

# Ecological emergence of thermal clines in body size

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## Abstract

The unprecedented rate of global warming requires a better understanding of how ecosystems will respond. Organisms often have smaller body sizes under warmer climates (Bergmann's rule and the temperature-size rule), and body size is a major determinant of life histories, demography, population size, nutrient turnover rate, and food-web structure. Therefore, by altering body sizes in whole communities, current warming can potentially disrupt ecosystem function and services. However, the underlying drivers of warming-induced body downsizing remain far from clear. Here, we show that thermal clines in body size are predicted from universal laws of ecology and metabolism, so that size-dependent selection from competition (both intra and interspecific) and predation favors smaller individuals under warmer conditions. We validate this prediction using  $4.1 \times 10^6$  individual body size measurements from French river fish spanning 29 years and 52 species. Our results suggest that warming-induced body downsizing is an emergent property of size-structured food webs, and highlight the need to consider trophic interactions when predicting biosphere reorganizations under global warming.

**Keywords:** Bergmann's rule, community interactions, food-web structure, life history, metabolic theory of ecology, niche theory, predator-prey size ratio, size distributions, temperature-size rule, thermal reaction norms

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## Introduction

Bergmann's rule (BR) posits that heat loss of an endotherm organism is proportional to its surface-to-volume ratio. Because body volume increases faster than body surface area with increasing body size, there is a selective advantage to a small body size (higher body surface-to-volume ratio and easy heat loss) in warm areas, and conversely to a large body size in colder climates (lower body surface-to-volume ratio and reduced heat loss). This thermodynamic argument inherent to BR is valid only for endotherms, but surprisingly ectotherms also develop smaller body sizes in warmer climates (Angilletta, 2009), a trend dubbed the temperature-size rule (TSR). The TSR suggests that BR might not provide the unique mechanism controlling thermal clines in endotherm body size. In addition, unlike for BR, we are still lacking universal proximate or ultimate mechanisms for the TSR in ectotherms (Angilletta, 2009; Ohlberger, 2013). These gaps in our knowledge impede a proper understanding of how warming impacts natural communities.

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Metabolic theory and experiments (Petchey *et al.*, 1999; Voigt *et al.*, 2003; O'Connor *et al.*, 2009; Rall *et al.*, 2010; Yvon-Durocher *et al.*, 2010; Vucic-Pestic *et al.*, 2011; Reuman *et al.*, 2013) predict that warming elevates consumer metabolism and food intake faster than primary production, so that resource biomass decreases and competition for resources is reinforced among consumers. In parallel, net energy gain (energy intake rate minus maintenance rate) increases faster with temperature for small consumers, which thus have a competitive advantage under warm conditions (Vasseur & McCann, 2005; Ohlberger *et al.*, 2011). This prediction has been derived independently by Ohlberger *et al.* (2011) using a perch (*Perca fluviatilis*)-specific physiological model, and (although less explicitly) by Vasseur & McCann (2005) using Arrhenius kinetics, suggesting that the pattern is robust (see Data S1 and Fig. S1). Hence, theory predicts that warming should favor a competition-induced selection for smaller body sizes. Metabolic theory also leads to predictions regarding the effects of temperature on predatory interactions. In a Holling type II functional response, warming should activate attack rate and decrease handling time (manipulation and digestion) by predators (Englund *et al.*, 2011; Vucic-Pestic *et al.*, 2011), thus resulting in

elevated predation rates on prey. Yet, if predators are non-size-selective or selectively target large prey, increased predation selects for earlier maturation at a smaller size in prey (Roff, 1992). Therefore, we predicted that warming-induced body downsizing should reflect an ecological shift in size-selective pressures from both competitors and predators toward favoring smaller body sizes. Importantly, these predictions are based on primary metabolic and ecological rules that apply virtually to all life forms including both endotherms and ectotherms (Brown *et al.*, 2004). However, ectotherms are better suited to test our predictions because they experience a wider range of body temperatures. Here, we empirically tested the prediction using long-term body size data on river fish communities in France (29 years, 52 species,  $n = 4.15 \times 10^6$  individual body sizes, see Table S1).

