

Quantifying the Likelihood of Co-existence for Communities with Asymmetric Competition

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Abstract Trade-offs in performance of different ecological functions within a species are commonly offered as an explanation for co-existence in natural communities. Single trade-offs between competitive ability and other life history traits have been shown to support a large number of species, as a result of strong competitive asymmetry. We consider a single competition-fecundity trade-off in a homogeneous environment, and examine the effect of the form of asymmetry on the likelihood of species co-existing. We find conditions that allow co-existence of two species for a general competition function, and show that (1) two species can only co-exist if the competition function is sufficiently steep when the species are similar; (2) when competition is determined by a linear function, no more than two species can co-exist; (3) when the competition between two individuals is determined by a discontinuous step function, this single trade-off can support an arbitrarily large number of species. Further, we show analytically that as the degree of asymmetry in competition increases, the probability of a given number of species co-existing also increases, but note that even in the most favourable conditions, large numbers of species co-existing along a single trade-off is highly unlikely. On this basis, we suggest it is unlikely that single trade-offs are able to support high levels of bio-diversity without interacting other processes.

Keywords Lotka–Volterra · Trade-offs · Community ecology · Niche · Life-history

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1 Introduction

There is no such thing in the natural world as a Darwinian demon which maximizes all possible life history traits (Law 1979), and instead individuals have to allocate resources to one life-history trait at the expense of others. This results in trade-offs between life history traits, so that, for example a plant species which allocates resource to rapid growth does so at the expense of its ability to withstand shading; or a species that has allocated much of the available resource to out-competing other species will suffer a decrease in its ability to disperse and colonise empty areas of the environment (e.g. Tilman 1994; Cadotte et al. 2006). Other classic life-history trade-offs include the offspring size-number trade-off (e.g. Venable 1992); the trade-offs between pathogen resistance and fecundity (e.g. Bowers et al. 1994); and competition and intra-guild predation (Amarasekare 2007).

Theory has shown that these trade-offs can allow two or more species to co-exist while competing for the same resources (e.g. Kisdi and Geritz 2003; Levins and Culver 1971; Bonsall and Mangel 2004), and consequently that trade-offs may be instrumental in the evolution of bio-diversity (Schluter 1995; White and Bowers 2005; Bonsall and Mangel 2004). In particular, Levins and Culver (1971) originally highlighted two such trade-offs, the competition-colonisation trade-off which has received much attention, and the trade-off between death rate and competitive ability which has received less attention. Levins and Culver argued that two species can co-exist if one experiences a lower death rate, but is a weaker competitor than the other species. Both trade-offs are closely related, and have received much attention, with Tilman (1994) showing that the competition-colonisation trade-off can potentially lead to infinitely many species co-existing.

However, the conditions under which species either competitively exclude, or co-exist alongside others due to trade-offs between competition and other life history traits might also be dependent on the existence and level of asymmetric competition between species (Adler and Mosquera 2000). Competition is called asymmetric if an individual with larger trait value (e.g. size) is bestowed some benefit over small trait valued neighbours, winning more than 50 % of contests by virtue of this difference in trait. This competition is deemed to be very asymmetric if there is a large difference in competitive ability between individuals which have slightly different trait values. Asymmetric competition is widespread in the natural world, forming the majority of inter-species competition in insects (Lawton and Hassell 1981); and is prevalent in plants where competition for light is expected to be size dependent, such that a larger plant may intercept nearly all the available light at the expense of a smaller individual (Weiner 1990). However, there is relatively little theory that investigates how the strength of competitive asymmetry may affect the maintenance of bio-diversity.

Adler and Mosquera (2000) demonstrated that, if the competition between two species is determined by a step function with infinite gradient when traits are the same, then the species richness, the number of species present in the community, is maximised in their model. They then used numerical simulations of their model to show how reducing the degree of competitive asymmetry reduces the number of species that can co-exist on the trade-off. Similarly, Kisdi (1999) showed that the gradient of the competition function at the point where two competing individuals

95 have the same trait value (i.e. the same size), is critical in determining the number
96 of species that may evolve in the long term. In other words, co-existence and the
97 evolution of a large community seem to be more likely if a small change in fecundity
98 translates into a large change in competitive ability.

99 Here, we build on this previous work and analyse a model with a single trade-off
100 between competitive ability and fecundity. We will find conditions required for two
101 species to co-exist, and demonstrate that while no more than two species can co-exist
102 when competition is a linear function of the trait value, if the mechanisms of the
103 competition between species allows for a discontinuity in the competition function,
104 then co-existence of any number of distinct species is possible. We also demonstrate
105 analytically for two species that this discontinuous competition gives an upper bound
106 on the likelihood of co-existence when compared with two convex–concave functions
107 that tend to the step function as parameters are altered. Niche theory suggests that as
108 species become more similar co-existence should become more unlikely, but few
109 studies have quantitatively investigated this in the context of life-history trade-offs.
110 Using rigorous proofs, we will show that competitive asymmetry and the gradient
111 of the competition function at the origin are important in determining the number
112 of species able to persist on one trade-off, but also show that even under the most
113 favourable conditions, large numbers of species co-existing on one trade-off is very
114 unlikely.

117 2 The Model

118
119 We examine co-existence criteria in a simple model where species differ only in
120 their per capita fecundity and their competitive ability. The per capita fecundity is
121 compared to competitive ability through assigning a trait value to each species. The
122 typical traits we have in mind are body size, or weight of armament, and a strong
123 competitor has a lower fecundity, creating a competition-fecundity trade-off. In do-
124 ing so, we assume a species which is a stronger competitor diverts resources into this
125 trait, perhaps by delaying reproduction and growing in size; whereas a weaker com-
126 petitor diverts more resources into reproduction at the cost of competitive ability. We
127 assume this trade-off, which restricts parameter space within the model, is conserved
128 across species, and that it can be described by two functions that relate a species' trait
129 value to (i) fecundity, and (ii) competitive ability. In particular, we will explore how
130 the shape of the latter function is important in determining the amount of species that
131 may be supported by the trade-off.

132 Let n denote the number of species present in the environment, with species i
133 having expected size x_i and population density N_{x_i} . We use Lotka–Volterra equations
134 to describe the population dynamics:

$$136 \frac{dN_{x_i}}{dt} = N_{x_i} \left(p(x_i) - \sum_{j=1}^n c(x_i - x_j) N_{x_j} \right), \quad (1)$$

139 where $p(x_i)$ is the intrinsic growth rate of species i when resources are not limiting
140 and the environment is free of competition; $c(x_i - x_j)$ is the competition kernel used
141

142 to quantify the impact of competition with species j on species i which depends only
143 on the difference in trait values $x_i - x_j$. For larger species, which have lower fecun-
144 dity, $p(x_i)$ is lower than for species with smaller trait values, so we assume that $p(x_i)$
145 is a strictly decreasing non-negative function of trait value x_i . The intrinsic growth
146 rate p is assumed to be greater than zero, as any species with a non-positive growth
147 rate would not be able to grow in even an empty environment. Since we are at liberty
148 to choose units for x , we choose $x_{\max} = 1$ since the maximum trait value for which
149 the growth rate is zero: $p(1) = 0$. Similarly, we let $x_{\min} = 0$ be the smallest permis-
150 sible trait value, meaning all extra resources are diverted into fecundity rather than
151 competitive ability. In what follows, we will mainly work with the linear growth func-
152 tion $p(x_i) = \rho(1 - x_i)$ where $\rho > 0$. However, we will use $p(x_i)$ wherever possible
153 in order to show how the method may be extended to non-linear growth functions.
154 Using these assumptions, our aim is to investigate the possibility and probability of
155 co-existence of species selected at random across the entire trait-space.

156 The continuous competition kernels $c(x_i - x_j)$ we consider are non-increasing
157 functions of the difference between the individual's trait value and that of its com-
158 petitor, i.e. non-increasing in $(x_i - x_j)$. This means that an individual with large trait
159 value experiences little competition from competing individuals with smaller trait
160 values, while small trait value individuals suffer a much larger competitive effect
161 from large individuals. For example, taller trees will clearly intercept light earlier
162 than shorter individuals, while shading shorter neighbours. However, shorter trees
163 will have limited shading effect on a tall neighbour. We use convex-concave func-
164 tions, to reflect the realistic assumption that two large species will have a similar
165 effect on a much smaller third species, while a large individual will suffer approx-
166 imately equal effects from two much smaller individuals. However, when all three
167 species are of similar size, the effects of the larger (smaller) two on the smallest
168 (largest) may vary significantly. The discontinuous competition is a suitable limit of
169 such continuous functions, and although it is less realistic, it allows for useful analyt-
170 ical upper bounds for the continuous cases.

