Published in final edited form as:
Biol Rev Camb Philos Soc. 2021 October 01; 96(5): 1933–1950. doi:10.1111/brv.12732.

Eco-evolutionary consequences of habitat warming and fragmentation in communities

Cara A. Faillace[1,*], **Arnaud Sentis**[1,2], **José M. Montoya**[1]

[1]Theoretical and Experimental Ecology Station, French National Centre of Scientific Research (CNRS), 2 Route du CNRS, Moulis, 09200, France

[2]INRAE, Aix Marseille University, UMR RECOVER, 3275 Route de Cézanne- CS 40061, Aix-en-Provence Cedex 5, 13182, France

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 the one hand, temperature influences traits related to metabolism, such as resource acquisition and activity levels. Such traits are also likely to have trade-offs with other energetically costly traits, like antipredator defences or dispersal. On the other hand, 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 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 (*i*) evolution in thermal performance of a species involved in a consumer−resource interaction, (*ii*) ecological or evolutionary changes to encounter and attack rates of consumers, and (*iii*) 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 with those solely based on ecological dynamics, for example, evolutionary responses 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 better to incorporate the role of

---

[*]Address for correspondence (Tel: +33 5 61 04 05 89; c.faillace@gmail.com).

Author contributions: C.A.F., A.S. and J.M.M. conceived the idea for the manuscript, C.A.F. developed the scenarios, and C.A.F., A.S., and J.M.M. jointly wrote the manuscript.

trade-offs among traits, and the role of eco-evolutionary dynamics in governing responses to warming in fragmented communities.

Keywords

climate change; consumer−resource dynamics; environmental warming; eco-evolutionary dynamics; habitat fragmentation; food webs; metacommunities

I Introduction

Anthropogenic climate change and habitat fragmentation are two of the largest current 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. the scales 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, or 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 timescales 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 and complexity (i.e. the set of species and interactions in which the evolving species is embedded) (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 noanalogue 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*. (2009*a*) 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 warming and fragmentation. 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 (i) evolution in thermal performance of a species involved in a consumer−resource interaction, (ii) ecological or evolutionary changes to encounter and attack rates of consumers, and (iii) 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.

II 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)]. In this review, we focus primarily on ecological and evolutionary responses associated with thermal performance of 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 timescales 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.*, 2016*a*). 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) 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. Johansson & Laurila (2017) 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*b*) 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 understand better the responses 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. For example, in experimental populations of the small forb *Arabidopsis thaliana*, after only six generations, evolving populations spread 200% further in fragmented landscapes than did nonevolving populations. By contrast, for populations evolving in continuous habitats, this difference was reduced to 11% (Williams, Kendall & Levine, 2016). Overall, intermediate levels of dispersal are most likely to promote local adaptation (Legrand *et al.*, 2017) (see online Supporting Information, Fig. S1). 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 impact emigration and immigration rates differently 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 or constitutive 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 is 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−environment correlation such that it can then increase opportunities for local adaptation (Urban *et al.*, 2008) (Fig. 2, outcomes C and D).

III 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 environmental change for a species also depends upon 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; ter-Horst *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 qualitatively to change predictions about thermal adaptation derived from single populations (Angilletta *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, despite the observed bacterial anti-predator evolution. Mismatches in the potential for evolutionary responses 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 changes in one species compared to those in other species, as well as to environmental changes. 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 and complexity, 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 modifications 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.* (2017) showed that when warming reduces predator body size it can increase predator survival at higher temperatures, leading to improved 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 gain versus metabolic loss (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 efficiencies and 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 *et al.*, 2017). Given that secondary and top consumers also frequently have smaller population sizes and longer generation times than their resources, warming may thus exacerbate differences in population sizes across trophic levels resulting in profoundly altered community structures, including losses of consumers, especially at higher trophic levels (Petchey *et al.*, 1999) (Fig. 2, outcome A).

(2) Responses to fragmentation

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

Because fragmentation can increase predation risk during dispersal, it can potentially select for prey phenotypes that increa sesurvival (Bestion *et al*., 2014), for example by increasing anti-predator traits or locomotor speed (Cote *et al*., 2017). 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 favour movement of some phenotypes over others (e.g. Gilliam & Fraser, 2001). In the presence of predators, aphids produce winged offspring that can disperse further away while avoiding terrestrial predators (Dixon & Agarwala, 1999). In addition, different phenotypes can be favoured in predator-free and predator-occupied patches. For example, Trinidadian guppies (*Poecilia reticulata*) evolve differences in life history, behaviour, morphology, and male colour in populations exposed to predators compared to those that are predator-free (Bassar *et al*., 2017). Taken together, because fragmentation can modify both dispersal rates and prey phenotypic traits, it should 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 concentrations 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 meta-community 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. 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* (Urban, 2008).

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). For example, experimental metacommunities containing populations of the host beetle, *Callosobruchus chinensis*, and its pteromalid parasitoid, *Anisopteromalus calanfdrae*, 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 potentially to 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 some 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. By 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 in a complex way with environmental temperature (De Block *et al.*, 2013; Tran *et al.*, 2016). For example, De Block *et al.* (2013) paired populations of the cladoceran *Daphnia magna* and their damselfly predator, *Ischnura elegans* from different latitudes in Europe in all possible combinations. Individuals of *I. elegans* differed in their genetically determined attack rates across latitudinal populations. The survival advantage experienced by southern *D. magna* at 24°C and northern *D. magna* at 20°C disappeared when they were paired respectively with southern *I. elegans* and northern *I. elegans*. These results show that local adaptation in both predators and prey can be important in eco-evolutionary dynamics. The degree of climate phenotype-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 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) and 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.

IV The Importance Of Fitness Tradeoffs In Eco-Evolutionary Dynamics

In Sections II and III 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 (*i*) be context dependent, modulated by resource availability, predator presence, and competitive interactions, and (*ii*) influence the distribution of phenotypes within populations by favouring those that are heat-resistant and maximise the cost−benefit balance of dispersal. This highlights the importance of intraspecific trait variation, fitness tradeoffs, and interspecific interactions to understand better the influence of warming and fragmentation on eco-evolutionary dynamics. In this section, we focus on the role of fitness tradeoffs 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. 3), such that selection on one trait is expected to alter performance in another trait or fitness attribute. In other words, ecological trade-offs occur when higher performance in one fitness attribute comes at the expense of performance in a second (Fig. 3). 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 thus has the potential to 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 coevolution 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 *versus* 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 versus heat-shock tolerance in pea aphids (*Acyrthosiphon pisum*) (Harmon, Moran & Ives, 2009a), and survival at extreme temperatures of *Tigriopus californicus* copepods versus their competitive ability (Willett, 2010). Changes in these trade-offs can then lead to altered consumer−resource dynamics (an ecological effect) (Gardner *et al.*, 2011; Sheridan & Bickford, 2011; Yvon-Durocher *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.

V Scenarios For Eco-Evolutionary Dynamics In Warmed And Fragmented Communities

We now provide several illustrative scenarios 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 responses to selection. These scenarios provide examples of 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 an 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. 4A). One result of the increased availability of the resource in cool patches could be an 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 [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) (Fig. 4B). 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 so doing, it could increase opportunities for additional local adaptation of the resource (Loeuille & Leibold, 2008), for instance, to increase defence against the consumer (evo) (Fig. 4C).

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) (Fig. S2). 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 with fragmentation than in an unfragmented community.

And thirdly, because the evidence with regard to the effects of warming on attack rate remains inconclusive, especially at evolutionary timescales, 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) (Fig. S3). 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) (Fig. S3).

(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 and increased investment in defence. 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) (Fig. S4).

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. 5A). 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. 5B). 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. 5C). 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.

VI 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 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 complexity 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; Bay *et al.*, 2018; Li *et al.*, 2018a,b). 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. 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 to understand the effects for interspecific interactions and community dynamics. Manipulative experiments using microcosms and mesocosms provide the necessary level of control to attribute unambiguously any observed evolutionary change to each factor and to evaluate initially the potential consequences of eco-evolutionary dynamics (Yoshida *et al.*, 2003; Harmon *et al.*, 2009b; Pantel, Duvivier & Meester, 2015; Scheinin *et al.*, 2015; Frickel, Sieber & Becks, 2016; Schaum *et al.*, 2017). We have generated predictions for how combinations of population traits and fragmentation will influence the likelihood of strong eco-evolutionary dynamics in Fig. 2, but these expectations remain untested. 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 as the conditions under which such dynamics have significant effects. Field-based experiments with local populations that differ in connectivity and temperature will then validate results from experimental populations (Hendry, 2019; see for example, Johansson, Quintela & Laurila, 2016b). In this way we can begin to detect heritable differences in thermal performance (Kenkel & Matz, 2017) and outcomes of interspecific interactions with implications for functioning in natural populations at longer timescales (Schaum *et al*., 2018).