Specifically, we based our approach to computing the strengths of competition and predation experienced by each individual fish on size-dependent niche theory (MacArthur & Levins, 1967). Then, we used statistical models to examine how temperature, competition (both intra- and interspecific), and predation interact on fish community body size, while accounting for multiple confounding effects of other abiotic covariates that affect habitat structure and productivity. We predicted that warming-induced body downsizing should emerge through both 'direct' (ecology-independent) and 'indirect' (ecology-mediated) effects of temperature. Direct effects should reflect thermal constraints on physiology and development as they appear in the TSR literature (Angilletta, 2009), in particular a limitation of oxygen diffusion path length at a large size as oxygen concentration becomes limited by higher temperatures (Pörtner *et al.*, 2008; Forster *et al.*, 2012), and/or an accelerated maturation due to a higher thermal sensitivity of gonad growth over soma growth (van der Have & De Jong, 1996; Zuo *et al.*, 2012). In turn, ecology-mediated effects of temperature on body size should emerge through shifts in competition- and predation-induced selection on body size. Our results support the view that both mechanisms are at work, but that ecology provides the overwhelming forces driving warming-induced thermal clines in fish body size.

## Materials and methods

Tests of BR and the TSR using multispecies data have been subject to criticism (Meiri & Thomas, 2007). The main problems arise from (i) averaging body sizes across large spatial scales, which artificially erases ecological noise; (ii) failure to account for the effect of species richness; and (iii) nonconsideration for the phylogenetic variability in body size. Here, we paid particular attention to avoid these pitfalls: (i) we used as

a response variable individual body length at a given sampling event, and spatial averaging is thus absent from our design; (ii) we included species richness as a predictor variable for body size in our model; and (iii) we allowed for a random, hierarchical taxonomic structure of body sizes in our model.

## The data

Our data set was extracted from the fish database of the French Office of Water and Aquatic Ecosystems (ONEMA). Fish were sampled from 1980 to 2008 during 20 602 sampling operations at 7024 sampling stations distributed among eight basins (North, Seine River, Channel Sea, Atlantic Ocean, Loire River, Garonne River, Rhône River, Mediterranean Sea) (Oberdorff *et al.*, 2002). Fish were caught by electric fishing using different methods (walking, by boat, mixed) and strategies Complete: whole station surface fully sampled; Ambiance: whole station surface partially sampled; Points: adapted from the Point Abundance Sampling method (Nelva *et al.*, 1979); Bank: only river banks were sampled; Other: other partial sampling strategies depending on river width and depth. Captured fish were counted, measured for total body length and returned to the river. If fish were too numerous, only a fraction of the catch was measured. Here, we excluded migratory species with a saltwater growth period, yielding  $n = 4\,145\,234$  individual body size measurements log-normally distributed among 52 species (Table S1).

Environmental variables were also recorded at each sampling station: river slope, depth, channel width (at upper banks), altitude, distance to the sea, distance to the source, and anthropogenic usage of the watershed (Corine Land Cover data). Air and water temperatures are highly correlated in rivers (Caissie, 2006), and we used air temperature that preceded each sampling operation as a proxy for river water temperature. The French meteorological services (Meteo France) provided us monthly temperature averages at 1085 meteorological stations spread across France for the 1978–2008 period. We interpolated corresponding monthly temperature averages at each of our fish sampling stations using thin plate regression splines of longitude and latitude, plus a spline effect of station altitude in the *mgcv* library of R (Wood, 2006). This approach yielded 348 models (one for each month) which provided a very good fit to the temperature data (mean  $\pm$  SD of deviance explained =  $0.94 \pm 0.02$ ). Fish sampling stations where latitude or longitude was beyond the range of latitudes and longitudes of the meteorological stations were removed from the analysis to avoid interpolation.

## Competition and predation

We based our estimation of the strengths of competition and predation experienced by individual fish on niche theory (see Data S1 and Fig. S2 for a full development). Briefly, body size correlates with individual prey size and type, ingestion rate, energy requirements, home range, and encounter rates (Woodward *et al.*, 2005), and a multidimensional resource-utilization niche may thus be collapsed onto one single body size axis where size distribution

defines the ecological niche (MacArthur & Levins, 1967). In this size-dependent niche theory, niche overlap and the strength of interactions are maximum at a given body size ratio between interactors. This ratio is equal to 1 (i.e. equal sizes) for competitors (MacArthur & Levins, 1967) and to 100 in body mass or 4.6 in body length for predators [predator/prey size (Brose *et al.*, 2006a)]. Hence, we defined the strength of competition experienced by a focal individual *i* from a competitor individual *j* as the lognormal (as in our data) probability density distribution:

