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# Species interactions under climate change: connecting kinetic effects of temperature on individuals to community dynamics

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Human-induced climate change, dominated by warming trends, poses a major threat to global biodiversity and ecosystem functioning. Species interactions relay the direct and indirect effects of climate warming on individuals to communities, and detailed understanding across these levels is crucial to predict ecological consequences of climate change. We provide a conceptual framework that links temperature effects on insect physiology and behaviour to altered species interactions and community dynamics. We highlight key features of this framework with recent studies investigating the impacts of warming climate on insects and other ectotherms and identify methodological, taxonomic and geographic biases. While the effects of increased constant temperatures are now well understood, future studies should focus on temperature variation, interactions with other stressors and cross-system comparisons.

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# Introduction

Human activities induce a rapid climate change that poses a major threat to global biodiversity and ecosystem

functioning [1]. Increasing and more variable temperatures that dominate future climate scenarios will affect all biota on Earth including insects, the most diverse and abundant group of terrestrial animals, which provides key ecosystem services such as pollination [2,3]. Understanding how temperature effects on individuals scale up to communities is thus crucial to assess and predict the ecological consequences of climate change.

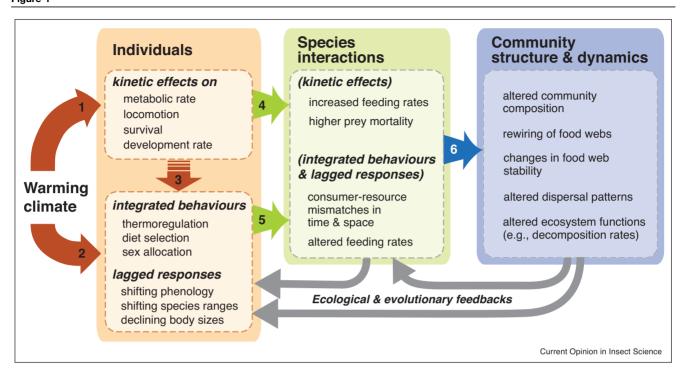
Altered temperature regimes can affect individuals, populations and communities directly and indirectly in multiple ways (Figure 1). Temperature directly alters metabolism and other physiological rates [4], modifying behavioural and life history traits of individuals [5,6] (Figure 1, arrows 1 and 2). These direct effects translate into altered species interactions (Figure 1, arrows 4 and 5), which in turn determine community structure and dynamics [7\*\*,8\*,9\*] (Figure 1, arrow 6) and provide ecological and evolutionary feedbacks on the individuals (grey arrows in Figure 1). We review recent evidence for this conceptual framework in insects with emphasis on species interactions, as both modelling [10] and experimental studies [11,12] show that trophic interactions modulate the strength of warming effects on individuals and communities. We omit related topics covered elsewhere in this issue: mismatches in predator and prey phenologies [13\*\*,14] and evolutionary and plastic responses to climate change [15,16].

# Recent advances: from individuals to species interactions

# Kinetic effects of warming on individuals

Environmental temperature directly underpins insect physiology and behaviour (Figure 1, arrow 1). Warming increases the kinetic energy of biochemical reactions, speeding up the rate of physiological processes to a maximum at an optimal temperature above which performance declines steeply [17]. Below the optimal temperature, warming leads to faster development (e.g. Refs. [18–20]) that often outpaces body growth and leads to smaller adult body sizes at warmer temperatures ([21], see below). More rapid development, fuelled by a faster metabolism (e.g. Ref. [22]), increases individual energetic demands and typically translates into higher feeding rates [23,24\*\*]. Higher feeding rates at higher temperatures can be driven by faster locomotion rates, more frequent encounters between individuals [25], or faster prey capture [26] (Figure 1, arrow 4).

