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Nature Rewires in a Changing World

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Abstract

Climate change is asymmetrically altering environmental conditions in space, from local to global scales, creating novel heterogeneity. Here, we argue that this novel heterogeneity will drive mobile generalist consumer species to rapidly respond through their behavior in ways that broadly and predictably reorganize—or rewire—food webs. We use existing theory and data from diverse ecosystems to show that the rapid behavioral responses of generalists to climate change rewire food webs in two critical ways. Firstly, mobile generalist species are redistributing into systems where they were previously absent and foraging on new prey, resulting in topological rewiring—a change in the patterning of food webs due to the addition or loss of connections. Secondly, mobile generalist species, which navigate between habitats and ecosystems to forage, will shift their relative use of differentially altered habitats and ecosystems, causing interaction strength rewiring—changes rerouting energy and carbon flows through existing food web connections that alter the food web's interaction strengths. We then show that many species with shared traits can exhibit unified aggregate behavioral responses to climate change, which may allow us to understand the rewiring of whole food webs. We end by arguing that generalists' responses present a powerful and underutilized approach to understand and predict the consequences of climate change and may serve as much-needed early warning signals for monitoring the looming impacts of global climate change on entire ecosystems.

Keywords: asymmetric impacts, behavioral response, climate change, early warning signals, food webs, interaction strength, mobile generalist species, novel heterogeneity, space, topology

Introduction

Following the poleward shift in species distributions observed with climate warming, Blanchard[1] quipped that the resultant massive compositional changes to the Arctic marine food web[2] are akin to nature "rewiring" itself. This northern range expansion is dominated by species that are relatively large, highly mobile, and foraging generalists, and so increases the Arctic marine food web's complexity[2]. This influx of generalists thus fundamentally alters the structure of this Arctic marine food web, making it both more connected and less modular, and also perhaps making interaction strengths weaker on average. This one example highlights a potentially global phenomenon: ongoing climate change will continue to fundamentally restructure—that is, "rewire"—ecosystem, and yet the ways that food webs will rewire are remain nebulous[2,3].

The rewiring of Earth's food webs with climate change should be first detectable as rapid behavioral responses that are most prominently exhibited by mobile generalist species (see Table 1 for key definitions)[4–6]. For example, Korstch et al.[2] found that as waters warm, the fish species advancing north in a marine ecosystem tend to be high-trophic-level consumers that are mobile and forage on a large range of resources. Similarly, many of the terrestrial species dispersing poleward in response to warming are capable of rapid, long-range movement[7,8]. Species that possess this set of key correlated traits (high mobility in terms of movement or dispersal and flexibility in both foraging and habitat use) comprise what are commonly referred to as generalists[2] (Table 1). Generalist species are often capable of responding to resource and environmental variation through their behaviour, linking various habitats and ecosystems transcending the boundaries between them traditionally deemed by ecologists. By linking otherwise distinct habitats and ecosystems, these species structure food webs in space[2,9,10]. The movement of generalist species clearly has potentially significant implications for material and energy flow within and across ecosystems[5,6,11,12], but behavioural

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responses have been largely overlooked by ecologists studying how food webs are rewiring with climate change.

In what follows, we argue that the responses of mobile generalist species rewire food webs in a changing world. We first show that climate change has asymmetrical impacts in space from global to local scales, producing novel heterogeneity in environmental conditions worldwide to which species are poised to respond (Figure 1). We then discuss emerging studies that show this novel heterogeneity drives generalist species to rapidly and predictably respond to novel conditions through their behaviour[11]. These generalists' responses alter food web in two related but qualitatively distinct ways: by changing food web topology (i.e., topological rewiring *sensu* Blanchard[1]), and changing the strengths of existing interactions (i.e., interaction strength rewiring). We illustrate rewiring driven by climate warming using two detailed example food webs, one aquatic (Box 1) and one terrestrial (Box 2), each made up of ectothermic organisms that are highly sensitive to changes in temperature[13]. We then illustrate how whole groups of species with shared traits can exhibit unified, aggregate community behavioral responses to climate change that could rewire entire food webs. We end by arguing that these results enticingly suggest that rapid behavioral responses of generalists to climate change represent a powerful tool in monitoring nature's responses to environmental change and can act as a potent addition to the early warning signals toolbox.

Climate Change Creates Novel Heterogeneity Across Scales

While many aspects of global change are thought to homogenize ecosystems and landscapes[14–16], climate change impacts are also expected to vary spatially, transforming environmental heterogeneity in subtle but significant ways across scales (Figure 1)[17]. The impacts of climate changes are well known to be asymmetrical at large spatial scales (i.e., one region or hemisphere is impacted more than another). At the global scale, rates of warming are asymmetric between hemispheres, with warming

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of land and oceans in the northern hemisphere outpacing the southern hemisphere[18,19] (Figure 1A). Other global-scale properties are being asymmetrically altered too, including precipitation[20], El Nino and La Nina frequencies[21], and ice extent[22]. Climate models also predict asymmetry in responses within hemispheres, with polar and temperate ecosystems being more strongly impacted than tropical and equatorial systems[18,23]. Regional effects of climate change include greater temperature increases on the Earth's land masses than in the oceans[24] (Figure 1B). Taken together, these asymmetrical impacts are leaving a complex large-scale footprint of climate change.

Asymmetrical climate change impacts are also expected at smaller scales, both within and across ecosystems, although they are not as well studied as global responses[18,21,23,25]. These smaller scale asymmetrical impacts will likely arise because ecosystems and the various habitats that comprise them have different physical and abiotic properties that differentially filter the impacts of climate change[11], comparable to the factors that create climate refugia[26]. The result is asymmetrical impacts of climate change in different habitats and ecosystems (e.g., one habitat or ecosystem, say, warms more or more rapidly than another), creating a small-scale heterogenous mosaic in space. While the surface waters of most lakes worldwide are warming, warming rates vary between lakes depending on local properties such as surface area, shape, and depth[27]. Within lakes, thermal stratification produces asymmetric warming between shallow nearshore and deep offshore macrohabitats because surface waters that warm under direct contact with the air do not mix with deeper waters, which remain cold even in the summer (Figure 1C)[22-24]. Similarly, in terrestrial systems, climate change is predicted to asymmetrically impact mountainous regions via feedbacks between latitude and elevation that depend on local topography, elevation, slope, and treelines[28–30]. At even smaller scales, global changes like warming or increased precipitation interact with nutrient conditions to increase the local heterogeneity in limiting factors in terrestrial ecosystems[28-31]. These asymmetric climate change impacts from micro to macro scales will produce a novel, transformed heterogenous palette of fine- and coarse-grained habitats and ecosystems.

