

Biodiversity of intertidal food webs in response to warming across latitudes

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Global warming threatens community stability and biodiversity around the globe. Knowledge of the mechanisms underlying the responses to rising temperatures depends heavily on generic food-web models that do not account for changes in network structure along latitudes and temperature gradients. Using 124 marine rock-pool food webs sampled across four continents, we show that despite substantial variation in ambient temperature (mean 11.5–28.4 °C), similar empirical food-web and body-mass structures emerge. We have used dynamic modelling to test whether communities from warmer regions are more sensitive to warming and found a general hump-shaped relationship between simulated biodiversity and temperature (gradient from 0–50 °C). This implies that an expected anthropogenic global warming of 4 °C should increase biodiversity in arctic to temperate regions while biodiversity in tropical regions should decrease. Interestingly, simulations of synthetic networks did not yield similar results, which stresses the importance of considering the specificities of natural food webs for predicting community responses to environmental changes.

Global warming is recognized as a major threat to species survival, community stability and ecosystem functioning¹. However, predicting the response of species communities to temperature increases is still subject to substantial uncertainties. Indeed, warming affects communities at all levels of biological organization, from species physiology to community structure and geographical distribution², leading to complex causality chains of interactions between these organization levels. At the individual level, temperature affects species biological rates, such as metabolism or activity^{3,4}, resulting in modifications of trophic interaction strengths⁵, trophic cascades⁶ and community body-mass structure^{7,8} – an essential driver of food-web structures⁹. These processes interact to determine the responses of communities at the ecosystem level, such as food-web stability¹⁰ or ecosystem functions¹¹.

A two-species consumer-resource model¹² predicted a decrease in resource biomass because of stronger top-down control at high temperatures. However, pioneering experimental studies considering the impact of warming on microcosm communities highlighted higher extinction probabilities of larger predators, even if their resources were increasing in density¹³. This inconsistency between experiments and models has been resolved by more accurate estimations of model parameters¹⁴. Contrary to prior results, models using the new parameters showed that the metabolic rates of predators increase faster with warming than their feeding rates, leading to starvation of larger predators when the temperature is high¹⁵ and to a decrease of species persistence¹⁰. Although these results are in line with microcosm studies¹³, they do not match recent empirical results for complex communities of natural stream ecosystems, which showed that biodiversity increases with local temperature allowing large predators to persist⁸. Hence, there is a discrepancy between complex food-web models predicting a collapse of large species at high temperatures¹⁰ and empirical studies of natural communities of similar levels of complexity showing better energy support of large species at higher temperature⁸. We show here that considering more precise biological information on food-web structures and body-mass distributions across species can resolve this paradox.

Indeed, a limitation of previous modelling approaches is that they did not completely bridge the gap between theoretical networks and real ecosystems. Conclusions are based on synthetic networks usually generated by a niche model¹⁶ instead of natural network structures, which imposes two strong limitations. First, it hampers an understanding of whether and how the network topology of natural communities changes with temperature as generative models such as the niche model produce synthetic networks without accounting for temperature. Second, the body-mass structures of these theoretical communities are usually determined by generic relationships between body mass and trophic levels, which ignores empirical evidence of differences between, for example, aquatic¹⁷ and terrestrial^{18,19} systems, despite their implications for community stability¹⁵. Thus, ecological studies have not yet considered the potential adaptations of network topology and body-mass distributions to local temperature and how they might interact with a perturbation such as warming.

Therefore, we aim to bridge the gap between purely theoretical and experimental approaches by using a global dataset of natural intertidal pool food webs from regions around the world across a temperature gradient²⁰, all sampled using the same methodology (Fig. 1). This allows us to study for the first time (1) the impact of environmental factors, including temperature, on food-web topology and (2) how local temperature conditions affect the response of natural food webs to simulated warming.

Effect of rock-pool temperature on food-web structure

Our dataset comprises 124 food webs from seven different regions (two beaches per region) across four continents (Fig. 1c, see Methods and ref. ²⁰ for more details). Overall, the summer sea temperature ranged from a minimum of 11.5 °C in Canada to a maximum of 28.4 °C in Brazil. We examined the effects of individual pool volume and temperature on network topology by considering 12 classical descriptors (see Supplementary Section 1 for mathematical definitions): number of species, number of links, connectance, mean omnivory, predator/prey ratio, mean generalism, proportions

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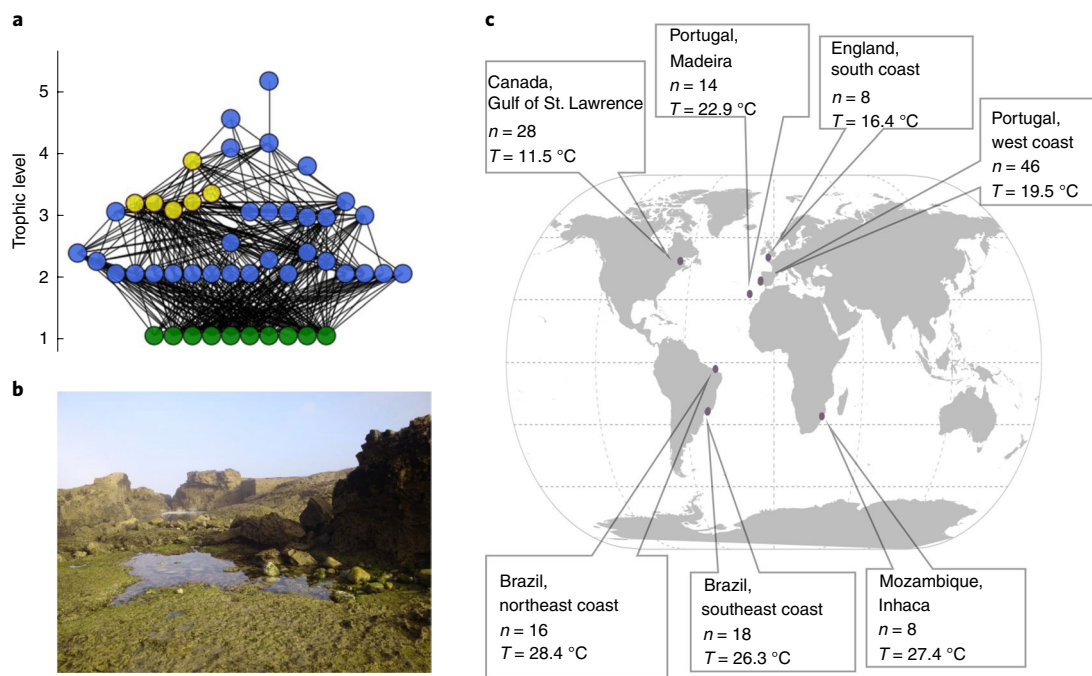