$$f(L_j, l_i, \sigma^2) = \frac{1}{L_j \sqrt{2\pi\sigma^2}} e^{-\frac{(\ln(L_j) - l_i + \sigma^2)^2}{2\sigma^2}}, \quad (1)$$

where  $L_j$  is body length of the competitor individual *j*,  $l_i$  is the log-transformed body length of the focal individual *i*, and in which competition strength is maximal when  $\ln(L_j) = l_i + \sigma^2$  is the variance of log-transformed body lengths for the focal species, which we took as an approximation of niche breadth. We provide in Fig. 1a an illustration of the resultant probability density distribution for competitors of a 116 mm focal roach (*Rutilus rutilus*). We then computed the

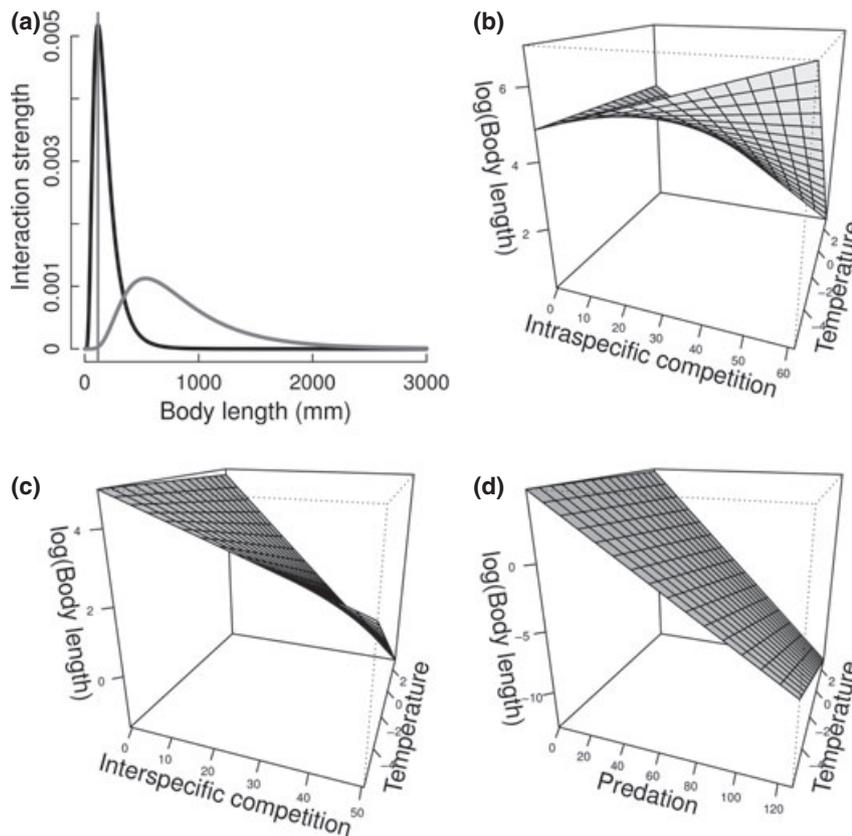
strength of competition *C* experienced by each focal individual *i* as

$$C = \sum_{j=1}^n f(L_j, l_i, \sigma^2), \quad (2)$$

where *n* is the number of nonfocal individuals *j* for the sampling operation. We computed separately intraspecific competition ( $C_{intra}$ ) for *js* as nonfocal conspecifics, and interspecific competition ( $C_{inter}$ ) for *js* as heterospecifics. Following a similar rationale, we modeled the log-normal size distribution of predators *j* as  $g(L_j, l_i, \sigma^2)$ :

$$g(L_j, l_i, \sigma^2) = \frac{1}{L_j \sqrt{2\pi\sigma^2}} e^{-\frac{(\ln(L_j) - l_i + \ln(4.6) + \sigma^2)^2}{2\sigma^2}}, \quad (3)$$

in which the strength of predation is maximal when  $\ln(L_j) = l_i + \ln(4.6)$ . We illustrate the resultant predator size distribution in Fig. 1a for the same focal roach individual as above. We then computed the strength of predation *P* experienced by each focal individual *i* as follows:



