

1 Running title: Evolutionary responses to conditionality

2 Evolutionary responses to conditionality in species interactions across environmental  
3 gradients

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## Abstract

The outcomes of many species interactions are conditional on the environments in which they occur. A common pattern is that outcomes grade from being more positive under stressful conditions to more antagonistic or neutral under benign conditions. The evolutionary implications of conditionality in interactions has received much less attention than the documentation of conditionality itself, with a few notable exceptions. Here, we predict patterns of adaptation and co-adaptation between partners along abiotic gradients, positing that when interactions become more positive in stressful environments, fitness benefits of interactors become more aligned and selection should favor greater mutualistic adaptation and co-adaptation between interacting species. As a corollary, in benign environments, if interactions are strongly antagonistic, we predict antagonistic co-adaptation resulting in Red Queen or arms-race dynamics, or reduction of antagonism through character displacement and niche partitioning. We predict no adaptation if interactions are more neutral. We call this the CoCoA hypothesis: **(Co)**-adaptation and **C**onditionality across **A**biotic gradients. Here, we describe experimental designs and statistical models allowing us to test predictions of CoCoA, with a focus on positive interactions. While only one study has included all the elements to test CoCoA, we briefly review the literature and summarize study findings relevant to CoCoA, and highlight opportunities to test CoCoA further.

## 50 Outcomes of biotic interactions depend on abiotic con- 51 ditions

52 The outcomes of biotic interactions are shaped by the conditions in which they occur. For  
53 example, warming temperatures cause corals to expel their zooxanthellae symbionts (Hoegh-  
54 Guldborg, 1999), increasing fire frequency and severity favors invasive over native grasses in  
55 competitive interactions (D’Antonio and Vitousek, 1992), and predation on pepper moths is  
56 altered by the prevalence of air pollution (Kettlewell, 1955). Conditionality in mutualisms  
57 is well known (Cushman and Whitham, 1989; Bronstein, 1994), and a meta-analysis of  
58 mutualism studies finds that mutualistic outcomes are variable across space and habitats  
59 (Chamberlain et al., 2014). We first discuss our predictions at the stressful, more mutualistic  
60 ends of environmental gradients and then predictions for the benign, more antagonistic ends  
61 of gradients.

62 Two well-developed and related models of species interactions seek to predict changing  
63 outcomes of interactions across gradients. First, economic models of mutualisms describe  
64 inequalities with respect to resources and predict conditional outcomes from mutualism to  
65 antagonism. When the resources a participant *receives* in trade from partners are those that  
66 are most limiting to the participant’s fitness, the benefits from trading are maximized; when  
67 resources the participant *provides* to partners limit the participant’s fitness, the costs of en-  
68 gaging in trade are maximized (Johnson, 1993; Schwartz and Hoeksema, 1998; Bever, 2015).  
69 Resource-based conditionality has been shown to exist for many “mutualisms” (Bronstein,  
70 1994), including between plants and mycorrhizal fungi, in which fungi provide soil nutri-  
71 ents in exchange for plant carbon: mycorrhizal fungi typically provide benefits to plants in  
72 low nutrient (stressful) conditions, but often impose costs when nutrient availability is high  
73 (Smith et al., 2010). Another model closely tied to environmentally conditional outcomes  
74 in species interactions is the Stress-Gradient hypothesis (SGH). The SGH posits that the  
75 relative importance of costs and benefits in biotic interactions changes across stress gradi-

76 ents (Bertness and Callaway, 1994), and that interactions will gradually shift from having  
77 neutral or negative outcomes under benign abiotic conditions to having beneficial outcomes  
78 under stressful conditions (Brooker and Callaghan, 1998; Malkinson and Tielbörger, 2010).  
79 A meta-analysis of SGH in plants found consistent shifts towards facilitation or reduced  
80 competition at high stress (He et al., 2013).

81 These separate theories are united by a focus on change in interaction benefits over  
82 gradients of increasing fitness-limitation by resource levels or abiotic stress: when interac-  
83 tions ameliorate fitness-limiting factors, they are expected to have positive effects on fitness,  
84 and when they exacerbate fitness-limiting factors, they should decrease fitness. The SGH  
85 and resource-based conditionality were originally detailed to explain changes from compe-  
86 tition to facilitation in plant interactions and changes from mutualism to antagonism in  
87 plant-microbe interactions, yet they apply to a diversity of interactions such as detritivore-  
88 detritivore (Fugère et al., 2012), herbivore-herbivore (Dangles et al., 2013), plant-herbivore  
89 (Daleo and Iribarne, 2009), and bacterial cross-feeding (Hoek et al., 2016), all of which be-  
90 come increasingly facilitative or decreasingly costly as a stress the interaction ameliorates  
91 increases.

92 The evolutionary implications of conditionality in interactions have received much less  
93 attention than the documentation of conditionality itself, with notable exceptions (Schwartz  
94 and Hoeksema, 1998; Thompson, 2005; Bronstein, 2009; Michalet et al., 2011). The geographic  
95 mosaic theory of coevolution (GMTC Thompson, 2005) suggests that as fitness consequences  
96 of interactions vary across space, selection pressure from these variable interactions will  
97 result in different evolutionary outcomes. The GMTC is well supported (Thompson, 2005;  
98 Schemske et al., 2009), yet lacks a framework for linking characteristics of the environment  
99 to specific evolutionary outcomes.

100 Here, we unite predictive frameworks for species interaction outcomes and evolutionary  
101 principles to develop a hypothesis that effects of limiting gradients on interaction outcomes  
102 to the degree of adaptation in interacting populations of species across stress gradients. We

103 first leverage existing theory of conditionality, stress gradients, and geographic mosaics to  
104 generate predictions. We then move to propose experimental and analytical methods for  
105 testing it and a discussion of existing relevant literature.

