# Eco-evolutionary consequences of habitat warming and fragmentation in communities

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**Running Head**: Eco-evolution with warming and fragmentation

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## ABSTRACT

Eco-evolutionary dynamics can mediate species and community responses to habitat warming and fragmentation, two of the largest threats to biodiversity and ecosystems. The eco-evolutionary consequences of warming and fragmentation are typically studied independently, hindering our understanding of their simultaneous impacts. Here, we provide a new perspective rooted in trade-offs among traits for understanding their eco-evolutionary consequences. On one side, temperature influences traits related to metabolism, such as resource acquisition and activity level. Such traits are also likely to have trade-offs with other energetically costly traits, like antipredator defence or dispersal. On the other side, fragmentation can influence a variety of traits (*e.g.*, dispersal) through its effects on the spatial environment experienced by individuals, as well as properties of populations, such as genetic structure. The combined effects of warming and fragmentation on communities should thus reflect their collective impact on the traits of individuals and populations, as well as trade-offs at multiple trophic

levels, leading to unexpected dynamics when effects are not additive and when evolutionary responses modulate them. Here, we provide a road map to navigate this complexity. First, we review single species responses to warming and fragmentation. Second, we focus on consumer-resource interactions, considering how eco-evolutionary dynamics can arise in response to warming, fragmentation, and their interaction. Third, we illustrate our perspective with several example scenarios in which trait trade-offs could result in significant eco-evolutionary dynamics. Specifically, we consider the possible 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. In these scenarios, we present a number of novel, sometimes counter-intuitive, potential outcomes. Some of these expectations contrast to those solely based on ecological dynamics, for example, evolutionary response in unexpected directions for resource species or unanticipated population declines in top consumers. Finally, we identify several unanswered questions about the conditions most likely to yield strong eco-evolutionary dynamics, how to better incorporate the role of trade-offs among traits, and the role of eco-evolutionary dynamics in governing responses to warming in fragmented communities.

**Key words:** climate change, consumer-resource dynamics, environmental warming, eco-evolutionary dynamics, habitat fragmentation, food webs, metacommunities

**CONTENTS**

## 1. INTRODUCTION

Anthropogenic climate change and habitat fragmentation are two of the largest threats to biodiversity and ecosystems (Opdam & Wascher, 2004; Tilman *et al.*, 2017). Despite the attention placed upon them separately in the literature, they have rarely been considered simultaneously as interacting factors driving ecological and evolutionary responses in communities and ecosystems. A few recent studies have addressed their combined effects at the individual species level (Bakker *et al.*, 2010; Cobben *et al.*, 2012; Martin *et al.*, 2012; Laurent, Schtickzelle, & Jacob, 2020), but impacts on species interactions and communities remain largely unexplored. This is surprising given both the multifaceted nature of global change, as well as the likelihood that the selective pressure induced by warming could be stronger in fragmented communities that have altered habitat connectivity and population genetic structure (Cobben *et al.*, 2012; Martin *et al.*, 2012; Laurent *et al.*, 2020). Fragmentation divides previously contiguous habitat into discrete patches surrounded by an inhospitable environmental matrix or by other barriers to movement of individuals. Temperature can be heterogeneous at local scales (*i.e.* at which sets of individuals interact directly) (Orizaola & Laurila, 2008), and under climate change some habitats can become warmer, while others may remain unchanged (Urban *et al.*, 2017). Fragmentation may consequently exacerbate thermal heterogeneity by creating additional habitat patches differing in thermal environment, which can have important consequences for species dispersal and evolutionary responses (Skelly & Freidenburg, 2000).

Warming and fragmentation can both affect the dispersal of individuals among habitat patches with potentially important ecological consequences at the metacommunity level (Tuff, Tuff, & Davies, 2016; Thompson & Gonzalez, 2017). For instance, altered dispersal in fragmented habitats can shift the relative importance of species interactions versus dispersal for colonization success, resulting in different compositions of local communities (Thompson & Gonzalez, 2017). Changes in dispersal can also alter gene flow among habitat patches and thus influence the likelihood of adaptive evolutionary responses. 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 (Richardson *et al.*, 2014). In addition, fragmentation can reduce opportunities for adaptive evolutionary responses through a number of processes [*e.g.*, through reduced genetic diversity, smaller population sizes, genetic drift, inbreeding depression (Joubert & Bijlsma, 2010; Legrand *et al.*, 2017)].

Alternatively, fragmentation may instead increase opportunities for local adaptation by creating heterogeneous landscapes and communities that result in complex selection mosaics within

metacommunities. This remains empirically understudied and its implications poorly understood for community and ecosystem dynamics (Legrand *et al.*, 2017). Nonetheless, the geographic mosaic theory of coevolution (Thompson, 2005) and the evolving metacommunity concept (Urban & Skelly, 2006) both posit that fragmented habitats can result in selection mosaics and local adaptation. They suggest that local adaptation spanning multiple generations across geographically structured populations is driven in part through variation in selection among habitat patches and a shifting genetic and evolutionary landscape (Gomulkiewicz *et al.*, 2000; Thompson & Cunningham, 2002). Thus, although variable local adaptation across a metacommunity is conceptually not a new idea, it remains largely underexploited for predicting the effects of habitat warming in fragmented landscapes.

The joint influence of fragmentation and warming on eco-evolutionary dynamics (defined as ecological and evolutionary dynamics that occur at contemporary time scales and affect one another (Fig. 1) remains similarly unexplored despite the pivotal role of eco-evolutionary dynamics for species persistence under rapid environmental change (Kinnison & Hairston, 2007). Selection acting upon traits for which correlations exist (*i.e.*, where selection on one trait is expected to alter performance in another trait or fitness attribute) is particularly likely to yield eco-evolutionary dynamics through ecological fitness trade-offs. Eco-evolutionary dynamics can have important consequences across levels of organization by altering phenotypic traits (Becks *et al.*, 2012; Stuart *et al.*, 2014), the dynamics of populations and communities (Yoshida *et al.*, 2007; Becks *et al.*, 2010; Faillace & Morin, 2016; Frickel, Theodosiou, & Becks, 2017), and the functioning of ecosystems (Palkovacs *et al.*, 2009; Bassar *et al.*, 2012; Walsh *et al.*, 2012).

Eco-evolutionary dynamics can be especially important in populations responding to novel environmental conditions, in part because they can depend upon the community context (de Mazancourt, Johnson, & Barraclough, 2008; Van Doorslaer *et al.*, 2009a, 2010; Osmond & de Mazancourt, 2013). For example, a novel species may invade a community when tracking optimal thermal conditions. In fact, temperate species have been documented moving northward and warm-adapted invasive species are colonizing temperate habitats (Parmesan & Yohe, 2003; Walther *et al.*, 2009). Fragmentation might simultaneously cause species to become "trapped" in no-analogue communities or climates (*i.e.*, ecological effect: eco) (Williams & Jackson, 2007; Feeley & Rehm, 2012). The presence of novel species interactions could then result in evolutionary changes to interacting species (*i.e.*, evolutionary effect: 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 by Faillace & Morin (2016). In fact, Van Doorslaer *et al.* (2009a) showed that

community context altered the response of populations of *Daphnia magna* evolving in response to habitat warming. Single-species cultures of *D. magna* evolved higher intrinsic growth rates, while community-embedded *Daphnia* evolved larger size at maturity (Van Doorslaer *et al.*, 2010). Given that habitat patches within a community can differ in both thermal environment and the species present, eco-evolutionary dynamics occurring in a community context are thus likely to prove important for fragmented communities responding to warming.

Here, we review the effects of fragmentation and warming for single species before expanding to consumer-resource interactions. In focusing on the effects of dispersal limitation and selection on traits and responses linked to metabolism, we identify gaps in the current knowledge regarding the interactive effects of fragmentation and warming. We argue that ecological trait trade-offs provide a useful avenue for examining the role of eco-evolutionary dynamics that emerge in response to simultaneous warming and habitat fragmentation (i.e. patch isolation) in multi-trophic communities. Building upon theoretical and empirically demonstrated effects of fragmentation and warming, we present the use of trade-offs by developing example scenarios for the eco-evolutionary consequences of habitat fragmentation and warming. We use scenarios of increasing complexity to illustrate the sometimes unexpected or counterintuitive outcomes that might emerge from considering the joint effects of both stressors in driving eco-evolutionary responses across multiple trophic levels. In this review, we ask: what are the potential eco-evolutionary consequences in fragmented landscapes 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 in top consumer body size in tri-trophic food chains. Finally, we present several unanswered questions guiding future research directions that provide opportunities to elucidate the potential role of eco-evolutionary dynamics under combined habitat warming and fragmentation.

## 2. SINGLE SPECIES RESPONSES TO WARMING AND FRAGMENTATION

Single species responses to both habitat warming and fragmentation have received a great deal of attention (Parmesan, 2006; Legrand *et al.*, 2017). Here we briefly review responses of individual species to provide necessary background before considering sets of interacting species, for which much less is known.

**(1) Responses to warming**

Species can exhibit a wide range of evolutionary and ecological responses to warming (although not all species will have the necessary evolutionary capacity; e.g. see Hoffmann & Sgró, 2011; Lindsey *et al.*, 2013; Quintero & Wiens, 2013; Buckley & Bridle, 2014; Kingsolver & Buckley, 2015). For this review, we focus primarily on ecological and evolutionary responses associated to thermal performance for species and their populations. We do not aim to be exhaustive and acknowledge that changes to additional traits, like phenology or behavioural thermoregulation, could also be of importance (see, e.g. Abram *et al.*, 2017; Boukal *et al.*, 2019).

