Review

Novel communities from climate change

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Climate change is generating novel communities composed of new combinations of species. These result from different degrees of species adaptations to changing biotic and abiotic conditions, and from differential range shifts of species. To determine whether the responses of organisms are determined by particular species traits and how species interactions and community dynamics are likely to be disrupted is a challenge. Here, we focus on two key traits: body size and ecological specialization. We present theoretical expectations and empirical evidence on how climate change affects these traits within communities. We then explore how these traits predispose species to shift or expand their distribution ranges, and associated changes on community size structure, food web organization and dynamics. We identify three major broad changes: (i) Shift in the distribution of body sizes towards smaller sizes, (ii) dominance of generalized interactions and the loss of specialized interactions, and (iii) changes in the balance of strong and weak interaction strengths in the short term. We finally identify two major uncertainties: (i) whether large-bodied species tend to preferentially shift their ranges more than small-bodied ones, and (ii) how interaction strengths will change in the long term and in the case of newly interacting species.

Keywords: climate change; ecological networks; body size; predator–prey interaction strength; range shifts; diet specialism

1. INTRODUCTION

Climate change affects different levels of biological organization. Early studies focused on population and species-level effects, and showed species range pole- and up-ward expansions following temperatures as climate warms, together with a number of phenological changes [1–3]. There is still a lack of strong and coherent theoretical and empirical foundation to incorporate species interactions and traits into climate change research [4]. This incorporation is crucial to develop better understanding, ecological forecasting and conservation planning of natural ecosystems.

Community- and ecosystem-level effects of climate change have received considerable attention over the last years, with a focus on how climate change affects species interactions and ecosystem processes [2,5,6]. At this level of biological organization, a fundamental question arises: Are there general patterns in the way species respond to climate change within and across ecosystems, or are responses merely idiosyncratic—i.e. each species responds differently? To answer this question, the challenge is to identify organism traits that may determine their sensitivity to climate change, and the consequences of their responses for species interactions.

If coexisting species have different sensitivities and differential responses to climate change, there will certainly be an emergence of new ecosystems with novel species combinations and/or changes in the distribution and strength of their interactions. This will probably alter their abundances, distributions and extinction probabilities [4]. However, our present understanding of the effects of climate change on species interactions in ecosystems is mired in idiosyncratic case studies and focused mainly on very small species interaction modules (e.g. reviewed in [5,7]).

Here, we ask whether it is possible to identify traits responsible for the differential sensitivities of species to climate change, and, on the basis of this, what novel communities from climate change would look like. We focus on two particular traits: species body size and diet specialization (i.e. diet breadth), presenting theoretical expectations and empirical evidence for the existence of trait-mediated sensitivities.

Body size is a commonly available surrogate of relevant life-history characteristics of species, namely dispersal ability, reproduction timing and frequency, population abundance or metabolism [8]. It is also a trait known to affect a number of biological processes, from the individual to the ecosystem level, including metabolism, fecundity, population growth rate, population density, trophic flows or ecosystem respiration [8,9]. Within trophic interaction networks, a number of studies have reported that body size determines food web structure and dynamics (see [10] for a review). For example, large predators tend to interact with more diverse prey items than smaller ones, and predator : prey size ratios determine biomass flux and interaction strength, ultimately regulating food web dynamics.

Declining body size is suggested as the third ecological universal response to warming, following poleward and altitudinal range shifts and species' phenological changes [11–13]. Similarly, changes in community size structure are likely to exert profound changes in the topology and dynamics of ecological networks [10]. Here, we will explore these changes and their likely consequences on novel communities in the face of climate change.

Diet breadth is a fundamental dimension of a species niche, and the balance of generalist and specialist species within communities determines the structure of species interaction networks and ecosystem functioning [14,15]. Diet breadth is systematically related to body size in food webs across ecosystem types [16], with larger predators feeding on more prey items than smaller ones. It is also likely that diet breadth is the key for predicting how species cope with climate change. For example, specialist enemies or mutualists with obligate interactions can be limited by other species when they shift their distribution range as climate changes, while generalists should be less constrained [17]. Along this line, the extinction risk of species, in the absence of warming, increases with the level of specialization in terms of the number of prey and the range in body sizes of the prey [18].