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

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

VII Conclusions

(1) In this review, we demonstrated how warming and fragmentation can individually alter selective pressures, as well as the size, structure, and connectivity of populations, interacting species, and more complex communities. We then examined the limited research available studying interactive effects of habitat warming and fragmentation. We used the available evidence to argue that ecological responses to concurrent habitat warming and fragmentation are likely to be mediated and complicated by eco-evolutionary dynamics.

(2) We generated four predicted broad outcomes for how combinations of population traits and fragmentation will influence the likelihood of eco-evolutionary dynamics compared to ecological responses, calling for greater attention to warming−phenotype matching, fragmentation-induced population structure, and community complexity.

(3) We suggest that a new perspective is needed to understand the simultaneous eco-evolutionary consequences of habitat fragmentation and warming for the dynamics of ecological communities. Such a perspective should be based on trade-offs among traits that emerge in response to warming and habitat fragmentation. Thermal environment affects traits related to metabolism, which are also likely to have trade-offs with other energetically costly ecological traits, such as antipredator defence or propensity to migrate. Traits additionally can be influenced by the spatial environment experienced by individuals.

(4) We illustrated this perspective with several example scenarios to generate novel, sometimes counter-intuitive predictions. For example, we predict that eco-evolutionary dynamics in tri-trophic chains could result in increases in abundance of intermediate consumers and even possibly unanticipated extinctions of top consumers, in marked contrast to expectations solely based on ecological dynamics.

(5) New research questions emerge that explicitly consider the consequences of eco-evolutionary dynamics in communities responding to fragmentation and habitat warming. Key questions 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.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements And Author Contributions

This research is supported by the French ANR through LabEx TULIP (ANR-10-LABX-41) and by the FRAG-CLIM Consolidator Grant, funded by the European Research Council under the European Union’s Horizon 2020 research and innovation programme (Grant Agreement Number 726176). We thank Simon Blanchet, Julien Cote, members of the Morin laboratory, and two anonymous referees for comments.

References

Abram PK, Boivin G, Moiroux J, Brodeur J. Behavioural effects of temperature on ectothermic animals: unifying thermal physiology and behavioural plasticity. Biological Reviews. 2017; 92: 1859–1876. [PubMed: 28980433]

Amarasekare P. Effects of temperature on consumer-resource interactions. Journal of Animal Ecology. 2015; 84: 665–679. [PubMed: 25412342]

Angilletta MJ Jr, Bennett AF, Guderley H, Navas CA, Seebacher F, Wilson RS. Coadaptation: a unifying principle in evolutionary thermal biology. Physiological and Biochemical Zoology. 2006; 79: 282–294. [PubMed: 16555188]

Arim M, Abades SR, Laufer G, Loureiro M, Marquet PA. Food web structure and body size: trophic position and resource acquisition. Oikos. 2010; 119: 147–153.

Bakker J, van Rijswijk MEC, Weissing FJ, Bijlsma R. Consequences of fragmentation for the ability to adapt to novel environments in experimental *Drosophila* metapopulations. Conservation Genetics. 2010; 11: 435–448.

Barraclough TG. How do species interactions affect evolutionary dynamics across whole communities? Annual Review of Ecology, Evolution, and Systematics. 2015; 46: 25–48.

Bassar RD, Bryan BL, Marshall MC, Pringle CM, Reznick DN, Travis J. Local adaptation of fish consumers alters primary production through changes in algal community composition and diversity. Oikos. 2017; 126: 594–603.

Bassar RD, Ferriere R, López-Sepuicre A, Marshall MC, Travis J, Pringle CM, Reznick DN. Direct and indirect ecosystem effects of evolutionary adaptation in the Trinidadian guppy (*Poecilia reticulata*). The American Naturalist. 2012; 180: 167–185.

Bay RA, Harrigan RJ, Le Underwood V, Gibbs HL, Smith TB, Ruegg K. Genomic signals of selection predict climate-driven population declines in a migratory bird. Science. 2018; 359: 83–86. [PubMed: 29302012]

Becks L, Ellner SP, Jones LE, Hairston NG Jr. Reduction of adaptive genetic diversity radically alters eco-evolutionary community dynamics. Ecology Letters. 2010; 13: 989–997. [PubMed: 20528898]

Becks L, Ellner SP, Jones LE, Hairston NG. The functional genomics of an eco-evolutionary feedback loop: linking gene expression, trait evolution, and community dynamics. Ecology Letters. 2012; 15: 492–501. [PubMed: 22417636]

Bestion E, Clobert J, Cote J. Dispersal response to climate change: scaling down to intraspecific variation. Ecology Letters. 2015; 18: 1226–1233.

Bestion E, Garcia-Carreras B, Schaum CE, Pawar S, Yvon-Durocher G. Metabolic traits predict the effects of warming on phytoplankton competition. Ecology Letters. 2018; 21: 655–664. [PubMed: 29575658]

Bestion E, Teyssier A, Aubret F, Clobert J, Cote J. Maternal exposure to predator scents: offspring phenotypic adjustment and dispersal. Proceedings of the Royal Society B: Biological Sciences. 2014; 281 20140701

Binzer A, Guill C, Brose U, Rall BC. The dynamics of food chains under climate change and nutrient enrichment. Philosophical Transactions of the Royal Society B: Biological Sciences. 2012; 367: 2935–2944.

Blanquart F, Kaltz O, Nuismer SL, Gandon S. A practical guide to measuring local adaptation. Ecology Letters. 2013; 16: 1195–1205. [PubMed: 23848550]

Bonsall MB, French DR, Hassell MP. Metapopulation structures affect persistence of predator-prey interactions. Journal of Animal Ecology. 2002; 71: 1075–1084.

Boukal DS, Bideault A, Carreira BM, Sentis A. Species interactions under climate change: connecting kinetic effects of temperature on individuals to community dynamics. Current Opinion in Insect Science. 2019; 35: 88–95. [PubMed: 31445412]

Branco P, Egas M, Elser JJ, Huisman J. Eco-evolutionary dynamics of ecological stoichiometry in plankton communities. The American Naturalist. 2018; 192: E1–E20.

Buckley J, Bridle JR. Loss of adaptive variation during evolutionary responses to climate change. Ecology Letters. 2014; 17: 1316–1325. [PubMed: 25104062]

Cadotte MW, Mai DV, Jantz S, Collins MD, Keele M, Drake JA. On testing the competition-colonization trade-off in a multispecies assemblage. The American Naturalist. 2006; 168: 704–709.

Cairns J, Moerman F, Fronhofer EA, Altermatt F, Hiltunen T. Evolution in interacting species alters predator life-history traits, behaviour and morphology in experimental microbial communities. Proceedings of the Royal Society B: Biological Sciences. 2020; 287 20200652

Cobben MMP, Verboom J, Opdam PFM, Hoekstra RF, Jochem R, Smulders MJM. Wrong place, wrong time: climate change-induced range shift across fragmented habitat causes maladaptation and declined population size in a modelled bird species. Global Change Biology. 2012; 18: 2419–2428.

Collins S, Bell G. Phenotypic consequences of 1,000 generations of selection at elevated CO2 in a green alga. Nature. 2004; 431: 566–569. [PubMed: 15457260]

Collins S, Bell G. Evolution of natural algal populations at elevated CO2. Ecology Letters. 2006; 9: 129–135. [PubMed: 16958877]

Comte L, Hugueny B, Grenouillet G. Climate interacts with anthropogenic drivers to determine extirpation dynamics. Ecography. 2016; 39: 1008–1016.

