Eco-evolutionary consequences of habitat warming in communities from fragmented landscapes

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Title: Eco-evolutionary consequences of habitat warming in communities from fragmented landscapes

Running Head: Eco-evolutionary consequences of habitat warming and fragmentation

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Abstract

Climate change and habitat fragmentation have emerged independently as two of the largest threats to biodiversity and ecosystems. In many cases, the ecological responses to these threats are mediated and complicated by eco-evolutionary dynamics. Here we present a new framework for understanding the simultaneous eco-evolutionary consequences of habitat fragmentation and warming for the dynamics of ecological communities. This framework is based on trade-offs among traits that emerge in response to warming and habitat isolation. Thermal environment affects traits related to metabolism, such as resource acquisition and activity level, which are also likely to have trade-offs with other energetically costly traits, like antipredator defense. Many such traits can be additionally influenced by fragmentation through its effects on the spatial environment experienced by individuals. We illustrate our framework with several example scenarios in which trade-offs among traits of interacting populations could result in eco-evolutionary dynamics with important consequences for communities. Theory and experiments that explicitly consider the consequences of eco-evolutionary dynamics in communities responding to fragmentation and habitat warming are urgently needed to yield more robust predictions for the long-term effects of multiple global change components.

Fragmentation modulates ecological and evolutionary responses to warming

Climate change and habitat fragmentation are two of the largest threats to biodiversity and ecosystems. Warming can have major impacts on species and communities [1,2], and thus ecosystem functioning [3], through a variety of plastic and evolutionary responses [4–6]. Within an organism's dispersal range, climate can differ across local scales [7]. Under climate change, some areas within the range can become warmer, while others may maintain their temperature or even cool. Isolation due to fragmentation may consequently exacerbate this effect by creating habitat patches that differ in thermal environment [8,9]. Moreover, altered dispersal in fragmented habitats can shift the relative importance of species interactions versus dispersal as determinants of colonization success, resulting in differences in composition and structure of local communities [8].

Changes in dispersal can alter gene flow among habitat patches. Fragmentation can thus additionally modify the opportunities for local adaptation to habitat warming [10,11]. Taken together, different local communities with limited dispersal can be exposed to disparate selective pressures in terms of both abiotic (*e.g.*, warming) and/or biotic (*e.g.,* predation pressure) factors [12]. Fragmentation can either reduce or increase opportunities for adaptive evolutionary response. It can reduce evolutionary responses through a number of processes involving reduced genetic diversity, smaller population sizes, genetic drift, inbreeding depression, and flow of maladaptive alleles [13,14]. The alternative, where fragmentation can instead increase opportunities for local adaptation (*i.e.*, *sensu* the evolving metacommunity concept [15]), remains empirically understudied and its implications poorly understood [14]. We suggest that a comprehensive view on the effects of fragmentation demands greater attention be placed on its potential to alter adaptive responses to warming through modifications of ecological interactions.

Eco-evolutionary feedbacks, species interactions, and multiple stressors

Ecological and evolutionary dynamics that occur at contemporary time scales and affect one another, defined as eco-evolutionary dynamics and feedbacks (Box 1 and Box 2), can have important consequences across levels of organization. They can alter phenotypic traits [16,17], the dynamics of populations and communities [18–21], and the functioning of ecosystems [22–24]. The community context of the evolutionary response can qualitatively alter the direction of the response and consequently the implications for community dynamics [25,26], which is likely to prove important for fragmented communities responding to warming. Populations experiencing novel selective pressures, such as those responding to anthropogenic environmental changes, may be especially likely to manifest reciprocal ecological and evolutionary responses with broad-reaching implications for communities and ecosystems.

Eco-evolutionary dynamics are especially important when populations experience selection upon traits for which important correlations among traits exist (Box 3), where selection on one trait is expected to alter performance in another trait or fitness attribute. Traits under selection in response to climate change, including those relating to metabolic function, can exhibit trade-offs with other traits important to life history, including growth [27,28], CO_2 assimilation [29], or interspecific interactions. For example, body size reductions driven by warming are taxon-specific and can differ across trophic levels. This then leads to altered consumer-resource dynamics (an ecological effect) [30–34]. This could thus potentially alter selection for traits that trade off with predator defense (an evolutionary effect), ultimately resulting in additional ecological changes within the community.

We believe that to gain a more complete understanding of the long-term effects of warming and fragmentation in communities we should investigate the consequences of eco-evolutionary dynamics on interspecific interactions in fragmented and warmed landscapes. Our goal is to highlight possible outcomes resulting from eco-evolutionary responses linked to consumer-resource interactions. We acknowledge that eco-evolutionary dynamics have the potential to yield multiple outcomes, hence we do not aim to provide an exhaustive exploration of possible outcomes. Instead, we limit ourselves to scenarios for which we find theoretical and empirical support for 1) ecological and evolutionary responses to warming and fragmentation, 2) trade-offs between traits, and 3) eco-evolutionary mechanisms assumed to be acting in the scenario.

To demonstrate our approach, we focus on the interactive effects of dispersal limitation and selection on traits and responses linked to metabolism (see Box 4 for effects on single species). We develop examples of predictions for the eco-evolutionary consequences of habitat fragmentation and warming for single consumer-resource interactions and linear food chains. Although we concentrate here on responses relating to metabolic functions (*e.g.*, thermal performance, attack rate, body size etc.), we stress that there are other possible effects of warming that will introduce opportunities for selection, such as changes to phenology. Specifically, we ask: in fragmented landscapes, what are the potential eco-evolutionary consequences of (1) evolution in thermal performance of a species involved in a consumer-resource interaction, (2) ecological or evolutionary changes to encounter and attack rates of consumers, and (3) changes to top consumer body size in tri-trophic food chains.

Effects of warming and fragmentation on consumer-resource dynamics

When selection occurs within an ecological community, the presence of multiple interacting species can result in additional direct and indirect effects [35], which is likely to qualitatively change predictions about thermal adaptation from single populations [36]. The opportunities for trade-offs and epistatic and/or antagonistic pleiotropic interactions increase. This can have a number of consequences. It can slow the rate of evolution[6,37]. It can prevent evolution from selection where it had previously been observed in single-species populations by overwhelming the directional selection. Or, as we highlight below, it can drive evolutionary response in otherwise unexpected ways [38,39].

