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**Spatial extinction or persistence: landscape-temperature interactions perturb predator-prey dynamics**

**Running title**: Landscape, temperature, and predator-prey dynamics

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**ABSTRACT**

Recognising that species interact across a range of spatial scales, we explore how landscape structure interacts with temperature to influence persistence. Specifically, we recognise that few studies indicate thermal shifts as the proximal cause of species extinctions; rather, species interactions exacerbated by temperature result in extinctions. Using microcosm-based experiments, as models of larger landscape processes, we test hypotheses that would be problematic to address through field work. A text-book predator-prey system (the ciliates *Didinium* and *Paramecium*) was used to compare three landscapes: an unfragmented landscape subjected to uniform temperatures (10, 20, 30 °C); a fragmented landscape (potentially hosting metapopulations) subjected to these three temperatures; and a fragmented landscape subjected to a spatial temperature gradient (~10 to 30 °C) - despite the prevalence of natural temperature ecoclines this is the first time such an analysis has been conducted. Initial thermal response-analysis (growth, mortality, and movement measured between 10 and 30 °C) suggested that as temperature increased, the predator might drive the prey to extinction. Thermal preferences (measured at 5 temperatures between 10 and 30 °C), indicated that both predator and prey preferred warmer temperatures, with the predator exhibiting the stronger preference, suggesting that cooler regions might act as a prey-refuge. The landscape level observations, however, did not entirely support the predictions. First, in the unfragmented landscape, increased temperature led to extinctions, but at the highest temperature (where the predator growth can be reduced) the prey survived. Second, at high temperatures the fragmented landscape failed to host metapopulations that would allow predator-prey persistence. Third, the thermal ecocline did not provide heterogeneity that improved stability; rather it forced both species to occupy a smaller realized space, leading toward extinctions. These findings reveal that temperature-impacted rates and temperature preferences combine to drive predator-prey dynamics and persistence across landscapes.

Temperature shifts, due to climate change, immediate anthropogenic divers, and natural phenomena, will alter the vital rates of organisms. Consequently, for decades, there has been interest in how species respond to temperature (e.g. Cossins and Bowler 1987). Individual species, however, rarely act in isolation. Rather, they are affected by processes such as competition and predation. There are, therefore, growing efforts through reviews, meta-analyses, and theoretical and empirical models to evaluate how temperature affects interactions, especially predator-prey dynamics (Montagnes et al. 2008, Gilman et al. 2010, Rall et al. 2010, Dell et al. 2011, Kordas et al. 2011, Sentis et al. 2012, Urban et al. 2012, Wisz et al. 2013, Abbot et al. 2014, Amarasekare 2014, Fussmann et al. 2014, Gilbert et al. 2014, Tomlinson et al. 2014, Öhlund et al. 2015). Although divergent views arise across such studies, collectively they recognise that temperature drives predator-prey interactions and appreciate the consequences to landscape ecology, ecosystem dynamics, and management strategies. Critically, few cases indicate temperature shifts as a proximal cause of extinctions or show a direct cause due to species experiencing temperatures outside their limits. Instead, it is species interactions, exacerbated by temperature changes that result in extinctions (Cahill et al. 2012).

Temperature also impacts on landscape-level processes, often through metapopulation dynamics (Gilman et al. 2010, Urban et al. 2012, Wisz et al. 2013, Classen et al. 2015, Duncan et al. 2015). The persistence of metapopulations relies on landscapes being composed of connected habitat patches that support asynchronous populations, each being at risk of local extinction. When local extinctions occur, colonisation from other patches ensures persistence across the landscape (Hanski 1999, Cooper et al. 2012). It follows that if temperature alters growth and mortality within habitat patches and dispersal between patches, these will affect metapopulation dynamics. For example, temperature rise across a landscape may increase dispersal, leading to synchrony across the metapopulation, which in turn results in destabilization (Thompson et al. 2015). Likewise as we show in this study, different thermal responses of the predator and prey may alter their persistence in isolated populations, and thus may affect metapopulations. We then take our analysis of metapopulations a step further: a sensible extension to assessing landscapes that experience a uniform shift in temperature is to evaluate spatial gradients. For instance, a temperature-ecocline may impose a range of attributes (e.g. refuges, shifts in dispersal, isolation of populations) on species within a fragmented landscape (Gilman et al. 2010), and these will undoubtedly influence predator-prey dynamics (Urban et al. 2012, Tunney et al. 2014). Predictions such as the “thermal accessibility hypothesis” that argues for structured effects of different temperatures on spatially coupled food webs (Tunney et al. 2014) have begun to explore this issue, but it requires further exploration.