**Fig. 1** Interactions between temperature and ecology on fish community body size. (a) An illustration of theoretical (Eqns 1 and 3) interaction strengths from competitors (black curve) and predators (gray curve) of varying body lengths on a 116 mm roach *Rutilus rutilus* (vertical gray line, see Materials and methods). (b–d) Surface plots for the interaction of temperature with (b) intraspecific competition, (c) interspecific competition, and (d) predation on fish community body size. The surfaces were predicted from the fixed effects in Eqn (6) and parameter estimates in Table 1, by letting focal variables vary from their minimum to their maximum value while fixing other variables to their mean value. Predictor variables were centered on 0 mean and scaled to unity standard deviation.

**Table 1** Thermal and ecological effects on fish community body length. Restricted maximum likelihood (REML) and pseudo-Markov chain Monte Carlo (MCMC) parameter estimates and their statistical significance for the fixed effects in Eqn (6). MCMC *P*-values correspond to twice the proportion of iterations in which the posterior distribution was positive (if posterior mode was negative) or negative (if posterior mode was positive) during 10 000 iterations.  $\Delta$ AIC indicates the change in model's Akaike's information criterion due to dropping the focal term from Eqn (6)

Predictor	Coefficient	Estimate		SE of the estimate		<i>T</i> -value	MCMC <i>P</i> -value	$\Delta$ AIC
		REML	MCMC	REML	MCMC			
Intercept	$\beta_0$	4.74E + 00	4.74E + 00	7.49E-02	7.07E-02	6.32E + 01	<0.0001	
<i>W</i>	$\beta_1$	-1.71E-02	-1.67E-02	1.09E-03	1.08E-03	-1.57E + 01	<0.0001	232
<i>S</i>	$\beta_2$	-1.07E-02	-1.11E-02	1.59E-03	1.41E-03	-6.70E + 00	<0.0001	31
<i>Spr</i>	$\beta_3$	3.27E-02	-3.29E-02	7.02E-04	7.03E-04	4.67E + 01	<0.0001	2160
<i>T</i>	$\beta_4$	-2.66E-02	-2.70E-02	1.83E-03	1.68E-03	-1.45E + 01	<0.0001	196
<i>C</i> <sub>intra</sub>	$\beta_5$	-3.80E-02	-3.79E-02	2.56E-04	2.52E-04	-1.49E + 02	<0.0001	21 974
<i>C</i> <sub>inter</sub>	$\beta_6$	-9.78E-02	-9.78E-02	2.82E-04	2.75E-04	-3.47E + 02	<0.0001	118 862
<i>P</i>	$\beta_7$	-1.23E-01	-1.23E-01	2.61E-04	2.42E-04	-4.72E + 02	<0.0001	217 099
<i>C</i> <sub>intra</sub> * <i>T</i>	$\beta_8$	-1.22E-02	-1.22E-02	2.72E-04	2.72E-04	-4.47E + 01	<0.0001	1985
<i>C</i> <sub>inter</sub> * <i>T</i>	$\beta_9$	-8.80E-03	-8.81E-03	3.29E-04	3.31E-04	-2.68E + 01	<0.0001	701
<i>P</i> * <i>T</i>	$\beta_{10}$	-5.58E-03	-5.41E-03	2.66E-04	3.57E-04	-2.10E + 01	<0.0001	425

$$P = \sum_{j=1}^n \Phi_j g(L_j, l_i, \sigma^2), \quad (4)$$

where *n* is the number of heterospecific individuals encountered and  $\Phi_j$  is the piscivory probability of species *j* defined as  $\Phi = 0$  for no piscivory,  $\Phi = 0.5$  for occasional piscivory, and  $\Phi = 1$  for piscivory, based on diet data from Fishbase (<http://www.fishbase.org/>, see Table S1). *C*<sub>intra</sub>, *C*<sub>inter</sub> and *P* are all expressed in weighted number of individuals, which provided a much better model fit than weighed densities (from either sampled surface area or sampled water volume).