A vast literature documents a number of changes in trophic interactions that occur separately in response to warming or to fragmentation. For instance, although increased encounter rates are possible in warmer conditions [40], some predators decrease their attack rates above a temperature threshold resulting from physiological constraints [41–43]. As feeding rates often scale with predator: prey body mass ratios [44,45], the pervasive body size reductions associated with environmental warming, which are most prevalent at higher trophic levels [31,32] (but see also [3]), can also alter consumer-resource dynamics.

Animal consumers frequently have smaller population sizes and longer generation times than their resources and warming may exacerbate differences in population sizes across trophic levels. Consumer metabolic rates are frequently more sensitive to increased temperatures than are their ingestion rates, which leads to decreased overall energetic efficiencies [46,47]. It may therefore be harder for animals at higher trophic levels to meet energetic demands than organisms at lower trophic levels. Declines in energetic efficiency are linked to increased risk of starvation for consumers at higher trophic levels and weaker top-down effects in communities [48–50].

Fragmentation can result in variability among local populations of attack rates by consumers on resources. Theory shows that habitat isolation, without temperature change, can result in increases in encounter rates affecting consumer and resource temporal population dynamics [51]. If habitat patches experience different temperatures, attack rates could vary plastically across the metacommunity, while at even larger scales (*e.g.*, latitudinal) local populations can differ in their genetically determined attack rates [52], which can interact complexly with environmental temperature [42,43,53,54].

Effects of trophic interactions and fragmentation on dispersal and habitat selection

The relationship between body size (and often trophic level) and dispersal capability remains unclear [55]. Actively dispersed consumers frequently exhibit superior dispersal relative to their prey [56,57], while in other cases, such as with passively dispersed organisms, resources can display greater dispersal capability than consumers [58].

Consumer-resource interactions can affect dispersal of both interacting species. Theory about density-dependent dispersal [59] and habitat matching/dispersal experiments indicate that, for instance, predators frequently disperse only below a critical threshold of prey abundance, while prey disperse when intraspecific competition is high or as a result of perceived predation risk [60,61]. Fragmentation can increase predation risk during dispersal, potentially leading to selection for prey phenotypes that increase survival (*e.g.*, dispersal syndromes as in [62]), for example by increasing antipredator traits or locomotor speed [63]. Conditions in the matrix surrounding patches can influence evolution similarly. Despite the increased risk associated with dispersal in the presence of predators, predators can nonetheless increase movement and dispersal of prey through the surrounding matrix, and can preferentially favor movement of some phenotypes over others (*e.g.*, larger individuals as in [64]). In addition, different phenotypes could be favored in predator-free and predator-occupied patches. Some individuals, for example, may preferentially choose habitats without predators [65,66]. Taken together, because fragmentation can modify both dispersal rates and a range of prey phenotypic traits, including those related to activity, speed, endurance, and thermal behaviors, fragmentation should change the flow of phenotypes that differ in metabolism and consumption. These same phenotypes could then also potentially differ in their responses to warming, as regulated through metabolic function.

Metacommunity dynamics can increase the time available for evolution to occur by improving the persistence of otherwise extinction-prone food webs [67,68]. Mismatches in the potential for evolutionary response across trophic levels may arise out of smaller population sizes and longer generation times at higher trophic levels. This can affect the standing genetic variability and the rapidity with which mutations arise relative to other species and environmental change. In fact, in consumer-resource interactions experiencing Red Queen dynamics (*i.e.*, a coevolutionary arms race between the interacting species), theory suggests that the most rapidly evolving partner is locally adapted while the other is not [69]. Predators can theoretically improve prey adaptation and persistence despite reductions in prey abundance. This could occur when the presence of predators reinforces directional selection and/or effectively reduces generation time by reducing prey population size to levels that maximize prey growth rate (thereby increasing the mutational rate) [70]. An evolutionary mismatch across trophic levels, combined with the documented changes to trophic interactions, suggests that eco-evolutionary dynamics may be particularly important for consumer-resource interactions during habitat warming.

Scenarios for eco-evolutionary dynamics in single predator-prey interactions

A number of eco-evolutionary dynamics can arise in this context. We present three. Firstly, if consumer-free habitat patches enable the resource species to evolve increased thermal tolerance (*e.g.*, if the predator was physiologically excluded from warm patches), its abundance could increase. This will result in increased dispersal among patches as density increases, and thus higher abundance in cool patches due to the influx of immigrants (Fig. 1A). This could happen with or without trade-offs between thermal performance and defense traits. In either case, a potential result of the increased availability of the resource in cool patches could be increased attack by the consumer. Increased attack by the consumer could result as either a density-dependent (*i.e.*, of the resource) ecological response or due to evolution to increase resource acquisition (Fig. 1B). Increased consumer pressure could then decrease the number of successfully dispersing individuals of the resource, increasing the degree of isolation among patches for the resource. In doing so, it could then increase opportunities for additional local adaptation of the resource, for instance, to increase defense against the consumer (Fig. 1C).

Secondly, an eco-evolutionary dynamic might occur if consumers are present in warm patches, but have reduced attack rates due to, *e.g.*, physiological constraints, a change in period of activity, or prey switching, (*i.e.*, a purely ecological response with no evolution in the consumer for changes in attack rate). In this scenario, warm patches would again function as prey refugia, leading to larger population sizes of prey and increasing opportunities for local adaptation to the thermal environment without trade-offs (Supplemental Fig. 2). In fact, if trade-offs between thermal performance traits and defense traits occur, evolution of increased thermal performance may prove to be more likely with spatial segregation than in a closed community.

And thirdly, because the evidence with regard to the effects on attack rate remain inconclusive especially at evolutionary time scales, we consider the possibility that attack rates also increase due to warming. For example, over time consumers may evolve in response to their thermal environment. If a consumer evolves increased attack rates in warm habitats and its abundance increases, the increased attack rates may decrease absolute number of dispersers of the resource among habitat patches (although dispersal rate itself could increase), resulting in increased opportunities for local adaptation of the resource (Supplemental Fig. 3). Even if the consumer reduces the abundance of the resource, it may facilitate local adaptation in the resource by maximizing its growth rate, thereby increasing the number of selective events per unit time, and by consuming maladapted individuals [70] (Supplemental Fig. 3).

