

Published in final edited form as:

Glob Chang Biol. 2016 June ; 22(6): 2013–2024. doi:10.1111/gcb.13255.

Morphological variation in salamanders and their potential response to climate change

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Abstract

Despite the recognition that some species might quickly adapt to new conditions under climate change, demonstrating and predicting such a fundamental response is challenging. Morphological variations in response to climate may be caused by evolutionary changes or phenotypic plasticity, or both, but teasing apart these processes is difficult. Here we built on the number of thoracic vertebrae (NTV) in ectothermic vertebrates, a known genetically-based feature, to establish a link with body size and evaluate how climate change might affect the future morphological response of this group of species. First we show that in old-world salamanders, NTV variation is strongly related to changes in body size. Secondly, using 22 salamander species as a case study, we found support for relationships between the spatial variation in selected bioclimatic variables and NTV for most of species. For 44% of species, precipitation and aridity were the predominant drivers of geographical variation of the NTV. Temperature features were dominant for 31% of species, while for 19% temperature and precipitation played a comparable role. This two-step analysis demonstrates that ectothermic vertebrates may evolve in response to climate change by modifying the number of thoracic vertebrae. These findings allow to develop scenarios for potential morphological evolution under future climate change, and to identify areas and species in which the most marked evolutionary responses are expected. Resistance to climate change estimated from species distribution models was positively related to present-day species morphological response, suggesting that the ability of morphological evolution may play a role for species' persistence under climate change. The possibility that present-day capacity for local adaptation might help the resistance response to climate change can be integrated into analyses of the impact of global changes, and should also be considered when planning management actions favouring species persistence.

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Keywords

amphibians; Bergmann's rule; ectothermic vertebrates; local adaptation; morphological evolution; NDVI; precipitation; temperature

Introduction

One of the biggest challenges of global change ecology is to explain and predict the evolution of complex traits in nature and in response to environmental stressors. Body size is known to be an integrative trait linked to individual fitness, highly heritable, and influenced by natural selection (Blanckenhorn, 2000). For instance, the body size of endotherms appears to increase in areas with lower temperature (and at higher latitudes, a phenomenon known as "Bergmann's Rule") reflecting the advantage of large body size in terms of thermoregulation (Meiri & Dayan, 2003). Nevertheless, it remains difficult to predict why a specific animal attains a specific size in a given habitat, or how body size might evolve, since multiple evolutionary forces determine body size-climate relationships (Ficetola *et al.*, 2010, Rypel, 2014). The situation is even more complex for ectotherms since most of them have a limited capacity for thermoregulation and they have been shown to exhibit wide interspecific variation in terms of body size-climate relationships. As a consequence, only part of ectotherms showed patterns consistent with the Bergmann's rule (Ashton & Feldmann, 2003, Adams & Church, 2008, Berke *et al.*, 2013, Rypel, 2014). Other evolutionary forces are likely to be at play, such as selection for desiccation tolerance or starvation resistance, and may explain the complex relationships between body size variation and climate in ectotherms (Adams & Church, 2008, Olalla-Tárraga *et al.*, 2009, Ficetola *et al.*, 2010; Table 1). Furthermore, demonstrating evolutionary relationships between individual body size and climate is particularly challenging in nature since body size variation among populations may also reflect plasticity, differences in age, and food availability (Caruso *et al.*, 2014, Merilä & Hendry, 2014, Rypel, 2014, Teplitsky & Millien, 2014, Connette *et al.*, 2015).

In this study we explore evolutionary responses to climatic variation in ectothermic vertebrates through the analysis of the number of thoracic vertebrae (NTV). Despite the existence of plastic responses, NTV shows a high level of genetic determinism in ectotherms (Itazawa, 1959, Dohm & Garland, 1993, Jockusch, 1997) and affects growth rate and body size evolution (Lindell, 1996, Head & Polly, 2007, Reece & Mehta, 2013), making it a perfect integrative trait. Intraspecific patterns for NTV are therefore expected to reflect genuine evolutionary variation (Jockusch, 1997). In multiple groups of ectothermic vertebrates, including salamanders, the evolution of body size was strongly related to the number of vertebrae (Wake, 1991, Head & Polly, 2007, Reece & Mehta, 2013, Arntzen *et al.*, 2015; see results section for an analysis on European salamanders), suggesting that the variation in the number of vertebrae is a key process in determining body size evolution. In other words, studying the relationships between climate and NTV, a trait with a strong genetic determinism that also determines body size, makes it possible to investigate the links with another trait, body size, which according to evolutionary theory may significantly evolve in response to climate change (Table 1). NTV is thus used here as a crucial link

between climate and body size. Even though some analyses on fish have assessed the role of climate on variation of NTV (McDowall, 2008, Shikano & Merila, 2011), studies have neither explicitly tested multiple hypotheses on processes determining the intraspecific variation for this trait, nor they have explored the consequences of NTV variation for species evolution and persistence in the context of global changes.

Using a comprehensive dataset of urodelan amphibians (salamanders) from Europe and the Middle East (supplementary material, Fig. S1), we analysed the relationships between present-day climate and intraspecific variation for NTV across species' ranges that potentially represent current local adaptations in response to climatic heterogeneity within their ranges. The observed relationships between NTV and climate were then used to explore the potential impact of climate change on morphological evolution, and to assess whether morphological responses to climate can help species to withstand climate change. Consensus projections extracted from multiple species distribution models (Thuiller *et al.*, 2009) and global climate models forced by the latest emission pathways scenarios (Moss *et al.*, 2010) were used to build reliable future distributions for all species. These projections were then related to the variation in NTV, assessing whether a morphological response would help the species to better withstand climate changes. Finally, we identified the areas where the most marked morphological responses are required in order to keep up with the pace of climatic variation.

Materials and methods

Data

Data on the number of thoracic vertebrae in Urodela species of Europe and the Middle East were collected from the literature (Veith, 1992, Veith *et al.*, 1992, Crnobrnja-Isailovic *et al.*, 1997, Lanza *et al.*, 2009). Only individuals for which data on collection locality were available were considered and those from contact zones of hybridizing species were excluded. Furthermore, only species with data for at least nine populations were considered. Overall, our datasets comprised 6,090 individuals, representing 462 populations and 22 species (Fig. S1). Taxonomy followed recent checklists of European amphibians (Sillero *et al.*, 2014).

