NOTE: COMMENTS ARE APPENDED TO THIS PAPER

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Geographic range size and speciation in Mediterranean land birds

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ABSTRACT

Background: Theory suggests that speciation rate should be a unimodal, monotonically decreasing or monotonically increasing function of range size. But few data exist to test these options adequately.

Goal: To develop and use a method to investigate the relationship between a species range size and its probability of speciation.

Data description: Extant species of Mediterranean land birds, their phylogeny, and their geographical distributions.

Method: For each endemic, select a candidate ancestor, i.e. its closest relative in the phylogeny. Accumulate a dataset of range sizes of all possible ancestors and their relatives within relatively broad clades (e.g. family). The point of the method is to compare the statistical distribution of ancestral range size with that of ancestral relatives to obtain the speciation–range size relationship. The method contains specific corrections for the following potential biases: (1) sampling from the macro-ecological distribution of range size (large ancestral ranges are expected to be more common in speciose clades); (2) phylogenetic inertia (clades may contain many ancestors, and so the analysis focuses at the clade level); (3) sampling effect of species diversity (more ancestors are expected from speciose range-size classes); and (4) wrongly assigned ancestors (since bird range size does not depend on phylogeny, the range size of wrong ancestors would be a random sample from the species pool, and so corrections 1 and 3 serve to erase any noise caused by wrong ancestors). The final outcome of the method is a plot that indicates the speciation–range size relationship. This plot can be tested for departure from a uniform distribution.

Conclusions: The speciation–range size relationship of these birds is unimodal and statistically different from a null, flat distribution. Speciation is more likely for species with intermediate range sizes. This pattern holds for absolute as well as relative range sizes.

Keywords: allopatric speciation, macroecology, macroevolution, Mediterranean region.

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INTRODUCTION

The influence of geographic range size on speciation remains unclear in macroecology and macroevolution. Perhaps the earliest idea on the speciation–range size relationship was that of Darwin (1859), who suggested that speciation should be concentrated in species with large ranges because these species tend to have more subspecies than ones with small ranges. Birds do show a positive relationship between range size and the number of subspecies (Phillimore *et al.*, 2007). But subspecies may or may not evolve to become separate species (*sensu* Grant and Grant, 2008). So there is a missing link in Darwin's argument.

A closer look at this question demands the consideration of four main issues (Gaston, 1998):

(a) Sampling effect of dispersal barriers by range size

Range size affects the opportunities for geographic isolation, which means opportunities for allopatric speciation (Rosenzweig, 1995). Allopatric speciation seems to be the critical speciation mode for explaining biodiversity and its dynamics (Rosenzweig, 1995; Coyne and Orr, 2004). Geographic barriers appear more or less randomly distributed on the Earth's surface, and thus the larger the range of a species, the higher the probability that it encounters a dispersal barrier. This implies a positive speciation–range size relationship (Rosenzweig, 1995). However, some ranges could be so large that they engulf some geographic barriers, which would reduce speciation opportunities. Combining the 'engulfing' effect with an enhanced probability of encountering a barrier yields a unimodal probability of speciation rate against range size, with intermediate ranges having the highest probability of speciation (Rosenzweig, 1975, 1978, 1995). However, unimodality may not be valid, at least in terrestrial biotas, because even the largest species ranges in terrestrial biogeographical provinces may be too small to result in an engulfing effect (Rosenzweig, 1975).

I know of only two empirical results pointing to positive speciation–range size relationships. Wagner and Erwin (1995) examined the influence of species range size on the number of descendants in two clades of Neogene Foraminifera and one clade of Ordovician Gastropoda. They found a positive relationship in forams only; in gastropods, the positive relationship was caused by the confounding effect of species longevity. At a different taxonomic scale, Krug *et al*. (2007) reported that the most speciose genera of marine bivalves, both regional and global, are those that have expanded their range out of the tropics. This suggests a positive speciation–range size relationship at the species level.

