

Metabolic scope of fish species increases with distributional range

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ABSTRACT

Background: Current models aimed at predicting the effect of climate change on future species distributions assume that all populations of a species are an undifferentiated collection of individuals with each individual having a tolerance range equal to that of the entire species. This assumption overestimates a species' ability to cope with climate change, but data to support better models are available only for a few species with commercial value. An alternative to detailed studies of intra-specific variation in plasticity is to identify global patterns in phenotypic plasticity. One such pattern may be the climatic variability hypothesis (CVH), which states that physiological flexibility should increase with climatic variability, and thus with latitude.

Goal: Evaluate the latitudinal pattern predicted by the climatic variability hypothesis.

Definitions: Routine metabolic rate (RMR) is the daily metabolic rate of an individual. Standard metabolic rate (SMR) is the minimum metabolic rate needed to sustain life processes at a given temperature. (Typically, RMR is nearly twice SMR.) Let metabolic scope (i.e. $RMR - SMR$) be a measure of physiological flexibility (see Naya *et al.*, 2012).

Methods: Download mass- and temperature-independent SMR and RMR for 38 fish species from the FishBase. Regress the metabolic scope of species against their body length, trophic position, distributional mid-point, distributional range, maximum depth, environmental temperatures, and thermal range within the distributional area.

Results: Metabolic scope was positively correlated with species' distributional range and marginally correlated with the thermal range within species' distributional area.

Conclusion: Given the pattern of variation in climatic variability with latitude in aquatic ecosystems, we expected that physiological flexibility in aquatic organisms should be closely related with species' distributional range rather than with latitudinal distributional mid-point, as was indeed the case for metabolic scope.

Keywords: climatic variability hypothesis, macrophysiology, metabolic rate, phenotypic plasticity, physiological flexibility.

INTRODUCTION

Earth's climate is changing rapidly. The data of the IPCC (2007–2008) signal a trend towards increasing global temperatures that is evident, yet not similar, on all five continents (Dillon *et al.*, 2010). Observed responses to recent climate change include shifts in phenology, geographic range shifts, disruption of ecological interactions, and changes in primary productivity (Walther *et al.*, 2002). Although these trends are expected to cause pervasive effects on the biota, the nature, span, and consequences of climate change must differ among species and even among populations of a given species along distributional ranges (Charmentier *et al.*, 2008).

Climate envelope models constitute one of the classic approaches to quantifying how species ranges will be modified under different climate change scenarios. These models are used to quantify the relationship between species' recognized distributional range and several climatic variables, and then using these correlations, to predict changes in species distributions under future climate scenarios (Guisan and Thuiller, 2005). Setting aside the fundamental assumption that there is an equilibrium between current species distributions and climate – that is, species are present in all climatically suitable areas and absent from all unsuitable ones – these models treat all populations of a species as an undifferentiated collection of individuals, with tolerance ranges equal to those of the entire species (O'Neill *et al.*, 2008). Clearly, this assumption could overestimate the real ability of a species to cope with environmental changes, and it is probable that current models are producing optimistic predictions regarding the effect of climate change on future species distributions. It is also true, however, that the quantification of mean values and its plasticity for several traits in a number of populations is an enormous undertaking. Consequently, the data needed to improve models are available only for a very small group of species with commercial value (O'Neill *et al.*, 2008; Benito-Garzón *et al.*, 2011).