171 We study the effects of asymmetric competition for two species considering
172 (1) a general function $c(z)$ and linear growth, with a focus on two examples; and
173 (2) for general growth $p(x_i)$ with linear and step function $c(x_i - x_j)$, which we also
174 consider for $n > 2$. As with the growth function, the general linear competition kernel
175 is studied, with

$$176 \quad c(x_i - x_j) = \kappa - \theta(x_i - x_j), \quad (2)$$

178 but additional restrictions are applied to the convex-concave and step functions
179 model. To ensure that the effect of this competition is never positive, such that the
180 model represents a predator-prey interaction or mutualism, it is necessary to have
181 $\kappa > \theta$. The intra-specific competition (i.e. when $x_i = x_j$) is assumed to be identical
182 across species, and can be scaled to one to reduce the number of parameters, and it
183 is assumed that the total negative effect of competition in an interaction between any
184 two individuals is the same. Ecologically, this means that there is a set amount of
185 resource to be shared between any two individuals. When the two individuals are the
186 same species and have equal trait values, each takes on average 50 % of the resource,
187 or wins the competitive contest roughly half of the time. When the trait values differ,
188

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189 the stronger competitor takes a greater percentage of the resource, leaving less for the
 190 weaker competitor. To reflect this, we study two continuous competition functions, a
 191 piecewise linear function given by

$$192 \quad c(x_i - x_j) = \begin{cases} 1 + \epsilon & x_i - x_j \leq -\Theta, \\ 1 - \frac{\epsilon}{\Theta}(x_i - x_j) & -\Theta < x_i - x_j < \Theta, \\ 1 - \epsilon & x_i - x_j > \Theta, \end{cases} \quad (3)$$

196 and a smooth function modified from that used by Kisdi (1999), which we consider
 197 as

$$198 \quad c(x_i - x_j) = 1 + \epsilon - \frac{2\epsilon}{1 + e^{-\frac{2(x_i - x_j)}{\Theta}}}. \quad (4)$$

202 As Θ tends to zero, these two functions both tend to a step function, that will be
 203 considered in detail for general n species dynamics. This function is given by

$$204 \quad c(x_i - x_j) = \begin{cases} 1 + \epsilon & x_i < x_j, \\ 1 & x_i = x_j, \\ 1 - \epsilon & x_i > x_j, \end{cases} \quad (5)$$

209 and is used as the discontinuous competition function throughout this study (see also
 210 Tilman 1994; May and Nowak 1994).

211 Our model is similar to those studied by Law et al. (1997) and Kisdi (1999), al-
 212 though both of their models only considered a concave–convex competition function
 213 in lieu of the linear and discontinuous functions considered for large n here. The
 214 function $c_{k,v}(z) = c(1 - 1/(v + e^{kz}))$ used by Kisdi, of which (4) is a modified ver-
 215 sion tends to a discontinuous step function of the type studied here as $\theta = 1/k$ tends
 216 to zero ($v > 0$ fixed). The use of simplified competition functions in this study allows
 217 for more analytical work than the more complex functions used in Kisdi’s analysis.
 218 We demonstrate in the two species case that our results for the discontinuous com-
 219 petition function are similar to those produced using the competition kernel given
 220 by (4) when θ is small, and hence allow for comparison with Kisdi’s competition
 221 model which shows qualitatively similar results for two species co-existence with
 222 linear growth.

223 When $\epsilon = 1$, our model with a step function $c(z)$ takes the same form as the spa-
 224 tially implicit model presented by Klausmeier (1998), which also demonstrates that
 225 co-existence is possible for general n . However, this current study builds upon this
 226 work to indicate both the likelihood of this co-existence, and the effects of weakened
 227 asymmetry in competition.

228 Before studying the effects of trade-offs on the co-existence of species, it is impor-
 229 tant to clarify what we mean by co-existence. In its strongest sense, co-existence can
 230 be taken to mean that all species present persist at a given positive equilibrium value.
 231 This means that any mathematical model of the system will exhibit co-existence
 232 if and only if there is a positive fixed point that is globally asymptotically stable,
 233 in the sense that all initial conditions for which each species has positive density
 234 end up at a positive equilibrium density. This is the notion of co-existence used
 235

236 by Strobeck (1973). Law and Morton (1996) uses a less stringent definition of co-
 237 existence, namely that the system exhibits co-existence if all species densities remain
 238 bounded and for all positive initial densities, there is a density $\delta > 0$ such that all the
 239 species eventually exceed δ , demonstrated mathematically by the concept of perma-
 240 nence. In this study, a collection of species is considered to exhibit co-existence if the
 241 model of those species exhibits permanence. However, as permanence is an imme-
 242 diate consequence of a globally asymptotically stable equilibrium in the interior, the
 243 existence of the latter is used to show co-existence in our discontinuous competition
 244 model.

245 In later sections, we study n-species communities and investigate the likelihood of
 246 co-existence given the model, and the trade-off function. Here, we assume commu-
 247 nities are assembled randomly from a regional species pool where all species (trait
 248 values) are present. We note that our results will be different to the expected number
 249 of species that will evolve via small mutations from a mono-specific community; or
 250 from community assembly by invasion of species one at a time; but in both cases
 251 relatively high levels of co-existence are required for large communities to occur.

253 3 Results

254 3.1 Linear Competition

255
 256
 257 Suppose that the competitive advantage held by one species over another is a linear
 258 function of the difference between the trait values of the two species. Then the com-
 259 petition coefficients $c(x_i - x_j)$ in (1) are determined by use of the function given
 260 in (2). In order to preserve the competition-fecundity trade-off, it is necessary that as
 261 fecundity decreases—and the function $p(x_i)$ decreases—the competitive advantage
 262 that the species holds over a fixed, weaker competitor is increasing. This translates
 263 to the mathematical condition $\theta > 0$. To simplify the calculations, it is assumed that
 264 $x_i > x_{i+1}$, but the results shown apply to any ordering of species and, therefore, trait
 265 values. The equations for the two species system are
 266

$$267 \frac{dN_{x_1}}{dt} = N_{x_1} \{ p(x_1) - \kappa N_{x_1} - (\kappa - \theta(x_1 - x_2)) N_{x_2} \}$$

$$268 \frac{dN_{x_2}}{dt} = N_{x_2} \{ p(x_2) - (\kappa - \theta(x_2 - x_1)) N_{x_1} - \kappa N_{x_2} \}.$$

269
 270
 271
 272 This model admits an interior fixed point when

$$273 \frac{\kappa}{\theta} \frac{p(x_2) - p(x_1)}{p(x_2)} < x_1 - x_2 < \frac{\kappa}{\theta} \frac{p(x_2) - p(x_1)}{p(x_1)}, \quad (6)$$

274
 275
 276 and this is globally stable whenever it exists, since $\kappa > 0$ by assumption. Therefore,
 277 co-existence is possible if the condition (6) is satisfied.

278 However, the limits of linear competition in giving rise to co-existence are shown
 279 if a third species is introduced to the system. We now demonstrate that regardless of
 280 the trait value this species holds, or the parameter values for κ, θ , it cannot form a
 281 permanent three species system with the two already species present.
 282

Note that when Eq. (2) is used, the 3×3 matrix of competition coefficients has a determinant of zero, i.e. is singular, and that therefore the model does not have a unique equilibrium point in the interior. In Lotka–Volterra systems, this means that the system does not exhibit permanence (Theorem 13.5.1 in Hofbauer and Sigmund 1998).

Therefore, no third species can form a permanent coalition with the two species already present. We conclude that with a linear function for competition, a maximum of two species can stably co-exist and when a third species is introduced, the model exhibits neither asymptotic stability nor permanence. The linear trade-off case is degenerate, but it is useful in illustrating the dependence of the model on the form of the competition function. We therefore switch our attention to a model utilising a non-linear competition function.

3.2 Generalised Competition in the Two Species Case

Consider a generalised competition function $c(x_i - x_j) = c(z)$, which is decreasing, such that $c(z) \leq 0$ for all z , for two species. These species are different in two aspects, competitive ability and population growth rate (effectively K and r , respectively), both of which are determined by a single parameter x_i for species i . We assume that growth rate decreases linearly with x_i , such that x_i can be considered as the proportion of non essential resource dedicated to competitive strength at the expense of population growth rate. It is simple to scale the model such that we can define this growth rate by the function $p(x) = 1 - x$. This therefore means that competitive ability must increase with x_i when the second species remains unchanged. We assume that the competition coefficients are a function of $x_1 - x_2$, so therefore can be treated by a function $c(z)$ of a single variable z . The competition coefficient c_{ij} gives the negative effect of species j on species i , and is defined by $c(x_i - x_j)$. This means that $c(z)$ must be a monotonically decreasing function of z . Note the model can be scaled to ensure $c(0) = 1$ without any loss of information.

If two species have identical competitive ability, but differ in growth rate, then the faster growing species would competitively exclude the slower grower, so an essential condition for co-existence is that $c'(0) < 0$.