Intraspecific variability in thermal performance traits among individuals or populations can be of similar magnitude as trait variability at the interspecific level (Herrando-Pérez *et al.*, 2020). Evolution of species' traits, such as changes in fecundity, growth, metabolic rates, and enzyme activities, has already been documented in response to warming (Van Doorslaer *et al.*, 2009b; Schulte, Healy, & Fangue, 2011; Merilä & Hendry, 2014; Geerts *et al.*, 2015; Padfield *et al.*, 2016; Schaum *et al.*, 2017, 2018). For instance, in the green alga *Chlorella vulgaris*, improved carbon use efficiency at higher temperatures can evolve in around 100 generations (Padfield *et al.*, 2016), while evolution of increased thermal tolerance has been observed in the freshwater alga *Chlamydomonas reinhardtii* in warmed semi-natural mesocosms after a period of multiple years (Schaum *et al.*, 2017). In the cladoceran *Daphnia magna*, clonal selection in semi-natural field conditions enabled populations to evolve rapidly in response to warming (Geerts *et al.*, 2015). Evolution in larger organisms can occur rapidly as well, on time scales relevant to ongoing climate warming (but see Quintero & Wiens, 2013). Natural selection has been observed for thermal critical maximum (i.e. the upper bound of an organism's thermal tolerance range) in the lizard *Anolis sagrei* (Logan, Cox, & Calsbeek, 2014). Similarly, Higgins *et al.* (2014) documented a broadening of the thermal performance curve in *Colias eurytheme* caterpillars, while caterpillars of the related *Colias eriphyle* have increased the thermal optimum of feeding over the past 40 years of climate warming. Evolutionary responses to the thermal environment have been documented at microgeographic scales as well (e.g. Skelly & Freidenburg, 2000). Overall, these examples highlight rapid evolution in the shape and position of thermal performance curves for a variety of biological traits.

In general, when evolution increases any of these biological rates at warmer temperatures, this results in improved thermal performance, leading to populations or species that are more successful in the warmer environmental conditions (Stoks, Geerts, & De Meester, 2014). However, traits under selection in response to climate warming, including those relating to metabolism, can exhibit trade-offs with other traits important to life history, such that improvement in one trait comes at the expense of

performance in a second trait (Simon, Machado, & Marroig, 2016). In *Escherichia coli*, for example, selection for improved fitness at moderate temperatures results in populations with reduced growth at temperature extremes (Cooper, Bennett, & Lenski, 2001). Similarly, in natural populations of the common pond snail *Radix balthica*, increased growth rate at warm temperatures potentially trades off against survival and tolerance at cold temperatures (Johansson *et al.*, 2016a). Selection on traits involved in trade-offs can yield unexpected results; for instance, algal lines of *C. reinhardtii* grown for many generations at high $CO_2$ concentrations have significantly lower growth and $CO_2$ affinity (Collins & Bell, 2004, 2006). In fact, Gilman *et al.* (2010) have suggested the existence of a widespread trade-off between growth rate and broad tolerance to temperature (i.e. wider thermal niches) in which warming may be expected to favour species or individuals with greater stress tolerance compared to those that are competitively dominant with rapid growth rates (Gilman *et al.*, 2010). Johansson and Laurila (Johansson & Laurila, 2017) have found that thermal critical maximum likely trades off with tolerance to chronic thermal stress in warm adapted populations of *R. balthica*. Evidence also suggests that the body size of some ectotherms is shrinking with warming (Daufresne, Lengfellner, & Sommer, 2009; Gardner *et al.*, 2011), which potentially improves tolerance to thermal stress (Sentis, Binzer, & Boukal, 2017). Finally, Van Doorslaer *et al.* (2009) showed that local adaption to warmer temperatures in *Daphnia* reduced establishment success of immigrant genotypes from warmer regions. When considered collectively, these studies reveal the importance of taking into account multiple potential trade-offs to better understand the response of single species to warming.

**(2) Responses to fragmentation**

Fragmentation alters the opportunities for evolution in response to local conditions (Cote *et al.*, 2017). 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. Habitat fragmentation can reduce dispersal among habitat patches as a result of increased inter-patch distances (Laurent *et al.*, 2020). For instance, in the ciliate *Tetrahymena thermophila*, fragmentation lowers dispersal by increasing inter-patch distances and dispersal costs. Ciliates became choosier in their decision to stay or leave their patches in a more fragmented landscape, which decreased the frequency of random dispersal events (Laurent *et al.*, 2020). Fragmentation can even promote the evolution of dispersal itself (Williams, Kendall, & Levine, 2016). For example, in experimental populations of the small forb *Arabidopsis thaliana*, after only six generations, evolving populations spread 200% farther in fragmented landscapes than did non-evolving populations. In contrast, for populations evolving in continuous

habitats, this difference was reduced to 11%. Overall, intermediate levels of dispersal are most likely promoting local adaptation (Legrand *et al.*, 2017) (Supplemental Fig. 1). However, in some cases, local adaptation can be enhanced even under higher potential gene flow as a result of habitat matching (Jacob *et al.*, 2017). As a result, fragmentation can differently impact emigration and immigration rates and thus modify ecological and evolutionary dynamics.

By creating habitat patches that differ significantly in local conditions, fragmentation can maintain higher intraspecific beta-diversity across patches in a metapopulation compared to that in a continuous landscape (Urban & Skelly, 2006). Coupled with its influence on dispersal (and gene flow) among patches, fragmentation may affect opportunities for adaptive evolution within patches (Hanski, 2012). Similar to thermal performance traits, the evolution of dispersal is likely to be constrained by trade-offs between dispersal ability and other fitness traits. For example, wingless aphids produce winged offspring in response to predators or crowding (Dixon & Agarwala, 1999; Srinivasan & Brisson, 2012). Winged aphids can disperse across long distances compared to wingless individuals, but developing wings is energetically costly, delays development, and reduces fecundity (Dixon, Horth, & Kindlmann, 1993). These costs are expected to outweigh the benefits when dispersal is unsuccessful. Dispersal ability thus trades off against fecundity, which should limit the evolution of dispersal traits. The impact of habitat fragmentation on dispersal traits is likely to depend on the balance between dispersal success and the cost of dispersal in a fragmented landscape. In fact, when dispersal is not successful, the frequency of winged aphids decreases in isolated populations, resulting in faster population growth (Sentis *et al.*, 2018).

**(3) Responses to simultaneous warming and fragmentation**

Evidence of the combined effects of warming and fragmentation is very limited. Interactions between warming and fragmentation are expected to occur when dispersal is non-random with regard to thermal conditions. For example, dispersal decisions in common lizards (*Zootoca vivipara*) can be related to their preferred thermal conditions and at least partially matched to phenotype-dependent survival (Bestion, Clobert, & Cote, 2015). Another example are natural populations of black-capped chickadees (*Poecile atricapillus*), whose overwintering populations in fragmented habitats were characterized by lower basal (i.e. maintenance) metabolic rates compared to populations from unfragmented habitats (Latimer *et al.*, 2018). Birds with lower summit metabolic rates (i.e. upper limit to body heat production) were less likely to survive the winter in fragmented habitats. 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.

At the species level, fragmentation and climate warming are generally expected to act synergistically to increase extinctions. For instance, habitat availability thresholds for species extinctions are predicted to decline when combined with general climate change (Travis, 2003). These theoretical predictions potentially occur in natural populations of British butterflies, where habitat modification, including fragmentation, combined with climate warming has led to population declines, with habitat generalists and better-dispersing species being favoured over those that are specialists or more sedentary (Warren *et al.*, 2001). In addition, recent research on several species of British butterflies suggests that persistence in the face of ongoing climate change would be achieved most effectively by incorporating semi-natural habitats that reduce effective fragmentation (Oliver *et al.*, 2015). Similarly, local extinction patterns of multiple freshwater fish species over a 20-year period are best explained by a combination of climate warming and habitat modification, including fragmentation (Comte, Hugueny, & Grenouillet, 2016).

Taken together, warming-induced changes to metabolism and fecundity have the potential to affect a population's viability, while fragmentation can result in increasing population isolation and changes to dispersal and gene flow. If habitat connectivity and gene flow are too low and population sizes within patches are small, fragmentation should favour drift, reducing or preventing local adaption (Gandon & Nuismer, 2009), while high habitat connectivity and gene flow are potentially more likely to yield solely ecological responses, like plastic responses and migration (Fig. 2, outcomes A and B). When the degree of gene flow and the population sizes within patches are sufficient to favour selection, fragmentation can instead increase the trait-environmental correlation such that it can then increase opportunities for local adaptation (Urban *et al.*, 2008) (Fig. 2, outcomes C and D).

## 3. INTERACTIONS OF CONSUMER-RESOURCE DYNAMICS WITH WARMING AND FRAGMENTATION

The previous section reviewed the range of single-species responses to both warming and fragmentation for a variety of taxa across different trophic levels. However, in nature, species are embedded in a community and the outcome of global change for a species also depends on changes in the nature and strength of interactions with other organisms within the community. We focus this section on the consequences of warming and fragmentation for consumer-resource interactions, the most important building block of communities.

Consumer-resource dynamics have a rich history of study in both ecology and evolution. In general, the presence of multiple interacting species can result in additional direct and indirect ecological and evolutionary effects (Tseng & O'Connor, 2015; Osmond, Otto, & Klausmeier, 2017; terHorst *et al.*, 2018; De Meester *et al.*, 2019; Tabi *et al.*, 2020). In terms of evolutionary responses to warming in fragmented landscapes, when selection occurs within an ecological community it is therefore likely to qualitatively change predictions about thermal adaptation derived from single populations (Angilletta Jr. *et al.*, 2006). For instance, Tabi *et al.* (2020) recently demonstrated that individual species' responses to temperature were insufficient to explain changes to community composition in experimental communities of protists feeding on bacteria. Similarly, in terms of evolutionary responses, the opportunities for trait trade-offs and epistatic (i.e. when the effect of one gene mutation depends on mutations in one or more additional genes) and/or antagonistic pleiotropic (i.e. when an allele that has a beneficial effect on one fitness component has a deleterious effect on a different fitness component) gene interactions increase with the number of interacting species. Such genetic effects and interactions can have important consequences, including slowing the rate of evolution or preventing it entirely (Etterson & Shaw, 2001; de Mazancourt *et al.*, 2008; Hoffmann & Sgró, 2011; Scheuerl *et al.*, 2020), and driving responses in otherwise unexpected ways (De Meester *et al.*, 2011; Barraclough, 2015; Cairns *et al.*, 2020). For example, in an experiment conducted by Cairns *et al.* (2020) protist predators exhibited unexpected higher population equilibrium densities when feeding on several evolved bacterial prey species compared to ancestral strains, despite anti-predator defence evolution in the bacteria. The authors suggested that this surprising result could have occurred as an indirect effect of bacterial resource evolution enabling higher prey densities, and thus predator densities, even in spite of the observed bacterial anti-predator evolution. Mismatches in the potential for evolutionary response across trophic levels are also possible and may arise out of smaller population sizes and longer generation times (Terhorst, Miller, & Levitan, 2010; Hague & Routman, 2016) frequently observed at higher trophic levels. This can affect the standing genetic variability and the rapidity with which mutations arise, and thus the relative importance of ecological and evolutionary change compared to other species and environmental change (Fig. 3). Ultimately, mismatches can result in significant differences in extinction risk across trophic levels (Quintero & Wiens, 2013; Dirzo *et al.*, 2014), as well as differences in the degree of local evolution (Fig. 2). In fact, in consumer-resource interactions experiencing Red Queen dynamics (i.e. a coevolutionary arms race between the interacting species), theory predicts that the most rapidly evolving partner is locally adapted while the other is not (Blanquart *et al.*, 2013). Predators can thus improve prey adaptation and persistence despite reductions

in prey abundance. This occurs 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 mutation rate) (Tseng & O'Connor, 2015; Osmond *et al.*, 2017). Clearly, both evolution itself, as well as ecological responses to evolutionary change, depend greatly on community context (i.e. the set of species and interactions in which the evolving species is embedded), with consumer-resource interactions having important consequences for both interacting species.