Eight bioclimatic variables were considered representing thermal environment, water availability, desiccation risk and primary productivity: mean annual temperature, mean temperature diurnal range, temperature annual range, mean annual summed precipitation, precipitation seasonality, summer precipitation, winter precipitation (calculated from the period 1950-2000 and obtained from the worldclim dataset; Hijmans *et al.*, 2005); the aridity index (Trabucco & Zomer, 2009) and the Normalized Difference Vegetation Index (NDVI), a proxy of primary productivity, obtained from the NOAA and the VEGETATION datasets (Gutman *et al.*, 1997 and <http://www.vgt.vito.be>). Cave salamanders (genus *Hydromantes*) generally remain underground during the summer (Lanza *et al.*, 2006, Lunghi *et al.*, 2015), so we only considered summed precipitation during autumn, winter and spring, instead of annual, winter and summer precipitations. Bioclimatic parameters might be related to body size evolution through multiple processes, as they affect thermoregulation, water balance, activity length, endurance, starvation resistance and food availability (Table 1; reviewed in

Ficetola *et al.*, 2010). Environmental parameters were extracted at a resolution of 30" for species in which all localities were defined with accuracy of less than 1 km (Table S1). For the remaining species, environmental parameters were extracted at a resolution of 2.5'.

Statistical analyses

Body size evolution and number of vertebrae—Phylogenetic generalized least squares (PGLS) were used to evaluate whether, at the interspecific level, the variation of body size was related to the number of vertebrae in European Urodela (see Wake, 1991 for examples on salamanders from other geographic areas). Data on the average number of vertebrae in the 22 study species (Table 2), plus eleven additional species for which data were available were used as the independent variable (Fig. S1). Data on the average body size of females (snout-vent length) were obtained from the literature (Lanza *et al.*, 1995, Colleoni *et al.*, 2014); we controlled for phylogeny by combining the trees used by previous comparative studies (Ficetola *et al.*, 2013a, Colleoni *et al.*, 2014). Available information was insufficient to test the relationships between the number of vertebrae and average body size at the intraspecific level.

Relationships between the number of vertebrae and bioclimatic variables—An information-theoretic approach was used to identify the combination of environmental variables most likely to influence intraspecific variation for the number of vertebrae (Burnham & Anderson, 2002). First, mixed models relating the number of vertebrae to all combinations of environmental variables were built. For each species, mixed models were estimated using maximum likelihood, and included population identity as a random effect. Strong intraspecific genetic structure can obscure relationships between morphology and climate (Romano & Ficetola, 2010). Therefore, for species comprising multiple subspecies, or when available genetic data indicated the existence of a strong intraspecific genetic structure, we included clade / subspecies identity as an additional random effect to take into account the potential effect of long- term evolutionary isolation (Steinfartz *et al.*, 2000, Babik *et al.*, 2005, Sotiropoulos *et al.*, 2007, Wielstra *et al.*, 2010, Canestrelli *et al.*, 2012). The models were then ranked using Akaike's Information Criterion corrected for small sample size (AICc) (Burnham & Anderson, 2002). AICc may select overly complex models, we therefore considered a complex model as a candidate only if it had an AICc that was lower than the AICc of all of its simpler nested models (Symonds & Moussalli, 2011). Furthermore, we allowed a maximum of two environmental variables per model for species with less than 20 populations, and a maximum of three variables for the remaining species. We excluded models with pairwise correlation among variables > 0.7 ; in all candidate models variance inflation factor was well below five, indicating lack of collinearity issues (Dormann *et al.*, 2013). We used Moran's *I* to test whether spatial autocorrelation may influence the results of our models. For all best-AICc models, residual autocorrelation was weak ($P > 0.05$ for all species), suggesting that autocorrelation did not bias our models (Dormann *et al.*, 2007). In our results, we first present the best-AICc models, which are particularly relevant when they have strong support. Subsequently, we also performed model averaging, which may be more suitable when there is not a single best model but rather a range of models that show good AICc values (Burnham & Anderson, 2002, Richards *et al.*, 2011). For model averaging, we calculated the Akaike weight (w) of all candidate models

including the intercept model, which is a measure of the support of the model, given the data (Burnham & Anderson, 2002). Model averaging was then used to obtain spatial projections of models under both present-day and future climatic conditions. If needed, environmental variables were transformed using square-root (annual, summer and winter precipitation) or logarithm (aridity) to improve normality and reduce skewness.

We used marginal and conditional R^2 (R^2_m and R^2_c , respectively) to assess the fit of the mixed-effect models (Nakagawa & Schielzeth, 2013). Both R^2_m and R^2_c convey unique information. Specifically, R^2_m represents the pure effect of fixed factors, while R^2_c is the variance explained by the entire model (Nakagawa & Schielzeth, 2013). R^2_m and R^2_c of best models were then used to define the present-day morphological response to bioclimatic variables. More specifically, we defined the present marginal response as R^2_m . The marginal response corresponded to the present-day morphological response to bioclimatic variables, after taking into account population- and clade-level effects. We defined the present global response as R^2_c , i.e. the response integrating the effects bioclimatic variables, population- and clade-level variation on morphology, and also including eventual joint effects between fixed and random variables. The global morphological response also aims at including eventual variation from local ecological factors not explicitly investigated here.

The models relating the number of vertebrae to bioclimatic variables were projected under multiple climate change scenarios on the basis of model-averaged models to obtain scenarios of how species might morphologically respond to climate change through rapid evolution in NTV and body size. We used the Hadley Centre Global Environment Model version 2–Earth System global circulation model (GCM) and four emission scenarios from the IPCC fifth assessment report, which are distinct “representative concentration pathways” (rcp): rcp2.6, rcp4.5, rcp6.0, rcp8.5. The four emission scenarios represent increasing emission pathways, leading to radiative forcing in 2100 of 2.6, 4.5, 6.0 and 8.5 Wm^2 (hereafter named: HE2.6, HE4.5, HE6.0 and HE8.5; Moss *et al.*, 2010). In order to explore variability among GCMs, three additional models were also considered [Geophysical Fluid Dynamics Laboratory Coupled Physical Model CM3 (GFDL-CM3); the Hadley Centre Global Environment Model version 2 – atmosphere (HadGEM2-AO); and the fifth version of the low resolution climate model of the Institut Pierre Simon Laplace (IPSL-CM5A-LR)], using one given rcp4.5 (hereafter named: GF4.5, HD4.5, IP4.5). These projections were available for all the climatic variables used in this study. However, NDVI was not projected over time but was kept constant. Data on temperature and precipitation under climate change scenarios were downloaded from <http://www.worldclim.org>. The aridity index under climate change scenarios was developed from these data, following Trabucco and Zomer (2009).

