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Niche and fitness differences relate the maintenance of diversity to ecosystem function: comment

Loreau, Michel ; Sapijanskas, Jurgis ; Isbell, Forest ; Hector, Andy

Abstract: The relationship between biodiversity and ecosystem functioning (BEF) has been one of the most vibrant research fields in ecology and environmental sciences over the past two decades. Hundreds of experiments have now manipulated species diversity to test its effects on a wide range of ecosystem properties. Methods that partition the effect of functional complementarity between species from that of selection for species with particular traits have been instrumental in clarifying the results of these experiments and in resolving debates about potential underlying mechanisms (Loreau and Hector 2001, Cardinale et al. 2007). Relatively few studies, however, have sought to disentangle the actual biological mechanisms at work in the effects of biodiversity on ecosystem functioning. Yet theory shows that different coexistence mechanisms can lead to different BEF relationships (Mouquet et al. 2002). Understanding the mechanisms that drive the functional consequences of biodiversity and their connections with those that determine the maintenance of biodiversity is key to making BEF research more predictive and more relevant to natural, non-experimentally manipulated ecosystems (Loreau 2010). The recent theoretical study by Carroll, Cardinale, and Nisbet (2011; hereafter CCN) makes a valuable contribution toward the goal of linking the maintenance of diversity and its functional consequences. CCN use MacArthur's (1972) classical consumer

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Niche and fitness differences relate the maintenance of diversity to ecosystem function: Comment

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22 The relationship between biodiversity and ecosystem functioning (BEF) has been one of the most
 23 vibrant research fields in ecology and environmental sciences over the past two decades. Hundreds
 24 of experiments have now manipulated species diversity to test its effects on a wide range of
 25 ecosystem properties. Methods that partition the effect of functional complementarity between
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 33 biodiversity is key to making BEF research more predictive and more relevant to natural, non-
 34 experimentally manipulated ecosystems (Loreau 2010).

 intimate

35 The recent theoretical study by Carroll, Cardinale and Nisbet (2011) (hereafter CCN) makes
 36 a valuable contribution toward the goal of linking the maintenance of diversity and its functional
 37 consequences. CCN use MacArthur's (1972) classical consumer–resource model to develop new
 38 measures of niche difference (ND) and relative fitness difference (RFD) between consumers. They
 39 then explore the relationships between these new measures and the widely used additive partition
 40 (AP) of the net biodiversity effect into a complementarity effect (CE) and a selection effect (SE),
 41 as well as the relative yield total (RYT), a measure closely related to CE (Loreau and Hector
 42 2001). Their analysis leads them to conclude that “post hoc statistical methods currently used to
 43 discern the mechanisms that drive effects of diversity on biomass do not necessarily reflect real
 44 biological processes that relate to mechanisms of species coexistence”. This conclusion serves as a

 existing literature

 in this context

45 reminder that, however useful, no post hoc analysis will ever be able to replace detailed
46 knowledge of the biological mechanisms at work.

47 But CCN also suggest that the ND and RFD metrics they devise are more appropriate than
48 AP for identifying mechanisms that drive BEF relationships; accordingly, they propose that future
49 theoretical and empirical work should focus on “predicting community biomass from three
50 independent variables: ND, RFD, and species richness”. As we explain below, we feel that these
51 additional conclusions are unwarranted; they are based on the implicit assumption that CCN’s new
52 approach is intrinsically better than AP without any independent demonstration that it does in fact
53 do a better job. On the other hand, CCN’s study raises valid questions about the scope and
54 limitations of AP, which has been sometimes liberally interpreted in the recent literature. In this
55 comment, therefore, we would like to (1) revisit the scope and limitations of the AP approach, (2)
56 discuss some of the limitations of CCN’s new proposed approach, and (3) briefly suggest some
57 directions that could be taken to move BEF research forward.

58 When two of us proposed AP ten years ago (Loreau and Hector 2001), it was in the context
59 of a raging debate about the interpretation of BEF experiments (Loreau et al. 2001). The main
60 interest of this approach was to allow testing of hypotheses that assume changes in numerical
61 dominance among species but no functional complementarity, such as the much-debated
62 “sampling effect” and “mass ratio” hypotheses. Essentially, these hypotheses propose that changes
63 in community production or biomass can be explained simply by zero-sum changes in the relative
64 abundances of species in mixture. The alternative — that communities are more (or less) than the
65 sum of their parts — has for a long time been termed overyielding (or underyielding). AP has
66 played a valuable role for testing these types of null hypothesis via its two components, SE and
67 CE.