An explicit or tacit acknowledgement arising from many of the studies cited above is that to evaluate the existing, divergent predictions, there is a need for empirical time-series data obtained across defined landscapes. Such data, especially those from natural landscapes, have proved difficult to gather (with recent exceptions, Classen et al. 2015; Thompson et al. 2015). Consequently, here we assess temperature effects on landscape processes using a model predator-prey system within microcosms (Jessup et al. 2004, Cooper et al. 2012, Li et al. 2013, Altermatt et al. 2015). In doing so, we test hypotheses associated with the effect of thermal and spatial-variability on predator-prey persistence across a 20 °C range. This is equivalent to daily and seasonal shifts in some regions or episodic events due to natural or anthropogenic drivers. More germane to the thermal accessibility hypothesis (Tunney et al. 2014), it corresponds to gradual changes across landscapes with altitudinal rises of 3000 m or latitudinal clines of 15° (Urban et al. 2012), and more locally to distances of meters in stratified waters, across intertidal zones, and along regions of arboreal shading.

Specifically, to examine the impact of temperature on metapopulation persistence we have chosen a predator-prey system that is inherently unstable in isolated patches: the predator drives its prey to extinction and then dies due to starvation (Cooper et al. 2012, Li et al. 2013). However, across a fragmented landscape the predator and prey tend to persist as metapopulations (Cooper et al. 2012). To provide initial predictions as to how temperature may alter predator-prey dynamics in isolated fragments and across a fragmented landscape we follow an often applied, albeit reductionist, approach and first characterise how a temperature shift (~10 to 30 °C) influences the growth and movement of our species: with increasing temperature the predator tends to reproduce faster than the prey, predator mortality increases, and there is a greater likelihood of contact due to increased swimming speeds (see Results). Collectively, these data suggest that as temperature rises the system will become destabilised. We then test this hypothesis by examining predator-prey dynamics in both isolated and fragmented landscapes (at 10, 20, 30 °C). Finally, for reasons raised above, we examine a temperature gradient (~10 to 30 °C) across the fragmented landscape. Here we posit two contrasting hypotheses, while recognising combinations of both could occur: *i.* the gradient will enhance predator-prey persistence by providing a heterogeneous environment (e.g. offering refuges, altering dispersal rates, isolating populations) or *ii.* the gradient will reduce persistence if the predator and prey have similar thermal preferences, resulting in them occupying the same space and negating the benefits of a fragmented environment. By conducting this tiered set of experiments, we provide evidence that distinct dynamics arise from a combination of temperature responses (e.g. growth, movement, thermal preference) across landscapes of varying structure. In doing so, we offer elucidation and guidance for further theoretical and field assessments of temperature impacts on landscape-species interactions (e.g. Angert et al. 2011, Tunney et al. 2014).

**Methods**

**Species and culture maintenance**

Using microcosm-based experiments, which act as good models of landscape processes (Jessup et al. 2004, Altermatt et al. 2015), we employed a text-book exemplar of predator-prey systems, the ciliates *Paramecium* (prey) and *Didinium* (predator). For ~80 years these model organisms have been instrumental in evaluating species interactions, temperature responses, and landscape dynamics (reviewed by Li et al. 2013). Specifically, we used clonal cultures of *Didinium nasutum* and *Paramecium caudatum* (obtained from Sciento, Manchester UK). Prey were maintained, following standard practices (Li et al. 2013), in Volvic® water containing 0.55 g L-1 protozoan pellets (Carolina Biological Supply, USA), which acts as nutrient resource for bacteria; pellets were crushed, and boiled for 30 min; then after cooling this was inoculated with the bacterium *Serratia marcescens* (a stock strain maintained at the Institute of Integrative Biology, University of Liverpool) and stored at 20 °C. Predators were also maintained in this media and fed prey*.*

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**Thermal responses of maximum specific growth rate and mortality due to starvation**

For >2 weeks prior to the experiment, the prey and predator were grown at satiating food concentrations (~108 bacteria ml-1, >40 prey ml-1, respectively, see Li et al. 2013) and were maintained at these levels throughout the growth experiment. Prior to measuring growth, both species were acclimated to temperatures for 48 h: 3, 6, 10, 13, 16, 20, 22, 25, 27, 30, and 33 °C. Individual predators (n = 12) were each placed in a 6-ml well, containing 4 ml of media and prey. Incubations lasted between 24 and 72 h, depending on the temperature, with no more than two generations occurring (i.e. conditions allowing exponential growth). Growth rate (d-1) was determined as the slope of *ln* abundance vs. time, with its mean and standard error determined from the replicates.