Rewiring Through Behavioral Responses

Novel heterogeneity stemming from climate change ought to elicit rapid behavioural responses by mobile generalist species. These responses could be due to either the direct physiological consequences of these new environmental conditions or from resultant changes in resource availability or distribution in space. Importantly, mobile high-trophic-level generalist species can navigate across the landscape, moving between habitats, ecosystems and even hemispheres, structuring food webs in space[10,31–33]. The responses of these species should therefore rewire food webs in two key ways (Table 1). Firstly, generalist species will expand into systems where they were previous rare or absent, resulting in topological rewiring—the addition or loss of food web connections or whole food web pathways. Topological rewiring is analogous to adding and removing "wires" in an electrical network. Secondly, generalist species will shift how they move and forage across multiple habitats and ecosystems, causing interaction strength rewiring—changes in the consumption rates of existing food web connections, thus rerouting energy flows through existing pathways. Interaction strength rewiring is akin to altering the "load" on the wires in an electrical network. Because the mobile generalist species that transcend the spatial boundaries between habitats and ecosystems link their energy and nutrient dynamics, their behavioural responses promise to fundamentally shift the interplay between sub-webs or food web compartments in different habitats and ecosystems. And when groups of generalist species with shared traits respond in concert to the altered spatial mosaic created by climate change, they have the potential to fundamentally reorganize the structures of whole ecosystems and biomes.

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Topological Rewiring

At the global scale, numerous studies have demonstrated the poleward movement of many species in various ecosystems worldwide, altering community structure and potentially restructuring local food webs [2,3,7,8,34–36]. Similar patterns exist across altitudinal gradients, as exemplified by upslope shifts in the distribution of bees, butterflies, and birds[37–39]. Importantly, these shifts tend to be dominated by generalist species, which are often more mobile and adapted to deal with spatial variation in resources and conditions[2,7,8,35,36]. These latitudinal and altitudinal advances of generalists strongly imply that local food webs should be experiencing species introductions and so undergoing topological rewiring as they gain new connections[1,2,40]. Local food webs may also lose connections because of the loss of species[36,40,41]. Notably, though, species ranges are expanding poleward and upslope faster than they are contracting, and the rate of species invasions appears to be outpacing the rates of local declines[7,42]. Taken together these changes suggest that, on average, we expect the reshuffling of species to skew local species diversity towards a more generalized set of species[3,43–45]. This skew towards generalists can fundamentally alter the topology of local food webs, increasing connectance and reducing modularity of the rewired food webs. These topological changes have potentially dramatic implications for stability and the maintenance of biodiversity[46–48], and topological rewiring from range expansion of tropical species has indeed been be associated with dramatic phase shifts in temperate marine food webs[49].

One clear example of topological rewiring comes from Kortsch et al.[2], who examined how climate change will impact the food web of the Barents Sea, which borders on the Arctic Ocean. They found that the boreal fishes moving poleward into the Barents Sea tended to be omnivorous generalist fish species. The addition of these generalists into the food web increased connectance and simultaneously reduced modularity by linking previously disparate modules corresponding to pelagic and benthic macrohabitats. Kortsch et al.[2] anticipate that the outcome of this topological rewiring in the Barents Sea food web will be altered patterns in carbon flow within this food web.

Interaction Strength Rewiring

Importantly, the asymmetrical impacts of climate change across scales are driving mobile generalist species to respond in ways other than redistributing across the globe and driving topological rewiring. Mobile generalist species may simultaneously alter the strengths of trophic interactions within food webs[50–52]. The distribution of interaction strengths, which is determined by the foraging actions of consumers, is a key part of food web structure that is well known to underlie the maintenance of diversity in and the stability of complex communities[46,48,52–55]. Research on food web rewiring has focused on topological changes in food web structure, with less emphasis on how interaction strengths will be altered by climate change. Some research has shown expected changes in average interaction strength with warming[56]. However, altered heterogeneity in space from climate change ought to change other aspects of interaction strength, such as strengthening some interactions and weakening others or rearranging the distribution of interaction strengths.

Many generalists forage across the landscape, coupling spatially distinct habitats and ecosystems[57]. Interaction strength rewiring can occur when these spatially distinct habitats and ecosystems are asymmetrically altered by climate change, driving generalist to change their relative use of resources in space. For example, asymmetrical warming between habitats may have physiological consequences for a generalist. The warming may increase metabolic demand, driving the generalist to increase its food consumption and thereby increasing the flow of energy through the existing food web pathways. However, if the metabolic consequences are too costly in the warmer habitat, a generalist may change its behaviour by decreasing use of food sources in the warmer habitat and increasing use of cooler habitats. This response would simultaneously reduce consumption on the

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existing food web pathways derived from the warmer habitat and increase consumption on the food web pathway from the cooler habitat. In this way, the amount of energy flow along existing warmed-up pathways (wires) is diminished, and the energy flow along other, less impacted pathways may be unchanged or increased. This change in mobile generalist consumers' behavior also results in the decoupling of adjacent habitats or ecosystems. Given that some migratory species, such as some whales and seabirds, couple the northern and southern hemispheres and adjust their behaviour with changes in climatic conditions[58], interaction strength rewiring also has the potential to play out at vast spatial scales.

