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REVIEW

# Evolutionary responses to global change in species-rich communities

Jennifer A. Lau<sup>1</sup>  and Casey P. terHorst<sup>2</sup><sup>1</sup>Department of Biology, Environmental Resilience Institute, Indiana University, Bloomington, Indiana. <sup>2</sup>Biology Department, California State University, Northridge, CaliforniaAddress for correspondence: Jennifer A. Lau, Department of Biology, Environmental Resilience Institute, Indiana University, Jordan Hall, 1001 E 3rd St., Bloomington, IN 47405. [jenlau@iu.edu](mailto:jenlau@iu.edu)

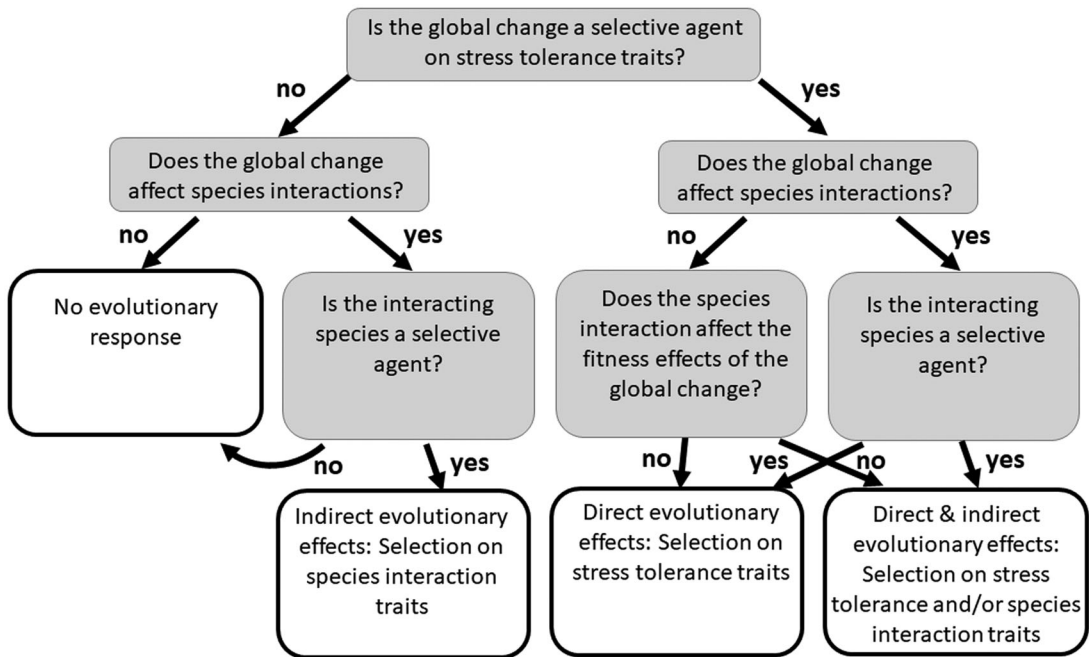
Evolution in nature occurs in the proverbial tangled bank. The species interactions characterizing this tangled bank can be strongly affected by global change and can also influence the fitness and selective effects of a global change on a focal population. As a result, species interactions can influence which traits will promote adaptation and the magnitude or direction of evolutionary responses to the global change. First, we provide a framework describing how species interactions may influence evolutionary responses to global change. Then, we highlight case studies that have explicitly manipulated both a global change and the presence or abundance of interacting species and used either experimental evolution or quantitative genetics approaches to test for the effects of species interactions on evolutionary responses to global change. Although still not frequently considered, we argue that species interactions commonly modulate the effects of global change on the evolution of plant and animal populations. As a result, predicting the evolutionary effects of the multitude of global changes facing natural populations requires both community ecology and evolutionary perspectives.

**Keywords:** adaptation; climate change; coevolution; contemporary evolution; context dependent; global warming; nutrient enrichment

## Introduction

Although ecologists now have a reasonable understanding of how global change will affect natural communities (population declines and extinctions,<sup>1–3</sup> changes in community composition,<sup>4</sup> and range shifts<sup>5</sup>), how populations will evolve in response to anthropogenic environmental change is less certain.<sup>6</sup> One challenge to investigate and predict evolutionary effects of global change is that evolutionary responses to global change occur in a community context of multiple interacting species. Because global changes frequently influence the outcome of species interactions<sup>7,8</sup> and because interacting species from mutualistic microorganisms<sup>9,10</sup> to antagonistic megafauna<sup>11</sup> frequently mitigate or exacerbate the fitness effects of global change, evolutionary outcomes are likely to vary across space and time depending on the presence and abundance of interacting species.

Any evolutionary response may result from either the direct effects of the global change or through indirect pathways that develop when the global change alters interactions between species (Fig. 1). Although accumulating evidence convincingly shows that some populations have adapted or can adapt to a wide range of global changes, including nutrient enrichment,<sup>12,13</sup> rising atmospheric CO<sub>2</sub> concentrations,<sup>14,15</sup> changes in precipitation,<sup>16</sup> global warming,<sup>17–19</sup> and biological invasions<sup>20,21</sup> (reviewed in Ref. 22), most studies have not identified the selective agents or ecological mechanisms (direct versus indirect effects) driving these evolutionary shifts.<sup>23</sup> The few studies that have explicitly manipulated species interactions in simulated global change scenarios (Table 1), however, reveal that the strongest evolutionary effects of global change sometimes result not from the direct effects of global change but because global changes alter



**Figure 1.** Global changes can cause evolutionary responses through both direct and indirect pathways. Direct evolutionary effects result in selection on stress tolerance traits (traits that minimize the negative fitness consequences or maximize the positive fitness consequences of global change). In contrast, indirect evolutionary effects result when either: (1) the global change alters the outcome of a species interaction that is a selective agent or (2) the species interaction affects the fitness effects of the global change. Increasingly, studies have tested how global changes affect natural selection; even more studies have shown how global changes affect species interactions, and decades of evolutionary ecology studies have illustrated the potential for interacting species to exert selection. In other words, each individual arrow in the diagram below is fairly well understood, but the cumulative outcome of these forces is less well documented. In particular, several big questions remain that can only be addressed when the community context is explicitly considered in tests of the evolutionary effects of global change: (1) what is the relative importance or frequency of direct versus indirect evolutionary effects of global change; (2) when are indirect evolutionary effects likely to be particularly important (e.g., diverse communities, tightly coevolved interactions, etc.); and (3) are the adaptive responses from direct versus indirect effects likely to be redundant, complementary, or even conflicting? Note that if an interacting species completely mitigates the fitness effects of the global change, then no selection on stress tolerance traits is likely to occur, even if the global change is a strong agent of natural selection in the absence of that interacting species.

interactions between species. In other cases, the presence of interacting species may influence evolutionary responses by reducing or intensifying the effects of global change on fitness and selection (the relationship between traits and fitness). In still other cases, interacting species can reduce or increase evolutionary constraints.<sup>24</sup> Although it is unknown whether species interactions commonly alter evolutionary responses to global change or reflect the unique conditions of this handful of studies explicitly testing for evolutionary effects in a community context, we suspect that such effects may be pervasive. For example, extinctions can be viewed as the ultimate evolutionary failure, and a meta-analysis found that altered species interac-

tions are the dominant driver of climate-induced extinctions.<sup>2</sup>

In this review, we focus on how the presence and/or abundance of interacting species (i.e., the community context) influences evolutionary effects of human-caused global changes because (1) the global change alters the strength of species interactions and the strength of selection imposed by species interactions, or reciprocally (2) species interactions alter the strength of selection imposed directly by global change (see Fig. 1 and Box 1). First, many types of global change, from nutrient enrichment to climate change, alter the likelihood or outcome of species interactions.<sup>7,8,25–29</sup> If species interactions are themselves strong agents of natural

**Table 1.** Example studies where both a global change and species interaction have been experimentally manipulated in the factorial design necessary for partitioning direct<sup>a</sup> and indirect effects of global change and where species interactions influence the magnitude or likelihood of evolutionary responses to global change

Global change	Species interaction	Effect on evolution	Direct effect? <sup>a</sup>
Elevated CO <sub>2</sub>	Plant competition	Elevated CO <sub>2</sub> effects on natural selection were greater in the presence of competition, because elevated CO <sub>2</sub> reduces the fitness (and selective) effects of competition. <sup>33–35</sup>	No
Elevated CO <sub>2</sub>	Plant competition?	Adaptation to elevated CO <sub>2</sub> only observed when the plant species richness of the test environment matched that of the selection environment. <sup>15</sup>	?
Biological invasion	Plant–herbivore	Herbivores increase selective effects of an invasive plant on a native plant species’ defenses and competitive ability, in part because the invasive plant increases herbivory on the native species and plant defense traits and competitive ability are genetically correlated. <sup>20,21</sup>	No
Global warming	Plant–pollinator	Only species with suitable pollinators available earlier in the season have evolved advanced flowering phenologies over the past 70 years. <sup>102</sup>	Unlikely
Global warming	Predator–prey	Adaptation to warming only observed in the presence of culling or predators, likely because culling and predation reduced intraspecific competition allowing for strong selection on rapid growth rates. <sup>36,37</sup>	No