To determine mortality,thepredator was treated as above but was maintained in media with no prey. Individual predators were each placed in one of 75 6-ml wells containing 4 ml of media; this was repeated at each temperature. Abundance in each well was then determined daily. If numbers increases, one randomly selected individual was removed. Death was recorded if the predator was entirely immobile or absent. Mortality rate was then determined as the negative slope of *ln* abundance (over the 75 wells) vs. time, with the standard error determined from the slope of the response (see Minter et al. 2011).

**The effect of temperature on swimming speed and distribution of prey and predator**

Literature data were used to assess temperature effects on the swimming speed of the two species (see Fig. 1 legend). To determine the effect of temperature on distribution (i.e. thermal preference), prey and predators were first maintained at 20 °C for >2 d. Tests were conducted on the two species separately. For each, ~100 individuals were introduced to the centre fragment of a 5-fragment corridor (Fig. 2a). The corridor was treated in two ways: maintained at 20 °C across the fragments (i.e. a control) or subjected to a gradient from 8 to 32 °C across the corridor. Each treatment was replicated (n = 5). Abundance in each fragment was determined every 2 h, for 10 h. After 10 h the distribution of individuals had stabilized (Appendix S2), so only the 10 h data are presented. As total abundance differed slightly between replicates, data were converted to decimal fractions of abundance. To determine the extent to which temperature affected the distribution of the two species, linear regression was applied to the data (decimal fraction of total individuals in a fragment vs. temperature) for all replicates, both for the constant 20 °C treatment and for the temperate gradient treatment.

**Temperature effect on predator-prey dynamics in isolated and fragmented landscape**

For isolated populations, prey (5 ml-1) and predators (0.125 ml-1) were inoculated into 8 ml of bacterized media in 10-ml wells; these included ~2.5 mg ml-1 of crushed boiled rice as a slow release resource for bacterial growth (following methods of Cooper et al. 2012). Cultures were maintained at 10, 20, and 30 °C (n = 2) for up to 24 d, or until at least one species reached extinction. Abundance was determined twice daily. Although the volume of these incubations (8 ml) is smaller than the total volume for the metapopulation incubations (total 100 ml, see below), the temporal predator-prey dynamics in the 8 ml incubations at 20 °C was similar to that in 64 ml containers, of a similar depth, also at 20 °C (see Results and Cooper et al. 2012, Fig. 3e), suggesting that the 8 ml incubations are at least indicative of trends in larger volumes.

For metapopulations, a fragmented landscape (henceforth, a microcosm, Fig. 2b) that supports *Paramecium*-*Didinium* metapopulations (Cooper et al. 2012) was used. Microcosm fragment were filled with 4 ml of bacterized media and rice (as above), initially with 10 prey in each fragment and one predator in every other fragment (i.e. 12 predators in the 25 fragments). Microcosms were not interfered with over the time-course, except for briefly (~10 min) removing them from incubators for counting. To determine abundances, microcosms were examined under a dissection microscope (variable power). Species rank abundance in each fragment was recorded daily for up to 32 d. For logistic reasons (e.g. to reduce shifts in temperature) abundance (individuals well-1) was scored categorically (rank = abundance range, ml-1): for prey: 0 = 0, 1 = 1-5, 2 = 6-15, 3 = 16-45, 4 = more than 46; for predators: 0 = 0, 1 = 1-3, 2 = 4-9, 3 = 10-27, 4 = more than 27.

Two temperature regimes were applied to microcosms: constant temperatures of 10, 20, and 30 °C and a gradient (henceforth TG) ranging from 8 to 32 °C (Fig. 2c). Prior to experimental incubations, individuals were maintained at their respective temperatures for 48 h; for the gradient, individuals were acclimated at 20 °C (average across the gradient was ~20 °C). Treatments were replicated twice.

