OPINION PAPER

The role of predators in driving warming-prey diversity relationships: An invertebrate perspective

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Abstract

Climate warming is one of the key driving forces of biodiversity loss. Yet, our understanding of underlying factors that link warming-biodiversity relationships at both local and regional spatial scales is limited. Here, I review how warming could change local-scale diversity of invertebrate animals. Specifically, I examine whether warming-prey diversity relationships are modulated by changes in predation at higher temperatures. I first review the predictions of bioenergetic models, and then carry out a systematic literature search to find empirical studies that have experimentally tested warming-prey diversity relationships together with warming-predation relationships as well as predation-prey diversity relationships both on land and in water. Empirical studies showed that warming consistently altered predation rates by either increasing or decreasing them. However, warming-prey diversity and predation-prey diversity relationships were inconsistent both on land and in water. Theoretical predictions of positive effects of warming on diversity in resource-rich environments were rarely tested by empirical studies. I suggest that warming-prey diversity and predation-prey diversity relationships can be better understood by incorporating three features of prey species: a) thermal tolerance, b) defense against predation, and c) ability to capture resources in warmer environments. I finally discuss the application of a prey trait-based conceptual framework to predict biodiversity changes from local to regional spatial scales in a warmer world.

Introduction

Ecosystems respond in several ways to rising surface and air temperatures. One of the major responses of ecosystems to increasing temperatures is changes in the structure of ecological communities (Gilman, Urban, Tewksbury, Gilchrist & Holt, 2010; Urban et al., 2016). Ecologists study these changes in community structure by measuring biodiversity changes within defined spatial and temporal units. Studies have shown that local scale biodiversity (usually the most common scale in ecological studies, i.e. plot level) may both decrease and increase in warmer environments, mostly depending on ecosystem type and study organism (Binzer, Guill, Rall & Brose, 2016; Thakur, Künne, Griffin & Eisenhauer, 2017; Yvon-Durocher et al., 2015). However, we currently lack a conceptual framework to encompass when climate warming might increase, decrease, or have neutral effects on local scale biodiversity within an ecosystem. Here, I discuss the role of warming-induced changes in predation rates as one of the potential drivers of variant warming-diversity relationships in invertebrate animals (Fig. 1A).

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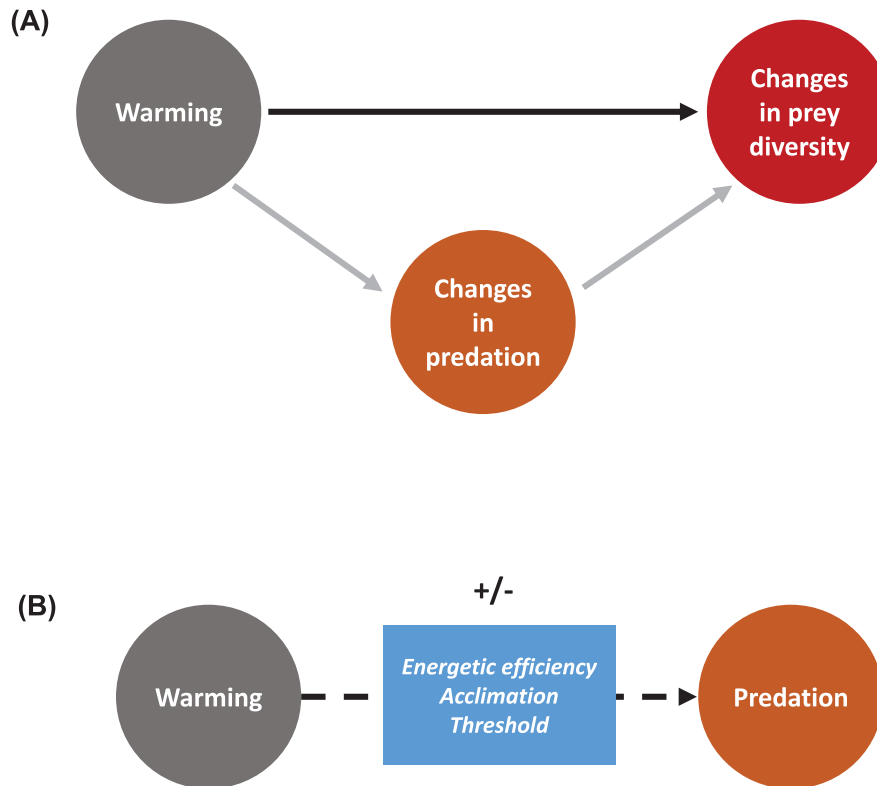 E-mail address: m.thakur@nioo.knaw.nl

(A)

(B)