In this paper, we aim at identifying general patterns and major unknowns on the structure and dynamics of novel communities that result from climate change. The paper is structured in three sections. The first section deals with climate warming impacts within closed and local communities, where we assume that populations cannot track changing climates across space by dispersal. Within closed communities, species can 'stay and adapt' or 'stay and become extinct'. In particular, we ask (i) whether climate change is reducing body size within populations and communities, (ii) whether there is a preferential loss of specialized interactions, and (iii) whether climate change affects consumer–resource interaction strengths.

The second section incorporates species movement as climate changes, considering open communities with species migration. In this section, we investigate which species are more likely to move and what are the consequences of differential species range shifts on the structure and dynamics of 'source' and 'sink' communities. In particular, we explore (i) whether larger species shift their ranges faster and further, (ii) whether trophic generalists are more likely to track changing climates, and (iii) to what extent interactions are lost or gained as species migrate.

The last section tries to summarize and connect the general patterns observed as well as the major unknowns identified in novel communities resulting from climate change. The implications of these patterns and unknowns for food web structure and dynamics and for community size structure are also discussed.

2. CLOSED COMMUNITIES

Closed communities with negligible immigration rarely exist in nature, with some oceanic islands or isolated mountain ranges as exceptional examples. However, climate change is acting on already highly degraded and fragmented landscapes, where species movements are constrained. In this section, we explore the effects of climate change on local communities where species are not tracking climate in space, in order to establish the baseline of local climate change effects making the simplifying assumption that species are not moving.

(a) *Climate change and body size shifts within populations and communities*

There are (at least) four rules concerning relationships between body size and temperature that are relevant in this context. The first three are summarized in [11], and are based on biogeographic and ecothermal gradients: first, Bergmann's rule (which states that warm regions tend to be inhabited by small-sized species); second, James' rule (saying that populations with smaller body size within a species are more likely to be found in warmer environments); third, the temperature-size rule (stating that the average size of individual ectotherms is inversely related to temperature [19]). The fourth one is the allometric size-scaling rule, which states that warming should lead to a decrease in the mean body mass and/or a decrease of population abundance at equilibrium [9]. Collectively, these rules predict that warming will reduce species body size and shift community size-structure towards smaller size-classes.

Starting at the population level, two recent reviews have shown heterogeneity in both the magnitude and the direction of size responses to warming [12,13]. The degree to which organism size is affected by temperature varies across taxa, but some general patterns can be recognized.

Both terrestrial and aquatic ectotherms have shown decreases in their body size. Numerous experiments have exposed organisms to increasing temperatures, and have shown decreases in species body size, including marine invertebrates, fish, beetles and salamanders, compared with controls ([13] and references therein). Both the rate and degree of shrinkage varies widely between taxa: from 1–3% in beetles to 14% in salamanders for each degree Celsius of warming. Evidence for mammals and birds also supports shrinking body sizes as the climate warms [13], although some works show equivocal responses or no change at all [12,20]. Only in some exceptional cases, the opposite trend is observed, with increasing body sizes for certain fish, lizards, birds and mammals. Along this line, studies such as those by Yom-Tov and collaborators [21,22] have shown an increase in body size in medium and small mammals (otters and shrews, respectively), with increasing temperatures during the last decades. The hypothesized mechanism behind this was an increase in productivity over the whole ecosystem owing to increasing temperatures, which in turn facilitated an increase in species body size. Most of these exceptions are from high latitudes [13,23], and it is expected that species inhabiting areas where increasing temperature and precipitation will lead to increased net primary productivity are likely to exhibit less clear shrinkage patterns.

Population and species body size changes would affect the distribution of body sizes at the community level. As expected from the previous rules and evidence

at the species level, warming is likely to favour small ectotherms to the detriment of large ones. This has been observed across different trophic levels. A recent meta-analysis revealed that mean body size of high trophic levels, fish in large French rivers in particular, has decreased significantly during the last 2–3 decades under gradual warming.