To investigate how treatments affected metapopulation dynamics within the microcosms, the level of synchrony of population across fragments was assessed by the Pearson product-moment correlation. Synchrony was calculated, independently for the prey and predator, from cross-correlations of specific growth rate: *ln* N*t*+1- *ln* N*t*, where N*t* is the abundance at time *t* (Bjørnstad et al. 1999, Dey and Joshi 2006, Vasseur and Fox 2009). Ranks were converted to mean abundances (cells ml-1) of the ranges they represented (see above): for prey: 0 = 0, 1 = 3, 2 = 10.5, 3 = 30.5, 4 = 90.5; for predators: 0 = 0, 1 = 2, 2 = 6.5, 3 = 18.5, 4 = 54.5. Two analyses of the coefficients of correlation were performed over time (18-32 days, depending on survival): for all the possible pairs of fragments (n= 300) and for just for pairs of fragments that were connected by a corridor (n= 40). These two analyses were conducted as the fragments across the landscape were not equally accessible; i.e. a population could only disperse directly to an adjacent fragment (Fig. 2b). We, therefore, first applied the simplest analysis, comparing all fragments, and then, recognising that synchrony will decay with distance (Bjørnstad et al. 1999), we applied a more stringent one, where only fragments that were directly connected were compared. Following recommendations of others (Holyoak and Lawler 1996, Fortin and Dale 2005, Dey and Joshi 2007), time-series were averaged, and means and standard errors from replicates treatment (10, 20, 30 ºC, TG) were determined. Linear regression was applied to the three uniform temperature-treatments, to assess if temperature affected synchrony. ANOVA followed by Tukey test was then applied across all treatments to assess how the TG-treatment differed from uniform treatments. All tests were performed using SigmaPlot 13, with α = 0.05).

**Results**

**Thermal responses of maximum specific growth rate, mortality rate, swimming speed, and temperature preference**

Food-saturated (maximum) prey growth rate increased monotonically between 3 and 30 °C, with a decrease at 33 °C; likewise, maximum predator growth rate increased monotonically between 6 and 27 °C, with a decrease above 30 °C (Fig. 1a). Ignoring the extremes, the slope of logpredator growth rate vs. temperature was significantly greater than the slope of the logprey growth rate (t-test, α = 0.05). When starved, predator mortality rate increased monotonically between 6 and 30 °C, with a substantial increase above 30 °C (Fig. 1b); ignoring the extreme at 30 °C, logpredator mortality rate exhibited a significant linear increase with temperature (t-test, α = 0.05). Prey mortality due to starvation was not assessed, as prey were always food-satiated in experiments.

Swimming speed of both species (Fig. 1c) exhibited significant linear increases with temperature, with no difference in their thermal responses (t-test, α = 0.05); swimming speed of the predator was on average ~0.6 mm s-1 faster than that of the prey (t-test, α = 0.05). Note though that these data from the literature do not cover the entire range examined in other parts of this study and may not be indicative of the entire range.

Dispersal incubations indicated that there was a significant increase in both species abundance at warmer temperatures (Fig. 1d,e), with predators exhibiting a stronger preference for warmer temperatures (t-tests, α = 0.05) and a larger proportion of the prey remaining at the colder end of the gradient.

**Temperature effects on predator-prey dynamics in isolated and fragmented landscapes**

Dynamics in unfragmented chambers, at all three temperatures, resulted in predator extinction, with the predator going extinct earlier as temperature increased. The prey were extirpated at the two lower temperature but persisted at the highest temperatures (Fig. 3a-f). In contrast, in the fragmented landscapes, the stability and persistence time of the predator-prey system declined with increasing temperature, with persistence of both species at 10 °C, predator extinction at 20 and 30 °C, and prey extinction at 30 °C, which would ultimately lead to predator extinction (Fig. 4). Landscape abundance maps (Fig. 5, Appendix S3) illustrate the wide and patchy spatial scale of metapopulation dynamics, which are also reflected by error bars (SE) on Fig. 4.

Dynamics in gradient-microcosms were initially stable over the incubation period but tended, over time, towards extinction or at least towards very low abundances of both species (Fig. 4g,h, Appendix S3). An emergent, aspect of gradient-driven dynamics was that both species tended to occur at or near 20 °C, the centre of the fragmented landscape (Fig. 5, Appendix S3).