### Statistical modeling

Our response variable was mean species body length at a given sampling event, log-transformed to normalize its distribution. We aimed at exploring the direct and interactive effects of temperature, competition and predation on fish body sizes, while controlling for the confounding effects due to other abiotic covariates affecting habitat structure and productivity, and due to nonindependence of observations arising from phylogeny, sampling ('Method', 'Strategy'), space ('Basin', 'Station'), and time ('Year'). In this context, we chose to analyze thermal and ecological effects on fish body size using mixed effects models:

$$y = X\beta + Zb + \epsilon, \quad (5)$$

where *y* is our response vector,  $\beta$  is a vector of fixed effects, *b* is a vector of normally distributed random effects, *X* and *Z* are the corresponding regressor matrices, and  $\epsilon$  is a vector of within-group, normally distributed and independent errors. To build the  $\beta$  vector of fixed effects, we first examined the contribution of the above-listed abiotic factors (see Data) to fish body size using binary recursive partitioning ('tree' function in R, Venables & Ripley, 2002). This nonparametric

method grows a regression (or decision) tree based on recursively partitioning the variance of a response variable as a function of predictor variables. We found that the most informative abiotic predictors (appearing near the root of the tree) to be included into the  $\beta$  vector were channel width (*W*), river slope (*S*), and the interpolated air temperature averaged across the 24 months that preceded sampling (*T*, ranged from 2.2 to 16.7 °C, mean = 11.8 °C, SD = 1.6 °C, which integrates thermal variation in both space and time). Averaging across 24 months provided a slightly better model fit than averaging across 12 months. We also included the following biotic variables: intraspecific competition *C*<sub>intra</sub>, interspecific competition *C*<sub>inter</sub> and predation *P* in the  $\beta$  vector which became the following:

$$\beta = \beta_0 + \beta_1 W + \beta_2 S + \beta_3 Spr + \beta_4 T + \beta_5 C_{intra} + \beta_6 C_{inter} + \beta_7 P + \beta_8 C_{intra} \times T + \beta_9 C_{inter} \times T + \beta_{10} P \times T, \quad (6)$$

where *Spr* is species richness at a given sampling operation (ranged from 1 to 27 species, mean  $\pm$  SD = 9.6  $\pm$  5.2; N.B. all fish body sizes measured during the same sampling event were assigned the same *Spr*). All predictor variables included in the  $\beta$  vector were standardized (zero mean and unity standard deviation) to avoid spurious scale effects. In Eq. 6, the *T* term captured direct, ecology-independent effects of temperature on body size, while ecology  $\times$  *T* terms captured indirect, ecology-mediated effects of temperature on body size. Second, we built our random effects vector *b* to account for the nonindependence structure in our data:

$$b = b_{\text{Phylum|Order|Spec}} + b_{\text{Str|Met}} + b_{\text{St|Bas}} + b_Y, \quad (7)$$

where 'l' means 'nested in', Phylum = either Agnatha, Clupeocephala, or Elopomorpha, Order = taxonomic order, Spec = species identity, Str = sampling strategy, Met = sampling method, St = sampling station, Bas = river basin, and *Y* = year. We did not include a taxonomic family effect

because it did not explain any variance beyond the *Order* effect. Taxonomy was established based on information from the US National Center for Biotechnology Information (<http://www.ncbi.nlm.nih.gov/taxonomy>). We ran our model in the lme4 library of R (Bates, 2005; R Development Core Team, 2012), which estimates parameters using restricted maximum likelihood (REML). lme4 also uses pseudo-Bayesian (Markov chain Monte Carlo, MCMC), post hoc sampling starting from REML estimates to compute MCMC parameters and p-values (from flat priors, 10 000 iterations after a burnin of 3000 iterations.). We further computed each model's Akaike's information criterion (AIC) =  $-2 \times \log\text{-likelihood} + 2 \times \text{npar}$  (where npar represents the number of parameters in the fitted model), as well as AIC change ( $\Delta\text{AIC}$ ) from the full model's AIC (4 794 987) when each fixed effect term was dropped separately from Eqn (6). This way, it is possible to evaluate the respective contributions of each fixed effect term to model's fit and parsimony. Note that removing any term from Eqn (6) increased model's AIC (Table 1), indicating that all fixed effect terms contributed to increase model's parsimony. Finally, we computed a pseudo- $R^2$  for the full model by regressing the response on model's fitted values, which yielded pseudo- $R^2 = 0.57$ .