A promising new trade-off between the large amounts of data needed to include differences in plastic responses among populations (of each species to be modelled) and the fairly low predictive power of current climate envelope models (Duncan *et al.*, 2009), is the identification of global patterns in phenotypic plasticity, which could then be easily incorporated into the models – if they exist. The climatic variability hypothesis (CVH) represents such a timely and promising possibility, since it directly connects phenotypic plasticity with climatic and geographic variables at a global scale. Specifically, the CVH states that as the range of climatic fluctuation experienced by animals increases with latitude, individuals at higher latitudes should have broader ranges of thermal tolerance and physiological flexibility that enable them to cope with the fluctuating environmental conditions (Janzen, 1967; Stevens, 1989; Chown *et al.*, 2004; Ghalambor *et al.*, 2006; Kellerman *et al.*, 2009; Bozinovic *et al.*, 2011; Naya *et al.*, 2011). Direct evidence supporting the CVH comes mainly from: (1) several articles evaluating thermal tolerance ranges in ectothermic animals [e.g. genus *Drosophila* (Hoffman and Watson, 1993; Overgaard *et al.*, 2011), diving beetles (Calosi *et al.*, 2008, 2010), insects (Addo-Bediako *et al.*, 2000), porcelain crabs (Stillman and Somero, 2000), fish (Brett, 1970), amphibians (Brattstrom, 1968; Snyder and Weathers, 1975), and lizards (Cruz *et al.*, 2005; Deutsch *et al.*, 2008)], and (2) a small and heterogeneous group of studies analysing flexibility in traits other than thermal ones, such as digestive and metabolic traits in rodents and birds (Naya *et al.*, 2008, 2012; Maldonado *et al.*, 2011, 2012), body size in lizards (A.J. Aguilar-Kirigin and D. Naya, unpublished manuscript), and ecophysiological and life-history traits in plants (Molina-Montenegro and Naya, 2012). The positive relationship between physiological (thermal) flexibility and distributional range observed in ectothermic animals has been termed the Brattstrom hypothesis (Bozinovic *et al.*, 2011), although it has to be recognized that

it is part of the overall CVH conceptual framework. Research into the evolution of physiological trait flexibility is essential for the interpretation of physiographic and ecographic patterns and these patterns should be verified on a broader taxonomical scale. In summary, recently published data strongly suggest that the latitudinal pattern in phenotypic flexibility predicted by the CVH could be real and apply beyond thermal tolerance ranges. Yet, we still know very little about regularities in this macrophysiological pattern in relation to the kind of traits evaluated, the taxa analysed, and the habitats of the organisms considered (Ghalambor *et al.*, 2006; Sunday *et al.*, 2011). Given this context, we assessed the relationship between metabolic scope – as a measure of physiological flexibility – and latitude for 38 fish species.

MATERIALS AND METHODS

Database

Standard metabolic rate (SMR) is the minimum metabolic rate needed to sustain life processes at a given temperature. Routine metabolic rate (RMR) is the daily metabolic rate of an individual. RMR is nearly twice as large as SMR. Metabolic scope equals $RMR - SMR$. We used metabolic scope as our measure of physiological flexibility (see Naya *et al.*, 2012). Recall that since metabolic rates were not assessed in the same individuals (and in some cases not even in the same study), our estimation of flexibility assumes that genetic relatedness is significantly greater within species than among species (see Gianoli and Valladares, 2012). To carry out the analyses, metabolic data were downloaded from FishBase (Froese and Pauly, 2011). We included all the species for which there were at least three data points – standardized at 20°C and obtained without applying any kind of stress – for SMR and RMR. Using these criteria, we retrieved a total of 1602 metabolic entries (699 for SMR and 903 for RMR) belonging to 38 fish species. Since the data were already standardized by temperature, we applied standardizations only for differences in body size.

First, we used the regression equation obtained for each of SMR and RMR separately [$\ln(SMR) = -1.552 (\pm 0.056) + 0.871 (\pm 0.013) \times \ln(m_b)$, $r = 0.93$; $\ln(RMR) = -1.445 (\pm 0.043) + 0.832 (\pm 0.012) \times \ln(m_b)$, $r = 0.92$], displacing each metabolic datum to the same body mass (m_b) value (100 g). Second, we downloaded for each species, and also from FishBase, the following ‘independent variables’: body length, trophic position, habitat (marine, freshwater or both), geographical zone (tropical, subtropical or temperate), latitudinal distributional mid-point, distribution range, and maximum depth (see evolutionary-ecology.com/data/2783Appendix.pdf). For five species, the distributional data were not reported in FishBase, so they were downloaded from the FishWise database (www.fishwise.co.za). In addition, we downloaded data on monthly variation in sea surface temperature (Sunday *et al.*, 2011) – sampled on a 5° × 5° grid basis and combining the Pacific, Atlantic, and Indian Oceans. These temperature data, together with the species distributional data, allowed us to obtain rough estimates of maximum and minimum temperatures and thermal range for each species.