Fig. 1 | Structure and distribution of natural rock-pool food webs. **a**, An exemplary food web depicting trophic interactions between species of a rock pool (Portugal). The colours define species metabolic types: green for plants, blue for invertebrates and yellow for ectothermic vertebrates. **b**, Photograph of a typical rock-pool ecosystem (Portugal). **c**, Distribution of the sampling regions. *n* is the number of pools sampled in a region and *T* is the average summer sea temperature of each region.

of basal, intermediate and top species, mean trophic level, mean trophic level of top species and average path length. We performed a principal component analysis (PCA) with these 12 descriptors. The two principal axes explained 68.1% of the data variability (Fig. 2a). When projected onto the PCA plane, the abiotic rock-pool characteristics (pool volume, pool temperature, elevation, difference from sea temperature, latitude and amplitude of variation in sea temperature in a year; blue arrows in Fig. 2a) were weakly correlated with the PCA axes (all correlation coefficients were less than 0.3, see Supplementary Section 2). Interestingly, the food-web structure was more, albeit weakly, related to the sea temperature (minimum, maximum and average temperature values for the year and for the summer, see Supplementary Section 2) than to the rock-pool temperature. Moreover, individual regressions between the 12 topological descriptors and sea temperature did not exhibit general trends (Supplementary Section 1) and the distribution of food-web data points on the PCA plane did not exhibit any pattern related to sea temperature (Fig. 2b). Together, these findings suggest that none of the different abiotic factors is a strong driver of food-web structure in our dataset.

Contrary to our expectations, the body-mass structure of the community (here, the scaling of body masses with trophic levels) did not respond systematically to temperature (Fig. 2c). A model selection procedure based on the Bayesian information criterion kept the species trophic levels as the only explanatory variable of species body masses in the model ($F_{1,3355} = 1,063.581$, $P < 0.001$, effect size = 0.57, confidence interval (CI) = [0.54, 0.61]), whereas temperature and the interaction between trophic levels and temperature were removed. Food-web identity nested into beach nested into region was considered as a random effect on the intercept (see Supplementary Section 3). The above-described results suggest that the network- and body-mass structures of the rock-pool communities are robust against differences in environmental temperature along the global gradient of our analyses.

Response of natural rock-pool food webs to simulated warming

Despite these structural similarities between the food webs across the natural temperature gradient, our simulations showed that the summer sea temperature of the rock pools influenced the response of food webs to simulated warming (Fig. 3). We used a dynamic model¹⁰ parameterized by species body masses and summer sea temperature (Methods) to compute species persistence (the proportion of species that survived until the end of the simulations) under warming of up to 4 °C. We chose to use summer sea temperature instead of individual rock-pool temperature as (1) sea temperature has a stronger effect on network structure than pool temperature and (2) summer corresponds to the sampling season. However, additional simulations with individual rock-pool temperature yielded similar conclusions (Supplementary Section 4).

For each of the 124 natural networks, we ran simulations of species dynamics along a warming gradient from 0 (local temperature of each individual rock pool) to 4 °C (local temperature plus warming of 4 °C) in steps of 0.1 °C. We used a mixed-effects model to test for the effects of simulated warming and summer sea temperature on species persistence (as proportions, data were logit-transformed; food-web identity nested into beach nested into region as a random structure). In this model, we used as covariates the variables that have the strongest effects on food-web structure according to the PCA analysis (see above): pool size, latitude, summer sea temperature, amplitude and pool elevation. Model selection by the parsimony criteria (Bayesian information criterion, see Supplementary Section 3) kept as variables summer sea temperature ($F_{1,5} = 1.7915$, $P = 0.238$, effect size = -0.0181, CI = [-0.114, 0.0783]) and simulated warming ($F_{1,2258} = 6.03$, $P = 0.0141$, effect size = 0.3369, CI = [0.309, 0.364]). The interaction between summer sea temperature and simulated warming was also significant ($F_{1,2258} = 593.42$, $P < 0.001$, effect size = -0.0173, CI = [-0.016, -0.0147]), because species persistence significantly increased with simulated warming for pools from colder regions (<22.9 °C) but significantly decreased

