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Biodiversity of intertidal food webs in response to warming across latitudes

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Abstract

Global warming threatens community stability and biodiversity around the globe. Knowledge on the underlying mechanisms depends heavily on generic food-web models that do not account for changes in network structure along latitudes and temperature gradients. Using 124 marine rockpool 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 used dynamic modelling to test if communities from warmer regions were more sensitive to warming and found a general humped-shaped relationship between simulated biodiversity and temperature (gradient from 0-50°C). This implies that an expected anthropogenic warming by 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.

1 **Main text**

2 Global warming is recognised as a major threat to species survival, community stability and
3 ecosystem functioning ¹. However, predicting the response of species communities to temperature
4 increases is still subject to substantial uncertainties. Indeed, warming affects communities at all
5 levels of biological organisation, from species physiology to community structure and geographical
6 distribution ², leading to complex causality chains of interactions between these organisation levels.
7 At the individual level, temperature affects species biological rates such as metabolism or activity
8 ^{3,4}, resulting in modifications of trophic interaction strengths ⁵, trophic cascades⁶ and community
9 body-mass structure^{7,8} – an essential driver of food web structures ⁹. These processes interact to
10 determine responses of communities at the ecosystem level, such as food web stability ¹⁰ or
11 ecosystem functions ¹¹.

12 A two-species consumer-resource model ¹² predicted a decrease in resource biomass because of
13 stronger top-down control at high temperatures. However, pioneering experimental studies
14 considering the impact of warming on microcosm communities highlighted higher extinction
15 probabilities of larger predators, even if their resources were increasing in density ¹³. This
16 inconsistency between experiments and models have been resolved by more accurate estimations of
17 model parameters ¹⁴. Contrary to prior results, models using the new parameters showed that
18 metabolic rates of predators increase faster with warming than their feeding rates, leading to
19 starvation of larger predators when temperature is high ¹⁵ and to a decrease of species persistence ¹⁰.

20 Although these results are in line with microcosm studies ¹³, they do not match recent empirical
21 results for complex communities of natural stream ecosystems, which showed that biodiversity
22 increases with local temperature allowing large predators to persist ⁸. Hence, there is a discrepancy
23 between complex food-web models predicting a collapse of large species at high temperatures ¹⁰ and
24 empirical studies of natural communities of similar levels of complexity showing better energy
25 support of large species at higher temperature ⁸. We show here that considering more precise

1 biological information on food-web structures and body-mass distributions across species can
2 resolve this paradox.

3 Indeed, a limitation of previous modelling approaches is that they did not completely bridge the gap
4 between theoretical networks and real ecosystems. Conclusions are based on synthetic networks
5 usually generated by a niche model ¹⁶ instead of natural network structures, which imposes two
6 strong limitations. First, it hampers an understanding of and how the network topology of natural
7 communities changes with temperature as generative models such as the niche model produce
8 synthetic networks without accounting for temperature. Second, the body-mass structures of these
9 theoretical communities are usually determined by generic relationships between body mass and
10 trophic levels, which ignores empirical evidence of differences between, for example, aquatic ¹⁷ and
11 terrestrial ^{18,19} systems, despite their implications for community stability ¹⁵. Thus, ecological studies
12 have not yet considered the potential adaptations of network topology and body-mass distributions
13 to local temperature and how they might interact with a perturbation such as warming.

14 Therefore, we aim to bridge the gap between purely theoretical and experimental approaches by
15 using a global dataset of natural intertidal pool food webs from regions around the world across a
16 temperature gradient ²⁰, all sampled using the same methodology (Fig. 1). For the first time, this
17 allows us to study (1) the impact of environmental factors including temperature on food-web
18 topology and (2) how these local temperature conditions affect the response of natural food webs to
19 simulated warming.

20

21 **Effect of rockpool temperature on food web structure**

22 Our dataset comprises 124 food webs from 7 different regions (two beaches per region) across five
23 continents (Fig. 1C, for more details, see SI I and ²⁰). Overall, the summer sea temperature ranged
24 from a minimum of 11.5°C in Canada to a maximum of 28.4°C in Brazil. We examined the effects
25 of individual pool volume and temperature on network topology by considering 12 classical
26 descriptors (see SI II for mathematical definitions): number of species, number of links,