Interaction strength rewiring has been documented in diverse ecosystems across the globe. Among the best-studied examples of interaction strength rewiring comes from boreal lake ecosystems in Canada that have lake trout (*Salvelinus namaycush*) as a top predator. The cold-water-adapted lake trout respond to the differential warming of the nearshore macrohabitat by retreating to the cooler offshore habitat and reducing its reliance on nearshore food resources (for details, see Box 1). Similarly, Barton, Schmitz, and co-authors[4,59–61] have shown interaction strength rewiring in grassland invertebrate food webs. When experimental warming shifts the vertical temperature gradient in grasslands, the active predatory spider *Phidippus rimator* moves down towards the relatively cool soil microhabitat, introducing novel intraguild predation causing extirpation of the sit-and-wait predatory spider *Phidippus mira*, reducing the feeding time of the grasshopper *Melanoplus femurrubrum*, and indirectly altering the biomass of grasses and herbs (for details, see Box 2). Additionally, Yurkowski et al.[62] show how the northward advance of a species due to climate change can cause interaction strength rewiring in Arctic marine ecosystems. As capelin (*Mallotus villosus*) move northward into Cumberland Sound, Nunavut, Canada, both beluga whales (*Delphinapterus leucas*) and Greenland halibut (*Reinhardtius hippoglossoides*) increase their foraging on forage fish, changing the summertime relationship between belugas and halibut from a primarily predator-prey interaction to a primarily competitive interaction (Figure 2A)[62]. A larger-scale example of across ecosystem interaction strength rewiring takes places at the sea-land interface. During periods of reduced sea ice, polar bears (*Ursus maritimus*) spend more time on land, spatially isolated from their preferred prey of ringed seals (*Pusa hispida*, see Figure 2B)[63,64]. At this time, the bears predate more on nesting seabirds and their eggs, altering the strengths of their interactoins with these resources[63,65]. This foraging switch is believed to be insufficient for them to maintain their condition, which is expected to negatively impact their populations[66]. Interaction strength rewiring may even occur on the largest spatial scales since migratory seabirds and whales, which couple hempisheres, now have to migrate farther poleward with climate change[67].

Spatially asymmetrical climate change may also drive interaction strength rewiring in more complex ways, such as by produinge phenological shifts. One intriguing example is that of Kodiak brown bears (*Ursus arctos middendorffi*), which feed on both terrestrial red elderberry (*Sambucus racemosa*) and on sockeye salmon (*Oncorhynchus nerka*)[68] (Figure 2C). While the productivity of these two resources were previously staggered in time, climate impacts pushed the elderberry to bloom earlier and now peak in synchrony with the relatively unaffected salmon spawns. This temporal synchronization effectively decoupled a connection between terrestrial and aquatic habitat that was mediated by bears[68]. Because climate change research has tended to initially cling to temperature changes (as noted by VanDerWal et al.[69]), many of our examples of rewiring focus on the impacts of asymmetrical warming. However, climate change is multifaceted, with many dimensions of climate change (e.g., precipitation) expected to be asymmetric in ways that similarly elicit rapid behavioral responses in mobile generalists and broadly rewiring food webs[70,71].

Aggregate Rewiring

The bulk of research on how climate change impacts food webs has focused on one or a small number of species, with less focus on how climate change may reorganize whole food webs[72]. Yet, the rewiring of food webs is likely not limited to a single generalist species response; entire suites of species within a food web may respond *en masse*, especially if they share key traits that drive their responses. To test this idea, we expand on the previous research showing how lake trout responses to climate change rewire lake food webs (described in Box 1). Lake trout responses result from reduced accessibility of the differentially-warmed nearshore macrohabitat in lakes. Lake trout are one of many cold-water adapted fishes that inhabit these lakes, and fish are generally relatively mobile[73]. Thus, reduced thermal accessibility of the nearshore macrohabitat may drive many of these species to exhibit similar behavioral responses to that of lake trout, generating a unified response of the entire cold-water thermal guild (Figure 3A). As expected, extensive spatial catch-per-unit-effort data from 721 lakes in Ontario, Canada[74] across a natural temperature gradient show that the cold-water guild is on average caught farther offshore (in deeper water) in warmer lakes (Figure 3B), indicating an aggregate behavioural response towards increased offshore habitat use. In addition, most of the 13 cold-water species, which span several trophic levels, individually were on average caught in deeper water in warmer lakes (Figure 3C). Because such shifts towards offshore habitat use are associated with decreased nearshore foraging[31,32], these unified behavioural results strongly imply significant rewiring throughout lake food webs, with major consequences for carbon flow in these ecosystems. Curiously, Dulvy et al[75] document similar aggregate behavioural responses in the North Sea. As the bottom temperature of shallow shelf seas warmed from 1980 to 2004, the whole bottom-dwelling fish assemblage comprised of 28 species moved into deeper waters[75]. The deepening of fish assemblages in these ecosystems exemplify two powerful case studies for the how rapid behavioral responses to climate change are rewiring interaction strengths at the whole food web scale. If groups of species with shared traits are widespread, these unified, aggregate responses may be common with climate change. Aggregate behavioural responses would allow us to scale from understanding how single species rewire food webs to understanding how whole food webs rewire with climate change. In combination with the aggregate range shifts documented for some groups of specie[75,76] aggregate responses may be vital to understanding food web rewiring with climate change.

Stability and Structural Early Warning Signals

Here, we have argued that the asymmetrical impacts of climate change ought to broadly and predictably rewire food webs in terms of both topology and interaction strength. The impacts of climate change are often strongly linked with simultaneous changes in other forms of human perturbations (e.g., species invasions) that may also drive rewiring[77,78]. These broadly imposed human impacts are allowing generalist species to redistribute around the globe, functionally homogenizing biodiversity, overwhelming more specialized species[79], and rewiring food webs[40,42,80]. Because food web structure and stability are inextricably linked[81], both topological rewiring and interaction strength rewiring have the potential to drastically alter stability. Despite the notion that heterogeneity largely plays a stabilizing role in ecosystems[82–86], the novel heterogeneity and behavioral responses we discuss here may not always act as a stabilizing force in newly rewired ecosystems[87]. The topological changes in Arctic marine food webs documented by Kortcsh et al[2]—increased connectance and reduced modularity—tend to be destabilizing because they synchronize whole food web responses to perturbations[46,53,54,88,89]. Yet, an influx of generalists may promote stability by weakening average interaction strengths[90] and allowing adaptive responses that mute variation[9]. Thus, in the interim, the exact ramifications of rewiring on stability may appear nebulous; however, the ultimate consequences of rewiring for stability are less ambiguous. With continuing asymmetrical climate change, some habitats and ecosystems will likely become completely inaccessible for the mobile generalists that couple them, leading to extensive decoupling that is well known to be destabilizing[91]. In addition, altered climatic conditions are likely to make ecosystems and habitats inhospitable for some species and impact key ecological and metabolic rates that are strongly liked to stability, making extinctions prevalent and inevitable and racking up extinction debt in many ecosystems[92]. Biodiversity loss on this scale is strongly linked to a loss in stability.

