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Why mountain passes are higher … for endemic amphibians and reptiles

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Crossing dispersal barriers with hostile environments is difficult for species with low environmental tolerance. Thus low environmental tolerance could result in small geographic ranges. In the case of mainland biotas, where mountain ranges are important dispersal barriers, this means species range size would decrease with the species inability to tolerate high altitude conditions. This idea predicts endemic species are more sensitive to elevational barriers than non-endemic species, other things being equal. Here, I test this prediction in the Mediterranean herpetofauna (southern Europe), using reported maximum altitude as a surrogate for tolerance to altitude. After correcting for sampling effects (influence of range size on reported altitude), phylogeny, and topographic biases (regional availability of maximum altitudes), a strong pattern is revealed: endemic amphibians and reptiles reach lower maximum altitudes than non-endemic counterparts. This suggests range size is controlled by the species ability to cross elevational barriers. Available data suggest this may be a general trend among endemics from mainland biotas.

Introduction

What affects species' geographic range sizes? This is a key question in ecology and biogeography (Brown 1995, Brown *et al*. 1996, Gaston 1998, Gaston and Blackburn 2000), since range size affects species ecological impacts, the origin of new species (Rosenzweig 1995, López-Villalta 2012) and extinction (Payne & Finnegan 2007). We can recognize three main factors influencing range size:

1. Dispersal ability: other things being equal, species whose propagules usually cover large distances would have large range sizes compared with species with poor dispersal ability. This is a very popular idea which holds well for fossil marine gastropods (Jablonski 1986), a group in which shell morphology reveals whether the larva was planktonic and thus, indirectly, the species dispersal ability. Range size also tends to increase with dispersal ability in *Chionochloa* grasses (Lloyd *et al*. 2003), *Sylvia* warblers (Böhning-Gaese *et al*. 2006), carabid beetles (Juliano 1983), Mediterranean littoral fishes (Macpherson & Raventos 2006) and marine endemic fishes from Hawaii (Eble *et al*. 2009). However, Lester *et al*. (2007) found no relationship between range size and dispersal abil-

ity, although potential phylogenetic biases weaken their results.

2. Time for dispersal: from speciation onwards, species disperse thus potentially increasing its geographic range. Hence, the older the species (evolutionary age), the larger its range size could be (Willis 1922). This prediction is generally not supported by available evidence. For example, in the taxon cycles of the Lesser Antillean bird fauna, the rule is that range size decreases with the age of endemic species (Ricklefs & Bermingham 2002). For bird species worldwide, range size does not tend to increase with species age: bird species usually achieve their largest ranges at intermediate evolutionary ages (Webb & Gaston 2000). The same pattern is observed in Cenozoic marine mollusks from New Zealand (Foote *et al.* 2007).
3. Environmental tolerance (niche breadth): a species which is able to survive and reproduce under a wide variety of environmental conditions (including the biotic environment) would also be able to cross dispersal barriers with relatively hostile conditions, or areas whose environment is “seen” by other species as hostile and thus as a dispersal barrier. Therefore, the higher the environmental tolerance of a species, the larger its expected geographic range (Brown 1995). A strong influence of environmental factors on species ranges matches well with the close correspondence between climate and ecoregion worldwide, although evolutionary history is also considered for ecoregion delimitation (Olson *et al.* 2001). At the regional scale, tolerance to soil water content is higher in grass species with larger ranges in New Zealand (Lloyd *et al.* 2003), and latitudinal range size increases with thermal tolerance in European aquatic beetles (Calosi *et al.* 2010). But biotic factors could also matter; for example, caterpillar dietary breadth is the best predictor of species range size in sphingid moths from the Indo-Australian tropics (Beck & Kitching 2007).

In mainland biotas, mountain ranges are important dispersal barriers which “prove” species environmental tolerance by means of hostile ecological conditions driven by altitude — essentially low temperatures, but also temperature extremes, desiccating winds, etc. (Hesse 1943, Huggett 1998). The role of mountains on range limitation is understandable when we consider that most extant species descend from tropical ancestors (Darlington 1957, Wiens & Donoghue 2004), who were probably adapted to the warm thermal regime of the tropics, thus being sensitive to high altitudes — a sensitivity which would have been inherited by many of their descendant species (tropical niche conservatism, Wiens & Graham 2005).

Adaptation to warm climate would make mountain passes harder to cross for tropical species, an idea which was proposed by Janzen (1967) in a controversial paper with a revealing title: “Why mountain passes are higher in the tropics”. Paraphrasing Janzen, in this work I will test whether mountain passes are higher for endemics, that is, if small range size is associated with low altitudinal tolerance. This hypothesis is supported by some evidence: endemic snails from Andalusia (S. Spain) tend to reach lower altitudes than their non-endemic relatives (López-Villalta 2011). Here, I address this hypothesis at a larger spatial scale and for different organisms, namely amphibians and reptiles from the Mediterranean Region (southern Europe).

