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Running title: Evolutionary responses to condtionality

Evolutionary responses to conditionality in species interactions across environmental gradients

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Statement of authorship: AO and SYS contributed to the development of the hypothesis. All authors contributed to the revising of the manuscript. AO proposed the hypothesis and provided the first draft of the manuscript.

Keywords: stress-gradient, biotic interactions, mutualism, climate adaptation, local adaptation, co-adaptation

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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 **Co**nditionality 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.

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Outcomes of biotic interactions depend on abiotic conditions

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

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

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

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

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

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

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

Evolutionary responses to conditionality: a hypothesis

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

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

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

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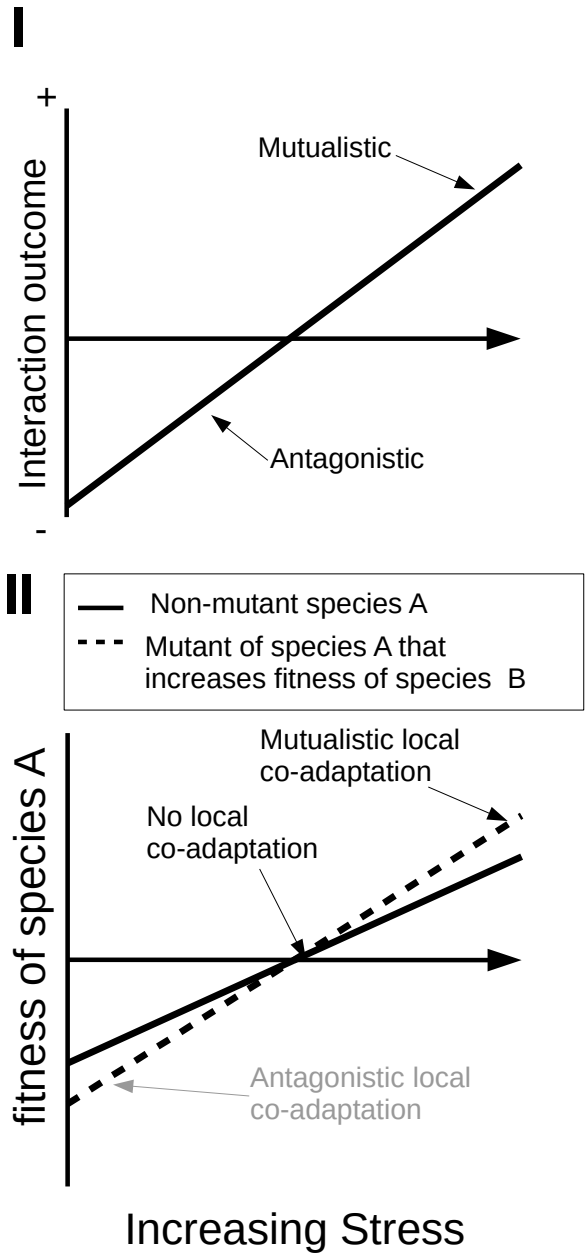

Figure 1: (I) The stress-gradient hypothesis (SGH) and limiting resource conditionality of mutualisms predict ecological stress-ameliorating interactions will be mutualistic at sites more limited by stress only. Note that relationships between limiting stresses and benefits are likely to be nonlinear, 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.

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

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

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

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

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

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

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

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Testing for CoCoA

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

Experimental design

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

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

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

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

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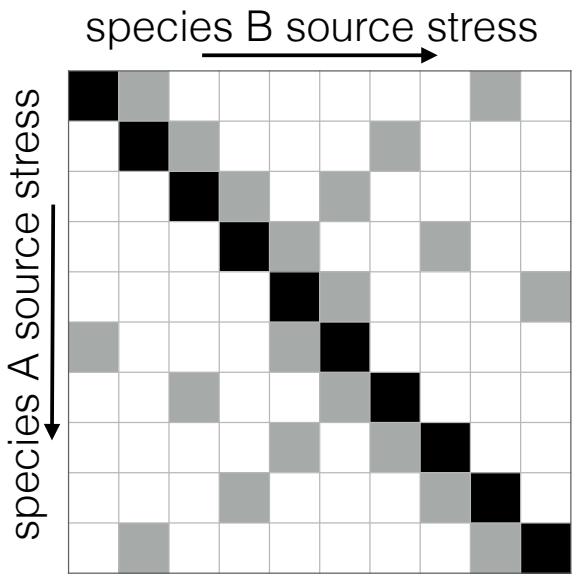