Given that generalist species responses critically influence stability, ecologists may be able to use the responses of generalist species as “structural” early warning signals to climate change impacts on ecosystems. Early warning signals (EWSs) have been successfully applied to forecast changes in diverse systems, from stock markets to ecosystems. Current ecological EWSs are largely based on time series of population abundance and have some significant challenges because empirical time series are often too short to decipher key signatures of a looming loss in stability, such as critical slowing down[93–95]. This aspect of EWSs is especially concerning for long-lived, higher-trophic-level organisms with population dynamic signatures like cycles and generation times that span multiple decades[96]. As a result, researchers have recently called for additional methods to be added to the EWS toolbox, including concomitant changes in spatial patterning within an ecosystem[97]. Our arguments here suggest that monitoring the behavior and foraging of high trophic level generalists can help detect key structural changes in food webs that indicate the imminent collapse of one or more species. Importantly, such behavioural assays using generalist species—the same species whose times series ought to be difficult to track—would expose pending collapse much shorter timescales and with much less intensive sampling efforts than time-series based approaches. For example, Guzzo et al.[31] use data collected over a period of 11 years to show rapid shifts in foraging behavior by lake trout in response to warming, which can live for decades. Given the rapid rate and large scale of environmental change worldwide, new structural indicators of looming change will be imperative to maintain the diversity and functioning of the biological systems on which we rely for critical ecosystem services[4,98,99]. With further research, we can harness generalists' responses to predict functional outcomes of climate change on the world's ecosystems.

Ecologists are already documenting rapid behavioral responses to changing environments conditions using a variety of tools that could serve as structural indicators of major changes to ecosystems. Increasingly common tools for diet analysis include biotracers like stable isotopes, fatty acids, and DNA barcoding, which can readily track changes in foraging behavior[100]. Yurkowski et al.[62] (Figure 2A) provide an excellent example of using stable isotopes to monitor ecosystem changes before and after the northward advance of a species with climate change. Theory suggests that the shift from a primarily predator-prey interaction to a primarily competitive interaction like Yurkowski et al.[62] document generally corresponds to a significant reduction in stability, perhaps foreshadowing major changes to this ecosystem. Another example of dietary monitoring comes from seabirds, which are known to couple across enormous spatial scales[58]. Seabirds that feed on multiple prey items (e.g., sardines, anchovies) have shown behavioral foraging shifts away from sardines that precede fishery surveys, which eventually indicated significant sardine population decline[58]. Diet-based tools could be particularly powerful when paired with traditional methods of detecting changes in animal movement with climate change, such as telemetry[31,101]. Perhaps these tools will reveal that generalists show increased behavioral variation prior to the looming major loss in system stability (e.g., loss of a key resource), analogous to the increased population abundance variance predicted by classical EWS theory. Because behavioral changes like movement are often accompanied by physiological changes, we might also expect a suite of organismal responses (e.g., growth, age at maturity, activity levels) in concert with climate change. Generalists' dietary, behavioral, and physiological responses together are likely to help address the unequivocal need for tools to detect looming collapses in ecosytems[102] and provide an across-scale-integrated approach to biomonitoring impacts of climate change[100].

Boxes

Box 1. The rewiring of lake food webs with climate change.

One well-documented example of rewiring comes from the well-studied north-temperate lake ecosystems that have cold-water lake trout (*Salvelinus namaycush*) as a top predator. Lake trout are highly mobile foragers that prefer cold water and can actively move and feed between shallow nearshore (littoral) and deep offshore (pelagic) macrohabitats[31]. The extent of littoral foraging by lake trout is governed by the thermal accessibility of the nearshore macrohabitat because lake trout experience a cost when making forays from their deep pelagic refuge into warmer littoral areas[31,32,100,103–106]. However, these two macrohabitats that lake trout couple will be differentially impacted by climate change, which is expected to warm the nearshore and surface macrohabitat faster than deep offshore macrohabitat[107,108]. This differential warming of the nearshore zone forces lake trout to respond by de-coupling from the nearshore, with lake trout moving into deeper colder waters and relying on less heavily on nearshore resources (Figure B1-A). The shift in habitat use by lake trout is revealed by long-term telemetry, which show increases the depth of detection as the nearshore macrohabitat warms (Figure B1-C data adapted from Guzzo et al.[31]). This is paralleled with a shift in lake trout diet that is apparent in stable carbon isotope signatures and stomach content analysis, which both show reduced reliance on nearshore food resources with increasing summer air temperature (Figure B1-B, adapted from Tunney et al.[32])[32,104]. Lake trout's behavioural response to the differentially-warmed littoral habitat thus represents rewiring of carbon flow through the whole lake ecosystems.