Cooper JK, Li J, Montagnes DJS. Intermediate fragmentation per se provides stable predator-prey metapopulation dynamics. Ecology Letters. 2012; 15: 856–863. [PubMed: 22639876]

Cooper VS, Bennett AF, Lenski RE. Evolution of thermal dependence of growth rate of Escherichia coli populations during 20,000 generations in a constant environment. Evolution. 2001; 55: 889–896. [PubMed: 11430649]

Cote J, Bestion E, Jacob S, Travis J, Legrand D, Baguette M. Evolution of dispersal strategies and dispersal syndromes in fragmented landscapes. Ecography. 2017; 40: 56–73.

Crooks KR, Soule' ME. Mesopredator release and avifaunal extinctions in a fragmented system. Nature. 1999; 400: 563–566.

Daufresne M, Lengfellner K, Sommer U. Global warming benefits the small in aquatic ecosystems. Proceedings of the National Academy of Sciences of the United States of America. 2009; 106: 12788–12793. [PubMed: 19620720]

de Block M, Pauwels K, van den Broeck M, de Meester L, Stoks R. Local genetic adaptation generates latitude-specific effects of warming on predator-prey interactions. Global Change Biology. 2013; 19: 689–696. [PubMed: 23504827]

de Mazancourt C, Johnson E, Barraclough TG. Biodiversity inhibits species' evolutionary responses to changing environments. Ecology Letters. 2008; 11: 380–388. [PubMed: 18248449]

de Meester L, Brans KI, Govaert L, Souffreau C, Mukherjee S, Vanvelk H, Korzeniowski K, Kilsdonk L, Decaestecker E, Stoks R, Urban MC. Analysing eco-evolutionary dynamics—the challenging complexity of the real world. Functional Ecology. 2019; 33: 43–59.

de Meester L, van Doorslaer W, Geerts A, Orsini L, Stoks R. Thermal genetic adaptation in the water flea Daphnia and its impact: an evolving metacommunity approach. Integrative and Comparative Biology. 2011; 51: 703–718. [PubMed: 21775388]

Dee LE, Okamtoto D, Gardmark A, Montoya JM, Miller SJ. Temperature variability alters the stability and thresholds for collapse of interacting species. Philosophical Transactions of the Royal Society B: Biological Sciences. 2020; 375 20190457

Denny M. The fallacy of the average: on the ubiquity, utility and continuing novelty of Jensen's inequality. The Journal of Experimental Biology. 2017; 220: 139–146. [PubMed: 28100801]

Dinh Van K, Janssens L, Debecker S, de Jonge M, Lambret P, Nilsson-Örtman V, Bervoets L, Stoks R. Susceptibility to a metal under global warming is shaped by thermal adaptation along a latitudinal gradient. Global Change Biology. 2013; 19: 2625–2633. [PubMed: 23640735]

Dinh Van K, Janssens L, Debecker S, Stoks R. Temperature-and latitude-specific individual growth rates shape the vulnerability of damselfly larvae to a widespread pesticide. Journal of Applied Ecology. 2014; 51: 919–928.

Dirzo R, Young HS, Galetti M, Ceballos G, Isaac NJB, Collen B. Defaunation in the Anthropocene. Science. 2014; 345: 401–406. [PubMed: 25061202]

Dixon AFG, Agarwala BK. Ladybird-induced life-history changes in aphids. Proceedings of the Royal Society B: Biological Sciences. 1999; 266: 1549–1553.

Dixon AFG, Horth S, Kindlmann P. Migration in insects: cost and strategies. The Journal of Animal Ecology. 1993; 62: 182–190.

Eggleston DB, Lipcius RN, Hines AH. Density-dependent predation by blue crabs upon infaunal clam species with contrasting distribution and abundance patterns. Marine Ecology Progress Series. 1992; 85: 55–68.

Etterson JR, Shaw RG. Constraint to adaptive evolution in response to global warming. Science. 2001; 294: 151–154. [PubMed: 11588260]

Faillace CA, Morin PJ. Evolution alters the consequences of invasions in experimental communities. Nature Ecology and Evolution. 2016; 1 0013

Feeley KJ, Rehm EM. Amazon’s vulnerability to climate change heightened by deforestation and man-made dispersal barriers. Global Change Biology. 2012; 18: 3606–3614.

Frickel J, Sieber M, Becks L. Eco-evolutionary dynamics in a coevolving host-virus system. Ecology Letters. 2016; 19: 450–459. [PubMed: 26898162]

Frickel J, Theodosiou L, Becks L. Rapid evolution of hosts begets species diversity at the cost of intraspecific diversity. Proceedings of the National Academy of Sciences of the United States of America. 2017; 114 201701845

Fronhofer EA, Legrand D, Altermatt F, Ansart A, Blanchet S, Bonte D, Chaine A, Dahirel M, de Laender F, de Raedt J, di Gesu L, et al. Bottom-up and top-down control of dispersal across major organismal groups. Nature Ecology and Evolution. 2018; 2: 1859–1863. [PubMed: 30397298]

Fussmann KE, Schwarzmüller F, Brose U, Jousset A, Rall BC. Ecological stability in response to warming. Nature Climate Change. 2014; 4: 206–210.

Gandon S, Nuismer SL. Interactions between genetic drift, gene flow, and selection mosaics drive parasite local adaptation. The American Naturalist. 2009; 173: 212–224.

Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R. Declining body size: a third universal response to warming? Trends in Ecology and Evolution. 2011; 26: 285–291. [PubMed: 21470708]

Geerts AN, Vanoverbeke J, Vanschoenwinkel B, van Doorslaer W, Feuchtmayr H, Atkinson D, Moss B, Davidson TA, Sayer CD, de Meester L. Rapid evolution of thermal tolerance in the water flea Daphnia. Nature Climate Change. 2015; 5: 665–668.

Gilliam JF, Fraser DF. Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. Ecology. 2001; 82: 258–273.

Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD. A framework for community interactions under climate change. Trends in Ecology and Evolution. 2010; 25: 325–331. [PubMed: 20392517]

Gomulkiewicz R, Thompson JN, Holt RD, Nuismer SL, Hochberg ME. Hot spots, cold spots, and the geographic mosaic theory of coevolution. American Naturalist. 2000; 156: 156–174.

Govaert L, Fronhofer EA, Lion S, Eizaguirre C, Bonte D, Egas M, Hendry AP, de Brito Martins A, Meliáan CJ, Raeymaekers JAM, Ratikainen II, et al. Eco-evolutionary feedbacks—theoretical models and perspectives. Functional Ecology. 2019; 33: 13–30.

Grainger TN, Gilbert B. Multi-scale responses to warming in an experimental insect metacommunity. Global Change Biology. 2017; 23: 5151–5163. [PubMed: 28556493]

Hague MTJ, Routman EJ. Does population size affect genetic diversity? A test with sympatric lizard species. Heredity. 2016; 116: 92–98. [PubMed: 26306730]

Hanski I. Eco-evolutionary dynamics in a changing world. Annals of the New York Academy of Sciences. 2012; 1249: 1–17. [PubMed: 22335524]

Harmon JP, Moran NA, Ives AR. Species response to environmental change: impacts of food web interactions and evolution. Science. 2009a; 323: 1347–1350. [PubMed: 19265021]

Harmon LJ, Matthews B, Des Roches S, Chase JM, Shurin JB, Schluter D. Evolutionary diversification in stickleback affects ecosystem functioning. Nature. 2009b; 458: 1167–1170. [PubMed: 19339968]

Hauzy C, Hulot FD, Gins A, Loreau M. Intra-and interspecific density-dependent dispersal in an aquatic prey-predator system. Journal of Animal Ecology. 2007; 76: 552–558. [PubMed: 17439471]

Hauzy C, Tully T, Spataro T, Paul G, Arditi R. Spatial heterogeneity and functional response: an experiment in microcosms with varying obstacle densities. Oecologia. 2010; 163: 625–636. [PubMed: 20213153]

Hendry AP. A critique for eco-evolutionary dynamics. Functional Ecology. 2019; 33: 84–94.

Herrando-Pérez S, Monasterio C, Beukema W, Gomes V, Ferri-Yanez F, Vieites DR, Buckiey LB, Araújo MB. Heat tolerance is more variable than cold tolerance across species of Iberian lizards after controlling for intraspecific variation. Functional Ecology. 2020; 34: 631–645.

Higgins JK, MacLean HJ, Buckley LB, Kingsolver JG. Geographic differences and microevolutionary changes in thermal sensitivity of butterfly larvae in response to climate. Functional Ecology. 2014; 28: 982–989.

