Adapt or disperse: understanding species persistence in a changing world

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Abstract

The majority of studies on environmental change focus on the response of single species and neglect fundamental biotic interactions, such as mutualism, competition, predation, and parasitism, which complicate patterns of species persistence. Under global warming, disruption of community interactions can arise when species differ in their sensitivity to rising temperature, leading to mismatched phenologies and/or dispersal patterns. To study species persistence under global climate change, it is critical to consider the ecology and evolution of multispecies interactions; however, the sheer number of potential interactions makes a full study of all interactions unfeasible. One mechanistic approach to solving the problem of complicated community context to global change is to (i) define strategy groups of species based on life-history traits, trophic position, or location in the ecosystem, (ii) identify species involved in key interactions within these groups, and (iii) determine from the interactions of these key species which traits to study in order to understand the response to global warming. We review the importance of multispecies interactions looking at two trait categories: thermal sensitivity of metabolic rate and associated life-history traits and dispersal traits of species. A survey of published literature shows pronounced and consistent differences among trophic groups in thermal sensitivity of life-history traits and in dispersal distances. Our approach increases the feasibility of unraveling such a large and diverse set of community interactions, with the ultimate goal of improving our understanding of community responses to global warming.

Keywords: adaptation, climate change, dispersal, interaction network, phenotypic plasticity, species interaction, temperature, thermal reaction norm, warming

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Introduction

There is no longer any doubt that climate change is affecting the distribution of species and composition of communities around the world (Parmesan *et al.*, 1999; Thomas *et al.*, 2001; Walther *et al.*, 2002; Pounds *et al.*, 2006). Data on many taxa in the northern hemisphere show a consistent trend of northward or westward expansion (Parmesan & Yohe, 2003) and spring advancement of phenology due to globally rising temperatures (Root *et al.*, 2003; Edwards & Richardson, 2004; Parmesan, 2007). The question of how climate change will alter the structure and functioning of eco-systems, however, remains unresolved. Estimates of global warming and precipitation levels at best vary greatly; the response of biological communities to one of the biggest human-induced experiments in evolution is even more uncertain. Estimates of species loss due to climate warming range from 3% to 78% of species going to become extinct (Thomas *et al.*, 2004; Thuiller *et al.*, 2004; but see Botkin *et al.*, 2007).

This wide range of scenarios can partly be explained by the inaccurate predictions on the rate and extent of global change. However, more importantly, it also results from the often-held assumption that community responses can be understood from single species behaviour. This approach lacks a mechanistic understanding and fails to take species interactions into account (Heikkinen *et al.*, 2006; Voigt *et al.*, 2007). Here, we question

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this approach and argue that multispecies interactions are fundamental to our understanding of the regulation of biodiversity and of the impact of environmental changes on communities.

Current approaches and outline

The traditional approach for forecasting change in community structure is typically phenomenological. This approach is based on (i) the 'species–area relationship', which aims to predict, for instance, the extent of species loss under habitat fragmentation from species–area curves (Seabloom *et al.*, 2002; Grelle *et al.*, 2005; Lewis, 2006), and (ii) the concept of 'environmental niche-based models' (otherwise known as 'Bio-envelope models') that are often used to project future geographic range of species from the current distribution of a species mapped in climate–space (Davis *et al.*, 1998; Pearson & Dawson, 2003; Hijmans & Graham, 2006; Araújo & New, 2007). Notwithstanding the value of such correlative studies for revealing general patterns in species diversity, much of the more detailed variation in community composition is left unexplained. Predictions have a large level of uncertainty. This variability in predictions can be explained by ecological and evolutionary processes that significantly alter the ranges of species, but are often not accounted for in models. For instance, in recently founded populations, the proportion of dispersive phenotypes at the border of the species range increase over non- or less-dispersive phenotypes, as is shown for thistles (Olivieri *et al.*, 1990), the speckled wood butterfly (Hill *et al.*, 1999), and bush crickets (Thomas *et al.*, 2001). This observation underlines predictions that when ranges expand, selection will tend to favour individuals with higher propensity for dispersal (Travis & Dytham, 2002). Phenomenological studies that are mainly descriptive and lack a mechanistic understanding of the underlying ecological and evolutionary processes, will fail to accurately predict species change.