Therefore, the system is given by

$$\dot{N}_1 = N_1(1 - x_1 - N_1 - c(z)N_2), \quad (7)$$

$$\dot{N}_2 = N_2(1 - x_2 - N_2 - c(-z)N_1), \quad (8)$$

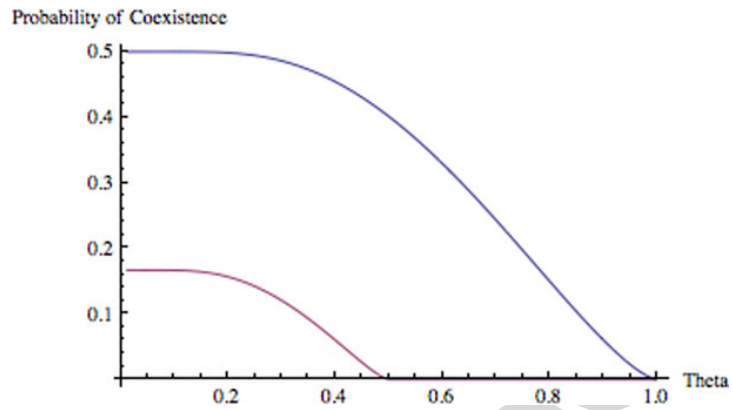
where $z = x_1 - x_2$. The condition for global stability of an interior fixed point is then given by $c(z)c(-z) < 1$, which is therefore a further condition on the function $c(z)$ for co-existence in the 2-species case.

It is simple to show that an interior fixed point is present when

$$1 - x_1 - c(z)(1 - x_2) > 0, \quad (9)$$

$$1 - x_2 - c(-z)(1 - x_1) > 0. \quad (10)$$

Fig. 1 How the probability of co-existence given by the convex–concave function (4) changes with the parameter Θ , which determines the steepness of the curve. Shown are the cases $\epsilon = 1$ and $\epsilon = 1/2$



By writing these as functions of z and x_2 , it is possible to rearrange to get

$$x_2 < \frac{1 - z - c(z)}{1 - c(z)}, \quad (11)$$

$$x_2 > \frac{(1 - z)c(-z) - 1}{c(-z) - 1}. \quad (12)$$

We now assume without loss of generality that species 1 is the competitively dominant species, i.e. $z > 0$. Then if we define z^* such that $1 - z^* - c(z^*) = 0$ and \hat{z} such that $1 - (1 - \hat{z})c(-\hat{z}) = 0$, (defined uniquely for convex–concave functions where $zc''(z) > 0$ for $z \neq 0$ and $c'(0) < -1$), then the area of co-existence can be found by

$$2 \left(\int_0^{z^*} dz \frac{1 - z - c(z)}{1 - c(z)} - \int_0^{\hat{z}} dz \frac{(1 - z)c(-z) - 1}{c(-z) - 1} \right), \quad (13)$$

where the factor of 2 is to include the other ordering of traits. It is relatively simple to show that with these assumptions, coupled with the fact that $c(-z) + c(z) = 2$, co-existence is only possible if $c'(0) < -1$ (Appendix A). This is in accordance with the work of Adler and Mosquera, who state that mono-culture will prevail when the steepness of the competition curve has magnitude less than 1.

As an example, we use the modified version of the function used by Kisdi (1999) given by (4), scaled such that the intra-specific competition coefficients are unity, and the parameter ϵ measured the greatest level of dominance possible, so $c(z) \in [1 - \epsilon, 1 + \epsilon]$ for all z . There is an issue in that z^* and \hat{z} as defined above cannot be found by simply rearranging these equations. However, as demonstrated in Fig. 1, when we numerically find the area of the region of co-existence, this area monotonically decreases as the parameter Θ is increased. The likelihood of co-existence is maximised at $\Theta = 0$, where the competition coefficients are determined by a step function. Using Taylor series expansions of the functions $F_1(z) = 1 - z - c(z)$ and $F_2(z) = (1 - z)c(-z) - 1$, we can show that the area of co-existence tends to the results presented in Sect. 3.3 as Θ approaches 0.

As a further example, we can investigate the piecewise linear function (3), where pairs of species with similar trait values will have different effects on one another than pairs with different trait values, but that once a threshold of dissimilarity is passed, all species have the same effect on one another. Note that this approximates the smooth

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function (4) considered above. This gives two cases, as the function $(1 - z)^{-1}$ will cross $c(-z)$ on the constant part for small Θ , but the sloped part for slightly larger Θ . The two cases are that where $\Theta < \frac{\epsilon}{(1+\epsilon)}$ and that where $\frac{\epsilon}{(1+\epsilon)} < \Theta < \epsilon$. In the case where Θ is small, we can write the above integrals as

$$\begin{aligned}
 & 2\left(\int_0^\Theta \frac{\epsilon - \Theta}{\epsilon} dz + \int_\Theta^\epsilon 1 - \frac{z}{\epsilon} dz - \int_0^\Theta \frac{\epsilon - \Theta}{\epsilon} - z dz - \int_\Theta^{\frac{\epsilon}{1+\epsilon}} 1 - \frac{1 + \epsilon}{\epsilon} z dz\right) \\
 &= 2\left(\Theta - \frac{\Theta^2}{\epsilon} + \frac{\epsilon}{2} - \Theta + \frac{\Theta^2}{2\epsilon} - \Theta + \frac{\Theta^2}{\epsilon} + \frac{\Theta^2}{2} + \frac{\epsilon}{2(1+\epsilon)^2} + \frac{\epsilon^2}{2(1+\epsilon)^2}\right. \\
 &\quad \left. - \frac{\epsilon}{1+\epsilon} + \Theta - \frac{\Theta^2}{2} - \frac{\Theta^2}{2\epsilon}\right) \\
 &= \frac{\epsilon^2}{1+\epsilon}.
 \end{aligned}$$

For larger Θ , we can write the integrals as

$$\begin{aligned}
 & 2\left(\int_0^\Theta \frac{\epsilon - \Theta}{\epsilon} dz + \int_\Theta^\epsilon 1 - \frac{z}{\epsilon} dz - \int_0^{\frac{\epsilon - \Theta}{\epsilon}} \frac{\epsilon - \Theta}{\epsilon} - z dz\right) \\
 &= 2\left(\Theta - \frac{\Theta^2}{\epsilon} + \frac{\epsilon}{2} - \Theta + \frac{\Theta^2}{2\epsilon} - \frac{1}{2} + \frac{\Theta}{\epsilon} - \frac{\Theta^2}{2\epsilon^2}\right) \\
 &= \frac{(\epsilon - \Theta)(\Theta + \epsilon(\epsilon + \Theta - 1))}{\epsilon^2}.
 \end{aligned}$$

We therefore find that the probability of two species co-existing is constant for small $\Theta < \epsilon/(1 + \epsilon)$, and a decreasing function of Θ when the competitive difference between similar species is smaller, i.e. when Θ is larger. Because in both this in the concave–convex case, the step function limit serves to maximise the probability of two species co-existing, we now consider the discontinuous case in more detail, as this will give an upper bound on the probability of co-existence for n species.

3.3 Discontinuous Competition

In a similar model to that presented here, Adler and Mosquera (2000) demonstrated how species richness increases with the gradient of the competition function at the origin (i.e. when two individuals have the same trait value), and this is supported by our results above. The logical extreme of this is that likelihood of co-existence will be maximised if the gradient at the origin is infinite, and we therefore now consider a step function for the competition coefficients, as given by (5). We note that Nowak and May (1994) used a very similar model, although they were studying the effects of superinfection on virulence in parasites rather than the number of different strains or species that the model could support. We recognise that such a competition gradient is unlikely to be found in nature (although Kubota & Hara found limited evidence of total competitive asymmetry in trees species in Northern Japan (Kubota

and Hara 1995)), but it is mathematically convenient to use this function to analytically investigate upper bounds for the levels of bio-diversity that can be supported on a single trade-off. As illustrated for the two species case above, our results will be very close to the case where the competition function is that used by Kisdi, and the piecewise linear function, mentioned above when Θ is small, and also to the competition-colonisation trade-off model of Tilman (1994) that assumes completely asymmetric competition between individuals of different trait values. Biologically, a species requires a positive growth rate $p(x_i)$ in order to be able to fixate in the environment even in the absence of competition. Therefore, the range of trait values x_i is restricted such that for all possible x_i , we have that $p(x_i) > 0$. While we continue to mostly consider the case $p(x_i) = 1 - x_i$, we return to the more generalised notation to illustrate that in this case, the methods can be used for non-linear $p(x_i)$. Note that for the case $p(x_i) = 1 - x_i$, the region of co-existence is unchanged from that considered in p -space.

Recall that the model with the step function (5) determining competition is given by

$$\frac{dN_i}{d\tau} = N_i \left(\bar{p}(x_i) - (1 - \epsilon) \sum_{j \in A_i} N_j - N_i - (1 + \epsilon) \sum_{j \in B_i} N_j \right), \quad (14)$$

where $\bar{p}(x_i) = p(x_i)/\rho$ (with $\rho = \max_{0 \leq x \leq 1} p(x)$), $\tau = \rho t$, $A_i = \{j : 1 \leq j \leq n, x_j < x_i\}$ is the set of all species j with a lower trait value than species i , and $B_i = \{j : 1 \leq j \leq n, x_j > x_i\}$ is the set of all species with trait value greater than that of species i . Note that either of these sets may be empty.

For convenience, we will now drop the bar on p , while remembering that now p has a maximum value scaled to unity. When $\epsilon = 0$, we get relative size independent, neutral competition, and because one species has the inherent advantage in that it experiences a higher population growth rate, only one species can exist, as shown in Appendix B. When $\epsilon > 0$, however, it is possible for more than one species to persist, as we now show, starting with the two-species case.