The present relationships between climate and NTV were used to predict the mean number of vertebrae in each grid cell under the present and future climatic scenarios. We then calculated the percentage of morphological variation for each map cell. Spatial projections were limited to areas within the range and, for species with large ranges not fully covered by sampled populations, to less than 500 km from sampled populations.

Variation in suitability: species distribution models—Correlative species distribution models (SDM) were used to assess relationships between the distribution of the

study species and climate, and to evaluate potential changes in suitability as a consequence of climate change. Within Europe, the SDM were calibrated assuming presence in cells where the species is present in the European Herpetological Atlas (Sillero *et al.*, 2014), refined at a 2.5' resolution by removing the cells outside the altitudinal limit of the species, or with unsuitable habitat (Ficetola *et al.*, 2015). Outside of Europe, the models were calibrated using the refined IUCN range maps (Ficetola *et al.*, 2015). For each species we used 5000 absence points, selected within the study area outside the cells where the species is recorded to be present. An ensemble of SDM forecasts (Araujo & New, 2007) was obtained for each species on the basis of the bioclimatic variables. The ensemble included projections with Generalized Additive Models, Boosting Regression Trees, Classification Trees, Multiple Adaptive Regression Splines and Random Forests. Models were developed using biomod2 (Thuiller *et al.*, 2009), and the probability of occurrence was projected under both current and future conditions as described in Thuiller *et al.* (2014). In order to obtain the remaining proportion of suitable species range in the future, probabilities of occurrence were transformed into binary maps (presence/absence) using the value maximising the true skill statistics as a threshold (Thuiller *et al.*, 2014). Future projections were limited to within the species range, due to the very limited dispersal capability of amphibians, particularly within the human-dominated landscapes of the study area (Araujo *et al.*, 2006, Early & Sax, 2011).

Species' resistance to projected climate change was estimated as the proportion of currently suitable range, that remains suitable under climate change scenarios. *Species exposure* was the mean absolute difference in environmental suitability between current and future conditions.

Relationship between morphological variation, changes in climatic suitability, and range size—Random-slope mixed models were used to measure the relationships between morphological variation, species resistance to climate change, exposure to climate change and species range (Table 2), under the seven climate change scenarios. First, we tested the relationship between exposure to climate change and future morphological response. Second, we evaluated whether species resistance to climate change was related to range size or present-day morphological variation. AICc was used to evaluate the support of potential predictors of resistance to climate change. In all models, species identity and scenario were considered as random effects. The results remained identical if the scenarios were considered as fixed factors. Uncertainty of variables was considerable, particularly given the differences among emission scenarios and GCMs. Therefore, as a dependent variable we did not use one single value per species (e.g. the mean across the seven climate change scenarios). Instead, for each species we used the projections under the seven scenarios, considering scenario and species identity as random effects, as we were interested in taking into account the heterogeneity across potential scenarios. In these mixed models, we used R^2_m as a measure of the pure effect of fixed factors. Some independent variables in these models (morphological variation, resistance to climate change and exposure to climate change) were not controlled by the researcher, with errors associated with their measurement. In this case, model II regression may be more appropriate (Legendre & Legendre, 2012), but unfortunately model II regressions are not easily implemented within

mixed models. We therefore re-analysed all the significant relationships with ranging major axis regression (Legendre & Legendre, 2012), using 999 permutations to obtain 95% confidence intervals of regression coefficients. All statistical analyses were performed using the R statistical environment (R Development Core Team, 2014), using the packages caper, lmodel2, nlme, MuMIn, SpatialPack, raster and rgdal (Orme *et al.*, 2013, Bivand *et al.*, 2014, Hijmans, 2014, Pinheiro *et al.*, 2014, Barton, 2015).

Results

Body size evolution and number of vertebrae

Across 33 species of salamanders from Europe and Asia, the variation of body size was strongly related to the number of vertebrae (PGLS: $F_{1,31} = 33.7$, $B \pm SE = 1.37 \pm 0.24$, $P < 0.0001$, $R^2 = 0.52$; Fig. S2). This result confirmed observations on other ectothermic vertebrates (Head & Polly, 2007, Reece & Mehta, 2013), and suggests that in salamanders the variation in the number of vertebrae is a key process determining body size evolution.

Relationships between climate and present-day number of vertebrae

The NTV showed variability in all the species with one exception (*Hydromantes genei*), even though this discrete parameter only has a limited number of values for each species (Table S2). Intraspecific variability, measured as coefficient of variation, clearly increased with geographic range (partial correlation taking into account sample size: $r = 0.67$, $N = 22$, $P < 0.001$).

For 16/22 species (73%), our information-theoretic approach detected support for relationships between environmental features and variation in the number of vertebrae; the strength of relationships was highly variable among species, being very low ($R^2_m < 0.1$) in three species, moderate ($0.1 < R^2_m < 0.3$) in nine species, and good ($R^2_m > 0.3$) in four species (Table 2, Figs. S3-S4). The best set of models explaining the variation in the number of vertebrae included variables representing precipitation, temperature and primary productivity (Table 2). The best models differed between species, and there was some uncertainty regarding the selection of the best models for several species (Table S1). For 44% of the 16 species with models, the weight of evidence for precipitation and aridity was predominant, temperature features were dominant for 31% of species, while for 19% temperature and precipitation variables played a comparable role (Table S3). Precipitation during the outdoor activity period (autumn to spring) was consistently included in the models for cave salamanders (*Hydromantes*), while patterns were more heterogeneous in the other genera.

The few species for which we did not detect any relationship with bioclimatic variables tended to be those with the smallest ranges, although we still detected clear relationships in some of the highly localised species (Table 2). Both marginal and global present responses were more marked in species with large ranges (partial correlations: range area vs. marginal response: $r = 0.62$, $P < 0.001$; range area vs. global response: $r = 0.76$, $P < 0.001$, Fig. 1). For two species (*L. helveticus* and *O. ophryticus*) R^2_m was zero, while R^2_c was 0.3, suggesting

that morphological variation might be caused either by historical factors, or by environmental factors not explicitly accounted here.

Interspecific variation in morphological response and resistance to climate change

Each species' morphological response to climate change was estimated as the mean relative change in the predicted number of vertebrae between current and future conditions. The future morphological response was highly variable among species and scenarios, ranging between 0.04% and 7.3% (Fig. 2a, Table S4). The future morphological response tended to increase in the most severe emissions scenarios (Fig. 2). Despite a high level of variability in the response (Fig. 2), the overall pattern was highly consistent across the different scenarios, as the species expected to have the most marked future response were consistently identified in all the scenarios (Spearman's correlations of future morphological response between scenarios always > 0.75).