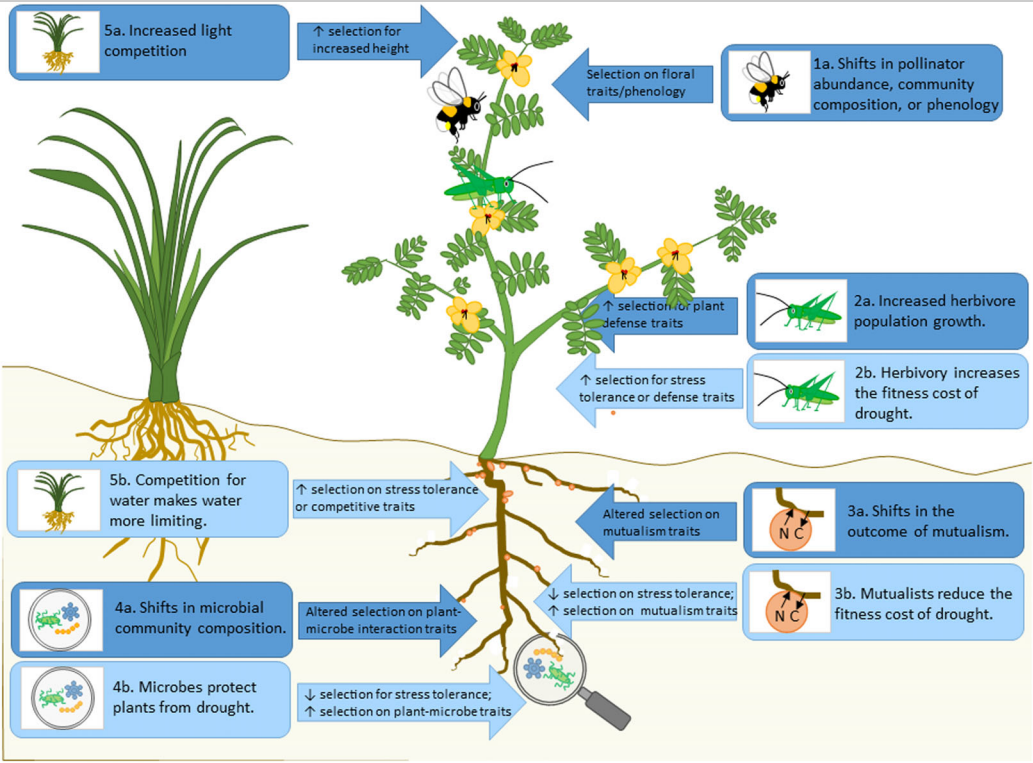
<sup>a</sup>Note that direct effects also include unmeasured indirect effects, such as effects mediated through other unstudied species occurring in the community.

selection,<sup>30</sup> then any change to the species interaction may alter evolution (Fig. 1). Indeed, recent theory illustrates how both mutualistic and antagonistic interactions may influence global change effects on evolutionary outcomes and extinction,<sup>27,31,32</sup> and empirical examples illustrate these effects in nature (Table 1). For example, in one of the case studies highlighted below (Box 2), elevated atmospheric carbon dioxide concentrations reduced the strength of interspecific competition, which would otherwise have imposed stronger selection on plant growth.<sup>33–35</sup> As a result, an effect of elevated CO<sub>2</sub> on evolutionary processes could only be detected in the presence of competitors. Similarly, *Daphnia* only evolved faster life histories (earlier ages at reproduction and larger clutch sizes) in response to elevated temperatures when predators were present.<sup>36,37</sup> This effect resulted because predators reduced *Daphnia* densities and high intraspecific competition selects for slower life histories, which otherwise directly cancels out the selective effects of warming (Box 3).  
Second, interacting species can either exacerbate or minimize the selective effects of the global

change through a variety of mechanisms. For example, theory illustrates how predators can accelerate prey evolutionary responses to global change by either preferentially consuming maladapted individuals, thereby increasing the strength of selection imposed by the global change, or by effectively reducing generation times by reducing prey density resulting in increased prey birthrates (the evolutionary hydra effect).<sup>38</sup> Conversely, other theoretical work suggests that increased competitor diversity reduces evolutionary responses to global change by increasing the likelihood that exapted species are already present in the species pool thereby limiting ecological opportunity.<sup>24</sup> In still other cases, species interactions may alter the strength of selection imposed by a global change by either increasing or decreasing the fitness effects, and potentially the selective effects, of the global change. In a simulated drought experiment, changes to the belowground microbial community protected plants from the negative consequences of drought stress.<sup>9</sup> As a result, these changes to the microbial community could potentially minimize selection imposed by

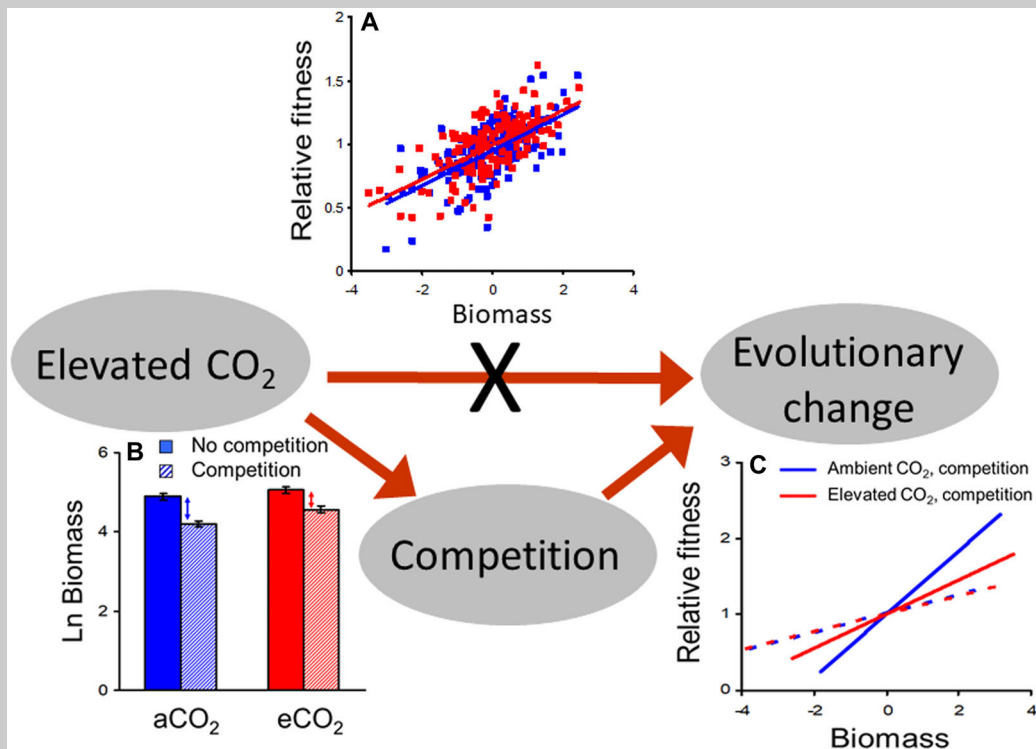
Box 1

Global changes, like global warming and drought, have the potential to affect the outcome of every interaction within a community. These altered species interactions can be potent agents of natural selection (dark blue boxes) and/or modifiers of the direct effects of global change on evolution (light blue boxes). Through the first mechanism (dark blue), global change alters the species interaction changing selection on the traits mediating the species interaction. Through the second mechanism (light blue), the global change may be a strong agent of selection on plant stress tolerance traits and the species interaction increases or decreases that selective force. Selection on traits underlying the species interaction also may be affected through this second mechanism because selection will favor traits promoting (or inhibiting) the species interaction depending on whether the species interaction ameliorates (or exacerbates) the negative effects of global change. The hypothetical interactions depicted here illustrate the following. (1) Global warming affects pollinator communities. Reduced pollinator abundances may select for floral traits that increase selfing or enhance floral display. (2a) Global warming may increase herbivore population growth rates, resulting in increased selection for plant defense. (2b) Herbivores also can exacerbate the negative fitness effects of drought stress, resulting in increased selection on both plant drought tolerance and plant defense traits. (3) Increased drought may influence the outcome of plant–microbe mutualisms, like the legume–rhizobium mutualism, altering selection on traits underlying the mutualism (3a) and potentially plant stress tolerance traits when the mutualism reduces the negative consequences of drought (3b). (4) Increased drought may have similar effects on more generalized plant–microbe interactions like those occurring between plants and the diverse microbial communities belowground or endophytic communities aboveground. (5a) When competitors are less harmed by drought than a focal species, light competition may be increased, increasing selection on competitive traits (e.g., plant height). (5b) By decreasing water availability, competition may also increase selection on drought tolerance traits and/or belowground traits that increase belowground competitive ability.