This rewiring of lake ecosystems has important consequences for both lake trout and whole lake ecosystems. Difficulty in garnering prey from the nearshore reduces both growth and condition factor in lake trout[31], suggesting a potential loss of stability (in that lake trout persistence is threatened) from reduced access to the littoral carbon pathway. Reduced nearshore foraging changes lake trout's

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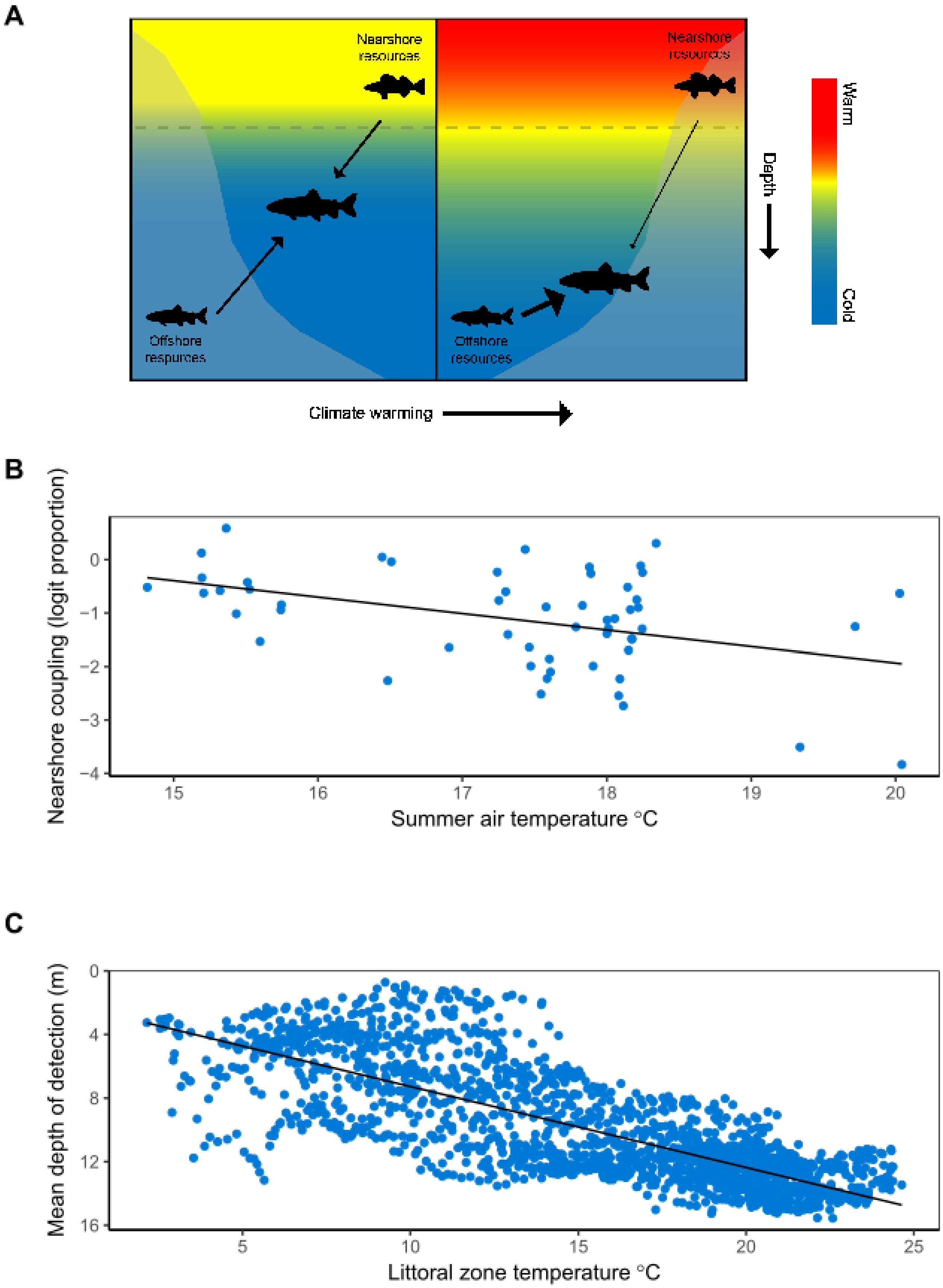
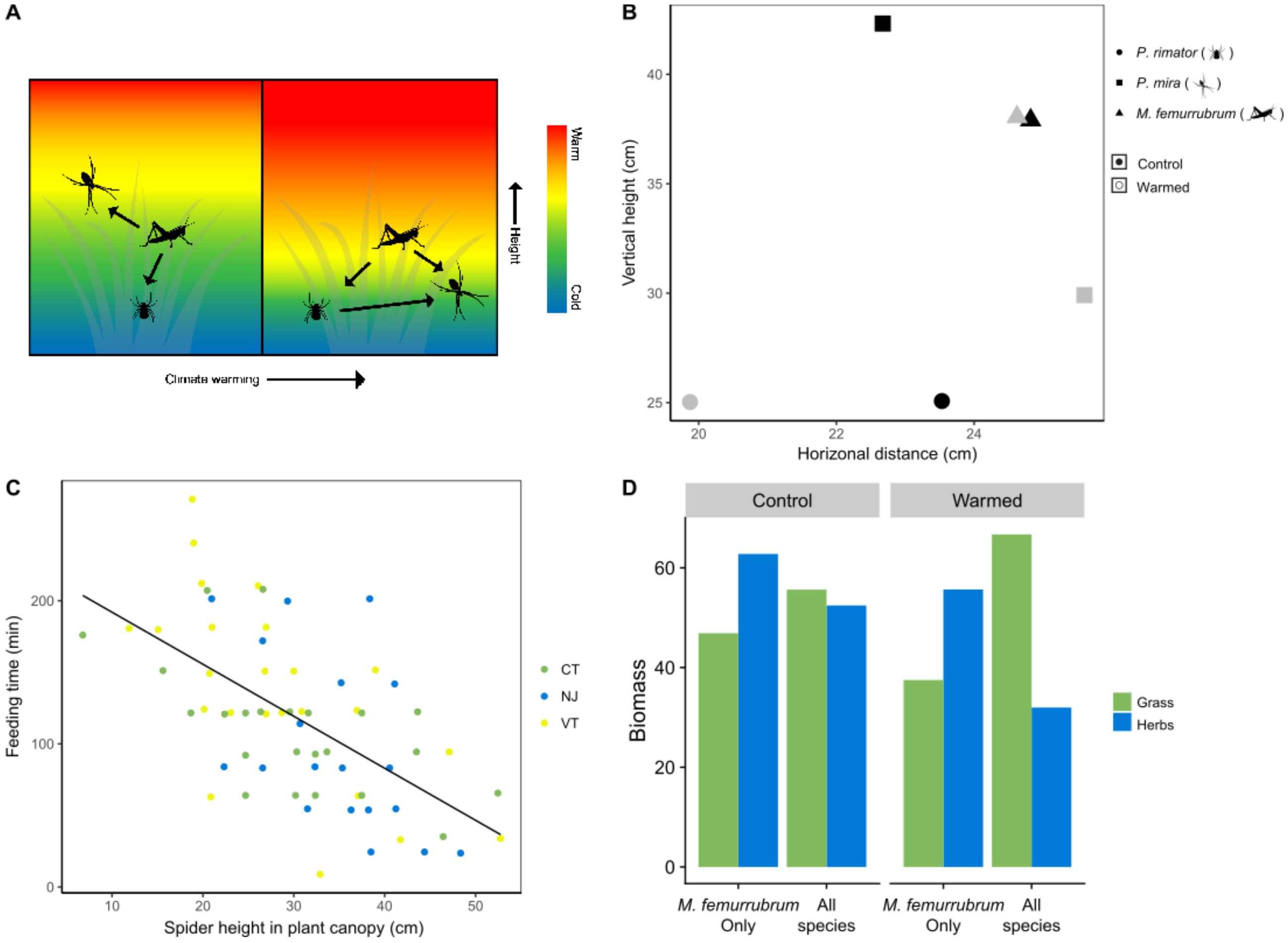
life history traits and reduce density in a way that may erode their top-down effects[100,109]. Temperate lake ecosystems are also highly seasonal environments, and lake trout show important seasonal shifts in behaviour and habitat use[31,106]. Climate change is altering various abiotic factors in lakes and affects some seasons more than others, suggesting that climate change will alter the seasonal flexes in lake food web structure. Such climate change impacts that are asymmetrical in time may also drive food web rewiring. Importantly, other species in boreal lake ecosystems, including the planktivorous cisco (*Coregonus artedi*) and the piscivorous walleye (*Sander vitreus*), both similarly display paired behavioral and dietary shifts away from the nearshore in increasingly warm lakes, showing that rewiring occurs at multiple places in lake food webs[109]. Such behavioural and dietary shifts may be a common response to thermally sensitive species in these lakes, producing unified aggregate behavioural responses to climate change (see *Aggregate Rewiring* and Figure 3).