## 106 **Evolutionary responses to conditionality: a hypothesis**

107 Because conditionality models predict that environmental or resource gradients result in pre-  
108 dictable variation in the nature of interaction outcomes, we suggest that evolution in these  
109 contexts might also result in predictable outcomes. Extending the predictions of condition-  
110 ality in interaction outcomes to coevolutionary dynamics, we predict selection should result  
111 in adaptation and co-adaptation in species interactions that are shaped by the same envi-  
112 ronmental gradients. Where interactions mutually ameliorate a limiting stress, we predict  
113 that, if a mutation arises in one species that reduces stress on the interacting partner, the  
114 effect of that mutation will feedback to positively affect fitness in both species (Sachs et al.,  
115 2004) and will be favored by selection. Genetic variation in the traits of one partner that  
116 ameliorate stress in the other should thus have large impacts on fitness of both partners  
117 in these stressful sites. As selection continues to fix mutations ameliorating the stress of  
118 partners, we predict mutualistic adaptation or co-adaptation should increase at stressful or  
119 resource-limited ends of environmental gradients (Figure 1). When changes in both part-  
120 ners (mutualistic co-adaptation) or just one partner alone (mutualistic adaptation) could  
121 contribute to this prediction of increasing mutual benefit of both partners.

122 At the ends of gradients that are “benign” with respect to stresses or resources, fitness  
123 will be instead limited by either costs of the interaction or by unrelated factors. Interactions  
124 between species may become neutral or shift towards antagonism (Johnson, 1993; Bertness  
125 and Callaway, 1994; Schwartz and Hoeksema, 1998), which we predict will result in a variety  
126 of coevolutionary outcomes.

127 If the interaction is neutral for one or more partners, we predict no co-adaptation, though

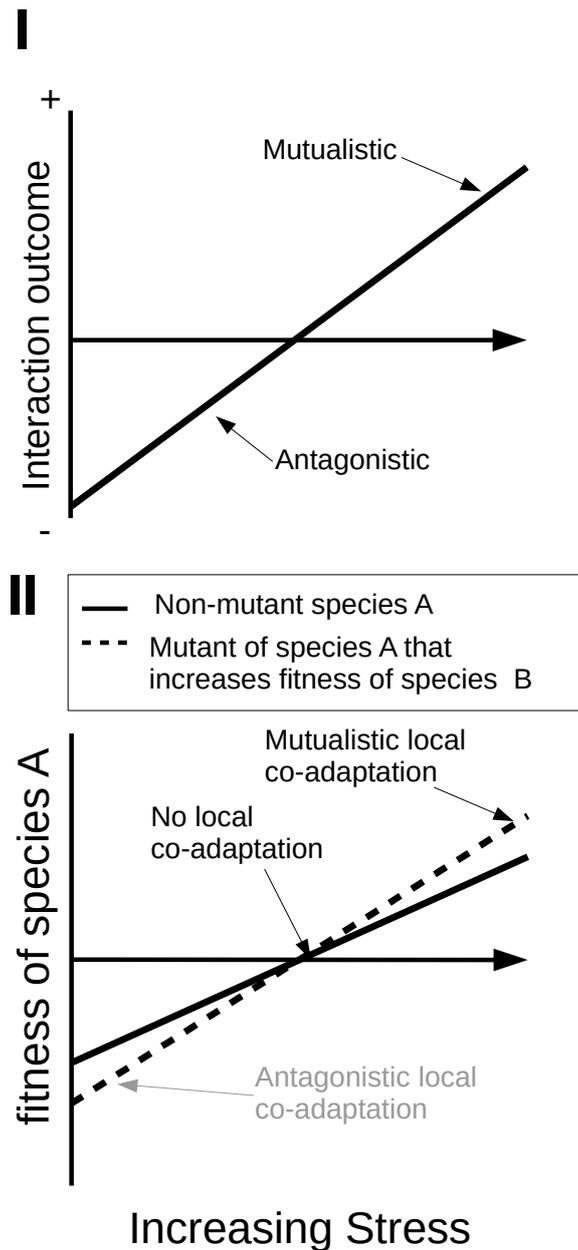


Figure 1: (I) The stress-gradient hypothesis (SGH) and limiting resource conditionality of mutualisms predict ecological stress-ameliorating interactions will be mutualistic at sites more limited by stress only. Note that relationships between limiting stresses and benefits are likely to be nonlinear, and benefits will taper off at extreme stress values (Malkinson and Tielbörger, 2010; Holmgren and Scheffer, 2010), but are simplified here for visual presentation. (II) Because selection favors alternate interaction strategies across the gradient, our hypothesis of interaction gradient adaptation (CoCoA) suggests increasing mutualistic local co-adaptation at high stress sites. Note that where interactions grade into increasing antagonism (+,- or -,-) in benign conditions, increasing antagonistic co-adaptation (primarily for parasitism) or adaptation to avoid interactions (primarily for competition) are favored.

128 if the interaction continues to negatively impact fitness of one partner, adaptation in this  
129 partner may still be influenced by interaction costs. Specifically, when interactions do not  
130 contribute to fitness, mutations that increase investment in interactions will drift, or will be  
131 removed by selection if the investment is costly to produce.

132 When the interaction is antagonistic in benign conditions, the interaction may again  
133 strongly affect fitness, now inflicting high costs on one or both partners. Reciprocal selection  
134 in mutually antagonistic interactions (e.g. competition) could act either to reduce antago-  
135 nistic interactions through avoidance (such as character displacement, Pfennig and Pfennig,  
136 2009), or to increase tolerance to the effects of the interaction (Bronstein, 2009). In more  
137 asymmetric interactions, such as trophic interactions (e.g. parasitism, predation), antago-  
138 nism can result in asynchronous or oscillating Red-Queen coevolutionary dynamics such as  
139 arms-races (Toju et al., 2011), or frequency-dependent selection (Decaestecker et al., 2007).  
140 In particular for arms-races, this intensified coevolution in benign conditions will drive esca-  
141 lation traits to the most extreme values (Hochberg and van Baalen, 1998; Benkman et al.,  
142 2003; Hanifin et al., 2008). Mutations affecting asymmetric interaction outcomes will have  
143 high fitness consequences for partners and will either swiftly fix or could exhibit cyclical  
144 dynamics under frequency-dependent selection.