In lower trophic levels, increasing temperatures decreased bacteria and phytoplankton cell size in temperature-controlled mesocosms [11]. Similarly, diatom cell size has decreased with increasing temperatures through the fossil record, suggesting that impending warming will shift phytoplankton communities towards smaller cells, where diatoms would be at a competitive disadvantage [24]. In another study, picophytoplankton (which comprise cyanobacteria and eukaryotic algae smaller than 2 μm) increased with temperature along a natural temperature gradient in the ocean, regardless of differences in trophic status or in inorganic nutrient loading [25]. Finally, studies in one of the areas experiencing the most extreme climatic warming on Earth, the Western Antarctic Peninsula, have shown that over the last 30 years there has been an increasing fraction of the largest components of phytoplankton, including diatoms and other large cells, in the southern (colder) region than in the northern (warmer) one [26].

Although climate change can affect different trophic levels within the food web, experiments considering multi-trophic communities have shown that warming does not affect the size-structure of different trophic levels equally. In a freshwater mesocosm study simulating expected warming for the end of the present century, mean phytoplankton body mass decreased by an order of magnitude between control and 4°C-warmed treatments, while mean zooplankton body mass remained constant. Compositional changes were observed, with warmed communities characterized by small phytoplankton species and by the absence of large species that were commonly found in controls. This compositional turnover was not observed for the zooplankton.

This result seems to contradict previous findings of higher trophic levels more sensitive to climate change than lower trophic levels [27], with larger extinction probabilities of higher trophic levels within bacteria–protist microcosms [27]. This apparent contradiction might be due to the combination of resource availability under warm conditions and close-to-lethal and lethal temperatures of different organisms. Higher metabolic demands of consumers high in the food web triggered by warming need to be compensated by higher availability of resources down the food web; otherwise, consumers will starve and eventually disappear. Yvon-Durocher *et al.* [28] showed a decrease in phytoplankton biomass, but it was compensated by an increase in phytoplankton turnover rate (as expected from the dominance of small organisms), and thus it was able to fuel higher zooplankton requirements with no concomitant effects higher up in the food web.

(b) *Lost and new interactions in closed communities*
(i) *Phenological mismatches and dietary shifts*
Differential responses of interacting species to climate change are affecting temporal/phenological coupling and decoupling, and are changing also consumer diets. This will eventually lead to the reorganization of consumer–resource interactions in ecological networks, with some interactions lost and new links emerging. Although idiosyncratic responses are sometimes claimed [6], it is important to search for general patterns. We discuss here how phenological mismatches and dietary shifts are related to species traits such as trophic position and diet breadth.

Habitat generalists with broader ecological niches have been shown to cope better with environmental change than specialist species with narrower ecological niches. In the past 10 years, numerous studies have reported that, in many ecosystems, generalist species are replacing specialist species, as predicted by niche theory, and causing biotic homogenization [29]. A reasonable assumption is that generalism in habitat use reflects broader diet breadth, and hence diet specialists should be more sensitive to climate change within closed communities than diet generalists.

Phenological mismatches have been found in plant–pollinator mutualisms [30], plant–insect interactions [31] and multi-trophic interactions [32]. Climate-driven phenological changes on higher trophic levels (i.e. secondary consumers) are slower than at lower trophic levels (with the exception of woody plant species), making the former especially vulnerable to phenological decoupling, as revealed in a recent review of terrestrial and aquatic ecosystems in the UK [33]. This is even more apparent when complex food chains consisting of several (more than two) trophic levels are considered. Phenological changes across trophic levels in a European deciduous forest over 25 years showed that the phenological phases of tree budburst advanced only slightly, while the next two trophic levels, the herbivores (represented by caterpillar biomass peaks) and insectivorous birds (represented by their hatching day), have advanced [32].

Diet specialists can be more severely affected by climate change than generalists. This has been documented for butterfly species with narrower larval diet breadth (i.e. number of food plant species), which have experienced relatively greater advances in their phenology than generalist butterflies [34]. Interestingly, other components of global change, namely the degree of intensification of human land use and aridity, affect generalist butterflies more severely than does climate change, while specialized butterflies showed serious richness and population declines with increasing temperatures [35].

Climate change is also producing dietary shifts on consumers. For generalist consumers, dietary shifts can simply reflect changes in the relative abundance of their prey as climate warms. These changes are characterized by Rall *et al.* [36] as a dominance of smaller prey items in consumers' diet. This has been shown for several apex predators in different habitats experiencing changes in ambient temperature. Trout in Arctic freshwater food webs showed marked changes in the invertebrate prey they fed upon along a natural temperature gradient [23]. Similarly, California sea lions shifted their diet composition from one dominated by market squid (*Loligo opalescens*), anchovy and rockfish to a diet predominantly composed of smaller sardines, rockfish and hake species [37]. Finally, 40 years of increasing temperatures affecting

five apex predators in the Bering Sea, including fur seals, two species of kittiwakes and two species of murres [38], changed their diet to a predominance of pollock species of small size [38].