If the model given by (1) and (5) has only two distinct species present, then it is possible for both species to co-exist providing there is a globally stable interior equilibrium point. Assuming $x_1 > x_2$ for simplicity of notation, and without loss of generality, the model takes the form

$$\begin{aligned} \frac{dN_1}{d\tau} &= N_1(p(x_1) - N_1 - (1 - \epsilon)N_2), \\ \frac{dN_2}{d\tau} &= N_2(p(x_2) - (1 + \epsilon)N_1 - N_2). \end{aligned} \quad (15)$$

For any interior fixed point to be stable the Jacobian matrix J at the fixed point $N^* = (N_1^*, N_2^*)$ must have negative trace and positive determinant. The trace $\tau(J) = -(N_1^* + N_2^*)$ is negative whenever the fixed point exists, and the determinant given by $\Delta(J) = \epsilon^2 N_1^* N_2^*$ is similarly positive whenever there exists an interior fixed point. Therefore, if the interior fixed point exists, it is globally stable. An interior steady state exists when the bracketed terms in (15) are set to zero and the solution for

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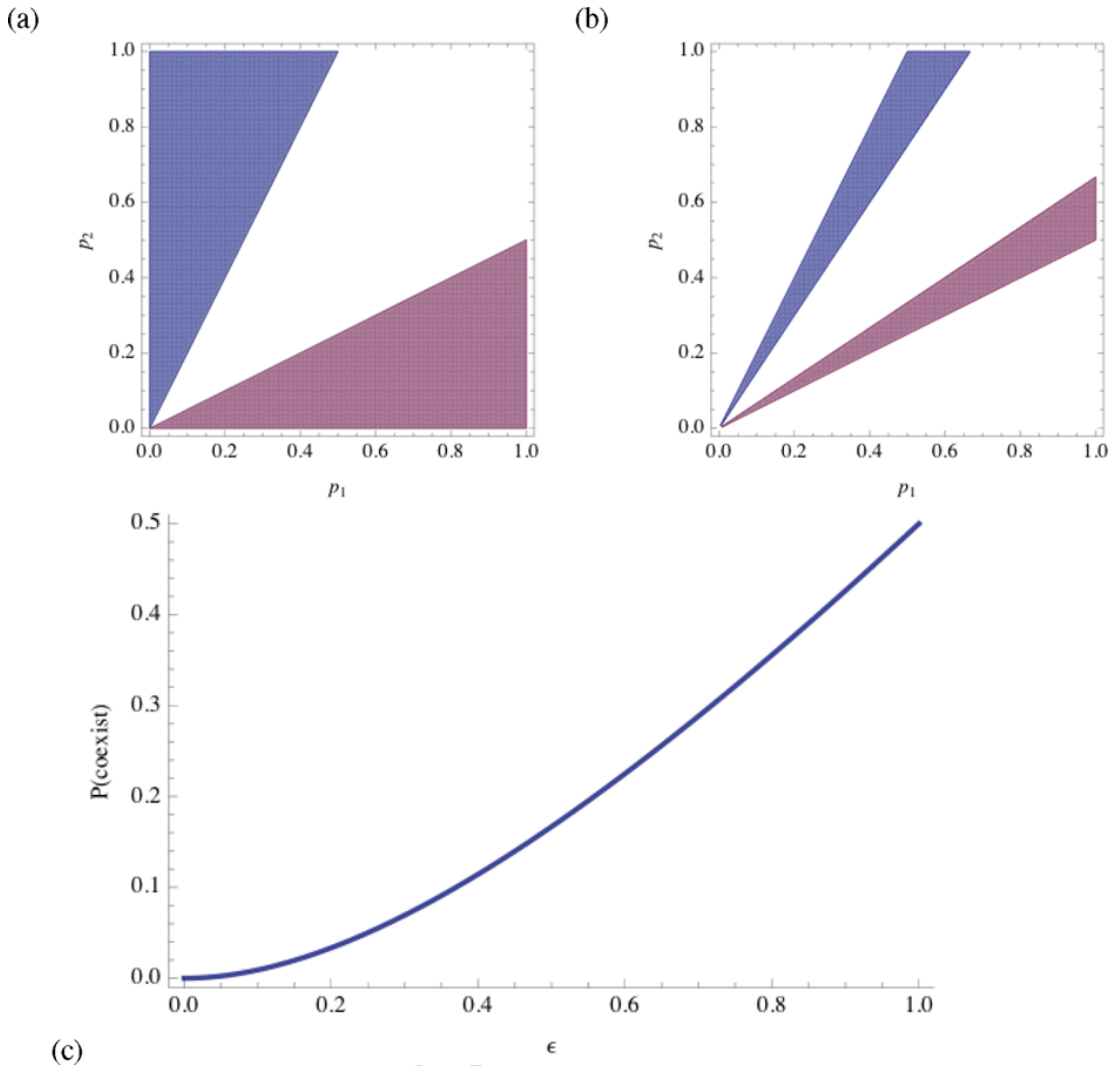


Fig. 2 The regions of co-existence for two species are plotted in p -space. (a) shows the co-existence regions for $\epsilon = 1$ while the case $\epsilon = 1/2$ is shown in (b). Shaded regions in the upper left half of the plot are where both species co-exist with growth rates $p_1 < p_2$, or equivalently trait values $x_1 > x_2$. The regions to the bottom right of the plots represent the alternative ordering $p_1 > p_2, x_1 < x_2$. (c) shows how the probability of co-existence increases with the asymmetry parameter ϵ , with large values indicating strong competitive asymmetry between individuals of different trait values

N_1, N_2 is positive. Therefore, the conditions for co-existence are given by

$$\frac{p(x_2)}{1 + \epsilon} > p(x_1) > p(x_2)(1 - \epsilon). \tag{16}$$

Since the trait values are limited to a finite range, it is possible to calculate the probability of co-existence for two species chosen at random from a uniform distribution on $x_1, x_2 \in [0, 1]$ by calculating the size of the area within the unit box $[0, 1]^2$ which satisfies (16) as well as the assumption $x_1 > x_2$. Here, we first find the area in p -space for which there exists an interior fixed point, and then from that calculate the area in x -space. Since p is a decreasing function satisfying $p(0) = 1, p(1) = 0$, it is invertible with increasing inverse p^{-1} that satisfies $p^{-1}(1) = 0, p^{-1}(0) = 1$, and hence the range of p^{-1} is $[0, 1]$. We first find the area in the p_1, p_2 plane, writing

$p_i = p(x_i)$ for simplicity of notation, for which

$$\frac{p_2}{1 + \epsilon} > p_1 > p_2(1 - \epsilon), \quad (p_1, p_2) \in [0, 1]^2, \quad (17)$$

and then map this to an area in x_1, x_2 space.

Since the case $p(x_i) = 1 - x_i$ is linear and maps $[0, 1]^2$ onto itself, the probability of co-existence is equal to the area of the x -space satisfying (16) which in turn equals the area in p -space satisfying (17).

The areas satisfying these conditions for $\epsilon = 1$ and $\epsilon = 1/2$ are shown in Fig. 2. To calculate the size of the area in the p_1, p_2 plane where both equilibrium populations are greater than zero, we note that when (17) intersects the unit box, it forms a triangle T with vertices $(0, 0)$, $(1 - \epsilon, 1)$ and $(1/(1 + \epsilon), 1)$. The area of T in the p_1, p_2 plane is therefore given by

$$\frac{1}{2} \left(\frac{1}{1 + \epsilon} - (1 - \epsilon) \right) = \frac{\epsilon^2}{2(1 + \epsilon)},$$

which is then multiplied by two to account for the other ordering of trait values $p_2 < p_1$ (i.e. $x_2 > x_1$) to give the area as

$$A = \frac{\epsilon^2}{1 + \epsilon}.$$

This area is an increasing function in ϵ , meaning that the greater the asymmetry observed in the competition between species, the more likely it is that two species can co-exist together, as anticipated by our numerical simulations of the concave-convex function and analytical work on the piecewise linear function. Note that the result here is identical to that when Θ is small in the piecewise linear case.

3.3.1 Communities with n -Species

In communities with $n > 2$ species present, any interior fixed point is unique and globally stable. While Nowak and May (1994) state that this result holds with a modification of the theory in Chap. 21.3 of Hofbauer and Sigmund (1998), we include our own proof in Appendix C.

