



Testing the heat-invariant and cold-variability tolerance hypotheses across geographic gradients



Francisco Bozinovic^{*}, María J.M. Orellana, Sebastián I. Martel, José M. Bogdanovich

Departamento de Ecología, Facultad de Ciencias Biológicas, Universidad Católica de Chile, Santiago 6513677, Chile

Center of Applied Ecology and Sustainability (CAPES), Facultad de Ciencias Biológicas, Universidad Católica de Chile, Santiago 6513677, Chile

ARTICLE INFO

Article history:

Received 11 July 2014

Received in revised form 13 August 2014

Accepted 13 August 2014

Available online 23 August 2014

Keywords:

Macrophysiology

Geographic ranges

Terrestrial isopods

Heat and cold-tolerances

Invariant thermal traits

Climate change

ABSTRACT

Changes in temperature across geographic gradients can occur on a wide temporal range, from fluctuations within hours as a result of day–night to those over many years. These events will drive many organisms towards their physiological limits of thermal tolerance. Recently, many reports support a limited scope for adaptive evolutionary responses to high temperatures, meaning a conserved heat tolerance among ectotherms in general. We address this problem and tested the heat and cold tolerance invariant–variant hypotheses in terrestrial isopods. We studied five different populations of *Porcellio laevis* and three populations of *Porcellio scaber*, spanning 30° S latitudinal gradient in Chile. The heat tolerance of woodlice was conserved with little variation along latitude and environmental temperatures, but cold tolerance decreases significantly with environmental temperatures and latitudes. Indeed, a significant and negative correlation was observed between cold tolerance and latitude. Also, significant and positive correlations were observed among cold tolerance and environmental temperatures. Conversely, heat tolerance was not significantly correlated with any of the environmental temperatures tested neither with latitude. This macrophysiological pattern indicated that heat and cold-tolerances of species and populations not always change across geographical gradients meaning that thermal tolerance responses to high temperatures may be evolutionary constrained.

© 2014 Elsevier Inc. All rights reserved.

1. Introduction

Over the past decade many climate-based hypotheses regarding variation in distribution range of species and populations have emerged (Pither, 2003). These hypotheses use data of physiological traits and environmental temperature (Spicer and Gaston, 1999) and, since temperature imposes geographic limits, both are key factors explaining the range and limits of distribution (Bozinovic et al., 2011a). Indeed, temperature is a critically important environmental factor for ectothermal organisms because of the direct effects of temperature on all biological processes underpinning the ecological and evolutionary success of species and populations across latitude and altitude (Pörtner et al., 2006). Thermal conditions vary over space and time, and thus populations and species are continually challenged to maintain homeostasis. Individuals are expected to evolve physiological adaptations, physiological tolerances, and acclimatization to local conditions in different and likely heterogeneous environments along geographic ranges. Accordingly, thermoregulatory constraints often have been invoked to explain animal distributions (e.g. Brattstrom, 1968; Root, 1988; Van Berkum, 1988; Bozinovic and Rosenmann, 1989; Hoffman and Watson,

1993; Addo-Bediako et al., 2000; Canterbury, 2002; Humphries et al., 2002; Rezende et al., 2004; Rodriguez-Serrano and Bozinovic, 2009; Swanson and Bozinovic, 2011; Naya and Bozinovic, 2012).

Changes in temperature across latitude and altitude can occur on a wide temporal range, from fluctuations within hours as a result of day–night or tidal cycles to those over many years as a result of global climate change (Pörtner et al., 2006). Indeed, the fifth assessment report (AR5) by the IPCC 2013 (www.ipcc.ch) indicates a trend towards increasing global temperatures and variability that is evident, yet not similar, in all continents. These events will drive many organisms towards their physiological upper limits of thermal tolerance, with potential negative impact on fitness (Finke et al., 2009; Clavijo-Baquet et al., 2014). Thus, understanding the nature of differential effects of global warming on biodiversity — from genes to ecosystems — is one of the many urgent challenges faced by contemporary science (Deutsch et al., 2008; Pörtner and Farrell, 2008). In this vein, recently, Araújo et al. (2013) tested if ectotherms, endotherms and plant species physiologically adapt their thermal tolerances to climate warming. These authors observed that tolerance to heat is largely invariant across lineages, but tolerance to cold varies. Sunday et al. (2014) also show that heat tolerance in terrestrial ectotherms is relatively invariant in comparison with cold limits. Besides, Schou et al. (2014) demonstrated a lack of increased heat resistance in replicate population of *Drosophila* exposed to augmented temperatures over time. All the above allow us

^{*} Corresponding author at: Departamento de Ecología, CAPES, Pontificia Universidad Católica de Chile, Santiago 6513677, Chile. Tel.: +56 2 354 2618.

