

# Intraspecific Variation Promotes Coexistence Under Competition For Essential Resources

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## Research Article

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1 **Title:** Intraspecific variation promotes coexistence under competition for essential resources

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11 competition, R\* model  
12

### 13 **Abstract**

14 Intraspecific variation may be key to coexistence in diverse communities, with some even  
15 suggesting it is necessary for large numbers of competitors to coexist. However, theory provides  
16 little support for this argument, instead finding that intraspecific variation generally makes it  
17 more difficult for species to coexist. Here we present a model of competition where two species  
18 compete for two essential resources and individuals within populations vary in their ability to  
19 take up different resources. We found a range of cases where intraspecific variation expands the  
20 range of conditions under which coexistence can occur, which provides a mechanism that allows  
21 the ecologically neutral evolutionary stable strategy (ESS) to become ecologically stable. We  
22 demonstrate that this result relies on nonlinearity in the function that describes how traits map  
23 onto ecological function. A sigmoid mapping function is necessary in order to model essential  
24 resources because it allows for variation in a unbounded trait while maintaining biologically  
25 realistic boundaries on uptake rates, and differs from other kinds of nonlinearity, which only  
26 unidirectionally increase or decrease ecological function. The sigmoid function's nonlinearity  
27 spreads individuals unevenly along the growth function, which allows positive growth  
28 contributions from some individuals to compensate for growth losses from others, leading to

29 coexistence. We discuss empirical systems beyond competition for essential resources in which  
30 discontinuous functions are important.

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32

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40 initial draft of the manuscript and DAV contributed to the final version of the manuscript.

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44

45 **Introduction**

46 Intraspecific variation is ubiquitous and, while its role has long been appreciated by  
47 evolutionary biologists, we have only recently begun to consider its impact on ecological  
48 processes and functions (Bolnick *et al.* 2011). A focal point of this work has been the study of  
49 coexistence of competing species. While many empirical studies have found that intraspecific  
50 variation promotes coexistence between competitors (Lankau and Strauss 2007, Clark 2010,  
51 Hausch *et al.* 2018), most theoretical work shows that intraspecific variation makes coexistence  
52 more difficult to achieve, except in a few specific contexts (Lichstein *et al.* 2007, Hart *et al.*  
53 2016, Barabás and D’Andrea 2016, Uriarte and Menge 2018). In this paper we utilize the  
54 essential resource competition framework first developed by León and Tumpson (1975) and  
55 popularized by Tilman (1980) to demonstrate that intraspecific variation can promote  
56 coexistence by allowing some individuals in the population to compensate for other individuals  
57 whose traits confer negative growth rates when traits map onto uptake rates through a nonlinear  
58 discontinuous function. Our work provides mechanistic insight into the processes by which  
59 intraspecific variation can promote coexistence, as well as those that limit the beneficial effects  
60 of intraspecific variation on coexistence, by focusing on the relationship between non-heritable  
61 intraspecific trait variation and ecological function.

62 Recent work describing intraspecific variation has stressed its significance in ecological  
63 processes (Kichenin *et al.* 2013, Forsman and Wennersten 2015), including competition and  
64 coexistence (Clark *et al.* 2007, Lankau and Strauss 2007, Lankau 2009, Clark *et al.* 2010, Ehlers  
65 *et al.* 2016, Hausch *et al.* 2018). Work on “intraspecific trait variation” (ITV) in competitive  
66 communities has typically focused on variation in quantitative functional traits related to  
67 resource use (Roughgarden 1972, 1974, Bolnick *et al.* 2003), for example, seed size in the diets

68 of desert granivores (Brown and Lieberman 1973), although variability can occur in any trait, not  
69 just those related to resource acquisition. This ITV can have important effects on the ecology of  
70 communities independently of the effects of selection and eco-evolutionary feedbacks. In part,  
71 these effects stem from alterations in their constituent populations' abilities to exploit resources  
72 (e.g. niche expansion – Berg and Ellers 2010), buffer environmental changes (Agashe 2009), and  
73 through the decrease in average fitness that can occur when traits vary around a peak in the  
74 fitness landscape (Bolnick 2001; Bolnick *et al.* 2011). In addition, when traits map onto an  
75 ecological effect via a non-linear function, variation can strongly influence the ecological effect  
76 due to Jensen's Inequality (Ruel and Ayers 1999).

77         Most empirical evidence supports the idea that ITV makes it easier for competing species  
78 to coexist, and can increase both equalizing mechanisms (Fridley and Grime 2010) and  
79 stabilizing mechanisms (Lankau and Strauss 2007). Stabilizing mechanisms are broadly defined  
80 as those which increase the invasion growth rate of all species in a competitive community  
81 (Chesson 2000). Stabilizing mechanisms (e.g. niche differences) permit the coexistence of  
82 species whose average fitness differs. Equalizing mechanisms, when combined with stabilizing  
83 mechanisms, contribute to stable coexistence by reducing average fitness differences between  
84 competitors and, without stabilizing mechanisms, can support unstable coexistence (Chesson  
85 2000).

86         Long term data on the individual growth rates of trees shows that random but  
87 ecologically important differences between individuals can allow species to coexist via high-  
88 dimensional niche partitioning (Clark *et al.* 2007). Although the high dimensionality of traits in  
89 the system makes coupling ITV to species-level niche differentiation difficult (Chase and Myers  
90 2011), it is possible that individual variation ensures that fitness differences among species are

91 small – thus allowing weak stabilizing mechanisms or neutrality to maintain a high diversity of  
92 species. Based on these data, Clark (2010) suggests that this ITV is a necessary condition for  
93 coexistence among a large number of competing species. In less diverse experimental  
94 populations, genetic variation in allelopathic secondary compounds has been shown to create an  
95 intransitive competitive hierarchy between the various *Brassica nigra* genotypes and their  
96 heterospecific competitors, which leads to mutual invasibility and, thereby, coexistence (Lankau  
97 and Strauss 2007). Such experiments are challenging to conduct, because experimental  
98 manipulation of ITV while controlling for selection requires careful consideration. ITV has been  
99 shown to help coexistence in experimental populations of congeneric bean weevils by increasing  
100 the probability that some individuals can exploit a non-overlapping niche during invasion  
101 (Hausch *et al.* 2018). However, demonstrating ITV's importance as fuel during the initial stages  
102 of invasion and establishment does not lend support to its importance for coexistence at  
103 equilibrium where character displacement is expected to reduce niche overlap. Unfortunately it is  
104 nearly impossible to increase stabilizing mechanisms (i.e. niche differentiation) without also  
105 affecting fitness differences (Song *et al.* 2019). The key question is therefore best posed: When  
106 and how does ITV increase stabilizing mechanisms more rapidly than fitness differences?

107         Theoretical work has shown that this is indeed a difficult requirement to achieve. Various  
108 theoretical approaches have been utilized to investigate the ecological effects of ITV on  
109 coexistence, including generalized Lotka-Volterra competition frameworks (Barabás and  
110 D'Andrea 2016, Hart *et al.* 2016, Uriarte and Menge 2018), competition between stage- or size-  
111 structured populations (Hartvig and Andersen 2013, Miller and Rudolph 2011), and zero-sum  
112 models of competition (Maynard *et al.* 2019), each other their own insights and limitations.  
113 These works differ markedly in many respects, but are consistent in their assumption that

114 variation in some trait or character maps smoothly and continuously onto variation in an  
115 ecologically relevant parameter (e.g. a competition coefficient, Hart *et al.* 2016). It is possible for  
116 ITV to enhance coexistence if competitors have large niche differences and individuals interact  
117 as strongly with conspecifics as they do with heterospecifics. However, ITV tends to weaken  
118 intraspecific competition, making this scenario unlikely (Hart *et al.* 2016). Intraspecific trait  
119 variation can also promote coexistence between competitors that experience a specialist-  
120 generalist tradeoff (Begon and Wall 1987, Barabás and D’Andrea 2016) because making the  
121 dominant competitor a generalist by increasing ITV decreases niche overlap. Uriarte and Menge  
122 (2018) found that intraspecific variation can facilitate coexistence if competitors are habitat  
123 specialists and the inferior competitor specializes on a habitat with a lower carrying capacity  
124 such that competition is less severe. In general, these mechanisms rely on carefully balanced  
125 assumptions about ITV itself, making them difficult to apply generally.

126         The way that quantitative traits map onto ecological function are a key piece in  
127 understanding how ITV will affect competitive outcomes. This is because mapping functions  
128 dictate how variation in a trait will influence an individual’s ecological role and, in turn, how that  
129 individual’s ecological role will influence stabilizing mechanisms. For example, a snake’s jaw  
130 morphology will determine the size of prey it can ingest, which, in turn, determines which  
131 species it will compete with for prey (Arnold 1983). Empirical evidence has shown that trait  
132 mapping functions can take on many different forms (e.g. Barbour *et al.* 2016). Furthermore, it is  
133 often the case that multiple traits control any one metric of function or performance in an  
134 individual. For example, roughly a dozen morphological and physiological traits, such as caudal  
135 fin size, white muscle volume, and number of vertebrae, can affect burst swimming speed in  
136 fishes (Ghalambor *et al.* 2003). Here, we are not concerned with reviewing or synthesizing the

137 current understanding of the forms of trait mapping functions. The more relevant question in the  
138 context of our study is: what might a trait mapping function need to look like in order for ITV to  
139 promote coexistence?

140         Variation within species is typically small relative to variation between species  
141 (Roughgarden 1974, Siefert *et al.* 2015, Rhoades *et al.* 2018, Des Roches *et al.* 2018), though  
142 there are exceptions (e.g. Burton *et al.* 2017). In addition, changes in traits between generations,  
143 as a result of selection, mutation or drift, tend to be relatively small in magnitude. For these  
144 reasons, a trait mapping function that allows ITV to contribute positively to stabilizing  
145 mechanisms needs to ensure that small differences in traits produce disproportionately large  
146 differences in ecological function, thereby creating the opportunity to substantially decrease the  
147 intensity of interspecific competition relative to intraspecific competition via small trait  
148 differences. One way to achieve this is through Jensen's inequality. In the context of trait  
149 mapping functions, Jensen's inequality means that when the mapping function is nonlinear, the  
150 ecological function evaluated at an average trait value is not equal to the average ecological  
151 function across all values for a variable trait. The direction of this difference depends on the  
152 concavity of the nonlinear function. As a result, when traits map onto ecological function via a  
153 nonlinear function, variation in the trait can have large effects on the ecological function (Ruel  
154 and Ayers 1999). Jensen's inequality has proven to be important in ecology due to the nonlinear  
155 nature of many ecological properties (Denny 2017).

156         Here we use a model of competition between two consumers, in which exploitative  
157 competition occurs through shared use of two non-living essential resources (León and Tumpson  
158 1975, Fox and Vasseur 2008). This model is a staple in studies of competition among aquatic  
159 autotrophs (e.g. Sommer 1989, Grover 1991, Fujimoto *et al.* 2003), where abiotic nutrients such

160 as phosphate and nitrite are essential (excess phosphate cannot compensate for a lack of nitrite  
161 and vice-versa; Rhee 1978). When resources are essential, growth can only be achieved when  
162 resources are provided in a fixed ratio (generally assumed to match the organism's  
163 stoichiometry). If the intake of resources does not match this ratio, one resource will be limiting  
164 for growth (Droop 1968). However, as resource densities or consumer traits such as uptake  
165 preference change, there can be a discontinuous shift to limitation by the alternative resource. To  
166 our knowledge, this is the first model to explore the effects of ITV on competition for essential  
167 resources, which represents a biologically plausible scenario in which discontinuities (i.e.  
168 thresholds) can have important effects on ecological function and coexistence. We demonstrate  
169 that non-heritable ITV expands the range of conditions under which coexistence is possible. We  
170 conclude by discussing the properties of the trait mapping function that allow ITV to promote  
171 coexistence and some systems in which functions of this form might be found.

## 172 **Methods**

### 173 *The Base Model*

174 We model resource competition among two consumers which differ in their  
175 stoichiometric requirements for growth using the formalism described in León and Tumpson  
176 (1975). The system is described by the following set of ordinary differential equations:

$$177 \quad \frac{dR_i}{dt} = D(S_i - R_i) - \sum_j \frac{N_j g_j}{y_{ij}} \quad (1a)$$

$$178 \quad \frac{dN_j}{dt} = N_j(g_j - d_j) \quad (1b)$$

179 where  $i, j = \{1, 2\}$ . The first term of Eq. 1a describes the dynamics of resources in the absence of  
180 consumers, where  $R_i$  is the abundance of the  $i$ th resource,  $S_i$  is the inflow concentration,  $D$  is the  
181 flow rate. The second term describes resource uptake by consumers, where  $N_j$  is the abundance  
182 of the  $j$ th consumer,  $g_j$  is the growth rate, and  $y_{ij}$  is a yield coefficient describing the units of

183 consumer  $j$  that can be produced with one unit of resource  $i$ . For Eq. 1b, the rate of change in  
184 consumer abundance  $N_j$  is determined by the growth rate  $g_j$  minus a constant background death  
185 rate of  $d_j$ .