(1**) Responses to warming**

A vast literature documents a number of ecological changes in trophic interactions that occur in response to warming. Warming typically increases consumer-resource encounter and feeding rates up to an optimal temperature above which rates decrease due to physiological constraints and behavioural modification induced by heat (Lang, Rall, & Brose, 2012; Sentis, Hemptinne, & Brodeur, 2012; De Block *et al.*, 2013; Tran *et al.*, 2016; Abram *et al.*, 2017). The non-linearity of thermal dependency of multiple biological rates (Amarasekare, 2015; Uszko *et al.*, 2017; Zhang *et al.*, 2017; Dee *et al.*, 2020; Uiterwaal & DeLong, 2020; Zhao, Liu, & Niu, 2020) can make predicting responses particularly difficult.

Feeding rates often scale with consumer-resource body mass ratios (Montoya *et al.*, 2009; Vucic-Pestic *et al.*, 2010). Therefore, the pervasive body size reductions associated with environmental warming can also alter consumer-resource dynamics. This can sometimes be compounded by trophic position as these changes may be most prevalent at higher trophic levels (Sheridan & Bickford, 2011; Ohlberger, 2013) (but see also Yvon-Durocher *et al.*, 2015). For instance, in a three-species food chain model, Sentis *et al*. (Sentis *et al.*, 2017) showed that when warming reduces predator body size it can increase predator survival at higher temperatures, leading to higher persistence of tri-trophic food chains at high temperatures. This possibility is particularly intriguing given that consumer metabolic rates often increase faster with warming than their ingestion rates, which leads to decreased overall energetic efficiencies, defined as the ratio of ingestion gains versus metabolic losses (Rall *et al.*, 2010; Vucic-Pestic *et al.*, 2011). Rall *et al.* (2010) found that for spiders and predatory beetles warming generally increased feeding rates and short-term interaction strengths, but decreased their ingestion efficiency and the long-term interaction strengths. Fulfilling energetic demands is typically harder for consumers at higher trophic levels than for organisms at lower trophic levels (Boukal *et al.*, 2019). In fact, the results reported by Rall *et al.* (2010) were striking as they suggest that warming can result in higher extinction risks from starvation for predators. Declines in energetic efficiency are also linked with weaker top-down effects in communities (Kratina *et al.*, 2012; Fussmann *et al.*, 2014; Iles, 2014; Sentis

356 *et al.*, 2017). Given that secondary and top consumers also frequently have smaller population sizes and
357 longer generation times than their resources (Fig. 3), warming may thus exacerbate differences in
358 population sizes across trophic levels resulting in profoundly altered community structures, including
359 losses of consumers, especially at higher trophic levels (Petchey *et al.*, 1999) (Fig. 2, outcome A).

360 **(2) Responses to fragmentation**

361 Fragmentation can similarly have a variety of effects on consumer resource interactions.
362 Consumer-resource interactions can affect dispersal of both interacting species. Theory about density-
363 dependent dispersal (Hauzy *et al.*, 2010) and habitat matching/dispersal experiments indicate potential
364 differences in drivers for predator and prey dispersal. Predators frequently disperse only below a critical
365 threshold of prey abundance, while prey disperse as a result of strong intraspecific competition or
366 perceived predation risk (Hauzy *et al.*, 2007; Fronhofer *et al.*, 2018). For example, for two protist
367 species, the prey species *Tetrahymena pyriformis* and the predator *Dileptus* sp., Hauzy *et al.* (2007)
368 determined that decreased density of *T. pyriformis* increased the dispersal of *Dileptus*, while increased
369 density of *Dileptus* increased the dispersal of *T. pyriformis*. Similarly, predatory water boatmen
370 (*Trichocorixa verticalis*) emigrated more rapidly from mesocosms when their cladoceran prey, *Moina*
371 *macrocopa*, was at low densities (Simonis, 2013). In fact, Fronhofer *et al.* (2018) tested the importance
372 of top-down and bottom-up control in dispersal decisions across numerous taxa, from protists to
373 vertebrates, finding that predation risk and resource limitation increased emigration rates across all taxa
374 and highlighting the importance of interactions with adjacent trophic levels.

375 Because fragmentation can increase predation risk during dispersal, it can potentially select for
376 prey phenotypes that increase survival (Bestion *et al.*, 2014), for example by increasing antipredator
377 traits or locomotor speed (Cote *et al.*, 2017). Despite the increased risk associated with dispersal in the
378 presence of predators, predators can nonetheless increase movement and dispersal of prey through the
379 surrounding matrix, and can preferentially favour movement of some phenotypes over others (e.g.
380 Gilliam & Fraser, 2001). In the presence of predators, aphids produce winged offspring that can disperse
381 further away while avoiding terrestrial predators (Dixon & Agarwala, 1999). In addition, different
382 phenotypes can be favoured in predator-free and predator-occupied patches. For example, Trinidadian
383 guppies (*Poecilia reticulata*) evolve differences in life history, behaviour, morphology, and male colour in
384 populations exposed to predators compared to those that are predator-free (Bassar *et al.*, 2017). Taken
385 together, because fragmentation can modify both dispersal rates and prey phenotypic traits, it should
386 change the flow of phenotypes that differ in fitness traits, including metabolism and consumption.

Fragmentation can result in variability of attack rates among local predator populations. For instance, in experimental populations of *Libellula* dragonflies, larval foraging rates were positively correlated with the degree of habitat fragmentation, with the individuals from the most isolated pools exhibiting significantly higher foraging rates than those from the most connected pools (McCauley, Brodin, & Hammond, 2010). Theory shows that habitat fragmentation can result in increased predator-prey interaction strengths through spatial compression (i.e. higher concentration of predator and prey individuals resulting in higher encounter rates), thereby affecting consumer and resource temporal population dynamics (McWilliams *et al.*, 2019). At even larger scales (e.g. latitudinal) populations can differ in their genetically determined attack rates. For instance, in *Nucella caniculata*, a predatory sea snail, populations differed significantly in their drilling rate on *Mytilus californianus*, their mussel prey. Common garden experiments demonstrated that the variation in attack rates was genetically determined, while gene flow was restricted among populations (Sanford *et al.*, 2003).

Importantly, because fragmentation can result in local patches that differ in the relative abundances of dominant consumers, disparate consumer-resource interactions across the metacommunity become possible, resulting in local patches that differ significantly in the strength of biotic selective pressures. For instance, Urban (2008) examined a metacommunity containing the salamander *Ambystoma maculatum* and several of its important larval consumers, including *Ambystoma opacum* and beetles of the genus *Dytiscus*. While *A. opacum* is a gape-limited predator that feeds primarily on small larval individuals of *A. maculatum*, larger larval individuals are instead more vulnerable to *Dytiscus* predators. These two predators exert opposing selection gradients upon *A. maculatum* larval growth rate (Urban, 2008). Densities of both predators are negatively correlated across ponds within the metacommunity, indicating that *A. maculatum* larvae can experience antagonistic selection regimes across the metacommunity depending on the abundance of the two predators in local habitat patches. This scales down the food web because the foraging rate of *A. maculatum* on its zooplankton prey is under selection as a result, in part, of predation pressure from *A. opacum*.

Theory shows that, in general, metacommunity dynamics favour the persistence of otherwise extinction-prone food webs, by decreasing local population fluctuations that can eventually lead to species extinctions (Bonsall, French, & Hassell, 2002; Ryall & Fahrig, 2006; Cooper, Li, & Montagnes, 2012). Experimental metacommunities containing populations of the host beetle, *Callosobruchus chinensis*, and its pteromalid parasitoid, *Anisopteromalus calandrae*, exhibit significantly prolonged persistence times compared to isolated communities (Bonsall *et al.*, 2002). By improving survival of both

consumers and resources, metacommunities therefore increase the time available for evolution to potentially occur.

**(3) Responses to simultaneous warming and fragmentation**

Research in the literature exploring the interaction between habitat fragmentation and warming for consumer-resource interactions remains scarce. Nonetheless, several studies, including several using latitudinal gradients, allow us to examine some interactive effects.

Habitat warming and dispersal can interact, with the effects of warming on dispersal rates likely to be context-dependent, modulated by resource availability and interspecific interactions. For instance, Grainger & Gilbert (2017) showed that when host plants are abundant, warming does not affect dispersal of herbivorous insects and increases their population size. In contrast, when host plants are limiting, warming increases dispersal rates and herbivore populations decline. When dispersal and warming both occur, the results for the community can be quite important. As an example, Perdomo, Sunnucks, & Thompson, (2012) examined the combined effects of a high-temperature event and habitat isolation on the assembly of natural moss micro-arthropod communities. In communities that had experienced warming, they found that two large springtail taxa (Collembola) became numerically dominant following community assembly, resulting in community size structures (i.e. body mass distributions at the community level) unlike those of unwarmed communities.

Variation in attack rates driven by genetic differences among predator populations can also interact complexly with environmental temperature (De Block *et al.*, 2013; Tran *et al.*, 2016). For example, De Block and co-authors paired populations of the cladoceran *Daphnia magna* and their damselfly predator, *Ischnura elegans* from different latitudes in Europe in all possible combinations (De Block *et al.*, 2013). Individuals of *I. elegans* differed in their genetically-determined attack rates across latitudinal populations. The survival advantage experienced by southern *Daphnia* at 24° C and northern *Daphnia* at 20° C disappeared when they were paired respectively with southern *Ischnura* and northern *Ischnura*. These results show that local adaptation in both predators and prey can be important in eco-evolutionary dynamics. The degree of climate-matching in interacting species in more complex communities is therefore likely to play a role in determining when eco-evolutionary dynamics result in cryptic outcomes (i.e. a “moving target” scenario such that ecological outcomes can mask the underlying evolutionary change) compared to more dramatic or visible outcomes (Fig. 2, outcome C). We may then expect that the dramatic eco-evolutionary outcomes will be particularly likely in complex communities

in which interacting species have mismatched climate phenotypes (e.g. as might occur in no-analogue communities) (Fig. 2, outcome D).