E-mail address: fbozinovic@bio.puc.cl (F. Bozinovic).

to propose the heat and cold tolerance invariant/variant hypotheses, which is, a conserved heat tolerance and a geographically variant cold tolerance among ectotherms in general (see also Addo-Bediako et al., 2000; Boher et al., 2010).

In this article we address these previous issues but at an altitudinal and latitudinal geographic range. We study the physiological responses (if any) in both cold and heat limits of tolerance respectively among populations and species of terrestrial isopods along different geographic and climatic localities (Fig. 1). We tested the heat and cold tolerance invariant/variant hypotheses in individuals from five different populations of *Porcellio laevis* and three populations of *Porcellio scaber*, spanning 30° S latitudinal gradient in Chile — including one of the southernmost populations of terrestrial isopods in the world (the common rough woodlouse *P. scaber*) — and from sea level to 1200 m above sea level (Fig. 1). Terrestrial isopods are good models to test hypotheses in spatial evolutionary ecology because they exhibit a broad distribution and must cope with extreme and variable abiotic conditions (Schultz, 1961, 1972; Miller and Cameron, 1987; Helden and Hassall, 1998). Particularly, species of the genus *Porcellio* are cosmopolitan and show plasticity in many traits in response to different environmental conditions (Warburg et al., 2001; Lardies and Bozinovic, 2006, 2008).

2. Materials and methods

2.1. Animals and environment

We collected individuals of *P. scaber* from three populations in a latitudinal gradient along Chile, namely Punta de Tralca ($n = 90$, 33°25'S; 71°41'W at 13 m above sea level), Puerto Montt ($n = 34$, 41°25'S; 73°05'W at 85 m above sea level) and Punta Arenas ($n = 171$, 53°00'S; 70°51'W at 37 m above sea level), see Table 1. Data of *P. laevis* were obtained from our previous studies (Castañeda et al.,

2004; Folguera et al., 2009). Localities for *P. laevis* were Antofagasta (23°38'S; 70°26'W at 125 m above sea level), La Serena (29°55'S; 71°15'W at 142 m above sea level), Santiago (33°23'S; 70°42'W at 520 m above sea level), San Carlos de Apoquindo (33°23'S; 70°31'W at 1230 m above sea level) and Viña del Mar (33°01'S; 71°32'W at 176 m above sea level). These data allow us to expand the latitudinal cline.

Environmental variables at each locality were obtained from the web site (<http://www.atmosfera.cl/HTML/climatologia/DATOS/DATOS.HTM>), being: latitude (Lat in °S), altitude (Alt in m above sea level), mean annual rainfall (Pp in mm), and the following annual ambient temperatures (mean = $T_{a\text{mean}}$; maximum = $T_{a\text{max}}$ and minimum = $T_{a\text{min}}$ in °C). All collected individuals from each population were placed in plastic containers and transferred to the laboratory. Animals were acclimated for three weeks at 22 ± 1 °C, a photoperiod 12 L:12D, and fed ad libitum with dry spinach. They were kept in plastic cages with a wet layer of plaster of paris covering the bottom of each cage, which is a good material to maintain moisture and obtain calcium (Lardies et al., 2004).

2.2. Experimental test

To test our hypothesis and calculate the critical thermal maxima (CT_{max}) and the critical thermal minima (CT_{min}), we followed the method proposed by Castañeda et al. (2004) and measured the righting response speed as an index of performance. The righting response speed (i.e. the speed for an individual to change from an inverse position to an upright position) is a common measure of the thermal sensitivity to ambient temperatures (Folguera et al., 2009). We placed a maximum of ten individuals at temperatures ranging from -3 °C to 39 °C, in plastic tubes of 3 mL which allowed us to separate each individual, and the mean value of CT_{min} and CT_{max} was calculated. Nevertheless, because