## Box 2

Case study A: elevated  $\text{CO}_2$  and competition. By manipulating the presence/absence of competitors along with atmospheric  $\text{CO}_2$  concentrations in a factorial design, Lau and coauthors<sup>33–35</sup> showed that elevated  $\text{CO}_2$  had minimal direct effects on natural selection (A) because all genotypes in the study population similarly benefit from elevated  $\text{CO}_2$ . However, elevated  $\text{CO}_2$  also minimized the fitness consequences of competition (B), reducing selection on aboveground biomass production when plants were grown in the presence of competitors (solid lines) (C). In this case, direct effects of elevated  $\text{CO}_2$  were virtually nonexistent (panel A and dashed lines in panel C), while indirect effects of elevated  $\text{CO}_2$  mediated by competition reduced selection intensities by up to 48%. Because the interactive effects of elevated  $\text{CO}_2$  and competition on the strength of selection were opposed by effects on the expression of genetic variation and genetic covariances, minimal evolutionary response to  $\text{CO}_2$  was predicted even in the presence of competitors.

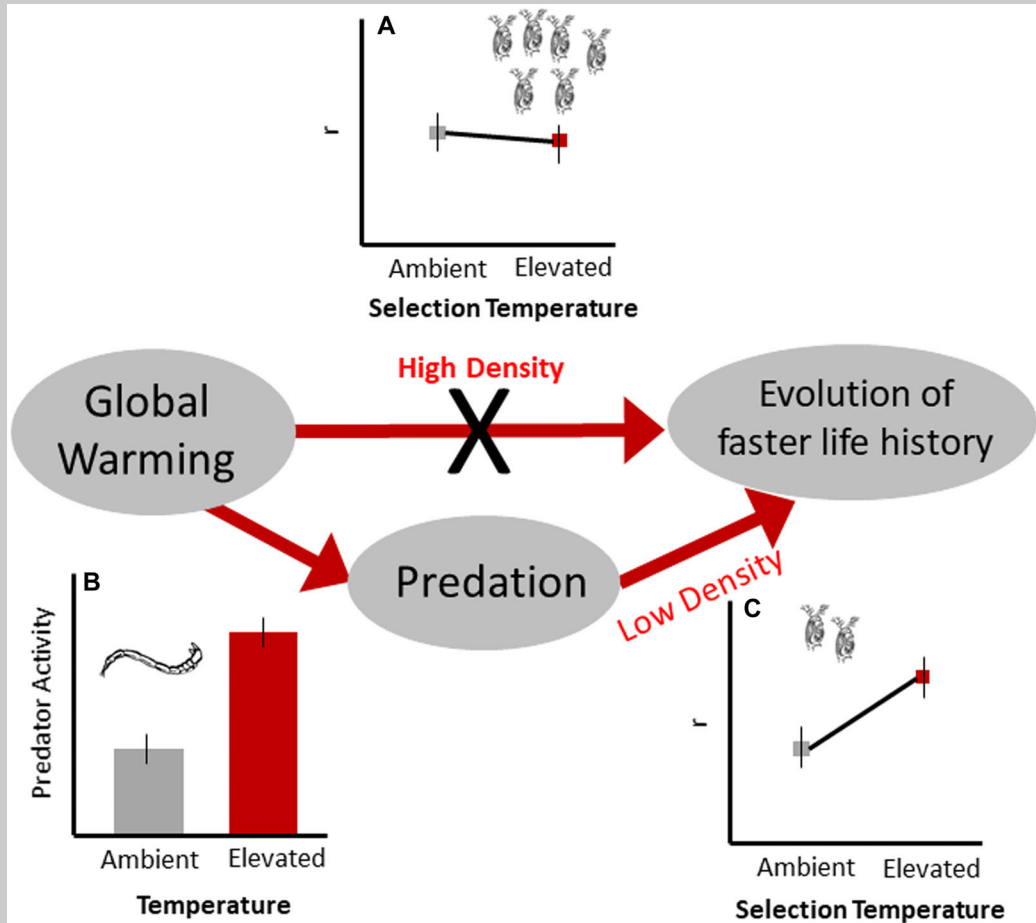


drought on classic plant drought avoidance and tolerance traits like flowering time, leaf morphologies, and physiological responses, and instead strengthen selection on traits promoting interactions with belowground microorganisms<sup>39</sup> (see also Fig. 1 and Box 1). In this case, because the belowground microorganisms greatly reduce the fitness effects of drought, an evolutionary effect on traditional plant drought tolerance traits might only be observed in the absence of the microbial community.

These two broad mechanisms (global changes influencing selection imposed by species interactions versus species interactions mitigating or exacerbating the selective effects of global change) can be difficult, if not impossible, to differentiate empirically. In both cases, the global change interacts with the presence or abundance of an interacting species to influence an evolutionary process and so can only be detected when both factors naturally vary independently of each other

### Box 3

Case study B: global warming and predator–prey interactions. Global warming has the potential to alter the evolution of life history traits, but this depends on the presence of predators in the community. Temperature increases *Daphnia* metabolic rates and selection favors individuals with faster life histories (early age of reproduction; more eggs per clutch). However, high *Daphnia* population densities impose selection in the opposite direction and prevent the evolution of faster life histories (A). Midge larvae are predators on *Daphnia* and reduce population sizes. At warmer temperatures, predator activity increases (B), significantly decreasing *Daphnia* population density, allowing for evolution of faster life histories in response to increased temperature (C). Adapted from Tseng and O'Connor (Ref. 37).



or are experimentally manipulated. However, the different mechanisms sometimes may shift the traits that are the target of selection (Box 1). For example, global warming may indirectly influence plant evolution by increasing herbivore population growth rates, resulting in increased herbivory and

causing increased selection favoring well-defended plants. However, herbivory may also increase the negative effects of global warming (or reduce the positive effects) on plant growth. If herbivory further increases plant water stress in warmer environments, warming may either select for increased



stress tolerance traits particularly when herbivores are present or increase selection favoring increased anti-herbivore defenses because the costs of herbivory are increased under global warming.

In addition to the two mechanisms leading to effects on natural selection described above, species interactions also may influence the magnitude of evolutionary effects of global change through several other mechanisms. Briefly, species interactions may limit adaptive responses to novel environments by reducing population sizes, or the likelihood of beneficial mutations,<sup>31,40</sup> or fitness differences and the opportunity for selection.<sup>41</sup> Global changes, and particularly those that introduce novel stressors or result in range shifts, may also influence the expression of genetic variation<sup>42–44</sup> and potentially genetic covariances<sup>45,46</sup> that can either accelerate or hinder short-term evolutionary responses (see, e.g., Ref. 47). Moreover, the strong selection that may accompany global change is also likely to alter G-matrices, sometimes in ways that reduce evolutionary responses, as revealed by artificial selection experiments.<sup>48</sup> Here, we focus on effects on natural selection because even fewer case studies have investigated how the community context influences the effects of global change on these other evolutionary processes; however, the lack of studies in this area highlights our incomplete knowledge about the net effects of global changes and species interactions on evolution. Our limited understanding of how global changes influence natural selection and these other evolutionary forces in complex communities may be the biggest challenge to predict evolutionary responses to global change and as a result, the effects of global change on biodiversity.

### *Species interactions as selective agents and their susceptibility to global change*

Species interactions can drive the evolution of phenological, morphological, biochemical, physiological, and life history traits. For example, pollinators are believed to be the selective force behind the extreme floral phenotypes found in nature, from 12-inch nectar spurs to the ornate orchid flowers that attract pollinators through deceit (reviewed in Ref. 49). Herbivores are the likely drivers of the arsenal of plant chemical and morphological defenses.<sup>50–52</sup> Competitors drive the evolution of size, gape widths, and foraging preferences in plants and animals (e.g., character displacement,<sup>53</sup>

reviewed in Ref. 54), and predators and pathogens are key selective agents on life history traits in many taxa (see, e.g., Refs. 55 and 56). Antagonists may even promote the evolution of sex.<sup>57,58</sup>

These same species interactions that are such potent evolutionary forces are also extremely susceptible to environmental conditions. Recent reviews highlight how global changes may destabilize mutualisms<sup>59</sup> and how global changes ranging from rising CO<sub>2</sub> concentrations to global warming alter the outcomes of many other types of species interactions<sup>8</sup> and the phenological synchrony of coevolved taxa.<sup>60</sup> At the very least, the strength of a particular species interaction as a selective agent may be reduced if the abundance of one of the partners declines in response to environmental change, or reciprocally, may increase if one of the partners increases in abundance.<sup>61,62</sup> For example, crossbills that are pine seed dispersers and squirrels that are pine seed predators can both impose selection on pine tree traits, but selection intensity is a function of interaction strength, which is partially determined by the abundance of the interacting species.<sup>61</sup> Notably, the effects of interaction strength on selection intensity differed for mutualistic and antagonistic interactions. Selection on pine tree traits lessened with increasing abundances of mutualistic seed dispersers but increased with increasing abundances of seed predators.<sup>61</sup> More general changes in community composition in more diffusely interacting species can elicit similar evolutionary responses. Eutrophication shifted the phytoplankton community in a European lake toward less nutritious and even toxic cyanobacteria. A resurrection approach revealed that this shift in prey community composition caused *Daphnia* populations to adapt to low-quality food resources.<sup>13</sup>