A second and even more essential limitation in the current research on climate change is that in the past many studies have concentrated on individual species. This makes the unrealistic assumption that species do not interact with other species (Harrington *et al.*, 1999; Parmesan, 2007; Walther, 2007), while species are a part of complex interaction networks. Importantly, these multispecies interactions can constrain the ability of single species to adjust to environmental change. Mismatches between species can occur, for instance, when interacting species differ in ecophysiological response to temperature change, do not share the same biogeographical or evolutionary history, are differently controlled (e.g. bottom-up by competition for resources vs.

top-down by predation), or differ in spatial and temporal scale (Adams & Wall, 2000; Klanderud & Totland, 2005; Hance *et al.*, 2007; Voigt *et al.*, 2007). The bioenvelope model approach fails to include these types of species interactions, even though current (and future) distributions of species reflect these fundamental influences (Davis *et al.*, 1998; Heikkinen *et al.*, 2006). Although these limitations of species–area relationships and bioenvelope models are recognized in the literature (Araújo & Luoto, 2007; Heikkinen *et al.*, 2007), they are neglected in many global change studies.

To our view it is important to emphasize the weaknesses behind these models because studies emerging from academia can directly influence climate change policy. To improve the forecasting on the impact of climate change, the focus needs to be on: (i) species composition of communities and the way these species interact, (ii) traits of the community constituents, (iii) how species attributes change with temperature, and (iv) how relevant traits affect interactions between species under climate change. Of course, the myriad of potential interactions between species makes a prediction of their impact on global warming daunting. Here, we suggest that a focus on broad categories of responses, namely (i) thermal sensitivity of metabolic rate and associated life-history traits and (ii) dispersal traits of species or species groups, can significantly increase our ability to forecast the effects of warming on communities. The crucial question is whether there are consistent differences between distinct species groups, in the way they respond to global warming, for instance defined by trophic position, location in the ecosystem, or life-history characteristics.

The obvious question is: why these traits? We highlight these traits in particular because they are the functional traits of species that are most likely to capture the strategy of a species in dealing with climate change; that is, adapt or disperse. First, thermal sensitivity of key life-history traits, in for instance an individual's relative growth rate or developmental rate, determines the ability of an individual to adapt to changes induced by temperature (Johnston & Bennett, 1995). There is an enormous diversity among species in the thermal response of key life-history traits to global warming (Fig. 1). Recent studies indicate that robustness of species interactions under climate change is determined by variation in the temperature sensitivity of their community components (Pounds *et al.*, 2006). Second, dispersal ability determines the potential to escape adverse direct and indirect consequences of temperature changes (Watkinson & Gill, 2002) by colonizing new habitats as they become available. There is a wide range in dispersal ability of species (Fig. 2). Here again, interactions between species must be stressed:
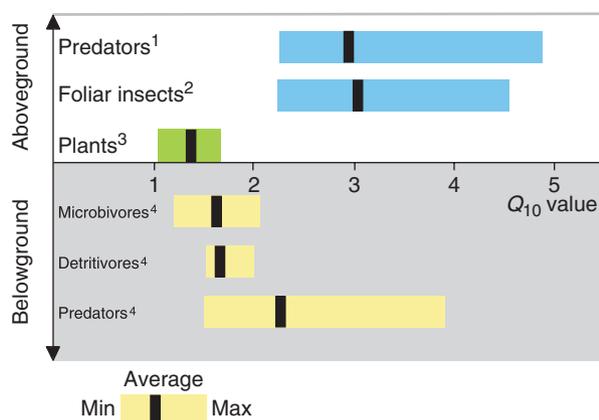
Fig. 1 Diversity in thermal sensitivity of metabolic rate and associated life-history traits. There is variation in thermal sensitivity of metabolic rate between trophic levels and within trophic levels. This figure shows the Q_{10}, a measure of thermal sensitivity, for metabolic rate and associated life-history traits for various invertebrate taxa. Horizontal bars indicate the range of Q_{10} (the increase in trait value from 15 to 25 °C divided by 10) for six trophic groups, while the vertical black lines give the average Q_{10}. Blue, yellow, and green refer to above- and belowground organisms and plants at the soil–air interface, respectively. This figure indicates that species living in habitats with relatively constant temperatures, such as the soil layer, have a weaker thermal response in traits compared with aboveground species, which live under more fluctuating regimes. Values are based on literature data; the numbers refer to the consulted literature. [1]Rohne (2002), Bell et al. (2003), Agboka et al. (2004), Pandey & Johnson (2006), Haghani et al. (2007), Krugner et al. (2007), Rahman et al. (2007), Sandanayaka & Ramankutty (2007) (Q_{10} inferred from development rate), [2]Stamp & Yang (1996), Kingsolver & Woods (1997), Frid & Myers (2002), Levesque et al. (2002), Kingsolver et al. (2007), Yang et al. (2007) (Q_{10} inferred from relative growth rate), [3]Tjoelker et al. (1998), Xiong et al. (2000), Medek et al. (2007) (Q_{10} inferred from relative growth rate), [4]Meehan (2006) (Q_{10} inferred from metabolic rate).

differences in timing and rates of dispersal between interacting species can result in shifts (and mismatches) of important temporal and/or spatial associations (Visser & Holleman, 2001; Parmesan, 2007). Therefore, we suggest that research aimed at focusing on species traits in combination with an analysis of thermal sensitivity of traits, will be highly productive, if particular attention is paid to differences among interacting species.

