REVIEW

Mechanisms driving change: altered species interactions and ecosystem function through global warming

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Summary

1. We review the mechanisms behind ecosystem functions, the processes that facilitate energy transfer along food webs, and the major processes that allow the cycling of carbon, oxygen and nitrogen, and use case studies to show how these have already been, and will continue to be, altered by global warming.

2. Increased temperatures will affect the interactions between heterotrophs and autotrophs (e.g. pollination and seed dispersal), and between heterotrophs (e.g. predators-prey, parasites/pathogens-hosts), with generally negative ramifications for important ecosystem services (functions that provide direct benefit to human society such as pollination) and potential for heightened species co-extinction rates.

3. Mitigation of likely impacts of warming will require, in particular, the maintenance of species diversity as insurance for the provision of basic ecosystem services. Key to this will be long-term monitoring and focused research that seek to maintain ecosystem resilience in the face of global warming.

4. We provide guidelines for pursuing research that quantifies the nexus between ecosystem function and global warming. These include documentation of key functional species groups within systems, and understanding the principal outcomes arising from direct and indirect effects of a rapidly warming environment. Localized and targeted research and monitoring, complemented with laboratory work, will determine outcomes for resilience and guide adaptive conservation responses and long-term planning.

Key-words: ecosystem function, ecosystem service, global warming, heterotrophs, resilience

Introduction

Recent global warming has been attributed to anthropogenic influence (Oreskes 2004; IPCC 2007), with one corollary being elevated species extinctions beyond background rates due primarily to the rapid rate of warming and a template of already degraded ecosystems globally (Thomas *et al.* 2004; Stork 2010). The last decade, and the last 5 years in particular, has witnessed a veritable explosion of ecological research quantifying the climate change–extinction nexus (Parmesan 2006; Brook, Sodhi & Bradshaw 2008; Dunn *et al.* 2009; Venter *et al.* 2009).

Global warming describes much more than elevated mean temperatures across biomes. It accounts for an increase in both minimum and maximum temperatures, with daily minimum temperatures rising more rapidly than maximum temperatures (Vose, Easterling & Gleason 2005). The ability of species to adapt to such changes will determine, to a large extent, the survival and reproduction of that species (Visser 2008). Further, higher temperatures will affect the interactions between auto- and heterotrophs, and organism phenology, leading to as yet unpredictable shifts in community structure and ecosystem function (Convey *et al.* 2002; Edwards & Richardson 2004).

Ecosystem function includes the processes that facilitate energy transfer along food webs, and the major processes

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that allow the cycling of carbon, oxygen and nitrogen. 'Function' also includes ecosystem services such as provision of food and material to humans, the regulation of climate, provision of clean water and fertile soils (see Hector & Wilby 2009). These are in turn influenced by the numerous interactions that occur within and among species, as well as between species and environmental gradients such as rainfall, temperature and geology.

As a general rule, ecosystem function is most resilient to change from disturbance where species diversity, or key functional species groups, are maintained (Fischer, Lindenmayer & Manning 2006). The loss of diversity through anthropogenic influence, such as habitat loss and over-harvest, is well documented as the primary form of such disturbances globally (Milner-Gulland, Coulson & Clutton-Brock 2000). In addition, recent retrospective studies have linked both climatic shifts and human predation to extinction events over longer time scales (such as the Eurasian mammoth *Mammuthus primigenius* – Nogues-Bravo et al. 2008). No doubt, habitat loss, harvest and the proliferation of invasive species will continue to act concomitantly with global warming to drive further extirpation of species (Brook et al. 2008), and while more studies discuss present-day decline in population abundance or range through climate change (see Ford et al. 2009; Gibson, van der Marel & Starzomski 2009), relatively little is known about the bottom-up loss of important ecological processes that will affect ecosystem functions (although see Wilmers et al. 2006).

Some empirical evidence does already suggest a shift in ecosystem processes through climate change; examples include modification of the carbon cycle via changes to vegetation structure (Cramer et al. 2001; Bradshaw, Warkentin & Sodhi 2009), alteration of net primary production, soil nitrogen cycling (Melillo et al. 1993) and pollination patterns (Fitter et al. 1995). Moreover, elevated temperatures can disrupt species interactions through shifts in phenology, survival, symbioses and other related pathways. For example, changes in dung beetle guild structure brought about by ambient warming can affect nutrient recycling and in turn modify herbivore foraging behaviour and distribution (Dunn et al. 2009).

An understanding of the mechanisms by which warming will affect ecosystem function has consequences beyond conservation biology. Indeed, basic services such as pollination have far-reaching implications for human society. Some recent studies have focused on the effects of climate change on species interactions, such as predator-prey (Parmesan 2006; Traill et al. 2009), parasite-host (Hance et al. 2007) and even invasive-native interactions (Occhipinti-Ambrogi 2007). To date though, there is no synthesis of the mechanisms behind shifts in ecosystem function through global warming.