Metabolic scope estimates

We calculated metabolic scope as an unbiased standardized mean difference – the Hedges’ difference, i.e. the difference between RMR and SMR means expressed in units of pooled

standard deviation and corrected for small sample bias – and its associated variance for each of the 38 species (evolutionary-ecology.com/data/2783Appendix.pdf). Because $SMR < RMR$, all true values of metabolic scope must be positive. The negative values we obtained in the first step must represent noise around very low levels of metabolic scope. So we replaced these negative values with zeros. Then, we evaluated the relationship between the magnitude of metabolic scope and independent variables through random-effect meta-analytical models with continuous predictor variables (body length, trophic position, distributional mid-point, distributional range, maximum depth, and environmental temperatures recorded within the distributional area) or categorical predictor variables (habitat and geographical zone), using the software Metawin® version 2.1 (Rosenberg *et al.*, 2000). We did not attempt to use phylogenetically informed analyses because the phylogenetic relationships between the species considered in our analysis are far from being solved [for several recent phylogenetic hypotheses for the taxon Percomorpha, see Setiamarga *et al.* (2008)].

RESULTS

Metabolic scope was positively correlated with species distributional range (Fig. 1), and marginally with the thermal range recorded within the distributional area (Table 1). Metabolic scope was not correlated with any other independent variable (Table 1), and did not differ among species from different geographic zones or among species with different habits (Table 2).

DISCUSSION

A relatively new approach to investigating physiological function in the context of exploring and understanding biodiversity has emerged with the integration of physiological ecology and macroecology, termed macrophysiology (Chown *et al.*, 2004). In general, this interdisciplinary

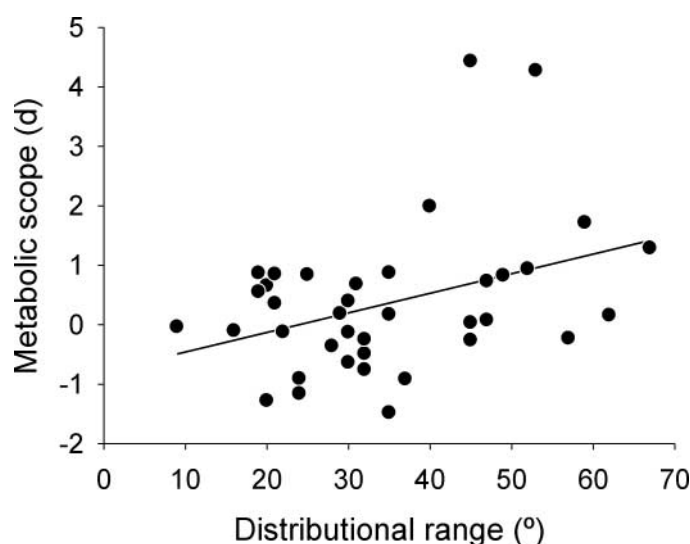


Fig. 1. Relationship between metabolic scope (quantified as the difference between routine metabolic rate and standard metabolic rate) and distributional range.

Table 1. Pearson product–moment correlation coefficients (and results of the meta-analytical models) for the relationships between metabolic scope and the continuous independent variables

Independent variable	Metabolic scope I	Metabolic scope II
Body length (cm)	$r = 0.05$ ($\chi^2 = 0.56$, d.f. = 36, $P < 0.45$)	$r = 0.02$ ($\chi^2 = 0.30$, d.f. = 36, $P < 0.59$)
Trophic position	$r = 0.11$ ($\chi^2 = 0.89$, d.f. = 36, $P < 0.35$)	$r = 0.07$ ($\chi^2 = 0.50$, d.f. = 36, $P < 0.48$)
Distributional mid-point (°)	$r = -0.03$ ($\chi^2 = 0.02$, d.f. = 36, $P < 0.90$)	$r = -0.04$ ($\chi^2 = 0.12$, d.f. = 36, $P < 0.73$)
Distributional range (°)	$r = 0.38$ ($\chi^2 = 7.18$, d.f. = 36, $P < 0.01$)	$r = 0.36$ ($\chi^2 = 6.32$, d.f. = 36, $P < 0.01$)
Maximum depth (m)	$r = 0.08$ ($\chi^2 = 0.37$, d.f. = 21, $P < 0.55$)	$r = 0.01$ ($\chi^2 = 0.10$, d.f. = 21, $P < 0.76$)
Maximum temperature (°C)	$r = 0.16$ ($\chi^2 = 0.89$, d.f. = 36, $P < 0.35$)	$r = 0.19$ ($\chi^2 = 1.23$, d.f. = 36, $P < 0.27$)
Minimum temperature (°C)	$r = -0.16$ ($\chi^2 = 1.55$, d.f. = 36, $P < 0.22$)	$r = -0.18$ ($\chi^2 = 2.15$, d.f. = 36, $P < 0.14$)
Thermal range (°C)	$r = 0.22$ ($\chi^2 = 2.64$, d.f. = 36, $P < 0.10$)	$r = 0.24$ ($\chi^2 = 3.72$, d.f. = 36, $P < 0.06$)