Fig. 1. (A) Direct and indirect effects of warming on prey communities, that is, whether warming effects on (prey) biodiversity is mediated via warming effects on predation (shown by gray thick lines). There might also be other factors explaining warming effects on (prey) biodiversity in addition to predation effects indicated by the thick line between warming and (prey) biodiversity. (B) Three interrelated determinants (energetic efficiency, acclimation to warming, and threshold temperature beyond which predators foraging declines) that drive the direction of warming-predation relationships. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The study of biodiversity changes in response to any environmental stress is a complex issue. The complexity mainly stems from the fact that biodiversity is a highly scale-dependent measurement (Chase et al., 2018 & Rosenzweig, 1995). In this review, I refer to two measures of biodiversity: alpha and beta diversity. Alpha diversity simply refers to a total number of species within a sampling unit area in a given time. Beta diversity is a slightly more complex measure, and usually refers to dissimilarity in species composition between two sampling units within a study area (at a given time). The greater the difference in species composition between the two sampling units the higher is beta diversity. Although most of this review deals with alpha (and occasionally beta) diversity changes at local scales, I also discuss how local scale diversity responses to warming can be incorporated to inform larger-scale biodiversity changes (e.g. at landscape scales).

Warming, predation and biodiversity change

Temperature rise augments metabolic rates in ectotherms (all predators discussed in this review are ectotherms) (Brown, Gillooly, Allen, Savage & West, 2004). An increase in metabolic rates enhances starvation risk in organisms, which subsequently leads to greater search for food and thus an increase in their foraging activity (Englund, Öhlund, Hein & Diehl, 2011) (Fig. 1B and 2A). Moreover, rise in foraging activity can only be sustained for a longer period if invertebrates are able to maintain higher or at least optimal energetic efficiency (the ratio of energetic loss to energetic gain) at warmer temperatures (Vucic-Pestic, Ehnes, Rall & Brose, 2011). Predators thus must acclimatize to warming for maintaining an optimal energetic efficiency over longer time periods (Sentis, Morisson & Boukal, 2015). Theoretical and empirical studies have shown that thermal acclimation in invertebrate consumers occur via phenotypic adjustments, such as reduction in individual body sizes (Reuman, Holt & Yvon-Durocher, 2013; Sheridan & Bickford, 2011), which could adjust metabolic demands in invertebrate species. At temperatures where an optimal energetic efficiency cannot be sustained, the foraging rates will progressively decrease resulting into starvation risks and death (Fig. 2A: region ii and iii). Indeed, these outcomes may vary between generalist and specialist invertebrate predators (e.g. parasitoids). More importantly, the energetic efficiency of invertebrates, their adaptation to maintain greater energetic efficiencies, and temperatures
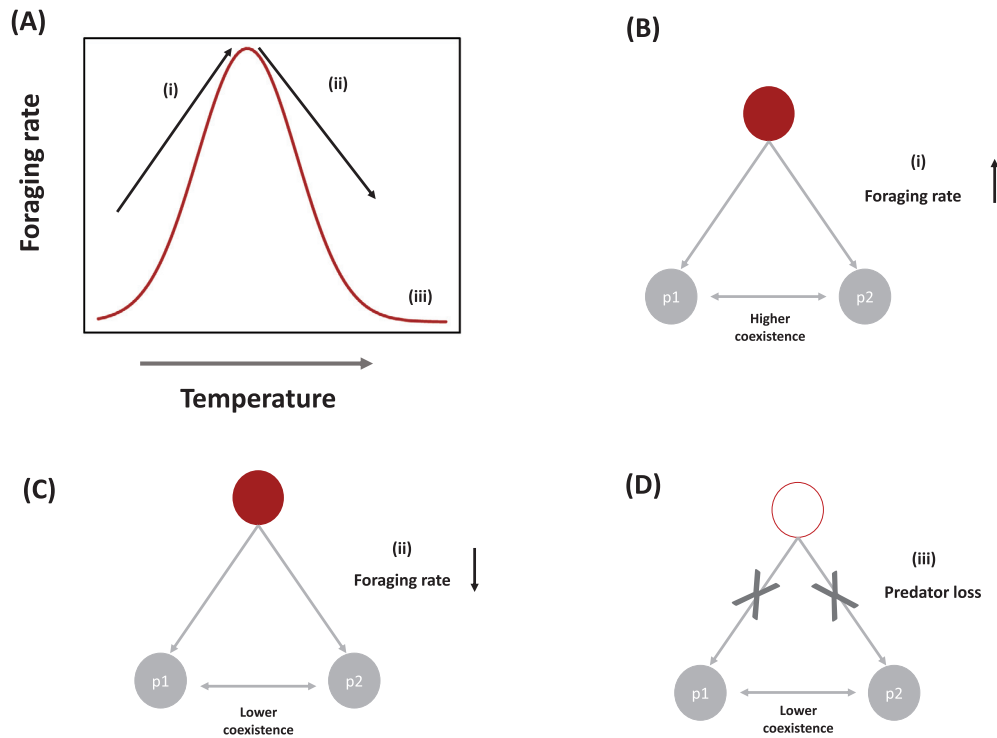
Fig. 2. (A) Warming-induced increase and decrease in foraging rates of predators. As temperature increases, foraging rates also increase according to metabolic principles, but once the threshold temperature is exceeded, foraging rates will decline leading to warming-induced starvation and mortality of predators. These curves are often called thermal performance curves and could vary among species. The three regions in this curve (depicted as i, ii, and iii) are argued to cause differential effects on prey coexistence (hypothesized based on predators' positive effects on prey coexistence; see main text for alternative possibilities) illustrated with one predator-two prey species scenarios in panels (B), (C) and (D). Notably, (C) and (D) could have similar outcomes for prey coexistence. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