68 SE is a straightforward application of a basic statistical approach: it is a covariance term that
69 relates the performance of a species in mixture (whether its relative yield increases or decreases
70 relative to expectations) to its monoculture biomass. It is positive when species with large
71 monoculture biomasses on average perform better in mixtures, and negative when the reverse is
72 true. When changes in relative abundances follow a zero-sum game, then SE (whatever its sign)
73 will explain the effects of diversity on mixture yield. Ecologists are familiar with covariances and
74 correlations; thus SE is relatively simple and easy to understand.

75 CE quantifiesoveryielding, i.e., an increase in mixture yield above the zero-sum expectation
76 (or underyielding when mixtures produce less than expected), which provides a simple,
77 operational way to define functional complementarity by its net effect at the community level.



78 Although technically CE has the dimension of absolute yield, one advantage is that it is closely
79 related to the relative yield and RYT concepts used in plant ecology and intercropping since the
80 1950s and they are therefore once again familiar to ecologists and relatively well understood. In
81 addition, CE and RYT have the nice property of being directly connected to the conditions for
82 stable coexistence in the classical Lotka-Volterra competition model (Vandermeer 1981, Loreau
83 2004).

84 In total, the AP and RYT frameworks are relatively simple and based on long-established
85 methodologies that are familiar to many ecologists. We therefore feel that, despite their
86 limitations, they will continue to have great value for performing tests of null hypotheses such as
87 the sampling effect and mass ratio hypotheses, and for generating alternative hypotheses about
88 possible mechanisms underlying BEF relationships detected in experiments.

89 It is important to note, however, that CE and RYT do not provide quantitative measures of
90 resource partitioning because they potentially combine the effects of a wide range of species
91 interactions, as one of us established clearly (Loreau 1998). A positive CE (or, equivalently, RYT

92 > 1) means that niche differentiation (partitioning of either resources or natural enemies), positive
93 interactions, or some combination thereof, are strong enough to outweigh interference competition
94 or other negative species interactions that might decrease relative yields in mixture. Conversely, a
95 negative CE (or RYT < 1) indicates that negative species interactions are strong enough to
96 outweigh the positive effects of niche differentiation and positive interactions on relative yields in
97 mixture. Thus, AP was devised as a tool to test hypotheses, not as a tool to identify the type and
98 strength of species interactions. It is the sign and relative magnitude of CE and SE that matter in
99 hypothesis testing, while their absolute magnitudes should be interpreted more cautiously because
100 of the range of biological processes that can affect them.

101 Liberal interpretations of AP as a means to identify and quantify species interactions may
102 have resulted from ambiguous usage of the term “mechanism” in the BEF literature as well as in
103 other areas of ecology. A “mechanism” denotes any lower-level process that contributes to
104 generating a higher-level “phenomenon” of interest. In this sense, although CE and SE, the two
105 components of AP, provide information about which mechanisms are compatible with the
106 observed effects of biodiversity on ecosystem functioning, they do not themselves correspond to
107 particular biological mechanisms because they combine the effects of a potentially wide range of
108 individual-level processes on the community-level phenomenon of yield, hence their appropriate
109 designation as “effects”. The literature, however (including Loreau and Hector 2001), has often
110 used the terms “mechanisms”, “classes of mechanisms” or “types of mechanisms” to describe CE
111 and SE, leading sometimes to the improper interpretation that they quantify individual-level
112 biological processes. Just as with any other approach, greater terminological and conceptual clarity
113 is likely to help better appreciate the scope and limitations of AP.

114 The new approach proposed by CCN relies on an attempt to formalize Chesson’s (2000)
115 conceptual distinction between stabilizing and equalizing coexistence “mechanisms”. They build

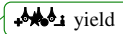
116 measures of ND and RFD that capture these two “mechanisms” based on the sensitivities of
117 species’ invasion rates to interspecific competition. Specifically, ND is measured as one minus the
118 geometric mean of these sensitivities, while RFD is measured as their geometric standard
119 deviation. CCN then show that both increasing ND and decreasing RFD increases RYT and CE, in
120 contrast to their intuitive expectations that only ND should affect RYT and CE based on the
121 assumption that the latter measure resource partitioning between species. This particular result
122 leads them to conclude that current measures of functional complementarity “give a largely
123 skewed estimate of resource partitioning”. There are, however, several fundamental problems with
124 this interpretation.