Overall, this suggests that, when temperature differs among habitat patches (e.g. Skelly & Freidenburg, 2000), attack rates are also expected to vary among patches (e.g. resulting from temperature-dependent attack rates, as in De Block *et al.*, 2013; Tran *et al.*, 2016). This leads to the prediction that fragmentation results in varying consumer-resource interactions among local habitat patches and that differences in these interactions then result in variable selection pressures at local scales within the metacommunity. Additionally, given the likelihood of evolutionary mismatches across trophic levels and the observed changes in trophic interaction strengths, we argue that the importance of eco-evolutionary dynamics for consumer-resource interactions during habitat warming and fragmentation is certainly underestimated.

## 4. THE IMPORTANCE OF FITNESS TRADE-OFFS IN ECO-EVOLUTIONARY DYNAMICS

In sections 2 and 3 we reviewed the effects of warming and fragmentation on isolated species and their interactions. These effects are likely to be non-additive and can have important ecological and evolutionary consequences at the population, community and landscape levels. In particular, the effects of warming and fragmentation on dispersal rates are likely to (1) be context-dependent, modulated by resource availability, predator presence, and competitive interactions, and (2) influence the distribution of phenotypes within populations by favouring heat-resistant phenotypes and those maximising the cost-benefit balance of dispersal. This highlights the importance of intraspecific trait variation, fitness trade-offs, and interspecific interactions to better understand the influence of warming and fragmentation on eco-evolutionary dynamics. In this section, we focus on the role of fitness trade-offs for eco-evolutionary dynamics and how these trade-offs can be used to anticipate the impact of warming and fragmentation on communities.

Eco-evolutionary dynamics are especially important when populations experience selection upon traits for which important correlations exist (Fig. 4), such that selection on one trait is expected to alter performance in another trait or fitness attributes. In other words, ecological trade-offs occur when higher performance in one fitness attribute comes at the expense of performance in a second (Fig. 4). Some examples of key fitness trade-offs include competition-colonization trade-offs (Cadotte *et al.*, 2006) and resource acquisition-defence trade-offs (Branco *et al.*, 2018). 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 within the food web as an evolutionary cascade, by rippling through the system as shifts in species abundances, resulting in altered community and ecosystem properties (Palkovacs, Wasserman, & Kinnison, 2011). Eco-evolutionary feedbacks can thus lead to unexpected ecological or evolutionary dynamics that cannot be adequately modelled or predicted without considering these feedbacks (Govaert *et al.*, 2019; Kaitala *et al.*, 2020). For example, in the case of experimental work by Hiltunen *et al.* (2018) examining the evolution of *Pseudomonas fluorescens* and its consumer *Tetrahymena thermophila* as a result of multistressor selection, a subsequent analysis by Kaitala *et al.* (2020) demonstrated that models including co-evolution between the two species best explained the observed dynamics.

Importantly, abiotic stressors (e.g. exposure to extreme temperatures) are predicted to alter trade-offs in a variety of ways that can result in eco-evolutionary dynamics that are environmentally-dependent (Theodosiou, Hiltunen, & Becks, 2019), which could be particularly important for communities in fragmented landscapes. 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 has documented effects from warming and/or fragmentation. For instance, warming can influence competitive outcomes (Bestion *et al.*, 2018) and resource acquisition and defence (De Block *et al.*, 2013), while fragmentation can influence dispersal and colonization (Cote *et al.*, 2017). Another documented trade-off is survival vs. growth-rate in relation to thermal performance. Examples include variable survival at different temperatures after laboratory selection for increased performance at high temperatures in *Escherichia coli* (Cooper *et al.*, 2001), growth rate vs. heat-shock tolerance in pea aphids (*Acyrthosiphon pisum*) (Harmon, Moran, & Ives, 2009a), and survival at extreme temperatures of *Tigriopus californicus* copepods vs. their competitive ability (Willett, 2010). Changes in these trade-offs can then lead to altered consumer-resource dynamics (an ecological effect) (Sheridan & Bickford, 2011; Yvon-Durocher *et al.*, 2011; Gardner *et al.*, 2011; Ohlberger, 2013; Sentis *et al.*, 2017) and, in turn, alter selection for traits that trade off with defence against a consumer (an evolutionary effect), ultimately resulting in additional ecological changes within the community (and an eco-evolutionary feedback).

Based upon these trends, we argue that investigation of fitness trade-offs and the consequences of eco-evolutionary dynamics on interspecific interactions in concurrently fragmented and warmed landscapes will provide a more complete understanding of the simultaneous long-term effects of these stressors. Using fitness trade-offs, our goal is therefore to highlight how eco-evolutionary responses linked to consumer-resource interactions may yield novel consequences in these systems.

## 5. SCENARIOS FOR ECO-EVOLUTIONARY DYNAMICS IN WARMED AND FRAGMENTED COMMUNITIES

We provide several illustrative scenarios next to demonstrate the ways in which eco-evolutionary dynamics may influence outcomes of consumer-resource interactions in communities experiencing simultaneous warming and fragmentation. We indicate whether each step in the dynamic is ecological (eco) or evolutionary (evo) to enable the reader to trace the feedbacks in the scenario. Acknowledging that eco-evolutionary dynamics have the potential to yield multiple outcomes, we do not aim to provide an exhaustive exploration of these possibilities. We do not argue that these scenarios are the only ones we should expect, or that they are likely to be the most common of all possible outcomes, but rather that they are likely to occur given the current theoretical and empirical evidence of the impacts of warming or fragmentation on species traits and response to selection. These scenarios provide examples on how eco-evolutionary dynamics can affect communities under warming and fragmentation, potentially yielding unexpected results compared to predictions based solely upon ecology or evolution.

### (1) Scenarios for single consumer-resource interactions

A number of eco-evolutionary dynamics, including feedbacks, can arise in consumer-resource interactions occurring in warmed and fragmented habitats. We focus on three that meet our criteria. 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) (evo), its abundance could increase (eco). A potential example of this phenomenon is with *Daphnia magna* in which isolated populations evolved increased growth rate in response to warming (Van Doorslaer *et al.*, 2010). This will result in increased dispersal among patches as density increases (Fronhofer *et al.*, 2018), and thus higher abundance in cool patches due to the influx of immigrants (eco) (Fig. 5A). One result of the increased availability of the resource in cool patches could be increased attack rate by the consumer. Increased attack by the consumer could result as either a density-dependent (*i.e.*, of the resource) ecological response (eco) (e.g. Eggleston, Lipcius, & Hines, 1992; Hossie & Murray, 2010) or due to evolution to increase resource acquisition (Fig. 5B) (e.g. populations differing in genetically determined attack rates evo) (Sanford *et al.*, 2003; De Block *et al.*, 2013; Dinh Van *et al.*, 2013, 2014). Increased consumer pressure can then decrease the number of successfully dispersing individuals of the resource (e.g. Yoder, Marschall, & Swanson, 2004), increasing the degree of isolation among patches for the resource (eco). In

doing so, it could then increase opportunities for additional local adaptation of the resource (Loeuille & Leibold, 2008), for instance, to then increase defence against the consumer (evo) (Fig. 5C).

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 (Tran *et al.*, 2016), a change in period of activity, or prey switching (eco). In this scenario, warm patches would again function as prey refugia, leading to larger population sizes of prey (eco) and increased opportunities for local adaptation to the thermal environment without trade-offs (evo) (Supplemental Fig. 2). In fact, if trade-offs between thermal performance traits and defence traits do occur (e.g. Janssens, Verberk, & Stoks, 2018; Tran *et al.*, 2019), evolution of increased thermal performance may prove to be more likely with spatial segregation associated to fragmentation than in a non-fragmented community.

And thirdly, because the evidence with regard to the effects of warming on attack rate remains inconclusive, especially at evolutionary time scales, we consider the possibility that attack rates also increase due to warming (De Meester *et al.*, 2011). For example, over time consumers may evolve in response to their thermal environment (evo). If a consumer evolves increased attack rates in warm habitats and its abundance increases, the higher attack rates may decrease the absolute number of successful dispersers of the resource among habitat patches (i.e. possibly as a result of reduced abundance of the resource, even though dispersal rate itself could increase; Dixon & Agarwala, 1999) (eco), resulting in increased opportunities for local adaptation of the resource as a result of increased effective patch isolation (evo) (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 (Osmond *et al.*, 2017) (Supplemental Fig. 3).

**(2) Scenarios for 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 (terHorst *et al.*, 2018). Evolutionary cascades become possible, with the potential for a shift in the trade-offs for one species to propagate through the food web as eco-evolutionary feedbacks. For example, landlocked populations of alewives (*Alosa pseudiharengus*) in lakes increase predation pressure (eco) on *Daphnia*. In response, the *Daphnia* have evolved faster growth, earlier maturation, and higher fecundity (evo) (Walsh & Post, 2011), an effect that cascades through the food chain in the form of altered

phytoplankton dynamics and ecosystem functioning (eco) (Walsh *et al.*, 2012). We thus focus on two scenarios with two different starting points that take into account the possibility of cascading effects in simple food webs.