Scenarios for eco-evolutionary dynamics in food chains

When expanding consumer-resource interactions to a tri-trophic food chain, the potential consequences of eco-evolutionary dynamics become more variable and difficult to predict [35]. Evolutionary cascades become possible, with the potential for a shift in the trade-offs for one species to propagate through the food web. We focus on two scenarios with two different starting points.

In the first one, a resource species evolves increased thermal tolerance. This could involve a trade-off with a trait important to defense against consumption or simply make it a more abundant, and thus readily available, resource. In either case, the intermediate consumer has an opportunity to evolve to increase investment in its own defense against a top consumer. This is most likely to occur in fragmented habitats, where the top consumers have smaller population sizes than in continuous habitats. In warm patches especially, top consumers that are physiologically sensitive to warming may be less abundant or absent entirely [71,72], providing partial refuge to the intermediate consumer. Specifically, as it becomes less costly to acquire the now more abundant resource, the intermediate consumer can be free to evolve decreased investment in expensive traits favorable to attack rate. Once this occurs, the top consumer, where present, would encounter less edible prey. For top predators, warming occurring in a fragmented landscape could thus lead to an increased likelihood of extinction (Supplemental Fig. 4).

The second scenario requires that the top and intermediate consumers experience the landscape at different scales. A top consumer for which individuals move regularly among patches may have a plastic reduction in body size due to metabolic constraints with increasing mean temperature across the landscape. This can trigger prey-switching [73], such that smaller predators are likely to target younger, smaller size classes of the intermediate consumer, *e.g.*, due to increasing gape limitation [74] (Fig. 2A). This, in turn, increases selection on the intermediate consumer to evolve faster growth rates and escape vulnerable size classes sooner. This agrees with early findings of faster growth rates of intermediate consumers in the presence of a top predator, although the possibility of evolutionary mechanisms acting in the system was not evaluated [75]. Faster growth rates can then result in increased attack rates by the intermediate consumer on the resource. Similarly, if the intermediate consumer escapes some degree of predation by the top consumer, it can evolve to increase investment in traits related to its attack on the resource at the expense of its own predator defense (Fig. 2B). With increased attack by the intermediate consumer, the resource might then evolve an increase in defense traits at the expense of its own resource acquisition (Fig. 2C). This, however, may vary among patches when individuals of the intermediate consumer only disperse infrequently among patches and when its physiological constraints depend on thermal environments within patches. For instance, attack rates may be especially high in cool patches if the intermediate consumer has physiological constraints in warm patches. In this situation, the evolution of the resource species' traits for defense or its own resource acquisition could occur unevenly across the landscape.

The two scenarios presented above can act simultaneously. If resource abundance increases as a result of increased thermal performance while the top consumer body size decreases, this results in predation escape by the intermediate consumer. The intermediate consumer would be able to invest in traits related to resource acquisition while its population abundance increases. With habitat fragmentation, changes in the resource population and in the top consumer would remain coupled since both occur in warm habitat patches, such that the changes at the two trophic levels could reinforce one another, possibly resulting in markedly increased abundance of the intermediate consumer not predicted without both habitat warming and fragmentation.

Conclusions and future directions

To date, a prevailing underlying assumption of many studies of climate change and fragmentation has been that observed differences in interspecific interactions can be attributed to purely ecological effects. Eco-evolutionary dynamics, however, can be cryptic and mostly visible as resultant changes in species abundances [76]; until we begin to study them directly in the context of warming and fragmentation, their importance is likely to remain mostly unknown. We argue that acknowledging the potential importance of eco-evolutionary dynamics occurring during climate change in fragmented landscapes opens up a new area of research.

To conclude, we present some experimental avenues and provide a roadmap to show how eco-evolutionary dynamics can be integrated into experiments to determine their role in governing responses to habitat warming and fragmentation across levels of biological organization. We suggest four ways forward.

1) Identification of evolutionary responses to warming in natural populations and experimental systems. Efforts to demonstrate the effects of eco-evolutionary dynamics should initially focus on the evo → eco direction. We believe that an initial evolutionary change that triggers ecological change is more tractable for manipulation. Nonetheless, eco-evolutionary dynamics that originate in the eco → evo direction will likely prove to be extremely important for two reasons. First, species change their abundances and behavior (*e.g.*, attack rates, phenology, activity periods, etc.) to cope with climate change. Second, climate change alters the community context through compositional and functional shifts. In this context, there is a growing body of work in the range expansion and invasion literature regarding the evolutionary impacts of species movements that might help to understand the effects of shifting community assemblages [20,23,77,78].

2) Disentangling the effects of purely ecological responses vs. cryptic eco-evolutionary dynamics in natural and experimental populations. This will require further acknowledgment among ecologists of the importance of intraspecific diversity within and among populations [79,80]. Genomic and transcriptomic analyses increasingly offer us opportunities to understand the targets of selection within genomes, providing novel information about how populations can evolve in response to local environmental conditions [81–84]. For example, by comparing genetic diversity before, during and after environmental stress, we can observe the outcomes of natural selection in response to novel environmental change, even within a single generation through shifts in allelic frequencies within a population [85,86].

3) Using controlled experiments to isolate the role of warming and fragmentation in driving evolutionary change and understanding the effects for interspecific interactions and community dynamics*.* Manipulative experiments using microcosms and mesocosms provide the necessary level of control to unambiguously attribute any observed evolutionary change to each factor and to initially evaluate the potential consequences of eco-evolutionary dynamics [87–92]. Careful experimental design will also ensure that we can test specific hypotheses regarding the circumstances most likely to result in eco-evolutionary dynamics, as well under which conditions such dynamics have significant effects.

4) Using field-based experiments with local populations that differ in connectivity and temperature to validate results from experimental populations. In this way we can begin to detect heritable differences in thermal performance [82] and outcomes of interspecific interactions with implications for functioning in natural populations at longer time scales [93].

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Author Contributions

CAF and JMM conceived the idea for the manuscript, CAF developed the framework, and CAF and JMM jointly wrote the manuscript.

Box 1. Glossary.