Figure 2: Possible sampling design and experimental combinations. Species A sources are in rows, arranged by increasing stress of source site from top to bottom. Species B sources are in columns, arranged by increasing stress of source site from left to right. Filled in squares are experimentally paired 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.

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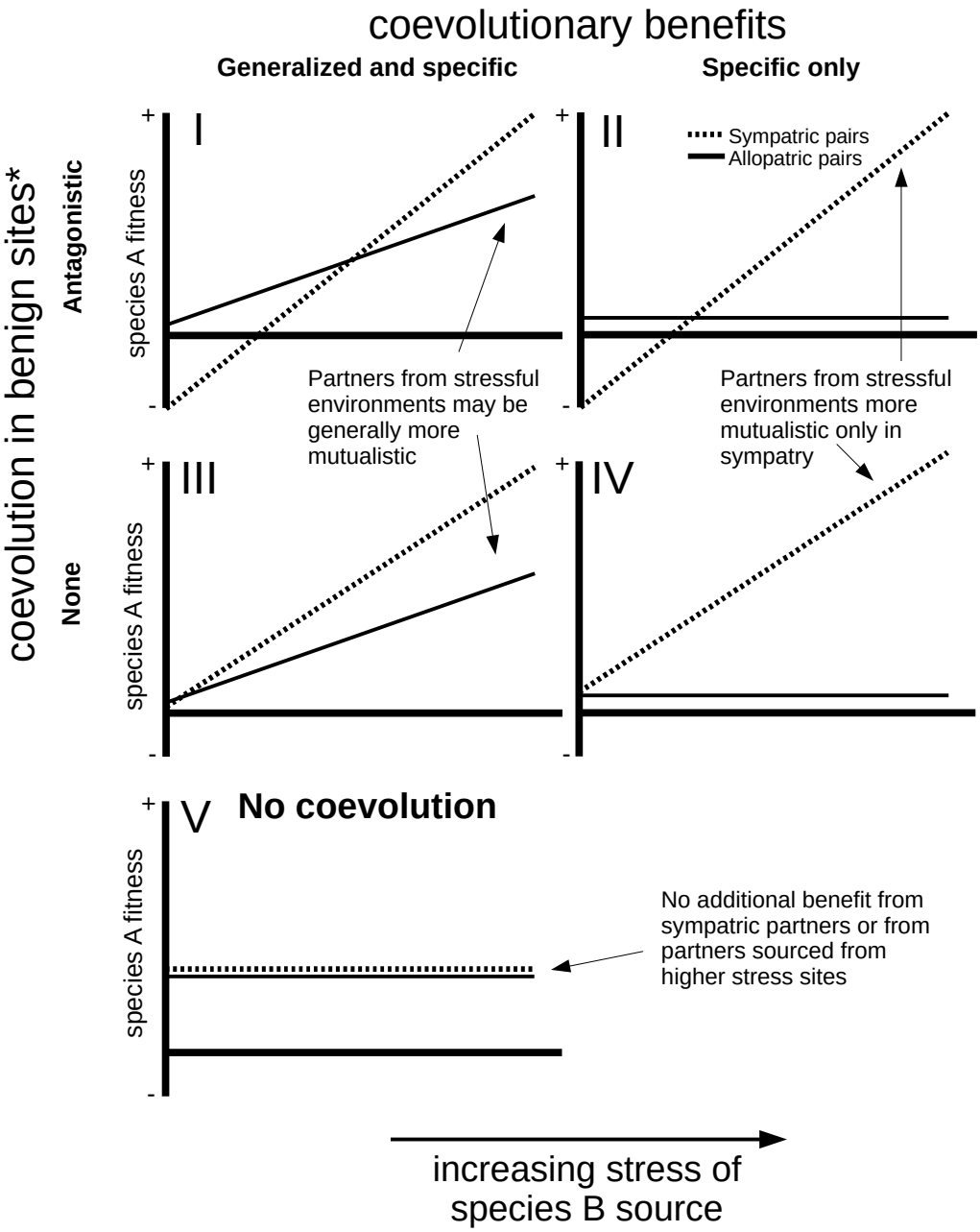