Note: Metabolic scope I was calculated using actual values, whereas Metabolic scope II was calculated by replacing negative values with zero (see Methods for explanations).

Table 2. Cumulative effect size for metabolic scope (E), 95% confidence interval (95% CI), number of comparisons (n), and statistics associated with each categorical analysis

Factor	Metabolic scope	95% CI	n	Statistics
<i>Geographic zone</i>	0.296	−0.020 to 0.652	38	$\chi^2 = 0.29$, d.f. = 35, $P < 0.87$
Tropical	0.227	−0.279 to 1.014	10	
Subtropical	0.248	−0.211 to 0.658	16	
Temperate	0.423	−0.171 to 1.206	12	
<i>Habitat</i>	0.296	−0.041 to 0.624	38	$\chi^2 = 1.28$, d.f. = 35, $P < 0.53$
Freshwater	0.158	−0.147 to 0.435	15	
Marine	0.194	−0.677 to 1.129	10	
Both	0.550	0.002 to 1.279	13	

Note: The 95% confidence intervals were estimated using a bootstrapping procedure with 1000 iterations.

convergence compares physiological features between individuals possessing different distributions (Gaston *et al.*, 2009; Stillman and Tagmount, 2009). Such an approach to biodiversity seeks to elucidate patterns of geographic physiological variability (physiographic patterns) within the framework of the hierarchical structure of biodiversity, and to understand the mechanisms that underlie these patterns. To predict responses to climate change, physiological and biophysical ecologists must understand the patterns of environmental variation and the mechanisms by which organisms cope with this variation. Hence, macrophysiology

represents a relatively straightforward method that includes realistic global patterns of phenotypic plasticity in models aimed at predicting the future distribution of species under different scenarios of global change. Obviously, this could be of great importance given the putative role of phenotypic plasticity on species' local persistence under the current scenario of global change (Berteaux *et al.*, 2004; Charmentier *et al.*, 2008; Deutsch *et al.*, 2008; Gienapp *et al.*, 2008; Hendry *et al.*, 2008; Teplitsky *et al.*, 2008; Hoffman and Sgro, 2011).

Within the above context, two results obtained in the present study are noteworthy. First, metabolic scope increases with species distributional range, but not with species distributional mid-point. Although intriguing at a first glance, these results are in line with the latitudinal pattern of variation in thermal range (i.e. the putative variable of phenotypic flexibility according to the CVH) in aquatic ecosystems. In contrast to terrestrial ecosystems, where thermal range clearly increases with latitude, the thermal range in aquatic ecosystems (at least in marine ones) varies very little with latitude (Fig. 2) (see also Sunday *et al.*, 2011). Accordingly, an increase in species distributional range implies a greater thermal range within species distributional area than an increase in species distributional mid-point (Fig. 2). Second, species distributional range was a better predictor of metabolic scope than thermal range. Interestingly, an analogous result is usually found for terrestrial ecosystems where latitude used to be a better predictor of phenotypic flexibility than thermal variability indexes. For these ecosystems, a set of explanations that may also hold for aquatic ecosystems has been proposed. For instance, it has been stated that: (i) latitude is probably a better predictor of long-term regimes of climatic variables than current climate values provided by weather stations; (ii) latitude is correlated with several other climatic, ecological, and historical factors that could affect phenotypic flexibility; and (iii) given the smooth variation of climatic variables in space, latitude could represent a weighted variable of climatic conditions acting over spatial scales more similar to those at which adaptation is expected to occur (Naya *et al.*, 2012).