1 connectance, mean omnivory, predator-prey ratio, mean generalism, proportions of basal
2 intermediate and top species, mean trophic level, mean trophic level of top species and average path
3 length. We performed a PCA analysis with these 12 descriptors. The two principal axes explained
4 68.1% of the data variability (Fig. 2a). When projected onto the PCA plane, the abiotic rockpool
5 characteristics (volume, pool temperature, elevation and difference to sea temperature, blue arrows
6 in Fig. 2a) were rather weakly correlated with the PCA axes (all correlation coefficients were lower
7 than 0.3, see SI III). Interestingly, the food web structure was more, albeit weakly, related to the sea
8 temperature: (minimum, maximum and average temperature values of the year and for summer, see
9 SI III) than to the rockpool temperature. Moreover, individual regressions between the 12
10 topological descriptors and sea temperature did not exhibit general trends (SI II), and the
11 distribution of food web data points on the PCA plane did not exhibit any pattern related to sea
12 temperature (Fig. 2b). Together, these findings suggest that none of the different abiotic factors is a
13 strong driver of food web structure in our dataset.

14 Contrary to our expectations, the body-mass structure of the community (here the scaling of body
15 masses with trophic levels) did not respond systematically to temperature (Fig. 2c). A model
16 selection procedure based on BIC kept the species trophic levels as the only explanatory variable of
17 species body masses in the model ($F_{1,3355} = 1063.581$, $p < 0.001$, effect size: 0.57, CI = [0.54,0.61]),
18 whereas temperature and the interaction between trophic levels and temperature were removed.
19 Food web identity nested into beach nested into region was considered as a random effect on the
20 intercept, see SI IV. The above-described results suggest that the network- and body-mass-structures
21 of the rockpool communities are robust against differences in environmental temperature along the
22 global gradient of our analyses.

23

24 **Response of natural rockpool food webs to simulated warming**

25 Despite these structural similarities between the food webs across the natural temperature gradient,
26 our simulations showed that the summer sea temperature of the rockpools influenced the response

1 of food webs to simulated warming (Fig. 3). We used a dynamic model¹⁰ parametrised by species'
2 body masses and summer sea temperature (SI I) to compute species persistence (the proportion of
3 species that survived until the end of the simulations) under warming of up to four degrees Celsius.
4 We chose to use summer sea temperature instead of individual pool temperature as (1) sea
5 temperature has a stronger effect on network structure than pool temperature and (2) summer
6 corresponds to the sampling season. However, additional simulations with individual rockpool
7 temperature yielded similar conclusions (SI V).

8 For each of the 124 natural networks, we ran simulations of species dynamics along a warming
9 gradient from 0 (local temperature of each individual rockpool) to 4 degrees Celsius (local
10 temperature plus warming of 4 degrees Celsius) in steps of 0.1. We used a mixed effects model to
11 test for the effects of simulated warming and summer sea temperature on species persistence (as
12 proportions, data were logit transformed; food web identity nested into beach nested into region as a
13 random structure). In this model, we used as covariates the variables that have the strongest effects
14 on food-web structure according to the PCA analysis (see above): pool size, latitude, summer sea
15 temperature, amplitude and pool elevation. Model selection by the parsimony criteria (BIC, see SI
16 IV) kept as variables summer sea temperature ($F_{1,5} = 1.7915$, $p = 0.238$, effect size: -0.0181, CI = [-
17 0.114, 0.0783]) and simulated warming ($F_{1,2258} = 6.03$, $p = 0.0141$, effect size: 0.3369, CI = [0.309,
18 0.364]). The interaction between summer sea temperature and simulated warming was also
19 significant ($F_{1,2258} = 593.42$, $p < 0.001$, effect size: -0.0173, CI = [-0.016, -0.0147]), because species
20 persistence significantly increased with simulated warming for pools from colder regions (<22.9)
21 but significantly decreased for warmer ones (> 22.9 degrees Celsius, no effect was found when sea
22 temperature was equal to 22.9). This interactive effect and the discrepancy in the response of food
23 webs from warm and cold regions can be explained by the general response of persistence of
24 empirical networks to warming across a temperature gradient from 0 °C to 50 °C. By zooming out
25 to this large temperature gradient, we can observe a hump-shaped relationship between persistence
26 and temperature (Fig. 4a) with a persistence peak between 20 and 30 degrees Celsius. Thus, the

1 absence of specific dependencies of food web topology and body-mass structure on regional
2 temperatures leads to a similar hump-shaped pattern in the scaling of food-web persistence across
3 our large temperature gradient (i.e. from 0 to 50 degrees Celsius). Hence, we can explain
4 differences in the responses of the different local food webs to the simulated warming by 4 degrees
5 Celsius by the position of their regional temperature on the large temperature gradient. The
6 temperatures of food webs from warmer regions are located on the decreasing part of the hump-
7 shaped relationship implying a decrease in persistence when exposed to warming, but the food webs
8 from colder region increase in persistence as their local temperatures are located on the left part of
9 the hump-shaped relationship.