leading to invertebrate starvation and mortality are crucial for understanding the foraging dynamics of any predators at higher temperature and their subsequent effects on prey diversity (Fig. 1B).

One of the earliest empirical examples of the effects of predation on prey diversity comes from the experimental work in inter-tidal rocky pools (Paine, 1974). By experimentally excluding one of the key predators of the system (sea stars), Paine (1974) showed that local species richness (of prey communities) declined by nearly four-fold within a few years mainly due to increase in mussels (one of the dominant prey species of sea stars). The coexistence among several prey species is thus magnified when predators can regulate the population of the prey that usually are the ones that can exploit the basal resources the most (Terborgh, 2015). In contrast, experiments have also shown that predator exclusions increase prey diversity particularly in systems with mobile predators and larger assemblages of prey species (Katano, Doi, Eriksson & Hillebrand, 2015).

Here for the sake of simplicity, let's assume that predation enhances prey diversity by regulating the dominant prey thereby relaxing interspecific prey competition. By plugging in warming effects on predation, we can come up with at least two scenarios for warming-predation-prey diversity relationships. First, when warming increases foraging

activity of predators and leads to stronger regulation of the dominant prey, prey diversity should increase (Fig. 2B). Second, when warming leads to decrease in foraging activity of predators or loss of predators, it is likely that prey coexistence within a system maintained by predators will weaken owing to increase in dominant prey species (Fig. 2C, D) (Zarnetske, Skelly & Urban, 2012). I reviewed extant bioenergetic models and performed a systematic literature search to examine these predictions.

What does theory predict?

Several theoretical studies have predicted warming effects on predator-prey dynamics using bioenergetic predator-prey models (Amarasekare, 2015; Gilbert et al., 2014; Rall, Vucic-Pestic, Ehnes, Emmerson & Brose, 2010; Reuman et al., 2013; Vasseur & McCann, 2005). Bioenergetic models (basic principles briefly discussed in Box 1) rely on temperature-dependent parameterization of key biological rates of both predator and prey that can predict their population dynamics using modified Lotka-Volterra models (e.g. consumer-resource models of Rosenzweig & MacArthur, 1963). Although bio-energetic models have rarely been used to predict prey biodiversity (exceptions like

Binzer et al., 2016; Stegen, Ferrière & Enquist, 2012), they have shown that increase in temperature can destabilize communities (via increased population oscillation of both predator and prey) particularly when temperature reduces prey biomass and magnifies predation (Vasseur & McCann, 2005). On the contrary, if warming leads to predator extinction, predator-prey systems may also stabilize but at the cost of reduced biodiversity of predators (Fussmann, Schwarzmüller, Brose, Jousset & Rall, 2014).

Box 1. **Bioenergetic models**

The key principle of bioenergetic models is based on mass and energy balance between predators and prey (or between consumers and resources). Several theoretical studies have utilized bioenergetic principles to predict population dynamics of predator and prey (Brose, Ehnes, Rall, Berlow & Scheu, 2008; Kalinkat et al., 2013; Reuman et al., 2013). Key biological rates like growth rates of prey and predators, handling time and attack rate by predators could be parameterized by temperature-dependence and body-size dependence (based on metabolic theory) in these models. The current practice of parameterizing these biological rates by temperature is based on the Arrhenius equation:

$$X_1 = X_0 \exp^{E_X \frac{T-T_0}{K.T.T_0}}$$

where X_1 is any biological rate, X_0 is a rate- and body mass-dependent normalization constant, E_X is the activation energy that influences the exponential effects of temperature on a given biological rate, T is the temperature of the system (treatment temperature), K is Boltzmann's constant (8.62×10^{-5} eV K^{-1}) and T_0 is the normalization temperature (control temperature). Notably, activation energy can vary between the processes, for instance Allen, Gillooly and Brown (2005) proposed a series of values for activation energy for respiration and photosynthesis, whereas Fussmann et al. (2014) reported various values of activation energy for processes like feeding rates and metabolic rates. Please note that in this opinion paper, I do not use bioenergetic models to make prediction(s) but reviewed studies that had used them to predict warming-biodiversity relationships (Section 3).

