

## Opinion piece



**Cite this article:** Thakur MP. 2020 Climate warming and trophic mismatches in terrestrial ecosystems: the green–brown imbalance hypothesis. *Biol. Lett.* **16**: 20190770. <http://dx.doi.org/10.1098/rsbl.2019.0770>

Received: 20 October 2019  
Accepted: 18 January 2020

**Subject Areas:**  
ecology, environmental science, evolution

**Keywords:**  
food webs, trophic asynchrony, phenology, climate warming, weak interactions, soil

**Author for correspondence:**  
Madhav P. Thakur  
e-mail: [m.thakur@nioo.knaw.nl](mailto:m.thakur@nioo.knaw.nl)

Electronic supplementary material is available online at <https://doi.org/10.6084/m9.figshare.c.4829340>.

# Climate warming and trophic mismatches in terrestrial ecosystems: the green–brown imbalance hypothesis

Madhav P. Thakur

Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

MPT, 0000-0001-9426-1313

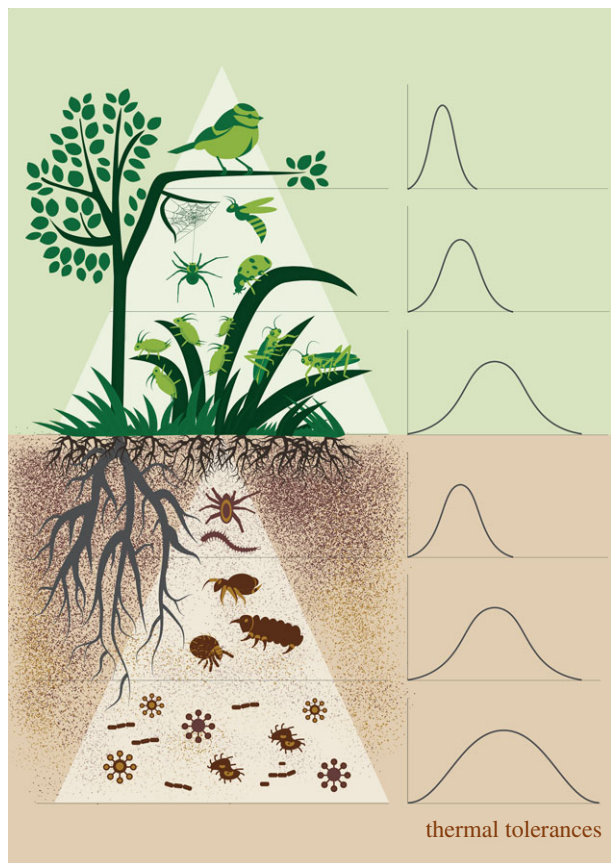
Anthropogenic climate change can give rise to trophic mismatches in food webs owing to differential responses of consumer and resource organisms. However, we know little about the community and ecosystem level consequences of trophic mismatches in food webs. Terrestrial food webs are broadly comprised of two types of food webs: green food webs aboveground and brown food webs belowground between which mass and energy flow mainly via plants. Here, I highlight that the extent of warming-induced trophic mismatches in green and brown food webs differ owing to a greater stasis in brown food webs, which could trigger an imbalance in mass and energy flow between the two food webs. I then discuss the consequences of green–brown imbalance on terrestrial ecosystems and propose research avenues that can help understand the relationships between food webs and ecosystem functions in a warmer world.

## 1. Green and brown food webs

Terrestrial food webs are composed of two interlinked food webs: the green food webs and the brown food webs (figure 1). Typically, the aboveground part of plants forms the base of green food webs, whereas the belowground part of plants (i.e. roots) together with the dead plant and animal materials form the base of brown food webs [1,2]. The balance of mass and energy flow in terrestrial ecosystems largely depends on how they flow between green and brown food webs via the interaction between plants and consumer organisms (microorganisms, invertebrates and vertebrates) living above and below the ground (figure 1). Recent studies have shown that different trophic levels in both green and brown food webs respond differentially to ongoing climate change (e.g. warming and drought) [3–7]. Differential responses of lower and high trophic levels within food webs result in trophic mismatches, which can make food webs potentially unstable with unwanted consequences for communities and ecosystems [8–12]. However, we know little about whether trophic mismatches in green and brown food webs also affect the interactions between green and brown food webs. Moreover, food web studies rarely integrate the simultaneous response of two food webs to climate warming [13,14]. Addressing this knowledge gap is important for understanding whether ongoing climate change can disrupt the balance of mass and energy flow between green and brown food webs (box 1).