125 The first problem follows directly from the above discussion of the concept of “mechanism”.
126 While Chesson’s distinction is useful to identify two types of constraints that affect coexistence,
127 we know of no evidence that these constraints reflect independent biological processes, and hence
128 that they correspond to distinct biological mechanisms. Just as with CE and SE, the so-called
129 stabilizing and equalizing “mechanisms” define effects at the community level (specifically, on
130 coexistence); these effects also summarize a wide range of species interactions, including resource
131 partitioning, natural enemy partitioning, facilitation, and interference. Even in the specific context
132 of consumer–resource interactions considered by CCN, deterministic niche differences between
133 species include differences in niche height (absolute level of resource consumption), niche
134 breadth, and niche overlap. Differences in niche height and niche breadth are usually implicitly
135 related to RFD, while low niche overlap is usually associated with ND (despite the fact that niche
136 overlap is only one component of niche differences) because it is a necessary condition for stable
137 coexistence. Differences in niche height and niche breadth, however, also affect quantitative
138 measures of niche overlap and the amount of niche overlap that is necessary to allow coexistence.
139 Therefore, except in special cases, ND and RFD should be expected to reflect the operation of a

140 number of overlapping lower-level processes. Thus, our first conclusion is that AP and the
141 distinction between stabilizing and equalizing “mechanisms”— or, more appropriately, effects —
142 are two alternative ways to sort the community-level effects of individual-level mechanisms.





143 A second conclusion follows immediately from the first. Since the two alternative
144 frameworks provide different ways to define and aggregate the community-level consequences of
145 individual-level processes and since they work with different quantities (sensitivity of invasion
146 rates to interspecific competition vs. yield), it is hardly surprising that they produce different
147 results. The fact that both ND and RFD affect CE and SE can be no more an argument for
148 rejecting the latter than the reciprocal fact that both CE and SE affect ND and RFD would be an
149 argument for rejecting ND and RFD. Therefore, without some independent confirmation, CCN’s
150 results neither justify their suggestion that ND and RFD are more appropriate than AP for
151 identifying mechanisms that drive the BEF relationships, nor do they support their claim that CE
152 gives a skewed estimate of resource partitioning.





153 This brings us to a third issue — the specific limitations of the ND and RFD metrics within
154 the context of BEF research. In contrast to AP, which was tailored to test hypotheses about the
155 effects of biodiversity on yield, ND and RFD bear no necessary relation to yield and other
156 ecosystem properties that are measured in biodiversity experiments. The simple relationships that
157 are often assumed between community-level resource depletion, production, and biomass at
158 equilibrium hold only under restricted conditions that may apply to annual plants but not
159 necessarily to other organisms (Loreau 2010). The connections between these equilibrium
160 properties and the sensitivity of species’ invasion rates to interspecific competition are bound to be
161 even weaker because the traits that govern a species’ ability to invade a subset of a community are
162 not necessarily the same as those that govern its yield once established in the full community.
163 There is mounting evidence that the strength of trophic interactions depends on the presence and

164 density of other species and that these trophic interaction modifications themselves interact
 165 (Golubski and Abrams 2011), generating a plethora of higher-order density-dependent effects in
 166 communities. For instance, Bogran et al. (2002) demonstrated phenotypic plasticity in host use by
 167 parasitoids along two niche axes, such that parasitoid species that appear redundant when studied
 168 independently may become complementary when they coexist. In such cases, niche differences
 169 measured using invasion rates have little to do with overyielding detected in biodiversity
 170 experiments. Experimental evidence also suggests that both the magnitude and the nature of
 171 biodiversity effects may change over time (Cardinale et al. 2007). Thus, while sensitivities of
 172 invasion rates are useful within the context of coexistence theory, it is doubtful that they will
 173 generally provide robust predictors of equilibrium ecosystem properties. It is also unclear how ND
 174 and RFD can be used to test some of the basic hypotheses of interest in BEF research. For
 175 instance, the sampling effect hypothesis assumes specifically that the species with the highest
 176 monoculture yield or carrying capacity outcompetes the others in mixtures. ND and RFD are
 177 unable to test this hypothesis because they are independent of the absolute value of carrying
 178 capacities (Appendix). For all these reasons, it seems to us that the AP approach has a distinct
 179 practical advantage for hypothesis testing in biodiversity experiments.