Theoretical predictions for temperature-biodiversity relationships based on trophic-interactions mainly depend on how temperature affects the supply of basal resources and predator-prey body size structures. Using a bioenergetic modeling framework, Binzer et al. (2016) showed that warming increases species diversity when basal resources are not limited by quantity but can lead to diversity decline when basal resources become limited. Fussmann et al. (2014) further showed that predator extinctions due to warming are more likely when predators are larger in body size than their prey. With an objective to predict large-scale temperature-biodiversity relationships using eco-evolutionary bio-energetic models, Stegen et al. (2012) also showed that greater resource supply can increase community diversity when exposed to warming.

Systematic literature search

I used a set of broad search terms to maximize the number of studies that examined warming-predation-prey biodiversity relationships. The search terms were: (temperature OR warming OR heat) AND (biodiversity OR species richness OR species diversity OR alpha diversity OR beta diversity OR coexistence OR co-occur*) AND (trophic interaction OR preda* OR top-down*). These search terms resulted in 837 published articles (accessed on July 1st, 2018 in ISI Web of Science) of which review papers, observational studies, and studies other than invertebrates (as prey communities) were excluded. The first screening (based on title and abstract) resulted in 43 experimental studies that studied temperature effects on predation and the subsequent effects on lower-trophic groups. I included studies that had temperature manipulations (mainly experiments), some measure of warming effects on predation (e.g. predator density or biomass responding to warming), have reported warming effects of prey diversity (alpha or beta or both) and also discussed or examined predation-prey diversity relationships (Table 1). Only 14 studies fulfilled these criteria (Table 1). Of 14 studies, four studies reported a positive warming-prey diversity relationship, three studies reported negative relationship and five studies showed a neutral pattern. Moreover, few studies highlighted context-dependent effects such as that of experimental or observational durations to drive warming-prey diversity relationships (Table 1).

The experimental or observational duration of warming substantially varied among studies. Experimental manipulations of warming were at least applied for a duration of one month (Table 1). All studies report that the duration of warming in their study system was adequate to induce thermal stress on their respective study organisms. The relationship between warming and alpha diversity (mainly species richness) of invertebrates ranged from neutral to negative to positive and even a unimodal relationship. Two studies further reported that sampling time (e.g. different seasons within a year) determined whether the warming- prey diversity relationship was positive, negative or neutral (MacLennan & Vinebrooke, 2016; Šorf et al., 2015). More importantly, temperature seemed to almost always affect predators - either by increasing the predation effect or decreasing it (Fig. 2A), which was independent of the duration of warming treatments. Warming-induced increases in predator foraging (presumably due to greater predator density or activity at higher temperature) often caused a negative temperature-prey diversity relationship, whereas decline in predators rendered warming-biodiversity relationships to be positive in several cases (Table 1). Thus, studies that reported prey biodiversity to increase at higher temperatures also showed decline in predator density at higher temperatures. These studies oppose the general expectation that the presence of predators maintains greater prey biodiversity (Paine, 1974; Terborgh, 2015). In fact, only three studies confirmed a positive relationship between predators and

Table 1. List of experimental studies from the systematic literature search and their key findings. Based on a systematic literature search, fourteen experimental studies report on warming effects on (prey) biodiversity, warming effects on predation, and potential relationship between predation and (prey) biodiversity. All studies experimentally manipulated temperature, except Woodward et al., 2010 that had natural thermal gradient within a locality (I excluded elevation or latitudinal studies in this review to focus on local-scale changes in species diversity).