## 2. Climate change and trophic mismatches in food webs

Recent understanding of trophic mismatches comes from empirical studies showing a mismatch between the phenology of consumer and resource organisms as a result of climate warming [10,20–22]. For instance, trophic mismatches in a food web occur when warming shifts the timing of reproduction and peak



**Figure 1.** Illustration of green and brown food webs. Different ranges of thermal tolerances at different trophic levels of food webs make them differentially responsive to warming. These often result in trophic mismatches in food webs.

abundance of resources but not that of their consumers [10]. While time-related biological events are central in the current understanding of trophic mismatches, differential thermal sensitivity of consumers and resources, such as in their feeding rates, can also trigger warming-induced trophic mismatches [4,23,24]. Moreover, trophic mismatches could also have a spatial component to it [25]. For example, spatial trophic mismatches occur when the response of a resource organism (e.g. plant) to climate warming is to migrate to newer areas while their consumers (e.g. herbivore) are unable to track their migratory range [26]. Such mismatches could result in the rewiring of food webs that can fundamentally change both the topology and interactions within food webs [27].

Trophic mismatches in green food webs have been shown for several systems, such as in Western European forests [10,22]. One notable example is that of the oak–caterpillar–great tits food web in the Netherlands [20]. Because of higher spring temperature, the caterpillar community showed an advancement in their maximal community biomass following the changes in oak phenology, however, the consumers (i.e. the great tit) of the caterpillar showed no adjustments in their egg production date [20]. Thus, this food web showed a mismatch between the timing of reproduction (great tits) and the peak resource abundance (caterpillars). A recent study carried out in UK also confirmed trophic mismatches in a similar green food web (oak–caterpillar–blue tits) across a latitudinal gradient [28], indicating a generality of such mismatches. Another study of terrestrial green food webs with multiple species (plant,

### Box 1. The nexus between green and brown food webs.

Green and brown webs in terrestrial ecosystems depend on above- and belowground plant production. Plants act as a conduit of resources for microorganisms and animals living above and below the ground. Plant derived organic resources flow into brown and green food webs and later are converted into inorganic resources from dead biomass that plants take up from the soil. Alterations at any trophic level (e.g. changes in plant, herbivore/detritivore and predator density or biomass) in either green or brown food webs can have effects on the other trophic levels via bottom-up and top-down effects [15,16]. For instance, plants consumed by herbivores in green food webs can affect the herbivores and detritivores of brown food webs via changes in plant's allocation of defences and plant's resource economics [15]. Shifts in the detritivore or herbivore communities of the brown food webs also show reciprocal effects [17]. Furthermore, changes in predator communities either belonging to green or brown food webs can cascade to other trophic levels of both compartments mainly via altering plant's direct interactions with herbivores and indirect interactions with detritivores (e.g. via the quality of litter) [18,19].

invertebrate and vertebrate) confirmed that phenological advancements in plants were maximal while that of vertebrates were minimal [29]. Such differential responses of resources and consumers (not only limited to phenological shifts) to climate warming are the key recipe of warming-induced trophic mismatches. Consumers can also prevent trophic mismatches when they are able to make physiological and behavioral adjustments (e.g. feeding rates, resource switching) to track the response of their resources in response to climate warming [30,31].