(b) Dispersal ability

Species dispersal, *sensu lato*, includes the environmental tolerance that allows the species to cross the hostile environment of a dispersal barrier (e.g. a high mountain range). A species with high dispersal ability would find limited opportunities for effective isolation (Mayr, 1963). Its high dispersal would interfere with the long-term isolation required for allopatric speciation and also facilitate the acquisition of a large geographic range. So high dispersal might produce an inverse speciation–range size curve (Gaston, 1998). We have strong empirical evidence linking dispersal ability and gene flow (Bohonak, 1999), but surprisingly little is known about the relationship between dispersal and range size. Some researchers suggest that dispersal tends to increase range size (López-Villalta, 2011), whereas others have reported no such influence (Lester *et al.*, 2007). Regardless, a link between range size, high dispersal ability, and low speciation rate certainly holds in fossil marine gastropods (Jablonski, 1986), where shell morphology reveals larval dispersal ability (i.e. whether the larva was planktonic).

In line with a strong effect of dispersal on speciation, Jablonski and Roy (2003) found that speciation declines with range size in marine mollusc species from the Late Cretaceous. They also suggested the same pattern holds for living molluscs, since sister group comparisons reveal that mean range size is inversely correlated with the number of species. However, they obtained mean range size as an average of species ranges, thus the approach is inadequate to infer the speciation–range size curve at the species level (which is the most realistic level to address this subject).

(c) Mutation rate

A large range often means higher abundance (Gaston and Blackburn, 2000), which would facilitate the origin of new alleles in the species (this would occur because individual mutation rate is multiplied by the number of individuals). A more rapid appearance of new mutations may increase speciation rate (Rosenzweig, 1995). Some evidence does indicate that particularly small populations hardly evolve (e.g. Greenbaum *et al.*, 1978; Walsh, 1995).

(d) Time-for-speciation effect

Since extinction risk decreases with range size (Raup, 1994), large ranges would have more time for speciation to develop (Gaston, 1998). Thus time-for-speciation predicts speciation rate increases with range size (Gaston, 1998).

Time-for-speciation has been suggested to be a possible explanation for higher numbers of species. Recall that Wagner and Erwin (1995) found a positive speciation–range size relationship among Ordovician gastropods that appears to be the outcome of differential species longevity. Extant genera of marine bivalves show a positive time–species relationship (Krug *et al.*, 2007), which may reflect the same for their underlying species. There is even some evidence that clade age is the main predictor of species diversity among major animal taxa (McPeek and Brown, 2007). Furthermore, in the form of species age, time also explains the number of bird subspecies (Phillimore *et al.*, 2007).

Yet the time-for-speciation effect conflates speciation and extinction, whereas theory and this paper try to measure speciation separately. I will return to this point in the Discussion.

In summary, there are theoretical models that suggest positive, negative, and unimodal relationships between speciation and range size. The sampling of dispersal barriers by the species range, the role of dispersal ability, mutation rate, and the time-for-speciation effect may all shape the patterns. Some empirical work has revealed positive but also negative relationships. Available evidence may be stronger for negative relationships, but the amount and taxonomic scope of these studies is too limited to extract general conclusions.

Empirical studies depend strongly on the fossil record (Wagner and Erwin, 1995; Jablonski and Roy, 2003). To my knowledge, all studies to date dealing with extant species have been indirect, dealing with species–genus ratios (Krug *et al.*, 2007) or means of species ranges (Jablonski and Roy, 2003). Here, I describe and employ a new method based on a more direct approach – that is, the estimation of speciation–range size curves using data from extant species. The critical assumption in the method is that range size is not subject to phylogenetic inertia, a condition that holds for birds, for example (Webb and Gaston, 2003).

In describing the method, I will focus on the origin of endemics within the Mediterranean bird fauna (land species only, in order to homogenize species ecological characteristics).

Many European bird species are fairly restricted to the Mediterranean region (Svensson *et al.*, 2010), but we can be reasonably sure of *in situ* speciation with endemic species only. The Mediterranean region is especially good for speciation studies because its islands, peninsulas, and mountain ranges harbour many endemic plant, invertebrate, and vertebrate species that have originated within the last few million years (Blondel and Aronson, 1999).