In order to find the region of trait space that permits an interior fixed point, we consider the model written in the form

$$\frac{dN_i}{d\tau} = N_i \left(p_i(x) - \sum_{j=1}^n c_{ij}(x) N_j \right), \quad (18)$$

where the $c_{ij}(x)$ competition coefficients combine to give the competition matrix $C(x)$. In Appendix D, we show that the volume of co-existence can be calculated from a determinant and is given explicitly by

$$V_n = \begin{cases} \frac{\epsilon^n}{(1+\epsilon)^{n-1}} & \text{even } n \geq 2, \\ \frac{\epsilon^{n-1}}{(1+\epsilon)^{n-1}} & \text{odd } n \geq 3. \end{cases}$$

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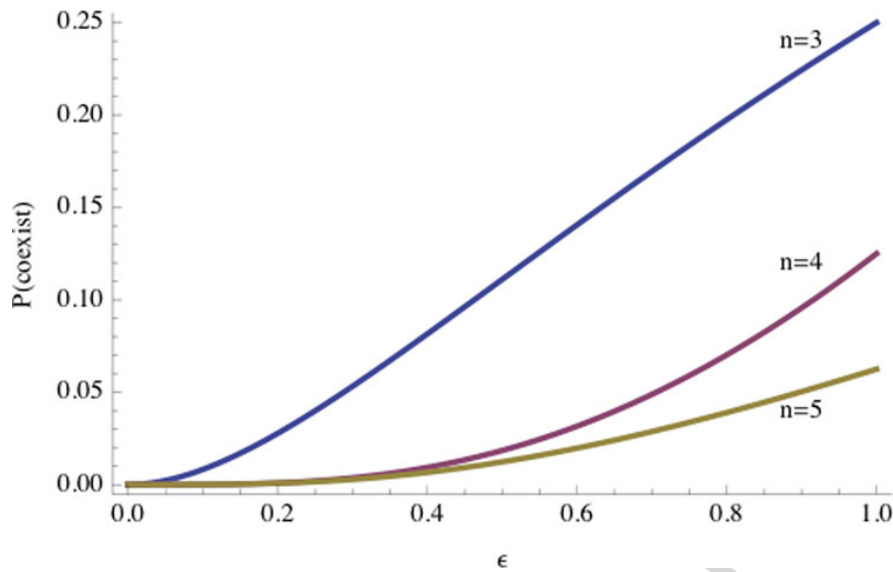


Fig. 3 How the probability of co-existence for different numbers n of species decreases with n is shown, along with how it changes with ϵ , shown for $n = 3, 4, 5$ species co-existence

Therefore, for all $0 < \epsilon \leq 1$, it is possible for any number n of species to co-exist along a single competition-fecundity trade-off. However, it is increasingly difficult for all species to co-exist as the number of species in the environment increases, as shown by Fig. 3.

4 Discussion

Life-history trade-offs have a rich history in helping to explain how competitors may co-exist, but relatively few studies have quantified how rapidly the likelihood of co-existence declines with increasing number of species within the community. Here, we have considered a trade-off between competitive ability and fecundity and have shown the probability of multiple species co-existence depends critically on the degree of asymmetry ϵ between them. Large values for ϵ indicate large competitive asymmetry between species with even nearby trait values, and it is here that co-existence is found to be most likely (see Fig. 3). However, as the number of species drawn from the pool increases, even small decreases in the competitive asymmetry can lead to rapid declines in the likelihood of co-existence. The probability of sustaining at least two species also depends on the slope of the competition function at $c(z = 0)$, and this is determined by the parameter Θ . As Θ decreases, the steepness of the competition curve increases, and so does the probability of the trade-off maintaining multiple species. Therefore, maximum co-existence is likely to be achieved at high ϵ and low Θ .

The trade-off considered here is essentially the same as the competition-colonisation trade-off, which has been much studied theoretically (e.g. Levin and Paine 1974; Hastings 1980; Tilman 1994) and empirically (e.g. Turnbull et al. 1999; Robinson et al. 1995; Cadotte 2007). Although early theory suggested any number of species might be able to co-exist on this trade-off (May and Nowak 1994;

612 Tilman 1994), as we have shown here, co-existence is dependent upon the steep-
613 ness of the trade-off function, and also on the amount of asymmetric competition
614 between the species. Recent theory that builds on this trade-off has shown that high
615 levels of co-existence are possible on a tolerance-fecundity trade-off, where species
616 with seeds that can tolerate wide ranges in environmental conditions are assumed to
617 be larger and, therefore, fewer in number (Muller-Landau 2010). However, this still
618 invokes strong competitive asymmetry because smaller seeded species are unable to
619 germinate in environments outside of their tolerance zone, and it is probable that even
620 some ability to germinate in non-preferred patches might greatly reduce the amount
621 of co-existence that is possible.

622 Our results connect to the results of Adler and Mosquera (2000), who showed
623 the shape of the trade-off to be important for the number of species that can co-
624 exist; and with HilleRisLambers and Dieckmann (2003) who found strong trade-
625 offs tend to enhance the co-existence of two species sharing one resource. We have
626 extended this work to consider how rapidly the area for coexistence in trait-space
627 diminishes with the number of species in the community. Our analyses reveal that
628 even with the trade-off assumptions that most favour co-existence, the likelihood of
629 co-existence diminishes very rapidly with the number of species, and this suggests
630 relatively few species are ever likely to be able to co-exist on one trade-off. Moreover,
631 our results reveal that competitive asymmetry becomes more important in generating
632 co-existence as the number of species increases (Fig. 3; Eq. (23)).

633 The methods we use are similar to those of Meszena et al. (2006) who calculated
634 the likelihood of an interior fixed point existing and its dependence on their model
635 parameters. However, we note the existence of an interior fixed point is not sufficient
636 for co-existence. For example, the symmetric May–Leonard model for three species
637 (May and Leonard 1975), always admits an interior equilibrium, yet the system only
638 exhibits permanence when for each species, intra-specific competition is greater than
639 twice the sum of the interspecific effects of the other two species. As such, their model
640 represents an upper bound to the likelihood of co-existence. In the current paper,
641 we address this by proving that the existence of an interior equilibrium is exactly
642 equivalent to the permanence of the system, therefore, adding to the conclusions made
643 by Meszena et al. (2006).

644 Our results therefore show how important competitive asymmetry is in generating
645 and maintaining large numbers of co-existing species; but how prevalent is com-
646 petitive asymmetry in natural communities? There is a large body of work to sug-
647 gest competitive asymmetry is common in animal (e.g. Lawton and Hassell 1981;
648 Morin and Johnson 1988; Resetarits 1995; Costanzo et al. 2005) and plant com-
649 munities (e.g. Weiner 1990; Connolly and Wayne 1996; Keddy et al. 1997). How-
650 ever, to our knowledge, except for seed size variation in plants (e.g. Turnbull et al.
651 1999), this competitive asymmetry has rarely been connected to a life-history trade-
652 off. It is worth noting that many of these studies consider only two species, and the
653 competition coefficients are often measured under one set of environmental condi-
654 tions, so it is not clear how much this asymmetry extends into large communities
655 of competitors, and whether there is a temporal fluctuation in the competitive hier-
656 archy. One exception to this is a study by Keddy et al. (1997) who measured the
657 competitive asymmetry between pairs of plant species drawn from a pool of 18
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species. Their work concluded that in fact competitive asymmetry increased with soil productivity, and this is because light rather than soil nutrients became the limiting factor, and generally competition for light is expected to be size asymmetric, whereas competition for soil nutrients is usually size symmetric (e.g. Weiner 1990).

The model we analyse here is biologically rather simple, and there is much scope for extensions that incorporate more realism. For example, as for most other models that study the competition-fecundity or competition-colonisation trade-offs, we assume that intra-specific competition is identical for all trait values (Eq. (14)); but it might be more realistic to assume that smaller individuals are better able to share resources than larger individuals, meaning the intra-specific competition term now has to be trait dependent as well. We believe relaxing this assumption would yield rather more complex dynamics than the current model, including the possibility of founder control (i.e. unstable interior equilibria). For example, Calcagno et al. (2006) incorporated priority effects, whereby an adult plant cannot be displaced by a seed, into a competition-colonisation model, and showed that this can actually increase co-existence. However, when maximum colonisation rate, analogous to our maximum population growth rate, is heavily limited, such preemptive competition generally ceases to be beneficial to co-existence. Therefore, this would reduce the amount of co-existence compared to that found here, and would place greater dependence on multiple trade-offs or other processes to generate co-existence between large numbers of species.

The models presented here have assumed linear intrinsic growth rate p in the absence of competition, and linear or piecewise constant competition for communities with three or more species. Non-linearity, with suitable monotonicity conditions, can be easily incorporated into the function p , and the volume in x -space can then be found through a change of variable in the volume integral. Moreover, changing p does not impact on the global stability of interior steady states, which as shown, depends solely on the competition matrix C . For models with three or more species, studying non-linear competition functions gives the difficulty of not only finding volumes in space enclosed between curved surfaces, but also determining which points in these volumes are globally stable. The alternative, focusing on co-existence measured by permanence, also presents a serious challenge due to the lack of necessary and sufficient conditions for permanence in general competitive Lotka–Volterra models for $n > 3$.

These extensions aside, we have shown here that competitive asymmetry could be very important in maintaining several species on a single trade-off; but that for large numbers of species multiple trade-offs; and/or other processes such as disturbance or natural enemies are required to maintain diverse competitive communities. Nonetheless, it is clear that competitive asymmetry which is widely observed in empirical studies could still interact with these other processes to increase, rather than decrease bio-diversity as has often been supposed (e.g. Keddy et al. 1997; Resutarits 1995).