The responses of brown food webs to various global change factors often depend on global change effects on plants, such as how plant quality and quantity change with a particular global change factor [32]. Warming-induced trophic mismatches in brown food webs are relatively less explored compared to that of green food webs [33,34], and therefore we still know less about trophic mismatches in brown food webs. However, given the differences in thermal tolerance across trophic groups in the soil (figure 1), warming can also induce trophic mismatches in soil food webs. For instance, if a top predator in the soil (e.g. a wolf spider) shifts its timing of egg production, but its prey (e.g. Collembola) do not in response to climate warming, a trophic mismatch is a likely scenario. A major challenge in soils is to track such phenological shifts of species in response to warming given the complexity of the soil habitat and a high density of species [33]. The indication of trophic mismatches in soils in response to climate warming thus mainly comes from studies that have shown differential responses among communities of different trophic levels of brown food webs [4,35,36], potentially also owing to interspecific variation in thermal tolerance between predators and prey communities [37]. These differences in responses are often measured in terms of microbial biomass and soil

invertebrate density. Studies also indicate trophic mismatches by measuring biological processes at different trophic levels of soil food webs, such as microbial respiration and invertebrate feeding activity in response to warming [34,38].

### 3. The green–brown imbalance hypothesis

The balance in mass and energy flow between green and brown food webs may shift because of the differences in responses of green and brown food webs to climate warming, referred here as the green–brown imbalance hypothesis. Indeed, other disturbance agents than warming can also trigger green–brown imbalances, such as drought [39] or grazing pressure [2], which are also caused by different sensitivity of green and brown food webs to a given disturbance. The focus of this essay is on green–brown imbalances owing to climate warming. Below, I discuss why two food webs may have different sensitivity to climate warming.

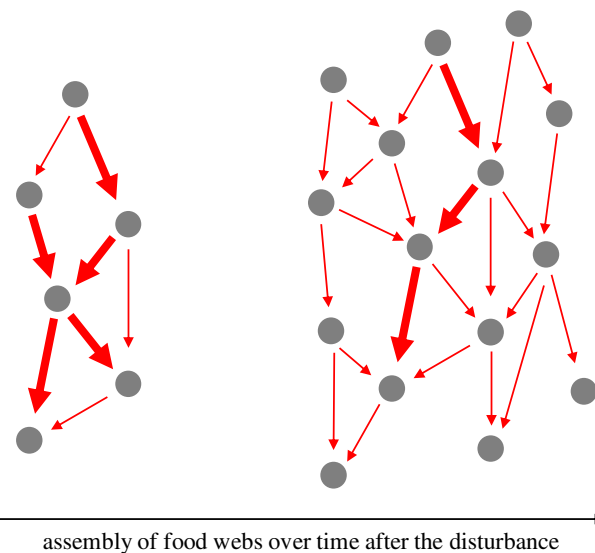
Let us first assume that a food web begins to assemble after a disturbance. A disturbance would locally eliminate species at different trophic groups and make it lower in species number (figure 2). As time progresses post-disturbance, species-poor food webs become species-rich via community assembly processes [40]. Food webs often assemble with several weak and few strong trophic links among consumers and resources (see [41] for details). The distribution of trophic relationships or interaction strength between consumer and resources in such a food web would skew towards weaker interactions. Such a food web is often considered to be more stable against perturbation or disturbance [41] (figure 2).

Trophic mismatches owing to climate warming are likely to push food webs away from such a stable state by altering interaction strengths [42]. The extent of such a trophic mismatch is likely to vary between food webs with different frequencies of strong versus weak interaction strengths. A food web with a greater number of strong interactions (e.g. specialized interactions) is more likely to exhibit trophic mismatches mainly owing to the inability of specialized consumers to track the dynamics of their resources when exposed to climate warming [10].

The shift of balance in mass and energy flow between green and brown food webs owing to climate warming is likely to result from a greater susceptibility of green food webs to trophic mismatches (leading to losses in feeding interactions) than brown food webs. There are at least two underlying reasons for the greater susceptibility of green food webs for trophic mismatches (i) differences in habitat features between green and brown food webs result in a greater frequency of stronger interactions in green food webs than in brown food webs, and (ii) wide thermal tolerance of soil microorganisms, which are a key basal resource of brown food webs.