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

$$190 \quad g_j = \min[y_{1j}u_jR_1, y_{2j}(1 - u_j)R_2] \quad (2)$$

191 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  
192 strict tradeoff. Each consumer has a different fixed stoichiometric ratio ( $y_{1j}/y_{2j}$ ), which  
193 ensures that species rely differently on the essential resources. Consumers maintain their  
194 stoichiometry by taking up resources in a fixed ratio according to the tradeoff between uptake  
195 preference for  $R_1$  and  $R_2$ . We assume that consumers either excreted in a non-usable form at no  
196 cost to the consumer (Vasseur and Fox 2011).

### 197 *The Trait Mapping Function*

198 We include ITV in consumer uptake preferences by assuming that individuals express  
199 differences in a quantitative trait  $\phi$  that determines their uptake rates  $u_j$ , according to the sigmoid  
200 function:

$$201 \quad u_j(\phi) = 0.5 + \pi^{-1}\text{ArcTan}(h\phi) \quad (3)$$

202 This sigmoid function, which provides a clear mapping of traits onto ecological function, is what  
203 generates the potential for ITV to promote coexistence. There are two properties of sigmoid  
204 functions that make them an appealing option for exploring the potential for ITV to promote  
205 coexistence. First, it is a nonlinear function that is concave up below the inflection point and

206 concave down above it (**Fig 1**). As previously stated, one way to ensure that small differences in  
207 traits have sufficiently large enough effects on interspecific niche differences to promote  
208 coexistence is through Jensen's inequality, which requires that traits map onto ecological  
209 function via a nonlinear function. The concavity of the nonlinearity determines the direction of  
210 this effect. For concave upward functions, the nonlinear average ecological function is less than  
211 what is expected based on the average trait value, while for concave downward functions the  
212 nonlinear average will be greater than expected based on the average trait. This generates a  
213 useful feature of sigmoid functions: adding trait variation around the inflection point means that  
214 average ecological function on either side will become increasingly different, thereby increasing  
215 niche differences and contributing to stabilizing mechanisms.

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

228 We focus on variation in uptake rate for two reasons. First, uptake rate has been  
229 empirically shown to vary within populations (Hughes et al. 2009, Abbott et al. 2017,  
230 Brandenburg et al. 2018), while other traits in the model, such as resource requirement ratios, are  
231 typically fixed within taxa (Rhee and Gotham 1980, Boersma and Elser 2006, Behmer and Joern  
232 2008, Göthlich and Oschlies 2012, Atkinson et al. 2020). Second, previous theoretical work (Fox  
233 and Vasseur 2008) has provided a biologically intuitive, well-behaved function that maps traits  
234 onto uptake rates (Eq. 3). Equation 3 is a numerically tractable continuous approximation of the  
235 partial derivative of consumer per capita growth rates with respect to uptake rates, where larger  
236 values of  $h$  and the use of other sigmoid functions do not change competitive outcomes (Fox and  
237 Vasseur 2008). Equations 1 and 2 can be used to accurately predict empirical competitive  
238 outcomes for populations that compete for essential resources without (Grover 1997) and with  
239 ITV (*Appendix VI: Competition Between Asterionella formosa and Cyclotella meneghiniana*).  
240 From a practical standpoint, Eq. 3 provides a biologically motivated way of constraining uptake  
241 rates between 0 and 1 while allowing traits to remain unbound. There is no biological motivation  
242 for constraining other parameters, like yield coefficients  $y_{ij}$ , which would instead continually  
243 evolve higher yields. More biological motivation is required before variation in other parameters  
244 like  $y_{ij}$  can be reasonably modeled.

#### 245 *The Modeling Details*

246 The colimitation point for a single consumer is the uptake rate which satisfies the  
247 equivalence of both terms inside the minimization function in Eq. 2:

$$248 \quad u_c = \frac{R_2 y_{2j}}{R_1 y_{1j} + R_2 y_{2j}} \quad (4)$$

249 (Fox and Vasseur 2008). Rearrangement of Eq. 4 then gives the value of the trait which  
250 coincides with colimitation,  $\phi_c$  as:

251 
$$\phi_c = \text{Cot}\left(\frac{\pi R_1 y_{1j}}{R_1 y_{1j} + R_2 y_{2j}}\right) \quad (5)$$

252 Equation 2 reflects the principle that only a single essential resource limits population  
 253 growth (except at the colimitation point) of each population. However, in the presence of ITV it  
 254 is possible that some individuals are limited by  $R_1$  while others are limited by  $R_2$ . We achieve  
 255 this distinction by introducing the parameter  $\omega_j$ , along with a pair of non-linear averages into a  
 256 new equation for growth:

257 
$$g_j = \omega_j y_{1j} \bar{u}_j R_1 + (1 - \omega_j) y_{2j} \overline{(1 - u_j)} R_2 \quad (6)$$

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

260 We determine the weighting parameter  $\omega_j$  by calculating the fraction of individuals of  
 261 population  $j$  whose trait value causes them to be limited by  $R_1$ , given the densities of  $R_1$  and  $R_2$ .  
 262 For mathematical tractability, we assume that ITV in a trait  $\phi$  is described by a uniform  
 263 distribution with a maximum  $\phi_{max}$  and minimum  $\phi_{min}$ ; however, our results are robust to other  
 264 trait distributions (*Appendix V: Other Trait Distributions*). The trait  $\phi$  maps onto uptake rates  
 265 according to a sigmoid function (see *Appendix I: Model Details* for full model details), which  
 266 allows us to explore an unbounded trait space while constraining  $u_j$  to the plausible range [0,1].  
 267 We further assume that this distribution is continually recreated via phenotypic variation (i.e. that  
 268 variation is not heritable). In this instance, the fraction of the population that falls below the  
 269 colimitation threshold, and is therefore limited by  $R_1$ , is:

270

271 
$$\omega_j = \begin{cases} 1 & \text{if } \phi_c < \phi_{min} \\ \frac{\text{Cot}\left(\frac{\pi R_1 y_{1j}}{R_1 y_{1j} + R_2 y_{2j}}\right) - \phi_{min}}{\phi_{max} - \phi_{min}} & \text{if } \phi_{min} < \phi_c < \phi_{max} \\ 0 & \text{if } \phi_c > \phi_{max} \end{cases} \quad (7)$$

272

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

274

$$275 \quad \bar{u}_j = \omega_j^{-1} (\phi_{\max} - \phi_{\min})^{-1} \int_{\phi_{\min}}^{\phi_{\min} + \omega_j (\phi_{\max} - \phi_{\min})} u(\phi) d\phi \quad (8a)$$

$$276 \quad \overline{(1 - u_j)} = 1 - (1 - \omega_j)^{-1} (\phi_{\max} - \phi_{\min})^{-1} \int_{\phi_{\max} - (1 - \omega_j)(\phi_{\max} - \phi_{\min})}^{\phi_{\max}} u(\phi) d\phi \quad (8b)$$

277

278 In order to contrast the model with and without trait variation, and to look at behavior across the

279 range of possible uptake rates, we use the following equations to determine the minimum and

280 maximum trait values in the population:

281

$$282 \quad \phi_{\min} = -\text{Tan}\left(\frac{\pi}{2 - \pi u_{\text{mid}}}\right) - \delta \quad (9a)$$

$$283 \quad \phi_{\max} = -\text{Tan}\left(\frac{\pi}{2 - \pi u_{\text{mid}}}\right) + \delta \quad (9b)$$

284

285 where  $u_{\text{mid}}$  represents the midpoint of the trait range and  $\delta$  is half of the range. In this way, we

286 create  $u_1, u_2$  combinations with expected coexistence outcomes based on Fox and Vasseur (2008),

287 and introduce different amounts of variation in one or both consumers to test the effect of

288 variation on those outcomes. Importantly, the model with and without variation are equivalent

289 because Eq. 6 converges upon Eq. 2 as the extent of ITV approaches 0 (see *Appendix 1: Model*

290 *Details*).

291 Given the assumptions above, Eq. 6 can be used to analytically solve the invasion growth

292 rate when a resident consumer does not have ITV (see *Appendix II: Invasion Analyses*). We

293 leverage this solution, and previous work on this framework (Fox and Vasseur 2008, León and

294 Tumpson 1975) to demonstrate how ITV in an invader alters the potential for invasion across the

295 full range of  $u_1, u_2$  parameter space. We complement the analytical solutions with numerical  
296 simulations to determine the outcome of competition (using a pair-wise invasion approach) and  
297 extend this to a scenario where just the resident and both the invader and resident have ITV  
298 (*Appendix III: Resident Variation*).

## 299 **Results**

300 Our model framework allows us to assess coexistence most effectively using an invasion  
301 analysis, where one consumer's (invader) growth rate is measured in an equilibrium community  
302 of its competitor (resident). **Fig 2** shows the expanded domain of coexistence when an invader  
303 has an optimal amount of ITV. When the invader has an optimal amount of ITV (that maximizes  
304 growth for a given  $u_1, u_2$  combination), conditions where the resident would otherwise  
305 outcompete the invader shift to form a larger contiguous coexistence region (**Fig 2b**) relative to  
306 the case without ITV (**Fig 2a**). The range of conditions supporting coexistence is also expanded  
307 when both the invader and resident have a fixed amount of ITV ( $\delta_1 = \delta_2 = 1$ ) and when the  
308 resident has a fixed amount of variation ( $\delta_2 = 1$ ) while the invader's ITV is optimized, although  
309 the expanded coexistence region is shifted and expanded slightly to accommodate the effects of  
310 fixed variation on the resident community at equilibrium in the latter case (**Fig 6**).

311 The aforementioned discontinuity plays a role in driving these patterns.

312 Competition for essential resources results in stable coexistence when consumers (i) are limited  
313 by different resources and (ii) consume a larger fraction of the resource that is most limiting for  
314 their growth (León and Tumpson 1975). These conditions together generate the four boundaries  
315 defining the diamond-shaped coexistence region in **Fig 2a** (where no ITV is incorporated).

316 Outside those boundaries, coexistence is not possible when all individuals are identical.

317 However, in the presence of ITV, some individuals can have uptake rates ( $u$ ) that span the  
318 discontinuity and place them inside the coexistence region (while the mean remains outside) .

319         Generating the appropriate conditions for coexistence in a subset of individuals is not  
320 sufficient for changing the outcome of coexistence unless that subset's rate of population growth  
321 is sufficient to compensate for losses in the remaining fraction. Given that we assume a  
322 symmetric distribution of ITV, if the mean trait lies outside the coexistence region, so too will  
323 more than half of the population. Thus, those individuals which exist inside the coexistence  
324 region must have a disproportionate positive effect on the population growth rate. This is  
325 achieved through Jensen's inequality, generated by the nonlinearity of the trait mapping function,  
326 which allows a subset of individuals with positive growth rates to have a disproportionately large  
327 effect on the total population growth rate. First, note that resource uptake ( $u_I$ ) maps linearly onto  
328 invasion growth rates (**Fig 3a**). If a population's average  $u_I$  falls outside of the coexistence  
329 region and variation spreads individuals evenly in both directions along the growth function, it is  
330 not possible for ITV to promote coexistence because crossing the discontinuity will only lead to  
331 lower average population growth rates. However, because of the nonlinearity of the sigmoid trait  
332 mapping function, ITV does not spread individuals evenly in both directions. Instead, the  
333 distribution spreads more rapidly into the middle of the function and slowly at the extremes (**Fig**  
334 **3a**). The transformed distribution  $T$  of  $u_j(\phi)$  (Eq. 3), assuming  $\phi$  is uniformly distributed, shows  
335 that individuals within the coexistence region is less densely packed than those at extreme  $u_I$   
336 values outside of the coexistence region (**Fig 3b**). However, those individuals within the  
337 coexistence region can contribute enough to the total population growth rate to allow for  
338 coexistence at an intermediate amount of ITV (**Fig 3c**). Whether or not these individuals

339 contribute enough to the total population growth rate to compensate for individuals outside of the  
340 coexistence region can be determine by calculating:

$$341 \int_{\phi_{\min}}^{\phi_{\max}} T(u_j(\phi)) g_j du_j \quad (10)$$

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

344 In our model, ITV does not promote coexistence simply by causing the expected value of  
345  $u_I$  to fall within the coexistence region. For example, incorporating a large amount of ITV  
346 resulted in a negative invasion growth rate even when  $E[u_j(\phi)]$  falls within the coexistence  
347 region for cases where  $u_{mid}$  was within the coexistence region and just outside of the coexistence  
348 region (**Fig 4a** and **4b**, respectively). Likewise, when  $u_{mid}$  was at an extreme value that was not  
349 near a coexistence boundary, large amount of ITV caused  $E[u_j(\phi)]$  to fall within the coexistence  
350 region but did not result in a positive invasion growth rate (**Fig 4c**). This is, again, because  
351 nonlinearity in the sigmoid function does not spread individuals evenly across the uptake rate  
352 parameter space such that  $E[u_j(\phi)]$  is not representative of the conditions that most individuals  
353 in the population are experiencing. It is also interesting to note that there are cases where a  
354 population's  $u_I$  distribution can expand outside of both the coexistence and persistence  
355 boundaries and still maintain a positive invasion growth rate (e.g. **Fig 4a**).