Both analyses of metapopulation synchrony (i.e. examining correlations of all fragments and of only ones connected by corridors; see Methods) provided similar results: as temperature increased there was a significant linear increase (α = 0.05) in the predator’s tendency to respond similarly across fragments, indicating a reduction in metapopulation dynamics with increasing temperature (Fig. 6a,b). In contrast, temperature had no significant effect on the prey, although there appeared to be an increase in correlation coefficients. For the prey, ANOVA indicated no significant differences (α = 0.05) in the correlation coefficient across all treatments, while for the predator, ANOVA, followed by Tukey’s multiple range test, indicated that the correlation coefficient for the gradient treatment did not significantly differ from those at 10 or 20 °C but was significantly lower than that at 30 °C, for both methods of assessing the data.

**Discussion**

The success of organisms experiencing changes in thermal conditions is commonly evaluated using data on maximum rates (e.g. food saturated), and these are often obtained from a range of sources (e.g. Rose and Caron 2007, Kordas et al. 2011, Dell et al. 2011, Urban et al. 2015). Following this approach, we initially examined the growth, mortality, and swimming speed of our model species (Fig. 1; although the ranges of speeds do not fully match those of our growth and mortality data). In general, the predator has a more pronounced thermal response, indicating that as temperature rises, it will rapidly increase in numbers when prey are abundant and die rapidly when prey are scarce. Likewise, the increase in swimming speed of both species with temperature should reflect increased encounter, and thus a decrease in prey abundance by ingestion. Assuming these responses can be applied to evaluate temporal dynamics, we might then predict that the predator will increase its ability to drive prey to extinction with increasing temperature, at least between 10 and 20 °C and possibly closer to 30 °C. This logic can then be applied to generate and assess hypotheses concerning interactions between temperature and spatial structure.

Our time-series of abundance generally support the prediction that increased temperature will reduce predator-prey persistence. Critically though, there are differences in how isolated and fragmented landscapes respond to temperature. These data, and the subsequent analysis, should now provide empirical evidence to stimulate development of more complex, mechanistic models for evaluating temperature effects on predator-prey (and ultimately metacommunity) dynamics in natural landscapes (Kearney and Porter 2009, Buckley et al. 2010, Urban et al. 2012). Specifically, we suggest that temperature-driven dispersal and growth rates across landscapes may alter their ability to sustain metapopulations (i.e. temperature rise synchronises metapopulations, Thompson et al. 2015) and should play a key role in the development of predictive models (Urban et al. 2012, Tunney et al. 2014). Finally, we provide, to our knowledge, the first exploration of how thermal gradients can affect predator-prey dynamics across fragmented landscapes, testing two alternate hypotheses (see Introduction).

**Response to uniform landscapes**

Predator-prey dynamics in the unfragmented landscape (Fig. 3) support arguments that higher trophic levels exhibit greater temperature-sensitivity, leading to destabilised predator-prey dynamics (Voigt et al. 2003, Dell et al. 2011, Kordas et al. 2011). As anticipated from the thermal response (Fig. 1), predator extinction occurred earlier as temperature increased. However, the time for prey to be driven to extinction exhibited a different response: at higher temperatures, a reduction in the predator’s growth rate and an increase in its mortality rate (Fig. 1a,b) likely contributed to its demise, allowing the prey to escape extirpation (Fig. 3e,f). These trends parallel, and may help to explain, other meso- and microcosm work that indicates environmental warming is likely to drive upper trophic level taxa towards extinction (Petchey et al. 1999, Thompson et al. 2015).

Although the above trends are instructive and may apply to some ecosystems, they were not entirely paralleled by predator-prey dynamics in the more realistic fragmented-landscape. First, as might be expected, metapopulation dynamics extended the persistence of the predator-prey dynamics (Hanski 1999, Cooper et al. 2012) for days, and potentially indefinitely at 10 °C (cf. Fig. 3a,b; 4a,d). At higher temperatures, however, increased movement of both species (Fig. 1c) likely aided in homogenising distributions across the landscape, reducing benefits of unsynchronized metapopulation dynamics (Thompson et al. 2015). This is reflected in the synchrony analysis that reveals a significant reduction in predator metapopulation dynamics with increasing temperature (Fig. 6a,b). Critically though, in contrast to the isolated population dynamics, in the fragmented landscape at 20 °C the predator became extinct and the prey survived, while at 30 °C there was a tendency for extinction of both species (cf Fig. 3 c-f, 4c-f). Undoubtedly, a range of temperature-driven processes (e.g. those presented in Fig. 1, but also ingestion rate, conversion efficiency, and other vital rates) interact to influence the stabilising benefits of metapopulation dynamics. Consequently, observations associated from a limited number of thermal responses must be viewed with caution. For instance, it may be inappropriate to apply predictions form isolated populations dynamics to those of metapopulations or assume that fragmented landscapes will always increase the likelihood of maintaining biodiversity (Anderson et al. 2015).