(c) *Climate change and interaction strength*
Climate change may also disrupt the strength of interactions among species, ultimately affecting community dynamics and functioning. Feeding rates depend on body mass and temperature (see [36] for a recent compilation of different functional responses). There are theoretical frameworks to investigate the effects of increasing temperatures on predator–prey interactions [36,39]. Vasseur & McCann [39] modelled consumer–resource dynamics, where metabolism and body size were dependent upon temperature, ultimately increasing consumer ingestion rate which shifted the system from a stable into an unstable (cycling) state. However, these authors assumed that the activation energy of consumption is higher than that of metabolism, which is not supported by recent meta-analyses [36,40]. In some cases, warming can stabilize population dynamics [41]. As a general theoretical expectation, increasing temperatures are likely to change the distribution of interaction strengths, with some interactions likely to become stronger.

Most empirical studies support this theoretical expectation, although evidence is not unequivocal. Top-down effects seem to get stronger as climate warms both in aquatic and terrestrial systems. In a seminal experiment, a marked increase in ingestion rates for the keystone predator seastar *Pisaster* of the dominant prey *Mytilus* was observed with higher water surface temperatures [42]. Similarly, warming increased the *per capita* interaction strength of the grazing amphipod *Ampithoe longimana* on the common macroalga *Sargassum filipendula* [43].

More generally, O'Connor and collaborators [44] showed that despite increases in primary productivity, warming strengthened consumer control of primary producers in a marine food web. This was due to shifts in food web structure towards greater heterotroph biomass relative to autotroph biomass, consistent with predictions based on the differential temperature scaling of respiration and photosynthesis metabolism [28,45,46].

Other authors found a somewhat similar effect of temperature on a predator–prey relationship between an insect and its larval anuran prey [47]. In this case, the proposed mechanisms behind the change in the interaction strength were different. An increase in temperature produced a general increase in the body size of the prey and this, in turn, rendered the gape-limited predator less able to capture prey. Tadpoles of a given size experienced a higher probability of capture, which had the potential of increasing the strength of this interaction. The overall effect of rising temperatures was a weakening of this predator–prey relationship, but there were direct as well as indirect effects involved in its change.

Warming is likely to affect both top-down and bottom-up control, but to a different extent. In greenhouse experiments using the aquatic community found in pitcher plants (*Sarracenia purpurea*), for example, warming increased mosquito predation on protozoa populations [48]. In contrast, bottom-up effects on protozoa were unaffected by temperature. Similarly, in terrestrial systems, Barton and co-workers considered direct and indirect effects in an old-field food web, showing that increasing temperatures did not change primary production, but the strength of top-down indirect effects on grasses and forbs increased by 30–40% per 1°C [49].

Whether bottom-up effects are generally unaffected by warming while top-down effects are strengthened requires further theoretical and empirical exploration (see [50]). Yet, if temperature influences the relative importance of top-down versus bottom-up effects, this would have major consequences for community dynamics and species persistence.

Changes in interaction strength are also a matter of time. In a series of theoretical and experimental papers, Rall and co-workers [51,52] showed that increasing temperatures tend to increase predator ingestion rate and *per capita* interaction strength in the short-term, while in the long-term temperature is likely to decrease interaction strength. They provide an elegant explanation by synthesizing metabolic and functional-response theory corroborated with experiments with terrestrial arthropods (beetles and spiders). What happens is that warming imposes energetic restrictions on predators in the long term by decreasing their energetic efficiencies (the ratio of feeding to metabolism), ultimately reducing interaction strength. However, this should be further explored, because in the long term other processes may compensate for increasing metabolism, such as increases in prey abundance or turnover rate [46].