THE METHOD

The method can be divided into five steps:

Step 1

Using published phylogenies, assign a candidate ancestor for each endemic species. The candidate ancestor of an endemic species is here defined as its sister species. If the endemic has no sister species but a sister clade, the most similar species within this clade will be taken as the possible ancestor. If the possible ancestor does not live in the Mediterranean region, the endemic will be excluded from the analysis (because no range size can be assigned to its ancestor). Also exclude the endemic if no clear ancestor can be proposed (due to phylogenetic or taxonomic uncertainty). Using these criteria, a wrong ancestor would be assigned if the published phylogeny is wrong, if the real ancestor is extinct, if the endemic is actually the ancestor of the proposed ancestor, or any combination of these circumstances. Wrongly assigned ancestors are ruled out in the following steps.

Step 2

Classify all possible ancestors into phylogenetic lineages (monophyletic families or similarly broad phylogenetic clades). Each lineage will contribute the same to the final results, in order to correct the phylogenetic inertia (i.e. the fact that different lineages may have different speciation–range size curves). This correction is performed in Step 5.

Step 3

Correct for any influence of clade species diversity on the range size of candidate ancestors. This is necessary since ancestor range size may increase with the number of species in a clade simply because large ranges are rare compared with smaller ones (Gaston and Blackburn, 2000) and may not show up at all until a clade contains many species. To examine this effect, one can plot the range sizes of candidate ancestors against the number of species in their corresponding clades (one species excluded in each clade, since the endemic does not count in the range size pool from which the ancestor is sampled). If there is any relationship between ancestral range size and clade species diversity, then the rest of the analysis must be done using, not ancestral ranges, but the range deviation of each ancestor from the best fit empirical model of this relationship (e.g. linear).

If there is no relationship between range size and the number of species in a clade, this correction is not necessary. In this case, range size values, and not range size deviations, will be the analytical units in the following steps.

Step 4

For each clade, obtain the frequency histogram of range size (or range residuals) for candidate ancestors. In this step, one must prevent clades with more than one candidate ancestor from introducing a phylogenetic bias. To avoid this bias, one weights the con-

tribution of each ancestor to the frequency distribution by the inverse of the number of ancestors in its clade (see Fig. 2). Thus the frequency unit in the distribution becomes, not the species, but the clade. Yet the resulting histogram has another sampling bias: more speciose range-size classes should produce more ancestors. This is a similar but different problem from that caused by clade species diversity alone (see the first paragraph of Step 3). The following step corrects this bias.

Step 5

Obtain the same kind of frequency histogram described in the previous step, but for all species in all clades. Now weight the frequency contribution of each species by the inverse of the number of species in its clade (Fig. 3). Here again, the frequency unit is the clade. This histogram is what we would expect if one ancestor per clade was sampled at random from the range size pool. Thus the differences between the ancestor histogram and this total histogram indicate how the range size of ancestors deviates from random expectations. The differences between the ancestor and total histogram can be plotted (difference vs. range-size class), which is in fact a surrogate of the speciation–range size relationship. The fit of this plot to linear and curvilinear regression will reveal whether this relationship is statistically different from a flat line (i.e. no relationship).

Correcting for wrongly assigned ancestors

Steps 3 and 5 also serve to eliminate any confounding effect caused by wrongly assigned ancestors (see Step 1). The key point in this correction is that range sizes of wrong ancestors would be a random sample of the range-size pool of their clades. Since Steps 3 and 5 correct for sampling issues, they also eliminate any problem wrong ancestors may cause. This is true even if the wrong ancestor is a close relative of the real one, because phylogenetic inertia has not been detected in bird range sizes (Webb and Gaston, 2003).

Do temporal changes in range size matter?

Our method does not take into account the fact that a species range size may change subsequent to its origination (Webb and Gaston, 2000). Thus the current range size of an ancestor may not represent its range size at the time it generated the new species. However, I know no reason to expect ancestral ranges to change with a bias in the same direction (expansion or retraction). Thus I assume ancestral ranges have changed in random directions. In this case, temporal changes in range size will add some noise to the real speciation–range size curve, but the main structure of this relationship would still be detectable if the noise is not too strong (otherwise, the relationship would converge to a horizontal line). Thus the method should be useful only for examining the speciation–range size curve of relatively recent species because the noise caused by temporal changes in ancestral ranges would probably increase with evolutionary time. Most Mediterranean endemic birds seem to have originated during the last part of the Tertiary onwards, and especially within the last 5–6 million years (Covas and Blondel, 1998; Blondel and Aronson, 1999). So endemic Mediterranean birds may be characterized as having evolved relatively recently.