	Study	System	Study type	Warming duration	Group/Taxa	Biodiversity	Warming- prey diversity relationship	Warming-predation relationship	Predation-prey diversity relationship
1	Antiqueira et al., 2018	Aquatic	Lab	4 months	Detritivores	alpha	Neutral	Not directly tested, but predation loss treatment was motivated by negative effects of warming on predators.	Loss of predators increased prey diversity.
2	Eklöf, Havenhand, Alsterberg & Gamfeldt, 2015	Aquatic	Lab (semi-open)	34 days	Macro-invertebrates	alpha	Positive	Warming decreased the biomass of the predator used in the experiment.	Predator removal increased the diversity of prey communities.
3	Hågvar & Klanderud, 2009	Terrestrial	Field	4 years	Soil micro-arthropods	alpha	Neutral	Warming increased the abundance of predators but mainly in N enriched soils.	Not directly tested, but indicative of unimodal relationship.
4	Harley, 2011	Aquatic	Field	52 years	Mussels	alpha	Not directly tested, but suggested to be negative	Predator-free space decreased with warming.	Predator exclusion at the warmest site increased biodiversity of mussels mainly via the increase in abundance of ecosystem engineers.
5	Lindo, 2015	Terrestrial	Lab	8 months	Soil micro-arthropods	alpha	Positive	Warming reduced predator density	Not directly tested but warming-induced decline in predator suggested to enhance prey richness.
6	Loewen & Vinebrooke, 2016	Aquatic	Outdoor meso-cosms	2 months	Zooplanktons	alpha	Neutral	Not directly tested but suggested that warming can reinforce predation effects.	Predation reduced species richness, which was further amplified in warmed water.
7	MacLennan & Vinebrooke, 2016	Aquatic	Lab	31 days	Zooplanktons	alpha	Positive (but also varied to neutral effects at different sampling times)	Not directly tested but suggested that warming can reinforce predation effects.	Predation by fish increased the species richness of zooplanktons.
8	Meadows, Ingels, Widdicombe, Hale & Rundle, 2015	Aquatic	Lab	2 months	Nematodes	alpha	Negative	Trophic diversity increased with warming.	Increase in trophic diversity at higher temperature could have negatively affected the diversity of prey and thus an overall diversity.

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Table 1 (*Continued*)

	Study	System	Study type	Warming duration	Group/Taxa	Biodiversity	Warming- prey diversity relationship	Warming-predation relationship	Predation-prey diversity relationship
9	Šorf et al., 2015	Aquatic	Outdoor meso-cosms	4 months	Zooplanktons	alpha	Dependent on the time of sampling (from positive to neutral to negative)	Predator abundance showed a unimodal response to warming.	Zooplankton diversity was attributed to warming-induced changes in predator density but only so at higher nutrient levels.
10	Thakur et al., 2017b	Terrestrial	Field	5 years	Nematodes	alpha	Positive and negative (dependent on resource availability in soils mediated via plant diversity)	Warming decreased predator density	Decrease in predator density was associated to warming-induced decrease in prey diversity in soils of plant monocultures.
11	Thakur et al., 2017a	Terrestrial	Lab	2 months	Litter micro-arthropods	alpha	Negative	Warming increased predator density	Greater predator density decreased prey coexistence.
12	Woodward et al., 2010	Aquatic	Field	Several years	Macro-invertebrates	alpha, beta	Unimodal	Warming increased the size of predators (fish) and switched their deit.	Not directly tested, but warming-induced dietary shifts and greater body size of predators were argued to reduce macro-invertebrate diversity at higher temperatures on top of physiological constraints.
13	Yvon-Durocher et al., 2015	Aquatic	Outdoor meso-cosms	5 years	Phytoplanktons	alpha	Positive	Zooplanktons were the predators and showed negligible response to warming.	Negligible zooplankton response and higher phytoplankton body sizes at higher temperature indicates weaker effects of trophic regulation on the observed higher biodiversity of phytoplanktons in warmed water.
14	Zhu et al., 2015	Terrestrial	Field	3 years	Aboveground insects	alpha	Neutral	Warming reduced predator diversity but had neutral effects on predator density	Greater predator density and prey (herbivore insects) richness were positively correlated at higher temperature.

prey biodiversity (MacLennan & Vinebrooke, 2016; Thakur et al., 2017b; Zhu et al., 2015).

The mixed findings of empirical studies suggest that warming effects on prey diversity only partly depend on warming regulation of predation (e.g. increase/decrease in predator density or diversity) and predation regulation of prey coexistence. The positive warming-prey diversity relationship, for instance, could be attributed to negative effects of predators on prey coexistence, and warming-induced negative effects on predators (Table 1). Further, some studies also reported neutral temperature-prey diversity relationships despite predation effects on prey diversity (Antiqueira, Petchey & Romero, 2018; Loewen & Vinebrooke, 2016; Zhu et al., 2015).