Eco-evolutionary dynamics- Ecological and evolutionary processes operating at contemporary time scales, in which one affects the other

Evolutionary cascade- When multiple interacting species have trade-offs relating to their interactions, a shift in the trade-off for one species has the potential to propagate or ripple through the food web through an eco-evolutionary feedback mechanism, resulting in altered community and ecosystem properties

Fragmentation- The division of previously contiguous habitat into discrete patches surrounded by an inhospitable environmental matrix or divided by other barriers to movement of individuals

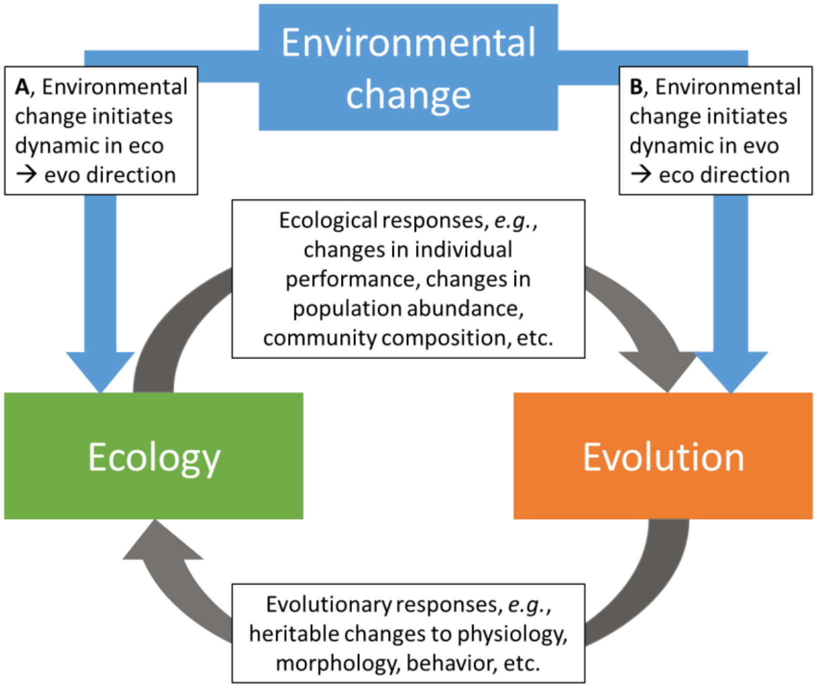
Local scales- The scale at which sets of individuals interact directly, such that population and community dynamics result directly from these interactions

Metacommunity- A set of communities interacting at the local scale that are linked by dispersal of individuals from populations of the interacting species

Phenotypic plasticity- Environmentally-induced changes to an individual organism's morphology, physiology, or behavior; while individual plastic responses are not themselves generally inherited, the degree of plasticity for a trait is itself is heritable

Thermal performance- The effect of temperature on a variety of biological rate processes across multiple biological levels of organization, *e.g.*, from biochemical reactions to whole organism responses like fecundity and metabolic rate

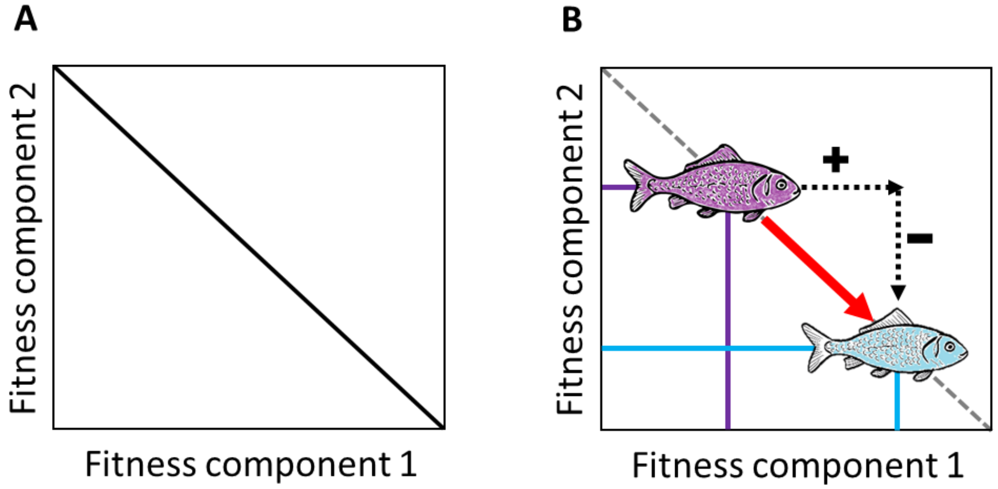
Box 2. Eco-evolutionary feedbacks.



Eco-evolutionary dynamics and feedbacks can originate as a result of ecological or evolutionary changes. In our conceptual diagram above, we assume that the dynamics are initiated in response to a change in the environment of a population.

Eco-evolutionary dynamics, where changes in the ecology of populations or communities result in evolutionary changes (A, above), or vice versa (B, above), can occur when ecology and evolution occur at contemporary timescales. Such dynamics are considered eco-evolutionary feedbacks when the secondary evolutionary (as in A) or ecological (as in B) response then results in an additional reciprocal ecological (A) or evolution (B) response. For example, we can imagine a scenario in which a novel species invades a community as it tracks habitat warming to remain within its thermal niche. Fragmentation might then simultaneously cause the species to become “trapped” in a non-analogue community (eco). The presence of novel species interactions could then result in evolutionary changes to interacting species (evo), which then causes additional changes to abundances of species and community composition (eco) (akin to the eco-evolutionary feedbacks resulting from experimental invasions observed in [20]).

Box 3. The importance of fitness trade-offs in eco-evolutionary dynamics.



A, Conceptual diagram of an ecological trade-off with two fitness components. **B**, When fitness trade-offs occur, evolution that improves performance in one fitness component results in a concomitant reduction in performance in a second fitness component. Here a starting population (purple fish) evolves increased performance in Fitness component 1 (blue fish), at the expense of performance in Fitness component 2, resulting in an overall shift along the trade-off curve (red arrow).

Ecological trade-offs occur when higher performance in one fitness attribute comes at the expense of performance in a second fitness attribute (A, above, conceptualized for simplicity as a linear relationship, although other relationships are possible). Some examples of fitness trade-offs studied in ecology include competition-colonization trade-offs [94] and resource acquisition-defense trade-offs [95].