*Phenotypic plasticity vs. genetic adaptation*

One of the most perceivable consequences of climate change is changing temperature. Even if we take the most conservative estimate of the total number of species on earth, well over 99.5% are ectothermal, meaning they are not able to regulate their body temperature at a constant level. Organisms must respond to the changing conditions to survive. Adjustment of species to global warming may be achieved by phenotypic plasticity in thermal responses or by changes in the genetic composition of populations (Pulido & Berthold, 2004). Genetic adaptation means that genetic variation, generated through mutations or genomic rearrangements results in differential performance and/or survival of genotypes. However, at the current time scale of global change phenotypic plasticity seems to prevail over genetic adaptation as a way species adjust to enhanced temperatures. In one of the few studies comparing the importance of phenotypic plasticity over genetic adaptation, a genetic analysis of a population of red squirrels in the Arctic indicated that over a 10-year period, 62% of the advancement in breeding dates can be attributed to phenotypic plasticity, whereas 13% was a result of genetic change in the population (Reale et al., 2003; Berteaux et al., 2004). This makes phenotypic plasticity a critical survival mechanism. Importantly, evolutionary and plastic responses to climate change are not mutually exclusive. This is best shown in the case of the *Aricia agestis* butterflies, and *Conocephalus discolor* grasshoppers, where adaptive evolution of host preference and dispersive phenotypes, respectively, occurred at the northern range boundary in response to temperature rise (Thomas et al., 2001). However, key genetic variation for host preference within this butterfly already existed and was fundamental for this shift. In such cases, evolutionary processes are not an alternative to range movement, but rather mediate the magnitude and dynamic of the range shift.

These observations indicate that although local evolutionary responses to climate change have occurred with high frequency, there is little evidence for changes in the absolute climate tolerance of a species. This view is supported by the disproportionate number of population extinctions documented along southern and low-elevation range edges in response to recent climate warming; species either go locally extinct or contract their ranges (Wilson et al., 2005; Franco et al., 2006).

Appreciating the diversity in temperature sensitivities

Adaptation to global warming may be achieved by temperature-induced phenotypic plasticity. Many aspects of the individual performance of ectotherms, such as behaviour, metabolic rate and associated growth rate, or reproduction rate, are strongly influenced by environmental temperature, due to an increase in physiological rates at higher temperatures. Typically, thermal responses of ectotherm traits show a characteristic shape, in which performance increases with increasing temperature, reaches a maximum, and then declines
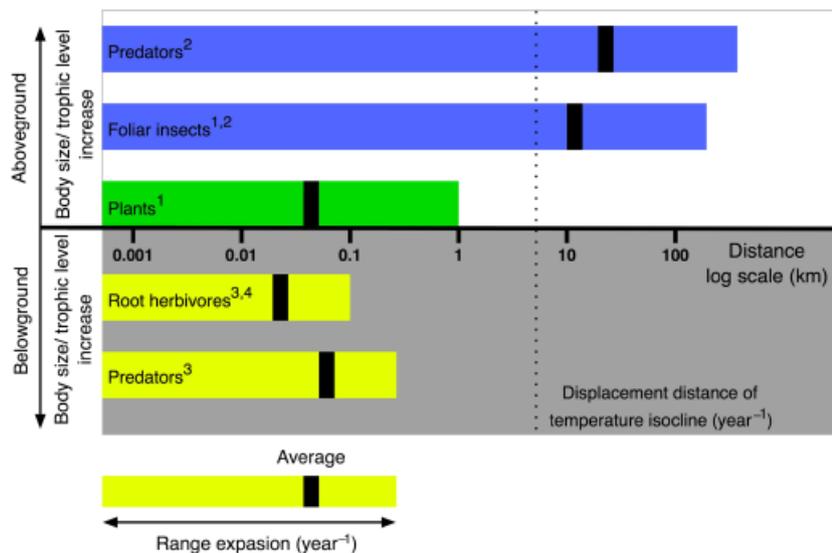
Fig. 2 Differential dispersal rates in organisms. There is variation in dispersal rates between trophic levels and within trophic levels. Horizontal bars indicate the range and maximum rate (y^{-1}, log scale) of dispersal, while the vertical black lines give the average rate of movement. Blue, yellow, and green refer to above- and belowground organisms and plants at the soil–air interface, respectively. Values are based on literature data; the numbers refer to the consulted literature. [1]Kinlan & Gaines (2003), McLachlan *et al.* (2005), [2]Holt (1996) (values inferred from the scale of resource use by aboveground predator vs. their prey), [3]Hedlund *et al.* (2004) (values inferred from the scale of resource use by belowground predator vs. their prey). The temperature isocline displacement distance for the temperate region is after Adams & Woodward (1992), Malcolm *et al.* (2002).