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

23 Surprisingly, our results thus suggest that the different response in community persistence to
24 simulated warming does not depend on local adaptations in network structure to environmental
25 temperature but instead on the different local temperatures that determine where the community is
26 positioned on the hump-shaped persistence-warming relationship. We examined this assertion more

1 carefully by comparing the persistence between food webs at their region-specific temperature
2 (natural temperature persistence) with food webs from other regions (with colder or warmer region-
3 specific temperatures) simulated at the same temperature. We did not observe a higher persistence
4 for food webs simulated at their natural temperature (SI VII) supporting our conclusion that the
5 rock-pool food webs do not have any specific systematic structural adaptations to local conditions.

7 **Differences between natural and synthetic food webs**

8 The hump-shaped pattern found across the large temperature gradient with natural food webs does
9 not hold for synthetic networks generated by the niche model that exhibit generally lower and
10 continuously decreasing persistence across the temperature gradient (Fig. 4b). This finding could be
11 explained by: differences in (1) the body-mass structure or (2) the network topologies between
12 synthetic and natural communities. We tested the first hypothesis by assigning synthetic body
13 masses to the species of the empirically established networks according to the generic relationship
14 between body mass and trophic level (eq. 5) that was also used to parameterise the synthetic
15 networks. The response in species persistence observed for this simulation was close to the one
16 observed for the natural food webs simulated with the natural body-mass distribution (Fig. 4c), but
17 persistence was generally lower. Only the site with an average summer sea temperature of 26.3 °C
18 (Fig. 4c, orange line) exhibited a pattern that is similar to the one observed for the niche model (Fig.
19 4b). Nevertheless, our results suggest that, in our case, network topology is an important factor
20 governing the response of communities to warming.

21 The different results observed for synthetic and empirical networks are associated with important
22 differences in network topology. First, synthetic models generate food webs with (1) higher trophic
23 levels (Fig. 5a, 5b), which increases the amount of energy lost during feeding interactions between
24 basal and top trophic levels^{23,24}. This decreases the energy fluxing upwards to highest trophic level
25 species, which reduces their energy supply and thus strengthens the predator starvation effect that is
26 responsible for the decrease in persistence at high temperatures. Second, synthetic models yield

1 systematically fewer upward feeding links per basal species leading to reduced herbivory pressure
2 (Fig. 5c). This prevents herbivore extinctions at low temperatures despite low productivity, which is
3 responsible for the increasing part of the hump-shaped temperature-persistence relationship.
4 Interestingly, food webs from the site with responses to warming similar to niche-model networks
5 are also the ones with topologies that match predictions from the niche model (Fig. 5, orange data
6 points).

7

8 **On the importance of considering natural food webs.**

9 Together, all these differences between results found with approaches using natural food webs or
10 synthetic models stress that the systematic use of generic modelling approaches can (1) bias
11 conclusions on the consequences of warming and (2) lead to misinterpretations of the underlying
12 mechanisms. Indeed, the use of natural food webs allowed us to solve the discrepancy between the
13 different results produced by models and empirical studies of complex communities. At these levels
14 of complexity, models predicted a decrease in species persistence with an increase in temperature ¹⁰,
15 which was explained by the starvation of large species from higher trophic levels ¹⁰. In contrast,
16 experimental results argued for better energy support of large species ⁸. We showed that the models'
17 underestimation of herbivory pressure and an overestimation of the number of trophic levels
18 (reducing the amount of energy reaching top species) in synthetic networks explains the
19 discrepancy between results found for generic food-web models and our predictions for natural food
20 webs. These differences argue for the use of natural networks to address the response of food-web
21 characteristics such as stability and functioning to environmental gradients, even in theoretical
22 studies.