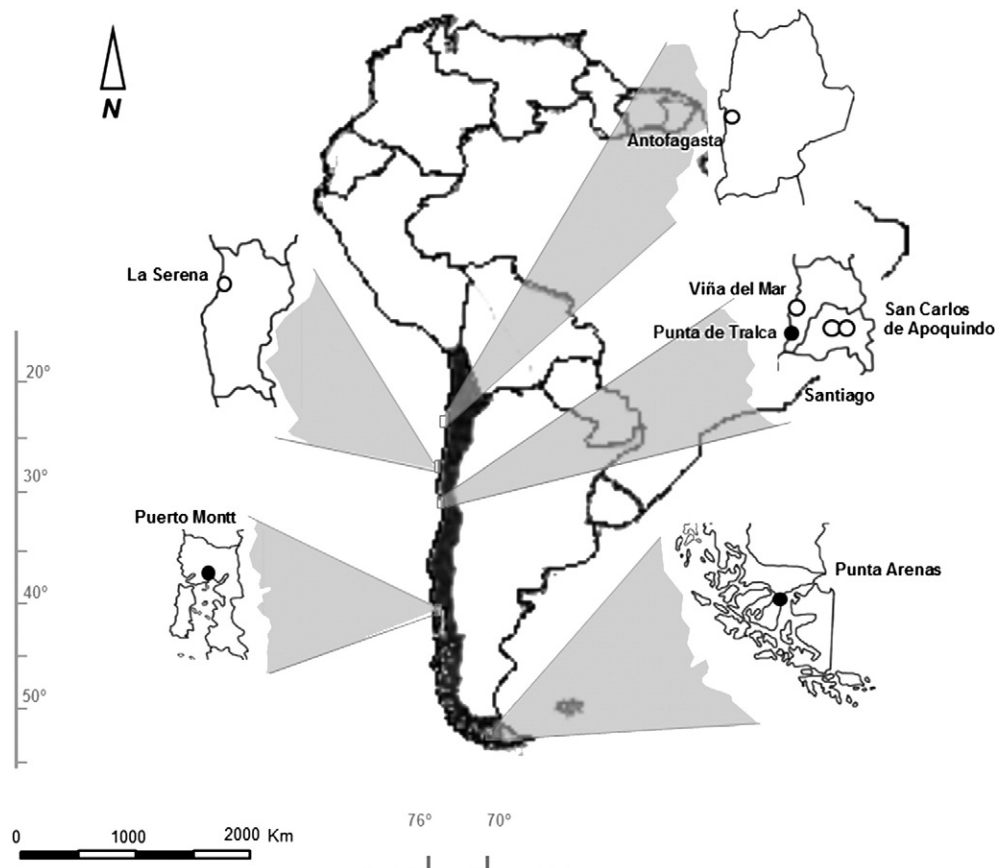


Fig. 1. Geographic localities of studied species and populations of *Porcellio laevis* (white circles) and *Porcellio scaber* (black circles) in Chile.

Table 1
Environmental conditions of species and populations of the terrestrial isopod *Porcellio laevis* and *Porcellio scaber* across geographic gradients in Chile. Latitude (*Lat*) in °S, altitude (*Alt*) in m above sea level, mean annual rainfall (*Pp*) in mm, and annual ambient temperatures (mean = $T_{a\text{mean}}$; maximum = $T_{a\text{max}}$ and minimum = $T_{a\text{min}}$) in °C.

Species/locality	Climate*	<i>Lat</i>	<i>Alt</i>	<i>Pp</i>	$T_{a\text{mean}}$	$T_{a\text{max}}$	$T_{a\text{min}}$
<i>Porcellio laevis</i>							
Antofagasta	Coastal desert	23.5	135	1.7	16.4	20.1	13.7
La Serena	Coastal semiarid	29.9	142	78.5	13.6	18.2	9.3
Santiago	Central Mediterranean	33.4	520	312.5	14.4	22.5	8.3
San Carlos de Apoquindo	Subandean Mediterranean	33.4	1,230	376.4	15.9	22.6	9.6
Viña del Mar	Coastal Mediterranean	33.0	41	372.5	14.0	17.5	11.2
<i>Porcellio scaber</i>							
Punta de Tralca	Coastal Mediterranean	33.5	13	48.0	16.3	21.3	11.3
Puerto Montt	Wet coastal temperate	41.4	85	1802.5	10.1	14.9	6.4
Punta Arenas	Cold steppe	53.2	37	376.4	5.9	9.7	2.7

* Climatic data at: <http://www.atmosfera.cl/HTML/climatologia/DATOS/DATOS.HTM>.

of a lower sample size, three to five animals from Puerto Montt were tested at each temperature. Tubes were located inside a water bath with antifreeze (Daihan Labtech Co.) at each experimental temperature, which was held constant (± 0.2 °C). After 30 min each woodlouse was placed at room temperature (22 ± 1 °C), and righting response speed was measured for a period of 10 min. Animals that died or exceeded 10 min until recovery were excluded. We used each woodlouse for just one temperature. Body mass (m_b) was measured prior to all experimental proceedings in an analytical balance (CHYO JK-180, precision ± 0.01 mg).