The effects of temperature on the strength of interactions may depend not only on the amount of the increase in temperature, but also on the time of exposure to these regimes. Pincebourde *et al.* [53] found that chronic exposures to high temperatures decreased the predatory pressure of *Pisaster* over *Mytilus*, whereas an acute exposure had an inverse effect, increasing the strength of this trophic interaction. This is particularly relevant to the study of ecosystems with highly variable intra-annual temperature regimes, where climatic warming may have opposite effects on interaction strengths in different times of the year.

3. OPEN COMMUNITIES
The overall picture in open communities is more complex, however, because some species will spatially track changing climates, while others will not, and thus dispersal differences among species will act on top of changes observed in closed communities. In this section, we consider whether species shifting (mostly expanding) their ranges are characterized by specific traits. We also consider the nature of new and lost species interactions resulting from these differential range shifts.

(a) *A few generalities on species range shifts tracking climate change*
Species range shifts are perhaps the best-documented biological response to climatic warming to date, but there is little consensus regarding the extent to which

different organisms will be able to establish populations in newly suitable habitats. This is particularly important given the rapid rate of climate change. Mounting evidence shows that species' ranges follow changing climates, with most observations coming from latitudinal or elevation shifts from temperate species [1,2].

Over the last *lustrum*, some studies have demonstrated species differential range shifts leading to spatial mismatches as a consequence of warming. This has led to similar consequences as those observed in closed communities, i.e. the formation of non-analogue communities, with new combinations of existing species and a re-mixing of species interactions [5].

Which traits predispose species to better track climate change? Intuitively, greater dispersal ability could increase the rate of spread, and better dispersers should be capable of tracking climate change more effectively and rapidly. But dispersal distance is difficult to quantify because rare long-distance dispersal events can have a disproportionate effect on the overall rate of spread [54].

Other life-history characteristics such as early reproduction, frequent reproduction and high fecundity should also increase colonization opportunity [55]. Details on most of these traits are lacking for most species, and to be useful for forecasting variation in responses to climate change, such knowledge should be available across many taxa and geographical regions. An alternative is to rely on more commonly available surrogates of relevant life-history characteristics. Here, we focus on two of them: body-size and ecological specialization.

(b) *Do larger species migrate faster and further?*

Body size shows positive correlations with some traits affecting the potential for shifting ranges under warming, including dispersal ability, home range size, trophic level, fecundity or competitive ability [9]. The general expectation should therefore be that larger species are more likely to migrate tracking climate changes, and they will be able to establish in new environments.

The natural experiment provided by the Late Pleistocene glaciation event is a good starting point to assess evidence. Roy and collaborators [56] analysed the range shifts of Californian marine bivalves from this period, and found that large-bodied species were more likely to shift their distribution in response to climate change. A similar pattern was observed for mammals over the same time period, with a positive correlation between range centroid distance shift and species body size [57]. Interestingly, these authors found that small-bodied species show a great deal of variation in the distance that they shift their range, with some having range shifts as large as some of the largest species [57]. By contrast, large-bodied species have much less variation in the distance they shifted their ranges.

Responses to recent climate change, however, are less unequivocal. Noticeably, only a few studies have explored differential range shifts related to species body size. Large butterflies, measured as female wing length, have shifted ranges more than small butterflies

in Finland between two time periods (1992–1996 and 2000–2004) [58]. However, a recent meta-analysis [55] has shown that at expanding range edges, body size has very low explanatory power for range expansion for datasets of diverse taxa, including North American Passeriformes, British Odonata and western North American small mammals (see also [59]).

Some studies actually show the opposite pattern. Pole-ward range margin shift of 116 southern Finnish bird species was larger for small-bodied species [60]. Similarly, North Sea fish species with shifting distributions tended to have smaller body sizes and faster life cycles, reflected in faster maturation and smaller sizes at maturity than non-shifting species [61].

No clear trend is therefore evident from the available data. A possible explanation is that, while some traits that are positively correlated with body size predispose large species to track climate changes in space, other traits benefit the establishment of small organisms. For example, traits that are likely to increase colonization opportunity, such as frequent reproduction and high propagule pressure, are usually negatively correlated with body size. As a conclusion, it will be the balance between 'beneficial' and 'detrimental' traits correlated with body size that determines whether large species will be able to move further and faster.

