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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 <sup>1</sup>. 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 <sup>2</sup>, 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 <sup>3,4</sup>, resulting in modifications of trophic interaction strengths <sup>5</sup>, trophic cascades<sup>6</sup> and community  
9 body-mass structure<sup>7,8</sup> – an essential driver of food web structures <sup>9</sup>. These processes interact to  
10 determine responses of communities at the ecosystem level, such as food web stability <sup>10</sup> or  
11 ecosystem functions <sup>11</sup>.

12 A two-species consumer-resource model <sup>12</sup> 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 <sup>13</sup>. This  
16 inconsistency between experiments and models have been resolved by more accurate estimations of  
17 model parameters <sup>14</sup>. 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 <sup>15</sup> and to a decrease of species persistence <sup>10</sup>.

20 Although these results are in line with microcosm studies <sup>13</sup>, 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 <sup>8</sup>. Hence, there is a discrepancy  
23 between complex food-web models predicting a collapse of large species at high temperatures <sup>10</sup> and  
24 empirical studies of natural communities of similar levels of complexity showing better energy  
25 support of large species at higher temperature <sup>8</sup>. 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 <sup>16</sup> 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 <sup>17</sup> and  
11 terrestrial <sup>18,19</sup> systems, despite their implications for community stability <sup>15</sup>. 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 <sup>20</sup>, 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 <sup>20</sup>). 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 model<sup>10</sup> 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<sup>21,22</sup>  
14 leading them to starvation<sup>15</sup>. 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 webs<sup>14</sup>. 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<sup>23,24</sup>. 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 <sup>10</sup>,  
15 which was explained by the starvation of large species from higher trophic levels <sup>10</sup>. In contrast,  
16 experimental results argued for better energy support of large species <sup>8</sup>. 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<sup>25,26</sup> and body mass distributions<sup>19,27</sup>.  
3 Incorporation of non-trophic interactions<sup>28</sup>, experimental studies manipulating external gradients  
4<sup>29,30</sup> or comparisons of food-web topology between ecosystem types<sup>31</sup> can provide insights in this  
5 direction. The extension of the allometric diet breath model<sup>32</sup>, incorporating temperature effects  
6 into optimal foraging theory<sup>33</sup> 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 predictions<sup>33</sup>. 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 functioning<sup>34</sup>. 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<sup>5,35</sup>. 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 adaptation<sup>36</sup> 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 dynamics<sup>37</sup>. 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 distributions<sup>38</sup>. Meta-community  
6 approaches including temperature effects<sup>39</sup> are for example a promising tool to improve the  
7 conceptual links between climatic models, food-web theory, and temperature size relationships<sup>40</sup>.

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 limit<sup>41</sup>, (2) the exponential scaling  
15 of biological rates with temperature causes higher increases in their biological rate per degree  
16 warming<sup>42</sup> and (3) the predator-starvation effect is leading to increasingly low abundances<sup>22</sup>.  
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 webs<sup>43</sup>. Additionally, the dynamically important body-mass  
2 structure of food webs also differs significantly among ecosystem types<sup>27</sup>, 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 m<sup>2</sup> - 33.00 m<sup>2</sup>,  
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  $\leq 0.5$  m<sup>2</sup>, two samples  
12 from pools with an area  $< 0.5$  m<sup>2</sup> and  $\leq 2$  m<sup>2</sup>, and three samples from pools with an area  $> 2$  m<sup>2</sup>,  
13 whenever the pool presented sediment at the bottom. Three quadrats of 5 cm<sup>2</sup> 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 <sup>1</sup>, based on the Yodzis  
 2 and Innes framework <sup>2</sup>. 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 attractors<sup>1</sup>. 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 model<sup>5</sup> and its correction<sup>6</sup>. 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)