23 While theoretical models generating food webs might be able to capture some common tendencies
24 in patterns (either food web topologies or body-mass distributions), the deviations of individual
25 systems from these average predictions appear to be essential and stress the limits of theoretical
26 models in addressing mechanisms occurring in-situ. Thus, it becomes urgent to address the causes

1 and consequences of these deviations. Exploring causes calls for a better understanding of
2 ecological factors constraining network topologies^{25,26} and body mass distributions^{19,27}.
3 Incorporation of non-trophic interactions²⁸, experimental studies manipulating external gradients
4^{29,30} or comparisons of food-web topology between ecosystem types³¹ can provide insights in this
5 direction. The extension of the allometric diet breath model³², incorporating temperature effects
6 into optimal foraging theory³³ to address how temperature might impact food web topology is a
7 first step towards the understanding of mechanistic processes underlying responses of food web
8 topology to temperature. Addressing the consequences of warming would call for a better
9 examination of food web properties deviating from generative model predictions and how they
10 relate to specific processes. Hence, one urgent question is whether this discrepancy in the warming
11 response between natural and generic food webs extends to other ecosystem types.

12

13 **Future steps**

14 Our analyses of food web responses to simulated warming is a step towards a better understanding
15 of the impact of global warming on natural communities. We showed that the use of dynamic
16 models and a set of replicated empirically estimated networks is a suitable tool to gain a
17 mechanistic understanding of the ecological processes underlying the consequences of warming.
18 However, we need to understand better how species change their feeding interactions under
19 temperature stress in order to get more accurate predictions³³. Indeed, the trophic links of the
20 empirical networks arose from static information, which does not account for temperature-driven
21 shifts in species' trophic interactions. Tackling this issue in the future would allow using a more
22 generic approach that would ultimately link studies considering the effects of warming on food
23 webs to ecosystem functioning³⁴. Moreover, we might also need to refine the classical Metabolic
24 Theory of Ecology and consider more complex responses of species rates such as hump-shaped
25 relationships with warming^{5,35}. This would increase model realism which is now uncertain when
26 species are above their optimal temperature. Considering this optimal temperature for biological

1 processes depending on a species' physiological adaptation³⁶ might also change the temperature of
2 maximal persistence, potentially shifting the highest persistence values to the local temperature
3 conditions and interacting with evolutionary dynamics³⁷. Then, an important future step will be to
4 incorporate this mechanistic understanding of warming effects on local communities to a more
5 global framework considering modifications of species distributions³⁸. Meta-community
6 approaches including temperature effects³⁹ are for example a promising tool to improve the
7 conceptual links between climatic models, food-web theory, and temperature size relationships⁴⁰.

8

9 **Conclusion**

10 Our results suggest that the local temperature condition of food webs determines their response to
11 warming. While warming tends to increase the persistence of species in the food webs from cold
12 regions, it tends to decrease the persistence of those from warmer places. In general, previous
13 studies have shown that tropical organisms are more sensitive to warming than their temperate
14 counterparts, because (1) they live closer to their physiological limit⁴¹, (2) the exponential scaling
15 of biological rates with temperature causes higher increases in their biological rate per degree
16 warming⁴² and (3) the predator-starvation effect is leading to increasingly low abundances²².
17 Together, these studies suggest that tropical food webs seem to be more vulnerable to warming than
18 food webs from colder regions. Our results confirm this expectation based on a general hump-
19 shaped pattern governing the response of natural rockpool food webs to a temperature gradient.
20 Strikingly, we only found this result using natural food-web structures, whereas differences in
21 predictions found in simulations using synthetic networks underline the importance of network
22 structure for species dynamics. These results stress to the importance of coupling an ecosystem-
23 specific understanding of network structures with predictive simulations of warming or other global
24 change gradients. While our results have shown that generic network models do not capture the
25 specific food-web structures that are important for the system response to warming, these generic
26 models also cannot cover ecosystem-specific signatures in network structures such as architectural

1 differences between soil and other food webs⁴³. Additionally, the dynamically important body-mass
2 structure of food webs also differs significantly among ecosystem types²⁷, which is not captured by
3 synthetic approaches. These shortcomings of generic network models may lead to substantial errors
4 in the predictions of ecosystem responses to global warming. Therefore, our results call for
5 employing system-specific natural network structures in the analyses of global warming, which
6 need to be integrated with effects on the population's biological rates, adaptation processes and new
7 communities due to range shifts. Altogether, this is a substantial research agenda, but unless we find
8 out how these patterns interact from species physiology to community structure up to geographical
9 distribution, predictions on future ecosystems in a warmed world remain highly uncertain.