In our first scenario, a resource species evolves increased thermal tolerance (evo) (e.g. Schaum *et al.*, 2017). This could involve a trade-off with a trait important to defence against consumption or simply make it a more abundant, and thus readily available, resource (eco). In either case, the intermediate consumer has an opportunity to evolve to increase investment in its own defence against a top consumer (evo). This is most likely to occur in fragmented habitats, where the top consumers have smaller population sizes than in continuous habitats (Crooks & Soulé, 1999). In warm patches especially, top consumers that are physiologically sensitive to warming may be less abundant or absent entirely (Petchey *et al.*, 1999; Binzer *et al.*, 2012), providing partial refuge to the intermediate consumer. Specifically, as it becomes less costly for the intermediate consumer to acquire the now more abundant resource, it is free to evolve decreased investment in expensive traits favourable 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 (eco) (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 (eco) (Teplitsky & Millien, 2014). This can trigger prey-switching (Truemper & Lauer, 2005), such that smaller predators are likely to target younger, smaller size classes of the intermediate consumer, potentially due to increasing gape limitation (Arim *et al.*, 2010) (Fig. 6A). This, in turn, increases selection on the intermediate consumer to evolve faster growth rates and escape vulnerable size classes sooner (evo). 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 this lake system was not evaluated (Persson *et al.*, 1996). Faster growth rates can cause increased attack rates by the intermediate consumer on the resource (eco). 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 defence (Fig. 6B). With increased attack by the intermediate consumer, the resource might then evolve an increase in defence traits at the expense of its own resource acquisition (evo) (Lind *et al.*, 2013) (Fig. 6C). This, however, may vary among patches when individuals of the intermediate consumer only

disperse infrequently 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 is physiologically constrained in warm patches. In this situation, the evolution of the resource species' traits for defence or its own resource acquisition could occur unevenly across the landscape.

The two scenarios presented above can act simultaneously. If the resource abundance increases while the top consumer body size decreases in warm patches, habitat fragmentation will couple changes in both populations. Changes at the two trophic levels could thus reinforce one another, possibly resulting in markedly increased abundance of the intermediate consumer not predicted without both habitat warming and fragmentation.

## 6. FUTURE RESEARCH DIRECTIONS

To date, a prevailing underlying assumption of many studies of climate change or fragmentation is that observed differences in interspecific interactions are explained by purely ecological effects. Eco-evolutionary dynamics, however, can be cryptic and mostly undetectable. For example, eco-evolutionary dynamics can be mostly apparent through consequential ecological changes in species abundances, increasing stability or dampening of ecological patterns in space (Kinnison, Hairston, & Hendry, 2015; Hendry, 2019; Urban *et al.*, 2020). 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 the degree of climate-phenotype matching, population properties related to fragmentation, and community context are important for determining the importance of eco-evolutionary dynamics in warmed and fragmented communities (Fig. 2), and that acknowledging their role opens up a new area of research.

Here, we present some experimental avenues and provide a roadmap to show how eco-evolutionary dynamics can be integrated into experiments to determine in what manner they govern responses to habitat warming and fragmentation across levels of biological organization, from single species studies to food webs. We present five key questions for future work.

**1) What hidden role do cryptic eco-evolutionary dynamics play in enabling populations and communities to respond to warming and fragmentation such that apparently no evolutionary response has occurred?** To disentangle cryptic eco-evolutionary dynamics from purely ecological responses will require further acknowledgment among ecologists of the importance of intraspecific diversity within and among populations (Raffard *et al.*, 2018; Therry *et al.*, 2018). 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 (Kenkel & Matz, 2017; Li *et al.*, 2018b, 2018a; Bay *et al.*, 2018). 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 (Pespeni *et al.*, 2012, 2013).

**2) To what extent does fragmentation allow eco-evolutionary dynamics in response to warming to vary at local scales across a metacommunity, and does this enable populations to retain higher levels of intraspecific diversity?** Uneven effects of warming are possible at local scales and local habitats that differ in selective forces can result in variable selection across a metacommunity. Taken together, fragmentation may have the ability to modulate eco-evolutionary dynamics in response to warming, but we currently do not have sufficient information to determine the extent to which it does so. Careful experimentation should evaluate the scales at which fragmentation and warming can interact such that local populations differ in their exposure to warming. Just as metacommunity dynamics potentially enable communities to retain higher interspecific beta diversity, they may allow populations to retain higher intraspecific beta diversity. This may be especially true when habitats vary in environmental conditions at local scales, favouring some genotypes more than others depending upon local conditions. Intraspecific diversity is likely an important component contributing to a population's resilience in the face of anthropogenic habitat change and is simultaneously expected to be an aspect of biodiversity that is diminished by anthropogenic habitat change, making this question particularly relevant in the face on ongoing warming and fragmentation.

**3) How frequently does fragmentation modulate the eco-evolutionary responses of populations and communities in response to warming and what combination of population and community-level factors will most frequently yield strong eco-evolutionary dynamics in this context?** Here we will benefit from 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 (Yoshida *et al.*, 2003; Harmon *et al.*, 2009b; Scheinin *et al.*, 2015; Pantel, Duvivier, & Meester, 2015; Frickel, Sieber, & Becks, 2016; Schaum *et al.*, 2017). We have generated predictions for how combinations of populations traits and fragmentation will influence the likelihood of strong eco-evolutionary dynamics in Figure 2, but these expectations remain untested. Careful experimental design will also ensure that we can test

667 specific hypotheses regarding the circumstances most likely to result in eco-evolutionary dynamics, as
668 well the conditions under which such dynamics have significant effects. Field-based experiments with
669 local populations that differ in connectivity and temperature will then validate results from
670 experimental populations (Hendry, 2019; see for example, Johansson, Quintela, & Laurila, 2016b). In this
671 way we can begin to detect heritable differences in thermal performance (Kenkel & Matz, 2017) and
672 outcomes of interspecific interactions with implications for functioning in natural populations at longer
673 time scales (Schaum *et al.*, 2018).

674 **4) How does the inclusion of trophic complexity alter predicted evolutionary outcomes in**
675 **warmed and fragmented habitats? In other words, how important are trade-offs between thermal**
676 **traits and traits related to resource acquisition and/or predator defence in governing eco-evolutionary**
677 **dynamics that emerge in response to warming?** Although logic suggests a role for trade-offs in driving
678 eco-evolutionary dynamics, and perhaps especially feedbacks, their importance is nonetheless far from
679 certain between interacting species. We argue that strong fitness trade-offs may be particularly
680 instrumental in driving the evolutionary cascades that enable eco-evolutionary feedbacks and loops to
681 arise, as demonstrated in the scenarios presented in Section 5. Careful hypothesis testing using
682 organisms for which traits and their trade-offs have been described will allow us to determine how eco-
683 evolutionary dynamics and feedbacks in response to warming and fragmentation are affected by the
684 presence or absence of trait trade-offs.

685 **5) What fitness trade-offs are important for eco-evolutionary dynamics in warmed and**
686 **fragmented communities and how does the shape of the trade-off curve, especially those related to**
687 **thermal traits, affect emerging eco-evolutionary dynamics in response to warming?** Traits have the
688 potential to respond and interact non-linearly. In fact, thermal traits described by thermal performance
689 curves, are frequently non-linear. Examples include resource growth rates, attack rates and handling
690 times ultimately determining interaction strength (Amarasekare, 2015; Uszko *et al.*, 2017; Zhang *et al.*,
691 2017; Dee *et al.*, 2020; Uiterwaal & DeLong, 2020; Zhao *et al.*, 2020). This non-linearity implies that
692 extrapolating performance over a temperature range from average performance at a constant
693 temperature can be inaccurate for organisms experiencing variable temperatures (Denny, 2017).
694 Similarly, ecological responses may be non-linearly density-dependent at the metacommunity scale
695 (*e.g.*, the response to predation depends upon both the risks and rewards to movement). Such non-
696 linear responses have the potential to complicate inferences, especially when trade-offs among traits
697 are considered. For this reason, it will be important to consider the importance of non-linear trade-offs
698 for eco-evolutionary dynamics involving responses to climate warming and fragmentation. Initially,

699 experiments must quantify the types of trade-off curves involved in eco-evolutionary responses.
700 Eventually, this information will allow a broader classification of how the shape of trait responses and
701 trade-offs influences eco-evolutionary dynamics.
702

703 **7. CONCLUSIONS**

704

705 (1) In this review, we demonstrated how warming and fragmentation can individually alter
706 selective pressures, as well as the size, structure, and connectivity of populations, interacting species,
707 and more complex communities. We then examined the limited research available studying interactive
708 effects of habitat warming and fragmentation. We used the available evidence to argue that ecological
709 responses to concurrent habitat warming and fragmentation are likely to be mediated and complicated
710 by eco-evolutionary dynamics.
711 (2) We generated four predicted broad outcomes for how combinations of populations traits
712 and fragmentation will influence the likelihood of eco-evolutionary dynamics compared to ecological
713 responses, calling for greater attention on the warming-phenotype matching, fragmentation-induced
714 population structure, and community complexity.
715 (3) We suggest that a new perspective is needed for understanding the simultaneous eco-
716 evolutionary consequences of habitat fragmentation and warming for the dynamics of ecological
717 communities. Such a perspective should be based on trade-offs among traits that emerge in response to
718 warming and habitat fragmentation. Thermal environment affects traits related to metabolism, which
719 are also likely to have trade-offs with other energetically costly ecological traits, such as anti-predator
720 defence or propensity to migrate. Traits can be additionally influenced by the spatial environment
721 experienced by individuals.
722 (4) We have presented this perspective with several example scenarios to generate novel,
723 sometimes counter-intuitive predictions. For example, we predict that eco-evolutionary dynamics in tri-
724 trophic chains could result in increases in abundance of intermediate consumers and even possibly
725 unanticipated extinctions of top consumers, in marked contrast to expectations solely based on
726 ecological dynamics.
727 (5) New research questions emerge that explicitly consider the consequences of eco-
728 evolutionary dynamics in communities responding to fragmentation and habitat warming. Key questions
729 to address include, but are not limited to: When does fragmentation allow for eco-evolutionary

dynamics in response to warming to vary among patches across a metacommunity? How do we disentangle cryptic eco-evolutionary dynamics from purely ecological responses? How does the inclusion of trophic complexity alter predicted evolutionary outcomes from single species studies in warmed and fragmented habitats? These and other questions require urgent investigation to yield more robust predictions for the long-term effects of multiple global change components.

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## 9. AUTHOR CONTRIBUTIONS

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

748 **Figure 1.** Conceptual diagram showing eco-evolutionary dynamics, where changes in the ecology of
749 populations or communities that result in evolutionary changes (**A**), or vice versa (**B**), can occur when
750 ecology and evolution occur at contemporary timescales. Such dynamics are considered eco-
751 evolutionary feedbacks when the secondary evolutionary (as in **A**) or ecological (as in **B**) response then
752 results in an additional reciprocal ecological (**A**) or evolutionary (**B**) response. As our focus is on
753 environmental change, we assume that the dynamics are initiated in response to a change in the
754 environment of a population.