145 Evidence exists that many traits affecting interaction outcomes have a genetic basis and  
146 can respond to selection. For example, variation in mutualistic benefit provided has been  
147 shown to have a genetic basis in many systems (e.g. Moran, 2001; Heath et al., 2012; Eaton  
148 et al., 2015; Chrostek and Teixeira, 2015; Klinger et al., 2016), as has variation in resistance  
149 to antagonists (e.g. Staskawicz et al., 1995; Lively and Dybdahl, 2000; Decaestecker et al.,  
150 2007), and thus both can be expected to respond to selection.

151 Both theoretical and empirical work suggest that as the strength of selection on beneficial  
152 or antagonistic interactions increases, mutations favoring interaction with local partners are  
153 more likely to fix (Parker, 1999; Nuismer et al., 2000; Kawecki and Ebert, 2004; Thompson,  
154 2005; Schemske et al., 2009). Strong selection coupled with low gene flow is predicted to result

155 in specific adaptation or co-adaptation between local populations. While extremely high gene  
156 flow would prevent adaptation along any gradient, intermediate gene flow could preclude local  
157 adaptation/co-adaptation within populations and instead promote general adaptation/co-  
158 adaptation among sets of populations. In Figure 3, we contrast expectations under high and  
159 low gene flow along a stress gradient where interactions grade towards mutualistic. Beneficial  
160 mutations that are specific to the genotypes of local partners (“specific benefits”) fix under  
161 low gene flow while those underlying benefits to and from multiple partners (“generalized  
162 benefits”, Figure 3) are predicted to be favored when gene flow between stressful sites is  
163 higher.

164 In sum, we predict that interactions shifting in the sign of outcomes along gradients  
165 generate the most adaptation or co-adaptation near gradient extremes and least midrange,  
166 where neutral outcomes for one or more species prevent fitness feedbacks. For interactions  
167 that exhibit conditionality across an abiotic or resource gradient, we predict evolution to-  
168 wards increasing mutualism and/or greater mutualistic co-adaptation in partners where the  
169 interaction most ameliorates fitness-limiting stress. In contrast, benign sites, where interac-  
170 tion outcomes are predicted to be more antagonistic, will generate antagonistic evolutionary  
171 dynamics, such as arms-races, or character displacement. We call this the **(Co)**-adaptation  
172 to **C**onditionality across **A**biotic gradients hypothesis, or CoCoA.

173 Below, we discuss designs that can test CoCoA. In designing a test for CoCoA, we focus  
174 primarily on the more limiting end of the abiotic gradient and mutualistic interactions, as  
175 we predict the coevolutionary outcomes will be consistent or increasing over time, making  
176 them most straightforward to test at a single timepoint. In contrast, as mentioned above,  
177 the often cyclical or temporally varying nature of antagonistic coevolution makes it much  
178 harder to detect from single time point experiments.

## 179 **Testing for CoCoA**

180 Tests of CoCoA need to include several things: (1) evidence of an environmental gradient that  
181 ranges from limiting to non-limiting for both partners; (2) evidence that the interaction alters  
182 the fitness of partners across the gradient; (3) measures of fitness outcomes in interactions  
183 with local and non-local partner pairs sourced from populations across the gradient to test  
184 for adaptation or co-adaptation. Throughout, we refer to populations of each species from  
185 the same site as sympatric and populations from different sites as allopatric. Measurements  
186 of partner effects on fitness must include both sympatric and allopatric partners to test  
187 for both generalized and specific benefits. Specific benefits could arise from both species  
188 adapting to each other at a site (specific co-adaptation), or from one partner adapting  
189 specifically to the traits of the partner population at that site (specific adaptation). Either  
190 scenario fits the predictions of CoCoA. Generalized benefits would arise if just one species  
191 adaptively increased in the benefit it provided to and extracted from any partner (generalized  
192 adaptation), or if at stressful sites both species increased benefits provided to any partner  
193 population (generalized co-adaptation). Below we have outlined experimental design, linear  
194 models, and results interpretation for tests of CoCoA.

### 195 **Experimental design**

196 The ideal test of CoCoA will quantify two things: the effects of interacting species on each  
197 other's fitness sampled from across the gradient and the extent of generalized and specific  
198 local benefits between partner species across the gradient. For illustration, we provide an  
199 example of the interaction between two species (species "A" and "B") along a gradient from  
200 stressful conditions, where CoCoA and conditionality hypotheses predict that species will  
201 mutually enhance each others' fitness, to conditions where at least one species is predicted  
202 to have a negative effect on the other. In other words, this is a gradient where we expect  
203 the interaction between A and B to vary from mutualistic to not mutualistic in outcome.

204 Testing CoCoA requires sampling populations of both species at sites along an identified

205 stress gradient. More populations always improves power, since population source site is  
206 the experimental unit, yet the number of populations must be balanced with the replication  
207 needed for each comparison. Under CoCoA, we predict increased generalized and specific  
208 benefits accruing from adaptation of partners at the stressful end of the gradient. In order  
209 to test for generalized adaptation (Figure 3, I and III, solid lines), one can regress the  
210 effect of Species B source population on Species A fitness across all populations of Species  
211 A sampled along the gradient. In order to quantify specific adaptation or co-adaptation  
212 between local populations of partners, it is necessary to assess the relative benefits received  
213 by both Species A and Species B with sympatric partners versus allopatric partners across  
214 the gradient (Figure 3, II and IV, difference between dashed and solid lines). While these  
215 comparisons may be made using all possible combinations of interacting partner populations  
216 of Species A & B, a fully crossed design is not required. We suggest designs that have twice as  
217 many allopatric as sympatric comparisons across the gradient to maximize statistical power  
218 for tests of local adaptation (as recommended by Blanquart et al., 2013), with both types  
219 of populations sampled across the full gradient. A variety of designs fit these requirements,  
220 and we provide one example in Figure 2.