Relating to theoretical frameworks, only few empirical studies tested whether resource availability could determine temperature effects on prey diversity via changes in predation. Hågvar and Klanderud (2009) showed that warming increased predation in N-rich soils but this neither led to positive nor negative warming-prey diversity relationship. Thakur et al. (2017b) indeed showed that warming effects on prey diversity within soil nematode communities were negative in plant monocultures (resource-limited environment) compared to that in diverse-plant communities, while warming also reduced predatory nematodes in plant monocultures. Hence, agreeing with the theoretical predictions, warming effects on prey biodiversity are likely to be negative when the quantity of basal resources is limited, and warming further leads to predator loss. Most empirical studies that showed negative effects of warming on prey diversity did not discuss whether the study systems were indeed limited in terms of resource quantity. If we follow theoretical predictions, one could assume these systems to be limited by resources, however, another experimental study Thakur et al. (2017a) revealed that the basal resource in the system increased with warming and despite of that, warming reduced prey coexistence due to increased predation. It is therefore likely that warming effects on prey diversity may also be independent of basal resource availability. I suspect this to be true where prey assemblages are species-poor (Thakur et al., 2017a) and could further depend on resource quality and not only quantity.

What may explain variable warming-biodiversity relationships?

In this opinion paper, I asked two questions: whether warming changes species diversity (focusing on invertebrate prey) and whether warming-induced changes in predation modulate warming-prey diversity relationships. There was one clear pattern from empirical studies: warming consistently shifted some measure of predation on prey invertebrates (Fig. 2A; the only exception being Yvon-Durocher et al., 2015; see Table 1 for details). In contrast,

warming-prey diversity relationships were highly variable. These variable relationships (neutral, negative and positive) can, in part, be explained by whether predators maintain or disrupt prey diversity at ambient temperatures (Table 1). Given that predation effects on prey diversity of invertebrates were also inconsistent, warming-predation-prey diversity (Fig. 1) relationships need to be further informed by biotic and abiotic conditions that regulate predation effects on prey diversity.

A long tradition in community ecology has been to point out the importance of bottom-up forces (resource or nutrient availability) as a key determinant of predator regulation of prey communities (Haddad, Crutsinger, Gross, Haarstad & Tilman, 2011; Hunter & Price, 1992; Moore, McCann, Setala & De Ruiter, 2003; Oksanen, Fretwell, Arruda & Niemela, 1981). Warming also regulates the dynamics of bottom-up forces thereby altering the strength of predator-prey interactions (Gilbert et al., 2014; Uszko, Diehl, Englund & Amarasekare, 2017) with subsequent effects on prey diversity regulation (Hoekman, 2010; Shurin, Clasen, Greig, Kratina & Thompson, 2012). Thus, one key aspect to examine for a better understanding of warming-prey biodiversity relationship is to test how resource (the ones that are consumed by prey) quantity and quality change with temperature. Warming can induce such changes in live resources via their direct effects on resource physiology, whereas changes in non-living resources (e.g. organic matter) may relate to temperature-induced increase in turnover rates of nutrients. If warming enhances resources for prey, the role of predation becomes more important in regulating the competitively dominant ones, and thus enhancing the prey diversity. If warming reduces resources for prey, predators at higher temperature can be lethal for rarer prey species, and thus could decrease prey diversity. However, this information is not always adequate for understanding how predation may modulate warming- (prey) biodiversity relationships (e.g. Thakur et al., 2017a).

In addition to how warming affects resources for prey, warming-prey diversity relationships could benefit from the insights on whether prey invests in traits to maximize resource capture or enhance their defense against predation, which is analogous to trade-offs between defense and growth. Gilman et al. (2010) had proposed a similar idea in their framework for understanding community interactions under warming but trade-offs between competitive superiority (ability to capture resource and grow fast) and higher tolerance to temperature (wider thermal niches). They suggested that warming most likely would favor prey with greater thermal tolerance than the competitively dominant ones (Gilman et al., 2010). Interestingly, a recent study showed that resource limitation (Phosphorus limitation) reduced thermal tolerance of phytoplankton species (Bestion, Schaum & Yvon-Durocher, 2018). Hence, warming effects on basal resource availability are further likely to drive tolerance-growth trade-offs.