A
Nearshore resources
Nearshore resources
Offshore resources
Offshore resources
Depth
Warm
Cold
Climate warming
B
Nearshore coupling (logit proportion)
0
−1
−2
−3
−4
15
16
17
18
19
20
Summer air temperature °C
C
Mean depth of detection (m)
0
4
8
12
16
5
10
15
20
25
Littoral zone temperature °C

Box 2. The rewiring of grassland food webs with climate change.

Temperate grassland food webs are expected to rewire in the face of climate change[4,59–61]. Grasslands have naturally occurring vertical temperature profiles corresponding to distance from the ground, creating distinct microhabitats near the soil surface and at the top of the grass canopy. Under ambient temperatures, the two spider predators are spatially separated, with the sit-and-wait predator *Phidippus mira* near the tops of the grasses and the active predator *Phidippus rimator* lower down near the soil (adapted from Barton & Schmitz[110]). Experimental warming shifts the entire temperature gradient[4,59–61], driving the sit-and-wait predator *P. mira* to respond by moving down closer to shaded thermal refugium near the soil surface at greater heights become too warm[4,33,110–112]. When *P. mira* responds by changing its microhabitat use by moving down, it spatially overlaps with the sit-and-wait predatory spider, *P. rimator*, driving intraguild predation that knocked out the *P. rimator* in Barton & Schmitz's[110] experimental microcosms. The behavioural response of *P. mira* impacted the foraging behaviour of herbivorous grasshoppers, *Melanoplus femurrubrum*. As *P. mira* moved down and farther away from *M. femurrubrum* with increasing temperature, *M. femurrubrum* showed increasing feeding time (adapted from Barton[61]). As a result, changes in top-down effects from predatory spiders drove indirect effects on herbaceous plant biomass, with the biomass of grasses and herbs in experimentally warmed mesocosms significantly altered when compared to control mesocosms (adapted from Barton & Schmitz[110]). This indirect effect is critical given that the direct effects of warming on plant biomass is less than the indirect effects of top-down control by spiders[60]. These studies also hint at the consequences of this grassland food web rewiring, with the loss of *P. rimator* suggesting possible impacts on stability and the change in plant biomass suggesting possible changes to ecosystem function. Barton and co-authors have also looked at how factors like wind and precipitation can also rewire terrestrial food webs[113,114], implying food web rewiring with other aspects of climate change. Intriguingly, Barton and Schmitz[115] show that daytime and nighttime warming having opposite effects on spider activity, producing opposite trophic cascades. These results suggest that climate change asymmetries in time may also drive food web rewiring. Taken together, these studies make a unique case study how the climate change asymmetries rewire grassland food webs.