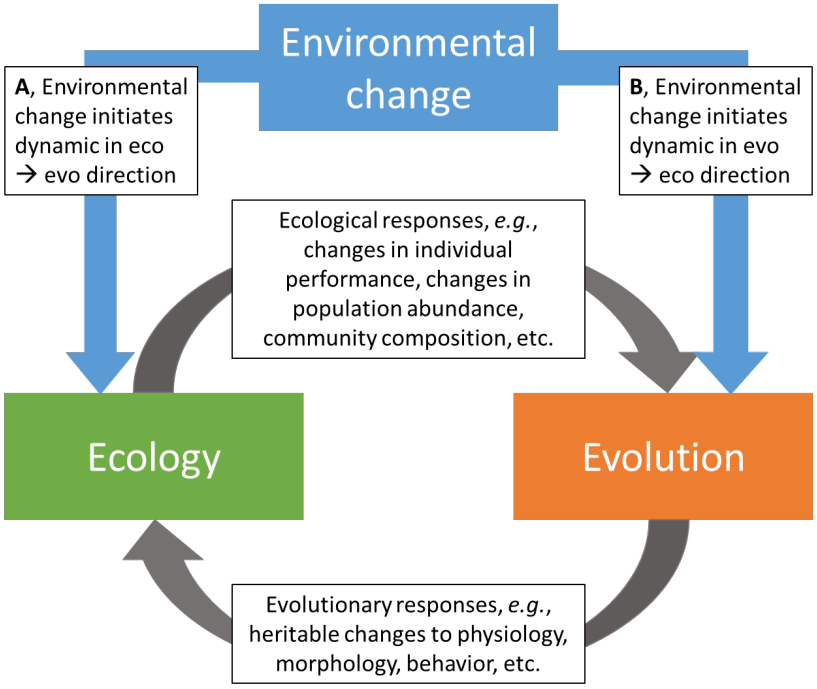


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**Figure 2. Likelihood of eco-evolutionary dynamics in response to warming and fragmentation as a function of species' traits (population size within a patch, genetic diversity, and environment-phenotypic matching), and community complexity.** For simplicity, two eco-evolutionary potential scenarios are presented and separated by the dotted grey line, corresponding to low and high eco-evolutionary potential. Grey-scale shading indicates the relative level from low to high of each factor. Colours on the bars show the expected range of each factor for a given outcome, **A** through **D (**detailed in the legend below the figure). For example, if warming-phenotype matching were high, we would expect very different outcomes depending on the eco-evolutionary potential. For low eco-evolutionary potential, local extinctions (A) or plastic responses and migration (B) are predicted, while for high eco-evolutionary potential, cryptic eco-evolutionary dynamics would be expected.

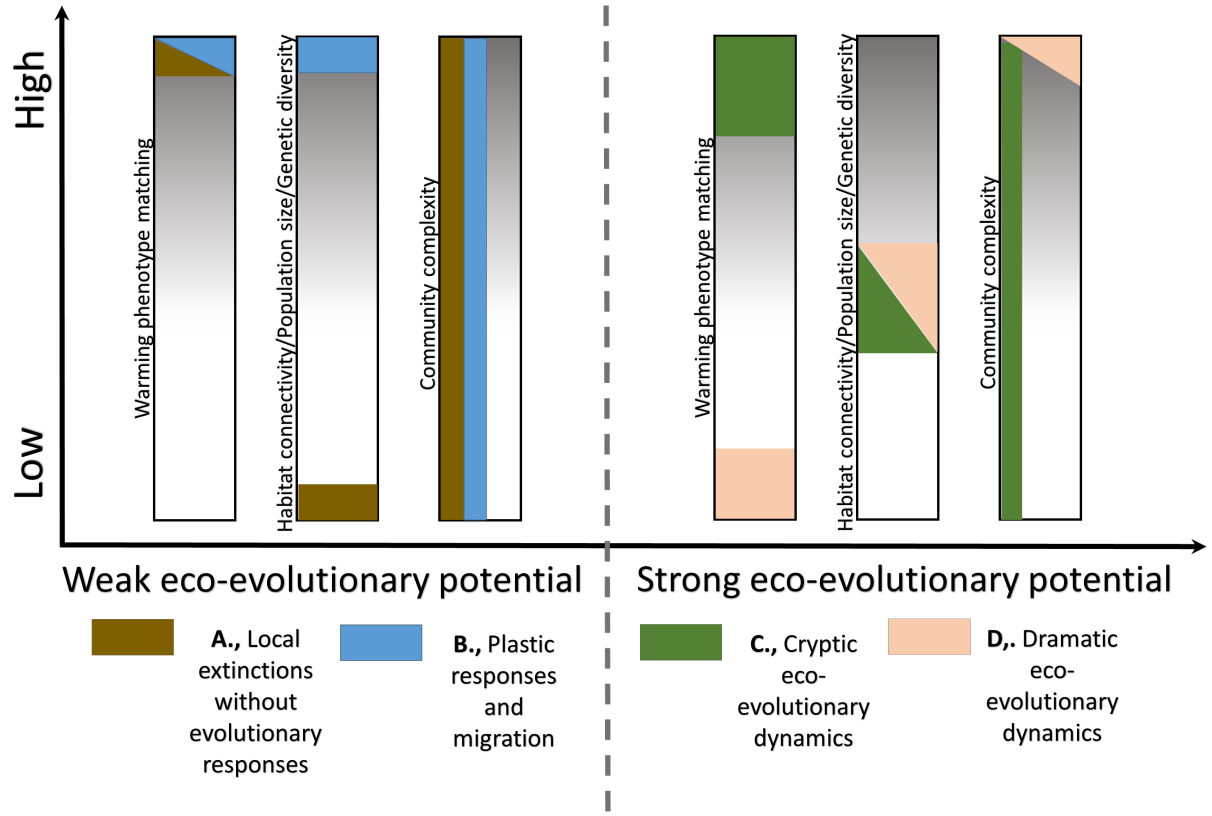


**Figure 3. Relative probability of the importance of ecological or evolutionary response of populations faced with environmental change when the rate of environmental change is scaled to generation time.** For species with very rapid generation times (krill), ecological and evolutionary responses may be similarly important. For species that experience climate change at scales that are intermediate to their generation time (fish), the relative importance of evolutionary response increases. For species with long generation times relative to the rate of climate change (whale), ecological responses (especially plastic responses and migration), may once again become relatively more important than evolutionary response. The position of interacting species (e.g., consumers and resources) in this graph determines the expected outcome and potential mismatches of their responses to environmental change.

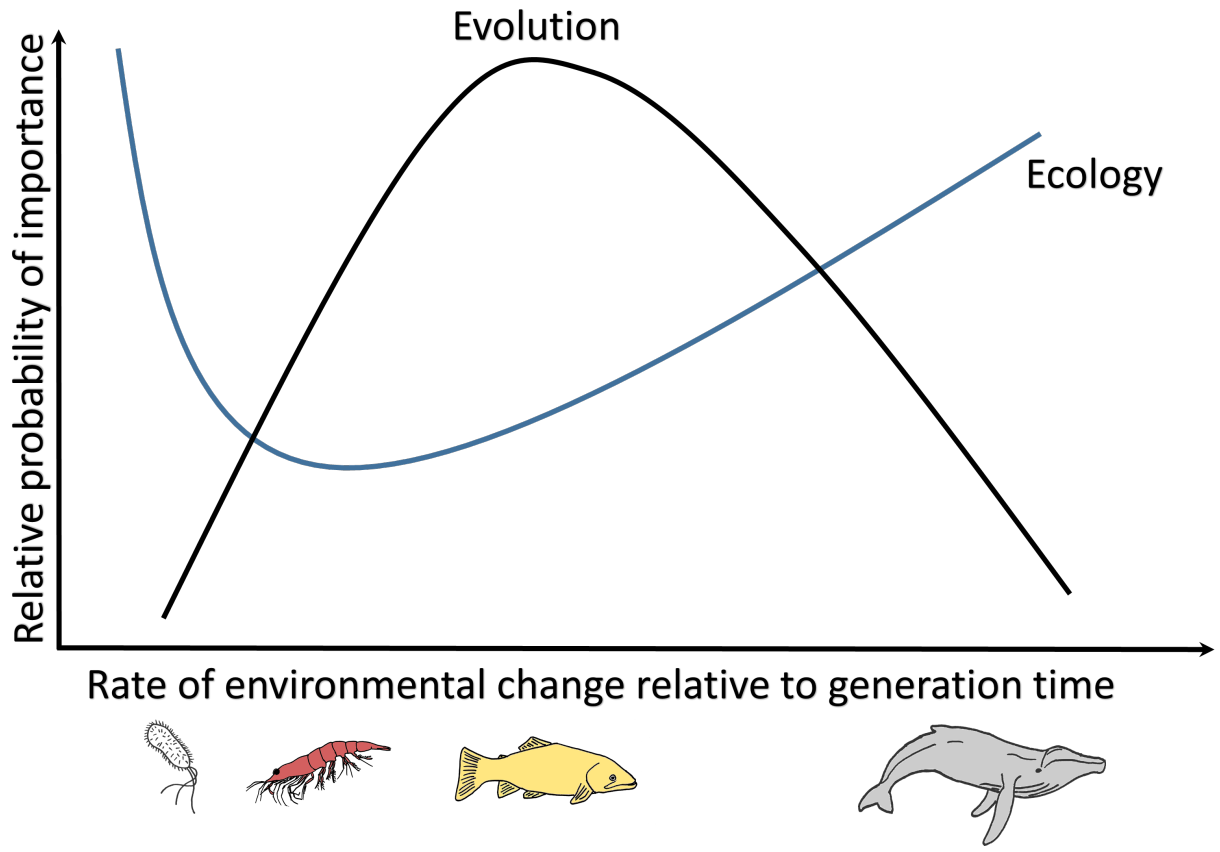


**Figure 4. A**, Conceptual diagram of an ecological trade-off with two fitness components (conceptualized as a linear relationship for simplicity). **B**, Evolution that improves performance in one fitness component results in a concomitant reduction in performance in a second fitness component. Here a starting population (pink fish) evolves increased performance in Fitness component 1 (x-axis trait), at the expense of performance in Fitness component 2 (y-axis trait), resulting in an overall shift along the trade-off curve (red arrow) for the evolved population (blue fish).