Even if both partners continue to persist at stable abundances, however, the selective effects of the species interaction may change when the outcome of the species interaction depends on environmental context (reviewed in Ref. 63). For example, increased nutrient availability reduces the benefits plants derive from plant–mycorrhizae and plant–rhizobium mutualisms<sup>64,65</sup> and some plant–plant and animal–animal interactions can shift along the spectrum from competitive to facilitative with increasing environmental stress.<sup>66–68</sup> These shifts in the outcome of species interactions are likely to

drive evolutionary change in one or more interacting taxa. Altered resource availability, for example, may cause evolutionary reductions in host investment in the mutualism<sup>69</sup> or the evolution of reduced cooperation in microbial symbionts,<sup>12</sup> and can alter the costs of resistance and host–parasite population densities that can accelerate the evolution of host resistance and parasite infectivity.<sup>70</sup>

### *Species interactions influencing the strength of the global change as a selective agent*

Many types of global change may themselves be strong selective agents (e.g., drought selecting for plant physiological traits that increase drought tolerance<sup>71</sup> and global warming selecting for increased thermal performance or altered phenology in reptiles and insects<sup>17,72,73</sup>), but the presence of interacting species may influence an organisms' fitness response to environmental change. For example, both aboveground fungal endophytes and diverse belowground microbial communities can reduce the negative consequences of drought for plants,<sup>9,10,74</sup> while herbivores sometimes intensify the negative effects of drought.<sup>75</sup> In these cases, the interacting species may reduce (e.g., microbes) or increase (e.g., herbivores) the evolutionary effects of the global change by minimizing or exacerbating the fitness impacts and, therefore, also affecting the fitness benefit of stress tolerance traits (Fig. 1 and Box 1). Similar effects are likely in animal systems, as the ability to horizontally acquire new microbial symbionts is correlated with the ability of sponge taxa to maintain high fitness under ocean acidification,<sup>76</sup> and transplantation of mice microbiomes that develop under cold conditions to sterile mice increases cold tolerance.<sup>77</sup>

Despite the potential for community members to influence fitness effects of global change, however, it is also possible that selection will remain unchanged in such scenarios, as fitness effects may not necessarily equate to selective effects. It is often assumed (and generally observed<sup>78</sup>) that strong ecological effects will result in strong effects on natural selection, because the opportunity for selection is inversely related to mean fitness resulting in an upper limit to the strength of selection.<sup>79</sup> Such effects do not always occur in the context of global changes, however, in part because a number of global changes increase fitness<sup>80</sup> and because environmental variables can change fitness trait rela-

tionships even in the absence of effects on mean fitness. In other words, some species interactions decrease mean fitness, but also reduce variance in relative fitness among individuals and the opportunity for selection in response to global change,<sup>41</sup> while in other cases a reduction in population fitness may increase the variance in relative fitness, leading to increased opportunity for selection.<sup>61</sup>

In addition to modifying the strength of the global change as an agent of selection on stress tolerance traits (i.e., traits that influence an organism's ability to maintain fitness in response to the direct effects of the global change), the interacting species may simply change which traits are the target of selection, as the importance of the species interaction to the focal organism's fitness may increase or decrease under the global change scenario (Box 1). For example, if endophytes reduce the fitness effects of drought stress on plants, they could potentially reduce the strength of drought as a selective agent on plant physiological traits promoting drought tolerance. Perhaps equally likely, microbial mutualists may cause increased selection for plant traits that help cultivate interactions with the endophytic microbes that protect them from drought (e.g., plant leaf or root traits that enhance endophyte colonization and growth).<sup>39</sup> The prevalence of such outcomes is unknown, largely because we still have surprisingly limited knowledge of the causes of natural selection<sup>23</sup> (but see Ref. 81) and often even the traits underlying adaptation, primarily because definitively identifying selective agents is extremely labor-intensive, requiring measures of selection or experimental evolution across environmental gradients or experimental manipulation of putative selective agents.<sup>82</sup>

### **Cases where species interactions are likely important mediators of evolutionary responses to global change**

Many studies illustrate the role species interactions play in evolution, and other studies show how global changes influence the outcome of species interactions or how species interactions influence the fitness effects of global change (Fig. 1). Few examples, however, have illustrated how species interactions or global changes alter selection imposed by the other (but see Boxes 2 and 3, and Table 1). Below we highlight these examples and also piece together data from several systems to illustrate the potential



for a diversity of species interactions to mediate evolutionary responses of bacteria, algae, plants, and animals to two commonly studied and pervasive anthropogenic environmental changes: nutrient enrichment and climate change. Species interactions also may be likely to influence evolutionary responses to other types of global change, such as habitat fragmentation, pollution, and urbanization, in part because these global changes often involve dramatic shifts in community composition. Although interest in the evolutionary consequences of both habitat fragmentation and urbanization has increased over the past several years (see, e.g., Refs. 83 and 84), studies considering effects of these types of global changes on natural selection remain rare and predominantly limited to plant–insect interactions (see, e.g., Ref. 85).

### *Nutrient enrichment*

Atmospheric CO<sub>2</sub> concentrations are increasing, as are nitrogen and phosphorus inputs to both terrestrial and aquatic systems. Thus, we are simultaneously increasing many of the most historically limiting resources required for plant and animal growth. Numerous studies have shown how CO<sub>2</sub>, N, and P alter competitive interactions between primary producers (reviewed in Refs. 26 and 86). Because these resources benefit most plant taxa, but benefit some more than others, changing nutrient availability creates “winners and losers.”<sup>86,87</sup> Increasing nitrogen concentrations tend to favor C3 grasses over legumes, nonvascular plants, and perennials,<sup>87,88</sup> and rising atmospheric CO<sub>2</sub> concentrations benefit fast-growing C3 herbaceous species over slower growing C3 species or C4 grasses.<sup>86</sup> We know from studies on many other plant and animal taxa that competition can alter patterns of natural selection<sup>89–91</sup> and the expression of genetic variation and the genetic covariances among traits (see, e.g., Ref. 35). Because changing nutrient availabilities can alter competition, both by changing the strength of competitive interactions and by shifting competition from one resource to a different resource, and because competition can be a potent evolutionary force, increasing nutrient concentrations are likely to alter the evolution of traits involved in competitive interactions (Box 1). In one example, differences in the strength of selection between ambient and elevated CO<sub>2</sub> environments were only observed in the presence of inter-

specific competition because elevated CO<sub>2</sub> reduced the strength of competition, which is a strong selective agent on plant growth traits. In contrast, the presence of competitors appeared to limit adaptation to elevated CO<sub>2</sub> in *Chlamydomonas* populations. Populations that evolved in single strain communities exhibited higher fitness than populations evolved in multistrain communities when grown in elevated CO<sub>2</sub> conditions.<sup>92</sup> The author suggests that this finding may be common because adapting to multiple novel selective agents (both competition and elevated CO<sub>2</sub>) may be more challenging than adapting only to the abiotic environment.<sup>92</sup> This idea is consistent with the idea that coevolutionary constraints might limit adaptation (*sensu* Ref. 93). However, as indicated by these two contrasting examples, general predictions may be elusive; recent theory illustrates how shifts in resource availability and competition interact to influence evolution, sometimes in complex and surprising ways where traits change in a direction counter to the shift in resource availability.<sup>31,32</sup>

Nutrient availability also influences trophic interactions. For example, elevated atmospheric CO<sub>2</sub> conditions alters plant–herbivore interactions because plant tissues typically have higher C:N ratios that frequently makes them less palatable to insect herbivores, although increased damage has also been observed in response to elevated CO<sub>2</sub>, as insect herbivores must consume more plant tissue to meet nutritional needs.<sup>94</sup> Similarly, N-fertilization typically decreases C:N ratios, increasing palatability to herbivores.<sup>25</sup> Because herbivores can be strong selective agents on plant defense traits like leaf toughness, trichomes, and phytochemicals,<sup>51,52</sup> changes in the amount of herbivory resulting from altered nutrient availability are likely to affect the evolution of these (and correlated) traits. Altered nutrient availability may also affect the inherent costs and benefits of plant defense. The classic resource availability hypothesis posits that low nutrient environments should favor slow-growing phenotypes that invest heavily in defense, while nutrient rich environments should favor fast growth and lower defense.<sup>95,96</sup> Interestingly, the effects of nutrient availability on plant defense evolution have been addressed primarily using comparative approaches among species (e.g., studies in Ref. 96) or populations inhabiting different resource environments, with few studies employing quantitative

genetic approaches to investigate resource effects on natural selection on plant defenses.