10

11 **Methods:**

12 **Data sampling and food web construction**

13 The food webs chosen for this work were those occurring in intertidal rock pools. The animal
14 community was composed of ectothermic species. Only pools occurring in the lower intertidal zone
15 of rocky shores were selected for sampling. Sampling took place in summer (2013-2015), during
16 spring tides. Summer was chosen, to ensure comparability since it is when biodiversity and species
17 abundance is highest in the intertidal rock pools, compared to other seasons. Two sites were selected
18 in each of the regions Canada (Gulf of St. Lawrence, site A - Pointe-au-Père – 48°29'33.0"N
19 68°29'33.0"W, site B – Sainte-Flavie - 48°36'43.0"N 68°13'44.3"W), United Kingdom (South
20 coast, site A – Mount Baten – 50°21'24"N 4°07'43"W, site B – Wembury – 50°19'00"N
21 4°04'57"W), Portugal-west coast (Portugal mainland, site A – Cabo Raso - 38°42'38.2"N
22 9°29'09"W and site B – Raio Verde - 39°17'11.4"N 9°20'23"W), Portugal-Madeira (Madeira Island,
23 northeast Atlantic, site A – Caniço – 32°38'44.4"N 16°49'26.5"W, site B – Porto da Cruz –
24 32°46'32.6"N 16°49'33.5"W), Brazil-São Paulo (southeast coast, site A – São Sebastião -
25 23°49'26"S 45°25'38"W and site B – Ubatuba - 23°28'01"S 45°03'36"W) and Brazil-Ceará
26 (Northeast coast, site A – Flecheiras - 3°13'04"N 39°15'29"W and site B – Guajirú - 3°14'14"N

1 39°13'44"W). In each region, sites A and B were separated by distances between 6 and 60 km from
2 each other. On each of these two sites per region, 2 to 4 beaches were targeted. In Mozambique only
3 one site was sampled, Inhaca (Praia do Farol – 25°58'36"S 32°59'38"E), two beaches were
4 targeted and four pools were sampled in each beach. All sampled intertidal rock pools were located
5 in the lower intertidal and their size range (depth: 0.05 m - 0.80 m; surface area: 0.15 m² - 33.00 m²,
6 as estimated from scaled digital photographs using the software ImageJ) ensured a minimum patch
7 size for the development of benthic assemblages, while still allowing a complete record of all
8 macro-organisms found in each pool. In total, 28 pools were sampled in Canada, 8 in the UK, 32 in
9 Portugal-west coast, 14 in Portugal-Madeira, 18 in Brazil-São Paulo (Brazil-SP), 16 in Brazil-Ceará
10 (Brazil-CE) and 8 in Mozambique. More information on site temperatures can be found in SI VII.
11 One bottom sediment sample of 50 ml was taken from pools with an area ≤ 0.5 m², two samples
12 from pools with an area < 0.5 m² and ≤ 2 m², and three samples from pools with an area > 2 m²,
13 whenever the pool presented sediment at the bottom. Three quadrats of 5 cm² of rock pool surface
14 were scrapped. Sediment and scraping samples were preserved in alcohol 70%, with Bengal rose,
15 and taken to the laboratory, where all organisms were identified with a binocular microscope. All
16 macro-organisms present in the pools were identified in situ, but samples were taken to the
17 laboratory whenever there were taxonomical issues, requiring more detailed observation in the
18 laboratory. In the latter case, marine organisms were identified with the aid of a stereomicroscope,
19 and when necessary by consulting identification keys and taxonomic experts.
20 Highly resolved food webs, depicting who eats whom, were compiled for each pool, based on
21 published information on each species diet. The networks analysed were trophic species versions of
22 the food webs. Trophic species are taxa that have the same set of prey and predators in order to
23 maintain comparability with food webs generated by the niche model which is based on the notion
24 of trophic species.

25

26 **Model of species dynamics**

1 To simulate the population dynamics, we used previously published model ¹, based on the Yodzis
 2 and Innes framework ². Species growth is determined by carrying capacity and intrinsic growth rate
 3 for basal species and energy input for non-basal ones; species lose energy through predation and
 4 metabolism:

$$5 \quad \frac{dB_i}{dt} = r_i B_i \left(1 - \frac{B_i}{K_i} \right) - \sum_P F_{Pi} B_P \quad \text{for producers, (1a)}$$

$$6 \quad \frac{dB_i}{dt} = \sum_p e_p F_{ip} B_i - \sum_P F_{Pi} B_P - x_i B_i \quad \text{for consumers. (1b)}$$