Ensemble forecasting of species distribution models was used to evaluate potential changes in the species' environmental suitability. The quality of the ensemble models was very good to excellent (Fig. S5). Exposure to climate change was a good predictor of the future morphological response. The species subjected to the highest levels of exposure (i.e., the ones suffering the strongest suitability changes under the climate change scenarios) were those which showed the most pronounced projected response in terms of morphology ($F_{1,89} = 18.2$, $P < 0.0001$, $R^2_m = 0.13$, Fig. 2b). For this analysis, a random intercept model was used because random slope models showed convergence problems, and the variance of random slope was 2.2×10^{-12} .

We tested the support of different predictors of resistance to climate change: geographical range (as widespread species often have broad ecological niches, and are thus hypothesised to better withstand climate change; Slatyer *et al.*, 2013), and the extent of present-day morphological response (either marginal or global). Present global response was the best predictor of resistance to climate change (Fig. 3), while the relationships between resistance and range size or marginal responses were weaker (Table 3). Major axis regression confirmed the results obtained using standard mixed models (Table S5).

Morphological response to climate change: intraspecific variation

For each species, we identified the areas where the most marked morphological response could be expected. Within the species' ranges the future morphological response was highly heterogeneous (Fig. 4, Fig. S6). For the 15 species with significant relationships between climate and the number of vertebrae (Table 2), we assessed whether the areas with the most marked future morphological response corresponded to those with the greatest variation in suitability, under the seven climate change scenarios. Only 22/105 correlations between morphological response and variation in suitability were significant, and just three of these remained significant after Bonferroni's correction (Table S6). This suggests that these two responses to climate change might be unlinked within the species' ranges. Overall, the most marked future morphological responses are expected to occur in the north-eastern portions of the study area (Fig. 5, Fig. S7), with consistent results across climate change scenarios (Table S7).

Discussion

The possibility of evolutionary responses to climate change is attracting growing interest, although evidence of such adaptive evolution remains limited (Holt, 1990, Carroll *et al.*, 2014, Merilä & Hendry, 2014, Teplitsky & Millien, 2014). Phenotype-environment correlations, investigating multiple potential drivers over broad scales, may provide important insights, but can only focus on traits with a strong genetic basis (Merilä & Hendry, 2014). Our study represents one of the first large-scale evaluations of potential evolutionary changes in response to climate change. This analysis was possible due to the genetic basis of among-population differences in NTV (Jockusch, 1997), the strong evolutionary link between NTV and body size (Fig. S2), and to the close relationships between NTV and climatic parameters in some salamander species (Table 2).

Species showing strong morphological responses to the climatic variation currently occurring within their range may better resist climate change (Fig. 3). The possibility that present-day capacity for local adaptation might help the resistance to climate change is an intriguing new hypothesis that can be integrated into analyses of the impact of global changes. Dispersal may be essential to spread favourable adaptations across populations (Bell & Gonzalez, 2011). However, if there are high levels of heterogeneity regarding adaptations the arrival of maladapted individuals may reduce fitness and impede rapid evolutionary changes to adapt to new conditions (Schiffers *et al.*, 2013). Our approach highlights the complexity of making evolutionary predictions, given the heterogeneity of interspecific responses and the complex spatial patterns of variation (Fig. 4).

Correlative analyses, such as phenotype-environment correlations and species distribution models have their own limitations. First, demonstrating a relationship with present-day data does not necessarily mean that the same effect will hold in the future (Merilä & Hendry, 2014). Second, the strength of relationships between present-day climate and morphological variation was highly heterogeneous among species, with some showing strong relationships, and others showing weaker or no effects. Relationships were often weak in species with very small geographical ranges, where populations experience less geographical variation for climatic conditions (Fig. 1, Table 2). The robustness of our conclusions might thus be variable among species. Third, the GCM and emission scenarios show high variability, and this determines variation in the expected morphological responses. For instance, the strongest future morphological responses are expected to occur in the north-eastern portions of the study area, but this trend is weaker in the less severe emission scenarios (Fig. S7). Model averaging and ensemble forecasting are some of the best approaches to account for the multiple uncertainties among models and future scenarios (Burnham & Anderson, 2002, Araujo & New, 2007), and our overall conclusions remain robust to multiple scenarios. Fourth, our analyses tested simple linear or quadratic relationships between present-day morphology and climate, but responses may be more complex, and extrapolations may be particularly uncertain when climate is projected beyond the current range of variability. Fifth, our models were built at rather fine spatial scales (if possible, 1-km resolution), but many amphibians select microhabitats at even finer scales (e.g. Ficetola *et al.*, 2013b). These microhabitats may have environmental conditions different from the ones estimated from broad-scale bioclimatic layers, such as mean temperature (Scheffers *et al.*, 2014), and might

act as micro-refugia, buffering against climate change effect (Dobrowski, 2011). More research is needed to assess how microhabitat selection may influence species resistance to global changes. Finally, NTV variation is only one piece of the evolutionary response puzzle, and species can employ other strategies to cope with change (e.g. behavioural changes, microhabitat shifts, evolution of other physiological or morphological parameters, etc.). Testing the reliability of our predictions would be challenging. Comparisons with fossils from periods with different climatic conditions may be an option (e.g. Fouquet *et al.*, 2010, Maiorano *et al.*, 2013), even though the number of fossil remains of urodeles is limited, and their taxonomic assignment often difficult (D'Orazi Porchetti *et al.*, 2012). Although we cannot state with certainty that our set of species will evolve as predicted, we do provide a new path for jointly exploring evolutionary and distributional responses to climate change.

Measuring the amount of variation explained by mixed models is not an intuitive task, and it is only recently that generalizable and consistent methods have been developed (Nakagawa & Schielzeth, 2013, Johnson, 2014). Given the structure of mixed models, the present-day morphological response should be quantified by jointly using two parameters (R^2_m and $R^2_{m^*}$), as both convey unique information (Nakagawa & Schielzeth, 2013). Marginal morphological response (i.e., R^2_m) was the amount of morphological variation solely determined by the analysed climatic parameters, after taking into account the population- and clade-level variation. Conversely, the global morphological response (R^2_C) was the overall amount of explained variation, and also taking into account population- and clade-level effects. Differences between marginal and global morphological response were variable among species. In some case, marginal and global responses were nearly identical, but in nearly half of species the global response showed considerably higher values (Table 2). This might occur because of multiple processes, such as genetic variation determined by historical or stochastic processes, or adaptation to parameters not considered in this study (e.g. features of aquatic or underground habitats). Species with broad geographical range generally exploit broader niches and are expected to better withstand climate change (Slatyer *et al.*, 2013).