To address this deficiency, we review (with case studies) the mechanisms of change of ecosystem function under rapid modern warming. We focus on animal species across taxa (heterotrophs) and across biogeographical regions, but exclude bacteria and fungi. We provide recommendations on how research and long-term monitoring projects can tease apart the mechanisms of change under projected global warming, thereby allowing adaptive response to prevent species extinctions. These will also help prevent the collapse of key ecosystem services such as pollination that underpin agricultural economies. Our review of the concept of function *per se* is necessarily cursory, as adequate description of this can be found in the primary and summarized literature (for example, Levin 2009). Further, our aim is not to document knowledge on ecosystem function; rather, we review how global warming will alter species interactions (and subsequent function), thereby providing background for targeted research. We address a paucity of information available for how warming will affect species interactions, rather than focus on single species or species-ecosystem interaction under global change (see also Meltofte et al. 2008).

Ecosystem function

The functioning of ecosystems is best seen as an umbrella term for a number of processes that operate within a system, and that ultimately facilitate the biogeographical flow of energy within and between ecosystems (Tilman et al. 2001; Levin 2009). Ecosystem *processes* include primary production and nutrient cycling (Vitousek et al. 1997; Hooper et al. 2005). Ecosystem *services* are an aspect of functions that are beneficial to humans, such as the provision of food and natural material and the sequestration of CO_2 (see Hector & Wilby 2009).

To go further, species interactions will influence the outcomes of ecosystem process and service in a number of ways. One obvious example is that of pollination – a result of a mutualistic interaction between animal and plant species. Species interactions can be neutral, mutualistic, commensal, competitive, predatory or parasitic. Nonetheless, the outcomes of such interactions will determine the extent of primary production and energy transfer along a food web (Hector & Wilby 2009). As a general rule, diverse communities tend to be more resilient to change and are thus favourable to the long-term maintenance of ecosystem function under environmental flux (Fischer et al. 2006).

Primary production is the first and basic form of energy storage following photosynthetic activity. Secondary production involves the assimilation of energy through consumption of primary producers (Hooper et al. 2005). Energy flow describes the route taken by energy from autotrophs through herbivores to higher trophic levels and eventual dissipation as heat (both through grazing and detrital chains). Nutrient processing includes the carbon, nitrogen, phosphorous, sulphur and oxygen cycles.

Global warming

There are many data available that support recent global warming, principally from observations of increased global mean air and ocean temperatures (Hansen & Lebedeff 1987; IPCC 2007). Indeed, the past decade ranks among the warmest in recorded history, with a 100-year linear trend (1906–2005) of 0·74 °C per year (IPCC 2007).

Observed recent warming patterns have revealed that raised temperatures vary not only seasonally, but are disparate across biogeographical regions (IPCC 2007; Visser 2008), with obvious implication for endemic species (Pounds, Fogden & Campbell 1999). Human activity is partly responsible for increased temperatures, that is, over-and-above background warming through solar irradiance and volcanism (Crowley 2000). We do not review global warming evidence or its causes; we focus instead on its observed and anticipated effects on ecosystem function. Adequate reviews of global warming are provided by the IPCC (2007), ACIA (2005) and Crowley (2000), and the consequences of this for species persistence by Walther *et al.* (2002), Thomas *et al.* (2004), Parmesan (2006) and Brook *et al.* (2008).

Mechanisms of change through global warming

ECOSYSTEM PROCESSES

Primary production

Actual production by autotrophs will be influenced largely by increased CO_2 concentration arising from climate change (see for example Melillo *et al.* 1993; Cramer *et al.* 2001). While warmer temperatures are anticipated to increase primary production (particularly in temperate regions), some studies suggest that high temperatures will engender a drop in gross primary productivity (Ciais *et al.* 2005). Laboratory-based research has also shown that warmed communities disproportionately lose top predators and herbivores, and become increasingly dominated by bacterivores and autotrophs (Petchey *et al.* 1999). Without doubt, the complexity of changes in productivity through climate change is enormous, and region-specific studies are required. As such, our review focuses on heterotrophs and warming and provides recommendations on how warming (and its effect on key heterotrophs) can be monitored.

Nutrient cycling

While there are a number of biogeochemical cycles that link biological systems, we hypothesize that warming will affect these mainly through changes to animal respiration, excretion and mortality. Much has been written on the increased concentration of CO_2 in recent times through the release of stored organic carbon as the burning of oil, coal and natural gas (e.g. Cox *et al.* 2000; Zachos *et al.* 2001), but less is known about the roles heterotrophs will play in a revised (warmer) system. Increased respiration and mortality will facilitate nutrient recycling, but of course autotrophic response to warming will be dissimilar across biogeographical regions, with differing rainfall regimes, mean temperatures and human use driving unique interactions (e.g. Melillo *et al.* 1993).