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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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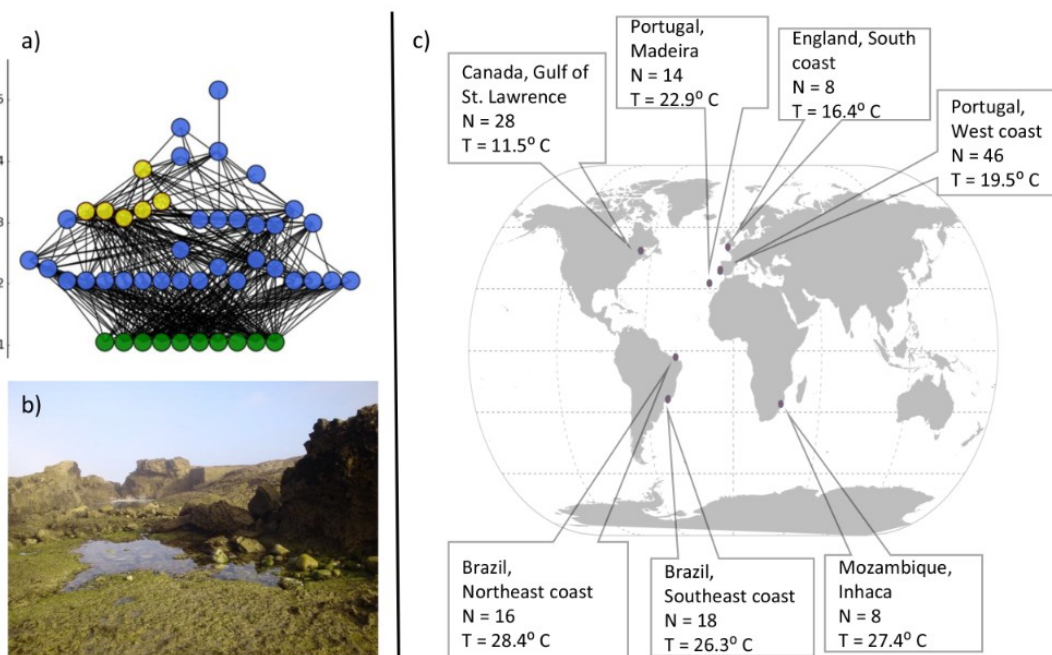
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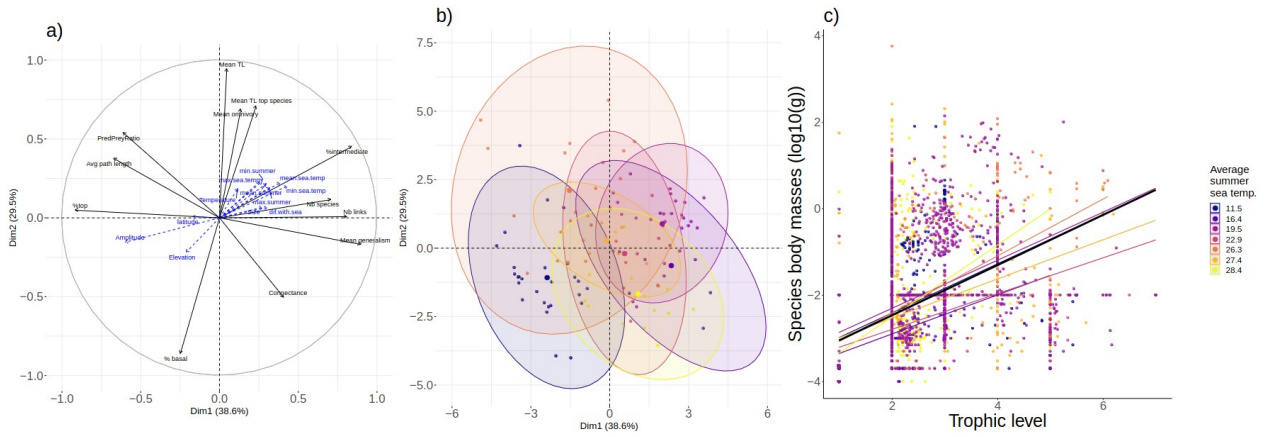
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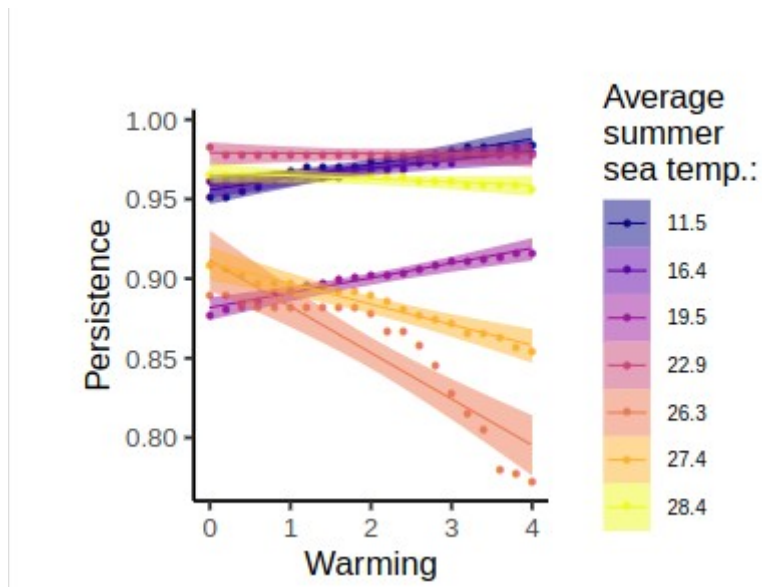