Biogeography and species data

The limits of the Mediterranean region are taken from Covas and Blondel's (1998) work on the Mediterranean avifauna. Following these authors, I consider the Mediterranean region to be divided into certain major subregions that are biogeographically meaningful for bird study in the basin (Fig. 1). Covas and Blondel (1998) recognized 17 subregions, but here I use only 13 due to the lack or uncertainty of distributional information in small subregions (Malta, Rhodes, and Elba) and the fact that the Canary Islands (Atlantic Ocean) are outside the Mediterranean basin (in fact, these islands have a subtropical climate).

Following the same authors, I define the range size of a bird species as the number of occupied subregions, where 'occupied' means that the species is regularly present within the subregion according to the distribution maps of Svensson *et al.* (2010). In this way, the presence of a species on an island counts the same as on a large peninsula, and so this measurement of range size can be seen as a surrogate of the colonization ability of the species over relatively long distances.

A species is here considered a Mediterranean endemic if and only if its known geographic range (breeding and wintering territory) is entirely contained within the limits of the Mediterranean region. Species ranges were consulted in Svensson *et al*. (2010), which covers the Western Palearctic. The same work served to compile regional species diversities and species range sizes for the lineages of the possible ancestors within the Mediterranean region. The method described in the previous section is valid for relative range sizes as well as absolute ones. In this paper, relative range sizes will be taken as percentages with reference to the range size interval of each phylogenetic clade.

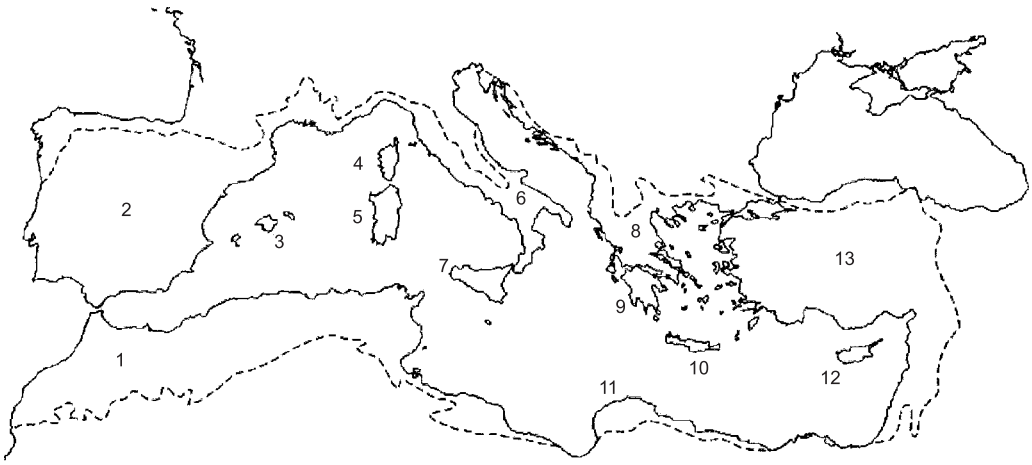

Fig. 1. The Mediterranean region and its subregions considered here. 1 = Maghreb, 2 = Iberian Peninsula (Mediterranean part only), 3 = Balearic Islands, 4 = Corsica, 5 = Sardinia, 6 = Italy and French *Midi* (up to the Pyrenees), 7 = Sicily, 8 = Balkans and Greek Peninsula (north), 9 = Peloponnese, 10 = Crete, 11 = Cyrenaica, 12 = Cyprus, 13 = Asia Minor. These subregions are recognized by Covas and Blondel (1998) with two exceptions: they separated Italy from the French *Midi*, and they considered Asia Minor to extend into the Caucasus, far from the Mediterranean basin. Modified from Quézel and Médail (2003).