Moreover, if stress-tolerant prey is favored by predators at higher temperature, predation can prevent the exclusion
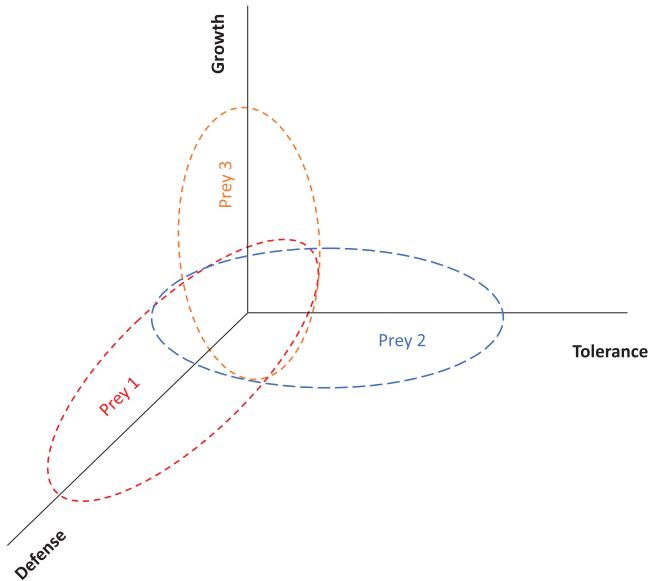
Fig. 3. Potential trade-offs among three categories of traits (defense against predators, tolerance of higher temperature, and growth) in prey species when confronted with warming and predation proposed as a conceptual framework to understand warming-biodiversity relationship via changes in predation. In the figure, Prey 1 is better in defending against predator, Prey 2 has higher thermal tolerance and Prey 3 grows faster when exposed to warming and predation. The implications of such trade-offs on prey diversity are discussed in the main text. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of resource-efficient prey. In such cases, predation would promote prey diversity. Prey species exposed to predation are further likely to invest in defense traits (Riessen, 2015). Therefore, tolerance-growth trade-offs can be extended by an additional axis of investment in defense traits in the context of warming-predation-prey diversity relationships (Fig. 3). In fact, a recent study highlighted a potential trade-off between growing large (to evade predation) and growing small (to minimize thermal stress) in a soil invertebrate species when confronted simultaneously to predation and warming (Thakur et al., 2018). We need studies that can examine such trade-offs by studying prey defense traits (e.g. greater or smaller body sizes, chemical defenses, harder integuments, faster movements to evade predation, etc.), prey growth (ability to exploit resources, growth rates, etc.) and their thermal tolerance (thermal performance curves, body temperature and body size, etc.) to provide better insights into the variant nature of warming-diversity relationships. It will further be important to consider trait plasticity in prey when exposed to predation and warming (Sentis, Hemptinne & Brodeur, 2017; Thakur et al., 2018; Thakur et al., 2017a) for a better understanding of prey trait trade-offs in a warmer world.

Outlook: scaling-up to regional diversity changes

Local changes in species diversity depend on the rate of exchange of species from regional pools to local scales (Ricklefs & Schulter, 1993). These exchange rates depend on several factors, ranging from dispersal capacity of species to climate-induced species migrations to biotic interactions among species. There is also a growing research interest in understanding predator-prey interactions in spatial context for improving biodiversity predictions from local to regional scales (Bartley et al., 2019; Grainger & Gilbert, 2016; Guzman et al., 2019; Holt & Hoopes, 2005). The trait framework (Fig. 3) discussed above can be extended to regional scales by adding spatial processes to it. For instance, prey species inferior in defense traits at higher temperature when exposed to enhanced predation can disperse to patches with lower predation pressure within a landscape. Moreover, dispersal of species from one patch to the other within a landscape can be constrained or facilitated by warmer temperatures (Barnes, Spey, Rohde, Brose & Dell, 2015; Kuparinen, Katul, Nathan & Schurr, 2009; Massot, Clobert & Ferrière, 2008). Dispersal of prey species will further depend on metabolic costs associated with their movement (Hirt, Jetz, Rall & Brose, 2017).