However, resistance to climate change was more strongly related to the global morphological response than to the extent of species range (Table 3). This suggests that the species showing the strongest morphological response also exploit the broadest niches, and this may improve their persistence under climate change.

Morphological response to bioclimatic variables was highly heterogeneous among species. Such heterogeneous responses were somewhat expected. Previous studies on the evolution of body size in amphibians have reported highly contrasting patterns, as some closely related species sometimes show opposite responses to the same climatic variables (Adams & Church, 2008): such heterogeneity in the responses may arise because each species is subjected to different evolutionary pressures (Ficetola *et al.*, 2010). However, identifying evolutionary processes determining body size variation is challenging, as body size is a highly plastic trait (Merilä & Hendry, 2014, Teplitsky & Millien, 2014). The pattern obtained through the analysis of the number of trunk vertebrae, a trait that is mostly genetically determined, was highly heterogeneous among species, and this result was

consistent with body size analyses (Adams & Church, 2008). For instance, some newt species showed a positive relationship between NTV and temperature, while others showed negative or no relationships (Table 2). This supports the idea that no general rules of body size evolution exist for ectotherms, as multiple evolutionary processes are at play (e.g. Table 1), and the importance of such processes is highly heterogeneous across species.

Species may persist under dramatic environmental changes by migrating towards newly suitable areas or through the evolution of new adaptations. However, species persistence requires a rate of adaptation that outpaces that of environmental change, and fast adaptation is only possible if populations harbour enough standing genetic variation (Holt, 1990). Morphological variability among individuals was frequent within the study populations, suggesting the existence of some genetic variation, but the within-population variability was still consistently lower than the overall variability across populations (Fig. S8). In practice, both evolutionary adaptations and migration would require a relevant flow of individuals, either across populations or towards new areas. Unfortunately, successful range shifts are unlikely for small vertebrates with limited dispersal due to the extreme fragmentation of habitats and gaps in climate paths (Araujo *et al.*, 2006, Early & Sax, 2011), thus more active management actions may be needed. Conservation biologists stress the importance of “evolutionary significant units” that should be independently managed to preserve intraspecific genetic variability and the evolutionary future of species (Latta, 2008). Our study offers new perspectives on how species with more variability might better withstand the challenge of climate change, but also poses conservation dilemmas. Species management might require the introduction of individuals showing adaptations to future climate conditions (Carroll *et al.*, 2014), but in turn this could lead to genetic homogenisation among populations and a loss of variability. Since the genetic variability underpinning local adaptations is often underappreciated, translocations may lead to unwanted loss of adaptations (Ficetola & De Bernardi, 2005, Latta, 2008). Managers may be faced with the trade-off between the risk of species extirpation, and the struggle to maintain intraspecific variation. Providing detailed evolutionary information to answer this dilemma will be a major challenge in the coming years.

Supporting Information

Refer to Web version on PubMed Central for supplementary material.

Acknowledgments

We thank V. Popescu, D. Moore, I. Auger and three reviewers for insightful comments on previous versions of the manuscript. GFF was partially funded by a grant of Univ. Milano-Bicocca. WT and JR received funding from the European Research Council under the European Community’s Seven Framework Programme FP7/2007- 2013 Grant Agreement no. 281422 (TEEMBIO). The LECA is part of Labex OSUG@2020, which supported this work (Investissements d’avenir – ANR10 LABX56). This paper is dedicated to Beatrice.

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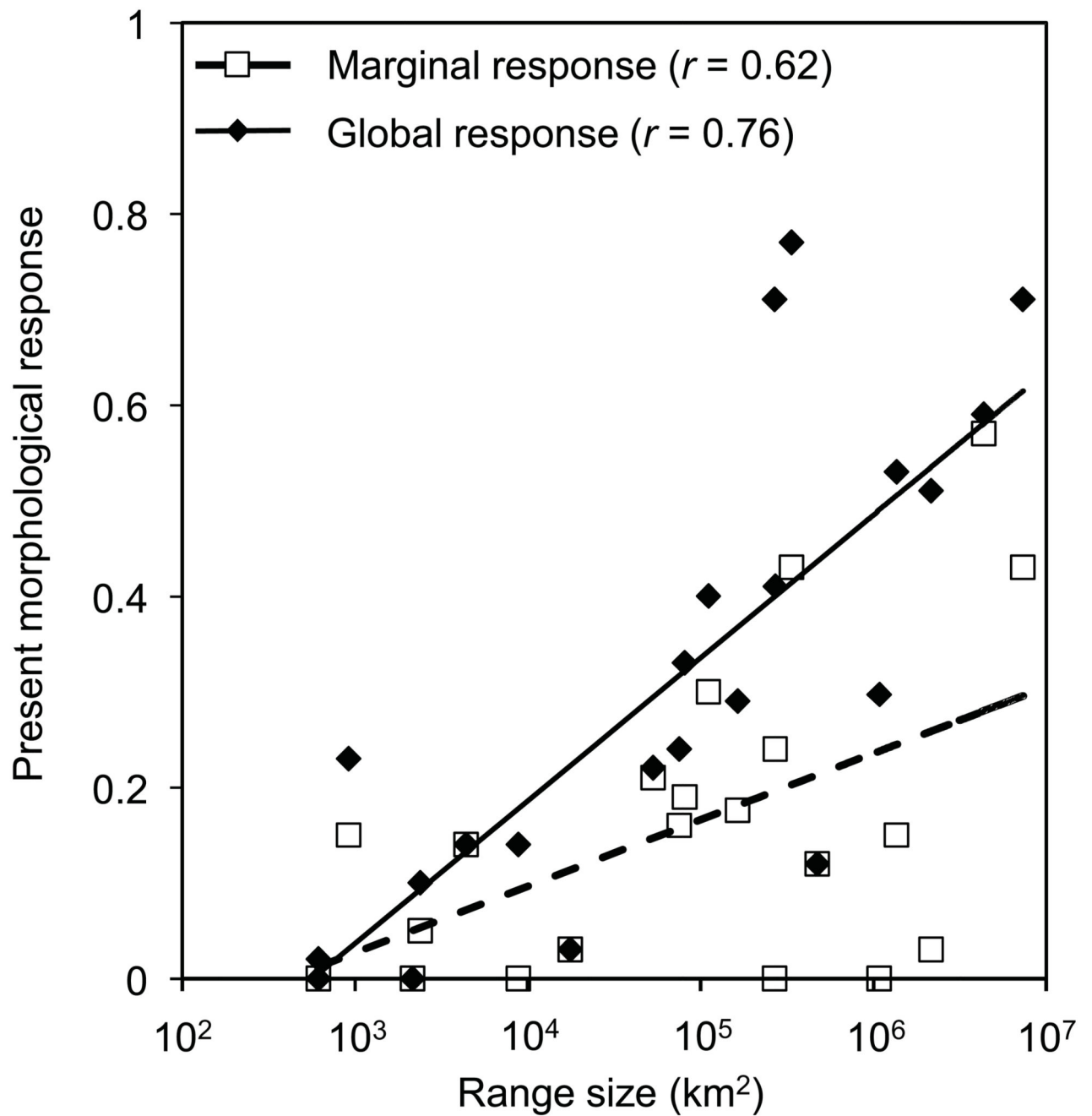


Figure 1. Current morphological response (R^2) in 22 species of salamanders. Relationship between range size, marginal and global present-day morphological responses.