2.3. Data analysis

Data of CT_{max} and CT_{min} were calculated from the relationships between ambient temperature and time (righting response) by adjusting the data to a polynomial function of second order using the software QTiPlot (www.qtiplot.com/index.html). The two solutions for $x = 0$ were used as estimators of thermal limits. As pointed out before and to expand the latitudinal geographic gradient of study, data of CT_{max} and CT_{min} of *P. laevis* were obtained from Castañeda et al. (2004) and Folguera et al. (2009), see Table 2, and recalculated through the same method. No significant differences between the patterns previously observed with *P. laevis* and those reported here observed. To test our hypothesis for the effect of environmental variables across the geographical gradient of species and populations on CT_{max} and CT_{min} we performed the most common measure of correlation, namely the Pearson Product Moment Correlation (PPMC) which is a measure of the strength of association between variables. All analyses were conducted using the statistical package Statistica® for Windows (StatSoft Inc., 2001).

3. Results

Values of m_b , CT_{max} and CT_{min} of *P. scaber* (this study) and *P. laevis* (our previous studies) are in Table 2. Mean CT_{max} was 39.6 ± 1.13 (SD) with variance = 1.3, whilst mean CT_{min} was 3.4 ± 2.22 (SD) with

Table 2
Mean body mass = m_b in mg, critical thermal maxima = CT_{max} in °C, and critical thermal minima = CT_{min} in °C of two species of terrestrial isopods from different populations along a geographical gradient in Chile.

Species/locality	m_b	CT_{max}	CT_{min}	Reference
<i>Porcellio laevis</i>				
Antofagasta	79	40.3	7.0	Castañeda et al. (2004)
La Serena	102	38.1	4.6	Castañeda et al. (2004)
Santiago	87	39.4	3.3	Castañeda et al. (2004)
San Carlos de Apoquindo	91	38.8	4.3	Folguera et al. (2009)
Viña del Mar	67	40.6	3.4	Folguera et al. (2009)
<i>Porcellio scaber</i>				
Punta de Tralca	50	40.1	3.3	This study
Puerto Montt	41	38.2	2.3	This study
Punta Arenas	55	41.1	-1.4	This study

variance = 4.9. Results of the PPMC test among physiological and environmental variables are in Table 3.

A significant and negative correlation was observed between CT_{min} and *Lat* (Table 3). Also, significant and positive correlations were observed among CT_{min} and $T_{a\text{mean}}$ and $T_{a\text{max}}$ and $T_{a\text{min}}$ (Fig. 2, Table 3). Conversely, CT_{max} was not significantly correlated with any of the environmental temperatures tested neither with *Lat* (Table 3, Fig. 2). Lastly, as expected, significant and negative correlations were observed among *Lat* and $T_{a\text{mean}}$ ($R = -0.914$, $P = 0.002$), $T_{a\text{max}}$ ($R = -0.797$, $P = 0.02$) and $T_{a\text{min}}$ ($R = -0.938$, $P < 0.001$).

4. Discussion

The key to the understanding of physiological responses to different environments is the analysis of mechanisms that cause variation in physiological traits, and the ecological and evolutionary consequences of this variation at different hierarchical levels (Spicer and Gaston, 1999). Constraints on this physiological diversity must be the (by-) product of complex interactions between specific physiological, phenological and ecological traits. Additionally, many of the primary traits may be phylogenetically conserved. Therefore the phylogenetic history must be included into any understanding and explanations of physiological limits (Bozinovic et al., 2011a).