Hiltunen T, Cairns J, Frickel J, Jalasvuori M, Laakso J, Kaitala V, Kunzel S, Karakoc E, Becks L. Dual-stressor selection alters eco-evolutionary dynamics in experimental communities. Nature Ecology and Evolution. 2018; 2: 1974–1981. [PubMed: 30455439]

Hoffmann AA, Sgró CM. Climate change and evolutionary adaptation. Nature. 2011; 470: 479–485. [PubMed: 21350480]

Hossie TJ, Murray DL. You can’t run but you can hide: refuge use in frog tadpoles elicits density-dependent predation by dragonfly larvae. Oecologia. 2010; 163: 395–404. [PubMed: 20130916]

Iles AC. Toward predicting community-level effects of climate: relative temperature scaling of metabolic and ingestion rates. Ecology. 2014; 95: 2657–2668.

Jacob S, Legrand D, Chaine AS, Bonte D, Schtickzelle N, Huet M, Clobert J. Gene flow favours local adaptation under habitat choice in ciliate microcosms. Nature Ecology and Evolution. 2017; 1: 1407–1409. [PubMed: 29046550]

Janssens L, Verberk W, Stoks R. A widespread morphological antipredator mechanism reduces the sensitivity to pesticides and increases the susceptibility to warming. Science of the Total Environment. 2018; 626: 1230–1235. [PubMed: 29898530]

Johansson MP, Ermoid F, Kristjánsson BK, Lauriia A. Divergence of gastropod life history in contrasting thermal environments in a geothermal lake. Journal of Evolutionary Biology. 2016a; 29: 2043–2053. [PubMed: 27364364]

Johansson MP, Laurila A. Maximum thermal tolerance trades off with chronic tolerance of high temperature in contrasting thermal populations of Radix balthica. Ecology and Evolution. 2017; 7: 3149–3156. [PubMed: 28480014]

Johansson MP, Quintela M, Laurila A. Genetic divergence and isolation by thermal environment in geothermal populations of an aquatic invertebrate. Journal of Evolutionary Biology. 2016b; 29: 1701–1712. [PubMed: 27208484]

Joubert D, Bijlsma R. Interplay between habitat fragmentation and climate change: inbreeding affects the response to thermal stress in Drosophila melanogaster. Climate Research. 2010; 43: 57–70.

Kaitala V, Hiltunen T, Becks L, Scheuerl T. Co-evolution as an important component explaining microbial predator-prey interaction. Journal of Theoretical Biology. 2020; 486 110095 [PubMed: 31783060]

Kenkel CD, Matz MV. Gene expression plasticity as a mechanism of coral adaptation to a variable environment. Nature Ecology and Evolution. 2017; 1 0014

Kingsolver JG, Buckley LB. Climate variability slows evolutionary responses of Colias butter flies to recent climate change. Proceedings of the Royal Society B: Biological Sciences. 2015; 282: 1–8.

Kinnison MT, Hairston NG. Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. Functional Ecology. 2007; 21: 444–454.

Kinnison MT, Hairston NG, Hendry AP. Cryptic eco-evolutionary dynamics. Annals of the New York Academy of Sciences. 2015; 1360: 120–144. [PubMed: 26619300]

Kratina P, Greig HS, Thompson PL, Carvalho-Pereira TSA, Shurin JB. Warming modifies trophic cascades and eutrophication in experimental freshwater communities. Ecology. 2012; 93: 1421–1430. [PubMed: 22834382]

Lang B, Rall BC, Brose U. Warming effects on consumption and intraspecific interference competition depend on predator metabolism. Journal of Animal Ecology. 2012; 81: 516–523. [PubMed: 22112157]

Latimer CE, Cooper SJ, Karasov WH, Zuckerberg B. Does habitat fragmentation promote climate-resilient phenotypes? Oikos. 2018; 127: 1069–1080.

Laurent E, Schtickzelle N, Jacob S. Fragmentation mediates thermal habitat choice in ciliate microcosms. Proceedings of the Royal Society B: Biological Sciences. 2020; 287 20192818

Legrand D, Cote J, Fronhofer EA, Holt RD, Ronce O, Schtickzelle N, Travis JMJ, Clobert J. Eco-evolutionary dynamics in fragmented landscapes. Ecography. 2017; 40: 9–25.

Li A, Li L, Wang W, Song K, Zhang G. Transcriptomics and fitness data reveal adaptive plasticity of thermal tolerance in oysters inhabiting different tidal zones. Frontiers in Physiology. 2018a; 9: 825. [PubMed: 30210351]

Li L, Li A, Song K, Meng J, Guo X, Li S, Li C, de Wit P, Que H, Wu F, Wang W, et al. Divergence and plasticity shape adaptive potential of the Pacific oyster. Nature Ecology and Evolution. 2018b; 2: 1751–1760. [PubMed: 30250157]

Lind EM, Borer E, Seabloom E, Adler P, Bakker JD, Blumenthal DM, Crawley M, Davies K, Firn J, Gruner DS, Stanley Harpole W, et al. Life-history constraints in grassland plant species: a growthdefence trade-off is the norm. Ecology Letters. 2013; 16: 513–521. [PubMed: 23347060]

Lindsey HA, Gallie J, Taylor S, Kerr B. Evolutionary rescue from extinction is contingent on a lower rate of environmental change. Nature. 2013; 494: 463–467. [PubMed: 23395960]

Loeuille N, Leibold MA. Evolution in metacommunities: on the relative importance of species sorting and monopolization in structuring communities. The American Naturalist. 2008; 171: 788–799.

Logan ML, Cox RM, Calsbeek R. Natural selection on thermal performance in a novel thermal environment. Proceedings of the National Academy of Sciences of the United States of America. 2014; 111: 14165–14169. [PubMed: 25225361]

Martin GS, van Dyck G-H, San Martin G, van Dyck G-H. Ecotypic differentiation between urban and rural populations of the grasshopper Chorthippus brunneus relative to climate and habitat fragmentation. Oecologia. 2012; 169: 125–133. [PubMed: 22108853]

McCauley SJ, Brodin T, Hammond J. Foraging rates of larval dragonfly colonists are positively related to habitat isolation: results from a landscape-level experiment. The American Naturalist. 2010; 175: E66–E73.

McWilliams C, Lurgi M, Montoya JM, Sauve A, Montoya D. The stability of multitrophic communities under habitat loss. Nature Communications. 2019; 10 2322

Merila J, Hendry AP. Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. Evolutionary Applications. 2014; 7: 1–14. [PubMed: 24454544]

Montoya JM, Woodward G, Emmerson MC, Sole’ RV. Press perturbations and indirect effects in real food webs. Ecology. 2009; 90: 2426–2433. [PubMed: 19769121]

Ohlberger J. Climate warming and ectotherm body size-from individual physiology to community ecology. Functional Ecology. 2013; 27: 991–1001.

Oliver TH, Marshall HH, Morecroft MD, Brereton T, Prudhomme C, Huntingford C. Interacting effects of climate change and habitat fragmentation on drought-sensitive butterflies. Nature Climate Change. 2015; 5: 941–945.

Opdam P, Wascher D. Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. Biological Conservation. 2004; 117: 285–297.

Orizaola G, Laurila A. Microgeographic variation in temperature-induced plasticity in an isolated amphibian metapopulation. Evolutionary Ecology. 2008; 23: 979.

Osmond MM, de Mazancourt C. How competition affects evolutionary rescue. Philosophical Transactions of the Royal Society B: Biological Sciences. 2013; 368 20120085

Osmond MM, Otto SP, Klausmeier CA. When predators help prey adapt and persist in a changing environment. The American Naturalist. 2017; 190: 83–98.

Padfield D, Yvon-Durocher G, Buckling A, Jennings S, Yvon-Durocher G. Rapid evolution of metabolic traits explains thermal adaptation in phytoplankton. Ecology Letters. 2016; 19: 133–142. [PubMed: 26610058]

Palkovacs EP, Marshall MC, Lamphere BA, Lynch BR, Weese DJ, Fraser DF, Reznick DN, Pringle CM, Kinnison MT. Experimental evaluation of evolution and coevolution as agents of ecosystem change in Trinidadian streams. Philosophical Transactions of the Royal Society of London B: Biological Sciences. 2009; 364: 1617–1628. [PubMed: 19414475]

Palkovacs EP, Wasserman BA, Kinnison MT. Eco-evolutionary trophic dynamics: loss of top predators drives trophic evolution and ecology of prey. PLoS One. 2011; 6 e18879 [PubMed: 21526156]

Pantel JH, Duvivier C, de Meester L. Rapid local adaptation mediates zooplankton community assembly in experimental mesocosms. Ecology Letters. 2015; 18: 992–1000. [PubMed: 26251339]

Parmesan C. Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics. 2006; 37: 637–669.