Figure 1



Overview of the conceptual framework linking direct effects of warming on individuals (arrows 1 and 2) to species interactions (arrows 4 and 5) and communities (arrow 6). We distinguish the immediate kinetic effects of temperature on biological rates of individuals and the lagged effects on individual behaviour and lagged shifts in species range, phenology and body size that are driven by temperature directly and indirectly through its kinetic effects (arrow 3). Warming-induced changes in community structure and dynamics and in species interactions also feedback on individuals (grey arrows).

This body of evidence corroborates previous studies showing that warming strengthens plant-herbivore interactions [24\*\*,27] and predator-prey interactions [22,28,29] (but see Ref. [26]) including intraguild predation [30] and cannibalism [31] in various insect groups. However, warming can also decrease the impact of predatory insects on prey populations. Energetic demands typically increase faster with temperature than feeding rates [24°,32°,33] which, in the long-term, can lead to starvation, prolonged development [18] and population extinctions, particularly at higher trophic levels [34,35]. Such a loss of top-down control may partly explain the growing impact of insect pests on crop yields with climate change [36,37].

## Beyond kinetics: integrated behaviours

In addition to short-term kinetic effects, warming imposes mid-term lagged effects on insect behaviour, phenology and phenotypic traits (Figure 1, arrows 2 and 3). Many insects can sense temperature and actively modify their behaviour [38\*\*]. These 'integrated behavioural effects' include behavioural thermoregulation. thermal orientation and thermosensory behavioural adjustments (i.e. use of integrated thermal information to modify behaviours [38°°]). While insects are likely to display one or more of these integrated responses to warming, few studies assessed their implications for species interactions (Figure 1, arrow 5). For instance, the egg parasitoid Trichogramma euproctidis modulates offspring sex-ratio allocation, increasing the proportion of males at high and low temperatures [39]. This altered sex-ratio could affect the population dynamics of the parasitoid and feedback on the host population [40].

Temperature also influences diet selection in insects and other ectotherms [7\*\*,41–44] (Figure 1, arrows 2 and 3). Two hypotheses currently link temperature, diet selection and food quality (i.e. C:N:P ratios). Under the 'growth rate hypothesis' [45], warming increases demand for phosphorus, fuelled by increased growth rates [46,47]; and for nitrogen, owing to increased protein denaturation and turnover rates [48]. Under the 'respiration hypothesis', warming increases demand for carbon over phosphorus or nitrogen, as respiration increases faster than growth with temperature [49°]. Despite the mixed results of experiments investigating the thermal effects on diet selection [7\*\*,41,44] and the lack of consensus on the underlying mechanisms, both hypotheses highlight the potential for warming-induced shifts in trophic interactions in ectotherm communities. Such shifts could alter the structure and stability of ectotherm-dominated food webs (e.g. in freshwaters); recent modelling studies demonstrated that prey quality can influence food web dynamics [50] and that warming-related extinctions are driven mainly by the indirect effects of temperature on trophic links, rather than by its direct effects on individual physiology [51].

### Beyond kinetics, three lagged responses: shifts in species range, phenology and body size

Climate change can influence species' phenotypes and spatial distribution through plastic or selective processes, leading to shifts in geographical ranges, phenology, and individual body sizes [2,52] (Figure 1, arrows 2 and 3). Even though these responses are lagged, they have important consequences for species interactions [22,24\*\*] (Figure 1, arrow 5, and Figure 2).

The distributional ranges of many European butterflies shifted northwards by 35-240 km during the 20th century in response to climate change [53], although some species also shifted southwards in Britain [54]. Similarly high variation in species-specific distributional range shifts, attributable to delayed species responses, differences in physiological constraints and alternative drivers of change, was reported in British ground beetles and grasshoppers [54]. These species-specific rates and extents of distributional range shifts may induce spatial mismatches in interacting species and disrupt current ecosystem processes, but this phenomenon is poorly understood [55].

Warming also influences the phenology of insects and their host plants. The green cover period lengthens by 3-4 days per decade due to advancing spring events and delayed leaf fall in autumn [56]. These phenological changes may lead to temporal mismatches between species and alter trophic and mutualistic interactions [13<sup>\*\*</sup>], covered elsewhere in this issue [14].