7
 8 where B_i , r_i , K_i , e_i and x_i respectively set the biomass, growth rate, carrying capacity, assimilation
 9 efficiency and metabolic rates of species i . p is the set of prey of species i and P its set of predators.
 10 e_i is equal to 0.45 for plants and 0.85 for animals. F_{ij} is the functional response term:

$$11 \quad F_{ij} = \frac{a_{ij} B_j^q}{1 + c_i + \sum_p Th_{ip} a_{ip} B_p^q} \quad (2)$$

12 where a_{ij} and Th_{ij} are the link specific attack rates and handling times, $q = 1.5$ determines the shape
 13 of the functional response. Parameters scale with body masses and temperature as:

$$14 \quad a_{ij}, Th_{ij} = d m_i^b m_j^c e^{\frac{E(T_0 - T)}{kT T_0}} \quad (3a)$$

$$15 \quad r_i, K_i, x_i = d m_i^b e^{\frac{E(T_0 - T)}{kT T_0}} \quad (3b)$$

16 where d is a constant, b and c are the allometric factors associated with respectively predator and
 17 prey body masses m_i and m_j . E is the activation energy and T the temperature in Kelvin. $T_0 = 293.15$
 18 is the temperature normalization factor. The values used are taken from Binzer *et al.* (2016) and are
 19 given in SI VIII.

20 Interference competition was defined as:

$$21 \quad c_i = d m_i^b (N_i - 1) e^{\frac{E(T_0 - T)}{kT T_0}} \quad (4)$$

1 where N_i is the number of individuals of species i . E was set to 0.65^3 and b to 0.21^4 . In absence of
2 other information, we considered d to be equal to 1.

3 Equations were solved using the *lsoda* method from *scipy* 1.0.0 with python 2.7 on a High-
4 Performance Computing Cluster. All simulations were ran for an equivalent of 3000 years to reach
5 stable attractors¹. We applied an extinction threshold at a biomass density of 10^{-12} .

6 7 **Niche model:**

8 We generated synthetic food webs using the niche model⁵ and its correction⁶. Species body masses
9 were determined using their trophic level with the following generic relationship:

$$10 \quad m_i = m_0 R^{L_i - 1 + \epsilon_i} \quad (5)$$

11 where m_0 is the body mass of the basal species ($m_0 = 0.01g$), R is the average body-mass ratio
12 between predators and prey (set to 100) and L_i is the trophic level of species i *sensu* Levine (1980).

13 **Statistical analyses:**

14 The PCAs analyses were performed using the PCA function from the FactoMineR (1.34) package.
15 The mixed effect models were performed using a two-sided approach with the lme function from
16 the nlme (3.1-143) package. Effect sizes reported correspond to the slopes associated to each
17 explanatory variable. Homoscedasticity was checked by a visual inspection of standardised residual
18 plots. Levine (1980)

19 20 **Method references:**

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14 **Data availability:**

15 The data that support the findings of this study are on archived public repository accessible at:
16 <https://doi.org/10.25829/ividiv.283-3-756>.

17 **Code availability**

18 The codes to run the model and to analyse the results are available on Github at
19 <https://doi.org/10.5281/zenodo.3578440>

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29 **Author contributions:**

1 BG and UB designed the study. VM and CV collected the data. BG wrote the first draft of the
2 manuscript and performed simulations. All authors contributed to the manuscript

3 **Competing interests:**

4 The authors declare no competing interests.

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Figure legends:

Figure 1: Structure and distribution of the natural rockpool food webs. a) An exemplary food web depicting trophic interactions between species of a rockpool (Portugal). Colours define species' metabolic types: green for plants, blue for invertebrates and yellow for ectotherm vertebrates. b) Picture of a typical rockpool 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.

Figure 2: Analysis of community structure. a) Principal component analysis of the normalised topological descriptors of the food webs. Black arrows represent the topological descriptors used in the analysis. Blue arrows represent abiotic variables projected on the PCA plan, but they were not used for the determination of PCA axes. TL means trophic level, and top species are consumers without predators. b) Each point represents one individual rockpool projected on the plane generated by the PCA, and its colour describes the associated summer sea temperature. Larger dots represent ellipses' centre of gravity. c) Relationship between species body masses and trophic levels depending on local temperature. Coloured lines represent the predictions of a linear regression for each region. Statistically, these different trends are not significantly different from each other (see SI IV), and the data are best described by an overall scaling relationship (black solid line).

Figure 3: Effect of simulated warming on species persistence. Each point represents the mean value at a given temperature; the solid line is the prediction from a linear model; the shaded-area shows the 95% confidence interval on the predicted values. Colours set the average see summer temperature within each region.