Parmesan C, Yohe G. A globally coherent fingerprint of climate change impacts across natural systems. Nature. 2003; 421: 37–42. [PubMed: 12511946]

Perdomo G, Sunnucks P, Thompson RM. The role of temperature and dispersal in moss-microarthropod community assembly after a catastrophic event. Philosophical Transactions of the Royal Society B: Biological Sciences. 2012; 367: 3042–3049.

Persson L, Andersson J, Wahlstrom E, Eklov P. Size-specific interactions in lake systems: predator gape limitation and prey growth rate and mortality. Ecology. 1996; 77: 900–911.

Pespeni MH, Garfield DA, Manier MK, Palumbi SR. Genome-wide polymorphisms show unexpected targets of natural selection. Proceedings of the Royal Society B: Biological Sciences. 2012; 279: 1412–1420.

Pespeni MH, Sanford E, Gaylord B, Hill TM, Hosfelt JD, Jaris HK, LaVigne M, Lenz EA, Russell AD, Young MK, Palumbi SR. Evolutionary change during experimental ocean acidification. Proceedings of the National Academy of Sciences of the United States of America. 2013; 110: 6937–6942. [PubMed: 23569232]

Petchey OL, McPhearson PT, Casey TM, Morin PJ. Environmental warming alters food-web structure and ecosystem function. Nature. 1999; 402: 69–72.

Quintero I, Wiens JJ. Rates of projected climate change dramatically exceed past rates of climatic niche evolution among vertebrate species. Ecology Letters. 2013; 16: 1095–1103. [PubMed: 23800223]

Raffard A, Santoul F, Cucherousset J, Blanchet S. The community and ecosystem consequences of intraspecific diversity: a meta-analysis. Biological Reviews. 2018; 94: 648–661. [PubMed: 30294844]

Rall BC, Vucic-Pestic O, Ehnes RB, Emmerson M, Brose U. Temperature, predator-prey interaction strength and population stability. Global Change Biology. 2010; 16: 2145–2157.

Richardson JL, Urban MC, Bolnick DI, Skelly DK. Microgeographic adaptation and the spatial scale of evolution. Trends in Ecology and Evolution. 2014; 29: 165–176. [PubMed: 24560373]

Ryall KL, Fahrig L. Response of predators to loss and fragmentation of prey habitat: a review of theory. Ecology. 2006; 87: 1086–1093. [PubMed: 16761585]

Sanford E, Roth MS, Johns GC, Wares JP, Somero GN. Local selection and latitudinal variation in a marine predator-prey interaction. Science. 2003; 300: 1135–1137. [PubMed: 12750518]

Schaum C-E, Barton S, Bestion E, Buckling A, Garcia-Carreras B, Lopez P, Lowe C, Pawar S, Smirnoff N, Trimmer M, Yvon-Durocher G. Adaptation of phytoplankton to a decade of experimental warming linked to increased photosynthesis. Nature Ecology and Evolution. 2017; 1 0094

Schaum C-E, Ffrench-Constant R, Lowe C, O'lafsson JS, Padfield D, Yvon-Durocher G. Temperature-driven selection on metabolic traits increases the strength of an algal-grazer interaction in naturally warmed streams. Global Change Biology. 2018; 24: 1793–1803. [PubMed: 29281766]

Scheinin M, Riebesell U, Rynearson TA, Lohbeck KT, Collins S. Experimental evolution gone wild. Journal of the Royal Society Interface. 2015; 12 20150056 [PubMed: 25833241]

Scheuerl T, Hopkins M, Nowell RW, Rivett DW, Barraclough TG, Bell T. Bacterial adaptation is constrained in complex communities. Nature Communications. 2020; 11: 1–8.

Schulte PM, Healy TM, Fangue NA. Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. Integrative and Comparative Biology. 2011; 51: 691–702. [PubMed: 21841184]

Sentis A, Bertram R, Dardenne N, Ramon-Portugal F, Espinasse G, Louit I, Negri L, Haeler E, Ashkar T, Pannetier T, Cunningham JL, et al. Evolution without standing genetic variation: change in transgenerational plastic response under persistent predation pressure. Heredity. 2018; 121: 266–281. [PubMed: 29959428]

Sentis A, Binzer A, Boukal DS. Temperature-size responses alter food chain persistence across environmental gradients. Ecology Letters. 2017; 20: 852–862. [PubMed: 28544190]

Sentis A, Hemptinne J-L, Brodeur J. Using functional response modeling to investigate the effect of temperature on predator feeding rate and energetic efficiency. Oecologia. 2012; 169: 1117–1125. [PubMed: 22271203]

Sheridan JA, Bickford D. Shrinking body size as an ecological response to climate change. Nature Climate Change. 2011; 1: 401–406.

Simon MN, Machado FA, Marroig G. High evolutionary constraints limited adaptive responses to past climate changes in toad skulls. Proceedings of the Royal Society B: Biological Sciences. 2016; 283 20161783

Simonis JL. Prey (*Moina macrocopa*) population density drives emigration rate of its predator (*Trichocorixa verticalis*) in a rock-pool metacommunity. Hydrobiologia. 2013; 715: 19–27.

Skelly DK, Freidenburg LK. Effects of beaver on the thermal biology of an amphibian. Ecology Letters. 2000; 3: 483–486.

Srinivasan DG, Brisson JA. Aphids: a model for Polyphenism and epigenetics. Genetics Research International. 2012; 2012: 1–12.

Stoks R, Geerts AN, de Meester L. Evolutionary and plastic responses of freshwater invertebrates to climate change: realized patterns and future potential. Evolutionary Applications. 2014; 7: 42–55. [PubMed: 24454547]

Stuart YE, Campbell TS, Hohenlohe PA, Reynolds RG, Revell LJ, Losos JB. Rapid evolution of a native species following invasion by a congener. Science. 2014; 346: 463–466. [PubMed: 25342801]

Tabi A, Pennekamp F, Altermatt F, Alther R, Fronhofer EA, Horgan K, Machler E, Pontarp M, Petchey OL, Saavedra S. Species multidimensional effects explain idiosyncratic responses of communities to environmental change. Nature Ecology and Evolution. 2020; 4: 1036–1043. [PubMed: 32572220]

Teplitsky C, Millien V. Climate warming and Bergmann's rule through time: is there any evidence? Evolutionary Applications. 2014; 7: 156–168. [PubMed: 24454554]

terHorst CP, Miller TE, Levitan DR. Evolution of prey in ecological time reduces the effect size of predators in experimental microcosms. Ecology. 2010; 91: 629–636. [PubMed: 20426322]

terHorst CP, Zee PC, Heath KD, Miller TE, Pastore AI, Patel S, Schreiber SJ, Wade MJ, Walsh MR. Evolution in a community context: trait responses to multiple species interactions. The American Naturalist. 2018; 191: 368–380.

Theodosiou L, Hiltunen T, Becks L. The role of stressors in altering eco-evolutionary dynamics. Functional Ecology. 2019; 33: 73–83.

Therry L, Cote J, Cucherousset J, Finn F, Buoro Y, Blanchet S. Genetic, plastic and environmental contributions to the impact of a rangeexpanding predator on aquatic ecosystems. Journal of Animal Ecology. 2018; 88: 35–46.

Thompson, JN. The Geographic Mosaic of Coevolution. The University of Chicago Press; Chicago: 2005.