In accordance with the criteria described in the Method section, I propose a candidate ancestor for 16 endemic species. These candidate ancestors belong to 10 different lineages. The dataset is summarized in Table 1 together with the references to the corresponding phylogenies. The complete dataset is available upon request.

In Table 1, five endemics appear both as new species and as candidate ancestors of another endemic (*Carduelis citrinella*, *Alectoris rufa*, *A. graeca*, *Sitta ledanti*, and *S. krueperi*). In both *Alectoris* and *Sitta*, this ambiguous situation arises because the closest relative for one endemic is the other endemic. In accordance with the method (Step 1), each endemic was selected as a candidate ancestor of the other and also as the possible descendant species of the other. Thus at least two wrong ancestors are included here, but the double correction of the method (Step 5) allows us to correct the resulting noise. This procedure pays because if we did exclude these ancestors, the signal of two potentially real ancestors would be lost.

The range size of candidate ancestors is virtually uncorrelated with the number of species in a clade ($r < 0.01$ for absolute range size; $r = 0.04$ for relative range size). Thus the correction described in Step 3 of the method was not required or performed on these birds.

The frequency histogram of ancestral range size (Step 4) and that for all species (Step 5) is shown in Fig. 2 and Fig. 3 respectively. The deviation of the first histogram with respect to the second (Step 5) reveals a unimodal curve both for absolute and relative range sizes (Fig. 4). The hypothesis that the curve does not differ from a horizontal line is not supported; the null expectation of $y = 0$ yields $r^2 < 0.001$. Meanwhile, the unimodal curves show excellent fits ($r^2 \geq 0.98$ for both absolute and relative range size curves). The fits are non-directional ($P < 0.02$ for the correlation coefficient). Thus, in the Mediterranean bird fauna, speciation most likely occurred in species with intermediate range sizes.

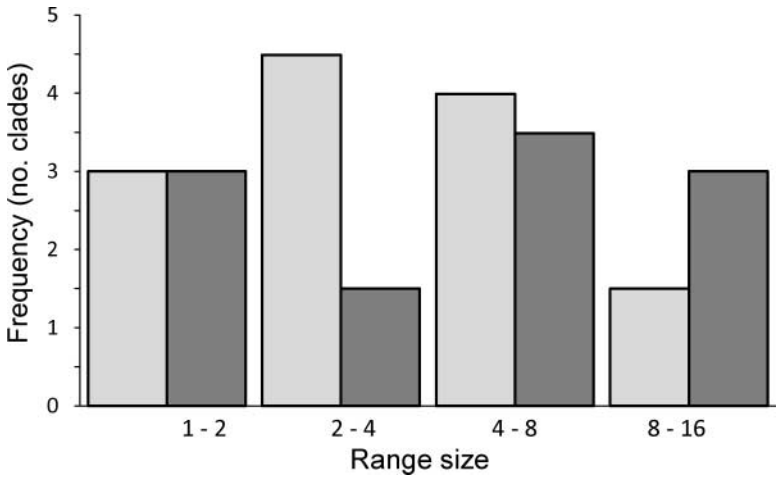

Fig. 2. Frequency histogram of ancestral range size. Light grey = absolute ranges; dark grey = relative ranges. Relative ranges (% clade range interval) are scaled from 1 to 16 to allow direct comparison with absolute ranges. If one clade (e.g. genus) contains, say, two candidate ancestors, then each ancestor will add 1/2 to its corresponding range-size class.

Table 1. The dataset describing the lineages analysed and the Mediterranean endemics they contain that are suitable for study because a possible Mediterranean ancestor can be proposed (see Method for details)