1 Figure 2.



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1 Figure 4.

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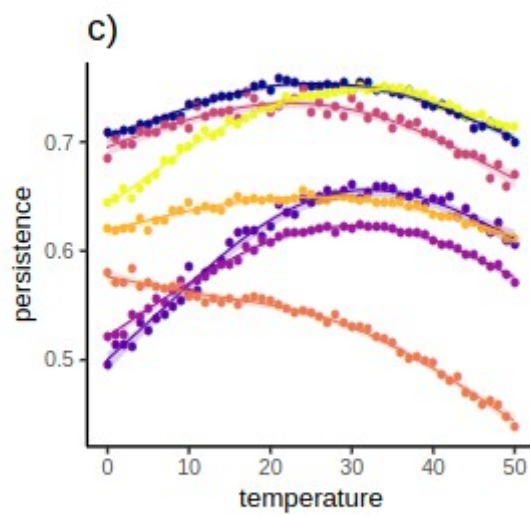
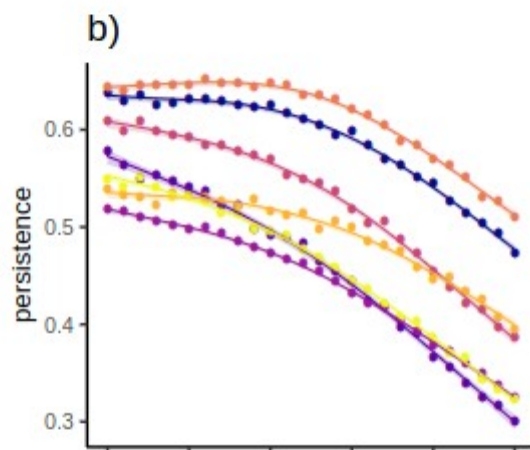
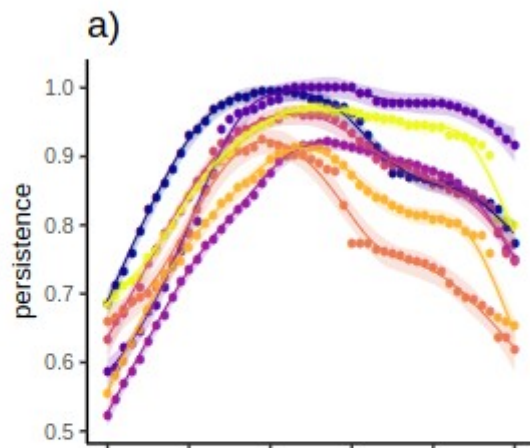
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1 Figure 5.