221 Experiments should be run under environments representative of those observed in nat-  
222 ural populations, as inappropriate conditions may alter expressed benefits or costs of asso-  
223 ciating with partners (Lau and Lennon, 2012). Ideally, fitness outcomes of sympatric and  
224 allopatric population interactions would be measured across several environments spanning  
225 the gradient. Running the experiment in multiple environments allows a test of the prediction  
226 that increasing stress shifts fitness outcomes towards increasing fitness alignment for Species  
227 A and Species B. Such a large experimental design, while optimal, may be possible only  
228 in systems where large amounts of replication are feasible, such as with microbe-microbe  
229 interactions. A reduced design tests outcomes only at the stressful ends of the gradient,  
230 where we predict to find a consistent signature of mutualistic adaptation or co-adaptation in  
231 sympatric populations, but only under stressful conditions. Here, we describe an experimen-

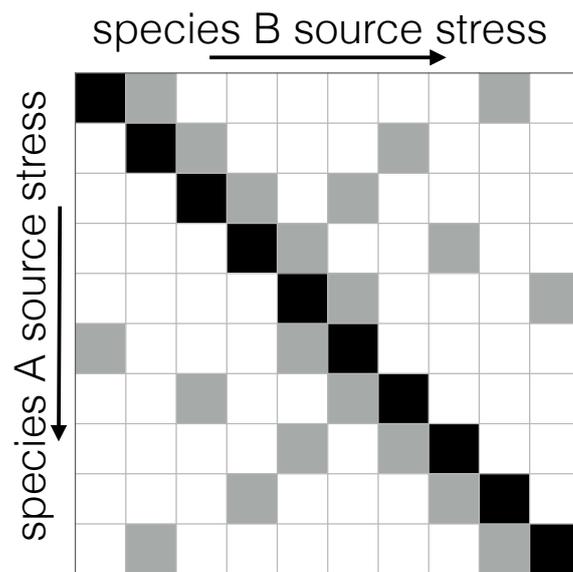


Figure 2: Possible sampling design and experimental combinations. Species A sources are in rows, arranged by increasing stress of source site from top to bottom. Species B sources are in columns, arranged by increasing stress of source site from left to right. Filled in squares are experimentally paired populations of A and B, including twice as many allopatric (grey) as sympatric (black) comparisons, and spreading sympatric and allopatric comparisons along the stress gradient for sources of both species A and species B.

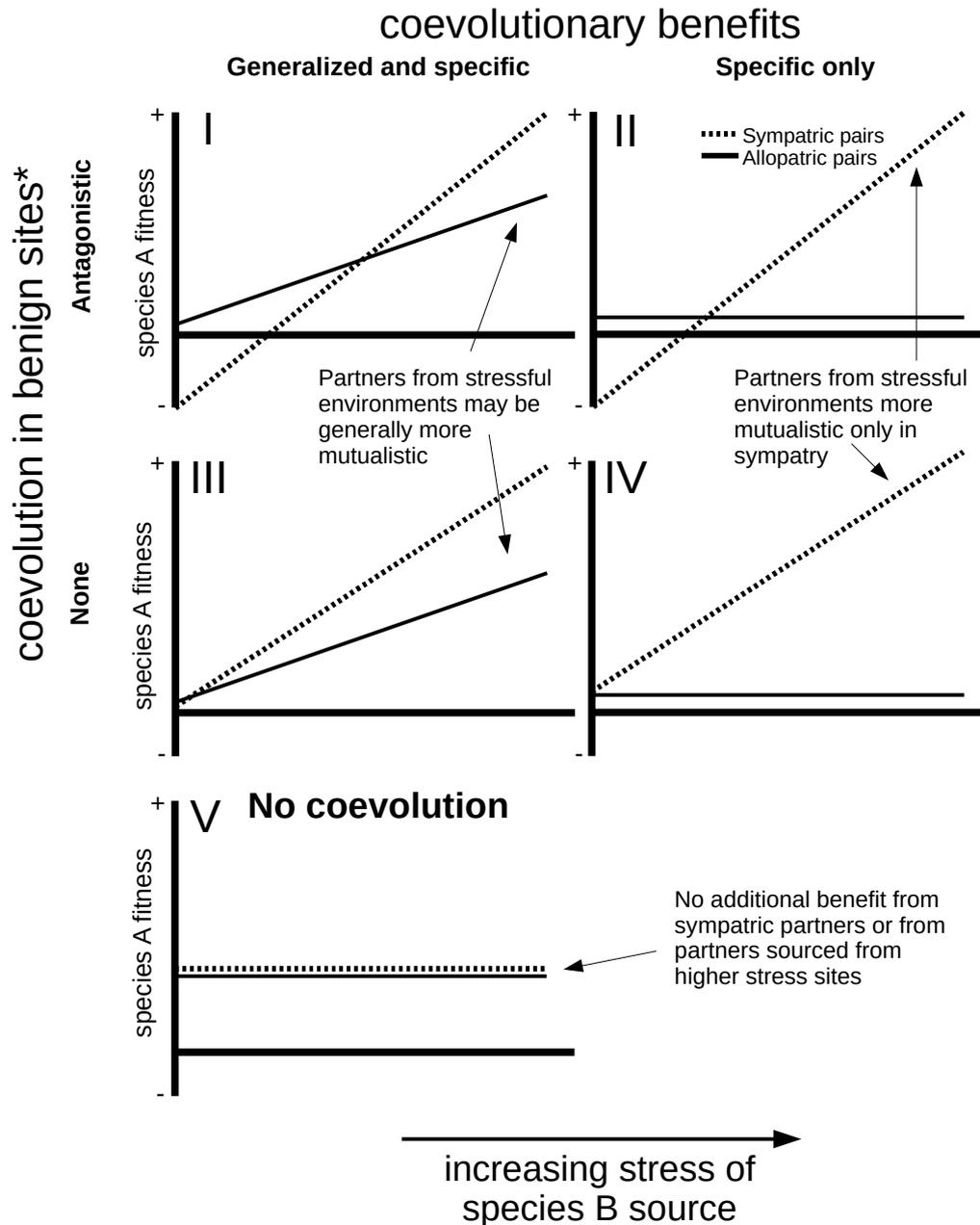


Figure 3: Possible experimental outcomes. CoCoA predicts greater fitness benefits provided by partners sourced from stressful sites across allopatric (solid lines) and sympatric (dashed lines) combinations (generalized benefits, panels I and III). CoCoA also predicts increasing fitness benefits of sympatric combination with source stress (specific benefits shown as the difference of dashed and solid lines, panels I-IV). Coevolutionary benefits may (see text) be specific to sympatric combinations (II, IV). For combinations with partners from benign sites, CoCoA predicts variable outcomes, and no (III, and IV) or negative (I and II) sympatric effects (see text). Without coevolution, the CoCoA expects no sympatric effects (V). Note that while this figure presents relationships between limiting stresses and benefits as linear, in many cases they increase nonlinearly (Malkinson and Tielbörger, 2010; Holmgren and Scheffer, 2010), reducing both benefits and adaptation at extreme stress.