Results here support the heat-tolerance invariant and cold-tolerance variant hypotheses at intra- as well as interspecific level in a geographic gradient. In other words, heat tolerance of ectothermic woodlice was conserved with little variation along latitude and environmental temperatures, but cold tolerance decreases significantly with environmental temperatures and latitudes and exhibited a large variability. Indeed, a 3.8 times increase in the variance of cold versus heat-tolerance was observed among woodlice species and populations. Interestingly, both heat and cold-tolerance limits were not correlated with altitude. However a note of caution is necessary here since more data of high altitude populations are necessary to confirm this finding. This macrophysiological pattern challenges the vision that physiological heat and cold-tolerances of species and populations always change across latitudinal and

Table 3
Results of the Pearson product moment correlation. Variables are: the critical thermal maxima, the critical thermal minima, body mass (m_b), latitude (*Lat*), altitude (*Alt*), mean annual rainfall (*Pp*), and annual ambient temperatures (mean = $T_{a\text{mean}}$; maximum = $T_{a\text{max}}$ and minimum = $T_{a\text{min}}$). *P*-values and correlation coefficient are indicated for each variable. Significant correlations are in bold.

	m_b	<i>Lat</i>	<i>Alt</i>	<i>Pp</i>	$T_{a\text{mean}}$	$T_{a\text{max}}$	$T_{a\text{min}}$
Critical thermal maxima							
<i>R</i>	-0.500	0.156	-0.571	-0.108	-0.186	-0.310	0.143
<i>P</i> -value	0.182	0.662	0.120	0.749	0.659	0.423	0.705
Critical thermal minima							
<i>R</i>	0.467	-0.978	0.223	-0.334	0.871	0.749	0.906
<i>P</i> -value	0.244	<0.001	0.596	0.419	<0.001	0.033	0.002

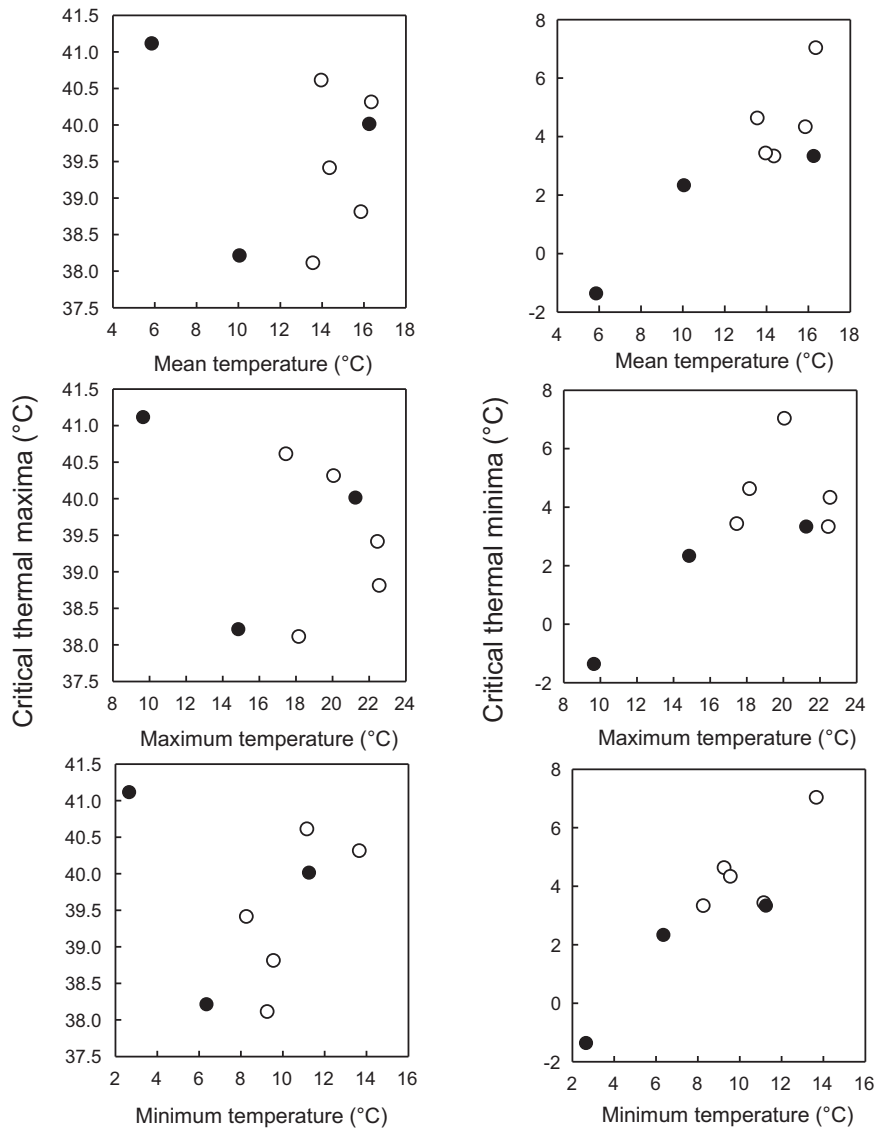


Fig. 2. Correlations between mean, maximum and minimum annual temperatures at each geographic locality and the critical thermal maxima and minima of *Porcellio laevis* (white circles) and *Porcellio scaber* (black circles) in Chile. Only the critical thermal minima were significantly correlated with annual temperatures (see text).