Species temporal response to warming will be seasonal (through phenology) and evolutionary by way of long-term adaptations (or failure of). Such scale of species'

response is also spatial, with localized, site-specific adaptations and broad-scale response to events such as El Niño (Forchhammer & Post 2004).

Dung beetles are an exemplar case study because these insects play an important role in the facilitation of nutrient recycling of animal waste. The endotherm *Geotrupes mutator* displays two well-defined thermoregulatory strategies throughout the day (Mena 2001). This species increases body temperature endogenously above ambient temperature to allow active search of dung pads by flying, whereas crepuscular and autumn-winter activity are possible by means of regional endothermy. Elevated temperatures can therefore confer enhanced foraging and activity during crepuscular and cool periods, consequently driving increased nutrient cycling. Competitive interactions will also be altered, with smaller dung beetle species that are restricted to daytime activity able to shift their niche and potentially compete with larger species (Davis 2002).

ECOSYSTEM SERVICES

The ecosystem services providing benefit to human society will be largely affected by global warming through the interactions that animals have with primary producers, such as the pivotal roles played by seed dispersers and pollinators. Ecosystem service implies more than just the provision of agricultural produce and timber supply; it also entails consumption of autotrophs such as domesticated and harvested animals. Even the provision of clean fresh water is a critical service (Verhoeven *et al.* 2006). Indeed, the study of ecosystem services is large, as many species directly or indirectly contribute to a service that is beneficial to humans.

We deal with this topic by focusing on case studies that provide examples of the ways by which warming can alter the interactions among species, and how these will lead to a shift in ecosystem function. First we address some of the changes expected in species' life history via elevated temperatures, including survival and recruitment, behaviour and distribution. We then discuss the mechanism of change that will occur at the population and species level with use of case studies.

LIFE HISTORY STRATEGIES

Survival and recruitment

Heterotrophs generally exhibit wide thermal tolerance. In extreme environmental conditions such as subfreezing winter temperatures, however, survival depends primarily on an animal's physiological tolerance envelope. Some animal species (mainly ectotherms) are freeze-intolerant and cannot overwinter in such regions (Block 1990). With rapidly increasing minimum winter temperatures reported due to global warming (Karl *et al.* 1991; Easterling *et al.* 2000), animal populations that experienced historical population reductions during the coldest season can now persist for longer and in greater numbers during the increasingly favourable winter

conditions. For example, in northern populations of the southern pine beetle *Dendroctonus frontalis*, it was proposed that a 3·3 °C increase in winter temperatures, from 1960 to 2004 facilitated beetle prepupae persistence during winter (Tran *et al.* 2007). On the other hand, in the highland forests of Monteverde, Costa Rica, population crashes of anurans are likely to have arisen because of a decline in mist frequency brought about by rising temperatures (Pounds *et al.* 1999).

An increase in mean or seasonal temperatures can affect species survival, and modify reproductive output and the duration of development (with recruitment defined as the proportion of offspring that survive to adulthood). In general, an increase in environmental temperature reduces developmental time in many insect species (Glenn 1922; Barlow 1962), such as the larvae of the nymphalid butterflies *Algais urticae*, *Inachis io* and *Polygonia album* (Bryant, Thomas & Bale 2002). Of note however, is that increased recruitment can be reversed where increasing temperatures cross optimal thresholds.

Phenological response

Rising ambient temperatures have been linked to changes in animal phenology, such as altering the emergence patterns of the tea leaf roller *Caloptilia theivora* (Satake *et al.* 2006) and some British butterflies (Sparks & Yates 1997). The reproductive phenology of other species has also changed in response to rising global temperatures (Hill, Thomas & Huntley 1999). For example, the estimated increment of 2 °C in annual temperature (from 1895 to 1998) has shifted semi-voltine to synchronous univoltine populations of the mountain pine beetle *Dendroctonus ponderosae* (Logan & Powell 2001).

Although phenological changes in species with temperature-dependent maturation rates can assist population growth in some cases, the reproduction and development duration of other organisms can be negatively affected by rising temperatures (Leather 1984). This is exemplified in the decreased survival of the hatchlings of red-eared slider turtles *Trachemys scripta elegans* due to residual yolk mass declines when exposed to warmer periods during post-hatching dormancy (Willette, Tucker & Janzen 2005). Such warming can also adversely affect ectotherm energy reserves through the elevated rate of store depletion that compromises survival during periods of nutritional stress generally occurring at obligate non-feeding stages (Willette *et al.* 2005). Further, synchronous relationships between consumers and resources such as predator-prey and herbivore-plant interactions, are at times based on a similar phenological response, but where these cues are slightly different, the shifts in seasonal temperatures will alter these (see Aizen & Patterson 1995), with potential for co-extinctions (Dunn *et al.* 2009).