232 tal design and analysis that tests CoCoA only in this stressful region of the gradient.(e.g.,  
233 under reduced resources, water availability, etc.).

234 We focus our tests and predictions around this range in interaction outcome because  
235 coevolutionary patterns from antagonisms may be difficult to detect without long-term sam-  
236 pling of trait changes and genotypes (Dybdahl and Lively, 1998; Decaestecker et al., 2007) or  
237 without long term partner removal experiments (Stuart and Losos, 2013). At any single time  
238 slice, one species may be “winning” the battle and appear locally adapted, but the winning  
239 species is likely to vary across time and space as evolution in the other species counteracts  
240 “gains” (e.g. Van Valen, 1974; Gandon and Michalakis, 2002; Nuismer, 2006).

## 241 **A linear model framework**

242 In classic tests of local adaptation, populations and sites are treated as discrete entities  
243 (Kawecki and Ebert, 2004; Blanquart et al., 2013). Incorporating degree of local adaptation  
244 along an environmental gradient, however, requires a continuous statistical approach. We  
245 suggest modeling effects of partners and environments on fitness in a linear framework, where  
246 fitness in one focal partner at a time is the response variable  $Y$  (below), and then repeating  
247 across the other partner so that species A and B fitnesses are response variables in separate  
248 models. This linear testing framework defines generally better and worse mutualists using  
249 average fitness benefits conferred to partners across partner combinations, which follows  
250 recent advances in theory (Frederickson, 2013; Porter and Simms, 2014; Jones et al., 2015).  
251 Below we show species A fitness as the response ( $Y_A$ ); the model for species B fitness would  
252 be specified by swapping all A and B terms.

$$Y_A \sim \alpha + \beta_{E_B} E_B + \beta_S S + \beta_{E \times S} E \times S + \beta_{E_A} E_A + \beta_Z Z + \varepsilon$$

253 The estimated parameter for the main effect of source environment in the non-focal  
254 partner (here, the environment of Species B population source,  $E_B$ , parameter  $\beta_{E_B}$ ) is a test  
255 of the CoCoA prediction that species B sourced from more stressful sites might be generally

256 more mutualistic for all species A populations than species B sourced from the less stressful  
257 parts of the gradient. CoCoA predicts that  $\beta_{E_B}$  should be positive.

258 Models should include a slope parameter for the binary term ( $S$ ) indicating whether  
259 origins of the interactors are sympatric ( $S = 1$ ) or allopatric ( $S = 0$ ) in addition to the slope  
260 parameter for the interaction between sympatry and the environmental gradient of source  
261 ( $\beta_{E \times S}$ ). Parameter estimates for effects of non-focal partner source environments ( $\beta_{E_B}$ )  
262 compared to estimates for the environment interaction with sympatry (an environment  $\times$   
263 sympatry interaction denoted as  $E \times S$ ) allow us to tease apart general benefits from specific  
264 benefits along the gradient (Figures 3 & 4). CoCoA predicts that  $\beta_{E \times S}$  should be positive;  
265 specifically that benefits accrued by sympatric partners from most stressful sites should be  
266 relatively greater than the benefits accrued by sympatric partners from other parts of the  
267 gradient, e.g. specific benefits are increased for stressful sites.

268 The focal partner source environment (here, the environment  $E_A$ ) is included to account  
269 for any main effects of population fitness along the gradient. Specifically, selection to reduce  
270 the fitness-limiting stress may not act only on interactions. Selection may also increase  
271 tolerance of stress without interactions (Espeland and Rice, 2007; Liancourt and Tielbörger,  
272 2011), or low resource environments might select for smaller individuals than high resource  
273 environments. Since the slope of species A fitness along increasing source site stress of B  
274 partners is built from the sum of  $\beta_{E_A}$ ,  $\beta_{E_B}$ , and  $\beta_{E \times S}$  (Figure 4), failure to account for  $\beta_{E_A}$   
275 can affect estimates of  $\beta_{E \times S}$  if fitness of Species A is positively or negatively correlated with  
276 the stress gradient. Estimating  $\beta_{E_A}$  allows us to account for either of these other sources of  
277 correlation (see Blanquart et al., 2013).

278 Our figures and models depict a linear relationship between fitness and the environmental  
279 gradient. To assess whether non-linear effects of gradients are better descriptors of the effects  
280 on fitness of species interactions along gradients (e.g. Malkinson and Tielbörger, 2010; Holm-  
281 gren and Scheffer, 2010), models with quadratic terms for  $E_B$  and  $E \times S$  should be compared  
282 with models using linear terms. Additional random effects that might be required, depend-