(c) *Generalism, specialism and range shifts*

Species with specialized niches and highly co-evolved interactions that have resulted in strong specializations might encounter great difficulty establishing populations in new habitats as they expand their ranges. On the contrary, ecological generalists with broader diet breadths will more easily find suitable resources and realized interactions in their new location. In addition, polyphagy may enhance the ability of species to track climate change. The flexibility of polyphagous generalist species with the incorporation of novel hosts may result in species having greatly enhanced abilities to track climate changes, leading to unexpectedly rapid range expansion.

A clear relationship exists between habitat generalists and diet generalists: species living in more habitat types will tend to have a broader resource range, as is the case for British butterflies [62]. Mounting evidence shows that habitat generalists shift ranges more easily than habitat specialists [63]. However, limited data exist directly on the dispersal abilities and degree of specialization for most species (but see [59] for an exception).

In a recent meta-analysis by Angert *et al.* [55], diet breadth was a good predictor of range expansion for North American Passeriformes, with generalists moving further than specialist species. However, diet breadth was a poor predictor for other taxa, e.g. western North American mammals. Similarly, the generalist butterfly *Polygonia c-album*, which is showing the greatest range expansion of any butterfly in Britain during on-going climate warming, has altered its host plant preference [64]. Current range expansion of this species is associated with the exploitation of more widespread host plants on which performance is improved. In addition, widely distributed host-plant generalist
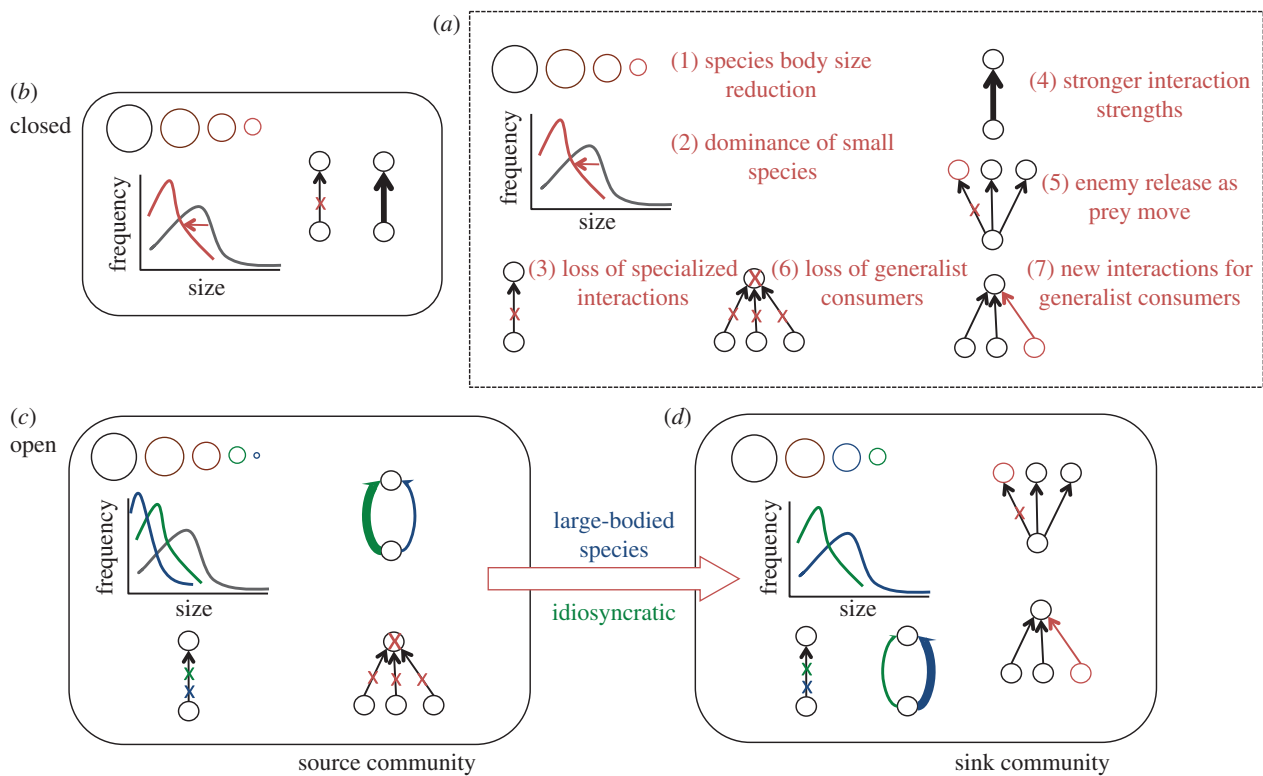
Figure 1. A summary of expected and unknown changes in size- and food web-structure in novel communities as a consequence of climate change. Cartoons in (*a*) correspond to the suite of changes addressed in this review. These include (1) reduction in species body size (population-level effect), (2) shifts in community size-distribution towards a dominance of small organisms, (3) loss of specialized reciprocal interactions, (4) increase in the strength of consumer–resource interactions, (5) enemy release as prey shift their ranges, (6) loss of consumers with broad diets as they preferably shift their ranges, and (7) appearance of novel interactions among migrating generalist consumers and native resources. Red colour indicates changes expected from climate change. (*b*) Corresponds to changes within closed communities as discussed in the main text. Lower panels correspond to open communities. For simplicity, it is illustrated with a source (*c*) and a sink (*d*) community, where, in addition to changes observed in closed communities, we consider changes due to migration of species from the source to the sink community, with no new species entering the source or leaving the sink community respectively. Two migration scenarios are considered to contemplate one of the major unknowns identified in our review: the preferential migration of large-bodied species (in blue) and the non-preferential, or idiosyncratic, migration of species—i.e. irrespective of their body size (in green). Changes in the source community are detailed in the main text.