Colouration

Animal colouration itself has many adaptive functions, not least of which is its role in mitigating body temperature

fluctuations for optimal physiological processes such as thermoregulation. The success of many (insect) species under global warming will be the ability to respond favourably to this. Behavioural preference of a habitat characterized by a specific thermal range can also be important for some animals, particularly when warming permanently alters the organism's colourations (see Lowe & Taylor 1964). For example, transient heat and cold shock exposure in the pupa of the butterfly *Colias eurytheme* alters the ultraviolet brightness and angular breadth of colour reflectance (Kemp, Vukusic & Rutowski 2006); a separate experiment on the same species using thermal shocks administrated during metamorphosis showed similar results in alteration of colour properties (Kemp & Rutowski 2007).

These thermal treatments strongly suggest that changes in temperatures can alter animal colouration permanently and indirectly affect the individual's physiology and appearance, thus potentially altering predator-prey dynamics and intraspecific interactions. Indeed, colouration plays a large part in prey selection among predatory invertebrates, with the potential for warming to alter selective pressures (see Losey *et al.* 1997).

Behaviour

The concomitant rise of seasonal temperature variation with climate change (Easterling *et al.* 2000) can adversely affect the development of behavioural thermoregulation; for instance, higher variance in incubation temperature compromises the post-hatching thermoregulatory behaviour of the Madagascar ground gecko *Paroedura pictus*, (Blumberg, Lewis & Sokoloff 2002). In coding moths *Cydia pomonella*, unmated adults select the lower extreme of temperature gradients to increase longevity and crypsis in the tree canopy (Kuhrt, Samietz & Dorn 2006). Elevated temperatures are also likely to alter animal behavioural responses and activity patterns. For example, the scarab beetles *Macrodactylus subspinosus* and *Popillia japonica* exhibit their strongest responses to chemical stimuli (pheromone attractants) at specific combinations of light and temperature (Heath, Williams & Phelan 2001). Warming will alter this response, with subsequent repercussions for breeding activity. Increased temperatures also enhance activity; for example, reproduction, biting activity and the rate of pathogen maturity in mosquito species rise with increasing temperature (Epstein 2001).

Range

Shifts in temperatures across the globe, and the variation within this (IPCC 2007) will initiate range shifts in some populations, particularly of specialized species adapted to specific environmental conditions. Regional warming has, for example, affected the geographical distribution of the checkerspot butterfly *Euphydryas edithai*, where the entire range of this species shifted northwards (Parmesan 1996). Indeed, in testing the effects of global warming on geographical shifts, Bryant *et al.* (2002) found that habitat shading (temperature

reduction) reduced development time in the nymphalid butterflies *Aglais urticae* and *Polygonia album*. Computer simulations predicted that projected temperature changes will result in a northward shift in these species' distributions by *c.* 200 km, and the extent of bivoltinism will shift northwards by *c.* 300 km (Bryant *et al.* 2002).

COMPLEMENTARITY

'Complementarity' describes the numerous interspecies interactions that facilitate ecosystem process and ultimately, function (Levin 2009). Here, we discuss some of the ways that global warming will alter the interactions between species, with case studies provided as examples.

Pollination and seed dispersal

Pollination plays an important role in agriculture, with many crops (*c.* 60%) dependent on natural pollination (Kearns, Inouye & Waser 1998; Allen-Wardell *et al.* 1998). The process, as well as seed dispersal, exemplifies ecosystem services to humankind. Climatic variation will modify (evolutionary) selection on flowering phenology as growing seasons expand or contract, which in turn will modify biotic interactions (Elzinga *et al.* 2007).

In two species of tropical wet forest, fragrance-foraging *Euglossa* and *Eulaema* bees, foraging behaviour is influenced by variation in the thermal environment. In particular, foraging is limited by low air temperatures in the morning and overheating in the late afternoon (Armbruster & Berg 1994), so predicted increases in temperature will limit the time available for pollen-collecting behaviour. Similarly, the early advancement of spring (due to elevated temperatures) resulted in the seed-set of bumblebee-pollinated *Corydalis ambigua* and small bee-pollinated *Gagea lutea* declining markedly relative to that of the fly pollinated plants *Adonis ramose* and *Anemone flaccida* (Kudo *et al.* 2004). Hence, warming can affect pollinator type as well as seed production in spring ephemerals, with more pronounced effects predicted for bee-pollinated plants (Kudo *et al.* 2004). Thermal radiation will further affect the behaviour of pollinators. For example, pollen germination of the Mediterranean marigold *Calendula arvensis* is limited by temperature. The fly *Usia aurata* foraging on *C. arvensis* captures heat passively from the inflorescences in order to warm itself sufficiently to sustain flight (Orueta 2002). Warming will provide *U. aurata* flies the opportunity for more foraging time, and less time required for basking.