Thompson JN, Cunningham BM. Geographic structure and dynamics of coevolutionary selection. Nature. 2002; 417: 735–738. [PubMed: 12066183]

Thompson PL, Gonzalez A. Dispersal governs the reorganization of ecological networks under environmental change. Nature Ecology and Evolution. 2017; 1 0162

Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C. Future threats to biodiversity and pathways to their prevention. Nature. 2017; 546: 73–81. [PubMed: 28569796]

Tran TT, Janssens L, Dinh KV, Op de Beeck L, Stoks R. Evolution determines how global warming and pesticide exposure will shape predator-prey interactions with vector mosquitoes. Evolutionary Applications. 2016; 9: 818–830. [PubMed: 27330557]

Tran TT, Janssens L, Dinh KV, Stoks R. An adaptive transgenerational effect of warming but not of pesticide exposure determines how a pesticide and warming interact for antipredator behaviour. Environmental Pollution. 2019; 245: 307–315. [PubMed: 30447473]

Travis JMJ. Climate change and habitat destruction: a deadly anthropogenic cocktail. Proceedings of the Royal Society of London Series B: Biological Sciences. 2003; 270: 467–473.

Truemper HA, Lauer TE. Gape limitation and piscine prey size-selection by yellow perch in the extreme southern area of Lake Michigan, with emphasis on two exotic prey items. Journal of Fish Biology. 2005; 66: 135–149.

Tseng M, O'Connor MI. Predators modify the evolutionary response of prey to temperature change. Biology Letters. 2015; 11 20150798 [PubMed: 26673935]

Tuff KT, Tuff T, Davies KF. A framework for integrating thermal biology into fragmentation research. Ecology Letters. 2016; 19: 361–374. [PubMed: 26892491]

Uiterwaal SF, DeLong JP. Functional responses are maximized at intermediate temperatures. Ecology. 2020; 101 e02975 [PubMed: 31944271]

Urban MC. Salamander evolution across a latitudinal cline in gape-limited predation risk. Oikos. 2008; 117: 1037–1049.

Urban MC, Leibold MA, Amarasekare P, de Meester L, Gomulkiewicz R, Hochberg ME, Klausmeier CA, Loeuille N, de Mazancourt C, Norberg J, Pantel JH, et al. The evolutionary ecology of metacommunities. Trends in Ecology and Evolution. 2008; 23: 311–317. [PubMed: 18439707]

Urban MC, Richardson JL, Freidenfelds NA, Drake DL, Fischer JF, Saunders PP. Microgeographic adaptation of wood frog tadpoles to an apex predator. Copeia. 2017; 105: 451–461.

Urban MC, Skelly DK. Evolving metacommunities: toward an evolutionary perspective on metacommunities. Ecology. 2006; 87: 1616–1626. [PubMed: 16922313]

Urban MC, Strauss SY, Pelletier F, Palkovacs EP, Leibold MA, Hendry AP, de Meester L, Carlson SM, Angert AL, Giery ST. Evolutionary origins for ecological patterns in space. Proceedings of the National Academy of Sciences of the United States of America. 2020; 117: 17482–17490. [PubMed: 32641501]

Uszko W, Diehl S, Englund G, Amarasekare P. Effects of warming on predator-prey interactions-a resource-based approach and a theoretical synthesis. Ecology Letters. 2017; 20: 513–523. [PubMed: 28266168]

van Doorslaer W, Stoks R, Duvivier C, Bednarska A, de Meester L. Population dynamics determine genetic adaptation to temperature in Daphnia . Evolution. 2009a; 63: 1867–1878. [PubMed: 19473405]

van Doorslaer W, Stoks R, Swillen I, Feuchtmayr H, Atkinson D, Moss B, de Meester L. Experimental thermal microevolution in community-embedded *Daphnia* populations. Climate Research. 2010; 43: 81–89.

van Doorslaer W, Vanoverbeke J, Duvivier C, Rousseaux S, Jansen M, Jansen B, Feuchtmayr H, Atkinson D, Moss B, Stoks R, De Meester L. Local adaptation to higher temperatures reduces immigration success of genotypes from a warmer region in the water flea Daphnia . Global Change Biology. 2009b; 15: 3046–3055.

Vucic-Pestic O, Ehnes RB, Rall BC, Brose U. Warming up the system: higher predator feeding rates but lower energetic efficiencies. Global Change Biology. 2011; 17: 1301–1310.

Vucic-Pestic O, Rall BC, Kalinkat G, Brose U. Allometric functional response model: body masses constrain interaction strengths. Journal of Animal Ecology. 2010; 79: 249–256. [PubMed: 19845811]

Walsh MR, DeLong JP, Hanley TC, Post DM, John P. A cascade of evolutionary change alters consumer-resource dynamics and ecosystem function. Proceedings of the Royal Society of London B: Biological Sciences. 2012; 279: 3184–3192.

Walsh MR, Post DM. Interpopulation variation in a fish predator drives evolutionary divergence in prey in lakes. Proceedings of the Royal Society B: Biological Sciences. 2011; 278: 2628–2637.

Waither GR, Roques A, Huime PE, Sykes MT, Pysek P, Kühn I, Zobei M, Bacher S, Botta-Dukat Z, Bugmann H, Czucz B, et al. Alien species in a warmer world: risks and opportunities. Trends in Ecology and Evolution. 2009; 24: 686–693. [PubMed: 19712994]

Warren MS, Hiii JK, Thomas JA, Asher J, Fox R, Huntiey B, Roy DB, Teifer MG, Jeffcoate S, Harding P, Jeffcoate G, et al. Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature. 2001; 414: 65–69. [PubMed: 11689943]

Wiiiett CS. Potential fitness trade-offs for thermal tolerance in the intertidal copepod Tigriopus californicus. Evolution. 2010; 64: 2521–2534. [PubMed: 20394668]

Wiiiiams JL, Kendaii BE, Levine JM. Rapid evolution accelerates plant population spread in fragmented experimental landscapes. Science. 2016; 353: 482–485. [PubMed: 27471303]

Wiiiiams JW, Jackson ST. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment. 2007; 5: 475–482.

Yoder JM, Marschaii EA, Swanson DA. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. Behavioral Ecology. 2004; 15: 469–476.

Yoshida T, Eiiner SP, Jones LE, Bohannan BJM, Lenski RE, Hairston NG Jr. Cryptic population dynamics: rapid evolution masks trophic interactions. PLoS Biology. 2007; 5 e235 [PubMed: 17803356]

Yoshida T, Jones LE, Eiiner SP, Fussmann GF, Hairston NG. Rapid evolution drives ecological dynamics in a predator-prey system. Nature. 2003; 424: 303–306. [PubMed: 12867979]

Yvon-Durocher G, Aiien AP, Ceiiamare M, Dossena M, Gaston KJ, Leitao M, Montoya JM, Reuman DC, Woodward G, Trimmer M. Five years of experimental warming increases the biodiversity and productivity of phytoplankton. PLoS Biology. 2015; 13 e1002324 [PubMed: 26680314]

Yvon-Durocher G, Montoya JM, Trimmer M, Woodward G. Warming alters the size spectrum and shifts the distribution of biomass in freshwater ecosystems. Global Change Biology. 2011; 17: 1681–1694.

Zhang L, Takahashi D, Hartvig M, Andersen KH. Food-web dynamics under climate change. Proceedings of the Royal Society B: Biological Sciences. 2017; 284 20171772

Zhao Q, Liu S, Niu X. Effect of water temperature on the dynamic behavior of phytoplankton-zooplankton model. Applied Mathematics and Computation. 2020; 378 125211