rapidly with further increases in temperature (King-solver *et al.*, 2007). The degree of thermal sensitivity is defined here as the change in trait value per unit of temperature change; in other words, high thermal sensitivity means a large change in trait value in response to temperature. Although the adaptive value of high or low thermal sensitivity is not equal across traits (Liefting *et al.*, 2009), it is clear from a comparison among multiple studies that the thermal sensitivity of key life-history traits shows pronounced differences among ectotherms (Fig. 1). For instance, distinctions based on trophic position show that growth rate of herbivores responds more strongly to temperature than growth rate of plants. Another remarkable difference is the much stronger thermal response of life-history traits for aboveground ectotherms than belowground ectotherms (Fig. 1).

It is this diversity among species that we need to appreciate in order to predict the effects of global warming on species survival. Quantifying thermal responses of traits for single species does not go far enough. However, when thermal responses of single species are studied in the context of multiple-species interactions, this can be a powerful approach. The effect of environmental change on species performance depends on the response of interacting organisms to these changes (Table 1). In the case of plants and herbivores this leads us to predict that the higher thermal sensi-

tivity of growth rate for herbivores compared with plants will increase grazing pressure on plants, potentially triggering outbreak population dynamics (Fig. 1). Another illustration of the strength of this approach is work on the causes of the widespread amphibian extinction over the last decades. Many studies have unsuccessfully attempted to link patterns of anuran extinction rates to changes in global temperatures. However, patterns of extinction can only be understood by taking into account a pathogenic chitrid fungus, *Batrachochitrium* sp. that grows on the skin of the tropical frogs (Pounds *et al.*, 2006; Whiles *et al.*, 2006). Studies of the thermal sensitivity of growth rate of frogs and the chitrid fungus, in combination with measurements of the microclimates experienced by both organisms, indicate that changes in climate have mainly benefited the chytrid fungus, but not the frogs. High elevation anurans such as *Atelopus* sp. exhibit a broad temperature range, meaning that their functional traits barely change with temperature (Navas, 2006). There is no evidence that the increase in air temperature directly stresses or increases the success of amphibians. The fungus, on the other hand, experiences temperature conditions that are mainly below its optimum temperature (Piotrowski *et al.*, 2004). Growth rate of the fungus rapidly increases with temperatures up to 23 °C. Temperature measurements indicate that both minimum and maximum temperatures are shifting towards the

Table 1 The reactions of species to environmental changes will, among others depend on their interactions with other organisms