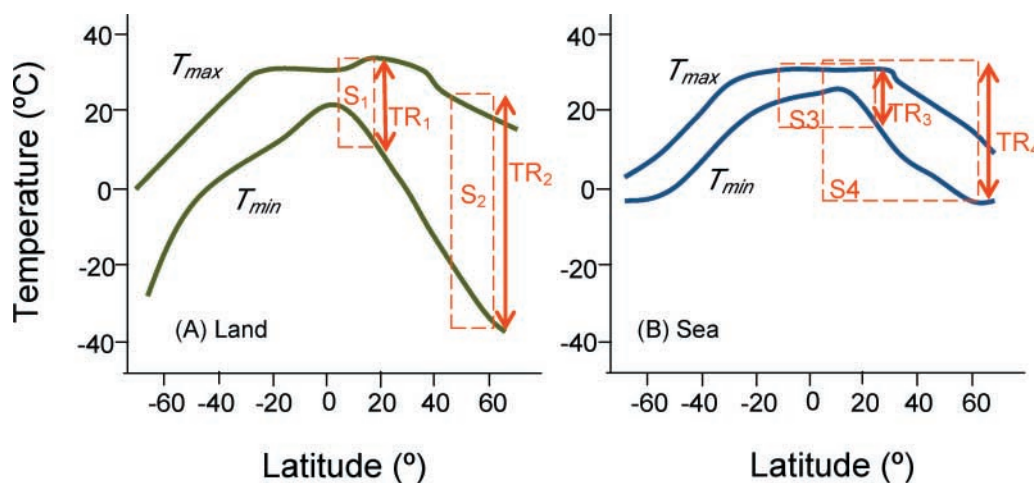


Fig. 2. Thermal ranges [TR_x (based on Sunday *et al.*, 2011)] for two hypothetical species occurring (A) on land (S_1 and S_2) and (B) in the sea (S_3 and S_4). Recall that on land an increase in thermal range occurs with a rise in a species distributional mid-point, whereas in the sea an increase in thermal range is more related to an increase in the species' distributional range (rectangles).

Finally, it is important to note some limitations of the present analysis. First, given that the phylogenetic relationships among the Acanthopterygii are far from being solved (Setiamarga *et al.*, 2008), we did not carry out phylogenetically informed analyses. Metabolic rates, however, are usually considered labile traits that can evolve in a few generations (Swallow *et al.*, 2009). Thus, given the large temporal scale considered in the analysis, we believe that it is not realistic to think that a phylogenetic constraint may affect the evolution of our focal trait (see Westoby *et al.*, 1995). Second, given that standard and routine metabolic rates were not assessed in the same individuals, an important amount of noise around species' real values of metabolic scope should be expected. As a consequence, a reduction in the power to detect any significant pattern should be expected. Nevertheless, we were able to detect the latitudinal pattern predicted by the CVH (modified for aquatic ecosystems), indicating that this global trend is a very strong one. This is a very relevant result since, as noted earlier, detecting global patterns in phenotypic plasticity represent a promising means to include plastic responses in models aimed at predicting the effect of climate change on species' persistence and future distribution.

In summary, the present study indicates that metabolic scope in fish increases with the species distributional range and, to some extent, with the range of temperature variability, as proposed by the climatic variability hypothesis. In the current scenario of climate change, there is a clear need to improve our current understanding of the relationship between species and population plastic responses, and its influence on the geographical distribution of taxa. Ultimately, this will lead to a better understanding of the relationship among tolerance, capacity, and plasticity, and guide the integration of these traits in the investigation of 'what determines a species range size'. The debate on how to integrate different physiological traits, or how to parameterize each and every trait considered fundamental for the modelling of species distribution range and its determinants, is a lively ONE (Kearney and Porter, 2009; Bozinovic *et al.*, 2011).