Finally, ectotherm body sizes vary systematically within and between species with temperature [52,57\*\*,58]. Decreasing body sizes with warming, known as the temperature-size rule [57\*\*], are common in insects, and documented long-term trends in body size have been linked to climate change [58]. The magnitude of body size change with temperature varies among insect taxa and habitats, with stronger size reductions in aquatic species and weaker or even reversed responses in terrestrial ones [59-61]. Absolute and relative consumerresource body sizes are key determinants of trophic interaction strengths and food web structure. Warming may thus indirectly alter predator-prey size ratios and modify species interactions and community dynamics [62,63] (Figure 1, arrows 5 and 6, and Figure 2). As aquatic food webs are more strongly size-structured than terrestrial ones, the ecological consequences of body size reductions are predicted to be stronger in aquatic than in terrestrial systems [8°].

#### Summary of current evidence

Temperature strongly influences the kinetic energy of biochemical reactions, which scales up to affect insect physiology, behaviour and interactions. Temperature can also induce lagged effects on the behaviour, spatial distribution, phenology and phenotypic traits of insect species. These can modulate the extent of the kinetic effects of temperature on insects as described above (Figure 1, arrows 1-3). While both the kinetic and lagged effects of warming are likely to be important for insects, as well as their interactions, most studies focused on the kinetic effects of temperature.

# Recent advances: from species interactions to community dynamics

# Importance of species interactions for population and communities in a warming world

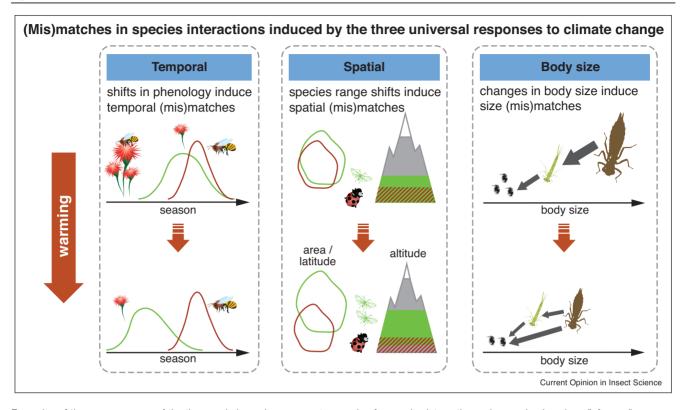
Species interactions are important for ecosystem stability and resilience to warming (Figure 1, arrow 6, and Figure 3). For example, impacts of herbivory on plant distribution can modify plant responses to climate change [10], as plantherbivore interactions can mediate the transition between dominant vegetation types at higher temperatures [10]. On the contrary, host-parasitoid interactions were found to alleviate the negative effects of heat shocks on aphid survival [12], suggesting that community complexity may buffer the negative effects of warming on individuals and populations as proposed in Ref. [11]. Even though trophic complexity may shield populations and communities, warming is likely to reduce this complexity and lead to cascading effects. The persisting species in altered communities may experience stronger negative effects of warming, that may further accelerate their decline [11] and increase the likelihood of regime shifts.

#### Effects of warming on community structure

Warming leads to long-term changes in ecological communities (Figure 3). For example, Floury et al. [64] found warming to increase functional diversity of invertebrates in streams and rivers across France. Long-term data on European freshwater communities show that vulnerability varies across functional groups, and species composition tends to shift towards generalist and tolerant species that often are or become invasive [64,65].

Community structure and food webs can be further modified by phenology mismatches, distribution range shifts and altered species interactions induced by warming ([14], arrow 6 in Figure 1, and Figure 2). Current theory predicts that warming-induced impacts on community structure and dynamics, owing to altered species interactions, depend on both direct and indirect thermal effects [9°]. Warming-induced changes in species composition or abundance can have cascading effects on other trophic levels [65]. For instance, Lister and Garcia [66] showed that climate warming decreased the abundance of

Figure 2



Examples of the consequences of the three main lagged responses to warming for species interactions: changes in phenology (left panel), distribution (middle) and body size (right); all of which can substantially alter species interactions. While changes in phenology and distributional areas are better understood in terrestrial ecosystems, the effects of changing body size are particularly important for aquatic habitats. Trophic link strength (right panel) indicated by arrow width; relative population sizes indicated by numbers of individuals.

forest arthropods, leading to a restructuring of the tropical forest food web in Puerto Rico.