Trade-offs imply that evolution to improve performance in one fitness attribute will affect performance in the second attribute (B, above). For performance attributes that affect the outcomes of interspecific interactions, evolution that results in movement along the trade-off curve will affect how species interact. When interacting species have trade-offs relating to their interactions, a shift in the trade-off for one species has the potential to thus propagate through the food web as an evolutionary cascade, or to ripple through the system through shifts in species abundances, resulting in altered community and ecosystem properties [77].

Trade-offs are most likely to have eco-evolutionary consequences for habitat warming in fragmented landscapes when at least one of the fitness attributes in the trade-off have documented effects from warming and/or fragmentation (and especially if different selective pressures on the two fitness components result). For instance, warming can influence competitive outcomes [96] and resource acquisition and defense [42], while fragmentation can influence dispersal and colonization [63]. Another documented trade-off is survival vs. growth-rate in relation to thermal performance, including variable survival at different temperatures after laboratory selection for increased performance at high temperatures [27]), growth rate vs. heat-shock tolerance [97], and survival at extreme temperatures vs. competitive ability [98].

Box 4. Single species responses to warming and fragmentation.

Evolution of thermal performance traits, including fecundity, growth, metabolic rates, and enzyme activities, has already been documented in response to warming [25,87,93,99–102]. In general, we can expect that when evolution results in improved thermal performance at warmer temperatures, the population or species will be more successful in the warmer environmental conditions. This evolution may, however, result in trade-offs in performance in different abiotic conditions or with regard to other life history components (see examples in Box 3).

Fragmentation alters the opportunities for evolution in response to local conditions [63]. Different genotypes can vary significantly in frequency and fitness among patches as a result of stochastic processes (*e.g.*, genetic drift), dispersal, and survival of individuals. Fragmentation can promote the evolution of dispersal itself [103]. Dispersal can be non-random with regard to environmental conditions. For example, dispersal decisions can be related to preferred thermal conditions and at least partially matched to phenotype-dependent survival [104]. Overall, intermediate levels of dispersal are expected to be the most likely to promote local adaptation [14] (Supplemental Fig. 1), however in some cases local adaptation can be enhanced even under higher gene flow [105].

By creating habitat patches that differ significantly in local conditions, fragmentation could maintain higher intraspecific beta-diversity across the metapopulation compared to in a continuous landscape. Coupled with its influence on dispersal (and gene flow) among patches, fragmentation may affect opportunities for adaptive evolution within patches. When the degree of gene flow and the population sizes within patches is sufficient to favor selection, fragmentation should increase the trait-environmental correlation such that it can increase local adaptation. If, however, gene flow is too small and population sizes within patches are small, fragmentation should favor drift. Fragmentation may therefore result in local populations within the metapopulation that differ in their phenotypic frequencies of thermal performance traits due to both stochastic and selective mechanisms.

Figure 1. Conceptual diagram (top panels) illustrating a hypothetical scenario for an eco-evolutionary feedback (evo→eco→evo) between a consumer species and its resource with evolutionary trade-offs visualized below each conceptual panel. Fragmentation in a habitat experiencing a thermal gradient results in patches that differ in thermal environment (color of background, with blue as cold, red as warm). In the conceptual panels, for each species the color of the illustration represents different genotypes (or phenotypes) within each population, while the size of the illustration represents the relative contribution of each phenotype to the population make-up. In the trade-off diagrams, the curve for the trade-off relationship is indicated with a grey dashed line, while evolutionary movement along the trade-off curve is indicated with a solid red arrow. Dashed black arrows show the positive (+) or negative (-) direction of the movement for each fitness attribute. **A,** The presence of habitat patches differing in their thermal environment results in evolution of the resource (algae) for increased thermal performance, and an increase in its abundance in warm patches. **B,** Increased abundance of the resource results in increased attack by the consumer (copepod) as an ecological (dashed red line off of the trade-off curve) or evolutionary response, a trait whose performance is not necessarily tied to thermal environment. **C,** Decreased dispersal of the resource occurs as a result of higher predation pressure, increasing the opportunity for local adaptation to increase defense against the predator.