On the other hand, pollination could decrease through increased ambient temperature. The downy inflorescences of the Himalayan snowball *Saussurea medusa* maintain higher-than-ambient temperatures to protect reproductive cells. Thick, hollow stems and overlapping bracts with epinasty (downward curvature) serve to retain heat in many species (Tsukaya, Fujikawa & Wu 2002). Heat accumulation within these inflorescences attracts pollinators in an otherwise cool environment (Kudo 1995), and

therefore elevated ambient temperatures could result in fewer potential pollinators.

As another example, the volatile compounds of some plants such as cycads have an important role in an odour-mediated push-pull pollination strategy (Terry *et al.* 2007). During pollination, *Macrozamia lucida* cones heat to 12 °C above ambient temperatures, with nearly a 200 000-fold increase in volatile emissions. Specific chemical components attract and repel the thrips *Cycadothrips chadwicki* from male cones, where pollen is available (Terry *et al.* 2007). It is plausible that an increase in temperature could disrupt this pollination process by interfering with cycad volatile emission, the thermal stability of the chemicals involved and the behaviour of pollinating thrips.

Seed dispersal is an essential process whereby future generations of many plant species depend on animal dispersers, and much of a disperser's ability depends on how environmental temperature affects the parent plant, or its own phenology. In New Zealand, increased temperatures could potentially enhance pre-dispersal insect seed predation, and reduce the ecological dominance of grasses such as those from the genus *Chionochloa* (McKone, Kelly & Lee 1998). Complex interactions among ant communities are, in part driven by temperature (Cerda, Retana & Cros 1997). Dominant ant species with low thermal tolerance displace their foraging activity towards dusk and dawn, whereas temperature-tolerant species forage during warmer periods to take advantage of reduced competition. Heat-tolerant species that forage at high temperatures might have a set of traits that makes them effective dispersers, a hypothesis derived from the observation that relatively heat-tolerant species have generally broader feeding spectra and can exploit scarce food items. Four of the ant species studied by Boulay *et al.* (2007) were effective dispersers of *H. foetidus* seeds. A rapid temperature increase also precedes carpel dehiscence in *H. foetidus*, thus potentially altering the interaction between *H. foetidus* and the associated ant community.

Predator–prey interactions

Climate warming has many repercussions for predator-prey interactions and herbivory (Wilmers, Post & Hastings 2007). Warming can influence the growth and recruitment of plants under herbivory (Holmgren *et al.* 2006), although elevated temperatures can also reduce the effect of herbivory through increased plant growth rates. Elevated temperatures also allow foraging over longer periods, or into regions that might have not been previously accessible to herbivores. For example, the increased abundance of invasive mountain pine beetles has led to the death of numerous lodge-pole pines that were formerly immune to infestation (Raffa & Berryman 1983). Likewise, recent warming possibly resulted in range expansion of the geometrid moths *Operophtera brumata* and *Epirrita autumnata* (Jepsen *et al.* 2008).

In larger ungulates such as caribou *Rangifer tarandus*, global warming trends are linked to reductions in calf body weight, presumably as a result of altered forage quality and

abundance (Weladji & Holand 2003). Climate variability will also affect the foraging behaviour of apex predators. For example, foraging wolves *Canis lupus* tend to hunt in larger packs in response to greater snowfall, leading to a decline in moose *Alces alces* abundance, and subsequent increase of their winter forage *Abies balsamea* (Post *et al.* 1999).

Folivorous insects usually take advantage of the 'phenological window' (usually lasting a few weeks) to feed exclusively on young developing leaves. Sometimes, however, alterations in regional climate change do not elicit synchronized changes in both the host plants and the herbivorous insects they attract because the cues involved in plant or insect phenology can differ. In the sycamore aphid *Drepanosiphum platanoidis* and its host *Acer pseudoplatanus*, egg hatching does not always synchronize closely with bud burst because weather affects the timing of bud burst (Dixon 1976).

A warming climate is predicted to influence a predator's reproductive success by changing prey availability. Advancement in spring arrival and its unequal consequence for the development and life stages of different species will disrupt synchrony of emerging predators and the prey upon which they depend (Durant *et al.* 2007). For example, a group of univoltine *Oedoparena* dipterans that forage on intertidal barnacles produce most larvae in late spring and early summer. Field experiments showed that an increase in *Oedoparena* larvae resulted in increased adult barnacle mortality (Harley & Lopez 2003). Of note however, is that dipteran flies have a heat tolerance threshold, and warming might exceed this, with subsequent release of predation pressure.

Because rising temperatures also have the capacity to shift animal colouration patterns, their role in crypsis developed by predators and prey will also be modified. Some examples of temperature-influenced animal colours support this idea. The positive correlation between temperature and colour brightness in the tree frog *Hyla cinerea* suggest that elevated microhabitat temperatures might influence body colourations and hence, habitat choice and predator-avoidance behaviour (King, Hauff & Phillips 1994).