Type of interaction	Organisms	Effect temperature increase	Mechanism	Effect of global warming	Reference
Two trophic levels					
1. Prey–predator	Aphid – Coccinelid beetle//Spruce budworm enemies	Temporal mismatch	Reproductive rate aphid lower than predator// reproductive rate spruce budworm higher than its enemies	Expected	Harrington et al. (2001)
2. Plant–pollinator symbiosis	Plant–butterflies	Temporal mismatch	Disrupt correlation between flowering period and pollinator activity. Decreased diet breath pollinators	Expected	Memmott et al. (2007), Hegland et al. (2009)
3. Plant–herbivore	Plant–Butterflies/aphids	Temporal mismatch	Development rate of insects is higher than plant, resulting in an increase in herbivory intensity due to higher growth rate and an additional generation of the insects within a year	Expected	Bale et al. (2002)
4. Plant–pathogen	Host plant–pathogen	Spatial mismatch	Dissimilarity in dispersal ability under global change	Observed	van Grunsven et al. (2007)
5. Host–endosymbiont	Parasitic wasp–Wolbachia/Aphid–Buchnera	Dissimilarity in lethal temperature	Elimination of endosymbionts by short term exposure to high temperatures restores bisexual reproduction, affect host fitness	Expected	Hance et al. (2007)
6. Host–parasitoid	Grasshopper–Entomophaga fungi/Host–braconid wasp	Dissimilarity in lethal temperature	Enhanced survival of parasitized host due to higher lethal temperature or increased host defense	Expected	Thomas & Blanford (2003)
7. Plant–mycorrhizal symbiosis	Anacardium–Glomus intraradices	Dissimilarity in thermal tolerance	Decreased root growth and changed root morphology results in failed AMF infection and elimination of plant–mycorrhizal association	Expected	Haugen & Smith (1992)
Three-trophic levels					
8. Plant–herbivore–predator	Oak–caterpillar–great tit	Temporal mismatch	Disrupt correlation between environmental cues used by oak and moth for growth. Phenotypic plasticity cannot maintain correlation. Advancement egg laying dates of birds not enough to match peak in caterpillar biomass	Observed	Visser & Holleman (2001), Visser et al. (1998)
9. Host–ectosymbiont–plant	Bark beetle–fungus–tree	Dissimilarity optimal temperatures of symbionts.	Shift of symbiont prevalence or loss of particular symbiont due to different optimal temperature ranges for sporulation in pupal chambers beetle. Symbiont shift affects beetle fitness. Possible consequences for tree mortality due to difference in fungal virulence	Expected	Six & Bentz (2007)

For different types of interactions the effect of an increase in temperature on interacting species (either observed or expected) and the underlying mechanism is given.

growth optimum of the fungus (Pounds *et al.*, 2006). This effectively encourages outbreaks of the fungus leading to increased frog infection. The result is the global loss of many species of frogs.

Temperature-induced changes can also result in a mismatch in phenologies that can have immediate and serious consequences. This is best illustrated by the oak–winter moth–great tit association. Bud burst of oak in western Europe has advanced 10 days over the last 40 years, due to increasing temperatures in late winter/early spring (Visser & Holleman, 2001). The egg-hatching of the winter moth larvae that feed on fresh oak leaves, however, has advanced 14 days, with the result that young moth larvae die from starvation. The cause of this disparity lies in the fact that the mechanisms determining the onset of development differ between both organisms. Oak bud burst is determined by a chilling sum and a subsequent warmth sum from the 1 November onwards (Kramer, 1994), whereas winter moth egg-hatching is determined by the spring temperature sum above 3.9 °C in combination with the number of frost days during the preceding winter. For great tit hatchlings, the caterpillars of the winter moth are the main food source. Great tits, however, have not been able to advance their laying date. The mistiming between oak and moth has led to a decreased recruitment in tit populations, as caterpillar densities have diminished at the time the tits feed their young (Visser *et al.*, 1998). This example shows that impact of a rise in temperature on biotic interactions can cascade through the food chain.

These examples, supplemented with the examples given in Table 1 show that even if we have information on the thermal sensitivity or plasticity of a particular trait of a species, this is not enough to effectively predict changes in its range due to global warming. Interactions with other species can result in a mismatch of temporal associations and may prevent or set limits to the range expansion of single species. Increased attention to thermal sensitivity of key traits in species, with a focus on broad categories of responses in a community context will help to forecast global warming effects. It is difficult to know beforehand which traits could be relevant in using thermal sensitivity as a parameter to predict responses of communities to thermal change. However, in ectotherms many key life-history traits strongly depend on metabolic rate, as shown by the toad-chitrid fungus and oak–caterpillar–tit examples. Therefore, thermal sensitivity of metabolic rate should be a relevant trait and provide a common metric. Figure 1 gives examples of variation in thermal sensitivity in metabolic rates and associated life-history traits, such as growth rate or development rate within and between trophic levels and ecosystem compartments. Unfortu- nately, at present, hardly any comparative data are presented on temperature sensitivities of these traits for species within communities.

Species on the move: discrepancy in dispersal ability

If thermal tolerance of an organism to temperature change is not sufficient for its continued survival, then moving to better conditions becomes imperative. Again, range shifts of interacting species under global warming cannot be predicted from information on individual species displacement distances. Variability in dispersal rate of interacting species can disrupt the spatial association between two species, for instance when the displacement distance under climate change of one species is larger than of the other species (Callaway *et al.*, 2004). A recent study shows that plant species that have colonized northwestern Europe from southern climate regions as a result of climate change may become temporary released from soil pathogenic activity (van Grunsven *et al.*, 2007). These plant species disperse faster than their natural enemies and this spatial mismatch results in a less net negative plant– soil feedback than similar native species in the new range. The exotic and native species grown in soil inoculated with soil conditioned by conspecifics shows a 13% and 35% reduction in the average biomass production, respectively. This enemy release pattern is also observed in artificially introduced invasive plant species (Reinhart *et al.*, 2003; Callaway *et al.*, 2004). As a consequence, the escape from enemies can increase the competitive ability, growth, and reproductive output of newly arrived plants over native plants, which compli- cates predictions of future distributions.