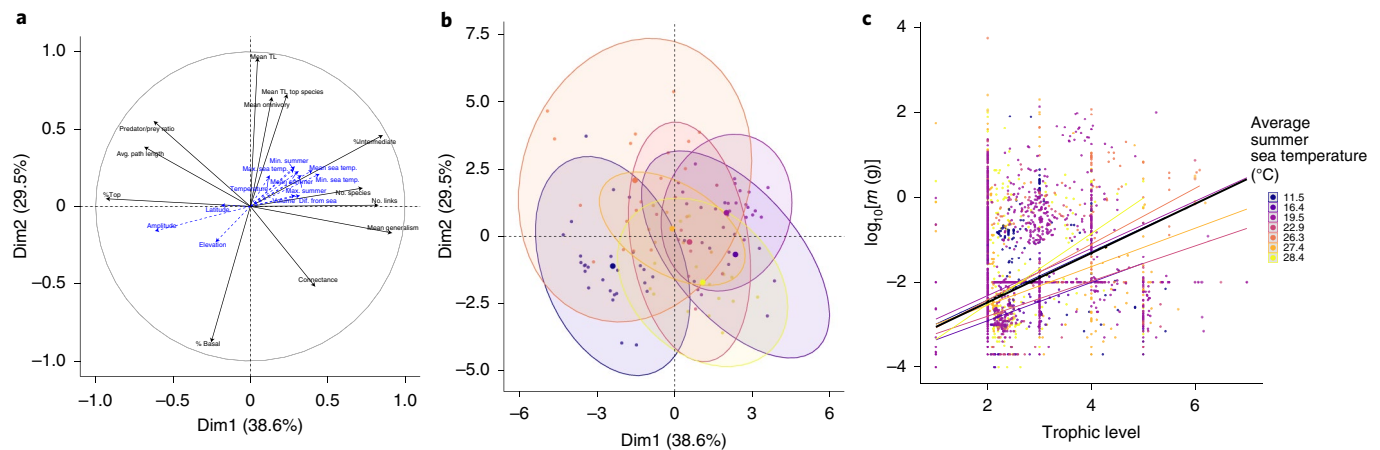


Fig. 2 | Analysis of community structure. **a**, PCA of the normalized topological descriptors of the food webs. Black arrows represent the topological descriptors used in the analysis. Blue arrows represent abiotic variables projected onto the PCA plane, but they were not used for the determination of the PCA axes. TL represents trophic level and top species are consumers without predators. **b**, Each point represents one individual rock pool projected onto the plane generated by the PCA and its colour describes the associated summer sea temperature (see key in **c**). Larger dots represent the centre of gravity of the ellipses. **c**, Relationship between species body masses (m) and trophic levels depending on local temperature. The coloured lines represent the predictions of a linear regression for each region. Statistically, these different trends are not significantly different from each other (see Supplementary Section 3) and the data are best described by an overall scaling relationship (black solid line).

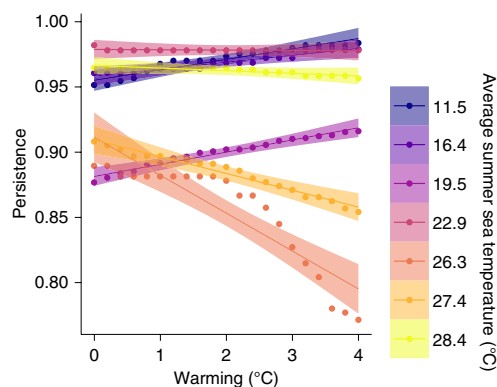


Fig. 3 | Response of persistence to temperature increase, depending on local temperature conditions. Each point represents the mean value at a given temperature. The solid lines are predictions from a linear model. The shaded areas show the 95% confidence interval on the predicted values. The colours represent the average sea summer temperature within each region.

for warmer ones ($>22.9^{\circ}\text{C}$, no effect was found when the sea temperature was equal to 22.9°C). This interactive effect and the discrepancy in the response of food webs from warm and cold regions can be explained by the general response of persistence of empirical networks to warming across a temperature gradient from 0 to 50°C . By broadening the temperature gradient, we observe a hump-shaped relationship between persistence and temperature (Fig. 4a) with a persistence peak between 20 and 30°C . Thus, the absence of specific dependencies of food-web topology and body-mass structure on regional temperatures leads to a similar hump-shaped pattern in the scaling of food-web persistence across our large temperature gradient (that is, from 0 to 50°C). Hence, we can explain the differences in the responses of the different local food webs to the simulated warming of 4°C by the position of their regional temperature on the large temperature gradient curves. The temperatures of the food webs from warmer regions are located on the decreasing part of the hump-shaped relationship, implying a decrease in persistence

when exposed to warming, but the food webs from colder regions increase in persistence as their local temperatures are located on the left part of the hump-shaped relationship.

Two mechanisms explain this hump-shaped relationship. At low temperature, the biomasses of basal species tend to be low because of low growth rates, leading to bottom-up extinction cascades to higher trophic levels. At high temperatures, basal species can persist with higher biomass densities, but the metabolic demands of larger predator species increase faster than their feeding rates^{21,22}, leading them to starvation¹⁵. A trade-off between these two phenomena explains the high persistence at intermediate temperatures, allowing sufficiently high biomass of basal species without leading to the highest metabolic rates and consumer starvation at higher trophic levels. This starvation effect observed at high temperatures, however, can be compensated by the nutrient supply of the food webs¹⁴. When the carrying capacity of basal species increases due to higher nutrient supply, the maximum persistence values are still reached at temperatures of 20 to 25°C , but the temperature at which persistence starts to decrease is shifted towards higher temperatures (Supplementary Section 5). Hence, tropical communities with high productivity could suffer less from warming than tropical communities from less productive areas.

Thus, surprisingly, our results suggest that the different response of community persistence to simulated warming does not depend on local adaptations in network structure to environmental temperature but instead on the different local temperatures that determine where the community is positioned on the hump-shaped persistence/warming relationship. We examined this assertion more carefully by comparing the persistence between food webs at their region-specific temperature (natural temperature persistence) with food webs from other regions (with colder or warmer region-specific temperatures) simulated at the same temperature. We did not observe a higher persistence for food webs simulated at their natural temperature (Supplementary Section 6), supporting our conclusion that the rock-pool food webs do not show any specific systematic structural adaptations to local conditions.