## Results

In line with the TSR literature reporting direct thermal constraints on physiology and development, we found that increased temperatures had a direct, negative effect on fish community body size across any level of competition or predation (Table 1, Fig. 1b–d). However, this direct effect was apparent mainly under medium to high strengths of ecological interactions (Fig. 1b–d). Removing the direct effect of temperature from the full model induced a large increase in model's AIC ( $\Delta\text{AIC} = 196$ , Table 1), indicating that this direct thermal effect was influential.

However, far more influential were the effects of competition and predation. Increased strengths of intraspecific and interspecific competition both favored smaller body sizes (Table 1), supporting the view that resources are limiting for body growth in river fish. Increased strength of predation also favored smaller prey sizes (Table 1), in line with predictions from life-history theory in which increased mortality from predation favors earlier maturation at a smaller body size in prey. Predation had the largest contribution to variation in fish body size ( $\Delta\text{AIC} = 217\ 099$ ), followed by interspecific competition ( $\Delta\text{AIC} = 118\ 862$ ) and intraspecific competition ( $\Delta\text{AIC} = 21\ 974$ ).

In line with our hypotheses on the ecological emergence of thermal clines in body size, we found that temperature and ecology significantly interacted on fish community body size. Importantly, the strength of ecology-mediated effects of temperature on fish body sizes overwhelmed the strength of direct thermal effects.

Specifically, increased temperature reinforced the negative effects of competition and predation on body sizes. This thermal magnification was particularly sharp for intraspecific competition ( $\Delta\text{AIC} = 1985$ ), which shifted from having a positive to negative effect on fish body sizes (Fig. 1b). Temperature also strongly reinforced the negative effects of interspecific competition ( $\Delta\text{AIC} = 701$ , Table 1, Fig. 1c) and predation ( $\Delta\text{AIC} = 425$ , Table 1, Fig. 1d) on fish body size. Totally removing temperature  $\times$  ecology interactions from the full model incurred a  $\Delta\text{AIC} = 5310$  (not shown in Table 1). Finally, a corollary of these temperature  $\times$  ecology interactions in a linear framework is that increased intensity of competition and predation magnified the negative effect of temperature on fish body sizes (increasingly negative slope of the temperature effect in Fig. 1b–d).

## Discussion

Our results highlight that ecology is crucial in driving thermal clines in fish body size. This is in sharp contrast with the current mechanisms proposed to explain BR and the TSR, which in their vast majority revolve around direct physiological constraints on individual homeostasis and development rates (van der Have & De Jong, 1996; Pörtner *et al.*, 2008; Angilletta, 2009; Forster *et al.*, 2012; Zuo *et al.*, 2012). Our results show that such direct physiological constraints are indeed at work, but are in fact not prominent in driving thermal clines in fish body size. Instead, as indicated by the  $\Delta\text{AICs}$ , the TSR in fish mainly emerged indirectly through a warming-induced magnification of the effects of competition and predation. In turn, the negative, apparently direct effect of temperature on fish body sizes was mainly present under medium to high strengths of ecological interaction (Fig. 1a–c), stressing that studies of BR and the TSR should not ignore ecology in their designs.

A major mechanism underlying the ecological emergence of thermal clines in body sizes involves a magnification of competitive asymmetry in favor of smaller individuals under warmer conditions. This result has been previously predicted theoretically from a physiologically structured population model for perch (Ohlberger *et al.*, 2011), and we show in the Supporting Information that a similar prediction may be independently derived from the metabolic theory of ecology (Vasseur & McCann, 2005). To our knowledge, our study is the first empirical validation of this theoretical prediction. Interestingly, we found that intraspecific competition slightly favored large fish at low temperature, in agreement with predictions from metabolic theory in which large fish starve less fast at low temperatures when there exists an 'ecological' (or