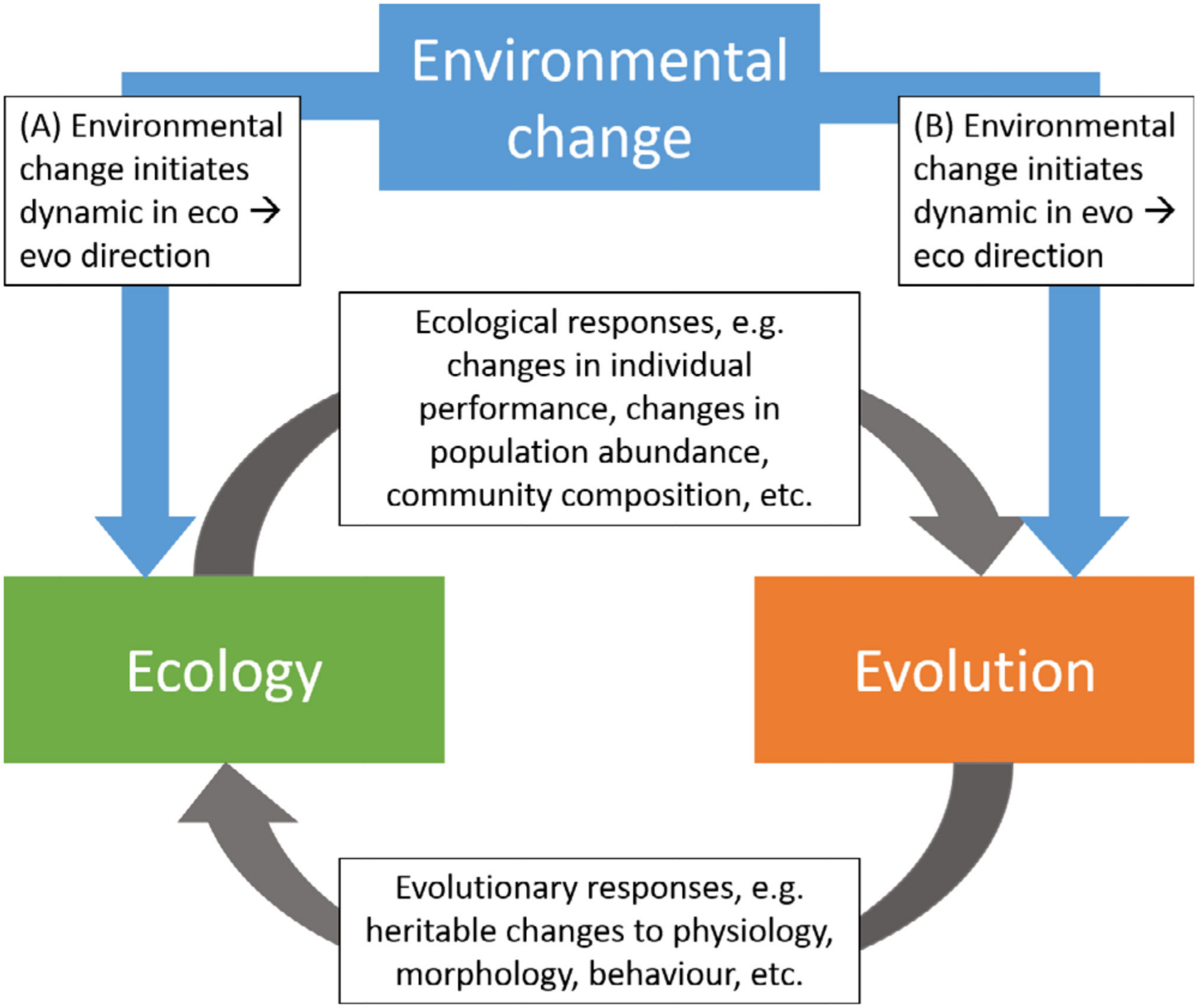

Fig. 1.

Conceptual diagram showing eco-evolutionary dynamics, where changes in the ecology of populations or communities that result in evolutionary changes (A), or *vice versa* (B), 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 evolutionary (B) response. As our focus is on environmental change, we assume that the dynamics are initiated in response to a change in the environment of a population.

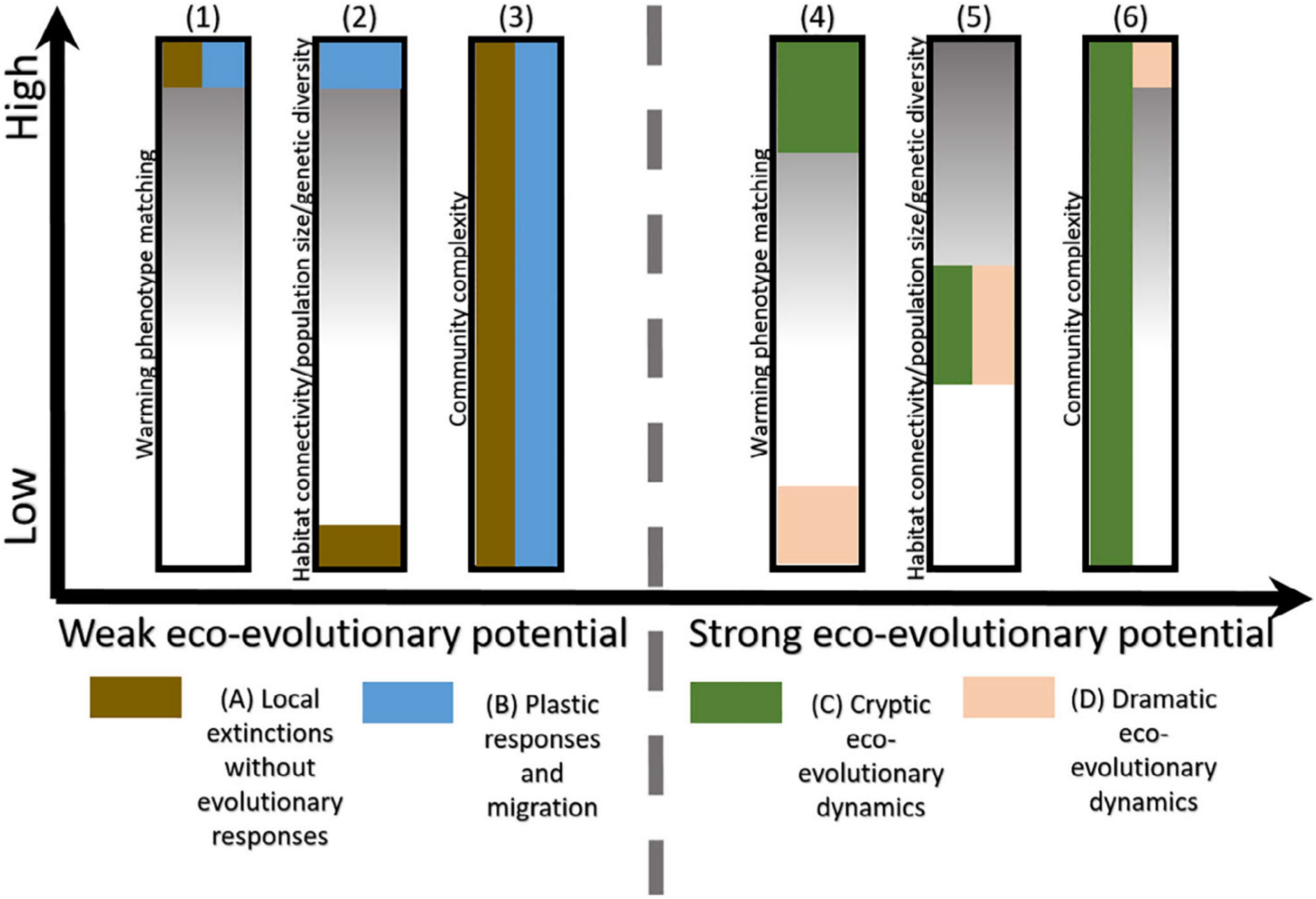

Fig. 2.

Likelihood of eco-evolutionary dynamics in response to warming and fragmentation as a function of species' traits, habitat connectivity, and community complexity. For simplicity, two potential eco-evolutionary scenarios are presented and separated by the dotted grey line, corresponding to weak and strong eco-evolutionary potential. Grey-scale shading indicates the relative level from low to high of each of the factors: 'warming phenotype matching', 'habitat connectivity/population size/genetic diversity', and 'community complexity'. Warming phenotype matching refers to the degree to which an organism's thermal phenotype matches the thermal environment in which it is found. We consider habitat connectivity, population size, and genetic diversity as a single factor in our figure because they are frequently positively correlated. Community complexity refers to the number of organisms and trophic levels, and consequently interspecific interactions, present in the community. We evaluate the role of each factor for weak (factor bars 1−3) and strong (factor bars 4−6) eco-evolutionary dynamics. Colours on the bars show the expected range of each factor for a given eco-evolutionary outcome (A−D). When an outcome is predicted for the entire range of a factor, for example, as in outcomes A and B that we predict across the full range of community complexity (3), the coloured bar spans the vertical range of the grey-scale factor bar. We identified four potential outcomes. Under weak eco-evolutionary potential, local extinctions without evolutionary responses (A) are predicted with high warming phenotype matching (1), low habitat connectivity/ population size/genetic diversity (2), and across a range of community complexity (3). Plastic responses and migration (B) are predicted under weak eco-evolutionary potential with high warming phenotype matching (1), high habitat connectivity/population size/genetic diversity (2), and across a range of community complexity (3). For responses with strong eco-evolutionary potential, we predict that cryptic eco-evolutionary dynamics (C) will be likely to occur with high warming phenotype matching (4), intermediate habitat connectivity/population size/genetic diversity (5), and a range of community complexity (6). The final outcome with strong eco-evolutionary potential, dramatic eco-evolutionary dynamics (D), is predicted to occur with low warming phenotype matching (4), intermediate habitat connectivity/population size/genetic diversity (5), and, high community complexity (6).