altitudinal geographical gradients (Araújo et al., 2013). Thus, species and populations with larger heat-tolerances do live in the warmest environments and also are found at colder high latitudes and altitudes. Finally and in agreement with recent studies, our results indicated that upper thermal limits of tolerance may be evolutionary constrained. This conclusion was experimentally confirmed recently by Schou et al. (2014) who, through a fruit-fly laboratory evolution experiment, demonstrated a limited scope for adaptive evolutionary responses in upper thermal limits (see also Gilchrist and Huey, 1999).

One consequence of invariance of heat tolerances is that estimated niches for cold-adapted species and populations will be likely to underestimate their heat-tolerance limits, so potentially enhancing estimations of risk from global warming (Araújo et al., 2013). On the contrary, species whose climatic preferences are close to their upper thermal limits will unlikely evolve physiological tolerances to increased global temperatures, and could be predictably more affected by global warming. In addition, recently Sunday et al. (2014) find among terrestrial ectotherms that they are not physiologically tolerant enough to high temperatures to survive and must behaviorally thermoregulate by using cover areas within their microhabitats. Interestingly, these authors find that that this phenomena can take place even at cold high-latitudes and altitudes. Previously, Boher et al. (2010) also assessed upper and lower lethal

temperature in *Drosophila* species. They used thermal limits to construct a thermal tolerance polygon that represents the total thermal range of each species after thermal acclimation. They observed that temperate species have broader thermal ranges than either tropical ones, but temperate species do not exhibit broader geographical range extensions. These authors also found that among studied *Drosophila*, upper lethal limits were more conserved than lower ones, supporting previous observations (e.g., Addo-Bediako et al., 2000). According to Boher et al. (2010) and despite that currently many *Drosophila* species are sympatric, temperate species with a cold Andean origin tolerate much lower temperatures than tropical ones suggesting a propensity of species to preserve ancestral traits. Niche conservatism in relation to lower limits of thermal tolerance can be outlined as an explanation (Wiens and Graham, 2005), where historical biogeography may be an important feature associated with cold thermal tolerance. This process allows species to track favored habitats rather than adapt to new ones, promoting stabilizing selection which is predicted to lead to niche conservatism through evolutionary time (Webb et al., 2002). Similarly, Kellermann et al. (2009), notice that tropical *Drosophila* species lack genetic variation for traits underlying cold tolerance. This piece of information suggests that species seem to retain similar traits over long periods of time. Future studies should test if a similar explanation can

be applied to *Porcellio* species because the possibility to track favored habitats or biogeography might not be the same.

On the other hand, explaining and predicting the responses of animals and plants to climate requires an understanding of the mechanistic basis of trait expression with the analysis of variation of these traits at higher levels of organization over broad geographical scales. Asymmetry in heat and cold-tolerance invariant and variant responses is probably the consequence of different biophysical processes operating near critical minimum and maximum thermal limits at lower levels of biological organization. Indeed, cell and organelle membranes are composed of lipids and proteins. The molecular composition, mainly the lipid compositions, may change in response to environmental conditions such as temperature. Hypothetically, this flexibility allows the adjustment of the biophysics of membrane structures so that they may work when environmental temperature changes. Nevertheless, if the environmental conditions are altered beyond the limits of tolerance, cell membranes frequently undergo gross structural changes. These changes include phase separation of the membrane molecular constituent and are associated with disturbances of function such as loss of membrane selective permeability and passive/active transport processes. As we previously suggested (Araújo et al., 2013), physiological variability in cold-tolerance limits is a consequence of differences in the thermodynamic effect of temperature on biochemical and biophysical reaction rates, and most likely those responsible for maintaining homeostatic regulation of ionic gradients. Indeed, the steady-state maintenance of asymmetric concentrations of ions is a major function of cell membranes and is temperature-dependent. On the contrary, variation in heat-tolerance is frequently a consequence of constraints over the destabilizing effects of high temperature on cell membranes and protein structures and functions. For instance a higher temperature can make the cell membrane lipids become more fluid, which allows the membrane phospholipids to rotate. Consequently, cell membranes become unstable and unselective. This biophysical process seems to be highly conserved across living systems and organisms (Gupta, 2003).

