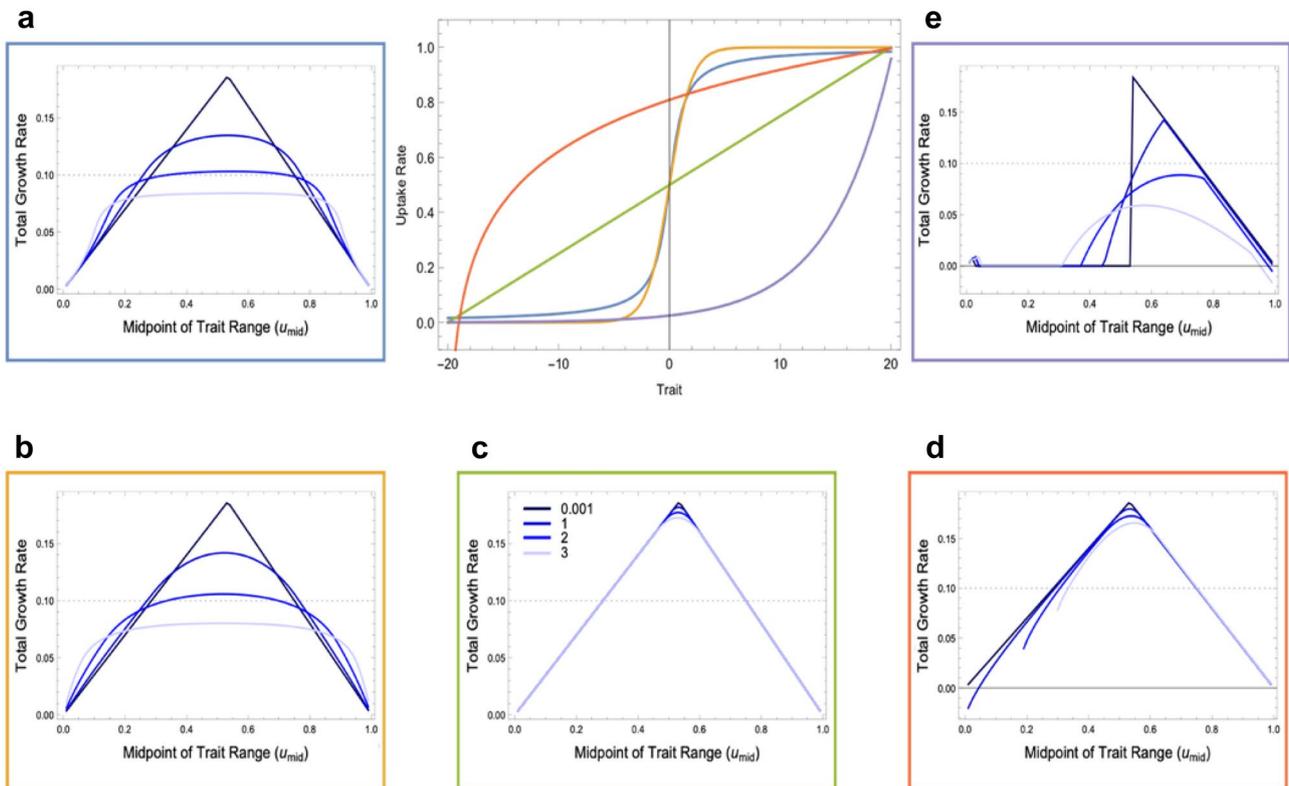


Fig. 11 The form of the function that maps quantitative trait ϕ onto uptake u_j is critical to how ITV affects the total population growth rate. Shown here is the total population growth rate as a function of the midpoint of the trait range at four levels of variation ($\delta = \{0.001, 1, 2, 3\}$). The five possible forms of this function include **a** the sigmoid

function used in the main text, **b** an alternative sigmoid function, **c** a linear function, **d** a saturating function, and **e** an exponentially increasing function. The horizontal dashed line indicates the death rate, above which growth is positive and below which growth is negative

though with only one kind of concavity, while the former has neither. As noted in the main text, sigmoid functions also provide a way of naturally constraining uptake preference to the plausible range (0,1) while still allowing the trait to be unbound in the range $(-\infty, \infty)$. None of the other functions presented in this appendix has this feature and must have additional constraints added to trait space in order to maintain the plausible range for uptake preference.

We used each functional to calculate the total population growth rate across different trait range midpoints u_{mid} and at four different levels of variation δ (Fig. 11). The two sigmoid functions produced qualitatively identical results, demonstrating that the details of the function are not as important as retaining the features of nonlinearity and piecewise shifts (Fig. 11a and b). In particular, adding a relatively small amount of variation when either sigmoid function is used expands the range of u_{mid} at which the invasion growth rate is positive. However, relatively large amounts of variation reduce the total growth rate across all u_{mid} values, indicating that too much variation is detrimental to coexistence (see Appendix 3. Sufficient amounts of intraspecific variation). When a linear function is used to map traits onto uptake preference, adding variation does not change the range of u_{mid} across which the invasion growth rate is positive (Fig. 11c). The saturating and exponentially increasing functions (Fig. 11d and e, respectively) both decrease the range of u_{mid} values over which growth rates are positive.

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Code availability Mathematica code will be made available through GitHub.

Declarations

Ethics approval Ethics approval was not necessary for this study.

Consent to participate Consent to participate was not necessary for this study.

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