Differences between natural and synthetic food webs

The hump-shaped pattern found across the large temperature gradient with natural food webs does not hold for synthetic networks

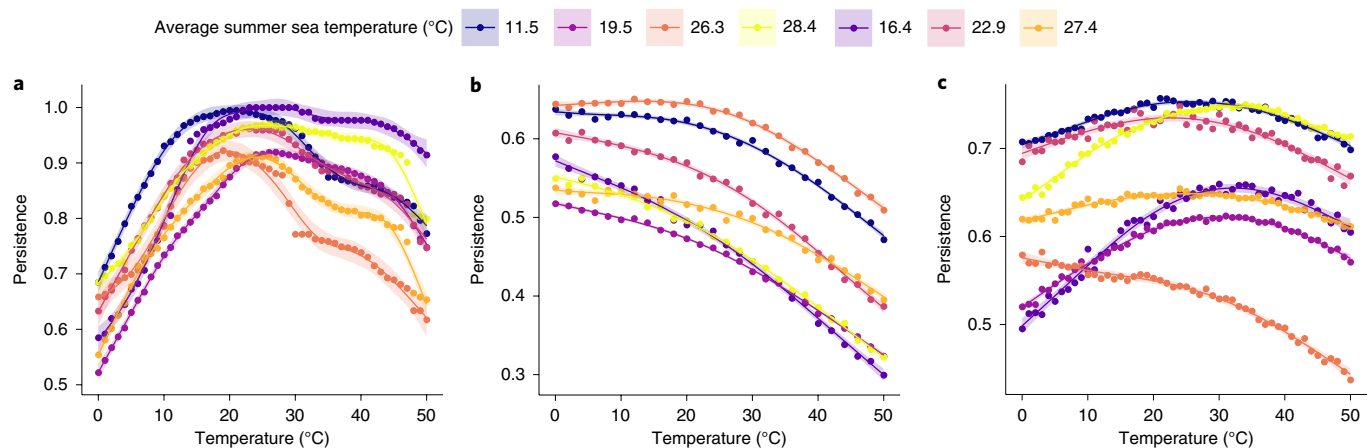


Fig. 4 | Relationship between species persistence and temperature in simulations. a–c, Natural food webs (**a**), niche model food webs (**b**) and natural food webs (**c**) in which species body masses were estimated with the same scaling law as used for niche models. Each point represents the mean value at a given temperature. The solid lines are the predictions from local moving regressions (locally estimated scatterplot smoothing (LOESS) technique). The shaded areas show the 95% confidence interval on the predicted values. The colours depict the average summer sea temperature within each region.

generated by the niche model, which exhibit generally lower and continuously decreasing persistence across the temperature gradient (Fig. 4b). This finding could be explained by differences in (1) the body-mass structure or (2) the network topologies between synthetic and natural communities. We tested the first hypothesis by assigning synthetic body masses to the species of the empirically established networks according to the generic relationship between body mass and trophic level given by equation (7) in the Methods, which was also used to parameterize the synthetic networks. The response of species persistence observed for this simulation was close to the one observed for the natural food webs simulated with the natural body-mass distribution (Fig. 4c), but the persistence was generally lower. Only an average summer sea temperature of 26.3 °C (Fig. 4c, orange line) exhibited a pattern that is similar to the one observed for the niche model (Fig. 4b). Nevertheless, our results suggest that, in our case, network topology is an important factor governing the response of communities to warming.

The different results observed for the synthetic and empirical networks are associated with important differences in network topology. First, synthetic models generate food webs with higher trophic levels (Fig. 5a,b), which increases the amount of energy lost during feeding interactions between the basal and top trophic levels^{23,24}. This decreases the energy fluxing upwards to the highest trophic level species, which reduces their energy supply and thus strengthens the predator starvation effect that is responsible for the decrease in persistence at high temperatures. Second, synthetic models yield systematically fewer upward feeding links per basal species leading to reduced herbivory pressure (Fig. 5c). This prevents herbivore extinctions at low temperatures despite low productivity, which is responsible for the increasing part of the hump-shaped temperature/persistence relationship. Interestingly, food webs from the site with responses to warming similar to niche-model networks are also the ones with topologies that match predictions from the niche model (Fig. 5, orange data points).

On the importance of considering natural food webs

Together, all these differences between results obtained with approaches using natural food webs or synthetic models stress that the systematic use of generic modelling approaches can (1) bias conclusions on the consequences of warming and (2) lead to misinterpretations of the underlying mechanisms. Indeed, the use of natural food webs has allowed us to solve the discrepancy between the different results produced by models and empirical studies of

complex communities. At these levels of complexity, models predicted a decrease in species persistence with an increase in temperature¹⁰, which was explained by the starvation of large species from higher trophic levels¹⁰. In contrast, experimental results argued for better energy support of large species⁸. We have shown that the models' underestimation of herbivory pressure and an overestimation of the number of trophic levels (reducing the amount of energy reaching top species) in synthetic networks explain the discrepancy between results obtained with generic food-web models and our predictions for natural food webs. These differences argue for the use of natural networks to address the response of food-web characteristics, such as stability and functioning, to environmental gradients, even in theoretical studies.

While theoretical models generating food webs might be able to capture some common tendencies in patterns (either food-web topologies or body-mass distributions), the deviations of individual systems from these average predictions appear to be essential and stress the limits of theoretical models in addressing mechanisms occurring in situ. Thus, it becomes urgent to address the causes and consequences of these deviations. Exploring causes calls for a better understanding of ecological factors constraining network topologies^{25,26} and body-mass distributions^{19,27}. The incorporation of non-trophic interactions²⁸, experimental studies manipulating external gradients^{29,30} or comparisons of food-web topology between ecosystem types³¹ can provide insights in this direction. Extension of the allometric diet breath model³², incorporating temperature effects into optimal foraging theory³³, to address how temperature might impact food-web topology is a first step towards the understanding of the mechanistic processes underlying responses of food-web topology to temperature. Addressing the consequences of warming would call for a better examination of food-web properties deviating from generative model predictions and how they relate to specific processes. Hence, one urgent question is whether this discrepancy in the warming response between natural and generic food webs extends to other ecosystem types.