Figure 4: Relationship between species persistence and temperature in simulations. a) natural food webs, b) niche model food webs and c) natural food webs, in which species body masses were estimated with the same scaling law also used for niche models. Each point represents the mean value at a given temperature; the solid lines are the prediction from local moving regressions (LOESS technique); the shaded-area shows the 95% confidence interval on the predicted values. Colours depict the average summer sea temperature within each region.

Figure 5: Comparison of mean trophic level, top trophic level and mean number of predators per basal species between niche and experimental networks. 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. Black line is the identity. Colours indicate the average sea summer temperature within each region.

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2 Figures

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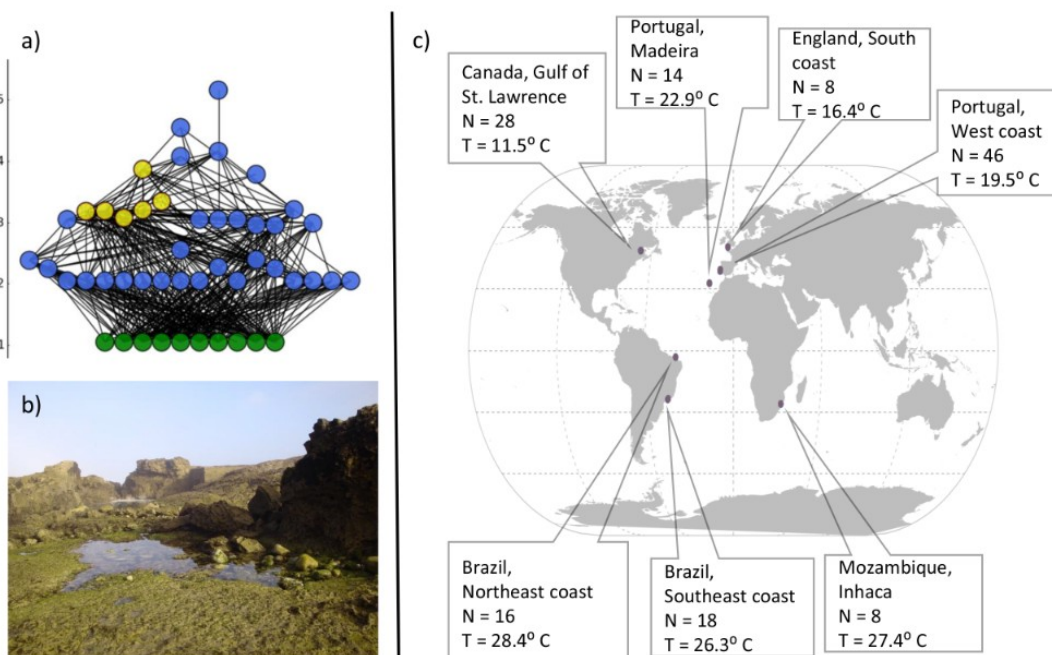
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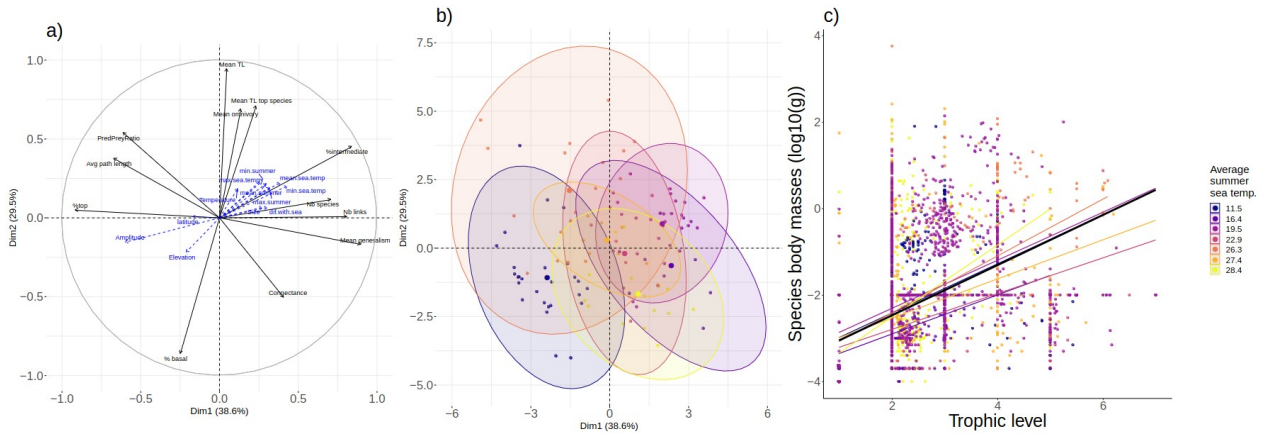
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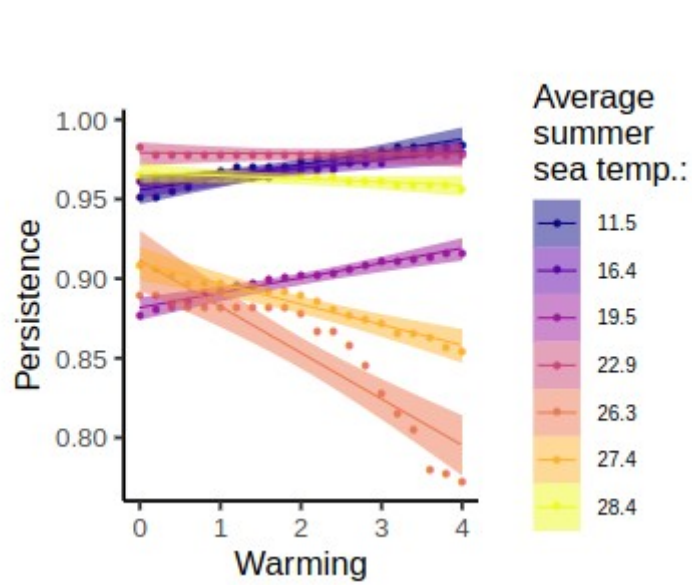