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180 Lastly, the results reported by CCN are largely restricted to 2-species systems, with some
 181 additional simulations for 3 and 4 species. Although the general trends they reveal seem to be
 182 robust, they should not mask some significant deviations from these trends, which confirm that
 183 ND and RFD bear no simple relations to overyielding, and hence that their use as tools to interpret
 184 biodiversity experiments would require more careful examination. In particular, CCN's central
 185 result that RYT (and hence CE) increases as ND increases and as RFD decreases does not always
 186 hold, even within the restricted scope of MacArthur's model. For some scenarios and parameter
 187 values, opposite patterns can be found.

 these trends

 exceptions

188 | To illustrate and understand this possibility, we use the continuous formulation of
 189 | MacArthur's model because it provides an explicit measure of niche differences (*sensu* niche
 190 | overlap) between species along a resource gradient (Sapjanskas and Loreau 2010), and we focus
 191 | on the specific example of 4 consumer species distributed in 2 functional groups. For simplicity,
 192 | we assume that the two species in each functional group i have the same niche width, σ_i , and that
 193 | the two functional groups are different enough (i.e., are spread out enough along the resource
 194 | gradient) that competitive interactions between groups is negligible. In this case, ND, RFD and
 195 | RYT can be obtained analytically (Appendix):

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$$196 \quad ND = 1 - \exp\left[-\frac{1}{8}\left(\frac{\Delta_1^2}{\sigma_1^2} + \frac{\Delta_2^2}{\sigma_2^2}\right)\right], \quad (1)$$

$$197 \quad RFD = \exp\left\{\frac{1}{8}\sqrt{\left(\frac{\Delta_1^2}{\sigma_1^2} - \frac{\Delta_2^2}{\sigma_2^2}\right)^2 + 32\left[\left(\log\frac{K_{1a}}{K_{1b}}\right)^2 + \left(\log\frac{K_{2a}}{K_{2b}}\right)^2\right]}\right\}, \quad (2)$$

$$198 \quad RYT = \frac{2 - \exp\left(-\frac{\Delta_1^2}{4\sigma_1^2}\right)\left(\frac{K_{1a}}{K_{1b}} + \frac{K_{1b}}{K_{1a}}\right)}{1 - \exp\left(-\frac{\Delta_1^2}{2\sigma_1^2}\right)} + \frac{2 - \exp\left(-\frac{\Delta_2^2}{4\sigma_2^2}\right)\left(\frac{K_{2a}}{K_{2b}} + \frac{K_{2b}}{K_{2a}}\right)}{1 - \exp\left(-\frac{\Delta_2^2}{2\sigma_2^2}\right)}, \quad (3)$$

199 | where K_{ia} and K_{ib} are the carrying capacities of the two species in functional group i , and Δ_i is the
 200 | distance between their niche centres along the resource gradient.

201 | As expected, ND decreases exponentially as niche overlap within functional groups
 202 | increases (remember that niche overlap between functional groups is assumed to be negligible).
 203 | RFD has two components: the first term under the square root in equation (2) is a measure of the
 204 | difference between the two functional groups in the amount of niche overlap within the group,
 205 | while the second is a measure of competitive dominance within the groups. Note that niche
 206 | overlap affects both ND and RFD, such that the two measures are not independent from each

207 other, as we suggested above based on intuitive arguments. But niche overlap and competitive
208 dominance interact more strongly in RYT since the relative yield total of each functional group
209 weighs the effect of niche overlap by competitive imbalance such that decreased niche overlap has
210 a disproportionately larger positive effect when species are competitively dissimilar (i.e., when
211 $K_{ia}/K_{ib} + K_{ia}/K_{ib}$ is larger). Since RYT incorporates the effects of niche overlap and competitive
212 imbalance in different ways than do ND and RFD, all sorts of relationships between these
213 measures are possible, including relationships that are opposite to those found by CCN — i.e.,
214 RYT can decrease, rather than increase, as ND increases and as RFD decreases (Fig. 1). Note that
215 these findings do not prove that there is anything intrinsically wrong with the approach based on
216 ND and RFD. But they do challenge the use of these metrics as some sort of self-evident reference
217 against which RYT and AP should be assessed. We see no justification for assuming the
218 superiority of the first approach over the second.