In this work, the Mediterranean Region is considered to be the temperate region with summer drought which surrounds the Mediterranean Sea (*see* Emberger 1930, Blondel & Aronson 1999, Quézel & Medail 2003, Thompson 2005). The mainland of this region is a complex array of elevational barriers of the Cenozoic, the Alpine range (Pyrenees–Alps–Dinaric Alps), which extends along the west–east axis isolating three large peninsulas (Iberia, Italy and Greece). These peninsulas acted as glacial refuges during the Pleistocene ice ages and are centres of origin for many endemic taxa (Blondel & Aronson 1999, Médail & Diadema 2009). Other mountain ranges — such as the Central System and Sierra Nevada (Spain), Apennine Mountains (Italy), Pindus (Greece) and Atlas Mountains (North Africa) — increase the topographic complexity of the region. These mountains, especially the Alpine range, are themselves centers of origin for many endemics and act as key dispersal barriers for many Mediterranean species (Blondel & Aronson 1999, Thompson 2005).

The richness of narrow-ranged endemics is the most outstanding feature of the Mediterranean biota (Blondel & Aronson 1999, Thompson 2005). For example, there are 63 species of amphibians and 165 of reptiles living in the northern bank of the region, of which 37 and 113 are endemics, respectively (Cheylan & Poitevin 1998). This means that 58.7% of the amphibians and 68.5% of the reptiles are endemics. These are the highest endemism levels known among the Mediterranean vertebrates (*see* Blondel & Aronson 1999). Many endemic amphibians and reptiles are island endemics, but there is also a high level of endemicity in the topographically complex mainland (Cheylan & Poitevin 1998).

Material and methods

The method consists of a corrected comparison (correcting for sampling effects, phylogeny and topographic biases) of maximum altitude between endemics and non-endemics. The data for reported maximum altitude were taken from Arnold and Ovenden (2007).

Reported maximum altitude is subjected to a sampling effect: species with a large range are more likely to have been found at higher altitudes simply because their ranges may cover more mountains and thus more opportunities of being observed at higher altitudes than that of species with narrower ranges but equal sensitivity to altitude. This sampling bias was corrected by obtaining the best fit regression model for the relationship between range size and maximum altitude, and then extracting for each species the difference between observed maximum altitude and that predicted by the model. In this correction, range sizes were measured for mainland herptiles from the Mediterranean region of Europe using the distributional maps in Arnold and Ovenden (2007) and a grid of quadrates of 200 × 200 km. The best fit regression model was selected from among linear, exponential, logarithmic, potential and polynomial models, and combinations of all of them. The residuals of maximum altitude with respect to the best fit model were taken as range-size-corrected data.

Phylogeny is another possible source of error (one lineage may have produced many altitude-insensitive endemics thus distorting the overall pattern). It was controlled by comparing pairs of closely related species at the genus level or below: one endemic taxon *versus* one non-endemic counterpart. This is recognized by Felsenstein (1985) as an elegantly simple method to control phylogenetic inertia. This procedure is usual when studying endemics (Thompson 2005), Mediterranean endemics included (Lavergne e*t al*. 2004, López-Villalta 2010, 2011).

Island endemics were excluded because their particular ecology could introduce confusion in the analysis (*see* Blondel & Aronson 1999 for ecological trends of Mediterranean island endemics). Mainland endemics are a more ecologically homogeneous group to focus in on the analysis.

The non-endemic relative of each endemic was selected following two criteria: (1) the taxon is as widespread as possible inside and outside the Mediterranean Region (i.e., is as "non-endemic" as possible, which strengthen the comparison), and (2) the taxon range overlaps with the endemic range as much as possible (the aim of this is to homogenize the environment in the comparison). With these criteria, I am isolating the factor of being a Mediterranean endemic as the main possible explanation for any pattern revealed in the comparison (*see* the same method in López-Villalta 2010).

After this selection process, I only included in the comparison those endemics whose geographic range clearly contains altitudes higher than that of the corresponding non-endemic relative (topographic maps were consulted). In this way, the lack of high elevations in endemic ranges cannot be invoked as an explanation to any altitudinal restriction in endemics. Notice this simple method rules out dispersal ability and the time-for-dispersal factor: if endemics reach lower altitudes than non-endemics, this will not be because endemics are currently not able to find higher altitudes than non endemics due to their present stage in range size dynamics. Thus the method will test the hypothesis of environmental tolerance only.