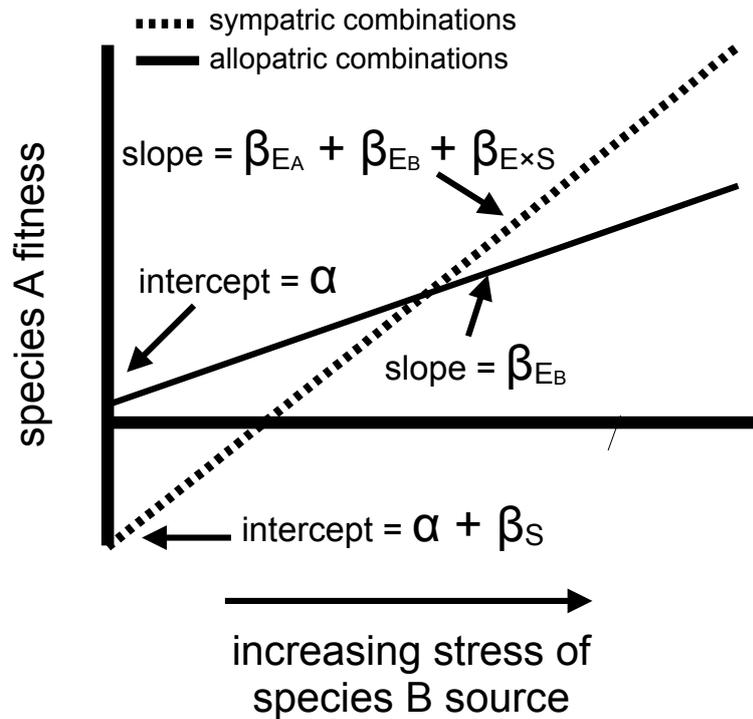


Figure 4: Here we show how parameters in the model relate to linear relationships between fitness and partner source. The relationship here is drawn from scenario I in Figure 3. Generalized coevolutionary benefits are tested by the parameter  $\beta_{E_B}$ , the slope of the allopatric comparisons (solid line), which is significantly positive here. Specific coevolutionary benefits are tested by the parameter  $\beta_{E \times S}$ , which, when added to  $\beta_{E_B}$  and  $\beta_{E_A}$ , is the slope of the sympatric (dashed) line.  $\beta_S$  only affects the intercept of the sympatric line.  $\beta_{E \times S}$  alone describes the increasingly positive difference between allopatric and sympatric combinations as the source site becomes more stressful. In some cases, both benefits and adaptation to them may be non-linear, requiring quadratic terms for  $E_B$  and  $E \times S$ .

283 ing on the design, could include: family effects, block effects, or year effects (represented  
284 here as a generic  $Z$ , with parameter  $\beta_Z$ ).

## 285 **Interpretation of results**

286 The predictions of CoCoA would be supported by the following outcomes: 1) if partners from  
287 more limiting sites provide greater benefits across focal species populations than partners  
288 from less limiting sites (generalized benefits,  $\beta_{EB}$  significantly positive) and 2) if partners  
289 from more limiting sites provide sympatric partners more benefit than the average benefits  
290 they provide allopatric populations of the partner species (greater specific benefits, indicated  
291 by a significant and positive  $\beta_{E \times S}$ ). When both  $\beta_{EB}$  and  $\beta_{E \times S}$  are significant and positive,  
292 both predictions of CoCoA would be supported, and both allopatric and sympatric lines  
293 have a positive slope (see Figure 4), but the sympatric line must be steeper to support local  
294 adaptation to interactions (illustrated in panels I and III in Figure 3).

295 Extensive gene flow between populations at stressful sites could result in more mutu-  
296 alistic partners from highly limited sites without increased local adaptation. For example,  
297 populations might experience isolation by environment more than isolation by distance (e.g.  
298 Sexton et al., 2016). This scenario is not plotted, but would be indicated by the case that  
299  $\beta_{E \times S}$  is non-significant and  $\beta_{EB}$  is significant and positive. The slope of the allopatric and  
300 sympatric lines would be identical (or differences would be due only to patterns in fitness of  
301 the focal species across the gradient,  $\beta_{EA}$ , unrelated to species interactions).

302 This section has focused on the stressful ends of gradients and mutualistic interactions. A  
303 similar experimental design and model would be required for tests of CoCoA in antagonisms  
304 or at benign ends of the gradients.  $\beta_S$  tests the main effect of sympatry, and is the intercept  
305 adjustment of the sympatric line relative to the non-sympatric line (Figure 4). This term  
306 reflects the difference between allopatric and sympatric pairings of A and B from benign  
307 sites. When this parameter is negative (as in Figure 3, panels I and II), it would indicate  
308 antagonistic adaptation in the non-focal species in benign sites. However, an estimate of  $\beta_S$

309 that is not different from 0 does not necessarily indicate a lack of antagonistic adaptation or  
310 coevolution, as adaptation in antagonistic interactions can generate non-significant effects  
311 (due to e.g. temporal or spatial variation in adaptation cycles). Repeating this design  
312 across samples from multiple time points (Decaestecker et al., 2007) or across experimental  
313 evolution (Pascua et al., 2011) may be required, and conclusions must be based on degree  
314 of trait change or rate of evolutionary dynamics across both abiotic gradients and time.

315 Experimental evolution would also facilitate testing whether mutualistic adaptation pro-  
316 ceeds reciprocally (co-adaptation) or if one species alone produces all patterns of adaptation.  
317 CoCoA expects the same patterns in increasing generalized and specific benefits with stress  
318 regardless of whether responses to selection are reciprocal (co-adaptation) or restricted to  
319 one species (adaptation only); pattern of benefits alone cannot distinguish co-adaptation  
320 from adaptation.

## 321 **Other considerations**

322 A non-trivial matter is how the gradient is defined and identified. Specifically, for CoCoA to  
323 hold, not only must sites be stressful, but interactions between partners must ameliorate the  
324 stress. CoCoA will be most predictive when conditions for the SGH and limiting resource  
325 conditionality are met: when a stress ranges from non-limiting to strongly limiting of fitness  
326 and is ameliorated by interaction between the focal species (He and Bertness, 2014). CoCoA  
327 will further be most predictive when population size is sufficiently large relative to gene flow  
328 and there is genetic variation on which selection can act in both partners. CoCoA will be less  
329 informative across weak, non-limiting, or multiple co-occurring gradients, where importance  
330 of interactions to fitness is less predictable (He and Bertness, 2014).

331 While extensive research on the SGH in plant-plant interactions generally supports the  
332 prediction of increasing facilitation with stress (He et al., 2013), peak facilitation may occur at  
333 moderate, rather than extreme limiting stress (Michalet et al., 2006; Holmgren and Scheffer,  
334 2010; Malkinson and Tielbörger, 2010). Intermediate peaks could be generated by non-linear

335 relationships between benefits (or costs) and abiotic gradients (Holmgren and Scheffer, 2010),  
336 or by low density of individuals at high stress sites causing missed interactions (Travis et al.,  
337 2006). Intermediate peaks appear to fit best in interactions that grade from increasing to  
338 decreasing access to a shared limiting resource (Maestre et al., 2009; Michalet et al., 2014), as  
339 opposed to interactions where limiting resources differ between partners. Peaks for positive  
340 outcomes in moderately stressful conditions, regardless of mechanism, have the consequence  
341 for CoCoA that mutualistic adaptation and co-adaptation would also peak at moderately  
342 stressful conditions, in which case, non-linear relationships of fitness with stress gradients  
343 would be the best models (see “A linear model framework” above).