I suggest that thermal heterogeneity within landscapes owing to climate warming (Sears, Raskin & Angilletta, 2011) is crucial to understand the exchange of predator and prey species from one patch to the other. Thermal heterogeneity in a landscape could act as both thermal corridors and barriers to dispersal of species (Fig. 4). Thermally tolerant prey species that are inferior in other two traits (defense and growth) but have greater dispersal ability can use warmer regions within a landscape as thermal corridors to disperse from local patches where predation pressure is higher, and resources become limiting with warming. Prey species with low thermal tolerance and poor dispersal ability are the ones likely to be trapped by thermal barriers, and thus with a higher probability of exclusion. These prey species could persist within a local patch when they can either defend themselves against predators or are better at exploiting resources. Moreover, these prey species could also utilize seasonal variations in thermal heterogeneity to disperse to newer patches (Boukal, Bideault, Carreira & Sentis, 2019). Interestingly, the colonization and local extinction of thermally inferior and/or superior prey species can dramatically rewire food webs with implications for ecosystem functioning (Zhang, Takahashi, Hartvig & Andersen, 2017). The scenarios of thermal corridors and barriers for invertebrate prey species are indeed speculative (Fig. 4) and most likely differ between terrestrial and aquatic systems, and among invertebrate species. Nevertheless, the spatial-dependence of warming-diversity relationships modulated by warming effects on predation (Fig. 1A) merit both theoretical and empirical scrutiny as also pointed out by recent studies (Bartley et al., 2019; Boukal et al., 2019).
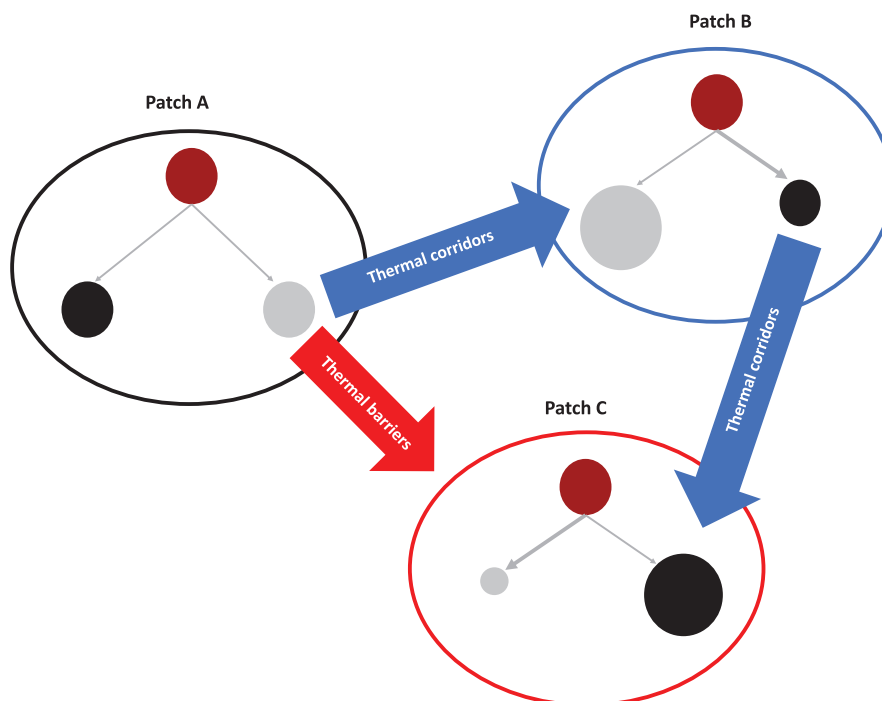
Fig. 4. Hypothetical scenarios of prey dispersal from one patch to another within a landscape to illustrate that dispersal could be constrained or facilitated by thermal barriers and corridors, respectively. Each patch is an assemblage of a predator (red circle) and its two prey species (one of which has higher thermal tolerance than the other: dark circles prey have greater thermal tolerance than the gray circles prey). Thermal heterogeneity in a landscape can facilitate and constrain prey dispersal from one patch to other and therefore can explain variations in local and regional patterns of prey diversity. Patch C is the warmest patch, whereas patch B has the lowest temperature. The population size of prey species is depicted by the size of the circles, and detrimental predation effects are indicated by the thickness of gray arrows within the patches. For prey species with lower thermal tolerance, dispersal will be towards the coolest patch via thermal corridors, whereas the same prey will not be able to move to patch C because of thermal barriers. Prey species with higher thermal tolerance will benefit by dispersing to patch C from patch B owing to competitive advantage over prey species in patch C. Greater predation on competitively inferior prey species is an assumption based on the findings from Thakur et al., 2017a, although this may differ when thermally inferior species are better at defense against predation (e.g. Fig. 3). Please refer to main text for the discussion of differences in the dispersal ability of prey species with higher and lower thermal tolerance. For the sake of simplicity, predator dispersal is not discussed in the text, however, a similar set of rules could also be applied for predators and their dispersal in thermally-heterogenous landscapes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Conclusions

As empirical studies showed that warming consistently altered predation in invertebrate animals, invertebrate prey community responses to warming could to some extent be explained by changes in predation. Moreover, studying traits of prey in relation to their defense, thermal tolerance and growth at higher temperature can help understand several forms of warming-prey diversity relationships influenced via warming-induced changes in predation. Extending these trade-offs in prey species to their dispersal strategies in thermally heterogenous landscapes could further provide local and regional context of biodiversity changes in a warmer world. Moreover, future studies can delve into how trade-offs in prey traits in warmer environments may vary between generalist and specialist predators. The warming-prey diversity framework via the effects of warming effects on predation discussed in this opinion paper has several limitations. For instance, I did not consider multiple global change effects in the proposed framework, which are likely to influence on each other's effects on biodiversity (Rillig et al., 2019; Thakur et al., 2019). Furthermore, increasing frequency of climatic extremes is likely to affect predictions based on metabolic principles alone. For instance, some climatic extremes can dramatically cause habitat losses with direct severe effects on both predator and prey biodiversity. Nevertheless, experimental studies guided by bio-energetic frameworks will continue to yield important insights on warming-biodiversity relationships both at local and regional scales particularly when they could incorporate prey trait information in the context of changing predation in a warmer world.

Declaration of Competing Interest

None

Acknowledgement

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