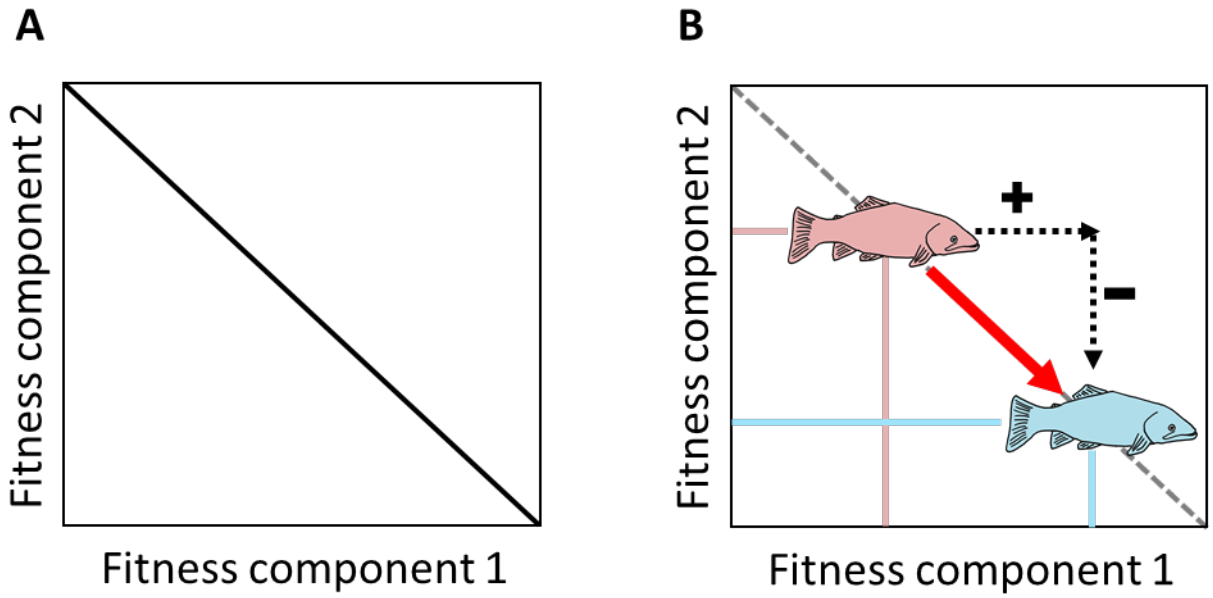


**Figure 5.** Conceptual diagram (top panels) illustrating a hypothetical scenario for an eco-evolutionary feedback (evo→eco→evo) between a consumer species and its resource with evolutionary trade-offs visualized below each conceptual panel. Fragmentation in a habitat experiencing a thermal gradient results in patches that differ in thermal environment (colour of background, with blue as cold, pink as warm). In the conceptual panels, for each species the colour 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 (alga) for increased heat-shock tolerance leading to an increase in its abundance in warm patches due to lower mortality under heat shock. **B,** Increased abundance of the resource results in increased attack by the consumer (daphnid) 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 defence against the predator.

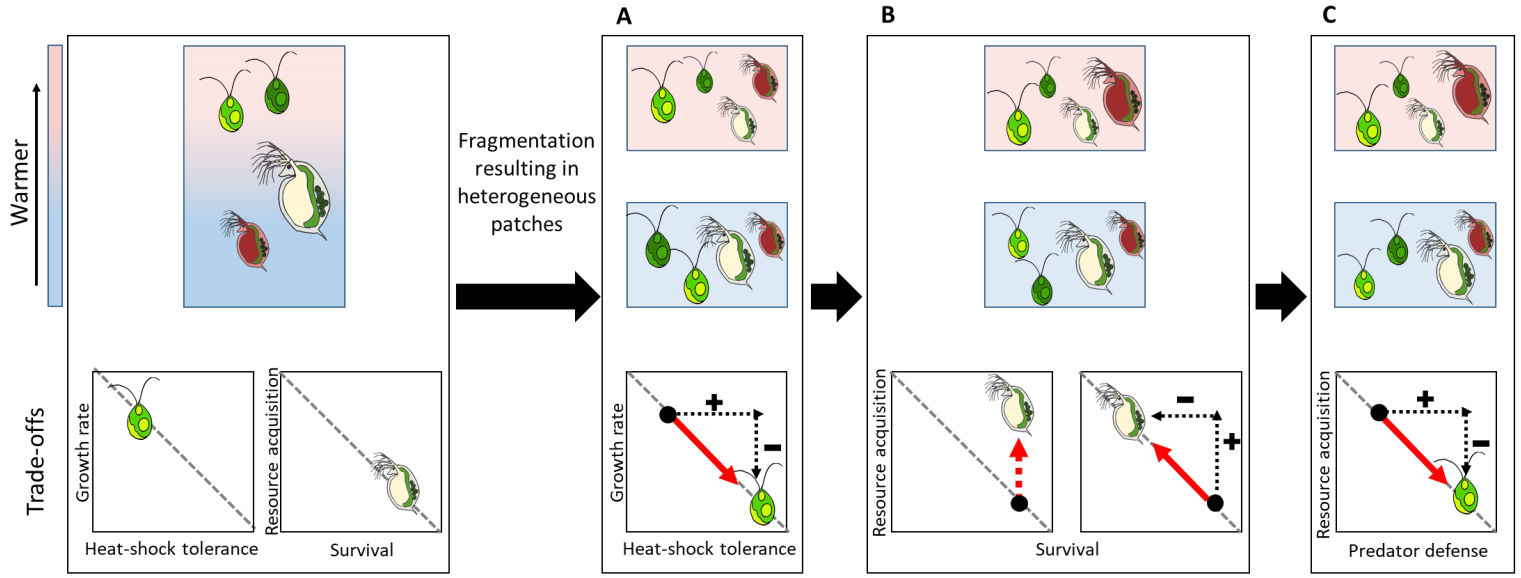
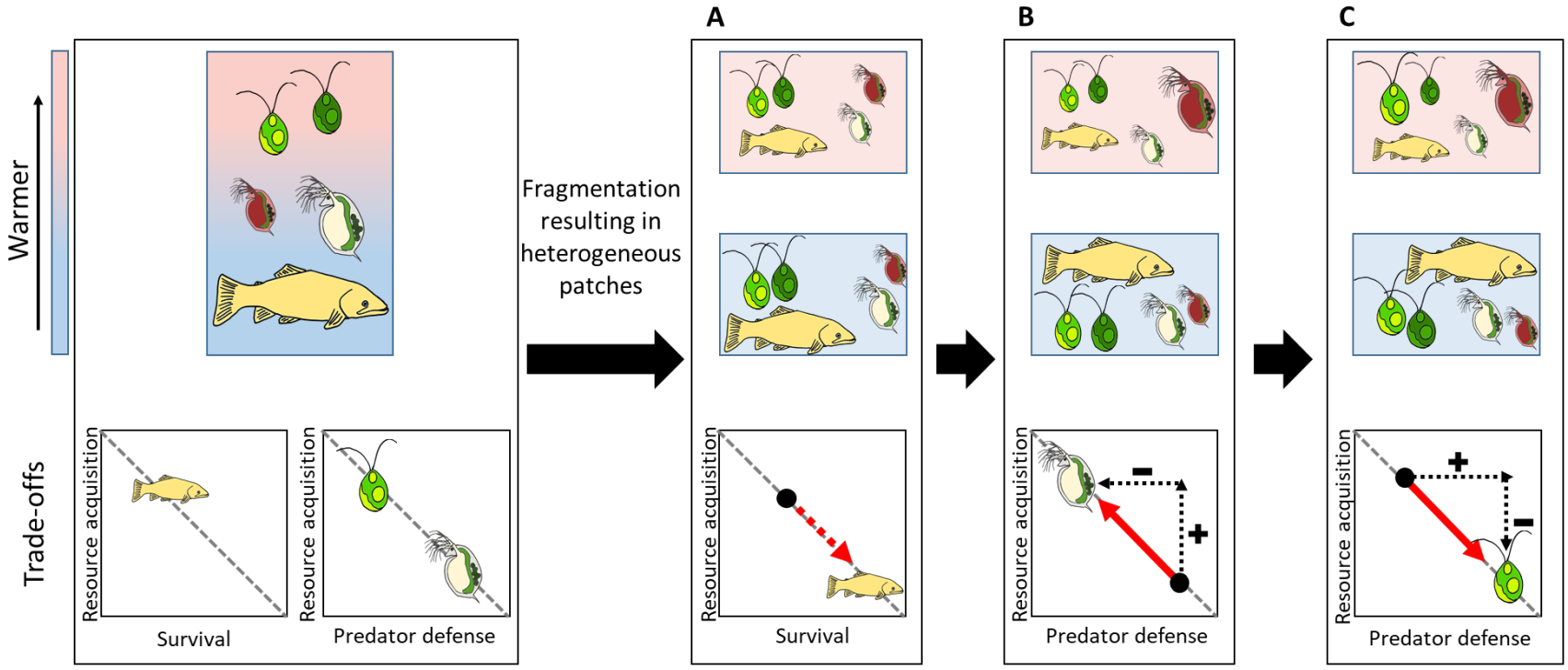


**Figure 6.** Conceptual diagram (top panels) illustrating a hypothetical scenario for an eco-evolutionary feedback (eco→evo→eco) for a tri-trophic food chain with evolutionary trade-offs visualized below each conceptual panel. See the caption for Fig. 5 for a description of the figure legend. **A,** The presence of habitat patches differing in their thermal environment results in a plastic reduction of top consumer (fish) body size (dashed red line on the trade-off curve). **B,** Decreased predation pressure linked to reduced fish body mass then allows the intermediate consumer (daphnid) to evolve increased resource acquisition. **C,** The resource (alga) evolves increased defence in response to higher predation pressure from the intermediate consumer.