After all these corrections, the residuals of maximum altitude of endemics were compared

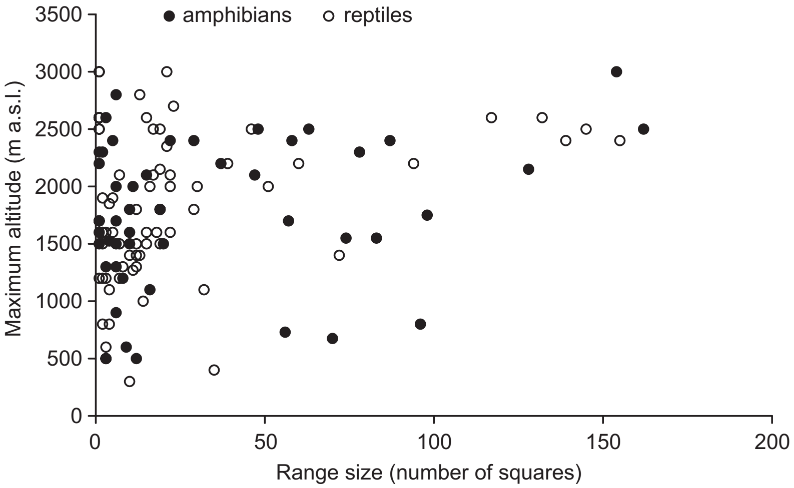

Fig. 1. Maximum altitude *vs.* range size in amphibians and reptiles from the Mediterranean Europe.

with those of non-endemics. If endemics are more sensitive to altitude, their residuals will be consistently lower than that of their corresponding non-endemic relatives. I counted the number of cases which satisfied this condition, and then I calculated the binomial probability of obtaining this number of "successes" assuming equal probabilities for the endemic to have either lower or higher value (corrected maximum altitude) than its non-endemic relative. This implies a random-walk evolution model for altitude sensitivity, with probabilities of 0.5 either for decreasing or increasing from ancestral values. If the calculated binomial probability is below 0.05, it will be taken here as evidence that endemics tend to have different sensitivity to altitude as compred with non-endemics (thus as usual, $\alpha = 0.05$).

Results

Fifteen pairs of endemic/non-endemic taxa were selected from the entire herpetofauna of Mediterranean Europe (Table 1). The variance of maximum altitude data changes with range size (Fig. 1), and this could introduce problems of heteroscedasticity when correcting for the sampling effect. This problem is decreased using log-transformed maximum altitude. The best-fit model for the relationship between maximum altitude (MA) and range size (R) in amphibians is:

$$\log_{10}(\mathrm{MA}) = 6 \times 10^{-6}R^2 - 6 \times 10^{-4}R + 3.1791 \quad (1)$$

and in reptiles is:

$$\log_{10}(\mathrm{MA}) = 5 \times 10^{-6}R^2 - 5 \times 10^{-4}R + 3.2226 \quad (2)$$

These models little explain the variance in the data ($r^2 = 0.08$ and 0.07, respectively). In both models, the residuals are virtually uncorrelated with range size ($r^2 < 0.001$).

When maximum-altitude data are corrected using these models, all endemics have lower values than their non-endemic counterparts. The binomial probability associated with this result is 0.00003. This highly improbable result means that Mediterranean endemic herptiles tend to be more sensitive to altitude than expected by chance. This conclusion will not change even if we reject the use of the sampling correction due to the poor fit of the models (Eqs. 1 and 2): using the crude data (Table 1), 14 out of 15 endemics have lower maximum altitude than their non-endemic relative, which yields a binomial probability of 0.0005.

Discussion

The results point that in Mediterranean herptiles range size is controlled by environmental tolerance: endemics (narrow range) are more sensitive to altitude thus being less able to cross mountain ranges. The same relationship was found in snails from Andalusia (S Spain) (López-Villalta 2011) and, among the Mediterranean mammals, at least in some genera (the shrews *Sorex* and *Crocidura*, the voles *Microtus*).

These examples suggest that the dependence of range size on altitude sensitivity may be a general trend in mainland biotas. This is also suggested by the north–south and west–east dimensions of species ranges. In North American reptiles, birds and mammals, the north–south dimension of narrow ranges tend to be greater than their west–east dimension, but the opposite is found for narrow ranges of European birds (Brown 1995: 163–165). This may be a response to multiple and simultaneous causes (Brown 1995), but one of the most outstanding is that narrow ranges would be limited by mountain barriers, which tend to follow the north–south axis in North America and the west–east axis in Europe. Thus the geographic ranges of altitude-sensitive species are expected to be smaller in the crossing direction, i.e. west–east in North America and north–south in Europe, and this is exactly what is observed in narrow ranges. This biogeographic pattern fits well the results reported here (higher sensitivity to altitude in endemics).