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Figures and Tables

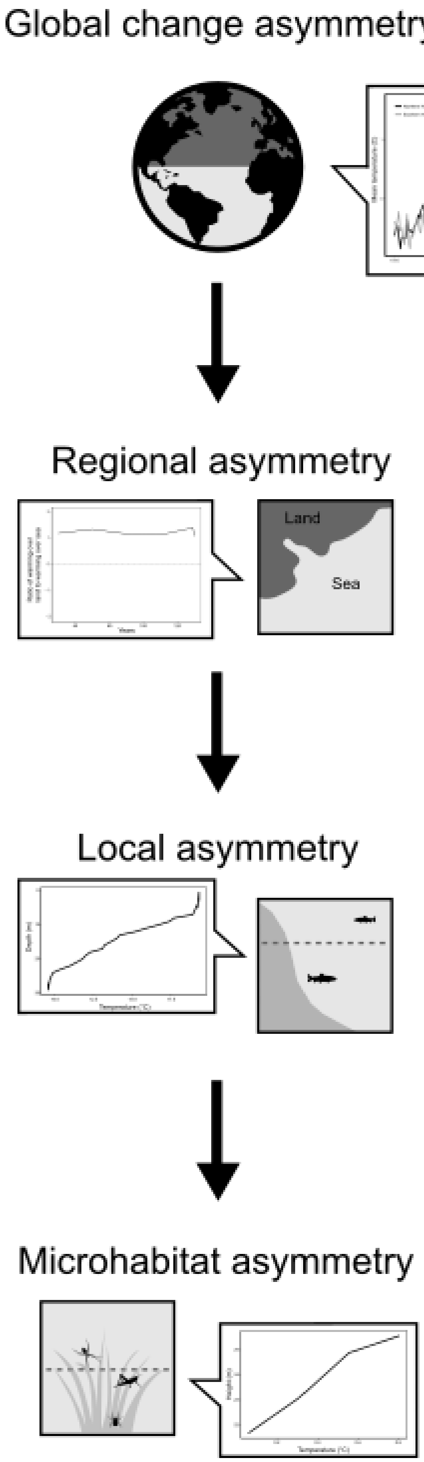

Figure 1. Examples of the asymmetrical impacts of climate change create novel heterogeneity across spatial scales, from local to global. (A) Global temperature data from 1880-2017 indicate

temperatures in the Northern hemisphere is increasing more rapidly than in the Southern hemisphere (adapted from Flato and Boer[18]). (B) The ratio of land/sea warming rates from many climate change models shows that land is warming faster than seas (adapted from Sutton et al.[24]). (C) Because of thermal stratification in lakes, indicated by this vertical temperature profile, the nearshore (littoral) areas and surface waters of lakes are warming faster than deep and offshore (pelagic) areas. (D) Temperature increases vertically farther to the soil surface to the top of grasses in grassland ecosystems (adapted from Barton and Schmitz[60]).

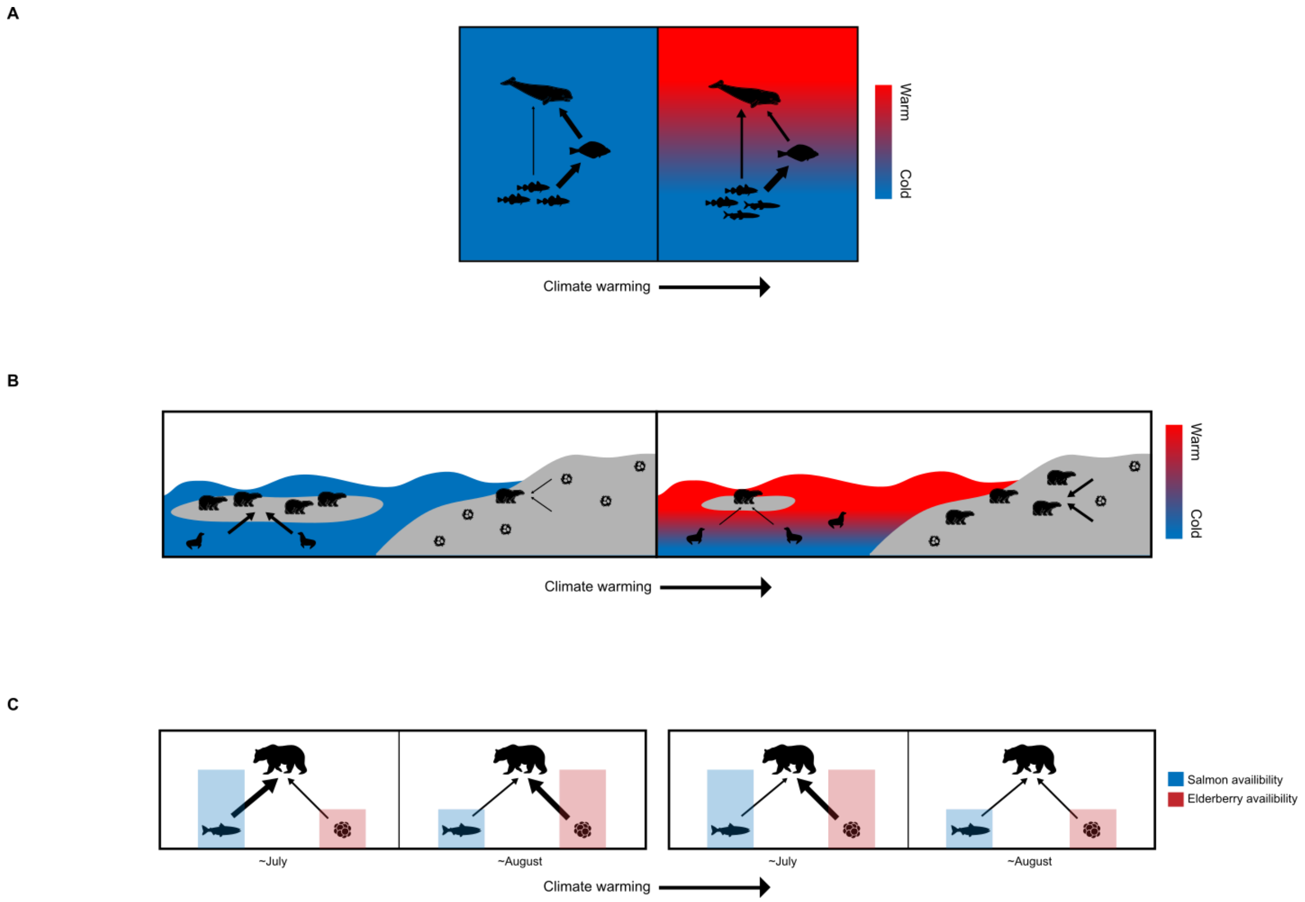

Figure 2. Three examples of food web rewiring from diverse ecosystems. (A) Rewiring of the arctic marine food web in Cumberland Sound, Nunavut, Canada. As capelin (*Mallotus villosus*) move northward into Arctic marine ecosystems, both beluga whales (*Delphinapterus leucas*) and Greenland halibut (*Reinhardtius hippoglossoides*) increase their foraging on forage fish. These responses change the summertime relationship between belugas and halibut from a primarily predator-prey interaction to a primarily competitive interaction (adapted from Yurkowski et al.[62]). (B) Rewiring of the food web across the Arctic land-sea interface. During periods of reduced sea ice, polar bears (*Ursus maritimus*) spend more time on land, spatially isolated from their preferred prey of ringed seals (*Pusa hispida*). While on land, the bears predate more on nesting seabirds and their eggs and less on ringed seals, altering the strengths of their interactoins with these resources