At present, we lack reliable data on dispersal rates, either active or passive, of many species, especially for species with a restricted habitat choice, resource specia- lists and species with limited dispersal abilities, such as most belowground organisms. Estimation of dispersal rates of interacting species in a community is a Hercu- lean task. However, the limited amount of existing studies on range extensions and dispersal ability of interacting species suggest that broad categories of responses, such as those based on (i) life history or (ii) trophic position, to global warming might be distin- guished. For instance, distinctions based on life his- tories can be made, such as between generalists and specialists. Many generalist species of nonmigratory European butterflies have expanded their range across large tracts of unsuitable territory (Parmesan *et al.*, 1999). Several upland butterfly species that rely for their larvae on ubiquitous host plants have moved their low- elevation boundary uphill by an average height equiva- lent to the uphill shift of isotherms (Wilson *et al.*, 2005).

Species with a generalist lifestyle can keep pace with global warming because range shifts will generally not be limited by resource availability. However, the consequences of temperature change may be different for specialists (Fig. 2). Most specialists are thought to be directly limited by the distribution of their prey/host plant, rather than abiotic conditions directly (Kinlan & Gaines, 2003; McLachlan *et al.*, 2005). So an important constraint to range expansion for specialist herbivores, for example, would be the rate of movement by their host plant or prey (Harrington *et al.*, 1999). In one of the few examples in which dispersal abilities of trophic groups are compared, Kinlan & Gaines (2003) show that plants move over smaller spatial scales than their herbivores. Estimated seed dispersal ranged from a few metres to 22 km, while phytophagous insects disperse over larger scales, from 8 to 42 km. In this example, specialist herbivorous insects are able to track the shift in temperature isoclines, but will be constrained because their plant resource will lag behind (Fig. 2). This pattern is predicted to be typical of many species interactions. Estimates of tree dispersal rates after the last glaciation, show that the overall rate of movement is too low for some species to keep up with the current projected shift in climatic isotherms (Watkinson & Gill, 2002; McLachlan *et al.*, 2005).

Besides specific life-history traits, a focus on the trophic position of species is another way to look at it. Generally, species with a high trophic position are believed to show a higher dispersal rate than species with a low trophic position, often because they have a larger body size, home range and spatial resource use (Holt, 1996). Strong data sets are still lacking, but belowground microbe-feeding microarthropods and their predators are likely to differ in displacement distance. Based on the spatial dimensions of resource use, microbe-feeding microarthropods actively move on a centimetre to metre scale (Bengtsson *et al.*, 1994), while the larger predaceous cantharid larvae of a higher trophic level actively move over larger scales, from metres to more than 100 m (Traugott, 2002). On the other hand, microbes and soil animals with a body size smaller than microarthropods might show a higher dispersal rate than species with a high trophic position, often because passive dispersal over long distances might be more important than active dispersal over short distances (Fenchel & Finlay, 2004). However, passive dispersal of small organisms with a body size <1 mm in length is nonintentional and nondirectional, and this may account for the temporary release of plants from soil pathogenic activity observed by van Grunsven *et al.* (2007). Subsequently, the probability to evade unfavourable environmental conditions or the possibility to benefit from an increase in the potential geographic range in response to the removal of ecological limitations by climate change will differ greatly among interacting species.

These examples indicate that information on the displacement ability of single organisms is not sufficient to understand range changes under global warming. Interacting species must be taken into account. We hypothesize that interaction effects can result in a mismatch in spatial associations and may prevent or set limits to the range expansion of single species. A focus on broad categories of responses in a community context, for instance plant–pathogen interactions or predator–prey interactions, might help to forecast global warming effects on communities.