Finally, melting of ice and snow are predicted to raise sea levels, thereby shifting tropical estuarine communities dependent on brackish water to more saline-tolerant mangroves (Mulrennan & Woodroffe 1998). This in turn, will affect food plant availability for herbivores like magpie geese *Anseranas semipalmata* and even Aboriginal human communities dependent on those herbivores for food (Traill *et al.* 2010).

Competition

Interspecific competition leads, through ecological and evolutionary pressures, to niche specialization and resource partitioning (Chesson 2000). The ultimate drivers of these interactions are rainfall, temperature regimes and soil type. Shifts in rainfall and temperature will affect autotrophic output, and subsequent shifts in plant community structure will have ramifications for dependent animal species. While global warming will have a 'bottom-up' effect, competitive interactions will also be influenced by phenology and the realized niches of competitors, with some species ultimately gaining a competitive edge. For example, thermal niche separation abounds among insect taxa. Differences in temperature and egg desiccation tolerances of the container-dwelling mosquitoes *Aedes albopictus* and *A. aegypti*, agents of many human diseases such as yellow and dengue fevers, influence whether the former (an invading species) coexists with or excludes the latter (Medley 2010). Local coexistence of both species is only possible because warm and dry climates, favoured by *A. aegypti*, alleviate competition with *A. albopictus* (Juliano *et al.* 2002). A wetter, hot climate will thus favour the invasive *A. albopictus*.

Thermal niche separation also occurs in other invertebrates and ectothermic vertebrates. Whip snakes *Demansia psammophis* are shuttling heliotherms with relatively high body temperatures and peak activity during daylight hours; in contrast, golden-crowned snakes *Cacophis squamulosus*, small-eyed *Cryptophis nigrescens* and marsh snakes *Hemiaspis signata* are more active at night, have relatively lower body temperatures and select lower ambient temperatures (Llewelyn, Shine & Webb 2005). Thus, different body temperatures among sympatric elapid species are likely to be correlated with times of activity, so that elevated day and night temperatures are predicted to alter interspecific interactions and possibly increase competition and competitive exclusion. In the cases described above, and likely many others, coexistence of species might be destabilized if global warming confers a physiological advantage to only one or a few species within thermally dependent guild structures.

Invasives

Invasion can be thought of as a type of competition, whereby non-native species gain a competitive advantage. Due to the deleterious changes that many invasives have on natural systems, and possible synergies between these under global change (Brook *et al.* 2008), we discuss the topic here in greater detail and through case studies.

Climate change has serious repercussion for the pace and ecological implications of biological invasions (Simberloff 2000; Orth *et al.* 2006; Occhipinti-Ambrogi 2007). Environmental warming has worldwide implications for the future geographical distribution of organisms; in particular, many animals previously not found in a particular region due to physiological or foraging constraints can invade these newly suitable habitats. For example, non-native Manila clams *Tapes philippinarum* introduced into European coastal waters have provided the Eurasian oystercatcher *Haematopus ostralegus* with a new food resource (Caldow *et al.* 2007). The presence of Manila clams has reduced the over-winter mortality of oystercatchers, providing an advantage to these populations that may not have previously been present. Some invasives gain advantage through physiological adaptations to greater temperatures. For example, the success of the invasive blue mussel *Mytilus galloprovincialis* along the western coast of North America is attributed to

physiological attributes that provide advantage at higher temperatures (Fields, Rudomin & Somero 2006). Indeed, Schneider & Helmuth (2007) found these invasives to be not only more heat-tolerant (than the native *M. trossulus*), but to have higher survival rates in wild conditions, conferring competitive advantage.

Although temperature shifts can alter invasive dynamics, the greatest effect of climate change in biotic communities arises from shifts in maximum and minimum temperatures rather than annual means (Stachowicz *et al.* 2002). These changes can give invasive species an early seasonal start, resulting in increased growth and recruitment relative to natives. In a temperate terrestrial ecosystem, invasive and native springtails differed in their phenotypic plasticity. Warmer conditions promoted survival during periods of desiccation in the invasive species, and reduced it in the native species (Chown *et al.* 2007). These results suggest that many invasives will expand their niche under warming, thereby outcompeting many natives (Slabber *et al.* 2007).

Parasite- and pathogen-host symbioses

There have been several recent comprehensive reviews of the effects of increased temperature on interspecific interactions such as parasitism, host-pathogen interactions and infectious diseases (Epstein 2001; Harvell *et al.* 2002). Predicted changes in these associations usually result from physiological or behavioural responses to elevated temperatures of at least one species in the symbiosis. We first summarize some of these processes with specific examples and then postulate how human-mediated global warming will affect trends in parasitism, infectious disease and host-pathogen interactions. Changing environmental temperatures for example, affect the mutualistic and antagonistic relationships between *D. frontalis* and their symbiotic mites and fungi (see Fig. 1).