#### (a) Differences in habitat features

Some habitat features of green and brown food webs are fundamentally different [1]. Species belonging to brown food webs reside in a highly complex structural habitat with a very fine (spatial) scale gradient of physio-chemical characteristics [43]. The habitat of green food webs is mainly characterized by the structural complexity owing to plant structures in the air. Given the greater habitat complexity in soils than in air, movement of organisms of brown food



**Figure 2.** Food web assembly after a disturbance leads to a greater number of weaker interactions. The weaker interactions are indicated by thinner red arrows, whereas stronger interactions are indicated by thicker arrows. In this opinion, I argue that the number of weaker interactions become higher in brown food webs than in green food webs during the food web assembly.

webs are highly constrained [1,44]. Because of this, predator–prey interactions are spatially obstructed more in brown food webs than in green food webs, which in turn enhance the number of weaker interactions in brown food webs [45]. Brown food webs indeed have a greater number of omnivory and intra-guild predation links (weak interactions) than specialized trophic relationships (strong interactions) observed in green food webs (e.g. host–parasitoid, specialist herbivores) [46–49]. Thus, both the likelihood of warming-induced trophic mismatches and its impacts on food web dynamics (e.g. mass and energy flow within food webs) will be greater in green food webs than in brown food webs.

#### (b) Thermal acclimation in soil microorganisms

In addition to habitat features which could lead to differences in green and brown food web responses, wider thermal tolerances of soil microorganisms can further reinforce a variation in sensitivity between the two food webs (figure 1). Soil microorganisms form a crucial base of the brown food webs, which is connected to several consumers of the soil [16]. It is increasingly shown that soil microorganisms can acclimate to warming by adjusting their metabolism and resource-use efficiency [50,51]. Microbial consumers are thus less likely to be deprived of microorganisms at higher temperatures. Brown food webs with greater thermal acclimation of soil microorganisms can, therefore, prevent thermally sensitive microbial consumers from starvation. This, in turn, is likely to minimize trophic mismatches (those arising from lack of resource availability) between soil microorganisms and their direct consumers. It is further likely that the complex structure of soils provides thermal refugia to several soil organisms that can also rescue them from warming effects [52]. However, thermal acclimation of soil microorganisms that are closely associated to plants (e.g. obligate symbionts) can depend on the dynamics of plant roots in warmer environments [53].

## 4. Consequences of the green–brown imbalance on ecosystem processes

The differences in the extent of trophic mismatches between green and brown food webs are likely to perturb mass and energy flow between the two compartments. Usually, the mass and energy feedback between the two compartments are crucial for maintaining ecosystem processes ranging from nutrient mineralization, carbon sequestration and primary production [16]. One way to think about the consequences of green–brown imbalance is via the differences in biomass entering from green to brown food webs, and in turn from brown to green food webs (electronic supplementary material, figure S1). We can expect two scenarios through which green–brown imbalance can affect ecosystem processes (electronic supplementary material, figure S1): (i) lower input of biomass entering from green food webs to brown food webs and (ii) higher input of biomass entering from green food webs to brown food webs. Both of these scenarios will depend on how warming affects plant production in green and brown compartments.

While our understanding of how these two scenarios affect ecosystem processes is limited, we could speculate that communities belonging to green and brown food webs are likely to change with the changes in mass and energy flow between the two. For instance, when the input from green food webs is at a shorter supply to brown food webs, one may expect adjustments in decomposition and mineralization rates in the soil with implications for microbial communities that can only thrive with a minimum of resources [54], with potential losses of some microorganisms. In such cases, if the brown webs are exposed to drought, it might further reinforce the imbalance by slowing down the input from brown to green food webs [38]. Experimental approaches can help understand the implications of green–brown imbalances on the community structure of green and brown food webs as well as associated ecosystem processes. Furthermore, the two compartments when unperturbed would tend to reassemble back to balanced states over time by balancing mass and energy flow. I suspect that the

reassembly of green and brown food webs from imbalanced to balanced states might result into shifts in community structure and potentially even the biodiversity (e.g. number of species) in either of the compartments.