Resource availability can also alter herbivore and predator evolution and predator–prey or host–parasite coevolution. As described earlier, nutrient enrichment caused shifts in phytoplankton communities, reducing food quality for zooplankton. As a result, *Daphnia* evolved to perform better to low-quality resources.<sup>13</sup> Productivity also increased the rate of coevolution in a *Pseudomonas fluorescens*–phage system, likely because: (1) increased population sizes of both host and a parasite lead to increased genetic variation in host resistance and parasite infectivity and increased encounter rates and (2) increased productivity reduces the costs of resistance in the host by reducing competition.<sup>70</sup>

Just as altered nutrient availability can affect antagonistic interactions with competitors, herbivores, and parasites, changes in nutrient availability also can alter interactions between plants and their resource mutualists, which can be important agents of selection on plant traits (see, e.g., Ref. 97). Both the legume–rhizobium mutualism and the widespread plant–mycorrhizae mutualism involve plants trading carbon for nitrogen fixed by their rhizobium symbionts or nitrogen and/or phosphorus foraged for by the extensive hyphae of their mycorrhizal symbionts. In both cases, when the availability of the traded resources shifts, the costs and benefits of the mutualism also likely change (see Ref. 98). From the plant's perspective, when soil nutrient availability increases, the benefits of associating with rhizobia or mycorrhizae decrease because the nutrients can be easily obtained directly from the soil. Similarly, when light availability decreases (a common side effect of adding nitrogen or phosphorus, which increases crowding and shading) and plant carbon stores are reduced, the carbon costs of supporting rhizobia or mycorrhizae are relatively increased (the plant must trade a resource that is now less abundant). As a result, nutrient enrichment may cause plants to evolve reduced dependence on microbial mutualists.<sup>69</sup>

### Climate change

The effects of different aspects of climate change, such as global warming or drought, on individual and population fitness and even evolution in nature are increasingly well documented.<sup>99</sup> The effects of climate change on selection, however, are likely to

be enhanced or mediated by species interactions. For example, although the evolution of body and beak size in Darwin's finches in the Galapagos is well known to evolve in response to drought that alters seed availability, this response is contingent on the presence of competitors in the community.<sup>100</sup> In the absence of competitors, *Geospiza fortis* evolved larger beaks and body sizes following drought, allowing them to exploit larger seeds. However, in the presence of larger competitive ground finches (*Geospiza magnirostris*), *G. fortis* evolved smaller body sizes following drought,<sup>100</sup> suggesting that even the direction of evolutionary response to drought was contingent upon competition.

Like drought, global warming can also cause evolutionary shifts that are contingent upon interactions with other species in the community. For example, the extent to which predators reduce *Daphnia* population sizes affects how those populations evolve in response to warming. In populations with greater predation pressure, *Daphnia magna* populations evolved a higher number of offspring in their first clutch when grown at elevated temperature, relative to populations grown at ambient temperature.<sup>36</sup> However, no evolutionary response was detected in populations with low predation pressure, where population densities were higher. Similarly, *Daphnia pulex* populations evolved increased population growth rates in response to warming, but only when dipteran predators were present (Box 3; see also Ref. 37). The effect of predators on this evolutionary response is likely mediated through a change in intraspecific competition. Although warming increases metabolic rates and selects for individuals with more rapid life history traits, those individuals are more favored when population density is low and there is little intraspecific competition. Predators reduce population sizes and create conditions that allow for selection on life history traits by global warming.

Positive species interactions also may affect the ability of populations to respond to climate change.<sup>27</sup> Theory suggests that the ability of species to evolve in response to climate change will depend on whether species are engaged in interactions with generalist mutualists or more specialized mutualisms.<sup>101</sup> Species engaged in generalist mutualisms are free to evolve into different trait spaces (e.g., earlier phenologies) because they will still

find compatible mutualists. However, for species engaged in obligate or more specialized mutualisms, strong selection by global warming may be opposed by reduced fitness in the new trait space if compatible mutualists are lacking. For example, climate change may select for earlier flowering phenologies to decrease the effects of summer drought and/or capitalize on longer growing seasons, but such selection will be greatly weakened if a self-incompatible species does not encounter specialist pollinators that have not yet emerged at this earlier time. In contrast, plants pollinated by generalist pollinators with varied phenologies, or plants that are self-compatible, will be more likely to evolve earlier phenologies in response to climate change.<sup>101</sup> Supporting this prediction, a study of 14 native, perennial plant species suggests that species that evolved earlier flowering phenologies in response to warming were typically those that experienced increased pollination when flowering was experimentally advanced. Those species that failed to evolve earlier flowering typically experienced reduced pollination when flowering was experimentally advanced.<sup>102</sup> Both models and empirical studies suggest similar outcomes in other systems. Evolutionary responses to a novel stress (antibiotics) are slowed when bacteria are engaged in obligate mutualism compared to populations that have not evolved to be obligate mutualists. Because fitness is limited by the least tolerant partner, selection for increased antibiotic resistance only acts on one partner at a time (Harcombe, unpublished data).

Climate change is likely to have substantial effects on other aspects of the evolutionary process, and the influence of species interactions on these effects is often unclear. Range shifts are a common response to climate change, with myriad taxa shifting their distributions toward higher latitudes or higher elevations.<sup>5</sup> Shifting ranges will inevitably lead to novel species interactions, resulting in evolutionary indirect effects of climate changes,<sup>103</sup> but are also likely to influence genetic diversity and gene flow. First, during any range shift event, founder effects are likely as dispersing individuals represent only a small subset of genotypes from the source population. Most models show that these processes cause reduced range-wide genetic diversity.<sup>104</sup> This reduced genetic variation may limit evolutionary responses to species interactions and other global changes. Alternatively, because the fitness effects of

herbivory and disease may be more intense when genetic diversity is reduced (see, e.g., Ref.<sup>105</sup>), the selective force of these antagonists on plant defense traits may be increased. Whether the increased strength of selection will overcome the effects of reduced genetic variation remains to be seen. Second, while genotypes expanding from warmer climates may introduce genes promoting survival and reproduction under global warming, their lack of coevolutionary history with antagonists and mutualists may alter their likelihood of successful colonization. Because of the spatial complexity of coevolutionary interactions,<sup>106,107</sup> it may be challenging to predict when gene flow and coevolutionary novelty may prove advantageous or disadvantageous to rapid adaptation.

### **Conclusions—why considering species interactions is important**

The examples above support the hypothesis that species interactions may commonly mediate evolutionary responses to anthropogenic environmental changes. As a result, studying evolutionary responses in a community context may be necessary for comprehensively predicting the long-term effects of global change for several reasons. First, rapid adaptation may be necessary for species to persist in the face of global change.<sup>103</sup> Although examples of evolutionary rescue exist, they are primarily from simplified laboratory<sup>108,109</sup> or glasshouse experiments.<sup>110</sup> Are populations occurring in the complex communities found in nature as likely to rapidly adapt? Or will the challenges of adapting to multiple selective agents simultaneously prevent the evolutionary responses that could enable persistence (see, e.g., Ref. 92)? Cases documenting rapid evolutionary responses in natural populations ranging from responses to global warming<sup>17–19</sup> to invasive species<sup>20,21</sup> to drought<sup>16</sup> suggest that at least in some systems, evolutionary changes will occur (reviewed in Ref. 22). Whether these changes will be substantial enough to rescue threatened populations remains to be seen but may be most likely when so-called “coevolutionary constraints”<sup>93</sup> are minimal. For example, one hypothesis for why invasive species are so successful in novel environments is that they have escaped many of the interacting species that otherwise might constrain adaptation.<sup>111</sup> Regardless, fully predicting biodiversity responses to global change

requires incorporating evolutionary responses into predictions.<sup>112</sup> When evolutionary responses are heavily influenced by species interactions (e.g., see Table 1), then a perspective combining evolution and community ecology is essential.