Temperature changes can interfere with many host-parasite interactions: in the pea aphid *Acyrthosiphon pisum* and its fungal pathogen *Erynia neoaphidis*, host susceptibility correlates negatively with temperature (Blanford *et al.* 2003). Further, damselflies *Lestes forcipatus* housed at higher-than-average temperatures had greater defence and resistance against their parasitic mite *Arrenurus planus* (Robb & Forbes 2005). Elevated temperatures can induce or enhance host susceptibility to parasites and reduce host survival and fertility. For example, the population size of red grouse *Lagopus lagopus scotica* synchronizes with climate. This is because environmental conditions affect the population size and density-dependent transmission of the gastro-intestinal nematode *Trichostrongylus tenuis*, an endoparasite that reduces host fertility (Cattadori, Haydon & Hudson 2005). Therefore, a rise in temperature is predicted to cause more outbreaks of infectious pests that can result in large, synchronized changes in red grouse abundance.

Warming can also enhance the proliferation of a parasite's infective stage (Poulin 2006). Increased cercarial production of parasitic trematodes in intertidal communities with rising
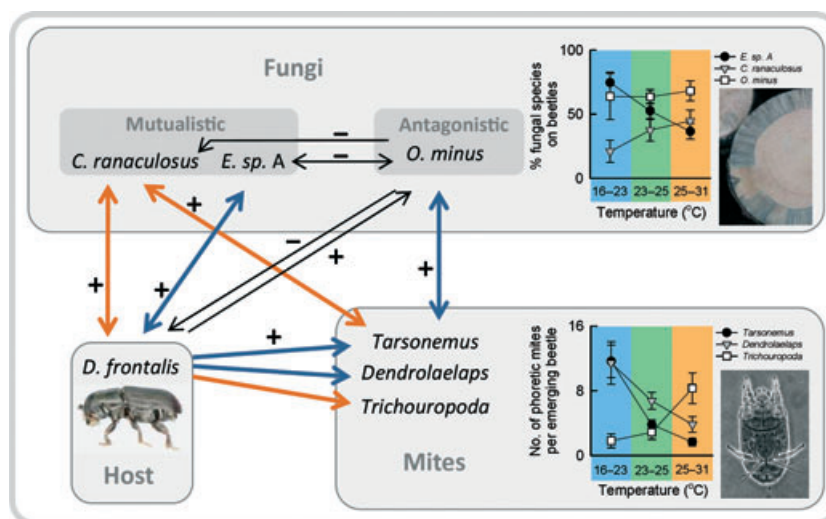
Fig. 1. Case study, How global warming affects pine beetle-pine tree parasitism and other interspecific interactions intricately linked to it. Effects of temperature on proportion of fungal species and abundance of phoretic mites on southern pine beetles *Dendroctonus frontalis*. Southern pine beetles are an important pest of pine forests in the United States. Hofstetter *et al.* (2007) investigated the effects of temperature on the interspecific interactions among beetles, mites and fungi. Billets taken from loblolly pine trees *Pinus taeda* infested with pine beetles were exposed to three temperature regimes (blue: 16–23 °C; green: 23–25 °C; orange: 25–31 °C). Mite–beetle and fungal–beetle associations were affected by variation in response to the number of mites per emerging beetle and fungal growth rates to different temperature regimes. Elevated (orange arrows) and lowered (blue arrows) temperatures can affect interaction intensity among mites (*Tarsonemus*, *Dendrolaelaps*, *Trichouropoda* species), bark beetles *D. frontalis*, beetle-mutualistic fungi *Entomocortium* sp and beetle-antagonistic fungus *Ophiostoma minus*. Inserts (clockwise from top): *O. minus* infestation of a pine tree (with permission, Alberta Sustainable Resource Development, www.mpb.alberta.ca); *Tarsonemus* (reproduced from *Sisäilma ja terveys - rakentajan opas*; published by the National Public Health Institute, now National Institute for Health and Welfare (THL), Finland; available at http://www.ktl.fi/attachments/suomi/julkaisut/julkaisusarja_b/2002b14.pdf); *D. frontalis* (with permission, David T. Almquist, Department of Entomology & Nematology, University of Florida, www.Bugwood.org.) Bars represent standard deviation. Redrawn with permission from Hofstetter *et al.* (2007).

temperatures (Poulin & Mouritsen 2006) illustrates this possibility well. In addition, elevated temperatures can also increase the emergence of infective stages of trematode parasites from snail hosts, thus promoting parasite transmission to the primary host (fish) and elevating total parasite abundance (Poulin 2006).