## 5. Outlook

Here, I have argued that the extent of trophic mismatches owing to climate warming will vary between green and brown food webs in terrestrial ecosystems. As a result, we could expect a green–brown imbalance, which can have multiple consequences on ecosystem processes ranging from changes in primary production to shifts in decomposition rates. Other global change factors than climate warming can also influence the green and brown food webs differentially. For instance, a drought experiment showed that aboveground herbivores suffered more from the drought than soil organisms [39]. Future experiments with compartmental (both green and brown food webs) and climate warming manipulations together with other global change factors can help understand the dynamics of green–brown imbalances and their consequences on ecosystem processes [55]. Both empirical and theoretical models will be important to understand the implications of green–brown imbalances for food web stability, multi-trophic biodiversity and ecosystem functions in a changing world.

**Data accessibility.** This article has no additional data.

**Competing interests.** We declare we have no competing interests.

**Funding.** The financial support came from the German Research Foundation (grant no. TH 2307/1-1). This is publication 6881 of the Netherlands Institute of Ecology.

**Acknowledgement.** I am grateful to four anonymous reviewers for suggestions on the previous versions of this manuscript. I am grateful to Wim H. van der Putten for his constant encouragement to write this manuscript. The manuscript benefitted from discussions with Nicole van Dam, Katja Steinauer, Henjo de Knecht, Ciska Veen, Casper Quist, Rutger Wilschut, Arjen Biere and Mark van Kleunen. I thank Friederike Arndt (info@formenorm.de) for her help in drawing figure 1.

## References

1. Van der Putten WH, Vet LEM, Harvey JA, Wackers FL. 2001 Linking above- and belowground multitrophic interactions of plants, herbivores, pathogens, and their antagonists. *Trends Ecol. Evol.* **16**, 547–554. (doi:10.1016/S0169-5347(01)02265-0)
2. Schrama M, Berg MP, Olf H. 2012 Ecosystem assembly rules: the interplay of green and brown webs during salt marsh succession. *Ecology* **93**, 2353–2364. (doi:10.1890/11-1102.1)
3. Voigt W *et al.* 2003 Trophic levels are differentially sensitive to climate. *Ecology* **84**, 2444–2453. (doi:10.1890/02-0266)
4. Thakur M, Griffin J, Kuenne T, Dunker S, Fanesi A, Eisenhauer N. 2018 Temperature effects on prey and basal resources exceed that of predators in an experimental community. *Ecol. Evol.* **8**, 12 670–12 680. (doi:10.1002/ece3.4695)
5. Thackeray SJ, Henrys PA, Hemming D, Bell JR, Botham MS, Burthe S, Wanless S. 2016 Phenological sensitivity to climate across taxa and trophic levels. *Nature* **535**, 241–245. (doi:10.1038/nature18608)
6. de Sassi C, Tylianakis JM. 2012 Climate change disproportionately increases herbivore over plant or parasitoid biomass. *PLoS ONE* **7**, e40557. (doi:10.1371/journal.pone.0040557)
7. Siebert J, Eisenhauer N, Poll C, Marhan S, Bonkowski M, Hines J, Koller R, Ruess L, Thakur MP. 2019 Earthworms modulate the effects of climate warming on the taxon richness of soil meso- and macrofauna in an agricultural system. *Agric. Ecosyst. Environ.* **278**, 72–80. (doi:10.1016/j.agee.2019.03.004)
8. Renner SS, Zohner CM. 2018 Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annu. Rev. Ecol. Evol. Syst.* **49**, 165–182. (doi:10.1146/annurev-ecolsys-110617-062535)
9. Doiron M, Gauthier G, Lévesque E. 2015 Trophic mismatch and its effects on the growth of young in an Arctic herbivore. *Glob. Chang. Biol.* **21**, 4364–4376. (doi:10.1111/gcb.13057)
10. Visser ME, Gienapp P. 2019 Evolutionary and demographic consequences of phenological mismatches. *Nat. Ecol. Evol.* **3**, 879–885. (doi:10.1038/s41559-019-0880-8)
11. Wolkovich EM, Allesina S, Cottingham KL, Moore JC, Sandin SA, De Mazancourt C. 2014 Linking the green and brown worlds: the prevalence and effect of multichannel feeding in food webs. *Ecology* **95**, 3376–3386. (doi:10.1890/13-1721.1)
12. Zou K, Thébaud E, Lacroix G, Barot S. 2016 Interactions between the green and brown food