356 We further visualize this mechanism using an extension of classic graphical technique  
357 (Tilman 1980), whereby a continuum of individual strategies can be plotted as a set of zero-net-  
358 growth isoclines (ZNGIs) that follow a boundary (Meszena and Metz 1999) or geometric  
359 envelope (Koffel et al. 2016) along axes of resource densities (**Fig 5**). Here the coexistence  
360 conditions are realized by the existence of an intersection between consumer ZNGIs and a  
361 correct orientation of consumption vectors with respect to the resource supply point (**Fig 5a**). It

362 is not sufficient to merely consider the average values for  $R_1^*$  and  $R_2^*$ . Instead, we consider the  
363 joint distributions of  $R_1^*$  and  $R_2^*$ , which more accurately reflects interactions between individuals  
364 whose traits are bound by a strict tradeoff (Eqs. 2 and 3). Intraspecific variation has effects on  
365 both the ZNGIs and, by association, on the consumption vectors as well. However, which effect  
366 drives coexistence depends on the location in parameter space. Along the curved persistence  
367 boundaries (left and top boundaries in **Fig 1**), the condition requiring consumption of the limiting  
368 resource is violated. Here, the distribution of consumption vectors generated by ITV leads to  
369 some individuals having the correct orientation (**Fig 5b**). Along the linear coexistence  
370 boundaries (right and bottom boundaries in **Fig 1**), the condition requiring an intersection among  
371 the ZNGIs is violated. Here, the distribution of ZNGIs generated by ITV leads to some  
372 individuals having the required intersection (**Fig 5c**).

### 373 **Discussion**

374 Previous work linking ITV to coexistence has produced conflicting results, with some  
375 finding that ITV is beneficial while others find that it is detrimental to coexistence. Those that do  
376 find support for the benefits of ITV for coexistence are typically constrained to cases where there  
377 are strict assumptions about the form of ITV itself. Here we focus on a critical piece to  
378 understanding how and when ITV will and will not be beneficial by asking which features of a  
379 trait mapping function would produce these beneficial effects and which might limit them. We  
380 found that two features – nonlinearity and discontinuity – are critical for determining how ITV  
381 will affect coexistence. Nonlinearity allows for the growth of individuals with beneficial traits to  
382 compensate for the losses generated by the rest of the population. Discontinuity is a double-  
383 edged sword in the sense that it can reduce niche overlap by allowing individuals with very

384 similar trait values to have a vastly different ecological role, but it also places an upper limit on  
385 the amount of ITV that can be beneficial.

386 Our model uses the well-established Droop function (Droop 1968; Eq. 2), which scales  
387 the growth rate to the density of the essential resource that is most limiting in the environment.  
388 This model is a staple in studies of competition among aquatic autotrophs (e.g. Sommer 1989,  
389 Grover 1991, Fujimoto *et al.* 2003), where abiotic nutrients such as phosphate and nitrite are  
390 essential (excess phosphate cannot compensate for a lack of nitrite and vice-versa; Rhee 1978).  
391 Tilman (1977, 1982) demonstrated that Droop's model predicted the outcome of competition for  
392 phosphate and silicon dioxide amongst the diatoms *Asterionella* and *Cyclotella*, failing to predict  
393 the outcome only when the supply of resources was sufficiently near the coexistence boundary.  
394 Although competitive exclusion may be slow near the coexistence boundary, this region also  
395 corresponds closely to that depicted in **Fig 2b** where ITV extends the coexistence region  
396 (*Appendix V: Competition Between Asterionella formosa and Cyclotella meneghiniana*).

397 The sigmoidal trait mapping function (**Fig 1**, Eq. 3) is critical to the observed outcomes  
398 in our model because of two specific components of the function. First, the discontinuity in the  
399 model (i.e. individuals are either limited by  $R_1$  or  $R_2$  depending on a continuous trait value)  
400 allows individuals with similar trait values to be functionally different. This type of system, in  
401 which smooth changes in a variable of interest produce abrupt (discontinuous) changes in  
402 behavior when a threshold is traversed, are commonly known as piecewise smooth systems  
403 (PWS) and are used to describe the behavior of many biological systems (May 1977, Dercole *et*  
404 *al.* 2007). Although we draw our conclusions from a model of competition for essential  
405 resources, this mechanism could easily be generalized to other systems of competition, including  
406 systems where prey switch occurs, in populations that undergo discontinuous shifts in life history

407 traits, and in size-structured populations. For example, damselfly naiads show frequency-  
408 dependent preferences for sessile *Simocephalus* or motile *Daphnia* prey. Naiads utilize two  
409 different foraging behaviors – walking and ambush – which influence their encounter rate of  
410 *Simocephalus* and *Daphnia* (Akre and Johnson 1979). Since naiads can use either foraging  
411 behavior, the proportion of time spent walking versus ambushing prey is a continuous behavioral  
412 trait that varies between individuals. Differences in this continuous trait alters an individual’s  
413 encounter rate with prey species and drives the observed discontinuous prey switching. In  
414 quantitative genetic threshold models, the underlying continuous trait is sometimes called the  
415 “liability” (Roff et al. 1997), which maps onto a response with a threshold, above which  
416 individuals have one trait and below a different trait. Liability traits in salmonid fishes, such as  
417 body size, influence discontinuous behavior in migratory tactics (smolting versus freshwater  
418 residency, Dodson *et al.* 2013), which can strongly affect dietary preferences (Rikardson *et al.*  
419 2000) and competitive interactions. Dietary overlap in threespine sticklebacks decreases when  
420 individuals differ in gape width (Bolnick and Paull 2008). In this system, ITV in gape width  
421 could allow individuals on either side of some threshold gape width to access prey items that  
422 heterospecific and conspecific competitors cannot. Interestingly, a continuous trait like gape  
423 width could have multiple discontinuous thresholds (ontogenetic shifts) at which individuals  
424 would be able to access novel prey, which creates even more opportunity for niche  
425 differentiation to promote coexistence. These kinds of discontinuous shifts in ecological function  
426 along a continuous range of trait variation have the potential to contribute to stabilizing  
427 mechanisms in the same way ITV in model does.

428         The discontinuity also creates a downturn in the  $u_I$ -growth rate mapping function (**Fig**  
429 **3a**) that generates an upper limit on the positive effects that ITV can have on coexistence. In

430 other words, we found that an intermediate amount of ITV maximizes invasion growth rates (**Fig**  
431 **4**). Without any such limit, ITV can increase without bounds, which would diminish niche  
432 differences which, without the assumption that ITV is much greater in the inferior competitor,  
433 would favor the superior competitor (Hart et al. 2016). Others overcome this by assuming that  
434 population variance trades off with mean performance (Lichstein et al. 2007). However, this  
435 assumption is restrictive and it is challenging to find mean-variance tradeoffs in empirical  
436 systems (Courbaud et al. 2012). In contrast, biological systems that show discontinuous shifts in  
437 function are fairly common in nature and may provide one alternative mechanism that limits the  
438 fitness advantages conferred by ITV. In particular, empirical systems tend to show more gradual  
439 switching in the presence of variation, which leads to nonlinearities like those presented here  
440 (van Baalen et al. 2001), while theoretical work often assumes that shifts occur rapidly due to  
441 difficulties in performing analytical analyses of equilibria in the presence of strong nonlinearity  
442 (Křivan 2007). Future work should explore the factors that limit the extent and benefits of ITV  
443 and how this might contribute to our understanding of when ITV will and will not promote  
444 coexistence between competitors.

445         Second, the nonlinearity of the sigmoid function, and more specifically the concavity of  
446 the nonlinearity, means that a small difference in trait values has a disproportionately large effect  
447 on the ecological function of individuals via Jensen's inequality. Jensen's inequality is common  
448 in many biological systems, where variability is often the rule rather than the exception, and has  
449 proven to be useful in explaining many biological phenomena (Denny 2017). The difference in  
450 concavity above (concave downward) and below (concave upward) the inflection point in the  
451 sigmoid function (**Fig 1**) creates a different kind of nonlinearity than what has been found to  
452 promote coexistence in other models where nonlinearity has a unidirectional effect that either

453 increases or decreases the response (e.g. Hart *et al.* 2016, Uriarte and Menge 2018). This form of  
454 nonlinearity spreads individuals unevenly across the uptake rate parameter space (**Fig 3a**) and  
455 highlights the necessity of carefully considering how to incorporate ITV into ecological  
456 frameworks. Consider a case where ITV is extremely large such that the majority of individuals  
457 in the population have an uptake rate of nearly 0 or 1 (e.g **Fig 9**). Although the  $E[u_j(\phi)]$  and  
458 average ZNGIs will be within the coexistence region, the majority of individuals will not be able  
459 to satisfy their stoichiometric requirements, resulting in negative population growth.

460         Another key component of our model is that a proportion of individuals in the population  
461 must grow fast enough to compensate for the proportion of individuals that are limited by the  
462 same resource as their competitor (Eq. 10, **Fig 4**). Broadly, this can be seen as a source-sink  
463 problem where the growth of the proportion of the population that is differentially resource  
464 limited (the “source”) can compensate for the growth of the proportion that is limited by the  
465 same resource as the heterospecific competitor (the “sink”). It is possible for emigration from a  
466 source population with positive growth rates to compensate for negative growth in a sink (i.e.  
467 “the rescue effect” Brown and Kodric-Brown 1977, Pulliam 1988, Gyllenberg and Hanski 1997),  
468 the genetic or developmental equivalent of which is phenotypic subsidy (Doebeli 1996, Bolnick  
469 *et al.* 2011). When populations or phenotypes vary in fitness but have sufficient rates of  
470 exchange between different subgroups, these processes can alter ecological interactions by  
471 decoupling a population or phenotype’s growth rate from its fitness (Bolnick *et al.* 2011). Meta-  
472 community models have shown that competitively inferior populations can be rescued from  
473 competitive exclusion when immigration from a competitively dominant source population is  
474 sufficiently high (Moquet and Loreau 2003). Similar ideas have been proposed in models of  
475 structured populations, where one stage acts as a “refuge” by overcompensating for high

476 mortality in another stage (Miller and Rudolph 2011). Further support comes from empirical  
477 work on genetic load in plant populations. It is often assumed that high genetic load is  
478 deleterious and should, therefore, be “purged” from the population by selection. However, meta-  
479 analyses have found no evidence of purging in plant populations and instead find that  
480 populations maintain suboptimal trait variation (Byers and Waller 1999, Byers 2005) in spite of  
481 the fact that theory suggests selection should eliminate such variation (Flaçoner and Mackay  
482 1996).

483         The functional forms and parameters sets we chose allow us to place our model in the  
484 context of previous work (Fox & Vasseur 2008). Competition for essential resources is common  
485 in nature among plants and phytoplankton (Salisbury and Ross 1992, Rhee 1978) and is  
486 theoretically well studied (León and Tumpson 1975, Tilman 1977, Abrams 1987, Huisman and  
487 Weissing 2001, Fox and Vasseur 2008). However, different parameter sets or functional forms  
488 might result in a larger effect size. Heterotrophs are more likely to compete for nutritionally  
489 complementary resources which would show less abrupt threshold behavior, and models such as  
490 this one have been adapted to include these kinds of utilization functions (Vasseur and Fox  
491 2011). The parameter set we chose assumes that competition is symmetric in that the internal  
492 stoichiometry of each species ( $y_{ij}$ ) is symmetric. However, asymmetric competition is common in  
493 plants and can alter competitive outcomes (Weiner 1990). Similarly, we assume that trait  
494 variation is symmetric and follows a uniform distribution. Though it does not qualitatively  
495 change our results (see *Appendix V: Other Trait Distributions*), different trait distributions have  
496 the potential to increase the observed effect size. Finally, we have restricted our analyses to a  
497 case with two consumers in order to leverage comparisons to previous work and aid in  
498 interpretation as well as visualization. However, by increasing the number of limiting resources,

499 it is possible to expand the model to three or more species. Others have explored the effects of  
500 ITV in multispecies competitive communities (Barabás and D’Andrea 2016).

