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

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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.

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

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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 = $T_a mean$; maximum = $T_a max$ and minimum = $T_a min$ 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

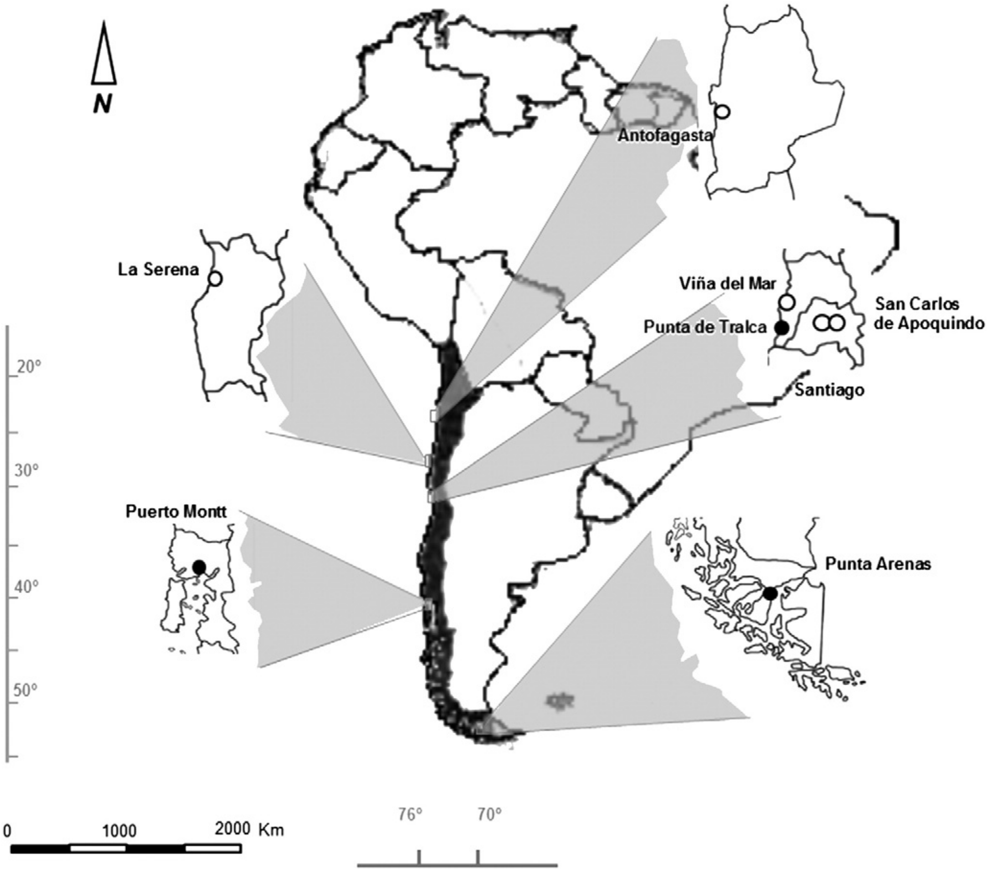

Fig. 1. Geographic localities of studied species and populations of *Porcellio laevis* (white circles) and *Porcellio scaber* (black circles) in Chile.