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## 11. SUPPORTING INFORMATION

**Index of supplemental figures.**

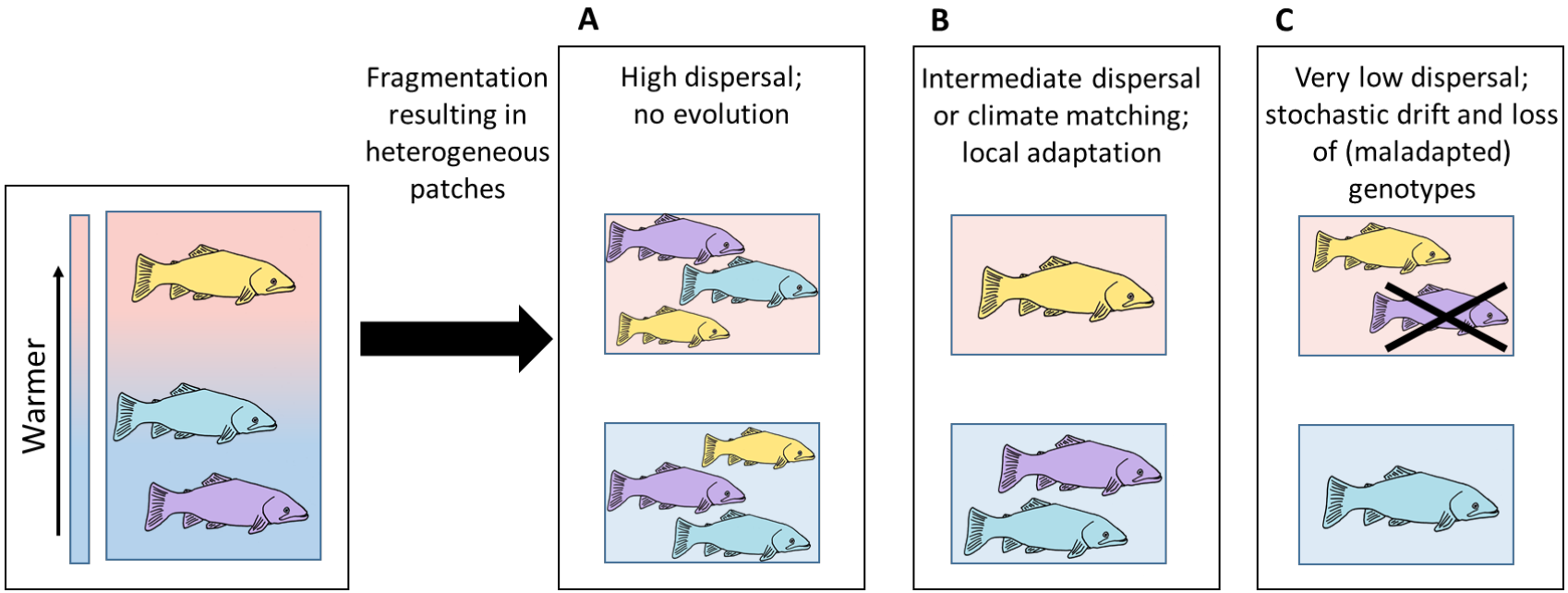
**Supplemental Figure 1.** Conceptual diagram illustrating how local adaptation to heterogeneous conditions among habitat patches after fragmentation depends on the degree and type of dispersal among habitat patches.

**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.

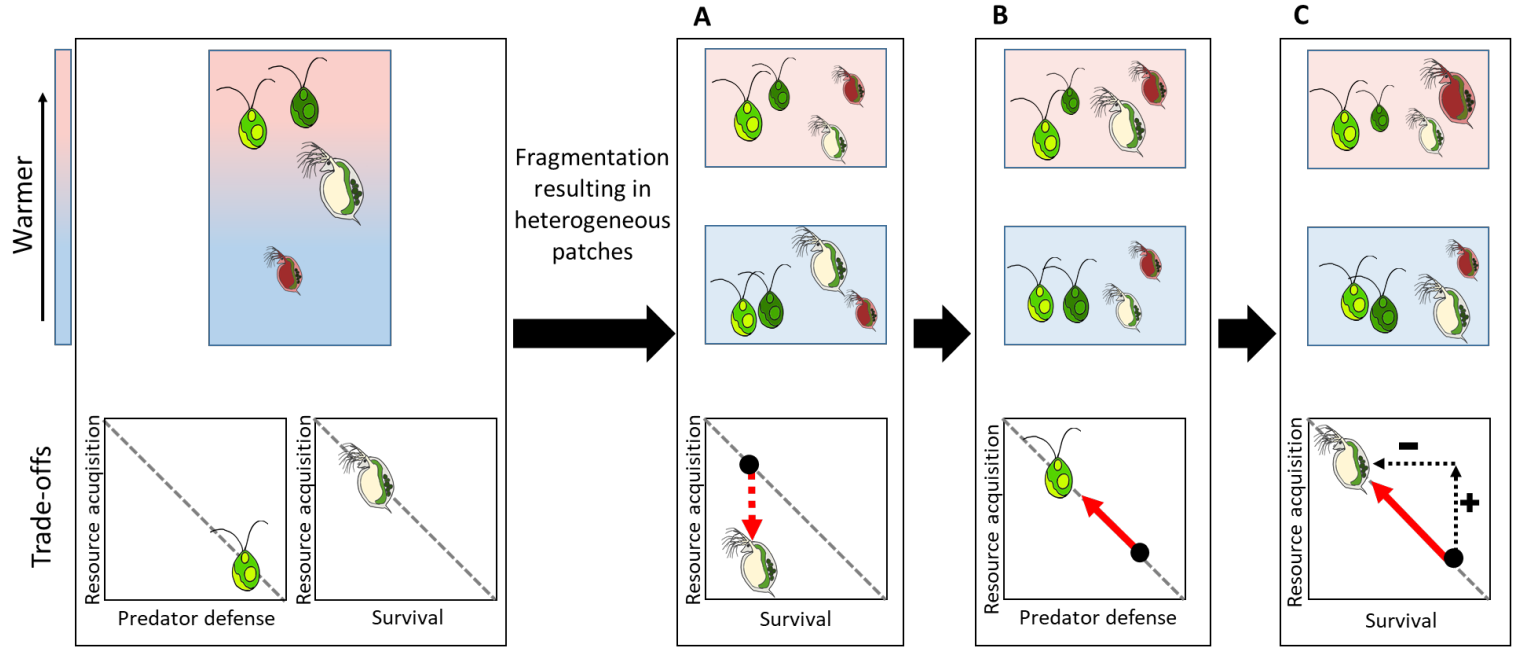
**Supplemental Figure 3.** Conceptual diagram illustrating a hypothetical scenario for an eco-evolutionary feedback (evo→eco→evo) between a consumer species and its resource initiated by evolution of increased attack rate by the consumer, with evolutionary trade-offs visualized below each conceptual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

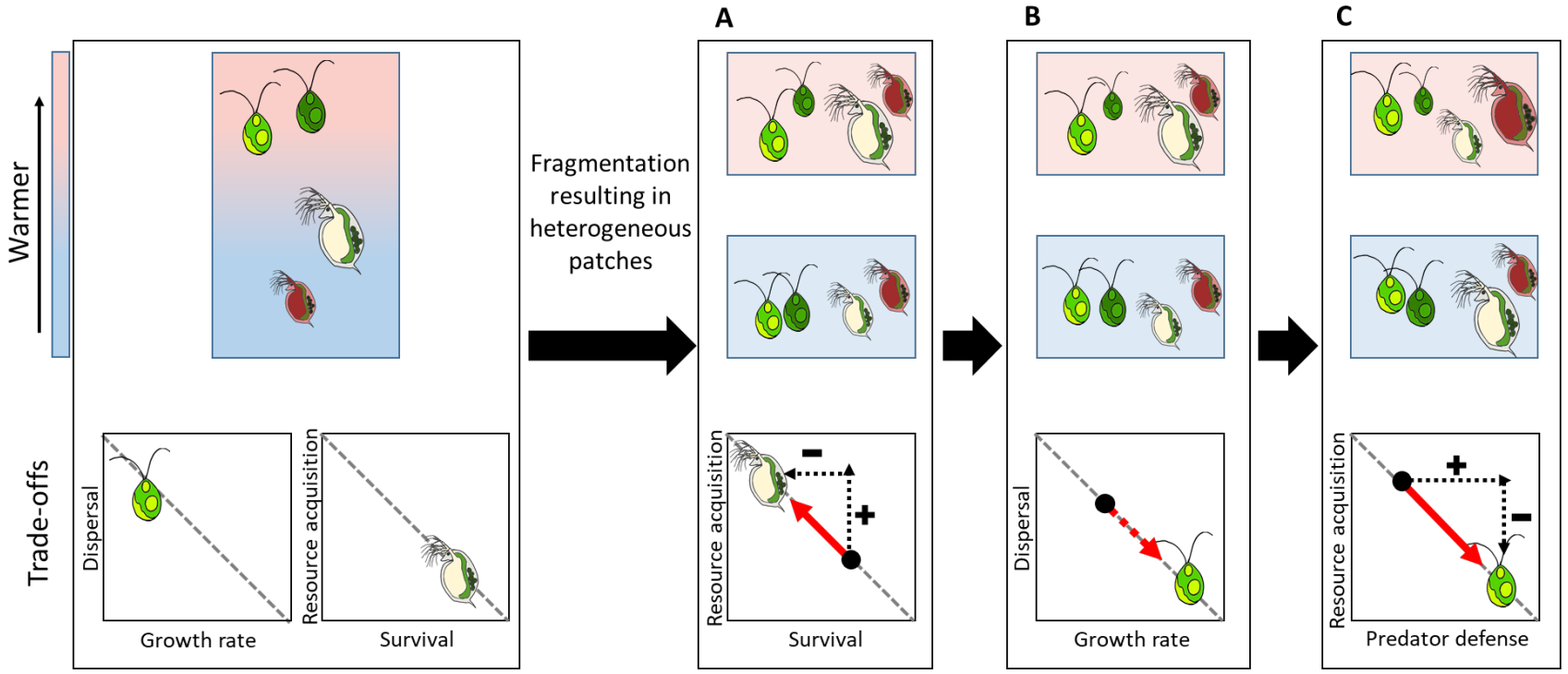
**Supplemental Figure 1A-C.** Conceptual diagram illustrating how local adaptation to heterogeneous conditions among habitat patches after fragmentation depends on the degree and type of dispersal among habitat patches. Fragmentation in a habitat experiencing a thermal gradient results in patches that different in thermal environment (colour of background, with blue as cold, pink as warm). The colour 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 (colour of background, with blue as cold, pink as warm). The colour 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 grey 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 (daphnid) 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 (alga). **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 (daphnid) 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 (alga) 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 defence 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 (alga) evolves increased thermal performance resulting in an increase in its abundance. **B,** The intermediate consumer (daphnid) evolves decreased investment in resource acquisition and increased investment in predator defence. **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.