501 To isolate the ecological effects of ITV, the trait distributions in our model are externally  
502 imposed and held constant while ecological interactions occur. We assume that the distribution is  
503 maintained regardless of population size, dynamics, and the effects of selection. An eco-  
504 evolutionary analysis of this model previously showed that the evolutionary stable strategy (ESS)  
505 exists at the intersection of the linear boundaries of the coexistence region (Fox and Vasseur  
506 2008). This point is directly adjacent to parameter regions where ITV can override competitive  
507 exclusion and yield coexistence. Thus, competitors which have evolved in sympatry may benefit  
508 from a “coexistence buffer” that is provided by ITV if a perturbation were to push the system  
509 outside the coexistence region. By expanding the coexistence region, ITV provides a mechanism  
510 by which the ecologically neutral ESS can become ecologically stable. Future work is needed to  
511 provide insight into how selection on the distribution of traits in the population is i) shaped by  
512 ecological and evolutionary forces and ii) changes the impact of ITV on coexistence.

513 We utilize the standard practice of assessing competitive outcomes using the invasion  
514 criterion, but recognize that this is precisely the scenario under which the assumption of trait  
515 variation makes the least sense (Tsutsui *et al.* 2000, Sakai *et al.* 2001, Allendorf and Lundquist  
516 2003). Our intent is not to imply that an invading individual must possess an impossible  
517 diversity of traits in order to be successful; rather we use this technique to measure the change in  
518 strength of coexistence mechanisms in the presence of ITV. Others have demonstrated that trait  
519 variation can be important during invasion because it increases the probability that some  
520 individual will have traits that promote growth (Hausch *et al.* 2018). Under such a scenario,  
521 selection acts as a filter for traits, but ITV itself does not have an effect, *sensu stricto*, on the

522 invasion growth rate. Our work focuses on the ecological mechanisms through which ITV alters  
523 competitive outcomes, while previous work has focused on the evolutionary effects of ITV as the  
524 fuel on which selection acts.

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

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537

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740 **Figure Legends**

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

746

747 **Fig 2** Shows the outcome of competition across the domain of uptake preferences for resident  
748 and invading consumers in for different scenarios incorporating (a) no ITV and (b) optimized  
749 ITV in the invader. The lines dividing outcome domains are adapted from Fox and Vasseur  
750 (2008) for the case without ITV and are shown in all panels for contrast. Adding ITV to the  
751 invader (b) increases the domain of coexistence (darker green) and the domain where the invader  
752 excludes the resident (violet). In panel (b), the extended regions show the outcome of  
753 competition for the extent of ITV ( $\delta$ ) which maximized the invasion growth rate (see *Appendix*  
754 *IV: Sufficient Amounts of Intraspecific Variation* for details on how much variation is necessary).  
755 Additional parameter values are given by  $S_1 = S_2 = 1$ ,  $y_{11} = y_{22} = 0.5$ ,  $y_{12} = y_{21} = 1$ ,  $D = d = 0.1$

756

757 **Fig 3** It is possible for ITV to promote coexistence because (a) although consumer preference for  
758  $R_1$  ( $u_I$ ) maps linearly onto invasion growth rate, the nonlinearity of the sigmoid trait mapping  
759 function spreads individuals (orange points) more rapidly around the discontinuity than it does  
760 outside of the coexistence region. The large dark orange point is  $E[u_j(\phi)]$ . Panel (b) shows the  
761 transformed distribution of  $u_I$  for  $\delta = \{0.5$  (blue),  $1$  (orange),  $2$  (green) $\}$  for  $u_{mid} = 0.77$ .

762 Panel (c) shows the contribution to population growth across the transformed distribution of  $u_I$   
763 values with corresponding values of  $\int_{\phi_{\min}}^{\phi_{\max}} T(u_j(\phi)) g_j du_j$

764

765 **Fig 4** Mechanisms supporting an expansion of the coexistence region rely upon the contributions  
766 from individuals within the coexistence boundaries. The zero net growth isoclines (lines),  
767 resource supply points (stars) and consumption vectors are shown for a parameter set (a) with no  
768 variation where stable coexistence is possible, (b) where variation ( $\delta = 0.5$ ) in uptake rate alters  
769 the consumption vector of the blue species ( $N_I$ ) such that stable coexistence occurs and (c)  
770 scenarios where variation ( $\delta = 0.5$ ) in uptake rate  $u_j$  alters the zero net growth isocline of the  
771 invader (blue) such that coexistence occurs where it would not be possible without variation.  
772 Variation that spans the critical boundary into parameter space supporting coexistence is shaded  
773 in darker tones. Note that in both (b) and (c), ITV alters isoclines and consumption vectors, but  
774 only the changes that matter for coexistence are shown

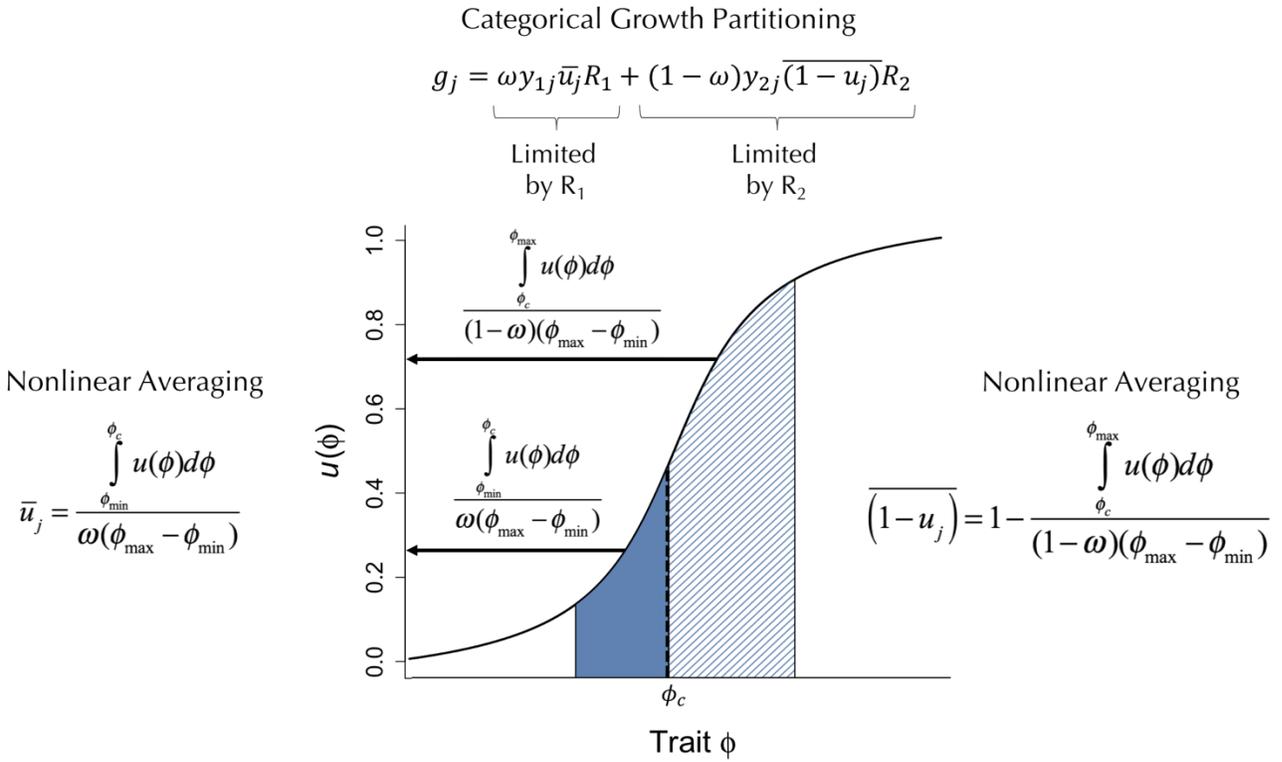
775

776 **Fig 5** The maximum and minimum preference for  $R_I(u_I)$  (black dotted lines) and expected value  
777 (red lines) as well as corresponding invasion growth rates (black lines) as a function of variation  
778 ( $\delta$ ) for (a)  $u_{mid}$  inside the coexistence region ( $=0.7$ ), (b)  $u_{mid}$  just outside of the coexistence  
779 region ( $=0.77$ ), and (c)  $u_{mid}$  far outside of the coexistence region ( $=0.24$ )