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706 **Appendix A**

707
 708 We note that since $c(z) + c(-z) = 2$ constant, we have that $c(-z) - 1 = 1 - c(z) > 0$
 709 for positive z . Therefore, we can subtract (12) from (11) to get

710
 711
$$\frac{(1 - z - c(z)) - ((1 - z)c(-z) - 1)}{c(-z) - 1} = \frac{z(c(-z) - 1)}{(c(-z) - 1)} = z.$$

712
 713
 714 Therefore, the upper and lower bounds for x_2 coincide at $z = 0$, and for $z > 0$ the
 715 upper bound is always greater than the lower, i.e. there is always a region where co-
 716 existence is possible. Therefore, if the upper bound (11) is non-increasing, both it and
 717 the lower bound (12) never exceed the value they achieve at $z = 0$, and there is only
 718 a region of co-existence in the positive quadrant when the limit

719
 720
$$\lim_{z \rightarrow 0} \frac{1 - z - c(z)}{1 - c(z)} > 0.$$

721
 722
 723 As both numerator and denominator tend to zero, we use l'Hopital's rule to get that
 724 this limit is given by

725
 726
$$\frac{-1 - c'(0)}{-c'(0)},$$

727
 728 which is positive for $c'(0) < -1$.

729 It remains to demonstrate that (11) is non-increasing for positive z . The derivative
 730 of the function is given by

731
 732
$$\frac{c(z) - 1 - zc'(z)}{(1 - c(z))^2}.$$

733
 734 If $c'(z) = 0$, then this becomes

735
 736
$$\frac{-1}{1 - c(z)} < 0,$$

737
 738
 739 since $c(z) < 1$ for all $z > 0$. When $c'(z) < 0$, then we note that the function is non-
 740 increasing for

741
 742
$$z \leq \frac{c(z) - 1}{c'(z)}.$$

743
 744 The derivative of the right-hand side is given by

745
 746
$$1 - \frac{c''(z)(c(z) - 1)}{c'(z)^2},$$

747
 748
 749 which is greater than one for all positive z . Therefore, this point increases faster
 750 than z . Noting that the derivative of (11) is zero when $z = 0$, we can therefore con-
 751 clude that for all $z > 0$, this upper bound is indeed non-increasing.
 752

Appendix B

Without losing any generality, we can order traits such that $x_1 > x_2 > \dots > x_n$ so that since p is decreasing, $p(x_1) < p(x_2) < \dots < p(x_n)$. When $\epsilon = 0$, Eqs. (14) become

$$\frac{dN_i}{d\tau} = N_i \left(p(x_i) - \sum_{j=1}^n N_j \right), \quad i = 1, \dots, n.$$

Thus, if $i < k$,

$$\frac{d}{d\tau} \log(N_i/N_k) = p(x_i) - p(x_k) < 0.$$

This shows that for $i < k$

$$N_i(\tau) = N_k(\tau) e^{(p(x_i) - p(x_k))\tau} \rightarrow 0, \quad \tau \rightarrow \infty,$$

since $N(t)$ is bounded. This shows that $N_i(\tau) \rightarrow 0$ as $\tau \rightarrow \infty$ for $i = 1, 2, \dots, n - 1$. It is intuitive that the remaining species density $N_n(\tau) \rightarrow p(x_n)$ as $\tau \rightarrow \infty$. This can be shown by first noting that the equation for the dynamic of N_n reduces to the time-dependent logistic equation:

$$\dot{N}_n = p(x_n) N_n \left(1 - \frac{N_n}{K(t)} \right), \tag{19}$$

where the time-dependent carrying capacity is given by

$$K(t) = p(x_n) e^{p(x_n)t} / \left(\sum_{i=1}^n e^{p(x_i)t} \right).$$

One may verify that the explicit solution to (19) is

$$N_n(t) = \frac{N_n(0) e^{p(x_n)t}}{1 + N_n(0) \sum_{i=1}^n \left(\frac{e^{p(x_i)t} - 1}{p(x_i)} \right)} \rightarrow p(x_n) \quad \text{as } t \rightarrow \infty.$$

We have thus shown that the species with minimum trait 0 will send any other species to extinction.

Appendix C

Lemma 1 *Whenever an interior fixed point exists for the n -species model given by (14), it is both unique and globally asymptotically stable relative to the interior of the region of space where all N_i are positive and, therefore, the system displays permanence.*

Proof It is well known that when (1) admits an interior steady state, it is globally stable (also known as LV-stable) if the matrix $-C = ((-c_{ij}(x)))$ is dissipative, that

is, there exists a positive diagonal matrix D such that the real symmetric matrix $D(-C) + (-C)^T D$ is negative definite and, therefore, has only negative eigenvalues (e.g. Hofbauer and Sigmund 1998). For the model with discontinuous competition, the competition matrix takes the form (in the region $x_1 > x_2 > \dots > x_n$) given by Eq. (22). Let D be a positive diagonal matrix with diagonal entries θ_i ($i = 1, \dots, n$). Then (1), with competition matrix C as in (22), admits a fixed point that globally attracts interior trajectories whenever the real symmetric matrix $A = (DC + C^T D)$, given by

$$\begin{pmatrix} 2\theta_1 & (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_2 & \dots & (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_n \\ (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_2 & 2\theta_2 & \dots & (1 - \epsilon)\theta_2 + (1 + \epsilon)\theta_n \\ (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_3 & (1 - \epsilon)\theta_2 + (1 + \epsilon)\theta_3 & \dots & (1 - \epsilon)\theta_3 + (1 + \epsilon)\theta_n \\ \vdots & \vdots & \ddots & \vdots \\ (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_n & (1 - \epsilon)\theta_2 + (1 + \epsilon)\theta_n & \dots & 2\theta_n \end{pmatrix}$$

has all positive eigenvalues, which is the case if all the leading principal minors are positive.

We have fixed $\theta_i > 0$ positive, so we restrict ourselves to looking at $m \times m$ leading principal minors of the matrix A with $m \geq 2$:

$$\begin{vmatrix} 2\theta_1 & (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_2 & \dots & (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_m \\ (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_2 & 2\theta_2 & \dots & (1 - \epsilon)\theta_2 + (1 + \epsilon)\theta_m \\ \vdots & \vdots & \ddots & \vdots \\ (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_m & (1 - \epsilon)\theta_2 + (1 + \epsilon)\theta_m & \dots & 2\theta_m \end{vmatrix}.$$

As the determinant of a matrix is not changed when one row or column is subtracted from another, we then subtract the $(m - 1)$ th column from the m th column, and the i th column from the $(i + 1)$ th column for all $1 \leq i \leq m - 1$ to obtain the matrix

$$\begin{vmatrix} 2\theta_1 & (1 + \epsilon)(\theta_2 - \theta_1) & \dots & (1 + \epsilon)(\theta_m - \theta_{m-1}) \\ (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_2 & (1 - \epsilon)(\theta_2 - \theta_1) & \dots & (1 + \epsilon)(\theta_m - \theta_{m-1}) \\ \vdots & \vdots & \ddots & \vdots \\ (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_m & (1 - \epsilon)(\theta_2 - \theta_1) & \dots & (1 - \epsilon)(\theta_m - \theta_{m-1}) \end{vmatrix}.$$

Removing the common factors in columns 2 up to m give that the determinant has a factor

$$(-1)^{m-1} \prod_{i=1}^{m-1} (\theta_i - \theta_{i+1})$$

which is then multiplied by

$$\begin{vmatrix} 2\theta_1 & 1 + \epsilon & 1 + \epsilon & \dots & 1 + \epsilon \\ (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_2 & 1 - \epsilon & 1 + \epsilon & \dots & 1 + \epsilon \\ (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_3 & 1 - \epsilon & 1 - \epsilon & \dots & 1 + \epsilon \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ (1 - \epsilon)\theta_1 + (1 + \epsilon)\theta_m & 1 - \epsilon & 1 - \epsilon & \dots & 1 - \epsilon \end{vmatrix}.$$

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847 Subtracting row $m - 1$ from row m , and row i from row $i + 1$ for all $i < m$ gives this
 848 determinant as

$$\begin{aligned}
 & \begin{vmatrix} 2\theta_1 & 1 + \epsilon & 1 + \epsilon & \cdots & 1 + \epsilon \\ (1 + \epsilon)(\theta_2 - \theta_1) & -2\epsilon & 0 & \cdots & 0 \\ (1 + \epsilon)(\theta_3 - \theta_2) & 0 & -2\epsilon & \cdots & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ (1 + \epsilon)(\theta_m - \theta_{m-1}) & 0 & 0 & \cdots & -2\epsilon \end{vmatrix} \\
 &= \begin{vmatrix} 2\theta_1 & 1 + \epsilon & 0 & 0 & \cdots & 0 \\ (1 + \epsilon)(\theta_2 - \theta_1) & -2\epsilon & 2\epsilon & 0 & \cdots & 0 \\ (1 + \epsilon)(\theta_3 - \theta_2) & 0 & -2\epsilon & 2\epsilon & \cdots & 0 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots \\ (1 + \epsilon)(\theta_m - \theta_{m-1}) & 0 & 0 & 0 & \cdots & -2\epsilon \end{vmatrix} \\
 &= (-1)^{m-1} \theta_1 2^m \epsilon^{m-1} - (1 + \epsilon)^2 (2\epsilon)^{m-2} (-1)^{m-2} (\theta_2 - \theta_1 + \theta_3 \\
 &\quad - \theta_2 + \cdots + \theta_m - \theta_{m-1}) \\
 &= (-1)^m (2\epsilon)^{m-2} ((1 - \epsilon)^2 \theta_1 - (1 + \epsilon)^2 \theta_m).
 \end{aligned}$$