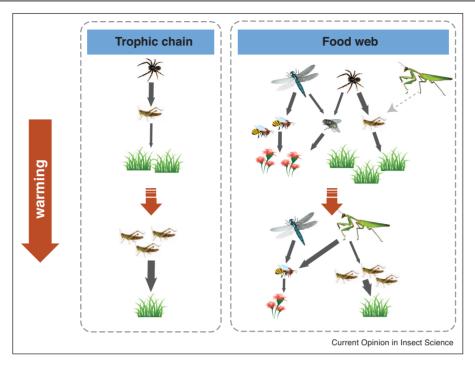
Asymmetric behavioural responses of predators and herbivores to warming can also affect trophic interactions, with potential cascading effects on local plant communities. A long-term mesocosm experiment using Pisuarina mira spiders (predator) and Melanoplus femurrubrum grasshoppers (prey) showed that, depending on the time of the day, warming can either weaken or strengthen a trophic cascade as spiders seek thermal refuge or become more active, with knock-on effects on grasshopper grazing pressure [67]. A field transplant experiment with five coupled populations of these two species found that the spiders selected cooler sites than the grasshoppers, which were less sensitive to warming. This led to reduced top-down control and higher grazing pressure, which in turn altered plant community composition [68].

#### Effects of warming on community stability

Beside structural changes, temperature-driven changes in consumer phenotypes at different trophic levels may lead to stabilizing or destabilizing cascading effects on communities (Figure 1, arrows 4-6). Decrease in stability is often predicted, as responses to warming vary across trophic levels [25,69,70] and thermal sensitivity varies substantially within and among species [71,72]. Plantherbivore interactions can also influence ecosystem resilience, increasing the rate of short-term responses of the vegetation to climate change (initial resilience) and reducing the long-term rate at which equilibrium is restored (asymptotic resilience) [10].

The generally greater thermal sensitivity of parasitoids, compared to their hosts, suggests that warming may disrupt the synchrony of host-parasitoid interactions [73] and lead to increased host abundance and fluctuations (e.g. in aphid-parasitoid interactions [74]). However, sensitivity does not always change monotonically with trophic level or body size, with potential implications for multi-trophic systems. For example, the critical thermal maximum (CT<sub>max</sub>) of the parasitoid wasp Cotesia congregata is substantially lower than in both its host caterpillar Manduca sexta and its own parasitoid wasp Conura sp. [71]. Similarly, a study on ant-hemipteranplant communities showed that plant growth and ant activity increased with temperature, while the hemipteran growth, abundance and size decreased [75].

Figure 3



Warming impacts community structure and dynamics through its effects on species interactions (solid lines; both trophic and non-trophic) and dispersal (dotted line). Typical responses include top predator losses that can trigger trophic cascades or change ecosystem stability, especially in simple communities (left panel). Arrival of more tolerant and often invasive species can rewire the entire food web (right panel). Community and food web complexity may buffer against these changes, owing to functional redundancy and multiple interactions (left versus right panel). Interaction strength indicated by arrow width; relative population size indicated by number of individuals.

# Effects of warming on dispersal and metacommunity dynamics

Along with species interactions, warming can alter species dispersal [76], but their combined effects remain poorly explored. Temperature affects dispersal rates directly by changing body size, behaviour and phenotypes (Figure 1, arrow 1), or indirectly by prompting dispersal away from low-quality resource patches [77] (Figure 1, arrow 6). For instance, Wang et al. [78] found that warming reduces the proportion of winged aphids, in turn altering their top-down control by ladybeetle predators. Warming may also affect arrival times and priority effects, leading to significant changes in communities and metacommunities, since early arrival offers competitive advantage [76]. Increased connectivity observed in metacommunity experiments suggests that higher dispersal rates may counter biodiversity loss resulting from warming [79].