Future steps

Our analyses of food-web responses to simulated warming is a step towards a better understanding of the impact of global warming on natural communities. We have shown that the use of dynamic models and a set of replicated empirically estimated networks is a suitable tool to gain a mechanistic understanding of the ecological processes underlying the consequences of warming. However, we

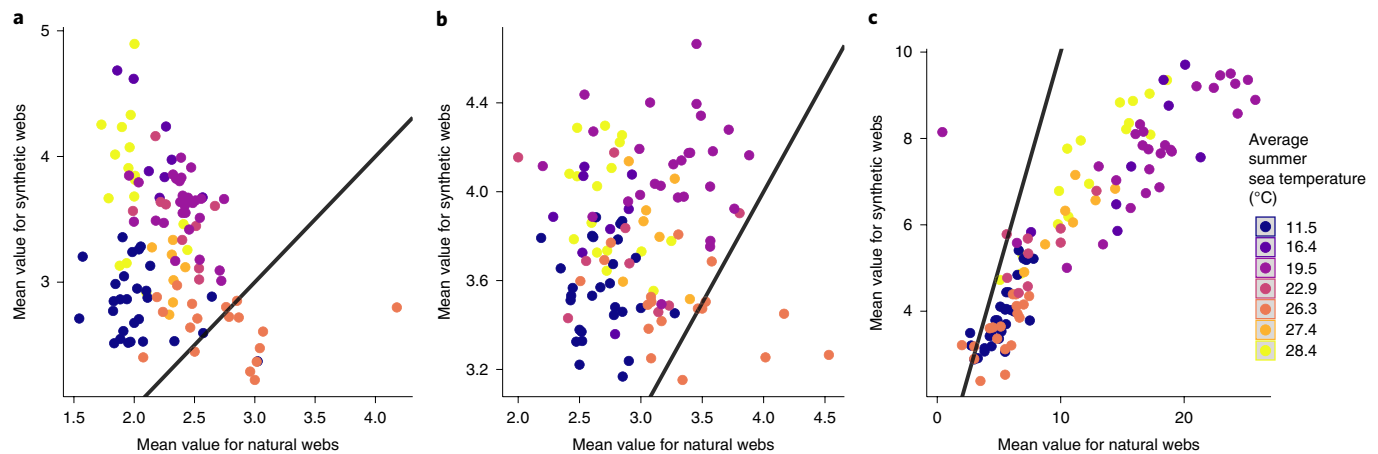


Fig. 5 | Comparison of trophic levels and herbivory links between niche and experimental networks. a–c, Mean trophic level (**a**), top trophic level (**b**) and mean number of predators per basal species (**c**). The connectance and species richness of each empirical food web were used to generate a set of 100 replicates of food with the niche model. The black lines represent the identity. The colours indicate the average sea summer temperature within each region.

need to understand better how species change their feeding interactions under temperature stress to achieve more accurate predictions³³. Indeed, the trophic links of the empirical networks arose from static information, which does not account for temperature-driven shifts in species' trophic interactions. Tackling this issue in the future would allow use of a more generic approach that would ultimately link studies considering the effects of warming on food webs to ecosystem functioning³⁴. Moreover, we might also need to refine the classical metabolic theory of ecology and consider more complex responses of species rates, such as hump-shaped relationships, to warming^{5,35}. This would increase model realism, which is now uncertain when species are above their optimal temperature. The biological processes of species can also adapt to their local temperature conditions³⁶. Accounting for this adaptation in our simulation might change the temperature of maximal persistence, potentially shifting the highest persistence values to the local temperature conditions and interacting with evolutionary dynamics³⁷. Then, an important future step will be to extend this mechanistic understanding of warming effects on local communities to a more global framework considering modifications of species distributions³⁸. Metacommunity approaches that include temperature effects³⁹ are, for example, a promising tool to improve the conceptual links between climatic models, food-web theory and temperature/size relationships⁴⁰.

Conclusion

Our results suggest that the local temperature condition of food webs determines their response to warming. While warming tends to increase the persistence of species in the food webs from cold regions, it tends to decrease the persistence of those from warmer places. In general, previous studies have shown that tropical organisms are more sensitive to warming than their temperate counterparts, because (1) they live closer to their physiological limit⁴¹, (2) the exponential scaling of biological rates with temperature causes higher increases in their biological rate per degree of warming⁴² and (3) the predator-starvation effect is leading to increasingly lower abundances²². Together, these studies suggest that tropical food webs seem to be more vulnerable to warming than food webs from colder regions. Our results confirm this expectation based on a general hump-shaped pattern governing the response of natural rock-pool food webs to a temperature gradient. Strikingly, we only found this result using natural food-web structures, with differences in predictions found in simulations using synthetic

networks underlining the importance of network structure for species dynamics. These results stress the importance of coupling an ecosystem-specific understanding of network structures with predictive simulations of warming or other global change gradients. While our results have shown that generic network models do not capture the specific food-web structures that are important for the system response to warming, generic models also cannot cover ecosystem-specific signatures in network structures such as architectural differences between soil and other food webs⁴³. Additionally, the dynamically important body-mass structure of food webs also differs significantly among ecosystem types²⁷, which is not captured by synthetic approaches. These shortcomings of generic network models may lead to substantial errors in the predictions of ecosystem responses to global warming. Therefore, our results call for the use of system-specific natural network structures in the analyses of global warming, which need to be integrated with effects on the population's biological rates, adaptation processes and new communities due to range shifts. Altogether, this is a substantial research agenda, but unless we find out how these patterns interact, from species physiology to community structure up to geographical distribution, predictions on future ecosystems in a warmed world remain highly uncertain.