862 Therefore, the $m \times m$ leading principal minor for $m > 1$ is given by

$$863 \quad - (2\epsilon)^{m-2} ((1 - \epsilon)^2 \theta_1 - (1 + \epsilon)^2 \theta_m) \prod_{i=1}^{m-1} (\theta_i - \theta_{i+1}). \tag{20}$$

872 It remains to be shown that the θ_i can be chosen such that all leading principal minors
 873 (20) are positive, which is the case when $((1 - \epsilon)^2 \theta_i - (1 + \epsilon)^2 \theta_j) < 0$ and $(\theta_i - \theta_j) >$
 874 0 for $i < j$. Setting

$$875 \quad \theta_i = n - \frac{1}{(1 + \epsilon)^{n+1-i}},$$

876 then we can use $j - i \geq 1$ to calculate that

$$\begin{aligned}
 877 \quad \theta_i - \theta_j &= \left(n - \frac{1}{(1 + \epsilon)^{n+1-i}} \right) - \left(n - \frac{1}{(1 + \epsilon)^{n+1-j}} \right) \\
 878 \quad &= \frac{(1 + \epsilon)^{j-i} - 1}{(1 + \epsilon)^{n+1-i}} \\
 879 \quad &\geq \frac{1 + \epsilon - 1}{(1 + \epsilon)^{n+1-i}} > 0.
 \end{aligned}$$

880 To show that $((1 - \epsilon)^2 \theta_i - (1 + \epsilon)^2 \theta_j) < 0$, we note that

$$\begin{aligned}
 881 \quad ((1 - \epsilon)^2 \theta_i - (1 + \epsilon)^2 \theta_j) &< ((1 - \epsilon)^2 \theta_1 - (1 + \epsilon)^2 \theta_j) \\
 882 \quad &< ((1 - \epsilon)^2 \theta_1 - (1 + \epsilon)^2 \theta_n)
 \end{aligned}$$

and that for $\epsilon = 0$, we have $((1 - \epsilon)^2\theta_1 - (1 + \epsilon)^2\theta_n) = 0$. Differentiating this with respect to epsilon gives

$$\begin{aligned} \frac{d}{d\epsilon}((1 - \epsilon)^2\theta_i - (1 + \epsilon)^2\theta_j) &= -4n + 1 + 2\frac{1 - \epsilon}{(1 + \epsilon)^n} + n\frac{(1 - \epsilon)^2}{(1 + \epsilon)^{n+1}} \\ &\leq -4n + 1 + 2 + n < 0 \end{aligned}$$

for all $0 \leq \epsilon \leq 1$ and $n \geq 2$. Therefore, since $\epsilon = 0$ is a root for the function, for any $\epsilon > 0$, we have

$$((1 - \epsilon)^2\theta_1 - (1 + \epsilon)^2\theta_n) < 0$$

and therefore

$$((1 - \epsilon)^2\theta_i - (1 + \epsilon)^2\theta_j) < 0.$$

Therefore, all the leading principal minors are positive, meaning that $A = DC + C^T D$ is positive definite. Therefore, $D(-C) + (-C)^T D$ is negative definite, as required for global stability. Global stability immediately implies permanence. \square

Appendix D

Here, we calculate the probability of co-existence for an n species version of (14). Since we are using the step function (5), the matrix $C(x)$ is piecewise constant. At the interior fixed point, the bracketed terms are equal to zero, which therefore reduces the model to $\mathbf{p}(x) = C(x)\mathbf{N}$, with \mathbf{p} the vector of the growth rate of each species and \mathbf{N} the vector with i th component N_i . Since $C(x)$ is non-singular, this is the rearranged to give the solution $\mathbf{N} = C^{-1}(x)\mathbf{p}(x)$. We are interested in the volume of x -space for which $\mathbf{N} = C^{-1}(x)\mathbf{p}(x) > \mathbf{0}$. To find this volume, we find the volume in p -space where $p_1 < p_2 < \dots < p_n$ which satisfies, since then $x_1 > x_2 > \dots > x_n$ and so $C(x)$ is a constant, and non-singular matrix C , so that

$$C^{-1}\mathbf{p} = \mathbf{0}. \tag{21}$$

Equation (21) defines a series of planes in p -space that all pass through the origin. When an ordering $p_n > p_{n-1} > \dots > p_1$ is assumed without any loss of generality, these planes form an n dimensional pyramid when intersected with the unit cube. The volume of this pyramid is then the probability of the n species model permitting an interior fixed point and, therefore, the probability of all n species co-existing due to the stability result in Appendix C.

With the ordering $p_1 < p_2 < \dots < p_n$, equivalent to $x_1 > x_2 > \dots > x_n$, the competition matrix C takes the form

$$C = \begin{pmatrix} 1 & 1 - \epsilon & 1 - \epsilon & \dots & 1 - \epsilon \\ 1 + \epsilon & 1 & 1 - \epsilon & \dots & 1 - \epsilon \\ 1 + \epsilon & 1 + \epsilon & 1 & \dots & 1 - \epsilon \\ \vdots & \vdots & \vdots & \ddots & \vdots \\ 1 + \epsilon & 1 + \epsilon & 1 + \epsilon & \dots & 1 \end{pmatrix}. \tag{22}$$

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It is relatively simple to show that C is non-singular, allowing us to calculate the volume of the n dimensional pyramid. We need to find the n points at which n of the planes intersect the face $p_n = 1$. To find these points, we note that the edges of the n dimensional pyramid must be orthogonal to each of the $n - 1$ planes in p -space defined by (21) that meet at that edge. Since $C^{-1}C = I_n$, each column of C is orthogonal to all bar one of the rows of C^{-1} . Therefore, the edges of the n dimensional pyramid point in the direction of the columns of C . These edges meet the plane $p_n = 1$ at the non-zero corners of the n dimensional simplex, so it is simple to show that these points are given by the columns of C , scaled such that the value of $p_n = 1$. Therefore, the n non-zero vertices of the simplex that lie in the plane $p_n = 1$ are given by

$$\begin{aligned} & \left(\frac{1}{1+\epsilon}, 1, 1, 1, \dots, 1 \right), \\ & \left(\frac{1-\epsilon}{1+\epsilon}, \frac{1}{1+\epsilon}, 1, 1, \dots, 1 \right), \\ & \left(\frac{1-\epsilon}{1+\epsilon}, \frac{1-\epsilon}{1+\epsilon}, \frac{1}{1+\epsilon}, 1, \dots, 1 \right), \\ & \vdots \\ & \left(\frac{1-\epsilon}{1+\epsilon}, \frac{1-\epsilon}{1+\epsilon}, \frac{1-\epsilon}{1+\epsilon}, \dots, \frac{1}{1+\epsilon}, 1 \right), \\ & (1-\epsilon, 1-\epsilon, 1-\epsilon, \dots, 1-\epsilon, 1). \end{aligned}$$

Theorem 1 *The probability of co-existence, is given by*

$$V_n = P(\text{coexist}_n) = \begin{cases} \frac{\epsilon^n}{(1+\epsilon)^{n-1}} & \text{even } n \geq 2, \\ \frac{\epsilon^{n-1}}{(1+\epsilon)^{n-1}} & \text{odd } n \geq 3. \end{cases} \quad (23)$$

Proof The volume of the n dimensional simplex is given by

$$\bar{V}_n = \frac{1}{n!} \begin{vmatrix} \frac{1}{1+\epsilon} & 1 & 1 & 1 & \dots & 1 & 1 \\ \frac{1-\epsilon}{1+\epsilon} & \frac{1}{1+\epsilon} & 1 & 1 & \dots & 1 & 1 \\ \frac{1-\epsilon}{1+\epsilon} & \frac{1-\epsilon}{1+\epsilon} & \frac{1}{1+\epsilon} & 1 & \dots & 1 & 1 \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots \\ \frac{1-\epsilon}{1+\epsilon} & \frac{1-\epsilon}{1+\epsilon} & \frac{1-\epsilon}{1+\epsilon} & \frac{1-\epsilon}{1+\epsilon} & \dots & \frac{1}{1+\epsilon} & 1 \\ 1-\epsilon & 1-\epsilon & 1-\epsilon & 1-\epsilon & \dots & 1-\epsilon & 1 \end{vmatrix}.$$