Species embedded in multispecies interaction networks

Multispecies interaction networks are even more complex than the linear interaction between two or more species described above (*sensu* Proulx *et al.*, 2005). Species interact with many other species in networks, and these interactions can differ in strength and in sign, either positive (facilitation), negative (inhibition), or neutral. For instance, in xerothermic grasslands, primary producers, arthropod herbivores and their predators all have different sensitivities to climate. These sensitivities are significantly ordered with increasing trophic rank. The vulnerability of predators to global warming (i.e. as defined by the mean temporal variation in organism abundance) is twice as high as the vulnerability of plants for temperature change (Voigt *et al.*, 2003). In aquatic food webs containing several functional groups, extinction risk of species of bacteria and Protozoa subjected to different temperature regimes also depends on their trophic position (Petchey *et al.*, 1999). Communities that are warmed 2 °C disproportionately loose more top predators (Petchey *et al.*, 1999) and herbivores, and become increasingly dominated by autotrophs and bacterivores. Increase in vulnerability of top trophic level organisms, can lead to community destabilization under climate change due to cascading effects down the food web, not simple geographic shifts (Voigt *et al.*, 2003). Changes in the relative distribution of organisms not only alter community composition and food web structure, but also initiate changes in ecosystem function beyond those expected from temperature-dependent physiological rates of individual species (Petchey *et al.*, 1999). For example, the greater extinction frequency for top consumers facilitates primary production by autotrophs resulting from reduced top-down control of producers, which could shift the carbon budget of ecosystems. On the other hand, in contrast to these two examples, short-term experiments show that global warming has minor effects on species

composition or species extinction (Grime *et al.*, 2000; Richardson *et al.*, 2002), or ecosystem function (Post & Pedersen, 2008). For example, in subarctic ecosystems warming shifted plant communities away from graminoid-dominated towards birch-dominated. In contrast, the increase in total community biomass by promoting growth of deciduous shrubs was mitigated by vertebrate herbivores when they were allowed to graze (Post & Pedersen, 2008). Multispecies networks will, therefore, set limits to the effect of temperature change on a particular species, making it difficult to derive predictions from single species effects.

Interaction networks of terrestrial ecosystems extend to both aboveground and belowground components that are closely interlinked (Wardle *et al.*, 2004; Bardgett *et al.*, 2005; De Deyn & van der Putten, 2005). Here, the direction and magnitude of change in the aboveground community in response to global warming will depend on how the soil-dwelling species are affected, and *vice versa*. Life-history strategy responses to global warming are likely to be more dramatic in aboveground species, exposed to the full climate variability, while belowground species experience microclimates that are buffered by the soil environment (Bale *et al.*, 2002). Above- and belowground organisms that belong to the same trophic group generally differ in thermal sensitivity of life-history traits (Fig. 1) and in body size, mobility, and dispersal range (Fig. 2), and these differences have the potential to significantly disrupt interactions. As such, recognition of these above- and belowground feedbacks in multispecies interactions is important for our understanding of the regulation of biodiversity and the impact of environmental changes on communities. It also causes the response of single species in a food web to be unpredictable from year to year (Bezemer & Knight, 2001).

A novel approach to understand future distributions

Simply scaling up the results of single-species response to global change is insufficient to understand effects on community composition and stability, and ecosystem functioning. Real communities contain such a diversity of organisms differing in the complex ways they respond to global warming. To reduce this diversity to manageable proportion we propose, as a first step, to (i) define strategy groups based on life histories used to adapt to global warming, (ii) identify key species in these groups and their interactions with species in other strategy groups, and (iii) find the relevant traits based on types of interactions as well as their sensitivity for global warming. This approach might help to find broad patterns in species interactions under climate change and might eventually be used to draw some predictions.

First, we suggest that a focus on species traits that relate to persistence under global warming can help to group species and their interactions in units, e.g. strategy groups, on which analyses of complex interactions can be based. For instance, Bale *et al.* (2002) have grouped insect herbivores according to the way they exploit plants with different growth forms. These plant growth forms and herbivore plant exploitation modes will be differentially affected by climate warming (Bale *et al.*, 2002). These groups include, for example, herbivores with long life cycles that depend mainly on climatic conditions rather than exploitation of specific host plants, herbivores with a single generation per year with a close synchrony with the host plant, and herbivores with a continuous development on a single host in a nonseasonal environment, with many generations per year. Plant growth form and seasonal availability of food strongly influence the life-history strategy of insects associated with them. Using an insect–plant life-history strategy matrix, Bale and colleagues predict that insect voltinism will increase with increased summer temperature, but not for insects with a single generation per year with a close synchrony with the host plant. The relative development rates of insects with this strategy and its host plant at different temperatures might set limits to host-specific insect herbivore species. Figure 1 shows that the development rate of insects reacts stronger to an increase in temperature than the growth rate of plants. In other words, in the northern, colder part of the range host plants may grow too slowly to support insect development, whereas in the southern, warmer part of the range, the plant develops too quickly.