Finally, this kind of analysis of physiological trait variation along geographical gradients is probably a powerful approach for evaluating how physiological traits evolve at both intra- and interspecific levels and to predict how organisms can live and cope with new climatic scenarios. This work illustrates the potential consequences of thermal change across space. It also should stimulate future studies tailored to climatic scenarios for specific regions and testing for the physiological impact of changes in the mean and variance of temperature as well as heat and cold waves or extremes in the context of nonlinear thermal performance (Bozinovic et al., 2011b; Estay et al., 2014).

Acknowledgments

Funded by FONDECYT 1130015 and Fondo Basal FONDECYT FB-002 (line 3) to FB. We acknowledge J.L.P. Muñoz for logistic support.

References

- Addo-Bediako, A., Chown, S.L., Gaston, K.J., 2000. Thermal tolerance, climatic variability and latitude. *Proc. R. Soc. B* 267, 739–745.
- Araújo, M.B., Ferri-Yáñez, F., Bozinovic, F., Chown, S.L., Marquet, P.A., Valladares, F., 2013. Heat freezes niche evolution. *Ecol. Lett.* 16, 1206–1219.
- Boher, F., Godoy-Herrera, R., Bozinovic, F., 2010. The interplay between thermal tolerance and life history is associated with the biogeography of *Drosophila* species. *Evol. Ecol. Res.* 13, 973–986.
- Bozinovic, F., Rosenmann, M., 1989. Maximum metabolic rate of rodents: physiological and ecological consequences on distributional limits. *Funct. Ecol.* 3, 173–181.
- Bozinovic, F., Calosi, P., Spicer, J.I., 2011a. Physiological correlates of geographic range in animals. *Ann. Rev. Ecol. Syst.* 42, 155–179.
- Bozinovic, F., Bastías, D.A., Boher, F., Clavijo-Baquet, S., Estay, S.A., Angilletta, M.J., 2011b. The mean and variance of environmental temperature interact to determine physiological tolerance and fitness. *Physiol. Biochem. Zool.* 84, 543–552.
- Brattstrom, B.H., 1968. Thermal acclimation in Anuran amphibians as a function of latitude and altitude. *Comp. Biochem. Physiol.* 24, 93–111.
- Canterbury, G., 2002. Metabolic adaptation and climatic constraints on winter bird distribution. *Ecology* 83, 946–957.
- Castañeda, L.E., Lardies, M.A., Bozinovic, F., 2004. Adaptive latitudinal shifts in the thermal physiology of a terrestrial isopod. *Evol. Ecol. Res.* 6, 579–593.
- Clavijo-Baquet, S., Boher, F., Ziegler, L., Martel, S.I., Estay, S.A., Bozinovic, F., 2014. Differential responses to thermal variation between fitness metrics. *Sci. Rep.* 4, 5349. <http://dx.doi.org/10.1038/srep05349>.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C., Martin, P.R., 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. U. S. A.* 105, 6668–6672.
- Estay, S.A., Lima, M., Bozinovic, F., 2014. The role of temperature variability on insect performance and population dynamics in a warming world. *Oikos* 123, 131–140.
- Finke, G.R., Bozinovic, F., Navarrete, S.A., 2009. A mechanistic model to study the thermal ecology of a southeastern pacific dominant intertidal mussel and implications for climate change. *Physiol. Biochem. Zool.* 82, 303–313.
- Folguera, G., Bastías, D.A., Bozinovic, F., 2009. Impact of experimental thermal amplitude on ectotherm performance: adaptation to climate change variability? *Comp. Biochem. Physiol. A* 154, 389–393.
- Gilchrist, G.W., Huey, R.B., 1999. The direct response of *Drosophila melanogaster* to selection on knockdown temperature. *Heredity* 83, 15–29.
- Gupta, R.S., 2003. Evolutionary relationships among photosynthetic bacteria. *Photosynth. Res.* 76, 173–183.
- Helden, A.J., Hassall, M., 1998. Phenotypic plasticity in growth and development rates of *Armadillidium vulgare* (Isopoda: Oniscidea). *Israel J. Zool.* 44, 379–394.
- Hoffman, A.A., Watson, M., 1993. Geographical variation in the acclimation response of *Drosophila* to temperature extremes. *Am. Nat.* 142, S93–S113.