780

781 **Figures**

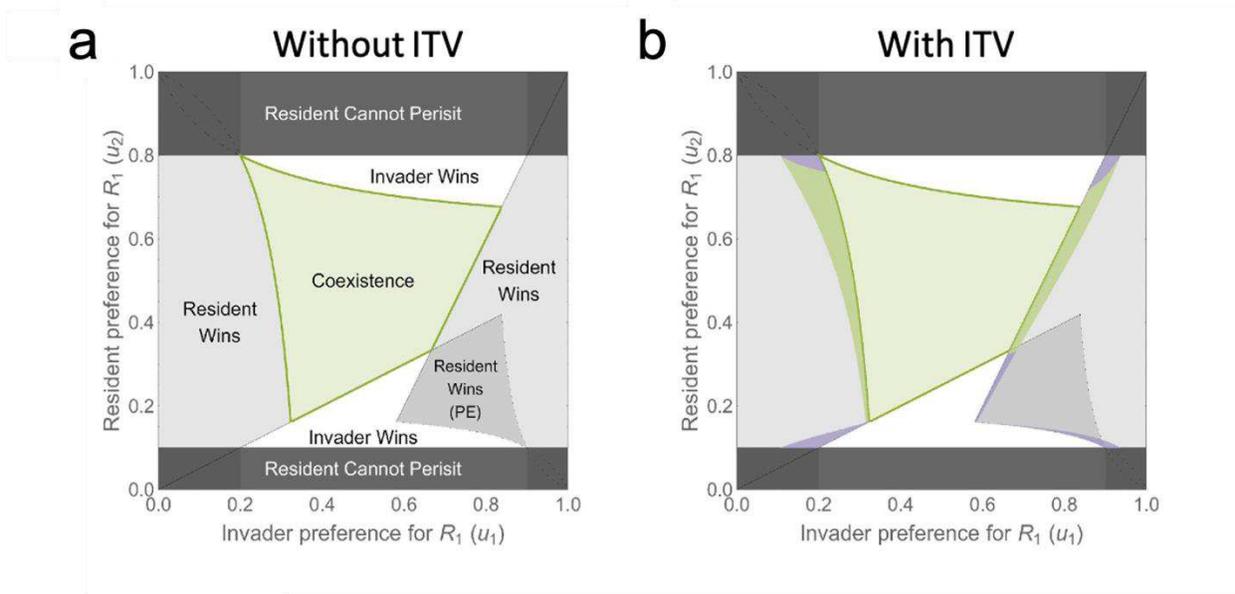
782 **Fig 1**



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785 **Fig 2**



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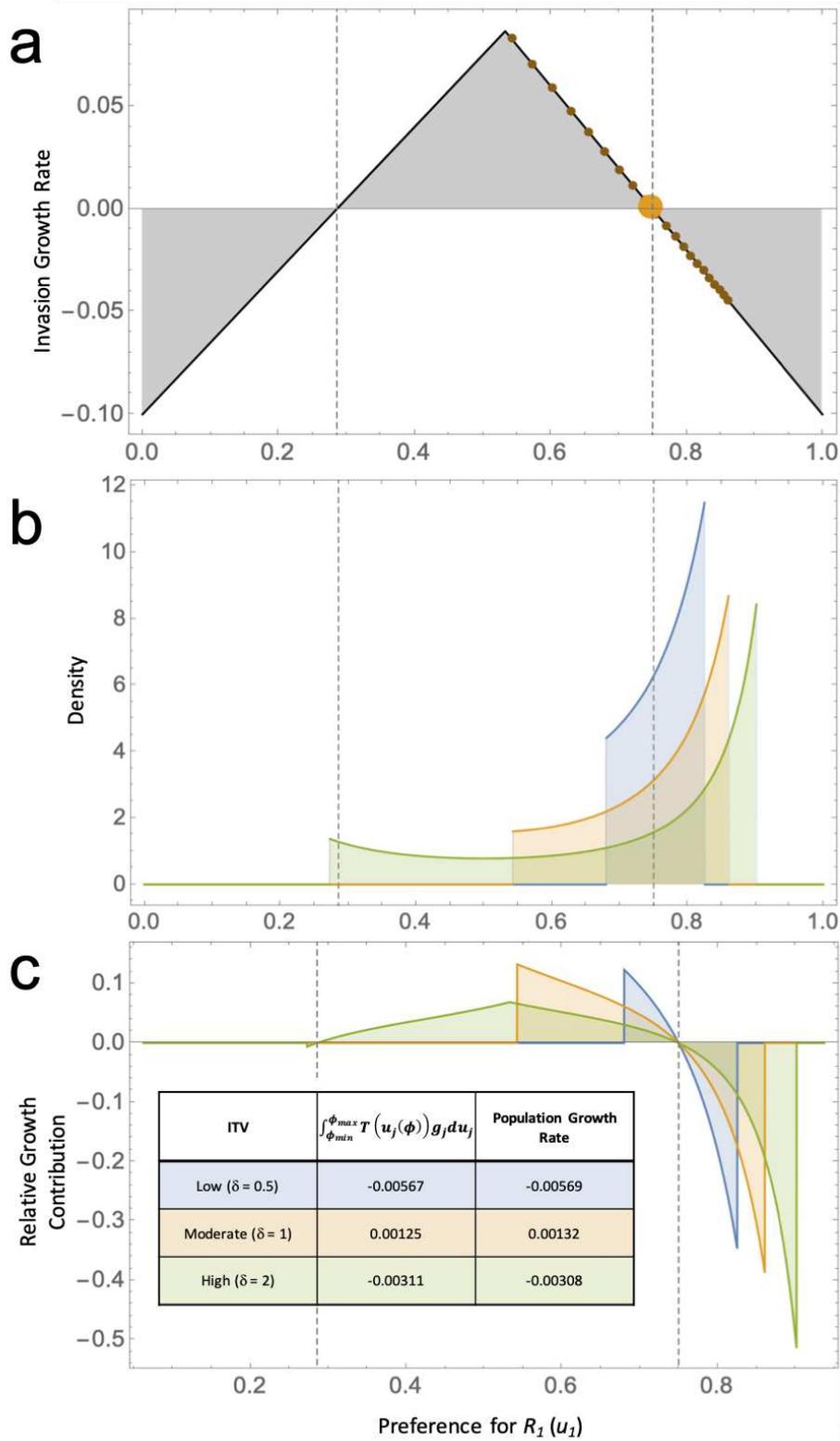
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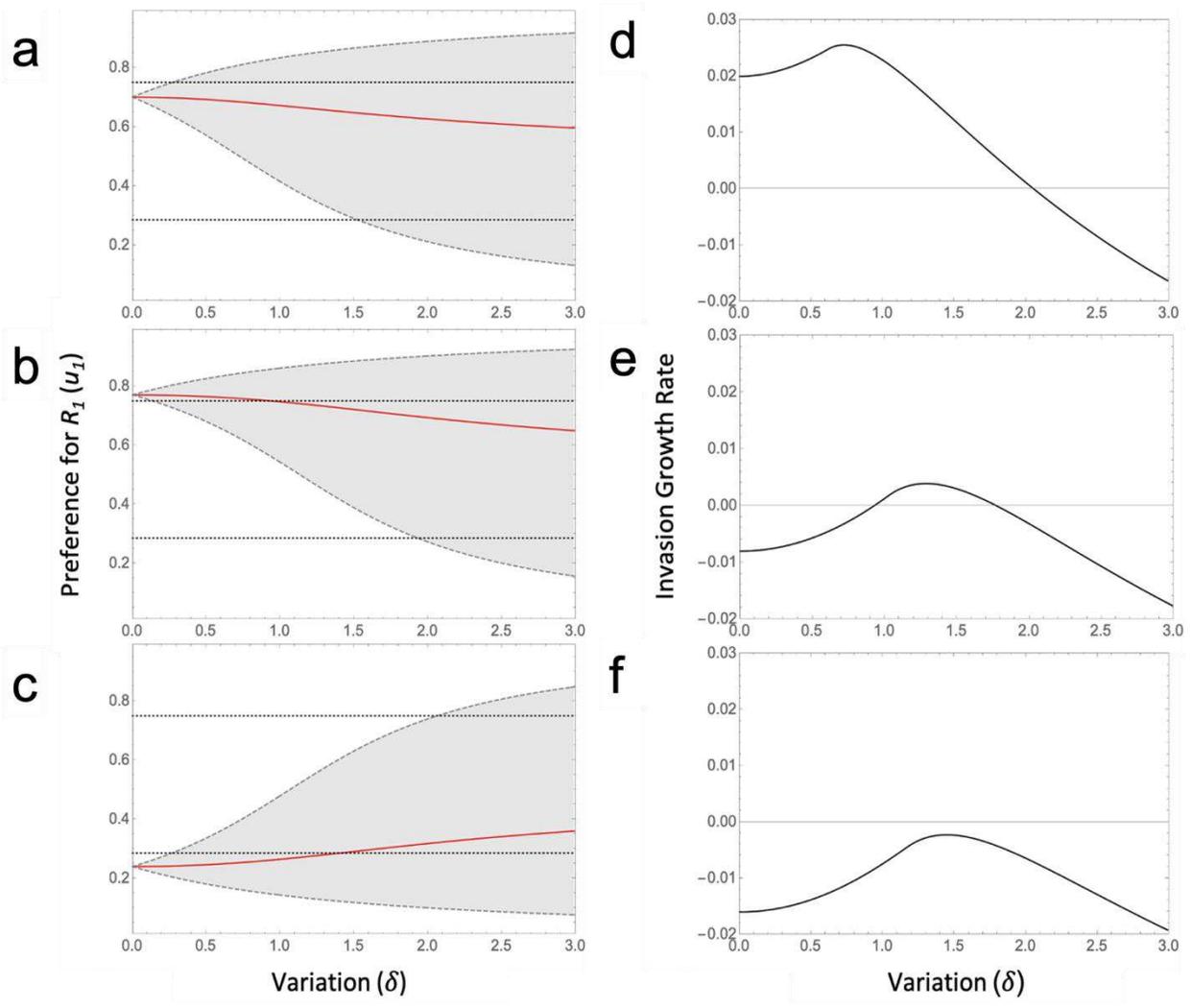
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795 **Fig 3**



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797 **Fig 4**



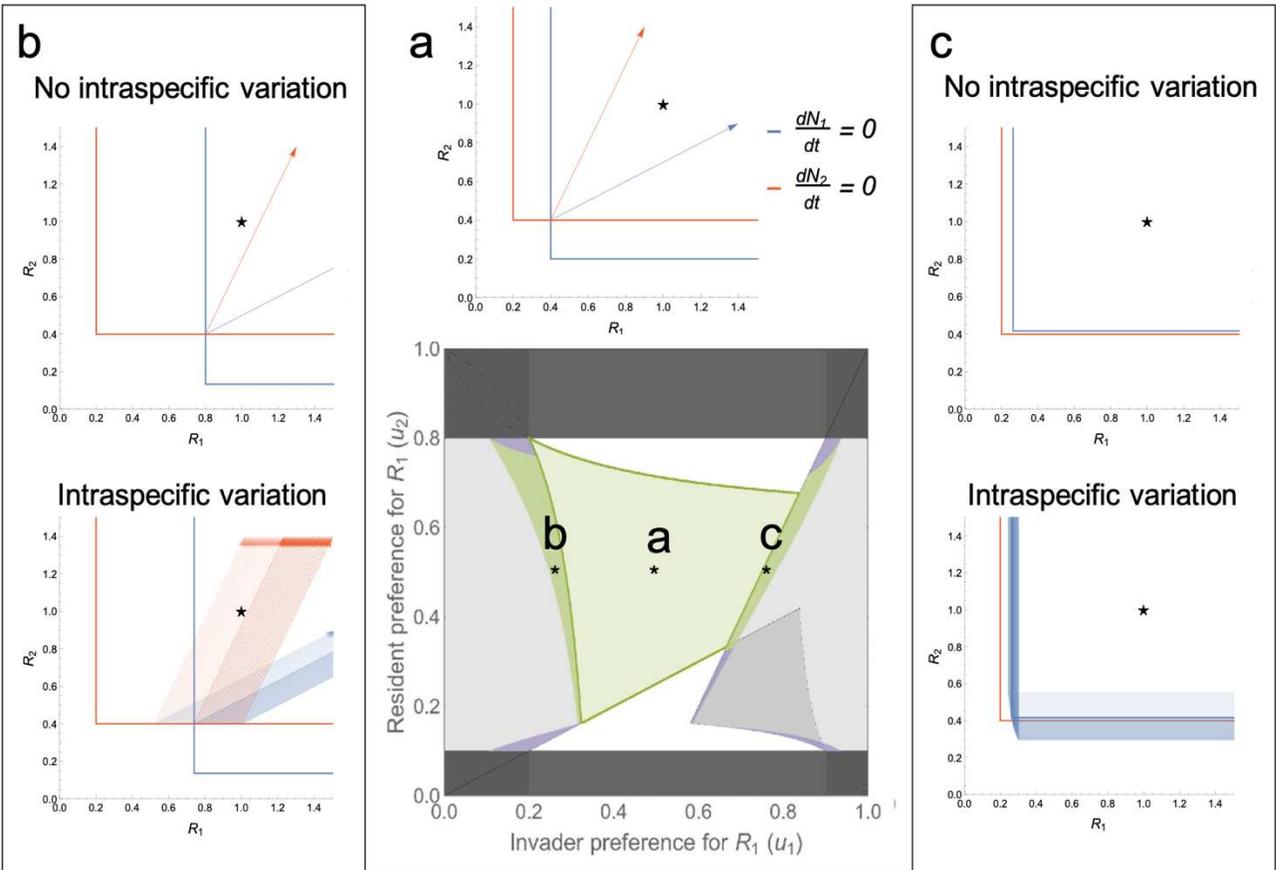
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800

801 **Fig 5**

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# 1 **Appendices**

## 2 *Appendix I: Model Details*

3 We determine the weighting parameter  $\omega_j$  by calculating the fraction of individuals  
4 whose trait value causes them to be limited by  $R_I$ , given the densities of  $R_I$  and  $R_2$  (Eq. 4). To  
5 solve  $\omega_j$ , we first assume that individuals express differences in a trait  $\phi$  that determines their  
6 uptake rates  $u_j$ , but not their yield coefficients, according to the sigmoid function:

7

$$8 \quad u_j(\phi) = 0.5 + \pi^{-1} \text{ArcTan}(h\phi) \quad (\text{S1})$$

9

10 The constant  $h$  determines the steepness of the tradeoff and therefore shapes how variation in  $\phi$   
11 translates into differences in  $u_j$ . Without loss of generality we assume  $h=1$ . The colimitation  
12 point for a single consumer is the uptake rate which satisfies the equivalence of both terms inside  
13 the minimization function in Eq. 2:

14

$$15 \quad u_c = \frac{R_2 y_{2j}}{R_1 y_{1j} + R_2 y_{2j}} \quad (\text{S2})$$

16

17 (Fox and Vasseur 2008). Rearrangement of Eq. S1 then gives the value of the trait which  
18 coincides with colimitation,  $\phi_c$  as:

19

$$20 \quad \phi_c = \text{Cot} \left( \frac{\pi R_1 y_{1j}}{R_1 y_{1j} + R_2 y_{2j}} \right) \quad (\text{S3})$$

21

22 To determine the effect of ITV on coexistence, analytically solve the invasion growth rate in a  
 23 community without ITV (Klausmeier *et al.* 2007, Fox and Vasseur 2008). We then compare this  
 24 to an invasion analysis of the model with intraspecific variation in one or both competitors  
 25 (*Appendix II: Invasion Analysis*) in order to inform our understanding of the importance of ITV  
 26 for coexistence.

27 Our model with variation is equivalent to the model without because our growth equation  
 28 (Eq. 6) converges to the growth equation without variation (Eq. 2) as variation approaches 0. As  
 29 variation approaches 0, the proportion of the population below the colimitation point  $\omega$  (Eq. 7)  
 30 will either be 1 (the whole population) or 0 (none of the population). For the case when  $\omega = 1$ ,  
 31 Eq. 6 reduces to:

$$32 \quad g_j = 1 y_{1j} \bar{u}_j R_1 + 0 y_{2j} \overline{(1 - u_j)} R_2 \quad (S4a)$$

33 which is equivalent to Eq. 2 when  $R_1$  is limiting. Similarly, when  $\omega = 0$  Eq. 6 reduces to

$$34 \quad g_j = 0 y_{1j} \bar{u}_j R_1 + -1 y_{2j} \overline{(1 - u_j)} R_2 \quad (S4b)$$

35 Note that the equation for  $\overline{(1 - u_j)}$  (Eq. 8b) contains an additional term to adjust the sign of this  
 36 second term so that it is positive and is equivalent to Eq. 2 when  $R_2$  is limiting.