**Response to temperature ecocline**

The fragmented landscape that was exposed to a temperature gradient provides further insights into temperature-driven predator-prey dynamics. As occurred for the single-temperature metapopulation dynamics, there seemed to be some stability imposed on the system by this fragmented landscape. However, there was a gradual decrease in both species, virtually to extinction for the predator (Fig. 4g,h), falling near those observed in the 20 °C fragmented landscape (Fig. 4c,d). This trend was somewhat reflected in the synchrony analysis that revealed similar levels between the temperature gradient and 20 °C landscapes (Fig. 6). In the Introduction, we offered two contrasting hypotheses regarding how a gradient might affect dynamics. Given the dearth of observational and modelling assessment on landscapes exposed to a temperature gradient, below, we explore these hypotheses and contrast plausible outcomes of such an ecocline against our observations.

For a metapopulation experiencing a temperature gradient, a range of predictions arise from the thermal responses (Fig. 1) and the time-series data at single temperatures (Fig. 3, 4a-f). For instance, as the predator has a preference for warmer temperatures and prey remain at cooler temperatures (Fig. 1d), the predator may become absent at the colder end of the gradient and this might create a prey-refuge, providing stability (Keppel et al. 2012). However, only when prey abundance was high did they occur in the coldest fragments, and as abundance decreased due to predation, there were virtually no prey in colder regions (Fig. 5, Appendix S3). Alternatively, warmer fragments might provide a prey-refuge where predators rapidly die due to starvation (Fig. 1b), as occurred in unfragmented landscapes (Fig. 3e,f), but this too was not so. Predators and prey were virtually absent from the warmest fragments, as presumably predators drove prey to extinction (i.e. as at 30 °C, Fig. 4e,f). Thus, warm and cold extremes did not seem to provide prey-refuges, as they may do over more extreme ranges (Tunney et al. 2014). Rather, both predator and prey populations peaked at intermediate temperatures (Fig. 5, Appendix S3).

The gradient, consequently, had a detrimental effect on species persistence, as the environmental ecocline gave rise to a biotic ecotone at intermediate temperatures. Concomitantly, the functional landscape was reduced, with fewer fragments occupied, leading to weaker metapopulation dynamics (e.g. Yaari et al. 2012). Ultimately then, this reduced landscape led to unstable dynamics that progressed towards extinctions. We suggest that such observations should encourage further investigations of distributions across natural thermal ecoclines, both experimentally and through field observations.

As a further caution, we note that recent studies have suggested that rapid evolution of predator-prey systems may occur in laboratory studies and in nature, altering predator-prey dynamics (e.g. Hiltunen et al. 2014). Such changes may then allow phenotypes to move to, and remain in, optimal fragments, following the “habitat matching” hypothesis (Jacob et al. 2015). Our work, however, was conducted on asexually reproducing, clonal populations that were sufficiently small to reduce the likelihood that species evolved over the ~30 day incubations. Furthermore, the ciliate macronucleus, which contains multiple copies of functional genes (Hausmann and Bradbury 1996) will be unlikely to express any mutations, to any great extent. It is, therefore, unlikely that such evolutionary shifts were a confounding factor in this study. However, further investigation over longer periods would clearly benefit from assessing genetic shifts across landscapes such as our model system.