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REFERENCES

- Addo-Bediako, A., Chown, S.L. and Gaston, K.J. 2000. Thermal tolerance, climatic variability and latitude. *Proc. R. Soc. Lond. B*, **267**: 739–745.
- Benito-Garzón, M., Alía, R., Robson, M.T. and Zavala, M.A. 2011. Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Glob. Ecol. Biogeogr.*, **20**: 766–778.
- Berteaux, D., Reale, D., McAdam, A.G. and Boutin, S. 2004. Keeping pace with fast climate change: can arctic life count on evolution? *Int. Comp. Biol.*, **44**: 140–151.
- Bozinovic, F., Calosi, P. and Spicer, J.I. 2011. Physiological correlates of geographic range in animals. *Annu. Rev. Ecol. Evol. Syst.*, **42**: 155–179.
- Brett, J.R. 1970. Temperature – animals – fishes. In *Marine Ecology*, Vol. 1 (O. Kinne, ed.), pp. 515–560. New York: Wiley.
- Brattstrom, B.H. 1968. Thermal acclimation in Anuran amphibians as a function of latitude and altitude. *Comp. Biochem. Physiol.*, **24**: 93–111.
- Calosi, P., Bilton, D.T. and Spicer, J.I. 2008. Thermal tolerance, acclimatory capacity and vulnerability to global climate change. *Biol. Lett.*, **4**: 99–102.

- Calosi, P., Bilton, D.T., Spicer, J.I., Votier, S.C. and Atfield, A. 2010. What determines a species' geographical range? Thermal biology and latitudinal range size relationships in European diving beetles (Coleoptera: Dystiscidae). *J. Anim. Ecol.*, **79**: 194–204.
- Charmentier, A., McCleery, R.H., Cole, L.R., Perrins, C., Kruuk, L.E.B. and Sheldon, B.C. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, **320**: 800–803.
- Chown, S.L., Gaston, K.J. and Robinson, D. 2004. Macrophysiology: large-scale patterns in physiological traits and their ecological implications. *Funct. Ecol.*, **18**: 159–167.
- Cruz, F.B., Fitzgerald, L.A., Espinoza, R.E. and Schulte, J.A., II. 2005. The importance of phylogenetic scale in tests of Bergmann's and Rapoport's rules: lessons from a clade of South American lizards. *J. Evol. Biol.*, **18**: 1559–1574.
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. *et al.* 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl. Acad. Sci. USA*, **105**: 6668–6672.
- Dillon, M.E., Wang, G. and Huey, R.B. 2010. Global metabolic impacts of recent climate warming. *Nature*, **467**: 704–707.
- Duncan, R.P., Cassey, P. and Blackburn, T.M. 2009. Do climate envelope models transfer? A manipulative test using dung beetle introductions. *Proc. R. Soc. Lond. B*, **276**: 1449–1457.
- Froese, R. and Pauly, D. 2011. *FishBase*, version 08/2011. Available at: www.fishbase.org.
- Gaston, K.J., Chown, S.L., Calosi, P., Bernardo, J., Bilton, D.T., Clarke, A. *et al.* 2009. Macrophysiology: a conceptual reunification. *Am. Nat.*, **174**: 595–612.
- Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J. and Wang, G. 2006. Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integr. Comp. Biol.*, **46**: 5–17.
- Gianoli, E. and Valladares, F. 2012. Studying phenotypic plasticity: the advantages of a broad approach. *Biol. J. Linn. Soc.*, **105**: 1–7.
- Gienapp, P., Teplitsky, J., Alho, S., Mills, A. and Merila, J. 2008. Climate change and evolution: disentangling environmental and genetic responses. *Mol. Ecol.*, **17**: 167–178.
- Guisan, A. and Thuiller, W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.*, **8**: 993–1009.
- Hendry, A.P., Farrugia, T.J. and Kinnison, M.T. 2008. Human influences on rates of phenotypic change in wild animal populations. *Mol. Ecol.*, **17**: 20–29.
- Hoffman, A.A. and Sgro, C.M. 2011. Climate change and evolutionary adaptation. *Nature*, **470**: 479–485.
- Hoffman, A.A. and Watson, M. 1993. Geographical variation in the acclimation response of *Drosophila* to temperature extremes. *Am. Nat.*, **142**: S93–S113.
- Janzen, D.H. 1967. Why mountain passes are higher in the tropics. *Am. Nat.*, **101**: 233–249.
- Kearney, M. and Porter, W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species ranges. *Ecol. Lett.*, **12**: 334–350.
- Kellerman, V., van Heerwaarden, B., Sgro, C.M. and Hoffmann, A.A. 2009. Fundamental evolutionary limits in ecological traits drive *Drosophila* species distributions. *Science*, **325**: 1244–1246.
- Maldonado, K., Bozinovic, F., Rojas, J.M. and Sabat, P. 2011. Within-species digestive tract flexibility in rufous-collared sparrow and the climatic variability hypothesis. *Physiol. Biochem. Zool.*, **84**: 377–384.
- Maldonado, K., Bozinovic, F., Cavieres, G., Fuentes, A.C., Cortés, A. and Sabat, P. 2012. Phenotypic flexibility in basal metabolic rate is associated with rainfall variability among populations of rufous-collared sparrow. *Zoology*, **115**: 128–133.
- Molina-Montenegro, M.A. and Naya, D.E. 2012. Latitudinal patterns in phenotypic plasticity and fitness-related traits: assessing the climatic variability hypothesis with an invasive plant species. *PLoS ONE*, **7**(10): e47620.