### 37 *Appendix II: Invasion Analyses*

38 The invasion growth rate is proportional to Eq. 3, but where  $R_1$  and  $R_2$  represent the equilibrium  
 39 resource densities in a community with a single (resident) consumer. Since all other parameters  
 40 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  
 41 would be symmetric for scenarios in which  $N_2$  is the invader. We proceed with  $N_1$  as the invader  
 42 and  $N_2$  as the resident.

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

45

46

$$\{R_{11}, R_{21}\} = \left\{ S_1 + \frac{d_1 + S_2(u_2 - 1)y_{22}}{y_{12} - u_2 y_{12}}, \frac{d_1}{y_{22}(1 - u_2)} \right\} \quad (S5a)$$

47

48 when  $R_I$  is the limiting resource and

49

50

$$\{R_{11}, R_{21}\} = \left\{ \frac{d_1}{y_{12}u_2}, \frac{S_1u_2y_{12} - S_2u_2y_{22} - d_1}{u_2y_{22}} \right\} \quad (S5b)$$

51

52 when  $R_2$  is the limiting resource. The point where resource limitation switches from  $R_I$  to  $R_2$ , as53 a function of  $u$ , can be determined as:

54

55

$$u_{c1} = d_1 \left( -2 + \frac{S_1y_{11} + S_2y_{21}}{d_1} + \sqrt{4 + \frac{(-S_1y_{11} + S_2y_{21})^2}{2(-S_1y_{11} + S_2y_{21})}} \right) \quad (S6)$$

56

57 There is an additional condition that defines the persistence boundary for the resident consumer.

58 When  $R_I$  and  $R_2$  cannot meet or exceed the inflow concentrations of the resources  $S_I$  and  $S_2$ , the59 consumer cannot persist ( $N_2=0$ ) and therefore  $R_{11} = S_1$  and/or  $R_{21} = S_2$ .

60 Using this set of conditions we calculate the invasion growth rate of consumer (with ITV) into a

61 resident community (without ITV) as:

62

63

$$I_{inv} = \omega_{inv}y_{1inv}\bar{u}_{inv}R_1 + (1 - \omega_{inv})y_{2inv}\overline{(1 - u_{inv})}R_2 - d_{inv} \quad (S7)$$

64

65 In cases where both the invading and resident consumer have ITV, Eq. S7 still represents the

66 invasion growth rate. However,  $R_I$  and  $R_2$  will deviate from the analytical values determined in

67 Eqs. S5a and S5b to reflect the effects of ITV. To analyze these cases we utilize numerical  
 68 simulation of the resident dynamics to determine the  $R_1$  and  $R_2$  at equilibrium (see below). We  
 69 use Eq. S7 to calculate the maximum invasion growth rate for any amount of ITV  $\delta$  (see **Fig 6**  
 70 and **7** for details on how much variation is necessary to produce various outcomes).

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

75

$$76 \quad g_{res} = \omega_{res} y_{1res} \bar{u}_{res} R_1 + (1 - \omega_{res}) y_{2res} \overline{(1 - u_{res})} R_2 \quad (S8)$$

77

78 which is then substituted into the following system of equations:  $\square$

79  $\square$

$$80 \quad \frac{dR_i}{dt} = D(S_{res} - R_{res}) - \frac{N_{res} g_{res}}{y_{ires}} \quad (S9a)$$

$$81 \quad \frac{dN_{res}}{dt} = N_{res}(g_{res} - d_{res}) \quad (S9b)$$

82

83 where  $i = \{1,2\}$ . This system of equations can then be numerically solved for  $R_1$  and  $R_2$  at  
 84 equilibrium. Invasion analyses can then proceed as described in the main text by substituting  
 85 these solutions into Eq. S7.

### 86 *Appendix III: Resident Variation*

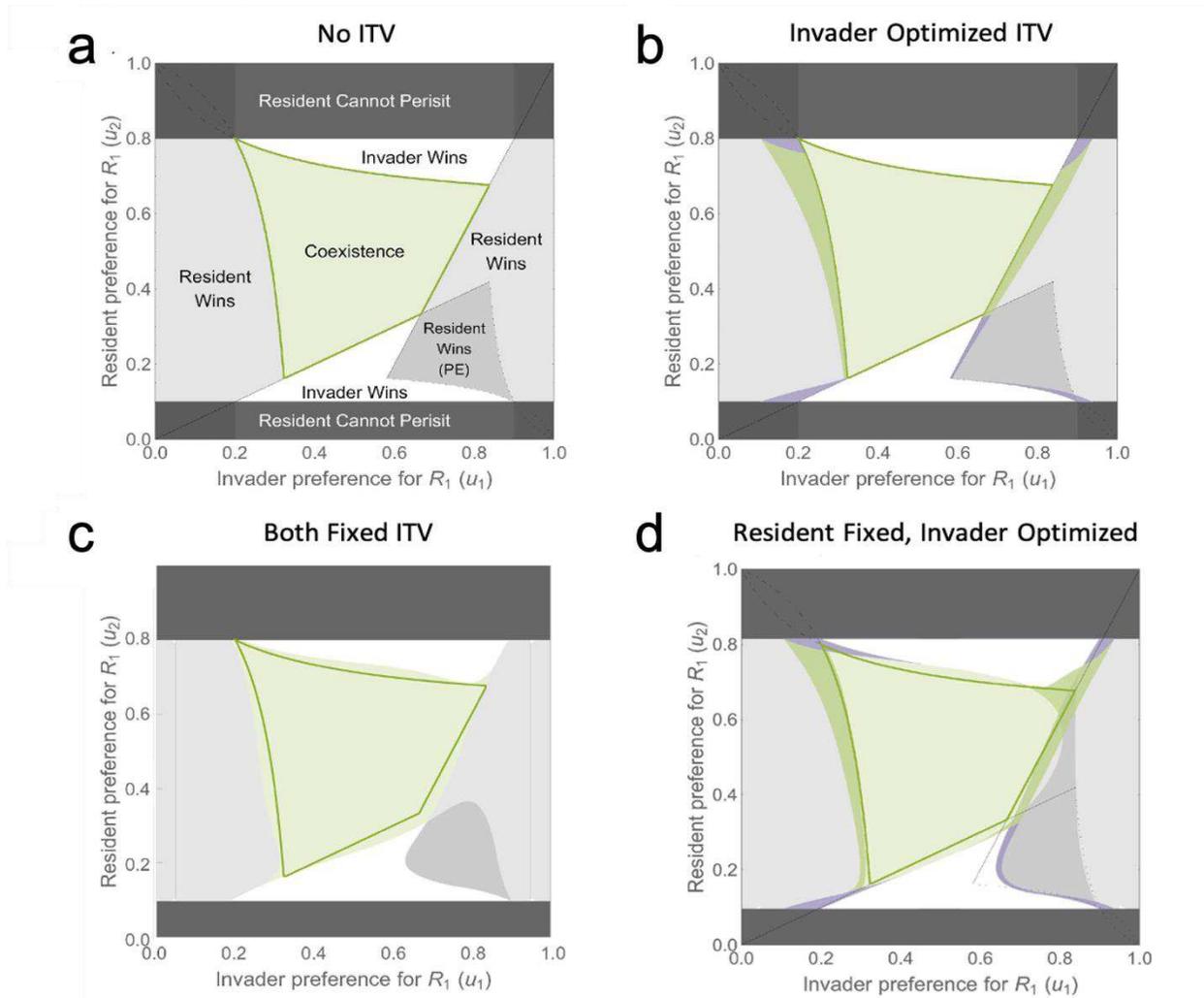
87 Previous work linking ITV to coexistence has found that the benefits of ITV are typically  
 88 constrained to cases where there are strict assumptions about the form of ITV itself. For  
 89 example, Barabás and D'Andrea (2016) found that two species with the same mean trait value

90 (on a single trait axis) could coexist if one had large ITV relative to the other. Here the  
91 generalist (large ITV) is successful outside the area of trait overlap while the specialist (small  
92 ITV) is dominant within this area. When the mean trait values differ among species, adding ITV  
93 in equal amounts to both competitors does not promote coexistence (Hart *et al.* 2016) but instead  
94 increases the niche overlap of species, leading to more intense interspecific competition and a  
95 weakening of the stabilizing mechanism. In contrast, we found that, in the case of essential  
96 resource competition, equal amounts of ITV in one or both competitors is capable to generating  
97 coexistence outside of the range of conditions under which coexistence is possible without ITV.

98 This is demonstrated in **Fig 6**, where in the absence of ITV, the invader has a negative  
99 invasion growth rate and both consumers are entirely limited by  $R_2$ . Increasing ITV in the  
100 invader leads to coexistence even when only a small fraction of individuals are limited by  $R_1$ ,  
101 because the contribution of those individuals to the population growth rate is outsized (**Fig 6b**).  
102 Similarly, when the resident competitor has ITV, coexistence occurs because a large enough  
103 fraction of the resident population shifts to limitation by  $R_1$  (**Fig 6c**). Even when only a small  
104 fraction of the population exists inside of the coexistence region, it can grow quickly enough to  
105 result in positive total population growth rates (**Fig 6d**).

106 The range of conditions that support coexistence expands more evenly along both axes if both  
107 the resident and the invader have fixed variation (**Fig 6c**). Fixed variation in both populations  
108 does not have any conditions under which the invader displaces the resident (**Fig 6c**), which can  
109 occur when the invader's variation is optimized for maximum invasion growth rate (**Fig 6d**).

110



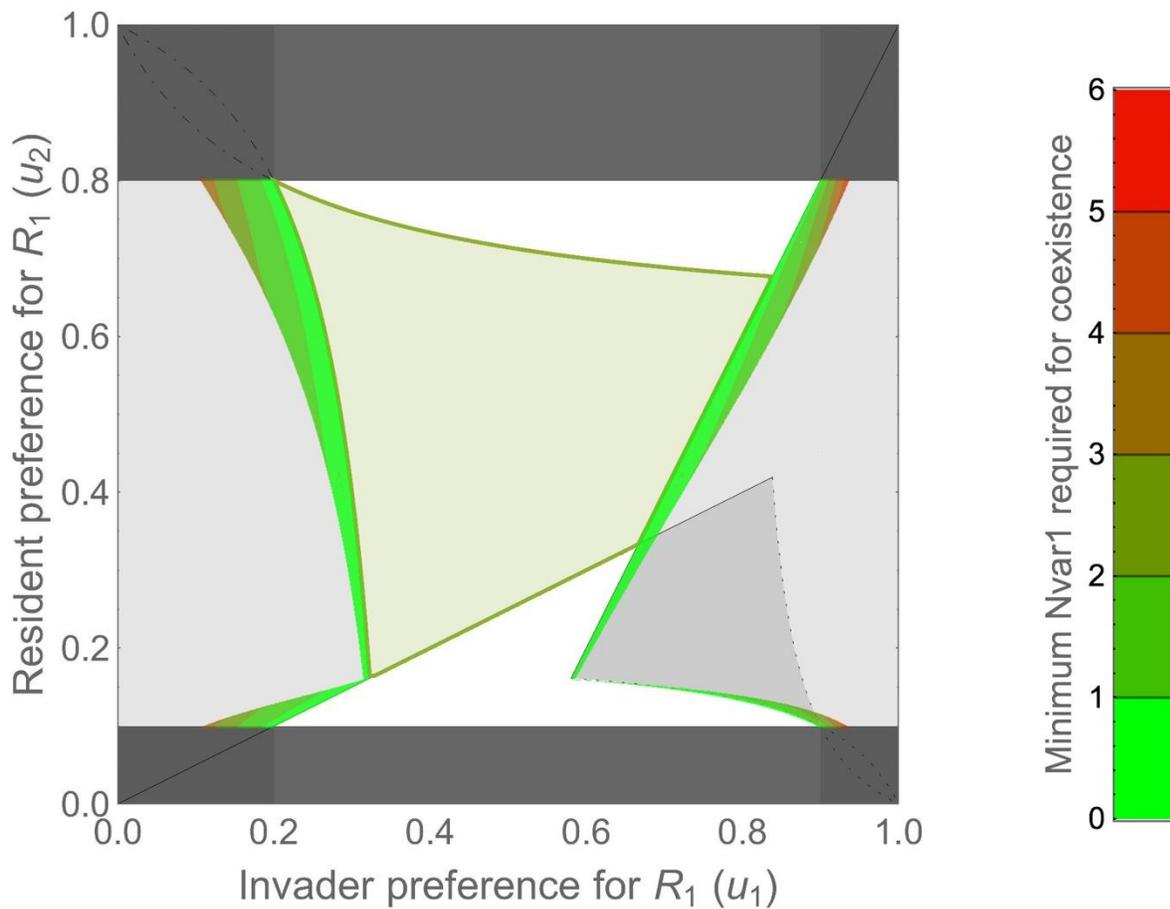
111  
 112 **Fig 6** Shows the outcome of competition across the domain of uptake preferences for resident  
 113 and invading consumers in for different scenarios incorporating (a) no ITV, (b) optimized ITV in  
 114 the invader, (c) a fixed amount of ITV in the resident and invader ( $\delta_1 = \delta_2 = 1$ ), and (d) fixed  
 115 variation in the resident ( $\delta_2 = 1$ ) and optimized variation in the invader. The lines dividing  
 116 outcome domains are adapted from Fox and Vasseur (2008) for the case without ITV and are  
 117 shown in all panels for contrast. Adding ITV to the invader (b) increases the domain of  
 118 coexistence (darker green) and the domain where the invader excludes the resident (violet).  
 119 Adding a fixed amount of ITV to the resident and invader (c) shifts the outcome domains and  
 120 acts in concert with ITV in the invader (d) to further increase the coexistence domain along all