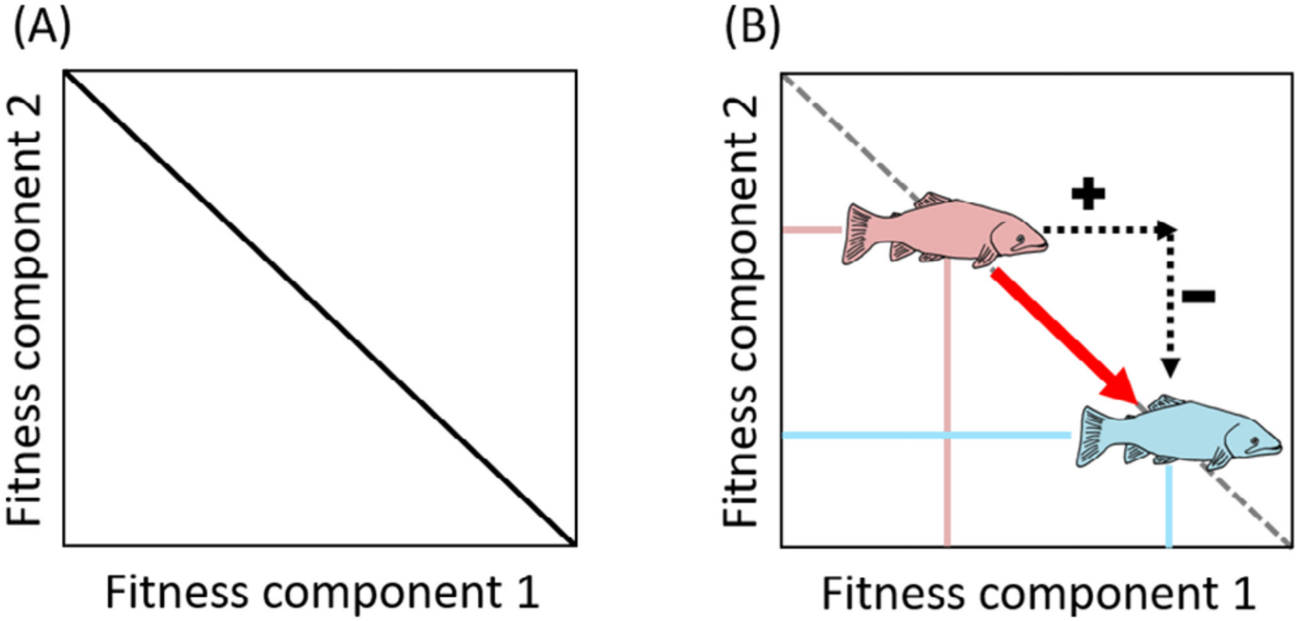

Fig. 3.

(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).

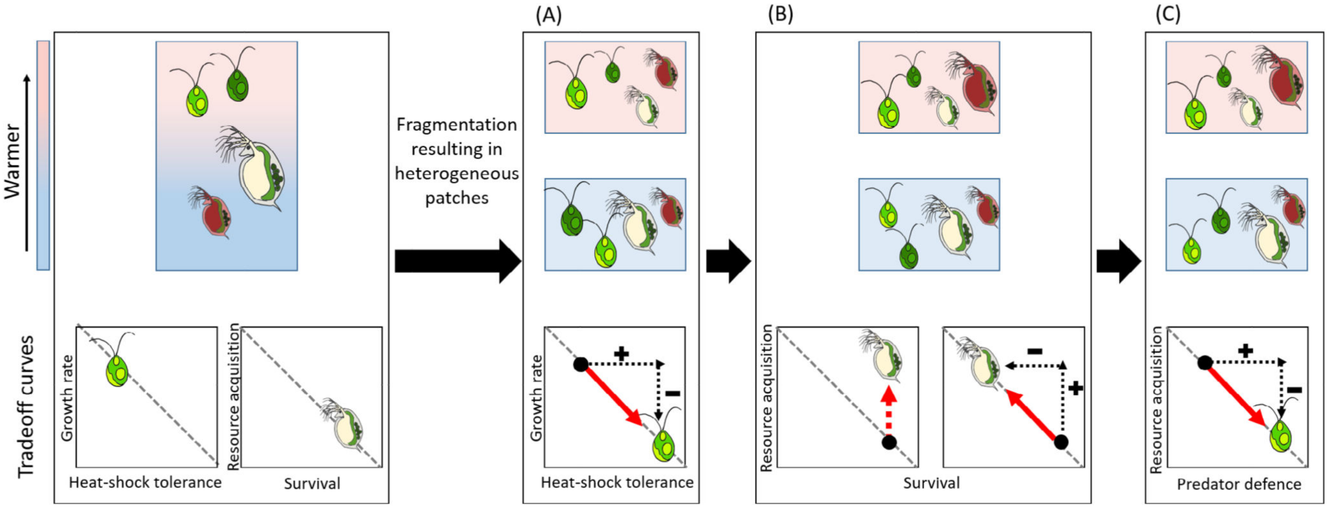

Fig. 4.

Conceptual diagram (top panels) illustrating a hypothetical scenario for an eco-evolutionary feedback (evoàeco àevo) 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 and 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 departing from 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.

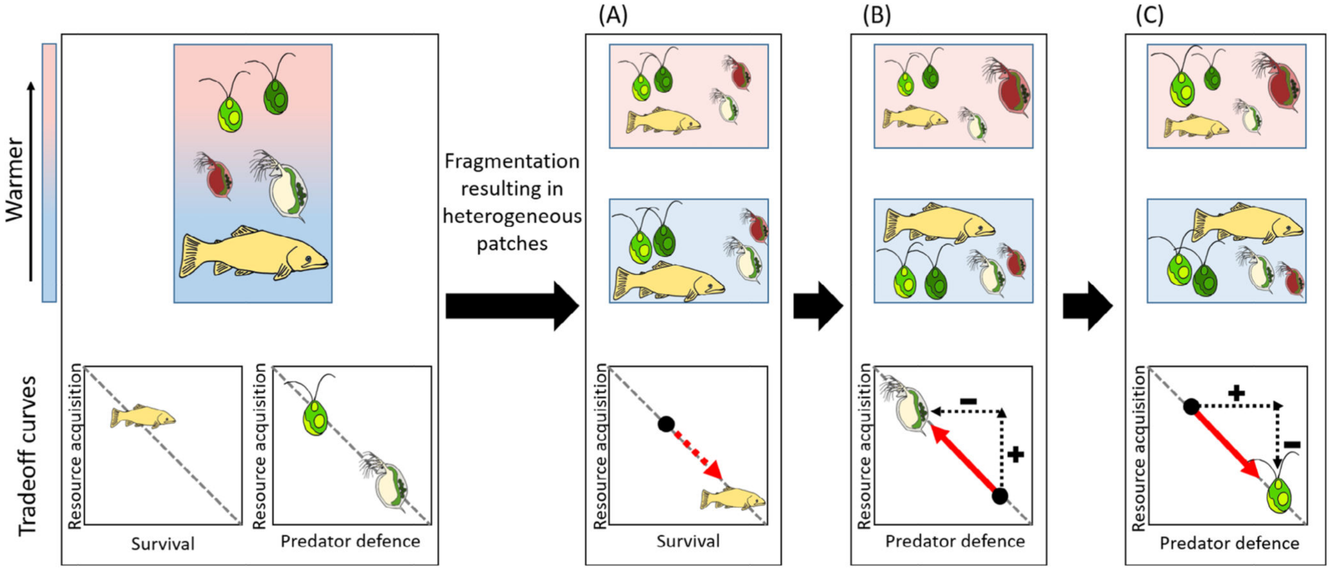

Fig. 5.

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 legend to Fig. 4 for further explanation. For the fish, size of the illustration corresponds to body mass rather than the relative contribution of a phenotype to the population make-up. (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.