resource) limitation for ingestion (Fig. S1a). In contrast, interspecific competition favored smaller fish across all temperatures, in agreement with predictions when there is a 'physiological' limitation for ingestion (ingestion is at its physiological maximum, Fig. S1c). Hence, our results might suggest that resources are more limiting in intraspecific competition and physiology is more limiting in interspecific competition. In parallel with its effects on competition, warming also amplified a strongly negative effect of predation on body sizes. Predators select for earlier maturation at a smaller size in prey when they are either non-size-selective or when they selectively target adult prey (Roff, 1992). A thermal magnification of this effect was expected because higher temperatures activate metabolic rates (Brown *et al.*, 2004), including attack rate and digestion by predators (Englund *et al.*, 2011; Vucic-Pestic *et al.*, 2011), thus resulting in elevated predation rates on prey. In summary, our empirical results perfectly validate predictions from universal laws of ecology and metabolism, and an ecological emergence of thermal clines in body size should thus occur in virtually all life forms. Accordingly, a number of studies suggest that our results should also hold (at least in part) in aquatic microorganisms (Petchey *et al.*, 1999), marine and freshwater plankton (O'Connor *et al.*, 2009; Yvon-Durocher *et al.*, 2010), fish (Ohlberger *et al.*, 2011), and terrestrial arthropods (Voigt *et al.*, 2003; Vucic-Pestic *et al.*, 2011).

If the magnitude of warming-induced body downsizing depends on the strengths of competition and predation in the community, in turn warming-induced body downsizing is likely to alter ecological dynamics in predictable ways. Body downsizing will likely induce a general destabilization of population and community dynamics. Indeed, smaller sizes reflect an earlier maturation (decreased generation time), younger age structure in the population, and increased population growth rate ( $r$ ) (Savage *et al.*, 2004; Daufresne *et al.*, 2009; Ohlberger *et al.*, 2011). Yet, an elevated  $r$  favors dynamic instability in populations following logistic growth (May, 1975), and younger populations have a lower ability to dampen the effects of environmental fluctuations (Hidalgo *et al.*, 2011). In size-structured populations, thermal magnification of competition and resultant body downsizing also tend to shift the dynamics from a fixed point toward cohort cycles (Ohlberger *et al.*, 2011). This dynamic destabilization arises because newborns deplete resources down to a level where adults cannot meet their maintenance requirements and starve to death (Persson *et al.*, 1998). At the food-chain level, increased competition due to warming is predicted to decrease consumer numbers and amplify consumer-resource limit cycles, thus increasing the effect of demographic stochasticity and

the extinction probability of top consumers (Petchey *et al.*, 1999; Voigt *et al.*, 2003; Vasseur & McCann, 2005; Arim *et al.*, 2007; Vucic-Pestic *et al.*, 2011). Finally, independent of warming, body downsizing (and reduced breadth of body size distributions in communities) is predicted to also destabilize more complex food webs (Brose *et al.*, 2006b; Heckmann *et al.*, 2012) and to trigger competitive exclusion at the base of the communities (Brose, 2008). Therefore, warmer ecosystems might be more prone to abrupt changes.

Over the longer term, increased extinction probability of top consumers under warmer conditions should further reinforce the strength of competition in ecosystems, because predators decrease density-dependent competition in their prey (De Roos *et al.*, 2008). Hence, there might be a runaway feedback driven by warming, where increased competition favors predator extinction, which in turn increases competition and top predator extinction. In such a runaway feedback, selection against a large body size will be reinforced and warming-induced body downsizing (i.e., BR and the TSR) will become increasingly apparent. In parallel, whole community architecture will likely be disrupted. Loss of top predators in food webs will tend to reduce vertical diversity and increased competition should elevate horizontal diversity. In particular, increased intensity of competition is predicted to result in less distinct trophic levels, higher species diversity, and increased food-web connectance and omnivory (Loeuille & Loreau, 2005), all of which are characteristic of tropical food webs relative to temperate food webs (Sala & Sugihara, 2005; Vander Zanden & Fetzer, 2007; Coat *et al.*, 2009). Hence, after an initial dynamic destabilization, warming and body downsizing should drive the architecture of temperate food webs toward structures more consistent with the tropics.

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### Author contribution

Eric Edeline, Gérard Lacroix and Stéphane Legendre designed the study, Nicolas Poulet provided the fish data, Christine Delire helped with the meteorological data, Eric Edeline analyzed the data and wrote the first draft of the manuscript, and all authors contributed to revisions.

## Conflicts of interest

The authors declare no competing financial interests.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Data S1.** The theory of temperature-dependent allometric scaling of net energy gain.

**Data S2.** The theory of log-normal distributions for size-dependent niches.

**Table S1.** Fish species included in our analysis.