### 344 **Existing literature pertinent to CoCoA**

345 In reviewing the literature, we found only one study that has addressed all criteria required  
346 to evaluate CoCoA. We found a number of studies in which most, but not all, of the criteria  
347 have been tested.

348 Experimentation on plant-microbe interactions offer the most complete tests. Johnson  
349 et al. (2010), which met all of the above criteria, found mutualistic local adaptation between  
350 a grass and its associated arbuscular mycorrhizal fungi across a phosphorus gradient. Plants  
351 are generally known to derive increased benefits from interacting with these fungi in low  
352 phosphorus conditions (Smith and Read, 2008). Fungi sourced from low phosphorous sites  
353 were more beneficial across plants but provided even greater benefits to sympatric plants  
354 (Johnson et al., 2010), supporting both the specialized and generalized benefits predictions  
355 of CoCoA. However, as only three sites were sampled, we remain cautious of inferring strong  
356 support for CoCoA.

357 Barrett et al. (2012) come very close to testing the full predictions of CoCoA by cross-  
358 inoculating acacia and microbes sampled along a soil nitrogen gradient (likely a limiting  
359 stress gradient). They found that the effects of the community of soil microbes sampled  
360 from low nitrogen sites provided the greatest benefit to acacias. In another study of plants

361 and nitrogen-fixing bacteria, bacterial genotypes sampled from high nitrogen sites (in which  
362 nitrogen is less limiting to plants) similarly provided less benefits than genotypes from low  
363 nitrogen sites (Weese et al., 2015). While the results of both these support the CoCoA  
364 prediction of increasing generalized benefits along stress gradients, neither test whether there  
365 are also increasing specific benefits (local adaptation or local co-adaptation).

366 In many ant-plant mutualisms, ants protect plants from herbivory and receive food from  
367 the plant. In Pringle et al. (2013), lower water sites were limiting for a plant host because  
368 insufficient water increased the risk of plant death from herbivory. This increased potential  
369 benefit from the interaction with ants, and both ant and plant partners have increased  
370 investments in the mutualism at these water-limited sites sites (Pringle et al., 2013). This  
371 example documents both the limiting gradient, which is ameliorated by the interaction, and  
372 greater reciprocal mutualistic benefits at the stressful portion of the gradient. It remains  
373 to be seen whether these benefits are adaptive differences or plastic behaviors, and whether  
374 they are generalized or specific.

375 In antagonistic interactions across gradients, there are also studies with support for a  
376 limited subset of CoCoA predictions. Bacteria-phage systems at the least limiting conditions  
377 (high nutrients) show strongest local adaptation (specific benefits) of phages to host bacteria  
378 (Pascua et al., 2011). Pascua et al. (2011) also showed increasing overall infectivity and  
379 resistance in high nutrients, suggesting greater trait escalation, as was found explicitly by  
380 another study, in which less limiting conditions led to evolution of increased defense traits  
381 in bacteria (Zhang and Buckling, 2016).

382 In contrast, one study finds evidence in conflict with CoCoA predictions. Across a puta-  
383 tive limiting gradient of increasingly cold conditions, plants show no local adaptation with  
384 rhizosphere biota and no evidence of increasing benefits from colder sourced biota (Kardol  
385 et al., 2014). While the limiting nature of extreme cold is a near certainty and the ability of  
386 plant-biota interactions to reciprocally ameliorate effects of extreme cold are untested, they  
387 are probable (Zhu et al., 2009).

388 In sum, while current evidence offers mixed support, only very few tests of CoCoA exist.  
389 Additionally, tests that do exist tend to test fitness patterns of only one partner, leaving  
390 mutual benefit unclear.

## 391 **Opportunities to test CoCoA**

392 Here we outline additional study systems where tests of some criteria of CoCoA have already  
393 been conducted, making them exciting opportunities for complete tests. The outcomes of  
394 interactions between plants and rhizosphere biota (a diverse community of microbes living in  
395 and near roots Hiltner (1904)) are highly influenced by environments (e.g. Zhu et al., 2009;  
396 Smith and Read, 2008; Lau and Lennon, 2012), and such conditionality suggests that plant-  
397 rhizosphere interactions are ripe for tests of CoCoA. Limiting soil nutrients have frequently  
398 been identified as the potential driver of the evolution of interactions with soil rhizosphere  
399 microbes (Johnson, 1993; Schwartz and Hoeksema, 1998; Kiers and van der Heijden, 2006;  
400 Bever, 2015), and meta-analysis finds local adaptation in plants and mycorrhizal fungi to be  
401 common but not universal (Rúa et al., 2016).

402 Plant-plant interactions across mesic-arid gradients are another system where CoCoA  
403 may be testable, as plant interaction outcomes across these gradients range from antagonis-  
404 tic to facilitative (He et al., 2013). Across the gradient from mesic to arid, competition in  
405 plant-plant interactions is expected to decrease in importance, leading to the prediction of  
406 CoCoA that adaptation to competitors would be greatest in mesic sites. Initial evidence does  
407 not reject CoCoA as a possibility, but also does not offer complete tests: genotypes from  
408 mesic (benign) sources were least affected by competition in multiple systems (Liancourt  
409 and Tielbörger, 2009; Liancourt et al., 2013), and another study suggests that neighbors  
410 may influence local adaptation in plants (Ariza and Tielbörger, 2011). However, two addi-  
411 tional examples in plant-plant interactions suggest that adaptive increases in stress-tolerance,  
412 rather than adaptive increase in benefits of interactions, may dominate patterns in stressful  
413 sites (Espeland and Rice, 2007; Liancourt and Tielbörger, 2011). Conclusions in plant-plant

414 interactions with respect to CoCoA must await more explicit tests.