- web determine ecosystem functioning. *Funct. Ecol.* **30**, 1454–1465. (doi:10.1111/1365-2435.12626)
13. Van Der Putten WH, Macel M, Visser ME. 2010 Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Phil. Trans. R. Soc. B* **365**, 2025–2034. (doi:10.1098/rstb.2010.0037)
  14. Schröter D, Brussaard L, De Deyn G, Poveda K, Brown VK, Berg MP, Wardle DA, Moore J, Wall DH. 2004 Trophic interactions in a changing world: modelling aboveground–belowground interactions. *Basic Appl. Ecol.* **5**, 515–528. (doi:10.1016/j.baee.2004.09.006)
  15. Bezemer TM, Van Dam NM. 2005 Linking aboveground and belowground interactions via induced plant defenses. *Trends Ecol. Evol.* **20**, 617–624. (doi:10.1016/j.tree.2005.08.006)
  16. Wardle DA, Bardgett RD, Klironomos JN, Setälä H, Van Der Putten WH, Wall DH. 2004 Ecological linkages between aboveground and belowground biota. *Science* **304**, 1629–1633. (doi:10.1126/science.1094875)
  17. Heinen R, Biere A, Harvey JA, Bezemer TM. 2018 Effects of soil organisms on aboveground plant–insect interactions in the field: patterns, mechanisms and the role of methodology. *Front. Ecol. Evol.* **6**, 1–15. (doi:10.3389/fevo.2018.00106)
  18. Thakur M, Herrmann M, Steinauer K, Rennoch S, Cesarz S, Eisenhauer N. 2015 Cascading effects of belowground predators on plant communities are density-dependent. *Ecol. Evol.* **5**, 4300–4314. (doi:10.1002/ece3.1597)
  19. Risch AC *et al.* 2018 Size-dependent loss of aboveground animals differentially affects grassland ecosystem coupling and functions. *Nat. Commun.* **9**, 1–11. (doi:10.1038/s41467-018-06105-4)
  20. Visser ME, Lessells CM, Van Noordwijk AJ, Tinbergen JM. 1998 Warmer springs lead to mistimed reproduction in great tits. *Proc. R. Soc. Lond. B* **265**, 1867–1870. (doi:10.1098/rspb.1998.0514)
  21. Kerby J, Wilmers C, Post E. 2012 Climate change, phenology, and the nature of consumer–resource interactions: advancing the match/mismatch hypothesis. In *Trait-mediated indirect interactions: ecological and evolutionary perspectives* (eds T Ohgushi, O Schmitz, R Holt), pp. 508–525. Cambridge, UK: Cambridge University Press.
  22. Post E. 2019 *Time in ecology: a theoretical framework [MPB 61]*. Princeton, NJ: Princeton University Press.
  23. Rall BC, Brose U, Hartvig M, Kalinkat G, Schwarzmüller F, Vucic-Pestic O, Petchey OL. 2012 Universal temperature and body-mass scaling of feeding rates. *Phil. Trans. R. Soc. B* **367**, 2923–2934. (doi:10.1098/rstb.2012.0242)
  24. Dell A, Pawar S, Savage V. 2011 Systematic variation in the temperature dependence of physiological and ecological traits. *Proc. Natl Acad. Sci. USA* **108**, 10 591–10 596. (doi:10.1073/pnas.1015178108)
  25. Post E, Pedersen C, Wilmers CC, Forchhammer MC. 2008 Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. *Proc. R. Soc. B* **275**, 2005–2013. (doi:10.1098/rspb.2008.0463)
  26. Schweiger O, Settele J, Kudrna O, Klotz S, Kühn I. 2008 Climate change can cause spatial mismatch of trophically interacting species. *Ecology* **89**, 3472–3479. (doi:10.1890/07-1748.1)