Online content

Any methods, additional references, Nature Research reporting summaries, source data, extended data, supplementary information, acknowledgements, peer review information; details of author contributions and competing interests; and statements of data and code availability are available at <https://doi.org/10.1038/s41558-020-0698-z>.

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References

1. Brose, U. et al. Climate change in size-structured ecosystems. *Phil. Trans. R. Soc. B* **367**, 2903–2912 (2012).
2. Scheffers, B. R. et al. The broad footprint of climate change from genes to biomes to people. *Science* **354**, aaf7671 (2016).
3. Ehnes, R. B., Rall, B. C. & Brose, U. Phylogenetic grouping, curvature and metabolic scaling in terrestrial invertebrates. *Ecol. Lett.* **14**, 993–1000 (2011).
4. Dell, A. I., Pawar, S. & Savage, V. M. Systematic variation in the temperature dependence of physiological and ecological traits. *Proc. Natl Acad. Sci. USA* **108**, 10591–10596 (2011).

5. Englund, G., Öhlund, G., Hein, C. L. & Diehl, S. Temperature dependence of the functional response. *Ecol. Lett.* **14**, 914–921 (2011).
6. Jochum, M., Schneider, F. D., Crowe, T. P., Brose, U. & O’Gorman, E. J. Climate-induced changes in bottom-up and top-down processes independently alter a marine ecosystem. *Phil. Trans. R. Soc. B* **367**, 2962–2970 (2012).
7. Daufresne, M., Lengfellner, K. & Sommer, U. Global warming benefits the small in aquatic ecosystems. *Proc. Natl Acad. Sci. USA* **106**, 12788–12793 (2009).
8. O’Gorman, E. J. et al. Unexpected changes in community size structure in a natural warming experiment. *Nat. Clim. Change* **7**, 659–663 (2017).
9. Eklöf, A. et al. The dimensionality of ecological networks. *Ecol. Lett.* **16**, 577–583 (2013).
10. Binzer, A., Guill, C., Rall, B. C. & Brose, U. Interactive effects of warming, eutrophication and size structure: impacts on biodiversity and food-web structure. *Glob. Change Biol.* **22**, 220–227 (2016).
11. Schwarz, B. et al. Warming alters energetic structure and function but not resilience of soil food webs. *Nat. Clim. Change* **7**, 895–900 (2017).
12. Vasseur, D. A. & McCann, K. S. A mechanistic approach for modeling temperature-dependent consumer-resource dynamics. *Am. Nat.* **166**, 184–198 (2005).
13. Petchey, O. L., McPhearson, P. T., Casey, T. M. & Morin, P. J. Environmental warming alters food-web structure and ecosystem function. *Nature* **402**, 69–72 (1999).
14. Rall, B. C. et al. Universal temperature and body-mass scaling of feeding rates. *Phil. Trans. R. Soc. B* **367**, 2923–2934 (2012).
15. Binzer, A., Guill, C., Brose, U. & Rall, B. C. The dynamics of food chains under climate change and nutrient enrichment. *Phil. Trans. R. Soc. B* **367**, 2935–2944 (2012).
16. Williams, R. J. & Martinez, N. D. Simple rules yield complex food webs. *Nature* **404**, 180–183 (2000).
17. Shurin, J. B., Clasen, J. L., Greig, H. S., Kratina, P. & Thompson, P. L. Warming shifts top-down and bottom-up control of pond food web structure and function. *Phil. Trans. R. Soc. B* **367**, 3008–3017 (2012).
18. Kéfi, S. et al. Network structure beyond food webs: mapping non-trophic and trophic interactions on Chilean rocky shores. *Ecology* **96**, 291–303 (2015).
19. Potapov, A. M., Brose, U., Scheu, S. & Tiunov, A. V. Trophic position of consumers and size structure of food webs across aquatic and terrestrial ecosystems. *Am. Nat.* **194**, 823–839 (2019).
20. Mendonça, V. et al. What’s in a tide pool? Just as much food web network complexity as in large open ecosystems. *PLoS ONE* **13**, e0200066 (2018).
21. Vucic-Pestic, O., Ehnes, R. B., Rall, B. C. & Brose, U. Warming up the system: higher predator feeding rates but lower energetic efficiencies. *Glob. Chang. Biol.* **17**, 1301–1310 (2011).
22. Fussmann, K. E., Schwarzmüller, F., Brose, U., Jousset, A. & Rall, B. C. Ecological stability in response to warming. *Nat. Clim. Change* **4**, 206–210 (2014).
23. Lindeman, R. L. The trophic-dynamic aspect of ecology. *Ecology* **23**, 399–417 (1942).
24. Lang, B., Ehnes, R. B., Brose, U. & Rall, B. C. Temperature and consumer type dependencies of energy flows in natural communities. *Oikos* **126**, 1717–1725 (2017).
25. Portalier, S. M. J., Fussmann, G. F., Loreau, M. & Cherif, M. The mechanics of predator–prey interactions: first principles of physics predict predator–prey size ratios. *Funct. Ecol.* **33**, 323–334 (2019).
26. Ho, H., Tylanakis, J. M., Zheng, J. X. & Pawar, S. Predation risk influences food-web structure by constraining species diet choice. *Ecol. Lett.* **22**, 1734–1745 (2019).
27. Brose, U. et al. Predator traits determine food-web architecture across ecosystems. *Nat. Ecol. Evol.* **3**, 919–927 (2019).
28. Kéfi, S. et al. More than a meal...integrating non-feeding interactions into food webs. *Ecol. Lett.* **15**, 291–300 (2012).
29. Tylanakis, J. M., Tschardtke, T. & Lewis, O. T. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature* **445**, 202–205 (2007).
30. Gauzens, B., Legendre, S., Lazzaro, X. & Lacroix, G. Intermediate predation pressure leads to maximal complexity in food webs. *Oikos* **125**, 595–603 (2016).
31. Riede, J. O. et al. Scaling of food-web properties with diversity and complexity across ecosystems. *Adv. Ecol. Res.* **42**, 139–170 (2010).
32. Petchey, O. L., Beckerman, A. P., Riede, J. O. & Warren, P. H. Size, foraging, and food web structure. *Proc. Natl Acad. Sci. USA* **105**, 4191–4196 (2008).
33. Petchey, O. L., Brose, U. & Rall, B. C. Predicting the effects of temperature on food web connectance. *Phil. Trans. R. Soc. B* **365**, 2081–2091 (2010).
34. Antikueira, P. A. P., Petchey, O. L. & Romero, G. Q. Warming and top predator loss drive ecosystem multifunctionality. *Ecol. Lett.* **21**, 72–82 (2018).
35. Amarasekare, P. Effects of temperature on consumer-resource interactions. *J. Anim. Ecol.* **84**, 665–679 (2015).
36. Fussmann, K. E., Rosenbaum, B., Brose, U. & Rall, B. C. Interactive effects of shifting body size and feeding adaptation drive interaction strengths of protist predators under warming. Preprint at *bioRxiv* <https://doi.org/10.1101/101675> (2017).
37. Weinbach, A., Allhoff, K., Thebault, E., Massol, F. & Loeuille, N. Selective effects of temperature on body mass depend on trophic interactions and network position. Preprint at *bioRxiv* <https://doi.org/10.1101/233742> (2017).
38. Van Der Putten, W. H., Macel, M. & Visser, M. E. 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 (2010).
39. Eklöf, A., Kaneryd, L. & Mürner, P. Climate change in metacommunities: dispersal gives double-sided effects on persistence. *Phil. Trans. R. Soc. B* **367**, 2945–2954 (2012).
40. Sentis, A., Binzer, A. & Boukal, D. S. Temperature-size responses alter food chain persistence across environmental gradients. *Ecol. Lett.* **20**, 852–862 (2017).
41. Tewksbury, J. J., Huey, R. B. & Deutsch, C. A. Putting the heat on tropical animals. *Science* **320**, 1296–1297 (2008).
42. Dillon, M. E., Wang, G. & Huey, R. B. Global metabolic impacts of recent climate warming. *Nature* **467**, 704–706 (2010).
43. Digel, C., Curtsdotter, A., Riede, J., Klarner, B. & Brose, U. Unravelling the complex structure of forest soil food webs: higher omnivory and more trophic levels. *Oikos* **123**, 1157–1172 (2014).