Dispersal decisions depend on the quantity and quality of local resources. Grainger and Gilbert [77] showed that, in the absence of resource limitations, warming did not affect dispersal and benefitted herbivore insects by increasing population size. Under resource limitations, increased dispersal rates and declines in insect populations are expected [77]. This suggests context-dependent effects of warming on dispersal rates, modulated by

resource availability and competitive interactions. Altogether, these results imply that climate warming will trigger restructuring of insect communities, but more studies are needed to determine the frequency and magnitude of these structural changes.

#### Summary of current evidence

Temperature-induced changes in species abundance, interactions and dispersal directly or indirectly impact community structure and ecosystem functioning. Evidence is mounting that warming will restructure communities. The various context-dependent warming effects on communities are also reliant on the system complexity and, therefore, difficult to disentangle. However, despite the inherent challenges, studies at higher levels of organisation will be critical to understand warming effects on biodiversity.

#### **Future directions**

Given the unpredictable nature of climate change over long timescales, robust predictions of climate change impact on species interactions and their consequences for community structure and dynamics remain elusive. While the effects of increased constant temperatures are now reasonably well understood, we argue that future studies should focus on temperature variation,

interactions with other stressors and comparisons across a wider range of taxa and systems.

In addition to warming, natural populations also experience predictable seasonal and daily variation, stochastic variation and extreme temperatures (e.g. 'heat waves'), which are projected to increase with climate change [80,81]. A recent review showed that thermal performance curves may be used to predict the effects of daily variation and heat waves on species interactions [82°], but data on many groups and community-level consequences are lacking.

Little is known about the interacting effects of temperature with other abiotic (e.g. pollution, eutrophication and droughts) [65] and biotic stressors (e.g. invasive species). Such interactions increase the risk of cascading effects and may strongly impact ecosystem diversity and functioning. For example, warming may accentuate drought and increased rainfall effects on the fitness of herbivorous insects and their predators by modulating food quality and predator-prey interactions [83,84]. In aquatic communities, warming and altered rainfall can have opposite effects on different functional groups [65]. Changes in rainfall are particularly important in small water bodies such as tank bromeliads, in which they disrupt trophic relationships [85]. Furthermore, warming may remove or weaken environmental barriers and thus facilitate the expansion of invasive, often cold-limited species (Figure 3), and change the nature of their impacts [34].

Despite recent advances, we also lack data on the effects of warming in many taxa and ecosystems, and have to rely on generalizations. Among terrestrial insects, current knowledge derives from several model tritrophic systems such as plant-aphid-parasitoid and plant-grasshopper-spider systems. Among aquatic insects, warming effects are best understood in larval odonates. Future work should encompass underrepresented taxa, such as wood-boring insects or aquatic insects breathing atmospheric oxygen.

Moreover, current research carries a temperate zone bias [86], although changes in trophic interactions driven by climate change are particularly relevant for Arctic and tropical regions. The Artic will experience the highest rates of temperature increase, with potentially high increases in invertebrate herbivory [27]. Tropical arthropods, due to their lower thermal tolerance, are highly vulnerable to climate warming [87] that has been identified as the main driver of arthropod abundance declines in a Neotropical rainforest, with strong impacts on higher trophic levels [66].

Finally, short-term effects of warming on the kinetic effects and trophic interactions (Figure 1, arrows 1 and 4) are much better understood and supported by theory [4,25]. Considerably less is known (but see Ref. [67]) about how changes in species interactions, measured over hourly to daily timescales, translate into long-term, multi-generational changes in complex communities (Figure 1, arrow 6). To this end, studies on thermal effects should also look beyond trophic interactions and investigate other interaction types such as non-trophic interactions or habitat provisioning [28].

## **Declaration of Competing Interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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