  27. Bartley TJ, McCann KS, Bieg C, Cazelles K, Granados M, Guzzo MM, MacDougall AS, Tunney TD, McMeans BC. 2019 Food web rewiring in a changing world. *Nat. Ecol. Evol.* **3**, 345–354. (doi:10.1038/s41559-018-0772-3)
  28. Burgess MD *et al.* 2018 Tritrophic phenological match-mismatch in space and time. *Nat. Ecol. Evol.* **2**, 970–975. (doi:10.1038/s41559-018-0543-1)
  29. Thackeray SJ *et al.* 2010 Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Glob. Chang. Biol.* **16**, 3304–3313. (doi:10.1111/j.1365-2486.2010.02165.x)
  30. Both C, Van Asch M, Bijlsma RG, Van Den Burg AB, Visser ME. 2009 Climate change and unequal phenological changes across four trophic levels: constraints or adaptations? *J. Anim. Ecol.* **78**, 73–83. (doi:10.1111/j.1365-2656.2008.01458.x)
  31. Vucic-Pestic O, Ehnes RB, Rall BC, Brose U. 2011 Warming up the system: higher predator feeding rates but lower energetic efficiencies. *Glob. Chang. Biol.* **17**, 1301–1310. (doi:10.1111/j.1365-2486.2010.02329.x)
  32. Tylianakis JM, Didham RK, Bascompte J, Wardle DA. 2008 Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* **11**, 1351–1363. (doi:10.1111/j.1461-0248.2008.01250.x)
  33. Eisenhauer N, Herrmann S, Hines J, Buscot F, Siebert J, Thakur MP. 2018 The dark side of animal phenology. *Trends Ecol. Evol.* **33**, 898–901. (doi:10.1016/j.tree.2018.09.010)
  34. Siebert J, Thakur MP, Reitz T, Schädler M, Schulz E, Yin R, Weigelt A, Eisenhauer N. 2019 Extensive grassland-use sustains high levels of soil biological activity, but does not alleviate detrimental climate change effects. *Adv. Ecol. Res.* **60**, 25–58. (doi:10.1016/b.saeacr.2019.02.002)
  35. Blankinship JC, Niklaus PA, Hungate BA. 2011 A meta-analysis of responses of soil biota to global change. *Oecologia* **165**, 553–565. (doi:10.1007/s00442-011-1909-0)
  36. Lindo Z, Whiteley J, Gonzalez A. 2012 Traits explain community disassembly and trophic contraction following experimental environmental change. *Glob. Chang. Biol.* **18**, 2448–2457. (doi:10.1111/j.1365-2486.2012.02725.x)
  37. Franken O, Huizinga M, Ellers J, Berg MP. 2018 Heated communities: large inter- and intraspecific variation in heat tolerance across trophic levels of a soil arthropod community. *Oecologia* **186**, 311–322. (doi:10.1007/s00442-017-4032-z)
  38. Thakur MP, Reich PB, Hobbie SE, Stefanski A, Rich R, Rice KE, Eddy WC, Eisenhauer N. 2018 Reduced feeding activity of soil detritivores under warmer and drier conditions. *Nat. Clim. Chang.* **8**, 75–78. (doi:10.1038/s41558-017-0032-6)
  39. Torode MD, Barnett KL, Facey SL, Nielsen UN, Power SA, Johnson SN. 2016 Altered precipitation impacts on above- and below-ground grassland invertebrates: summer drought leads to outbreaks in spring. *Front. Plant Sci.* **7**, 1–12. (doi:10.3389/fpls.2016.01468)
  40. Morrien E *et al.* 2017 Soil networks become more connected and take up more carbon as nature restoration progresses. *Nat. Commun.* **8**, 14349. (doi:10.1038/ncomms14349)