Second, if species interactions commonly mediate both ecological and evolutionary effects of global change, then global change effects are likely to vary substantially across communities, making predicting the long-term effects of global change exceedingly difficult and only possible by fully understanding the role species interactions play in evolutionary outcomes.<sup>113</sup> In an intriguing example, adaptation to elevated CO<sub>2</sub> was observed after 14 years in the perennial plant *Poa pratensis*, but these adaptive responses were only manifest when the plant species diversity of the test environment matched the diversity of the selection environment. In other words, CO<sub>2</sub> adaptation in populations from high-diversity environments must involve traits that do not promote CO<sub>2</sub> adaptation in low-diversity environments, and reciprocally CO<sub>2</sub> adaptation in populations from low-diversity environments must involve traits that fail to promote CO<sub>2</sub> adaptation in high-diversity situations.<sup>15</sup>

Even more challenging is the reality that communities are composed of coevolving populations. Beyond variation in community composition, the evolutionary history of interacting species may further influence evolutionary responses to global change. Although rarely considered, new data indicate that warm-adapted algal prey facilitated *Daphnia* adaptation to warmer temperatures compared to algal prey that had evolved under colder environments.<sup>114</sup> Conversely, coevolving *Pseudomonas* hosts reduced phage adaptation to increasing temperature compared to when *Pseudomonas* hosts were not allowed to evolve.<sup>115</sup> Importantly, these coevolutionary interactions can also feedback to influence the ecological effects of global change. For example, theoretically, coevolution can act to reduce or increase the effects of global change on population densities, depending on whether the coevolutionary interaction is conflicting (i.e., changes in trait values of one species harm the other) or nonconflicting (i.e., changes in trait values of one species do not directly harm the other species).<sup>116</sup>

Ultimately, we may be able to predict when species interactions are likely to alter evolution-

ary effects of global change if we are able to predict which global changes and species interactions are likely to be strong selective agents, how global changes influence species interactions, and the community contexts most likely to result in indirect evolutionary effects (Fig. 1). Unfortunately, this may be a more daunting task than expected as even the seemingly intuitive hypothesis that human-caused environmental change will exert strong selection has received limited empirical support.<sup>80</sup> That said, there are now thousands of estimates of natural selection on hundreds of populations, and a subset of these data that included replicate populations across space or time identified precipitation (but not temperature) as a strong selective agent.<sup>81</sup> Tackling past calls for large-scale observational studies or experimental manipulations to test for selective agents and to identify targets of selection (see, e.g., Refs. 23 and 82) may be the Herculean effort needed to make the evolutionary consequences of global change a predictive science.

Although we have focused on how species interactions influence the selective effects of global change, natural selection is only one component of the evolutionary process. Genetic variation and covariation among traits also will influence the likelihood and magnitude of evolutionary response. Theory and empirical work illustrate how stress and/or novel environments influence the expression of genetic variation<sup>42,117,118</sup> and environmental conditions can also influence genetic covariances among traits,<sup>45</sup> yet it is unclear how frequently global changes will accelerate evolution by increasing the expression of genetic variation and breaking the covariances that constrain rapid evolutionary responses. Although novel stressors are predicted to increase the expression of genetic variation,<sup>117</sup> other stressors may reduce the expression of genetic variation.<sup>118</sup> Some human-caused environment changes, such as pollutants, insecticides, and herbicides, are clearly novel, but many others are not and have been experienced to some extent in the recent evolutionary past (e.g., warming due to climate change). Still other global changes are gray areas that represent a gradient of continual increase or decrease in a potential selective agent (e.g., atmospheric CO<sub>2</sub> concentrations). In Box 2, elevated CO<sub>2</sub> increased the expression of genetic variation, opposing the effect of elevated CO<sub>2</sub> reducing the strength of natural selection on

plant size traits, resulting in minimal predicted evolutionary response.<sup>35</sup> The extent to which global change effects on the expression of genetic variation and selection act synergistically versus antagonistically is unknown, largely because the effects of global change on the G-matrix are rarely quantified.

In sum, community context may mediate or exacerbate evolutionary responses to global change in important ways. However, the extent to which species interactions commonly affect evolutionary outcomes remains unknown, largely because most studies do not explicitly consider them. Given that many studies quantifying evolutionary effects of global change are conducted under relatively simplified conditions in greenhouses, growth chamber, or lab environments where species interactions are minimized, we may be significantly misunderstanding the evolutionary consequences of global change. Only by manipulating the presence or intensity of species interactions, ideally in natural field environments, can we begin to predict when and how rapid adaptation may be most likely to occur and ultimately the population, community, and ecosystem effects of that adaptation.<sup>119</sup> Manipulation of community context in even simple systems often reveals large effects on evolution and the ecological outcomes of evolutionary change. In one elegant study, species evolving in complex communities exhibited greater rates of evolutionary change during adaptation to a novel lab environment and the resulting coevolved community was much more productive than communities reassembled from taxa that had evolved in monoculture.<sup>120</sup> If such effects occur in nature, then further integration of community ecology with evolutionary ecology is required to understand the long-term consequences of global change.

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## Competing interests

The authors declare no competing interests.

## References

1. Brook, B.W., N.S. Sodhi & C.J.A. Bradshaw. 2008. Synergies among extinction drivers under global change. *Trends Ecol. Evol.* **23**: 453–460.
2. Cahill, A.E., M.E. Aiello-Lammens, M. Caitlin Fisher-Reid, *et al.* 2013. How does climate change cause extinction? *Proc. R. Soc. B.* **280**. <http://doi.org/10.1098/rspb.2012.1890>.
3. Urban, M.C. 2015. Accelerating extinction risk from climate change. *Science* **348**: 571–573.
4. Walther, G.-R. 2010. Community and ecosystem responses to recent climate change. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **365**: 2019–2024.
5. Parmesan, C. & G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* **421**: 37–42.
6. Gienapp, P., C. Teplitsky, J.S. Alho, *et al.* 2008. Climate change and evolution: disentangling environmental and genetic responses. *Mol. Ecol.* **17**: 167–178.
7. Blois, J.L., P.L. Zarnetske, M.C. Fitzpatrick & S. Finnegan. 2013. Climate change and the past, present, and future of biotic interactions. *Science* **341**: 499–504.
8. Tylianakis, J.M., R.K. Didham, J. Bascompte & D.A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* **11**: 1351–1363.
9. Lau, J.A. & J.T. Lennon. 2012. Rapid responses of soil microorganisms improve plant fitness in novel environments. *Proc. Natl. Acad. Sci. USA* **109**: 14058–14062.
10. Gehring, C.A., C.M. Sthultz, L. Flores-Renteria, *et al.* 2017. Tree genetics defines fungal partner communities that may confer drought tolerance. *Proc. Natl. Acad. Sci. USA* **114**: 11169–11174.
11. Post, E. 2013. Erosion of community diversity and stability by herbivore removal under warming. *Proc. R. Soc. B.* **280**: 20122722. <http://doi.org/10.1098/rspb.2012.2722>.
12. Weese, D.J., K.D. Heath, B.T.M. Dentinger & J.A. Lau. 2015. Long-term nitrogen addition causes the evolution of less-cooperative mutualists. *Evolution* **69**: 631–642.
13. Hairston, N.G., Jr. W. Lampert, C.E. Cáceres, *et al.* Rapid evolution revealed by dormant eggs. *Nature* **401**: 446.
14. Sandrini, G., X. Ji, J.M.H. Verspagen, *et al.* 2016. Rapid adaptation of harmful cyanobacteria to rising CO<sub>2</sub>. *Proc. Natl. Acad. Sci. USA* **113**: 9315–9320.
15. Kleynhans, E.J., S.P. Otto, P.B. Reich & M. Vellend. 2016. Adaptation to elevated CO<sub>2</sub> in different biodiversity contexts. *Nat. Commun.* **7**: 12358.
16. Franks, S.J., S. Sim & A.E. Weis. 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proc. Natl. Acad. Sci. USA* **104**: 1278–1282.
17. Bradshaw, W.E. & C.M. Holzapfel. 2001. Genetic shift in photoperiodic response correlated with global warming. *Proc. Natl. Acad. Sci. USA* **98**: 14509–14511.
18. Schaum, C.-E., S. Barton, E. Bestion, *et al.* 2017. Adaptation of phytoplankton to a decade of experimental warming linked to increased photosynthesis. *Nat. Ecol. Evol.* **1**: 94.
19. Schlüter, L., K.T. Lohbeck, M.A. Gutowska, *et al.* 2014. Adaptation of a globally important coccolithophore to ocean warming and acidification. *Nat. Clim. Change* **4**: 1024–1030.