noctuid moths were more mobile than host-plant specialists with more restricted distributions [65]. In summary, diet breadth may or may not be a good predictor, depending on the taxa considered: good for birds, butterflies and moths, bad for small mammals. As a conclusion, diet breadth is a good candidate predictive trait for more mobile taxa (birds, some groups of flying insects) and a poor predictor for less mobile taxa such as small mammals [66].

(d) Novel interactions and ecological release
We have seen before how climate change within closed communities can break existing species interactions and create new ones. The differential range shifts of species also remove and add interactions, both in the 'source' (where species are coming from) and 'sink' (where species arrive) communities (figure 1). It is hypothesized [7,67] that climate change could create ecological release for species that track changing temperatures better than their enemies. Victims can leave their natural enemies behind during a range expansion [32,67,68].

Research conducted in soil communities support this hypothesis. A number of range-shifting plant species

have less negative soil feedback in their expansion range than related native species [68]. For example, *Tragopogon dubius* is currently expanding from southern into northern West Europe. Along this expansion range, the plant has a better performance than closely related *T. pratensis*, which has a natural occurrence along the entire latitudinal gradient, owing to a combination of release from soil-borne enemies from its original range and accumulation of beneficial soil-borne organisms from the expanding range [68].

However, one of the biggest unknowns of range-expanding species is whether and of what nature new interactions with natives will be. Although theoretical explorations are available [67,69], direct empirical evidence is lacking. Lurgi *et al.* [59] is an exception, showing that most vertebrates migrating upwards in mountains as a consequence of climate change tend to interact with a more restricted suite of species than native vertebrates, modifying fundamental food web properties. Novel interactions can have a large influence on fitness because moving species lack co-evolutionary history with the new partner. This can cause local extinctions (e.g. increase in predation rates) but also might permit persistence otherwise impossible (e.g. a novel prey expanding into a predator's range) [7].

4. DISCUSSION AND CONCLUSIONS

Evidence presented here shows that species within a community will not respond equally to climate change. Some may adapt better and some may track changing climates faster than others. These responses will not be merely idiosyncratic, and species traits such as diet specialism and, to a lesser extent, body size are good predictors of which and how species will adapt to changing conditions. Differential species responses will affect the structure and dynamics of species interaction networks both by breaking already established interactions and by the appearance of novel interactions, as we discuss in this section.

In summary, we have identified three major expected broad changes and two major unknowns of novel ecosystems from climate change, which are illustrated in figure 1. For simplicity, let us consider an open system composed of a source community (figure 1c) from which species migrate and a sink community (figure 1d) where those species that shift their ranges arrive. This, of course, is an extreme and simplified example, because some species may simply expand their ranges, and thus will not disappear entirely from the source community.