- Naya, D.E., Bozinovic, F. and Karasov, W.H. 2008. Latitudinal trends in physiological flexibility: testing the climatic variability hypothesis with data on the intestinal length of rodents. *Am. Nat.*, **172**: E122–E134.
- Naya, D.E., Catalán, T., Artacho, P., Gaitan-Espitia, J.D. and Nespolo, R.F. 2011. Exploring the functional association between physiological flexibility, climatic variability and geographical latitude: lesson from land snails. *Evol. Ecol. Res.*, **13**: 647–659.
- Naya, D.E., Spangenberg, L., Naya, H. and Bozinovic, F. 2012. Latitudinal pattern in rodent metabolic flexibility. *Am. Nat.*, **179**: E172–E179.
- O'Neill, G.A., Hamman, A. and Wang, T. 2008. Accounting for population variation improves estimates of the impact of climate change on species' growth and distribution. *J. Appl. Ecol.*, **45**: 1040–1049.
- Overgaard, J., Kristensen, T.N., Mitchell, K.A. and Hoffmann, A.A. 2011. Thermal tolerance in widespread and tropical *Drosophila* species: does phenotypic plasticity increase with latitude. *Am. Nat.*, **178**: S80–S96.
- Rosenberg, M.S., Adams, D.C. and Gurevitch, J. 2000. *METAWIN*, version 2.1. Statistical Software for Meta-Analysis. Sunderland, MA: Sinauer Associates.
- Setiamarga, D.H.E., Miya, M., Yamanoue, Y., Mabuchi, K., Satoh, T.P., Inoue, J.G. *et al.* 2008. Interrelationships of Atherinomorpha (medakas, flyingfishes, killifishes, silversides, and their relatives): the first evidence based on whole mitogenome sequences. *Mol. Phylogenet. Evol.*, **49**: 598–605.
- Snyder, G.K. and Weathers, W.W. 1975. Temperature adaptations in amphibians. *Am. Nat.*, **109**: 93–101.
- Stevens, G.C. 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat.*, **133**: 240–256.
- Stillman, J.H. and Somero, G.N. 2000. A comparative analysis of the upper thermal tolerance limits of Eastern Pacific porcelain crabs, genus *Petrolisthes*: influences of latitude, vertical zonation, acclimation, and phylogeny. *Physiol. Biochem. Zool.*, **73**: 200–208.
- Stillman, J.H. and Tagmout, A. 2009. Seasonal and latitudinal acclimatization of cardiac transcriptome responses to thermal stress in porcelain crabs, *Petrolisthes cinctipes*. *Mol. Ecol.*, **18**: 4206–4226.
- Sunday, J.M., Bates, A.E. and Dulvy, N.K. 2011. Global analysis of thermal tolerance and latitude in ectotherms. *Proc. R. Soc. Lond. B*, **278**: 1823–1830.
- Swallow, J.G., Hayes, J.P., Koteja, P. and Garland, T., Jr. 2009. Selection experiment and experimental evolution of performance and physiology. In *Experimental Evolution* (T. Garland, Jr. and M.C. Rose, eds.), pp. 301–351. Berkeley, CA: University of California Press.
- Teplitsky, C., Mills, J.A., Alho, J.S., Yarrall, J.W. and Merila, J. 2008. Bergmann's rule and climate change revisited: disentangling environmental and genetic responses in a wild bird population. *Proc. Natl. Acad. Sci. USA*, **105**: 13492–13496.
- Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C. *et al.* 2002. Ecological responses to recent climate change. *Nature*, **416**: 389–395.
- Westoby, M., Leishman, M.R. and Lord, J.M. 1995. On misinterpreting the 'phylogenetic correction'. *J. Ecol.*, **83**: 531–534.