- Humphries, M.M., Thomas, D.W., Speakman, J.R., 2002. Climate-mediated energetic constraints on the distribution of hibernating mammals. *Nature* 418, 313–316.
- Kellermann, V., Van Heerwaarden, B., Sgro, C.M., Hoffmann, A.A., 2009. Fundamental evolutionary limits in ecological traits drive *Drosophila* species distributions. *Science* 325, 1244–1246.
- Lardies, M.A., Bozinovic, F., 2006. Geographic covariation between metabolic rate and life history traits. *Evol. Ecol. Res.* 8, 455–470.
- Lardies, M.A., Bozinovic, F., 2008. Genetic variation for plasticity in physiological and life-history traits among populations of an invasive species, the terrestrial isopod *Porcellio laevis*. *Evol. Ecol. Res.* 10, 747–762.
- Lardies, M.A., Bacigalupe, L.D., Bozinovic, F., 2009. Testing the metabolic cold adaptation hypothesis: an intraspecific latitudinal comparison in the common woodlouse. *Evol. Ecol. Res.* 6, 567–578.
- Miller, R.H., Cameron, G.N., 1987. Effects of temperature and rainfall on populations of *Armadillidium vulgare* (Crustacea: Isopoda) in Texas. *Am. Midl. Nat.* 117, 192–198.
- Naya, D.E., Bozinovic, F., 2012. Metabolic scope of fish species increase with distributional range. *Evol. Ecol. Res.* 14, 769–777.
- Pither, J., 2003. Climate tolerance and interspecific variation in geographic range size. *Proc. R. Soc. B* 270, 475–481.
- Pörtner, H.O., Farrell, A.P., 2008. Physiology and climate change. *Science* 322, 690–692.
- Pörtner, H.O., Bennett, A.F., Bozinovic, F., Clarke, A., Lardies, M.A., Lucassen, M., Pelster, B., Schiemer, F., Stillman, J.H., 2006. Trade-offs in thermal adaptation: the need of a molecular to ecological integration. *Physiol. Biochem. Zool.* 79, 295–313.
- Rezende, E.L., Bozinovic, F., Garland, T., 2004. Climatic adaptation and the evolution of basal and maximum rates of metabolism in rodents. *Evolution* 58, 1361–1374.
- Rodriguez-Serrano, E., Bozinovic, F., 2009. Interplay between global patterns of environmental temperature and variation in nonshivering thermogenesis of rodent species across large spatial scales. *Glob. Chang. Biol.* 15, 2116–2122.
- Root, T., 1988. Energy constraints on avian distributions and abundances. *Ecology* 69, 330–339.
- Schou, M.F., Kristensen, T.N., Kellermann, V., Schlötterer, C., Loeschke, V., 2014. A *Drosophila* laboratory evolution experiment points to low evolutionary potential under increased temperatures likely to be experienced in the future. *J. Evol. Biol.* <http://dx.doi.org/10.1111/jeb.12436>.
- Schultz, G.A., 1961. Distribution and establishment of a land isopod in North America. *Syst. Zool.* 10, 193–196.
- Schultz, G.A., 1972. Ecology and systematics of terrestrial isopod crustaceans from Bermuda (Oniscidea). *Crustaceana* 3, 79–99.
- Spicer, J.I., Gaston, K.J., 1999. *Physiological Diversity and its Ecological Implications*. Blackwell Science, Oxford.
- StatSoft Inc., 2001. *Statistica*, Version 6 (data analysis software system), (Tulsa, OK).
- Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T., Huey, R.B., 2014. Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc. Natl. Acad. Sci. U. S. A.* 111, 5610–5615.
- Swanson, D.L., Bozinovic, F., 2011. Metabolic capacity and the evolution of biogeographic patterns in oscine and suboscine passerine birds. *Physiol. Biochem. Zool.* 84, 185–194.
- Van Berkum, F.H., 1988. Latitudinal patterns of the thermal sensitivity of sprint speed in lizards. *Am. Nat.* 132, 327–343.
- Warburg, M.R., Calahorra, Y., Amar, K., 2001. Non-seasonal breeding in a porcellionid isopod. *J. Crustac. Biol.* 21, 375–383.
- Webb, C.O., Ackerly, D.D., McPeck, M.A., Donoghue, M.J., 2002. Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.* 33, 475–505.
- Wiens, J.J., Graham, C.H., 2005. Niche conservatism: integrating evolution, ecology, and conservation biology. *Annu. Rev. Ecol. Syst.* 36, 519–539.