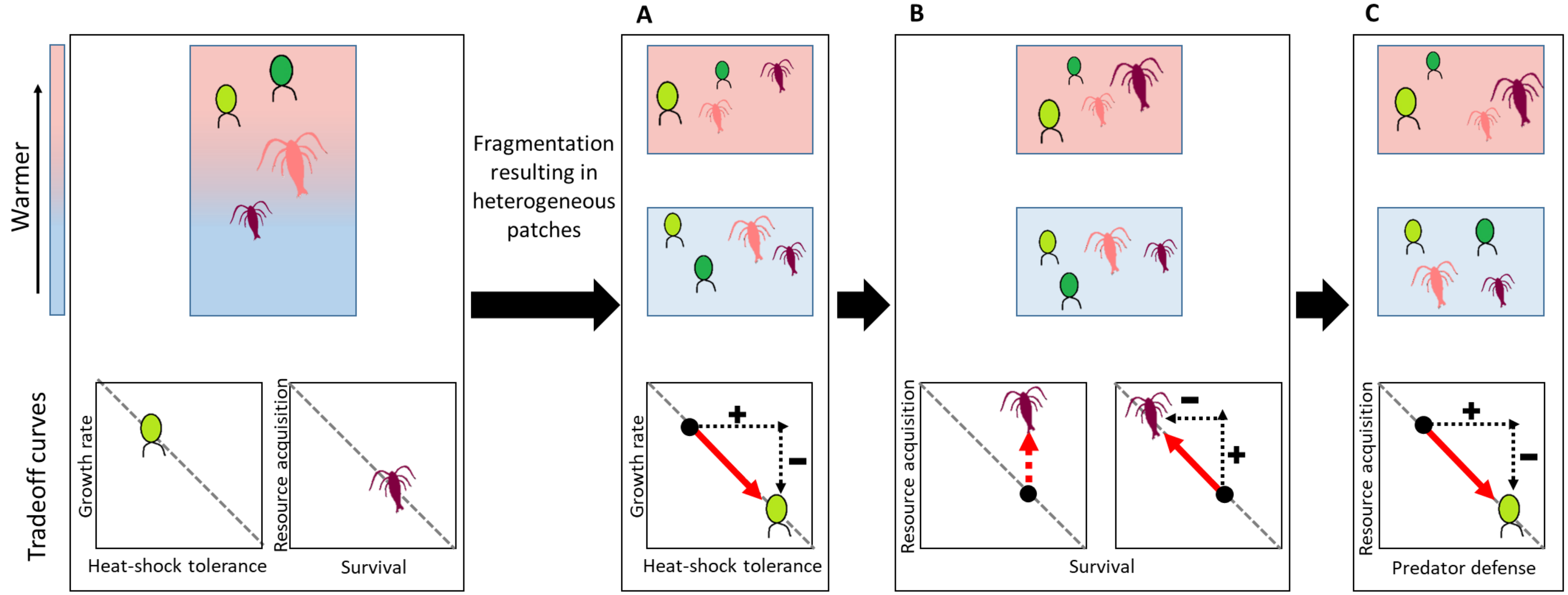
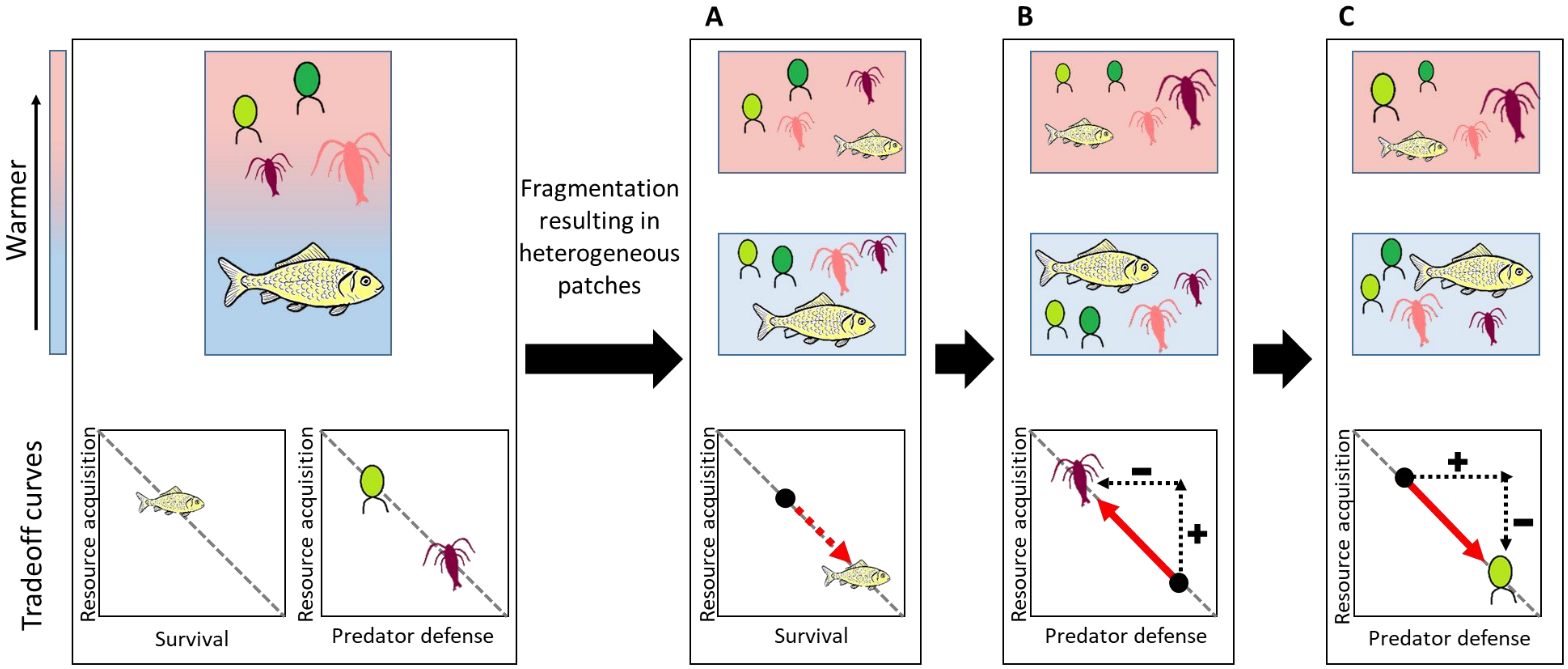


Figure 2. Conceptual diagram (top panels) illustrating a hypothetical scenario for an eco-evolutionary feedback (eco→evo→eco) it a tri-trophic food chain with evolutionary trade-offs visualized below each conceptual panel. See the caption for Fig. 1 for a description of the figure legend. **A,** The presence of habitat patches differing in their thermal environment results in a plastic reduction of top consumer (fish) body size (dashed red line off of the trade-off curve). **B,** Decreased predation pressure linked to reduced fish body mass then allows the intermediate consumer (copepod) to evolve increased resource acquisition. **C,** The resource (algae) evolves increased defense in response to higher predation pressure from the intermediate consumer.



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SUPPLEMENTAL FIGURES

Index of supplemental figures.