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1 Figure 4.

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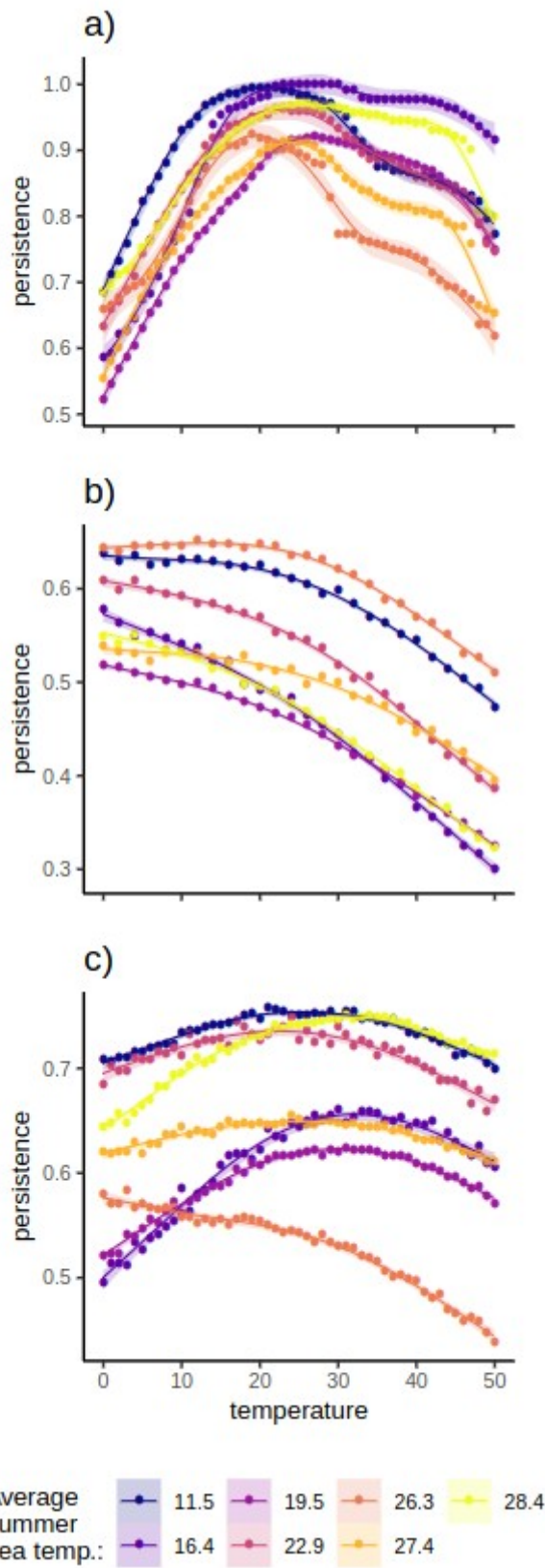
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1 Figure 5.