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Methods

Data sampling and food-web construction. The food webs chosen for this work were those occurring in intertidal rock pools. The animal community was composed of ectothermic species. Only pools occurring in the lower intertidal zone of rocky shores were selected for sampling. Sampling took place in summer (2013–2015), during spring tides. Summer was chosen to ensure comparability because it is when biodiversity and species abundance are at their highest in intertidal rock pools. Two sites were selected in each of the regions: Canada (Gulf of St. Lawrence, site A – Pointe-au-Père – 48° 29' 33.0" N, 68° 29' 33.0" W; site B – Sainte-Flavie – 48° 36' 43.0" N, 68° 13' 44.3" W), the United Kingdom (south coast, site A – Mount Batten – 50° 21' 24" N, 4° 07' 43" W; site B – Wembury – 50° 19' 00" N, 4° 04' 57" W), Portugal-west coast (Portugal mainland, site A – Cabo Raso – 38° 42' 38.2" N, 9° 29' 09" W; site B – Raio Verde – 39° 17' 11.4" N, 9° 20' 23" W), Portugal-Madeira (Madeira Island, northeast Atlantic, site A – Caniço – 32° 38' 44.4" N, 16° 49' 26.5" W; site B – Porto da Cruz – 32° 46' 32.6" N, 16° 49' 33.5" W), Brazil-São Paulo (southeast coast, site A – São Sebastião – 23° 49' 26" S, 45° 25' 38" W; site B – Ubatuba – 23° 28' 01" S, 45° 03' 36" W) and Brazil-Ceará (northeast coast, site A – Flecheiras – 3° 13' 04" N, 39° 15' 29" W; site B – Guajirú – 3° 14' 14" N, 39° 13' 44" W). In each region, sites A and B were separated by distances of between 6 and 60 km. For each of these two sites per region, two to four beaches were targeted. In Mozambique only one site was sampled, Inhaca (Praia do Farol – 25° 58' 36" S, 32° 59' 38" E), two beaches were targeted and four pools were sampled on each beach. All sampled intertidal rock pools were located in the lower intertidal zone and their size range (depth: 0.05–0.80 m, surface area: 0.15–33.00 m², as estimated from scaled digital photographs using the software ImageJ) ensured a minimum patch size for the development of benthic assemblages while still allowing a complete record of all macroorganisms found in each pool. In total, 28 pools were sampled in Canada, 8 in the UK, 32 in Portugal-west coast, 14 in Portugal-Madeira, 18 in Brazil-São Paulo (Brazil-SP), 16 in Brazil-Ceará (Brazil-CE) and 8 in Mozambique. More information on site temperatures can be found in Supplementary Section 7.

One bottom sediment sample of 50 ml was taken from pools with an area ≤0.5 m², two samples from pools with an area >0.5 and ≤2 m², and three samples from pools with an area >2 m², whenever the pool presented sediment at the bottom. Three quadrats of 5 cm² of rock-pool surface were scraped. Sediment and scraping samples were preserved in 70% alcohol, with Rose bengal, and taken to the laboratory, where all organisms were identified with a binocular microscope. All macroorganisms present in the pools were identified *in situ*, but samples were taken to the laboratory whenever there were taxonomical issues requiring more detailed observation in the laboratory. In the latter case, marine organisms were identified with the aid of a stereo microscope, and when necessary by consulting identification keys and taxonomic experts.