Second, even within trait-based groups (*sensu* Bale *et al.*, 2002) a diversity of organisms may be present differing in the complex way they respond to global warming. We suggest that the species involved in key interactions, important for community stability and ecosystem functioning, are identified in strategy groups, to be able to understand the vulnerability of communities or ecosystems to changes in climate. For these species, the slope of their temperature response curve for key life-history traits, and their dispersal rates should be compared to determine if interacting species differ in either temperature sensitivity (temporal mismatch) or in displacement distance (spatial mismatch). If slopes and displacement distance differ between interacting species then mismatches in time and space can be anticipated.

Finally, when species and their key interactions are identified (as in Table 1) the proper traits should be selected. The examples in Table 1 suggest that climate change induced effects on species interactions with a strong seasonal component relate to a different set of traits, such as growth rate or reproductive rate (Table 1,

interaction types 1–3 and 8), in comparison to species interactions with a less strong seasonal component, which depend more on thermal threshold levels, for instance lethal temperatures or optimal temperatures (Table 1, interaction types 5–7, and 9). As climate becomes less favourable for species development, synchrony becomes a more critical feature, and relevant traits such as growth rate and development rate are becoming more important. This trait selection procedure serves only as a first approximation, and a meta-analysis on interaction-type life-history trait should be performed to reveal the generality of the observed pattern. Moreover, such an analysis might also reveal if interactions with a strong seasonal component may have a higher potential to disrupt species interactions compared with nonseasonal interactions.

In summary, the approach we advocate first defines strategy groups, then identifies the key species and their interactions within these groups, and, finally, selects traits to be studied on the basis of the type of interaction and the sensitivity of the interactions for seasonality. Comparison of response curves of interacting species could then be a useful indication of how a rise in temperature will affect the outcome of the interaction.

What does the future hold?

Observational data over the last 50 years has shown us that some species are much more adept at adapting to climate change than others (Root et al., 2003); these details are paramount to understanding underlying mechanisms. For instance, in contrast to sessile species and species with low potential of dispersal, highly mobile organisms are expected to respond more readily to global warming by evading unfavourable environments. Poor dispersers, however, must adapt. If all species were to respond uniformly to global warming, all ecosystems would just shift towards the poles and 'only' the boreal species would be at risk. Most importantly, there are interspecific differences in the potential for ecological and evolutionary responses, and it is exactly this disparity between interacting species that may perturb community composition.

The approach we advocate points to several key research questions that still need to be addressed in order to obtain a better understanding of the impacts of global warming on ecosystems. These questions are: (1) Which traits enable species to adapt to global warming? We argue that dispersal and thermal sensitivity of key life-history traits are two important factors when considered in a community context, but not in isolation. Future work should identify additional functional traits that can be used to predict the response of species to global change. (2) What is the speed of adaptation and

to which extent does this vary among species? Species with high rates of movement can quickly reach new profitable places, while those which move slowly might fail to detect suitable habitats. Hence, selection might act on dispersal traits for species with a high rate of movement, while for slow moving species selection might be on persistence traits that will enable local adaptation. We need to take account of phenotypic and genotypic flexibility and niche width, which is at least in part determined by temperature regime (Bale et al., 2002). (3) What is the amplitude of intraspecific sensitivity towards global warming? Species do not behave equally throughout their range. The type of response seems to depend on the geographic position of an organism in its area (Root et al., 2003). At the low latitude end of its area, habitat quality for a particular species might not change that much but the number of competitive species might increase (McCarty, 2001). At the high latitude end of their area individuals react more strongly to changes in temperature and may expand their range towards the poles. Hence, information on the geographic position of interacting species may be valuable to understand why and how species adapt to global warming. Lastly, (4) is there a trade-off between thermal tolerance of key life-history traits and dispersal ability? Trade-offs between a variety of life-history traits and dispersal ability have been reported (Roff, 2001). Hence, the question whether species with a low thermal tolerance for, for example, growth rate have higher dispersal abilities is not only intriguing but also crucial to understand responses of communities to environmental change.

In conclusion, expected increases in global temperature are typically well within the range of the temperature tolerance of most species. In general, most species will not be threatened by the direct effect of temperature alone. In our view, changes in species distribution and abundance will primarily be determined by the impact of temperature on species interactions rather than the thermal tolerance or the dispersal ability of individual species. We argue that by concentrating on temperature change in relation to the interactions between key species or functional species groups inferences can be made about the vulnerability of ecosystems as a whole. The use of life-history traits or trophic position of species as a basis to aggregate interactions between species in units of analysis of workable dimensions will improve our predictions with respect to the effect of global warming on communities.

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