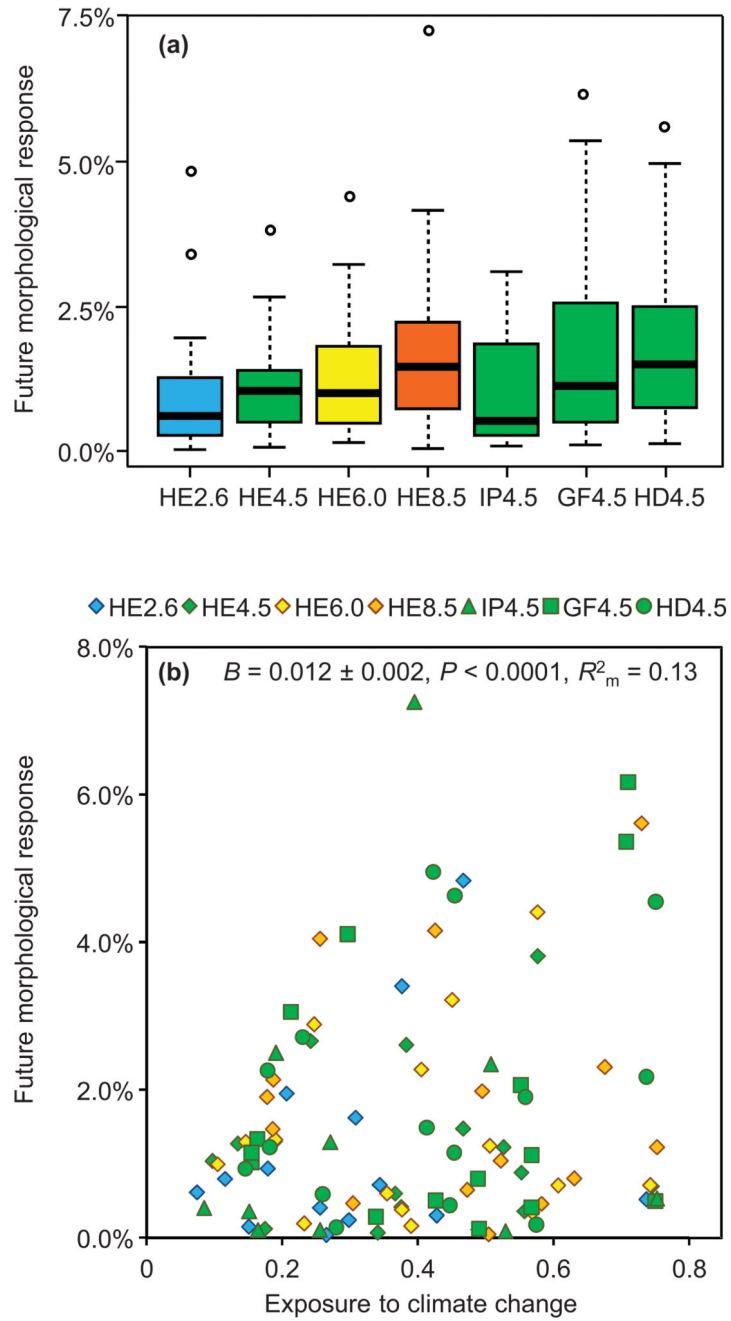


Figure 2. (a) Future morphological response expected under seven scenarios of climate change. (b) Relationship between exposure by climate change (i.e. the average variation in climatic suitability across the range) and future morphological response, under seven climate change scenarios. Different colours and symbols represent distinct emission scenarios and global circulation models, as depicted above the (a) panel.