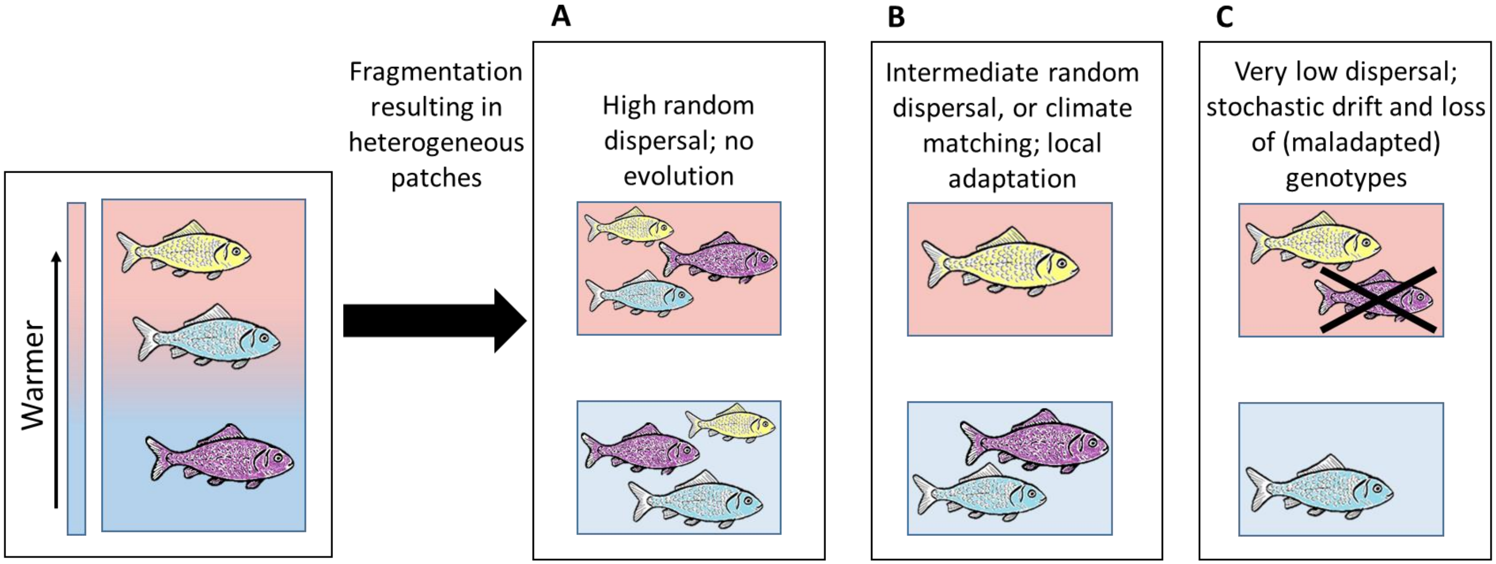
Supplemental Figure 1. Conceptual diagram illustrating how local adaptation to heterogeneous conditions among habitat patches after fragmentation depends on the degree and type of dispersal among habitat patches.

Supplemental Figure 2. Conceptual diagram illustrating a hypothetical scenario for an eco-evolutionary feedback (eco→evo→eco) between a consumer species and its resource initiated by a plastic reduction in attack rate by the consumer, with evolutionary trade-offs visualized below each conceptual panel.

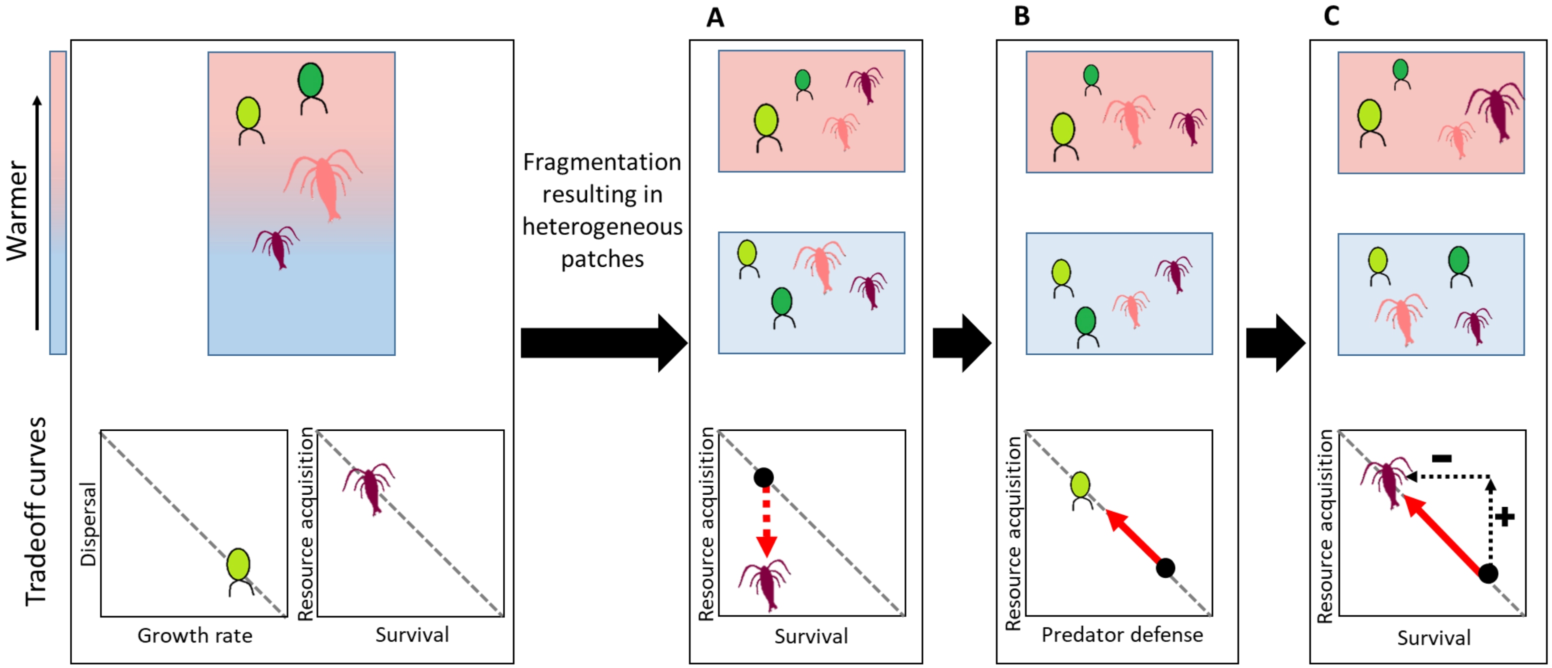
Supplemental Figure 3. Conceptual diagram illustrating a hypothetical scenario for an eco-evolutionary feedback (evo→eco→evo) between a consumer species and its resource initiated by evolution of increased attack rate by the consumer, with evolutionary trade-offs visualized below each conceptual panel.

Supplemental Figure 4. Conceptual diagram illustrating a hypothetical scenario for an eco-evolutionary feedback (evo→eco→evo) in tri-trophic food chain initiated by evolution of increased thermal performance in the resource, with evolutionary trade-offs visualized below each conceptual panel.