**Summary**

Through meta-analysis, Cahill et al. (2012) revealed that few studies indicate that climate change is the proximal cause of species extinctions, and none show a direct cause due to species being forced to cope with levels outside their limits. Instead, they suggest species interactions, exacerbated by temperature changes, result in extinctions. We have explored how changing temperature and landscape alter predator-prey interactions (growth, mortality, movement, dispersal), potentially leading to extinctions. We show that fragmented landscapes do not sustain metapopulations at higher temperatures, with synchrony increasing with temperature across the fragmented landscape, likely arising from increased dispersal. Likewise, we indicate that a thermal ecocline does not necessarily offer structure that improves stability; rather it may force the species to occupy a smaller realized space, with ensuing detrimental effects. In short, we reveal that thermal accessibility, tolerance, and preference combine to drive complex predator-prey dynamics. These findings highlight the need for continued assessment of thermal responses on a range of factors (including and beyond those we measured) and the need to improve parameterisation of landscape-based thermal response models associated with metapopulations and metacommunities.*Acknowledgments* - There was no UK or Mexican funding for this study; all resources were obtained from slush funds from DJSM. HQ was supported by funding from Tianjin Agricultural University, China. WZ was supported by the National Nature Science Foundation of China. Thanks are given to several colleagues, the Editor, and two anonymous reviewers who provided comments on drafts of the manuscript. Thanks are also given to Oliver Beveridge for access to his data on swimming speed of *Didinium*.

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**Figure legends**

**Figure 1** Thermal responses for the preyandpredator (*Paramecium, Didinium*, respectively). a. For both species, the response of food saturated (maximum) specific growth to temperature. b. The response of specific mortality rate of the predator (in the absence of prey) to temperature. c. Response of swimming speed of both species to temperature; predator data were obtained from Beveridge et al. (2010); prey data were obtained from Tawada and Oosawa (1972), Tawada and Miyamoto (1973), Toyotama and Nakaoka (1979), and Bräuker et al. (1994) (see also Appendix S1); solid lines are the least squares regression though the data (grey points >30 °C are prey-values that are not included in the regression, as at these high temperatures there is a deviation from linearity), and dashed lines are the 95% CI. d, e. the dispersal response of both species (after 10 h, when the response stabilised, Appendix S2) in (d) a corridor (Fig. 2a) that experiences a temperature gradient (Fig. 2c) or (e) a constant “control” temperature of 20 °C; solid lines are the least squares regression though the data. For all panels, prey are represented by solid circles, predators are represented by open circles, and where presented error bars are 1 SE.

**Figure 2** Experimental microcosms. a. A corridor of 5, 6-ml wells (containing 4 ml of media), connected by 2.5 ± 0.5 mm holes, used for dispersal experiments. b. A fragmented landscape composed of 25, 6-ml wells (containing 4 ml of media), connected by 0.70 ± 0.15 mm holes, used for metapopulation experiments. c. The temperature gradient imposed on dispersal experiments and some metapopulation experiments.

**Figure 3** Predator-prey abundance in time-series incubations from unfragmented landscapes at three temperatures (a,b =10 °C, c,d = 20 °C, e,f = 30 °C); each temperature is replicated. Prey are represented by solid circles and predators by open circles.

**Figure 4** Predator-prey rank-abundance (see text) in time-series incubations from fragmented landscapes (Fig. 2 b) at three temperatures (a,b =10 °C, c,d = 20 °C, e,f = 30 °C) and in the landscape experiencing a temperature gradient (g,h; see Fig. 2c); each temperature is replicated. Prey are represented by solid circles and predators are represented by open circles. Error bars are 1 SE of the mean across the landscape, reflecting the range in rank abundance.

**Figure 5** Abundance maps as an indication of the spatial distribution of prey and predator across the fragmented landscape (Fig. 2b) at three temperatures (a = 10 °C, b = 20 °C, c = 30 °C) and in the landscape experiencing a temperature gradient (d, note: the top of the panel is cold and the bottom is warm, see Fig. 2c). These are examples-days from the time-series (day number in top right of panel) representing the initial distribution (Pre-bloom), the peak abundance across the landscape (Bloom), the distribution after the bloom (Post-bloom), and the distribution at the end of the time-series (End); for the full data set of both (replicated) time-series see Appendix S2. Species abundance is presented as rank abundances (see Methods for details). Note, the colour-contour algorithm approximates abundance across the landscape, resulting in fragments containing multiple colours; these maps thus represent trends rather than absolute levels.

**Figure 6** Synchrony analysis of predator and prey metapopulation dynamics (Fig. 4) across fragmented landscapes (Fig. 2b), experiencing constant (10, 20, 30 °C) or a temperature gradient (TG, see Fig. 2c). Two analyses of the coefficients of correlation were performed: (a) for all the possible pairs of fragments and (b) for just for pairs of fragments connected by a corridor (see Materials and Methods for details). Error bars are SE. The solid line indicates the significant increase in predator coefficients of correlation and temperature; dashed lines are the 95% CI.