20. Lau, J.A. 2006. Evolutionary responses of native plants to novel community members. *Evolution* **60**: 56–63.
21. Lau, J.A. 2008. Beyond the ecological: biological invasions alter natural selection on a native plant species. *Ecology* **89**: 1023–1031.
22. Palumbi, S.R. 2001. Humans as the world's greatest evolutionary force. *Science* **293**: 1786–1790.
23. MacColl, A.D. 2011. The ecological causes of evolution. *Trends Ecol. Evol.* **26**: 514–522.
24. de Mazancourt, C., E. Johnson & T.G. Barraclough. 2008. Biodiversity inhibits species' evolutionary responses to changing environments. *Ecol. Lett.* **11**: 380–388.
25. Throop, H.L. & M.T. Lerdau. 2004. Effects of nitrogen deposition on insect herbivory: implications for community and ecosystem processes. *Ecosystems* **7**: 109–133.
26. Brooker, R.W. 2006. Plant-plant interactions and environmental change. *New Phytol.* **171**: 271–284.
27. Gilman, S.E., M.C. Urban, J. Tewksbury, *et al.* 2010. A framework for community interactions under climate change. *Trends Ecol. Evol.* **25**: 325–331.
28. Zarnetske, P.L., D.K. Skelly & M.C. Urban. 2012. Biotic multipliers of climate change. *Science* **336**: 1516–1518.
29. Romero, G.Q., T. Gonçalves-Souza, P. Kratina, *et al.* 2018. Global predation pressure redistribution under future climate change. *Nat. Clim. Change* **8**: 1087–1091.
30. Vermeij, G.J. 1994. The evolutionary interaction among species: selection, escalation, and coevolution. *Annu. Rev. Ecol. Syst.* **25**: 219–236.
31. Johansson, J. 2008. Evolutionary responses to environmental changes: how does competition affect adaptation? *Evolution* **62**: 421–435.
32. Van Den Elzen, C.L., E.J. Kleynhans & S.P. Otto. 2017. Asymmetric competition impacts evolutionary rescue in a changing environment. *Proc. R. Soc. B.* **284**: 20170374. <http://doi.org/10.1098/rspb.2017.0374>.
33. Lau, J.A., R.G. Shaw, P.B. Reich, *et al.* 2007. Strong ecological but weak evolutionary effects of elevated CO<sub>2</sub> on a recombinant inbred population of *Arabidopsis thaliana*. *New Phytol.* **175**: 351–362.
34. Lau, J.A., R.G. Shaw, P.B. Reich & P. Tiffin. 2010. Species interactions in a changing environment: elevated CO<sub>2</sub> alters the ecological and potential evolutionary consequences of competition. *Evol. Ecol. Res.* **12**: 435–455.
35. Lau, J.A., R.G. Shaw, P.B. Reich & P. Tiffin. 2014. Indirect effects drive evolutionary responses to global change. *New Phytol.* **201**: 335–343.
36. Van Doorslaer, W., R. Stoks, C. Duvivier, *et al.* 2009. Population dynamics determine genetic adaptation to temperature in *Daphnia*. *Evolution* **63**: 1867–1878.
37. Tseng, M. & M.I. O'Connor. 2015. Predators modify the evolutionary response of prey to temperature change. *Biol. Lett.* **11**. <http://doi.org/10.1098/rsbl.2015.0798>.
38. Osmond, M.M., S.P. Otto & C.A. Klausmeier. 2017. When predators help prey adapt and persist in a changing environment. *Am. Nat.* **190**: 83–98.
39. Lau, J.A., J.T. Lennon & K.D. Heath. 2017. Trees harness the power of microbes to survive climate change. *Proc. Natl. Acad. Sci. USA* **114**: 11009–11011.
40. Rich, S.S., A.E. Bell & S.P. Wilson. 1979. Genetic drift in small populations of *Tribolium*. *Evolution* **33**: 579–584.
41. terHorst, C.P., J.A. Lau, I.A. Cooper, *et al.* 2015. Quantifying nonadditive selection caused by indirect ecological effects. *Ecology* **96**: 2360–2369.
42. Hoffmann, A.A. & J. Merilä. 2000. Heritable variation and evolution under favourable and unfavourable conditions. *Trends Ecol. Evol.* **14**: 96–101.
43. Salmela, M.J., B.E. Ewers & C. Weinig. 2016. Natural quantitative genetic variance in plant growth differs in response to ecologically relevant temperature heterogeneity. *Ecol. Evol.* **6**: 7574–7585.
44. Rowiński, P.K. & B. Rogell. 2017. Environmental stress correlates with increases in both genetic and residual variances: a meta-analysis of animal studies. *Evolution* **71**: 1339–1351.
45. Wood, C.W. & E.D. Brodie III. 2015. Environmental effects on the structure of the G-matrix. *Evolution* **69**: 2927–2940.
46. Björklund, M., A. Husby & L. Gustafsson. 2013. Rapid and unpredictable changes of the G-matrix in a natural bird population over 25 years. *J. Evol. Biol.* **26**: 1–13.
47. Etterson, J.R. & R.G. Shaw. 2001. Constraint to adaptive evolution in response to global warming. *Science* **294**: 151–154.
48. Careau, V., M.E. Wolak, P.A. Carter & T. Garland, Jr. 2015. Evolution of the additive genetic variance-covariance matrix under continuous directional selection on a complex behavioural phenotype. *Proc. R. Soc. B.* **282**: 20151119. <http://doi.org/10.1098/rspb.2015.1119>.
49. Harder, L.D. & S.D. Johnson. 2009. Darwin's beautiful contrivances: evolutionary and functional evidence for floral adaptation. *New Phytol.* **183**: 530–545.
50. Fraenkel, G. 1959. The raison d'être of secondary plant substances. *Science* **129**: 1466–1470.
51. Mithöfer, A. & W. Boland. 2012. Plant defense against herbivores: chemical aspects. *Annu. Rev. Plant Biol.* **63**: 431–450.
52. Agrawal, A.A. & M.G. Weber. 2015. On the study of plant defence and herbivory using comparative approaches: how important are secondary plant compounds. *Ecol. Lett.* **18**: 985–991.
53. Brown, W.L. & E.O. Wilson. 1956. Character displacement. *Syst. Zool.* **5**: 49–64.
54. Pfennig, D.W. & K.S. Pfennig. 2010. Character displacement and the origins of diversity. *Am. Nat.* **176**: S26–S44.
55. Reznick, D.A., H. Bryga & J.A. Endler. 1990. Experimentally induced life-history evolution in a natural population. *Nature* **346**: 357–359.
56. Martin, T.E. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* **65**: 101–127.
57. Otto, S.P. 2009. The evolutionary enigma of sex. *Am. Nat.* **174**: S1–S14.
58. Jokela, J., M.F. Dybdahl & C.M. Lively. 2009. The maintenance of sex, clonal dynamics, and host-parasite coevolution in a mixed population of sexual and asexual snails. *Am. Nat.* **174**: S43–S53.
59. Kiers, E.T., T.M. Palmer, A.R. Ives, *et al.* 2010. Mutualisms in a changing world: an evolutionary perspective. *Ecol. Lett.* **13**: 1459–1474.
60. Kharouba, H.M., J. Ehrlén, A. Gelman, *et al.* 2018. Global shifts in the phenological synchrony of species interactions