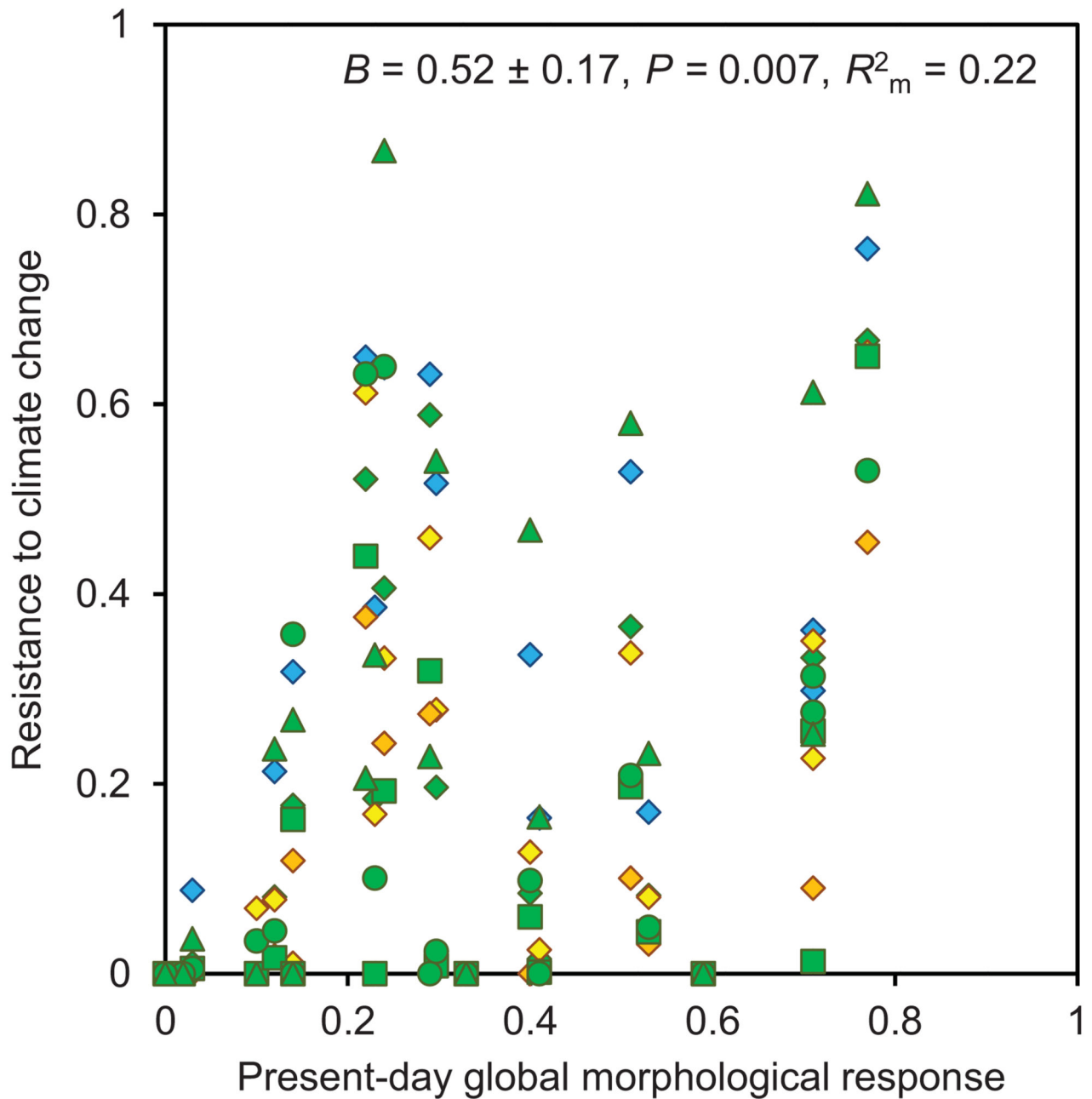


Figure 3.

Relationship between present-day global morphological response (R_c^2) and resistance to climate change (i.e. the proportion of species range that remains suitable). Different colours and symbols represent distinct emission scenarios and global circulation models, as depicted above the panel.

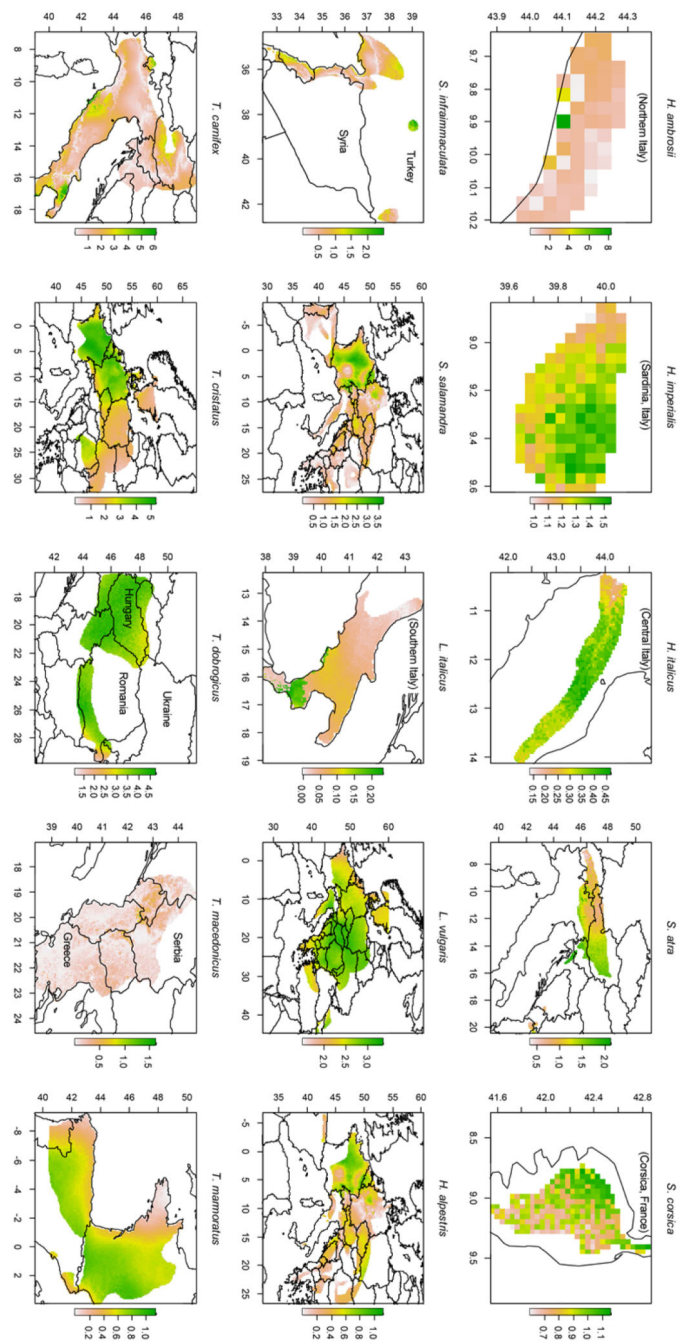


Figure 4.

Intraspecific variation in morphological response (%) expected in 15 salamander species under the climate change scenario HE4.5. See Fig. S6 for patterns under different climate change scenarios. Panels represent different areas and have very heterogeneous scales; the figures on the margins of each panel represent the geographic coordinates (lat-long) of each area.