219 Where does all this leave the BEF research field? Methods based on relative yield, in
220 particular AP, have been the primary tool used in identifying biodiversity effects over the last
221 10–15 years. CCN's study reiterates that CE cannot be directly equated to resource partitioning,
222 and shows that CE and SE do not correspond to stabilizing and equalizing coexistence effects.
223 This is not surprising because CE and SE were not developed to quantify resource partitioning or
224 coexistence mechanisms. Instead, CE and SE are useful tools to test hypotheses. For example,
225 Cardinale (2011) used AP in the analysis of a recent experiment where SE and CE appear to do a
226 good job in identifying the signatures of species dominance and complementarity, respectively.
227 Unfortunately, the ND and RFD measures proposed by CCN are also unable to quantify biological
228 processes such as resource partitioning because, like CE and SE, they are net measures of multiple
229 biological processes. Thus, it is unclear how they can contribute to enhance our ability to detect
230 biological mechanisms.

231 Given the limitations inherent in all pre-existing post hoc statistical methods (reviewed in
232 Hector et al. 2009) and CCN's new approach, how can we make further progress in understanding
233 the mechanisms that explain the maintenance of biodiversity and its functional consequences? We
234 believe that such progress requires at least two key ingredients. The first is expanding theory that
235 connects the microscopic mechanics of species interactions and the macroscopic properties of
236 whole ecosystems. There have been recent developments in this area (Loreau 2010), and we
237 welcome CCN's work as a new contribution toward this shared goal. The main challenge for
238 theory development will be to keep a unifying perspective while examining the mechanistic details
239 of species interactions. The distinction between stabilizing and equalizing coexistence effects
240 provides one possible unifying framework, but others are conceivable. One of the important roles
241 of ecological theory should be to build and explore alternative unifying frameworks that link the
242 microscopic and macroscopic properties of ecosystems. Second, we need a new generation of
243 experiments that analyze the individual- and population-level processes that generate the effects of
244 biodiversity on ecosystem functioning. When two of us proposed the AP methodology (Loreau
245 and Hector 2001), we concluded that this methodology "cannot replace direct experimental
246 investigations into the mechanisms at work in responses to biodiversity changes at the ecosystem
247 level, which are now critical to further progress in this area". This conclusion is still topical today.
248 A few pioneering studies have experimentally manipulated available niche space
249 (Dimitrakopoulos and Schmid 2004, Cardinale 2011) or species' niches through evolution (Gravel
250 et al. 2011) to test for the role of resource partitioning in shaping BEF relationships. Others have
251 manipulated intra- and interspecific population densities simultaneously to disentangle the roles of
252 resource partitioning and facilitation in overyielding (Gross et al. 2007, Northfield et al. 2010).
253 Still others have manipulated the presence of mutualists (van der Heijden et al. 1998) or pathogens
254 (Maron et al. 2011, Schnitzer et al. 2011) to test for their role in driving BEF relationships. But

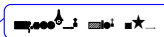
255 overall the number of studies that have tested underlying mechanisms explicitly is still too limited
256 to draw general conclusions on the lower-level processes that drive BEF relationships and the way
257 these processes interact. Combining innovative theory and experiments that allow us to
258 disentangle these processes and bring them together in a coherent unifying framework should now
259 be a major research focus in community and ecosystem ecology.