Large species-ranges do not seem to follow the direction of mountain ranges, since their west–east dimension tend to be greater than their north–south dimension in North America and Europe. This is not surprising provided that species with large ranges are more altitude tolerant, as the present work reveals. Being more tolerant, wide-ranged species would not be as limited by mountain ranges as narrow-ranged species. Wide-ranged species are probably not confined by altitudinal sensitivity but by latitudinal changes in abiotic factors. Thus two different dynamics can be hypothesized for mainland species-ranges: altitudinal limited (endemics) *vs*. latitudinal limited (large ranges).

The tempo and mode of the relationship between elevational barriers and endemic ranges is debatable. According to the hypothesis by Janzen (1967), high sensitivity to altitude would result from specialization to higher-temperature regimes, which is expected in organisms adapted to tropical climates. From the warm climate of the Eocene onwards, the northern hemisphere has cooled until the Pleistocene glaciation (Stanley 1999, Thompson 2005). Since the Mediterranean herpetofauna is quite ancient, with most lineages being established from the Eocene to the mid-Miocene (Blondel & Aronson 1999), then the most parsimonious history of

Table 1. Species pairs included in the comparison.

Non-endemic species	Max. altitude (m a.s.l.)	Endemic species	Max. altitude (m a.s.l.)	Where could the endemic reach higher altitudes than the non-endemic?
Salamandra salamandra[1]	2500	*S. terdigitata*	1500	Western Apennines
Triturus marmoratus	2100	*T. carnifex*	1800	Apennines, Alps, Dinaric Alps
Lissotriton vulgaris	2150	*L. italicus*	1525	Central Apennines
Alytes obstetricans	2400	*A. dickhilleni*	2300	Sierra Nevada
Pelodytes punctatus	1500	*P. ibericus*	900	Sierra Nevada
Hyla arborea	2300	*H. meridionalis*	1000	Eastern Pyrennees
Rana dalmantina[2]	1700	*R. italica*	1700	Central Apennines
Rana perezi[3]	2400	*R. epeirotica*	500	Pindus
Emys orbicularis	1400	*Mauremys leprosa*	1000	Many inner Iberian mountains
Lacerta viridis and *L. bilineata*[4]	2200	*L. trilineata*	1500	Pindus
Podarcis muralis	2500	*P. sicula*	2000	Alps, Central Apennines
Chalcides striatus	1800	*C. chalcides*	1270	Central Apennines
Anguis fragilis	2400	*A. cephalonicus*	1200	Peloponnese
Hierophis caspius	1600	*H. gemonensis*	1400	Pindus, Rhodope Mountains, Dinaric Alps
Zamenis longissimus	2000	*Z. lineatus*	1600	Southern Italy, Sicily

[1] the closest relative of *Salamandrina* among the non-endemic Mediterranean salamanders (Zhang *et al.* 2008); [2] brown frogs; [3] green frogs; [4] considered the same species (*see* Arnold and Ovenden 2007).

adaptation to temperature regime would be that altitude-sensitivity is an ancestral state in these amphibians and reptiles. In this scheme, Mediterranean endemics are expected to be basal in phylogenies with respect to their non-endemic relatives. The presence of some archaic relicts among the Mediterranean endemic herpetofauna supports this option — for example, *Salamandrina terdigitata* is the most basal known member of the family *Salamandridae* (Zhang *et al*. 2008). However, there are also endemics which seem definitely derived, such as the toad *Alytes dickhillenii* (Martínez-Solano *et al*. 2004). Thus, further work is needed to clarify this subject.

The high sensitivity to altitude in Mediterranean endemics raises the possibility that current global warming would reduce their extinction risk. The reason is that global warming would weaken the barrier effect of mountain ranges by increasing the temperature at any given altitude. Thus altitude-sensitive species would find that mountain passes became “lower” due to global warming. Eventually, some of them would be able to cross the mountain ranges that previously limited their geographic range. With a suitable habitat, they would expand their ranges and this would mean a reduced extinction risk, since range size is one of the most critical factors affecting the probability of extinction (Brown 1995, Brown *et al*. 1996, Gaston 1998), may be the key factor (Cardillo *et al*. 2005, Payne & Finnegan 2007). Araújo *et al*. (2006) provides additional support to the idea that climate warming may be less dangerous than previously thought (Thomas *et al*. 2004) for European amphibians and reptiles. Anyway, these predictions depend on dispersal ability and habitat availability, and thus caution is recommended.

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