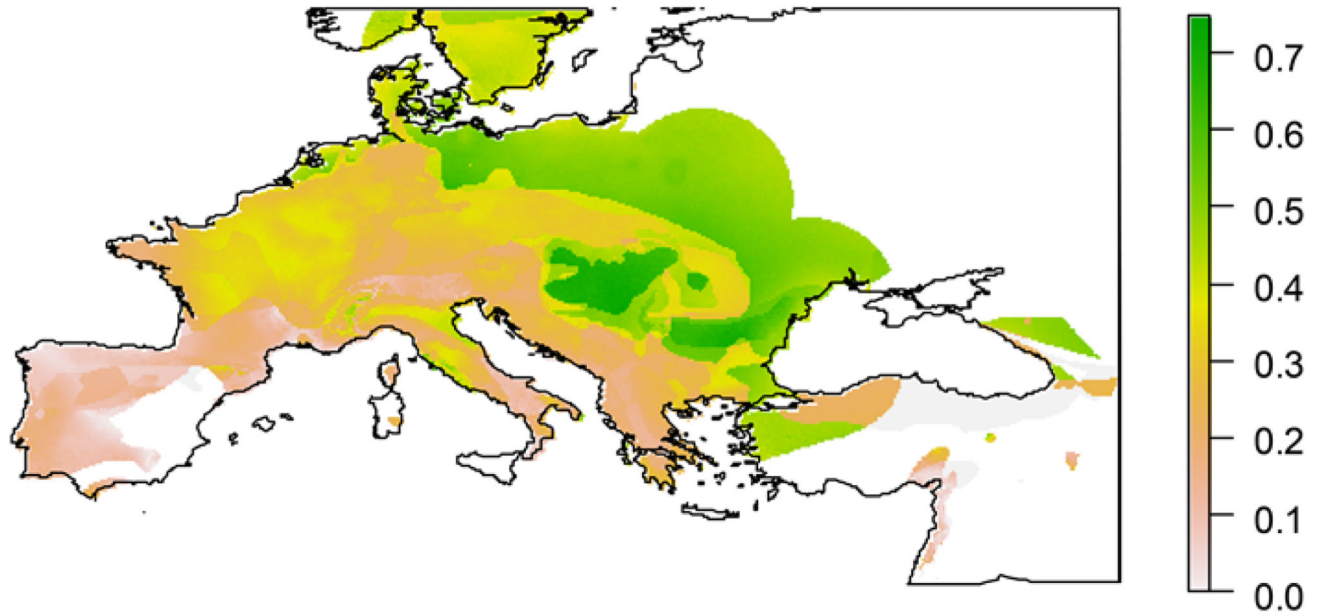


Figure 5.

Intraspecific variation in morphological response averaged across multiple salamander species, and across seven climate change scenarios. The map is the average of the expected morphological responses under seven GCM and emission scenarios, each standardized between 0 and 1. See Fig. S7 for the expected responses under each of the seven scenarios. For each scenario, expected morphological responses are the average of all the species showing a relationship between number of vertebrae and ecogeographical variables, plus the species not showing a relationship with eco-geographical variables, but with range > 100 000 km².

Table 1

Proposed evolutionary processes linking body size evolution to environmental variables variation in amphibians. Multiple processes can also interact, thus leading to complex and nonlinear relationships. See also Ficetola *et al.* (2010) for additional details.

Hypotheses	Proposed process	Implicated bioclimatic variable(s) considered in this study
Heat balance	Large body size advantageous for thermoregulation in cold environments because increases thermal inertia (Olalla-Tárraga & Rodríguez, 2007)	Mean temperature
Endurance	Large body size favoured in areas with high thermal excursion, because it is associated to more fat reserves (Ashton, 2002)	Thermal excursion
Seasonality	Large body size favoured in areas with long growing season (Mousseau, 1997, Schutze & Clarke, 2008)	Temperature, thermal excursion, precipitation seasonality*
Starvation resistance	Large individuals have more reserves and can better survive during periods of food shortage, thus large body size is favoured in seasonal/cold environments where animals are inactive for long periods (Arnett & Gotelli, 2003, Ashton & Feldmann, 2003)	Temperature, thermal excursion, precipitation seasonality*
Water availability	Large body size is favoured in dry climates because it reduces desiccation tolerance (Ashton, 2002)	Precipitation, aridity
Primary productivity	Evolution of large body size favoured in more productive environments, where food supply is higher (Olalla-Tárraga & Rodríguez, 2007, Ficetola <i>et al.</i> , 2010)	Normalized Difference Vegetation Index (NDVI)

*amphibian activity depends on both temperature and water availability

Table 2

Study species and variables selected by the best-AIC models. See Tab. S1 for a complete list of candidate models and their weights. *N*: number of populations / individuals for each species; (+): positive relationships; (-): negative relationships; (Q): quadratic relationships. Mean and range of the number of vertebrae for each species are reported in Tab. S6.

Species	<i>N</i>	Range area (km ²)	<i>R</i> ² _m	<i>R</i> ² _c	Variables in the best AICc model
<i>Hydromantes ambrosii</i>	14/84	920	0.15	0.23	Precipitation seasonality (+), Precip. Sept-May (Q)
<i>H. flavus</i>	10/42	616	0	0	
<i>H. genei</i>	15/123	2155	0	0	
<i>H. imperialis</i>	13/116	2391	0.05	0.10	Precipit. Sept-May (-), Temp. annual range (+)
<i>H. italicus</i>	19/100	17675	0.03	0.03	Precipit. Sept-May (+)
<i>H. strinatii</i>	42/315	8836	0	0.14	
<i>H. supramontis</i>	12/87	616	0	0.02	
<i>Salamandra atra</i>	9/45	111164	0.30	0.40	Temp. diurnal range (-), Winter precipit. (-)
<i>S. corsica</i>	11/43	4413	0.14	0.14	Temp. mean (-), Temp. diurnal range(+)
<i>S. infraimmaculata</i>	14/599	80949	0.19	0.33	Temp. annual range (Q)
<i>S. salamandra</i>	89/2679	2162890	0.03	0.51	Precip. Seasonality (Q)
<i>Lissotriton helveticus</i>	9/55	1082200	0	0.30	
<i>L. italicus</i>	13/114	75324	0.16	0.24	Winter precip. (+), NDVI (Q)
<i>L. vulgaris</i>	40/276	7340650	0.43	0.71	Aridity (+), Temp. mean (-)
<i>Ichthyosaura alpestris</i>	40/326	1364076	0.15	0.53	Precip. seasonality (+), NDVI (Q)
<i>Ommatotriton ophryticus</i>	9/80	268433	0	0.71	
<i>O. vittatus</i>	13/49	53232	0.21	0.22	NDVI (-)
<i>Triturus carnifex</i>	28/300	337089	0.43	0.77	Summer precip. (Q), Winter precip. (+)
<i>T. cristatus</i>	18/142	4366886	0.57	0.59	Temp. annual range (+), Winter precipit. (+)
<i>T. dobrogicus</i>	14/127	272023	0.24	0.41	Temp. mean (+), Temp. diurnal range (+)
<i>T. macedonicus</i>	17/341	163791	0.15	0.30	Aridity (Q), NDVI (+)
<i>T. marmoratus</i>	13/47	474709	0.12	0.12	Aridity (-)

Table 3

Comparison of potential predictors of resistance to climate change across salamander species. All models are mixed models, including species identity and climatic scenarios as random factors.

Model rank	Predictor	<i>F</i>	d.f.	<i>P</i>	R^2_m	AICc
1	Present global response	9.15	1,20	0.007	0.22	0
2	Geographical range	4.32	1,20	0.051	0.17	5.62
3	Present marginal response	3.38	1,20	0.081	0.10	10.56
4	Null model	-	-	-	-	40.66