The first expected broad change is the shift in the distribution of body sizes towards smaller sizes. Locally (within closed communities, figure 1b), most available evidence reports shrinking body sizes and a larger dominance of smaller species with respect to larger ones. However, we identified a first major unknown that might compensate for or exacerbate this reduction: will large-bodied species tend to preferentially shift (or expand) their ranges more than small-bodied ones? If they will, the source community will be characterized by a size distribution even more extreme due to the combination of shrinking body sizes at the population level and the loss of large species from the community due to migration (figure 1c in blue). Sink communities will in turn compensate for shrinking body sizes within populations with the arrival of large species, resulting in small changes in community size distribution but important compositional changes. In particular, former large species in the food web will reduce their size and be replaced by those that have expanded their ranges. The alternative scenario, i.e. idiosyncratic migration not related to body size, will result in similar community size-structure of the source and sink communities (figure 1c in green).

The second pattern is that the distribution of diet specialists and generalists is likely to change towards a major dominance of generalized interactions (some of them newly established interactions) and the loss of specialized reciprocal interactions. The loss of specialized interactions will be observed both at the sink and source communities, independently of the migration scenario considered –preferential migration of large-bodied species or idiosyncratic (figure 1c,d). Within closed communities (figure 1b), this will result primarily from phenological mismatches mostly affecting specialists. This can have important implications for biodiversity, because specialized interactions, although less frequent than previously expected [70], often result from highly coevolved interactions, and hence it could represent the loss of important evolutionary history. Moreover, some specialized interactions can be crucial for ecosystem functions such as pollination and biological control [15], and the loss of specialized pollinators and parasitoids, respectively, may largely affect ecosystem performance, given the low species redundancy characteristic of specialized interactions (i.e. it is difficult to replace their role by other species).

Source and sink communities, however, will differ in terms of the loss of generalized interactions. We have shown that consumer species with broader diet breadths follow changing climates better than specialists. Thus, source communities will tend to lose generalist consumers (figure 1c), whereas sink communities will acquire them (figure 1d). It is likely that generalist consumers that migrate will establish new interactions with resources in the sink community not present in the source community they come from. This would result in changes in population dynamics of those resources exploited by the generalist consumer through changes in apparent competition.

Similarly, enemy release of prey as they shift their ranges would trigger dynamic changes. In source communities predators will lose an important prey item (figure 1c), while in sink communities new prey species will experience less predation (figure 1d). This could eventually lead to increases in population size of newcomers in the community to the detriment of native prey with stronger top-down control, ultimately changing abundance distributions. This, however, could be compensated for if new interactions are established between range-expanding generalist consumers and prey populations that did not interact with each other in the source community.

The third broad pattern is the shift in the distribution of species interaction strengths. In the short term, and in closed communities, warming will strengthen some of the existing interactions (figure 1b). However, changes in interaction strengths will be different between source and sink communities if large-bodied species migrate preferentially (figure 1c,d). This is based on the scaling of predator–prey interaction strengths with predator : prey body size ratios—the larger the difference in size between predators and prey, the larger their interaction strength [10]. If large-bodied species from high trophic levels and large individuals within a species preferentially migrate, then interaction strengths in the source community would become weaker (loss of large predator : prey size ratios; figure 1c in blue) and they would become stronger in the sink community (gain of large predator : prey size ratios; figure 1d in blue). This would imply important changes in top-down control and community dynamics across ecosystems as a function of whether they act as source or sink communities of large predators shifting their ranges. This would act in synergy with reported changes in top-down versus bottom-up control in closed ecosystems. Whether bottom-up effects are generally unaffected by warming while top-down effects are strengthened requires further theoretical and empirical exploration (as shown in [50]). Yet, if temperature influences the relative importance of top-down versus bottom-up effects, and large species preferentially migrate, this would have major consequences for community dynamics and species persistence.

Finally, the second major unknown is how the strength of already established interactions will

change in the long term, mainly owing to changes in resource availability and accessibility. For example, predators with a diverse prey base might compensate for the smaller size of some of their prey items by shifting their diets to consume a larger proportion of bigger prey, rearranging the distribution of strong and weak interaction strengths within food webs. In addition, it is uncertain how strong interaction strengths among newly interacting species will be, especially in the case of idiosyncratic migration of species irrespective of their body size. Altogether, these uncertainties will render community dynamics within novel ecosystems from climate change a fundamental issue that still needs a solid theoretical and experimental framework.

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