415 There are several systems that are particularly promising for tests of CoCoA in antag-  
416 onisms. Increased trait escalation at high productivity has been found in camellia-weevil,  
417 newt-predator, and squirrel-rattlesnake antagonisms (Toju et al., 2011; Stokes et al., 2015;  
418 Holding et al., 2016). Defensive (Stokes et al., 2015; Holding et al., 2016) or both defensive  
419 and offensive (Toju et al., 2011) traits appear to have escalated more in environments where  
420 abiotic stress is low, as measured by increasing habitat productivity (Toju et al., 2011) or  
421 increases in physiological function (Stokes et al., 2015; Holding et al., 2016). These systems  
422 show some of the patterns CoCoA would predict, but whether stress-gradients led to these  
423 patterns, and whether patterns reflect adaptation to interactions must still be tested.

424 In sum, complete tests of CoCoA are within reach in many systems. Tests of some criteria  
425 already exist in these systems, and suggestive results indicate that complete tests of CoCoA  
426 like those outlined above would be worthwhile.

## 427 Discussion

428 Different models of conditionality in species interactions across environmental gradients make  
429 convergent predictions. Economic models of mutualisms predict that when a species is lim-  
430 ited by the resources provided by a partner, fitness benefits from engaging in interactions  
431 with that partner increase (Johnson, 1993; Schwartz and Hoeksema, 1998). The stress-  
432 gradient hypothesis (SGH) predicts that species should have more mutualistic interactions  
433 when they are occurring under abiotic stress and more neutral or antagonistic ones when in  
434 benign conditions (Bertness and Callaway, 1994; Brooker and Callaghan, 1998; Malkinson  
435 and Tielbörger, 2010). Predictions of one or both of these conditionality models are sup-  
436 ported by a number of studies in plant-plant (reviewed in He et al., 2013), animal-animal  
437 (e.g. Daleo and Iribarne, 2009; Dangles et al., 2013), and plant-microbe interactions (Smith  
438 et al., 2010).

439 We present here an extended hypothesis from these models of conditionality, which we  
440 term Co-adaptation to Conditionality across Abiotic gradients (CoCoA). CoCoA predicts  
441 evolutionary responses to predictable changes in interaction outcomes along environmental  
442 gradients. CoCoA, economic (Johnson, 1993; Schwartz and Hoeksema, 1998; Werner et al.,  
443 2014; Bever, 2015) and behavioral models (Revillini et al., 2016) all predict that selection in  
444 resource-limiting environments should favor increased benefits provided to partners in the  
445 mutualism. Other models of co-adaptation also focus on environmental gradients, making  
446 predictions based on levels of environmental productivity and biological diversity (Thrall  
447 et al., 2007). CoCoA differs from these models in its focus on adaptation patterns in both  
448 partners, its inclusion of fitness-limiting stresses beyond resources, and thus its applicability  
449 to a wide variety of conditional interactions.

450 CoCoA predicts that when an interaction is mutually positive across a portion of a stress  
451 gradient, fitnesses of partners are aligned at the stressful end of the gradient, resulting in  
452 mutualistic adaptation. At the benign end of the gradient, where the stress is not lim-  
453 iting fitness of these species, there are multiple possible evolutionary outcomes predicted  
454 by CoCoA. If the interaction outcome is neutral, we predict no local adaptation between  
455 partners. If the outcomes become antagonistic, such as in relationships that shift to par-  
456 asitism, CoCoA predicts intensification of evolutionary dynamics driven by possible Red  
457 Queen (or similar) coevolutionary scenarios: escalatory arms-races or frequency-dependent  
458 cycles, which can cause traits involved in the interaction to reach extreme values. If the  
459 outcomes become mutually negative, such as increased competition (as predicted by SGH)  
460 coevolution or adaptation to avoid interactions such as character displacement (Pfennig and  
461 Pfennig, 2009), or habitat partitioning (Martin, 1998; Germain et al., 2016) are also possi-  
462 ble. Adaptation at the benign end of the gradient would be difficult to detect in single time  
463 samples of populations, in contrast to outcomes at the stressful end of the gradient, which  
464 are more straightforward to test owing to their predicted temporal and spatial consistency.

465 CoCoA implies that selection for specialization may be common at both ends of the

466 stress gradient continuum, i.e. in both antagonistic and mutualistic interactions. While it  
467 is generally accepted that parasitism often promotes specialization and increases the rate of  
468 evolution (Paterson et al., 2010), it is debated whether mutualism commonly imposes selec-  
469 tion for specialization (Thompson, 2005). There is, however, some evidence that mutualism  
470 can be at least as strong a driver for specialization as parasitism (Kawakita et al., 2010),  
471 and mutualists may evolve at faster rates than non-mutualist sister lineages (Lutzoni and  
472 Pagel, 1997; Rubin and Moreau, 2016).

## 473 **Concluding Remarks**

474 As climatic conditions become more extreme and stressful under global change (Pachauri  
475 et al., 2014), we predict that adaptation to these environments may be heavily influenced  
476 by biotic interactions. Numerous studies have focused on single species processes that limit  
477 ranges, such as source-sink dynamics or maladaptive gene flow (see Sexton et al., 2009, for  
478 review), but our CoCoA hypothesis suggests more research on multi-species dynamics may  
479 be fruitful (Sexton et al., 2009; van der Putten et al., 2010).

480 Emerging evidence supports mutualism-dependent range limits for plants and rhizosphere  
481 biota: plants interacting with ectomycorrhizae have shown greater southern range contrac-  
482 tions than plants associated with endomycorrhizae (Lankau et al., 2015), and soil mutualists  
483 are facilitating pine invasion of novel habitat (Hayward et al., 2015). CoCoA contributes  
484 to a growing body of literature highlighting the importance of biotic interactions in deter-  
485 mining limits of species distributions on abiotic gradients (e.g. HilleRisLambers et al., 2013;  
486 Afkhami et al., 2014), even in climatically stressful environments (e.g. Brown and Vellend,  
487 2014) where abiotic variables have often been thought to be of greater importance (Brown  
488 et al., 1996; Hargreaves et al., 2014; Louthan et al., 2015). Biotic filters on abiotic variables  
489 that exacerbate or ameliorate abiotic effects may thus have widespread consequences for  
490 range shifts and other responses to global change.

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