Figure 3: Possible experimental outcomes. CoCoA predicts greater fitness benefits provided by partners sourced from stressful sites across allopatric (solid lines) and sympatric (dashed lines) combinations (generalized benefits, panels I and III). CoCoA also predicts increasing fitness benefits of sympatric 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.

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

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

A linear model framework

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

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

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

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

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

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

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

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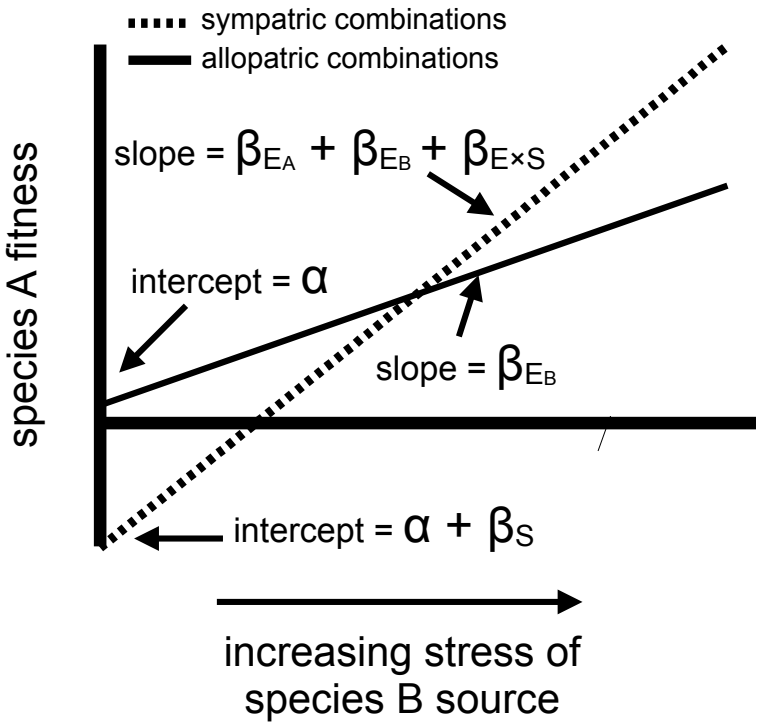

Figure 4: Here we show how parameters in the model relate to linear relationships between fitness and partner source. The relationship here is drawn from scenario I in Figure 3. Generalized coevolutionary benefits are tested by the parameter β_{E_B}, the slope of the allopatric comparisons (solid line), which is significantly positive here. Specific coevolutionary benefits are tested by the parameter $\beta_{E\times S}$, which, when added to β_{E_B} and β_{E_A}, is the slope of the sympatric (dashed) line. β_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 $E \times S$.

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

Interpretation of results

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

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

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

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

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

Other considerations

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

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

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

Existing literature pertinent to CoCoA

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

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

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

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

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

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

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

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

Opportunities to test CoCoA

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

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

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interactions with respect to CoCoA must await more explicit tests.

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

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

Discussion

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

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

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

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

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

Concluding Remarks

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

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

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Acknowledgements

AO was supported by NSF GRFP grant DGE-1148897 and NSF grant DEB-0919559 to SYS.

J.R.I. would like to thank support from NSF Plant Genome project IOS-1238014.

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