- over recent decades. *Proc. Natl. Acad. Sci. USA* **115**: 5211–5216.
61. Benkman, C.W. 2013. Biotic interaction strength and the intensity of selection. *Ecol. Lett.* **16**: 1054–1060.
  62. Vanhoenacker, D., J. Ågren & J. Ehrlén. 2013. Non-linear relationship between intensity of plant-animal interactions and selection strength. *Ecol. Lett.* **16**: 198–205.
  63. Chamberlain, S.A., J.L. Bronstein & J.A. Rudgers. 2014. How context dependent are species interactions? *Ecol. Lett.* **17**: 881–890.
  64. Hoeksema, J.D., V.B. Chaudhary, C.A. Gehring, *et al.* 2010. A meta-analysis of context-dependency in plant response to inoculation with mycorrhizal fungi. *Ecol. Lett.* **13**: 394–407.
  65. Taylor, B.N. & D.N.L. Menge. 2018. Light regulates tropical symbiotic nitrogen fixation more strongly than soil nitrogen. *Nat. Plants* **4**: 655–661.
  66. Bertness, M. & R.M. Callaway. 1994. Positive interactions in communities. *Trends Ecol. Evol.* **9**: 191–193.
  67. Maestre, F.T., R.M. Callaway, F. Valladares & C.J. Lortie. 2009. Refining the stress-gradient hypothesis for competition and facilitation in plant communities. *J. Ecol.* **97**: 199–205.
  68. Kawai, T. & M. Tokeshi. 2007. Testing the facilitation-competition paradigm under the stress-gradient hypothesis: decoupling multiple stress factors. *Proc. R. Soc. B.* **274**: 2503–2508.
  69. Schultz, P.A., R.M. Miller, J.D. Jastrow, *et al.* 2001. Evidence of a mycorrhizal mechanism for the adaptation of *Andropogon gerardii* (Poaceae) to high- and low-nutrient prairies. *Am. J. Bot.* **88**: 1650–1656.
  70. Lopez-Pascua, L.D.C. & A. Buckling. 2008. Increasing productivity accelerates host-parasite coevolution. *J. Evol. Biol.* **21**: 853–860.
  71. Franks, S.J. 2011. Plasticity and evolution in drought avoidance and escape in the annual plant *Brassica rapa*. *New Phytol.* **190**: 249–257.
  72. Higgins, J.K., H.J. MacLean, L.B. Buckley & J.G. Kingsolver. 2014. Geographic differences and microevolutionary changes in thermal sensitivity of butterfly larvae in response to climate. *Funct. Ecol.* **28**: 982–989.
  73. Logan, M.L., R.M. Cox & R. Calsbeek. 2014. Natural selection on thermal performance in a novel thermal environment. *Proc. Natl. Acad. Sci. USA* **111**: 14165–14169.
  74. Giauque, H., E.W. Connor & C.V. Hawkes. 2019. Endophyte traits relevant to stress tolerance, resource use and habitat of origin predict effects on host plants. *New Phytol.* **221**: 2239–2249.
  75. Bansal, S. 2015. The interactive effects of drought and herbivory on ecophysiology of trees. In *Combined Stresses in Plants*. R. Mahalingham, Ed.: 245–259. Switzerland: Springer International Publishing.
  76. Ribes, M., E. Calvo, J. Movilla, *et al.* 2016. Restructuring of the sponge microbiome favors tolerance to ocean acidification. *Environ. Microbiol. Rep.* **8**: 536–544.
  77. Chevalier, C., O. Stojanović, D.J. Colin, *et al.* 2015. Gut microbiota orchestrates energy homeostasis during cold. *Cell* **163**: 1360–1374.
  78. Caruso, C.M., R.A. Martin, N. Sletvold, *et al.* 2017. What are the environmental determinants of phenotypic selection? A meta-analysis of experimental studies. *Am. Nat.* **190**: 363–376.
  79. Rundle, H.D. & S.M. Vamosi. 1996. Selection may be strongest when resources are scarce: a comment on Wilson. *Evol. Ecol.* **10**: 559–563.
  80. Fugère, V. & A.P. Hendry. 2018. Human influences on the strength of phenotypic selection. *Proc. Natl. Acad. Sci. USA* **115**: 10070–10075.
  81. Siepielski, A.M., M.B. Morrissey, M. Buoro, *et al.* Precipitation drives global variation in natural selection. *Science* **355**: 959–962.
  82. Wade, M.J. & S. Kalisz. 1990. The causes of natural selection. *Evolution* **44**: 1947–1955.
  83. Jacquemyn, H., L. De Meester, E. Jongejans & O. Honnay. Evolutionary changes in plant reproductive traits following habitat fragmentation and their consequences for population fitness. *J. Ecol.* **100**: 76–87.
  84. Santangelo, J.S., L.R. Rivkin & M.T.J. Johnson. 2018. The evolution of city life. *Proc. R. Soc. B.* **285**: 20181529. <http://doi.org/10.1098/rspb.2018.1529>.
  85. Irwin, R.E., P.S. Warren & L.S. Adler. 2018. Phenotypic selection on floral traits in an urban landscape. *Proc. R. Soc. B.* **285**: 20181239. <http://doi.org/10.1098/rspb.2018.1239>.
  86. Porter, H. & M.L. Navas. 2003. Plant growth and competition at elevated CO<sub>2</sub>: on winners, losers, and functional groups. *New Phytol.* **157**: 175–198.
  87. Suding, K.N., S.L. Collins, L. Gough, *et al.* 2005. Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proc. Natl. Acad. Sci. USA* **102**: 4387–4392.
  88. Midolo, G., R. Alkemade, A.M. Schipper, *et al.* 2019. Impacts of nitrogen addition on plant species richness and abundance: a global meta-analysis. *Global Ecol. Biogeogr.* **28**: 398–413.
  89. Miller, T.E. 1995. Evolution of *Brassica rapa* L (Cruciferae) populations in intra- and interspecific competition. *Evolution* **49**: 1125–1133.
  90. Shaw, R.G., G.A.J. Platenkamp, F.H. Shaw & R.H. Podolsky. 1995. Quantitative genetics of response to competitors in *Nemophila menziesii*—a field experiment. *Genetics* **139**: 397–406.
  91. Stanton, M.L., D.A. Thiede & B.A. Roy. 2004. Consequences of intraspecific competition and environmental variation for selection in the mustard *Sinapis arvensis*: contrasting ecological and evolutionary perspectives. *Am. Nat.* **164**: 736–752.
  92. Collins, S. 2011. Competition limits adaptation and productivity in a photosynthetic alga at elevated CO<sub>2</sub>. *Proc. R. Soc. B.* **278**: 247–255.
  93. Antonovics, J. 1976. The nature of limits to natural selection. *Ann. Mo. Bot. Gard.* **63**: 224–247.
  94. Stiling, P. & T. Cornelissen. 2007. How does elevated carbon dioxide (CO<sub>2</sub>) affect plant-herbivore interactions? A field experiment and meta-analysis of CO<sub>2</sub>-mediated changes on plant chemistry and herbivore performance. *Global Change Biol.* **13**: 1823–1842.
  95. Coley, P.D., J.P. Bryant & F.S. Chapin. 1985. Resource availability and plant antiherbivore defense. *Science* **230**: 895–899.

96. Endara, M.-J. & P.D. Coley. 2011. The resource availability hypothesis revisited: a meta-analysis. *Funct. Ecol.* **25**: 389–398.
97. Batstone, R.T., E.M. Dutton, D. Wang, *et al.* 2017. The evolution of symbiont preference traits in the model legume *Medicago truncatula*. *New Phytol.* **213**: 1850–1861.
98. Johnson, N.C., J.H. Graham & F.A. Smith. 1997. Functioning of mycorrhizal associations along the mutualism-parasitism continuum. *New Phytol.* **135**: 575–585.
99. Hoffmann, A.A. & C.M. Sgrò. Climate change and evolutionary adaptation. *Nature* **470**: 479–485.
100. Grant, P.R. & B.R. Grant. 2006. Evolution of character displacement in Darwin's finches. *Science* **313**: 224–226.
101. Gilman, R.T., N.S. Fabina, K.C. Abbott & N.E. Rafferty. 2012. Evolution of plant-pollinator mutualisms in response to climate change. *Evol. Appl.* **5**: 2–16.
102. Rafferty, N.E. & A.R. Ives. 2011. Effects of experimental shifts in flowering phenology on plant-pollinator interactions. *Ecol. Lett.* **14**: 69–74.
103. Davis, M.B., R.G. Shaw & J.R. Etterson. 2005. Evolutionary responses to changing climate. *Ecology* **86**: 1704–1714.
104. Pauls, S.U., C. Nowak, M. Balint & M. Pfenninger. 2013. The impact of global climate change on genetic diversity within populations and species. *Mol. Ecol.* **22**: 925–946.
105. Schmitt, J. & J. Antonovics. 1986. Experimental studies of the evolutionary significance of sexual reproduction. IV. Effect of neighbor relatedness and aphid infestation on seedling performance. *Evolution* **40**: 830–836.
106. Forde, S.E., J.N. Thompson & B.J.M. Bohannan. 2004. Adaptation varies through space and time in a coevolving host-parasitoid interaction. *Nature* **431**: 841–844.
107. Thompson, J.N. 2005. *The Geographic Mosaic of Coevolution*. Chicago, IL: University of Chicago Press.
108. Bell, G. & A. Gonzalez. 2009. Evolutionary rescue can prevent extinction following environmental change. *Ecol. Lett.* **12**: 942–948.
109. Szűcs, M., M.L. Vahsen, B.A. Melbourne, *et al.* 2017. Rapid adaptive evolution in novel environments acts as an architect of population range expansion. *Proc. Natl. Acad. Sci. USA* **114**: 13501–13506.
110. Bodbyl Roels, S.A. & J.K. Kelly. 2011. Rapid evolution caused by pollinator loss in *Mimulus guttatus*. *Evolution* **65**: 2541–2552.
111. Strauss, S.Y. 2014. Ecological and evolutionary responses in complex communities: implications for invasions and eco-evolutionary feedbacks. *Oikos* **123**: 257–266.
112. Urban, M.C., G. Bocedi, A.P. Hendry, *et al.* 2016. Improving the forecast for biodiversity under climate change. *Science* **353**. <http://doi.org/10.1126/science.aad8466>.
113. Turcotte, M.M., M.S.C. Corrin & M.T.J. Johnson. 2012. Adaptive evolution in ecological communities. *PLoS Biol.* **10**: e1001332.
114. Tseng, M., J. Bernhardt & A. Chila. 2019. Species interactions mediate thermal evolution. *Evol. Appl.* **12**: 1463–1474.
115. Zhang, Q.-G. & A. Buckling. 2011. Antagonistic coevolution limits population persistence of a virus in a thermally deteriorating environment. *Ecol. Lett.* **14**: 282–288.
116. Northfield, T.D. & A.R. Ives. 2013. Coevolution and the effects of climate change on interacting species. *PLoS Biol.* **11**: e1001685.
117. Holloway, G.J., S.R. Poverly & R.M. Sibly. 1990. The effect of new environment on adapted genetic architecture. *Heredity* **64**: 323–330.
118. Charmantier, A. & D. Garant. 2005. Environmental quality and evolutionary potential: lessons from wild populations. *Proc. R. Soc. B.* **272**: 1415–1425.
119. De Meester, L., K.I. Brans, L. Govaert, *et al.* 2019. Analysing eco-evolutionary dynamics—the challenging complexity of the real world. *Funct. Ecol.* **33**: 43–59.
120. Lawrence, D., F. Fiegna, V. Behrends, *et al.* 2012. Species interactions alter evolutionary responses to a novel environment. *PLoS Biol.* **10**: e1001330.