(adapted from Prop et al.[63], Hamilton et al.[64], and Smith et al.[65]). (C) Rewiring of the food webs of coastal Pacific North America. Kodiak brown bears (*Ursus arctos middendorffi*) feed on both terrestrial red elderberry (*Sambucus racemosa*) and on sockeye salmon (*Oncorhynchus nerka*). While these two resources were previously staggered in time, climate impacts pushed the elderberry to bloom earlier and now in synchrony with salmon, effectively forcing the decoupling of between terrestrial and aquatic habitat that was mediated by bears (adapted from Deacy et al.[68]).

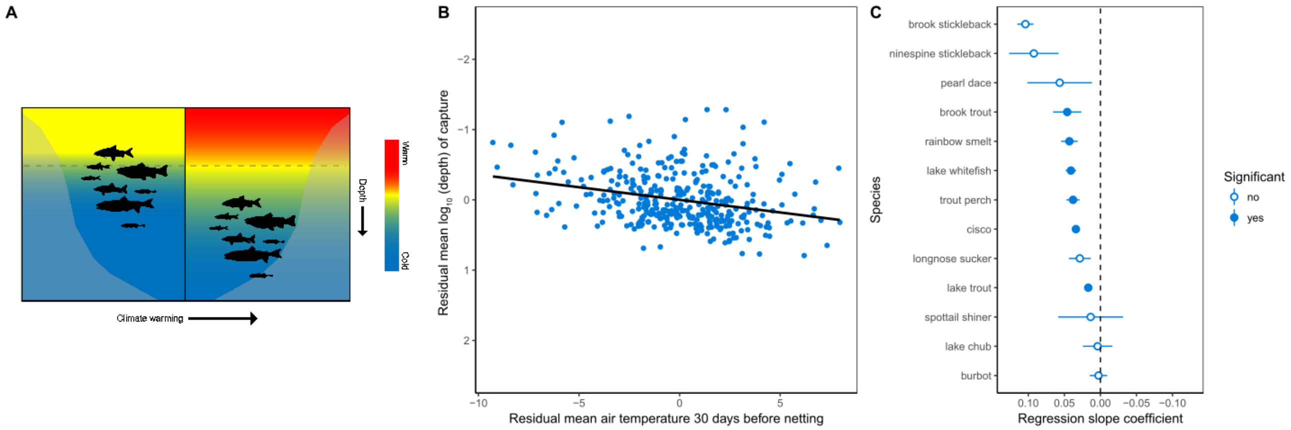

Figure 3. (A) The aggregate behavioural response of coldwater fishes to move into deeper, offshore waters with climate warming, which suggests the rewiring of boreal shield lake food webs. (B) The residual average $\log_{10}$ depth of capture for 13 coldwater fish species increases across a gradient of increasing average recent air temperature based on spatial catch-per-unit-effort data from 721 lakes in Ontario, Canada, showing that cold-water species were on average caught in deeper water in warmer lakes (adapted from Bartley[109], see Supplementary Information). (C) The slope coefficient (with standard error) for regression models of the residual average log10 depth of capture across a spatial gradient of average recent air temperature for each of 13 cold-water species, showing many species contribute to the unified behavioural response of these species to increased temperature (adapted from Bartley[109], see Supplementary Information).

Table 1. Key terms and concepts relating to the rewiring of the world's food webs with climate change

rewiring	Fundamental changes in the structure of a food web that alter the pathways of nutrients and/or energy in an ecosystem. Rewiring can occur from changes in either food web topology (topological rewiring) or changes in interaction strengths (interaction strength rewiring).
topological rewiring	Changes in the topology of a local food web (i.e., who eats whom), which often result from novel species introductions and/or the loss of local species.
interaction strength rewiring	Changes in the strengths of interactions in a local food web (i.e., the magnitude of the effect on the energy flow from one species on another), which often result from changes in the consumptive demand of a consumer associated with changes in the consumer's behaviour.
novel heterogeneity	Unprecedented, increased distinctiveness in the relative environmental conditions of habitats that arises from the asymmetrical impacts of climate change. These asymmetrical impacts of climate change occur at various scales, from within ecosystems to between entire hemispheres.
behavioral response	Changes in behaviour by a species or suite of species, such as dispersal, movement, habitat use, and foraging actions, that occur in reaction to changes in environmental conditions.

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mobile generalist species	Species that tend to possess high mobility (in terms of movement or dispersal) and flexibility in both foraging and habitat use. As a result, these species tend to have a large dietary breadth and link macrohabitats through their foraging actions, allowing them to behaviourally respond to environmental variation in space and time.
structural early warning signal	Properties in food web structure (topology and interaction strengths) that suggest imminent and drastic changes in ecosystems, such as major shifts in stability or regime shifts.

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Author Contributions

T.J.B. and K.S.M. conceived the concept for and contributed equally to this paper. All authors contributed to the development of the ideas and to the writing and editing of the text, led by T.J.B. and K.S.M. T.J.B. and M.G. prepared the figures using data from T.J.B., T.D.T., and M.M.G. as well as other sources. T.J.B. and K.S.M. led the final draft preparation and submission stages with comments from all authors being received prior to submission.

Competing interests

In relation to the work here, the authors acknowledge no competing interests.

Additional Information

The data used to produce figures 1 and 3 can be found online at 10.5281/zenodo.1158733