260

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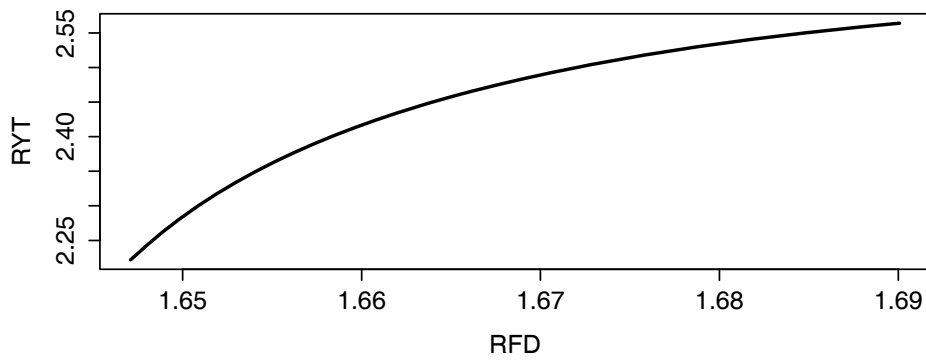
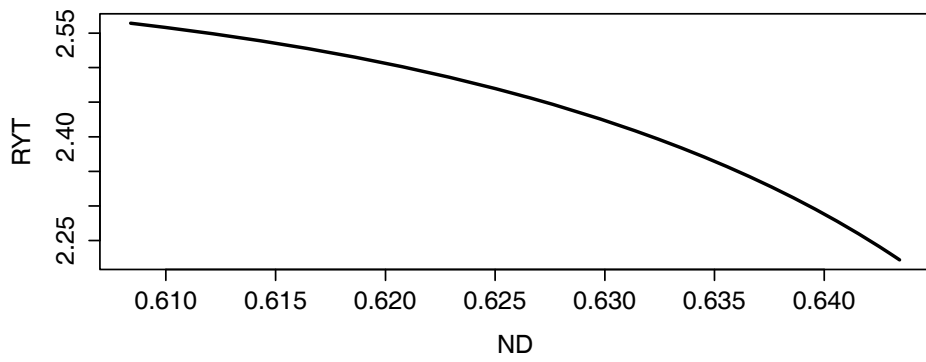
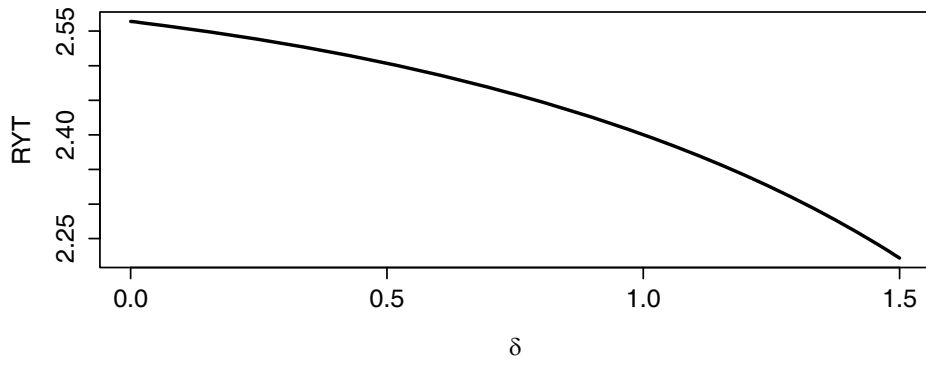
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324

Figure legend

325

326 **Fig. 1.** Changes in the relative yield total, RYT, and the resulting relationships between RYT and
 327 ND or RFD when niche overlap varies in a community of 4 species distributed in 2 functional
 328 groups (equations 1–3). Niche overlap is here varied in opposite directions in the two functional
 329 groups using the transformation $\left\{ \frac{\Delta_1^2}{\sigma_1^2}, \frac{\Delta_2^2}{\sigma_2^2} \right\} \rightarrow \left\{ \frac{\Delta_1^2}{\sigma_1^2} - \delta, \frac{\Delta_2^2}{\sigma_2^2} + 1.5\delta \right\}$, where δ is increased from an
 330 initial value of zero. Parameters were chosen such there is both greater niche overlap ($\Delta_1/\sigma_1 <$
 331 Δ_2/σ_2) and greater competitive imbalance ($K_{1a}/K_{1b} + K_{1b}/K_{1a} > K_{2a}/K_{2b} + K_{2b}/K_{2a}$) in the first
 332 functional group. ND and RFD are increasing and decreasing functions, respectively, of δ . Yet,
 333 RYT decreases with δ because the competitive imbalance between the two groups is sufficiently
 334 large for the positive effect of reduced niche overlap in the second group ($\Delta_2^2/\sigma_2^2 + 1.5\delta$) to
 335 overwhelm the negative effect of increased overlap in the first ($\Delta_1^2/\sigma_1^2 - \delta$) (Appendix). In this
 336 example, $\Delta_1^2/\sigma_1^2 = 3$, $\Delta_2^2/\sigma_2^2 = 4.5$, $K_{2a} = K_{2b}$, and $K_{1a} = 2K_{1b}$. Stable coexistence of the four
 337 species requires $\delta < 1.4$.



338

339

Figure 1