Since there are $n!$ of these volumes, one for each ordering of the traits, so the total volume is $V_n = n! \bar{V}_n$. Let $U_n = n!(1+\epsilon)^{n-1} \bar{V}_n$. Then

$$U_n = \begin{vmatrix} 1 & 1+\epsilon & 1+\epsilon & 1+\epsilon & \cdots & 1+\epsilon & 1+\epsilon \\ 1-\epsilon & 1 & 1+\epsilon & 1+\epsilon & \cdots & 1+\epsilon & 1+\epsilon \\ 1-\epsilon & 1-\epsilon & 1 & 1+\epsilon & \cdots & 1+\epsilon & 1+\epsilon \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \\ 1-\epsilon & 1-\epsilon & 1-\epsilon & 1-\epsilon & \cdots & 1 & 1+\epsilon \\ 1-\epsilon & 1-\epsilon & 1-\epsilon & 1-\epsilon & \cdots & 1-\epsilon & 1 \end{vmatrix}.$$

We now show that $U_n = \epsilon^2 U_{n-2}$. To see this, first subtract the second row from the first row. Having done this, in the new determinant subtract the first column from the second column. This gives

$$U_n = \begin{vmatrix} \epsilon & 0 & 0 & 0 & \cdots & 0 & 0 \\ 1-\epsilon & \epsilon & 1+\epsilon & 1+\epsilon & \cdots & 1+\epsilon & 1+\epsilon \\ 1-\epsilon & 0 & 1 & 1+\epsilon & \cdots & 1+\epsilon & 1+\epsilon \\ \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \\ 1-\epsilon & 0 & 1-\epsilon & 1-\epsilon & \cdots & 1 & 1+\epsilon \\ 1-\epsilon & 0 & 1-\epsilon & 1-\epsilon & \cdots & 1-\epsilon & 1 \end{vmatrix},$$

which gives $U_n = \epsilon^2 U_{n-2}$ as required. Now quick calculations show that $U_2 = \epsilon^2$ and $U_3 = \epsilon^2$ so that $U_n = \epsilon^n$ for $n \geq 2$ even and $U_n = \epsilon^{n-1}$ for $n \geq 3$ odd.

$$\begin{aligned} \bar{V}_n &= \frac{1}{n!} \frac{\epsilon^n}{(1+\epsilon)^{n-1}} \quad n \text{ even,} \\ &= \frac{1}{n!} \frac{\epsilon^{n-1}}{(1+\epsilon)^{n-1}} \quad n \text{ odd.} \\ V_n &= \begin{cases} \frac{\epsilon^n}{(1+\epsilon)^{n-1}} & \text{even } n \geq 2, \\ \frac{\epsilon^{n-1}}{(1+\epsilon)^{n-1}} & \text{odd } n \geq 3. \end{cases} \quad \square \end{aligned}$$

References

- Adler, F., & Mosquera, J. (2000). Is space necessary? Interference competition and limits to biodiversity. *Ecology*, *81*, 3226–3232.
- Amarasekare, P. (2007). Trade-offs, temporal variation, and species coexistence in communities with intraguild predation. *Ecology*, *88*, 2720–2728.
- Bonsall, M., & Mangel, M. (2004). Life-history trade-offs and ecological dynamics in the evolution of longevity. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, *271*, 1143–1150.
- Bowers, R., Boots, M., & Begon, M. (1994). Life-history trade-offs and the evolution of pathogen resistance: competition between host strains. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, *257*, 247–253.
- Cadotte, M. (2007). Competition-colonization trade-offs and disturbance effects at multiple scales. *Ecology*, *88*, 823–829.
- Cadotte, M., Mai, D., Jantz, S., Collins, M., Keele, M., et al. (2006). On testing the competition-colonization trade-off in a multispecies assemblage. *The American Naturalist*, *168*, 704–709.
- Calcagno, V., Mouquet, N., Jarne, P., & David, P. (2006). Coexistence in a metacommunity: the competition–colonization trade-off is not dead. *Ecology Letters*, *9*, 897–907.

Quantifying the Likelihood of Co-existence for Communities

- 1035 Connolly, J., & Wayne, P. (1996). Asymmetric competition between plant species. *Oecologia*, 108, 311–
1036 320.
- 1037 Costanzo, K., Mormann, K., & Juliano, S. (2005). Asymmetrical competition and patterns of abundance of
1038 *Aedes Albopictus* and *Culex pipiens* (Diptera: Culicidae). *Journal of Medical Entomology*, 42, 559.
- 1039 Hastings, A. (1980). Disturbance, coexistence, history, and competition for space. *Theoretical Population*
1040 *Biology*, 18, 363–373.
- 1041 HilleRisLambers, R., & Dieckmann, U. (2003). Competition and predation in simple food webs: interme-
1042 diately strong trade-offs maximize coexistence. *Proceedings of the Royal Society of London. Series*
1043 *B, Biological Sciences*, 270, 2591–2598.
- 1044 Hofbauer, J., & Sigmund, K. (1998). *The theory of evolution and dynamical systems*. New York: Cam-
1045 bridge University Press.
- 1046 Hofbauer, J., & Sigmund, K. (1998). *Evolutionary games and population dynamics*. Cambridge: Cam-
1047 bridge University Press.
- 1048 Keddy, P., Twolan-Strutt, L., & Shipley, B. (1997). Experimental evidence that interspecific competitive
1049 asymmetry increases with soil productivity. *Oikos*, 80, 253–256.
- 1050 Kisdí, É. (1999). Evolutionary branching under asymmetric competition. *Journal of Theoretical Biology*,
1051 197, 149–162.
- 1052 Kisdí, E., & Geritz, S. (2003). On the coexistence of perennial plants by the competition-colonization
1053 trade-off. *The American Naturalist*, 161, 350–354.
- 1054 Klausmeier, C. (1998). Extinction in multispecies and spatially explicit models of habitat destruction. *The*
1055 *American Naturalist*, 152, 303–310.
- 1056 Kubota, Y., & Hara, T. (1995). Tree competition and species coexistence in a sub-boreal forest, northern
1057 Japan. *Annals of Botany*, 76, 503.
- 1058 Law, R. (1979). Optimal life histories under age-specific predation. *The American Naturalist*, 114, 399–
1059 417.
- 1060 Law, R., & Morton, R. (1996). Permanence and the assembly of ecological communities. *Ecology*, 77,
1061 762–775.
- 1062 Law, R., Marrow, P., & Dieckmann, U. (1997). On evolution under asymmetric competition. *Evolutionary*
1063 *Ecology*, 11, 485–501.
- 1064 Lawton, J., & Hassell, M. (1981). Asymmetrical competition in insects. *Nature*, 289, 793–795.
- 1065 Levin, S., & Paine, R. (1974). Disturbance, patch formation, and community structure. *Proceedings of the*
1066 *National Academy of Sciences of the United States of America*, 71, 2744.
- 1067 Levins, R., & Culver, D. (1971). Regional coexistence of species and competition between rare species.
1068 *Proceedings of the National Academy of Sciences of the United States of America*, 68, 1246–1248.
- 1069 May, R., & Leonard, W. (1975). Nonlinear aspects of competition between three species. *SIAM Journal*
1070 *on Applied Mathematics*, 29, 243–253.
- 1071 May, R., & Nowak, M. (1994). Superinfection, metapopulation dynamics, and the evolution of diversity.
1072 *Journal of Theoretical Biology*, 170, 95.
- 1073 Meszner, G., Gyllenberg, M., Pasztor, L., & Metz, J. (2006). Competitive exclusion and limiting similarity:
1074 a unified theory. *Theoretical Population Biology*, 69, 68–87.
- 1075 Morin, P., & Johnson, E. (1988). Experimental studies of asymmetric competition among anurans. *Oikos*,
1076 53, 398–407.
- 1077 Muller-Landau, H. (2010). The tolerance–fecundity trade-off and the maintenance of diversity in seed size.
1078 *Proceedings of the National Academy of Sciences of the United States of America*, 107, 4242.
- 1079 Nowak, M., & May, R. (1994). Superinfection and the evolution of parasite virulence. *Proceedings of the*
1080 *Royal Society of London. Series B, Biological Sciences*, 255, 81.
- 1081 Resetarits, W. Jr (1995). Competitive asymmetry and coexistence in size-structured populations of brook
trout and spring salamanders. *Oikos*, 73, 188–198.
- Robinson, G., Quinn, J., & Stanton, M. (1995). Invasibility of experimental habitat islands in a California
winter annual grassland. *Ecology*, 76, 786–794.
- Schluter, D. (1995). Adaptive radiation in sticklebacks: trade-offs in feeding performance and growth.
Ecology, 76, 82–90.
- Strobeck, C. (1973). N species competition. *Ecology*, 54, 650–654.
- Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75, 2–16.
- Turnbull, L., Rees, M., & Crawley, M. (1999). Seed mass and the competition/colonization trade-off: a
sowing experiment. *Journal of Ecology*, 87, 899–912.

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- 1082 Venable, D. (1992). Size-number trade-offs and the variation of seed size with plant resource status. *The*
1083 *American Naturalist*, 140, 287–304.
- 1084 Weiner, J. (1990). Asymmetric competition in plant populations. *Trends in Ecology & Evolution*, 5, 360–
1085 364.
- 1086 White, A., & Bowers, R. (2005). Adaptive dynamics of Lotka–Volterra systems with trade-offs: the role of
1087 interspecific parameter dependence in branching. *Mathematical Biosciences*, 193, 101–117.

UNCORRECTED PROOF

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