  41. McCann K. 2000 The diversity stability debate. *Nature* **405**, 228–233. (doi:10.1007/978-1-4615-9968-5\_10)
  42. Rall BC, Vucic-Pestic O, Ehnes RB, Emmerson M, Brose U. 2010 Temperature, predator–prey interaction strength and population stability. *Glob. Chang. Biol.* **16**, 2145–2157. (doi:10.1111/j.1365-2486.2009.02124.x)
  43. Young IM, Crawford JW. 2004 Interactions and self-organization in the soil–microbe complex. *Science* **304**, 1634–1637. (doi:10.1126/science.1097394)
  44. Berg MP. 2012 Patterns of biodiversity at fine and small spatial scales. In *Soil ecology and ecosystem services* (ed. DH Wall), pp. 136–149. Oxford, UK: Oxford University Press.
  45. Bellmore JR, Baxter CV, Connolly PJ. 2015 Spatial complexity reduces interaction strengths in the meta-food web of a river floodplain mosaic. *Ecology* **96**, 274–283. (doi:10.1890/14-0733.1)
  46. Digel C, Curtsdotter A, Riede J, Klamer B, Brose U. 2014 Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels. *Oikos* **123**, 1157–1172. (doi:10.1111/oik.00865)
  47. Neutel AM, Heesterbeek JAP, Van De Koppel J, Hoenderboom G, Vos A, Kaldewey C, Berendse F, De Ruiter PC. 2007 Reconciling complexity with stability in naturally assembling food webs. *Nature* **449**, 599–602. (doi:10.1038/nature06154)
  48. Thakur M, Geisen S. 2019 Trophic regulations of the soil microbiome. *Trends Microbiol.* **27**, 771–780. (doi:10.1016/j.tim.2019.04.008)
  49. Brose U, Scheu S. 2014 Into darkness: unravelling the structure of soil food webs. *Oikos* **123**, 1153–1156. (doi:10.1111/oik.01768)
  50. Dacal M, Bradford MA, Plaza C, Maestre FT, García-Palacios P. 2019 Soil microbial respiration adapts to ambient temperature in global drylands. *Nat. Ecol. Evol.* **3**, 232–238. (doi:10.1038/s41559-018-0770-5)
  51. Bradford MA. 2013 Thermal adaptation of decomposer communities in warming soils. *Front. Microbiol.* **4**, 1–16. (doi:10.3389/fmicb.2013.00333)
  52. Classen AT, Sundqvist MK, Henning JA, Newman GS, Moore JA, Cregger MA, Moorhead LC, Patterson CM. 2015 Direct and indirect effects of climate change on soil microbial and soil microbial–plant interactions: what lies ahead? *Ecosphere* **6**, art130. (doi:10.1890/ES15-00217.1)
  53. Parts K, Tedersoo L, Schindlbacher A, Sigurdsson BD, Leblans NIW, Oddsdóttir ES, Borken W, Ostonen I. 2019 Acclimation of fine root systems to soil warming: comparison of an experimental setup and a natural soil temperature gradient. *Ecosystems* **22**, 457–472. (doi:10.1007/s10021-018-0280-y)

54. van der Wal A, de Boer W. 2017 Dinner in the dark: illuminating drivers of soil organic matter decomposition. *Soil Biol. Biochem.* **105**, 45–48. (doi:10.1016/j.soilbio.2016.11.006)
55. Ohgushi T, Wurst S, Johnson S. 2018 Current knowledge and future challenges of aboveground and belowground community ecology. In *Aboveground–belowground community ecology* (eds T Ohgushi, S Wurst, S Johnson), pp. 345–361. Cham, Switzerland: Springer International Publishing.