Ecological competitiveness through global warming

It is worth mentioning here that much of the ecological literature focussing on the projected impact of global warming on biodiversity and keystone species describes negative outcomes. Some species and localized populations will however likely benefit from warming; indeed, this could even be a sizeable minority. For example, the loggerhead turtle *Caretta caretta* is more quiescent at lower temperatures and often enters into a state of underwater hibernation, but above 10 °C, they have the ability to move and forage (Hochscheid *et al.* 2007). An increase in temperature of the regional waters, coupled with increased food intake, will result in faster growth rates and improve reproductive output.

Further, sea level rise resulting from warming will shift many tropical low-lying coastal regions toward (salt-tolerant) mangrove communities (Mulrennan & Woodroffe 1998). Specialized species adapted to mangrove type environments will likely flourish, as will their predators. That said, the ultimate outcomes for biodiversity under global change will take place at localized and broad spatial and temporal scales (as per Forchhammer & Post 2004).

Recommended research directions

Our review has provided example of changes that have occurred in recent times through warming, and it is inevitable now that changes will continue over the coming decades or even centuries. While debate continues on emission reduction, ecologists are advised to consider how best to mitigate the impacts (Brook, Rowley & Flannery 2007). A first step to take in monitoring and understanding the outcomes of global warming (on the revised role that heterotrophs will play) is to break this down by region. The IPCC (2007) provides documentation of change across the globe by major geographical regions. Change will not be homogenous across these regions, or even across similar biomes (see Meltofte *et al.* 2008). Research and monitoring programs therefore need to consider the nature of change within the region of interest, and the spatial variation of that change (Meltofte *et al.* 2008). Moreover, warming *per se* might not be the most serious biodiversity threat in some areas. For example, in low-lying coastal regions, sea level rise (largely as an indirect result of warming) poses a substantial threat to biodiversity, and ultimately coastal ecosystem functions (Finlayson *et al.* 2006; Craft *et al.* 2009).

A next step will be the identification of key species within ecological systems that provide essential functions for ecosystem resilience (Walker 1992; Fischer *et al.* 2006). These will undoubtedly include large mammals that play an important role in ecosystem structure, such as African elephants *Loxodonta africana* (Jacobs & Biggs 2002), or invertebrates that provide a crucial link in function, such as the dung beetles and pollinators described herein. Not only must these be identified, their status and distribution will require regular quantification [such as through the IUCN (2009) Red List].

High species richness acts to stabilize systems under change, so even species identified now as having minor functional roles could become essential components of future ecosystems defined by altered climates (Loreau *et al.* 2005). Indeed, the management of species diversity across functional groups will be one the most important tasks given ecologists in the coming decades (Fischer *et al.* 2006). Ecosystem function relies on a healthy biodiversity, and high species diversity provides resilience to change (Walker 1992; Hector & Bagchi 2007). Species diversity assessment should be a core element of research and monitoring that measure ecosystem change under warming, and indeed all aspects of global change including the increase in CO_2 concentration.

Occupying a similar priority is the maintenance of key species interactions: the identification of important interactions such as pollinators and dispersers. Identification of key species will compliment the identification of important interactions between these and other species. The development of competing hypotheses that test the response of these to altered climatic and environmental parameters will underscore future research programmes (Burnham & Anderson 2001). Key threats to biodiversity and ecosystem function require consistent and enhanced investigation, including the effects of invasive species, habitat loss (through land-use change and conversion) and pathogen spread. The development of laboratory and field-based research that tests competing hypotheses on the response of these (invasives, pathogens and parasites) to climatic shifts will therefore feature prominently (e.g. Willi & Hoffmann 2009). In some cases, the impacts of change will be attenuated or reversed by ecosystem process (Suttle, Thomsen & Power 2007). This is an important point, and emphasizes the need to maintain system biodiversity and thus resilience under change.

Long-term monitoring necessary for documenting the extent of change through time and across biogeographical gradients is essential to this endeavour. Broad transects can be developed across biomes to monitor environmental conditions (temperature, CO_2) and species shifts. Indeed, such monitoring will allow predictive models to be updated through time and projections revised (e.g. Brook *et al.* 2009).

Concluding Comments

Global warming, subsequent rising sea levels and increased atmospheric CO_2 concentration will alter present-day ecosystems and ecosystem function, but the extent of these anticipated changes cannot be predicted with any real accuracy yet. Given the important of ecosystem function, and particularly service to humans, a 'bottom-up' approach to

determine this is important. Some studies have already shown how warming can alter important ecological interactions between species, with subsequent effects on service and function (Mena 2001). Ecologists therefore need to focus on the mechanisms of change, or the mechanics by which warming will affect species behaviour, physiological and evolutionary response, population- and species-level interactions and the knock-on effects for species diversity, system resilience and function. By teasing apart these mechanisms through field and laboratory research, as well as long-term monitoring, we will be able to adapt to shifts in biodiversity structure and function, and mitigate the effects of climate change.

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