Highly resolved food webs, depicting who eats whom, were compiled for each pool on the basis of published information on each species' diet. The networks analysed were trophic species versions of the food webs. The trophic species are taxa that have the same set of prey and predators to maintain comparability with food webs generated by the niche model, which is based on the notion of trophic species.

Model of species dynamics. To simulate the population dynamics we used a previously published model¹⁰ based on the Yodzis and Innes framework⁴⁴. Species growth is determined by carrying capacity and intrinsic growth rate for basal species and energy input for non-basal ones; species lose energy through predation and metabolism:

$$\frac{dB_i}{dt} = r_i B_i \left(1 - \frac{B_i}{K_i}\right) - \sum_p F_{pi} B_p \quad \text{for producers} \quad (1)$$

$$\frac{dB_i}{dt} = \sum_p e_p F_{ip} B_i - \sum_p F_{pi} B_p - x_i B_i \quad \text{for consumers} \quad (2)$$

where B_i , r_i , K_i , e_i and x_i , respectively, are the biomass, growth rate, carrying capacity, assimilation efficiency and metabolic rates of species i , p is the set of prey of species i and P its set of predators, e_i is equal to 0.45 for plants and 0.85 for animals, and F_{ij} is the functional response term:

$$F_{ij} = \frac{a_{ij} B_j^q}{1 + c_i + \sum_p \text{Th}_{ip} a_{ip} B_p^q} \quad (3)$$

where a_{ij} and Th_{ij} are the link specific attack rates and handling times, c_i is the interference competition and $q = 1.5$ determines the shape of the functional response. The parameters scale with body masses and temperature as:

$$a_{ij}, \text{Th}_{ij} = dm_i^b m_j^c e^{\frac{E_{ij} - T}{kT_0}} \quad (4)$$

$$r_i, K_i, x_i = dm_i^b e^{\frac{E_i - T}{kT_0}} \quad (5)$$

where d is a constant, b and c are the allometric factors associated with predator and prey body masses m_i and m_p , respectively, E is the activation energy, T is the temperature in kelvin and $T_0 = 293.15$ K is the temperature normalization factor. The values used are taken from Binzer et al.¹⁰ and are given in Supplementary Section 8.

Interference competition is defined as:

$$c_i = dm_i^b (N_i - 1) e^{\frac{E_{ii} - T}{kT_0}} \quad (6)$$

where N_i is the number of individuals of species i , E was set to 0.65 (ref. ⁴¹) and b to 0.21 (ref. ⁴⁵). In the absence of other information, we considered d to be equal to 1.

The equations were solved using the lsoda method of SciPy 1.0.0 with Python 2.7 on a high-performance computing cluster. All simulations were run for an equivalent of 3,000 years to reach stable attractors¹⁰. We applied an extinction threshold at a biomass density of 10^{-12} .

Niche model. We generated synthetic food webs using the niche model¹⁶ and its correction⁴⁶. Species body masses were determined using their trophic level with the following generic relationship:

$$m_i = m_0 R^{L_i - 1 + e_i} \quad (7)$$

where m_0 is the body mass of the basal species ($m_0 = 0.01$ g), R is the average body-mass ratio between predators and prey (set to 100), L_i is the trophic level of species i sensu Levine (ref. ⁴⁷) and e_i is a random variable sampled from a normal distribution with a mean of 0 and a standard deviation of 1 that prevents species with a similar trophic level all having the same body mass.

Statistical analyses. The PCAs were performed using the PCA function of the FactoMineR (1.34) package⁴⁸.

The mixed-effect modelling was performed using a two-sided approach with the lme function of the nlme (3.1–143) package⁴⁹. The effect sizes reported correspond to the slopes associated with each explanatory variable. Homoscedasticity was checked by a visual inspection of standardized residual plots.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data that support the findings of this study are archived in a public repository accessible at: <https://doi.org/10.25829/ndiv.283-3-756> (ref. ⁵⁰).

Code availability

The codes used to run the model and to analyse the results are available on Github at <https://doi.org/10.5281/zenodo.3578440> (ref. ⁵¹).

References

- Yodzis, P. & Innes, S. Body size and consumer-resource dynamics. *Am. Nat.* **139**, 1151–1175 (1992).
- Hirt, M. R., Lauerhmann, T., Brose, U., Noldus, L. P. J. & Dell, A. I. The little things that run: a general scaling of invertebrate exploratory speed with body mass. *Ecology* **98**, 2751–2757 (2017).
- Allesina, S., Alonso, D. & Pascual, M. A general model for food web structure. *Science* **320**, 658–661 (2008).
- Levine, S. Several measures of trophic structure applicable to complex food webs. *J. Theor. Biol.* **83**, 195–207 (1980).
- Lé, S., Josse, J. & Husson, F. FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.* **25**, 1–18 (2008).
- Pinheiro, J., Bates, D., DebRoy, S. & Sarkar, D. nlme: Linear and nonlinear mixed effects models. R package version 3.1-143 (2019).
- Brose, U. GlobALL daTabasE of traits and food Web Architecture (GATEWAY) version 1.0. *iDiv* <https://doi.org/10.25829/ndiv.283-3-756> (2018).
- Gauzens, B. The temporal dynamics of intertidal pool communities. *Zenodo* <https://doi.org/10.5281/zenodo.3578553> (2020).

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Author contributions

B.G. and U.B. designed the study. V.M. and C.V. collected the data. B.G. wrote the first draft of the manuscript and performed simulations. All authors contributed to the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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