121 four of its boundaries. In panels **(b)** and **(d)**, the extended regions show the outcome of  
122 competition for the extent of ITV ( $\delta$ ) which maximized the invasion growth rate (see *Appendix*  
123 *IV: Sufficient Amounts of Intraspecific Variation* for details on how much variation is necessary).  
124 Additional parameter values are given by  $S_1 = S_2 = 1$ ,  $y_{11} = y_{22} = 0.5$ ,  $y_{12} = y_{21} = 1$ ,  $d = 0.1$   
125 *Appendix IV: Sufficient Amounts of Intraspecific Variation*

126 Throughout the main text, we discuss competition outcomes with intraspecific variation.  
127 Here, we describe how much variation is necessary for these outcomes to occur. Relatively  
128 modest amounts of variation ( $\delta < 1$ ) can result in positive invasion growth rates and coexistence  
129 where it would otherwise not be possible (**Fig 7**), particularly when the resident's preference for  
130  $R_1$  and  $R_2$  are close to symmetrical (i.e.  $u_2 = \sim 0.5$ ). Larger amounts of variation are necessary to  
131 produce positive invasion growth rates when the resident's resource preferences become strongly  
132 skewed in either direction (**Fig 7**), which roughly corresponds to the regions where intraspecific  
133 variation leads to displacement of the resident by the invader rather than coexistence (see **Fig 2b**  
134 in the main text).

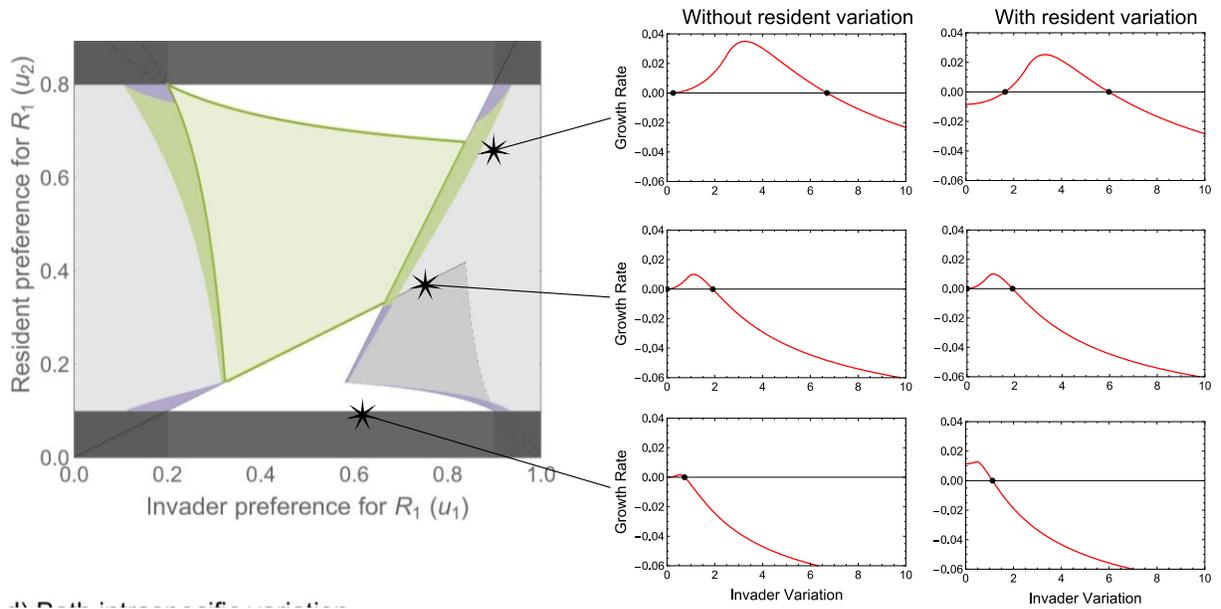
135 In some cases, when variation increases beyond a certain point (i.e. becomes "too large"),  
136 it is no longer beneficial for invasion. We demonstrate this by calculating invasion growth rates  
137 for a range of  $\delta$  from 0 to 10 for three fixed  $u_1, u_2$  combinations just outside of the coexistence  
138 boundary (**Fig 8**). If variation spreads the trait distribution in such a way that a large proportion  
139 of the population has an uptake ratio that skews heavily toward being limited by the same  
140 resource as its competitor, the proportion that is limited by the opposite resource is unable to  
141 compensate for the high degree of niche overlap experienced by the rest of the population (**Fig**  
142 **8**). As a result, overall population growth rates will be negative.

143 Since ITV's effect on coexistence is the product of nonlinearity in the uptake function  
 144  $u(\phi)$  (Eq. S1), it is useful to consider how different values of  $\delta$  change the distribution of uptake  
 145 rates. As ITV increases, the distribution of uptake rates in the population becomes increasingly  
 146 bimodal (**Fig 9**), consistent with the conclusion that continuous change in the trait  $\phi$  mapped onto  
 147 the sigmoid uptake function  $u(\phi)$  results in individuals being spread unevenly across the uptake  
 148 rate parameter space. The steepness of the nonlinearity in the function depends on the shaping  
 149 parameter  $h$  (Eq. S1), which we assume is equal to 1 throughout our analyses. Larger amounts of  
 150 ITV would be necessary for individuals to traverse this discontinuity for values of  $h < 1$ .  
 151 However, our results remain qualitatively the same.  
 152



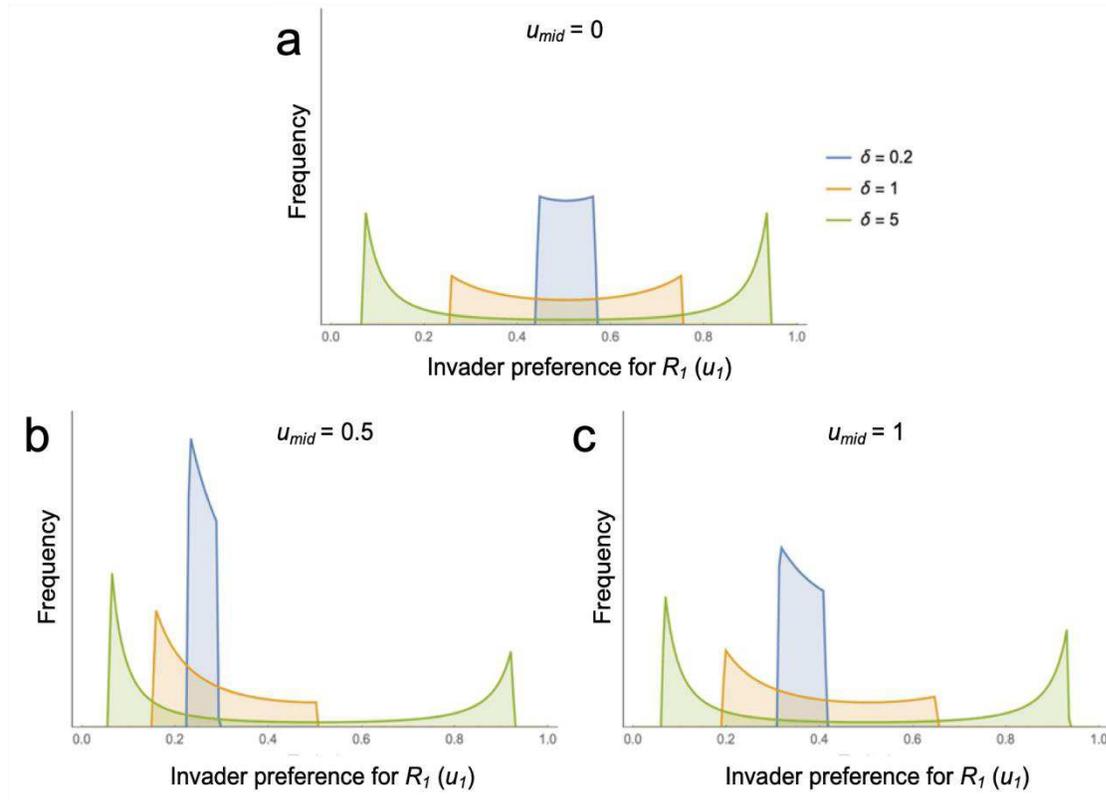
153

154 **Fig 7** Phase plane of the  $u_1, u_2$  surface showing the minimum amount of variation  $\delta$  needed to  
 155 produce a positive invasion growth rate  $I_{inv}$



156  
 157 **Fig 8** Invasion growth rates  $I_{inv}$  over a range of intraspecific variation values  $\delta$  at three points  
 158 along the coexistence boundary, with and without resident variation

159



160

161 **Fig 9** As the magnitude of variation ( $\delta$ ) increases, populations show an increasingly bimodal  
 162 distribution of uptake rates ( $u_1$ ). Shown here are distributions of uptake rates for populations with  
 163 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  
 164 green curved respectively). Note that the distribution of uptake rates converges upon the same  
 165 distribution regardless of  $u_{mid}$  as  $\delta$  increases

166 *Appendix V: Other Trait Distributions*

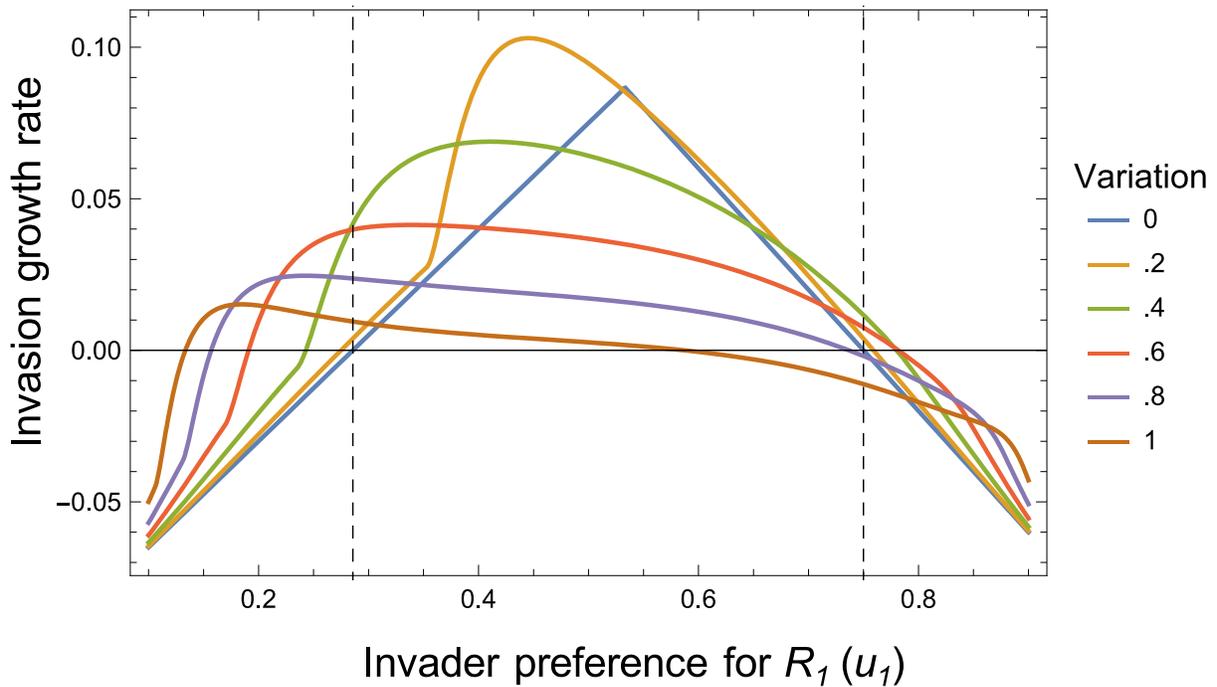
167 Although we assume a uniform distribution for our analyses to aid in mathematical  
 168 tractability, our results are robust to other trait distributions. For example, if trait variation takes  
 169 the form of a normal distribution such that  $\omega$  is calculated as

170

171 
$$\omega_j = \begin{cases} 1 & \text{if } \phi_c < \mu - 3\sigma \\ \frac{\Phi(\phi_c) - \Phi\left(-\text{Tan}\frac{\pi}{2 - \pi(\mu - 3\sigma)}\right)}{\Phi\left(-\text{Tan}\frac{\pi}{2 - \pi(\mu + 3\sigma)}\right) - \Phi\left(-\text{Tan}\frac{\pi}{2 - \pi(\mu - 3\sigma)}\right)} & \text{if } \mu - 3\sigma < \phi_c < \mu + 3\sigma \\ 0 & \text{if } \phi_c > \mu + 3\sigma \end{cases} \quad (\text{S10})$$

172

173 where  $\Phi$  is the cumulative distribution function of a normal distribution with a mean  $\mu$  and a  
 174 standard deviation  $\sigma$ , and  $\phi_c$  is the colimiting trait value, we show that variation in uptake rates  
 175 still allows for positive invasion growth rates outside of the region where they are possible  
 176 without variation (**Fig 10**).