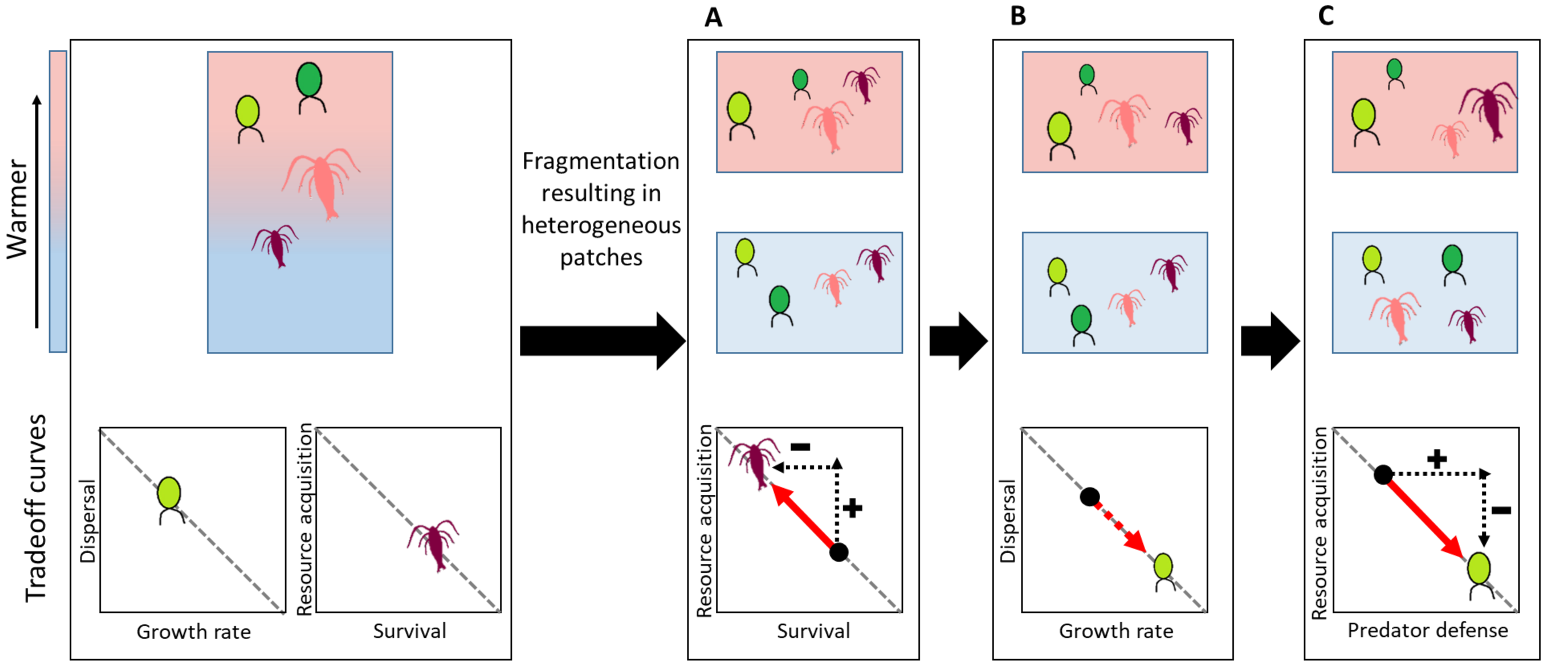
Supplemental Figure 1A-C. Conceptual diagram illustrating how local adaptation to heterogeneous conditions among habitat patches after fragmentation depends on the degree and type of dispersal among habitat patches. Fragmentation in a habitat experiencing a thermal gradient results in patches that different in thermal environment (color of background). The color of the illustration represents different genotypes (or phenotypes) within each population, while the size of the illustration represents the relative contribution of each phenotype to the population make-up. **A,** With high random dispersal, populations are not expected to exhibit adaptation to local conditions within patches. **B,** With intermediate random dispersal or with habitat matching, populations are expected to evolve to increase adaptation to the local environmental conditions within patches. **C,** With very low dispersal, populations are expected to exhibit loss of genetic diversity as a result of stochastic drift and the loss of maladapted genotypes.



Supplemental Figure 2A-C. Conceptual diagram (top panels) illustrating a hypothetical scenario for an eco-evolutionary feedback (eco→evo→eco) between a consumer species and its resource with evolutionary trade-offs visualized below each conceptual panel. Fragmentation in a habitat experiencing a thermal gradient results in patches that different in thermal environment (color of background). The color of the illustration represents different genotypes (or phenotypes) within each population, while its size represents its relative contribution to the population make-up. In the trade-off diagrams, the curve for the trade-off relationship is indicated with a gray dashed line, while evolutionary movement along the curve is indicated with a solid red arrow. Dashed black arrows show the direction of the movement for each fitness attribute. **A,** In warm patches the consumer (copepod) experiences a plastic reduction in attack rate (dashed line off of the trade-off curve) such that warm patches become partial refugia of reduced predation pressure for the prey (algae). **B,** Reduced predation pressure enables prey in warm patches to increase local adaptation (increased resource acquisition) and achieve higher abundance. **C,** The predator eventually evolves increased attack rates in warm patches.



Supplemental Figure 3A-C. Conceptual diagram (top panels) illustrating a hypothetical scenario for an eco-evolutionary feedback (evo→eco→evo) between a consumer species and its resource with evolutionary trade-offs visualized below each conceptual panel. See the caption for Supplemental Fig. 2 for a description of the figure legend. **A,** The presence of habitat patches differing in their thermal environment results in evolution of the consumer (copepod) for increased attack rate, and an increase in its abundance in warm patches. **B,** Increased predation pressure results in decreased dispersal and/or increased population growth rate of the resource (algae) as an ecological response (dashed red line on the trade-off curve). **C,** Decreased dispersal then increases the opportunity for local adaptation of the resource to increase defense against the predator.



Supplemental Figure 4A-D. Conceptual diagram (top panels) illustrating a hypothetical scenario for an eco-evolutionary feedback (evo→eco→evo) in tri-trophic food chain with evolutionary trade-offs visualized below each conceptual panel. See the caption for Supplemental Fig. 2 for a description of the figure legend. **A,** In warm patches the prey (algae) evolves increased thermal performance resulting in an increase in its abundance. **B,** The intermediate consumer (copepod) evolves decreased investment in resource acquisition and increased investment in predator defense. **C,** The abundance of the top consumer (fish) declines in warm patches and it might even be driven to extinction in warm patches. **D,** Once released from predation pressure, the intermediate consumer evolves increased investment in resource reacquisition.