177

178 **Fig 10** Invasion growth rates assuming a normal distribution for trait variation in uptake ranging  
 179 from  $\delta = 0$  to 1 when the resident preference for  $R_1(u_2) = 0.5$ . The region between the vertical  
 180 dashed lines is the range of  $u_1$  values over which positive invasion growth rates are possible  
 181 without variation

182 *Appendix VI: Competition Between Asterionella formosa and Cyclotella meneghiniana*

183 We show that ITV in uptake rates can alter zero-net growth isoclines and consumption  
184 vectors such that coexistence is possible under resource conditions that would otherwise lead to  
185 competitive exclusion (**Fig 3** in the main text). Tilman (1977) performed competition  
186 experiments with the diatoms *Asterionella formosa* and *Cyclotella meneghiniana* under various  
187 resource conditions. Tilman (1982) further shows that the competitive outcomes of these  
188 experiments generally agree with the graphical predictions based on zero-net growth isoclines  
189 and consumption vectors parameterized for these species. However, two data points that fall  
190 within the graphical region where *C. meneghiniana* should win resulted in coexistence in the  
191 experiments. Using yield and death rate parameters from Tilman (1977) and  $R^*$  values from  
192 Tilman (1982) (**Table 1**), we calculated uptake rates of each resource for each species using

193

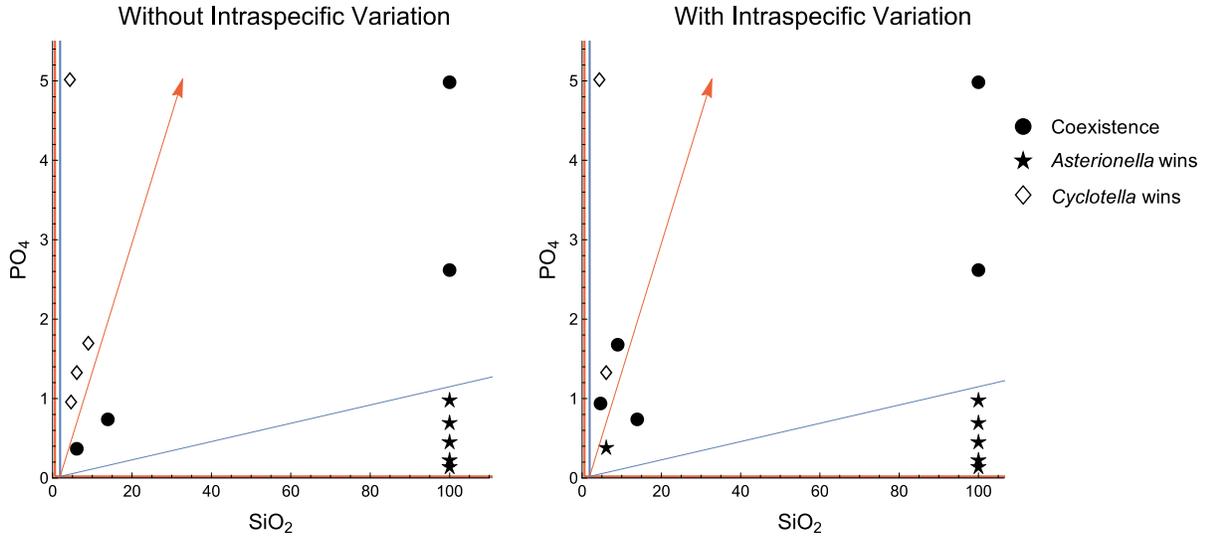
194

$$u_{ij} = \frac{d_j}{R_{ij}^* y_{ij}} \quad (\text{S11})$$

195

196 where  $i, j = \{1, 2\}$ . We then used resource supply values ( $S_1, S_2$ ) extracted from Tilman (1982)  
197 using ImageJ (Schneider *et al.* 2012) to numerically solve our model for the outcomes of  
198 competition with and without ITV in the uptake rates of *A. formosa*. Without ITV, the outcomes  
199 are as predicted by the graphical model (**Fig 11**). Intraspecific trait variation in the uptake rates  
200 of *A. formosa* alter the outcomes of competition at three data points, including the two that do  
201 not align with the prediction in the original data set (**Fig 11**).

202



203

204

**Fig 11** Intraspecific trait variation can alter zero-net growth isoclines and consumption vectors

205

such that coexistence is possible under resource conditions where it is not possible without ITV.

206

Using parameters from Tilman (1977, 1982), we determined the outcome of competition

207

between diatoms *Asterionella formosa* (blue) and *Cyclotella meneghiniana* (red) with and

208

without ITV in uptake rates for *A. formosa*. In the original experiments, two data points resulted

209

in coexistence where the model without variation predicts that *C. meneghiniana* should win. The

210

model with ITV in *A. formosa* leads to coexistence in the same two data points, here denoted by

211

the two points that change from diamonds in the left panel to circles in the right panel.

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

212

213

**Table 1** Parameter values from Tilman (1977, 1982) used to numerically solve our model for

214

competitive outcomes between *A. formosa* and *C. meneghiniana* with and without ITV in the

215

uptake rates of *A. formosa*.

216

217

### Appendix VII: Other Functional Forms

218

In the main text, we consider what a trait mapping function that would allow ITV to

219

promote coexistence might look like. The sigmoid trait mapping function (Eq. 3) used in our

220 model is the critical component that allows ITV to contribute to stabilizing mechanisms and,  
221 thereby, promote competition. In this appendix, we consider other functional forms of trait  
222 mapping.

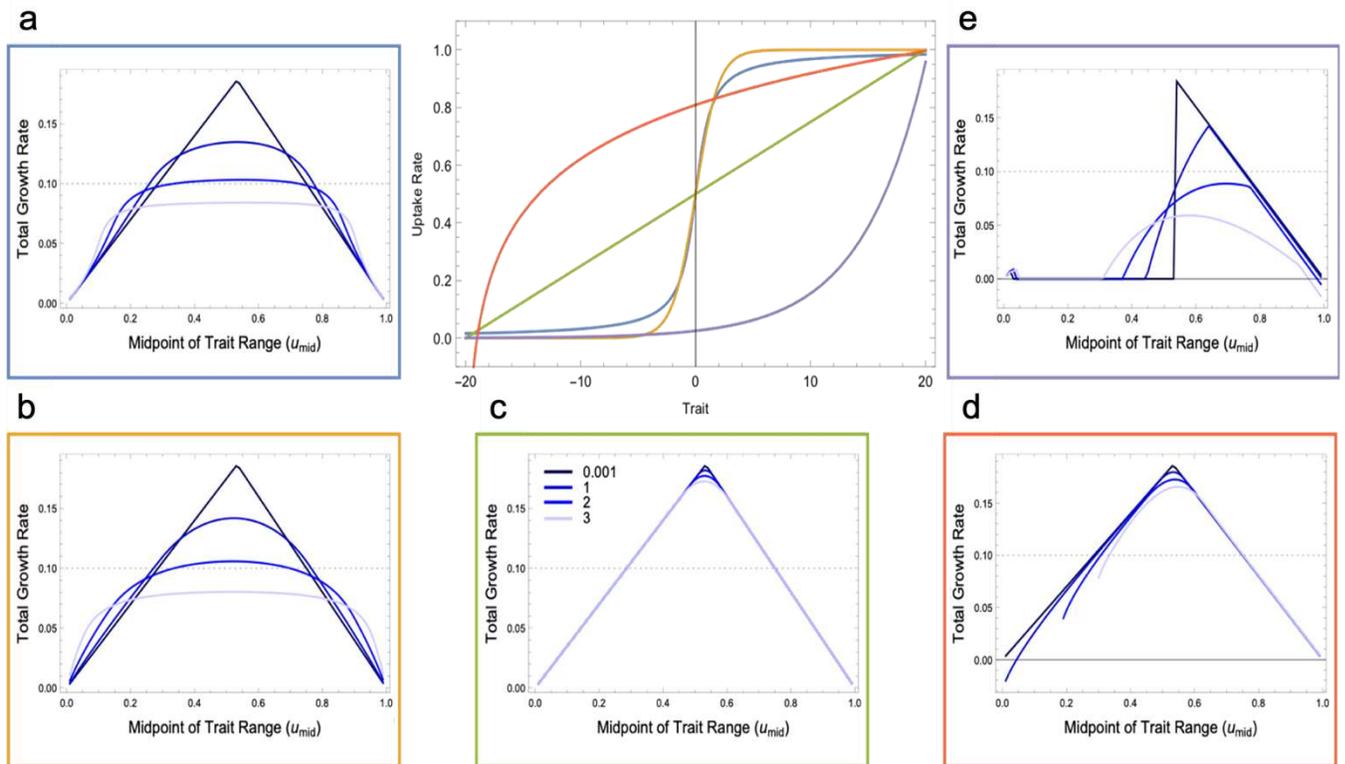
223 Here we consider four alternatives (**Table 2**) to the trait mapping function used in the  
224 main text (Eq. 3). We consider a sigmoid function that differs in detail from the sigmoid function  
225 used in the main text but produces a qualitatively similar function form. Importantly, it retains  
226 the two key features of Eq. 3 – nonlinearity and discontinuity. We also consider linear,  
227 saturating, and exponentially increasing functions. The latter retain the feature of nonlinearity,  
228 though with only one kind of concavity, while the former has neither. As noted in the main text,  
229 sigmoid functions also provide a way of naturally constraining uptake preference to the plausible  
230 range  $[0,1]$  while still allowing the trait to be unbound in the range  $[-\infty,\infty]$ . None of the other  
231 functions presented in this appendix have this feature and must have additional constraints added  
232 to trait space in order to maintain the plausible range for uptake preference.

233 We used each functional for to calculate the total population growth rate across different  
234 trait range midpoints  $u_{mid}$  and at four different levels of variation  $\delta$  (**Fig 12**). The two sigmoid  
235 functions produced qualitatively identical results, demonstrating that the details of the function  
236 are not as important as retaining the features of nonlinearity and discontinuity (**Fig 12a** and **12b**).  
237 In particular, adding a relatively small amount of variation when either sigmoid function is used  
238 expands the range of  $u_{mid}$  at which the invasion growth rate is positive. However, relatively large  
239 amounts of variation reduce the total growth rate across all  $u_{mid}$  values, indicating that too much  
240 variation is detrimental to coexistence (see *Appendix IV: Sufficient Amounts of Intraspecific*  
241 *Variation*). When a linear function is used to map traits onto uptake preference, adding variation  
242 does not change the range of  $u_{mid}$  across which the invasion growth rate is positive (**Fig 12c**). The

243 saturating and exponentially increasing functions (**Fig 12d** and **12e**, respectively) both decrease  
 244 the range of  $u_{mid}$  values over which growth rates are positive.

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

245 **Table 2** Summary of functional forms of the trait mapping function considered in *Appendix VII*:  
 246 *Other Functional Forms.*



247 **Fig 12** The form of the function that maps quantitative trait  $\phi$  onto uptake  $u_j$  is critical to how  
 248  
 249 ITV affects the total population growth rate. Shown here is the total population growth rate as a  
 250 function of the midpoint of the trait range at four levels of variation ( $\delta = \{0.001, 1, 2, 3\}$ ). The five  
 251 possible forms of this function include (**a**) the sigmoid function used in the main text, (**b**) an

252 alternative sigmoid function, **(c)** a linear function, **(d)** a saturating function and **(e)** an  
253 exponentially increasing function. The horizontal dashed line indicates the death rate, above  
254 which growth is positive and below which growth is negative.