Lineage	Mediterranean endemics	Possible ancestor and reference
Basal clade of Accipitridae[a]	*Aquila adalberti* Brehm 1861	*Aquila heliaca* Savigni 1809 (Hiraldo *et al.*, 1976)
Alaudidae	*Chersophilus duponti* Vieillot 1820	*Eremalauda dunni* Shelley 1904 (Sibley and Ahlquist, 1990)
Fringillidae	*Carduelis corsicana* Koenig 1899	*Carduelis citrinella* Pallas 1764 (Förschler *et al.*, 2009)
	Carduelis citrinella Pallas 1764	*Carduelis carduelis* Linnaeus 1758 (Arnaiz-Villena *et al.*, 1998)
Galliformes[b]	*Alectoris barbara* Bonnaterre 1791	*Alectoris chukar* Gray 1830 (Randi *et al.*, 1992)
	Alectoris rufa Linnaeus 1758	*Alectoris graeca* Meissner 1804 (Randi *et al.*, 1992)
	Alectoris graeca Meissner 1804	*Alectoris rufa* Linnaeus 1758 (Randi *et al.*, 1992)
Passerida	*Passer italiae* Vieillot 1817	*Passer domesticus* Linnaeus 1758 *Passer hispaniolensis* Temminck 1820 (Hermansen *et al.*, 2011)[c]
Picidae	*Picus vaillantii* Malherbe 1847	*Picus viridis* Linnaues 1758 (Sibley and Ahlquist, 1990; Pons *et al.*, 2010)
Certhioidea[d]	*Sitta krueperi* Pelzeln 1863	*Sitta ledanti* Vielliard 1976 (Pasquet, 1998)
	Sitta ledanti Vielliard 1976	*Sitta krueperi* Pelzeln 1863 (Pasquet, 1998)

Sturnidae + Cinclidae[e]	*Sturnus unicolor* Temminck 1820	*Sturnus vulgaris* Linnaeus 1758 (Zuccon *et al.*, 2008)
Sylvia[f]	*Sylvia melanothorax* Tristram 1872	*Sylvia rueppelli* Temminck 1823 (Shirihai *et al.*, 2001)
	Sylvia sarda Temminck 1820	*Sylvia undata* Boddaert 1783 (Shirihai *et al.*, 2001)
Oenanthe + *Phoenicurus* + allies[g]	*Oenanthe leucura* Gmelin 1789	*Oenanthe leucopyga* Brehm 1855 (the most similar of the wheatears of the region)
	Phoenicurus moussieri Olphe-Galliard 1852	*Phoenicurus phoenicurus* Linnaeus 1758 (Sangster *et al.*, 2010)

[a] This part of Accipitridae includes the branch of *Aquila adalberti* and the sister clade with *Gyps* vultures, according to the phylogeny of Wink and Sauer-Gürth (2004). In this way, the number of species considered within the lineage is reasonably similar to that from other lineages.
[b] This order has been preferred as the phylogenetic unit for analysis because the two families it contains (*Phasianidae* and *Tetraonidae*) each has very few species in the Mediterranean region.
[c] Two ancestors are considered here because *Passer italiae* is a hybrid species.
[d] This superfamily (Cracraft *et al.*, 2004) was chosen with the aim of increasing the few species provided by the family *Sittidae* in the Mediterranean. In the region, Certhioidea contains Sittidae, Certhiidae, and Troglodytidae. The endemic *Sitta whiteheadi* Sharpe 1884 was excluded since its closest relative (*S. villosa*) is not Mediterranean (Pasquet, 1998).
[e] Sturnidae is species-poor in the region. The closest family (see Voelker and Spellman, 2004) is added here.
[f] The genus *Sylvia* is enough here to obtain a species richness similar to that of the other lineages.
[g] Our view on the phylogeny of the former families Turdidae and Muscicapidae is rapidly changing. Here, following the most recent phylogenetic reconstruction available, I select a clade with reasonable species richness containing the genera *Oenanthe*, *Saxicola*, *Monticola*, and *Phoenicurus*, thus forming a single and complete clade (for the Mediterranean region) in accordance with Sangster *et al.* (2010) – Clades D3i, D3h, D3g, and D3f within *Saxicolinae* (see their Figure 1).

Some excluded species:
Eleonora's falcon (*Falco eleonorae* Gene 1839) is not a Mediterranean endemic, as usually read. It breeds almost exclusively within the basin, but it winters in Madagascar.
Poecile lugubris Temminck 1820 (Paridae) was excluded because its closest known relative is *P. davidi* (Gill *et al.*, 2005), which is not in the Mediterranean region.
Oenanthe cypriaca Homeyer 1884 is not an endemic: it breeds only in Cyprus, but it winters in Africa far from the Mediterranean part (Svensson *et al.*, 2010).

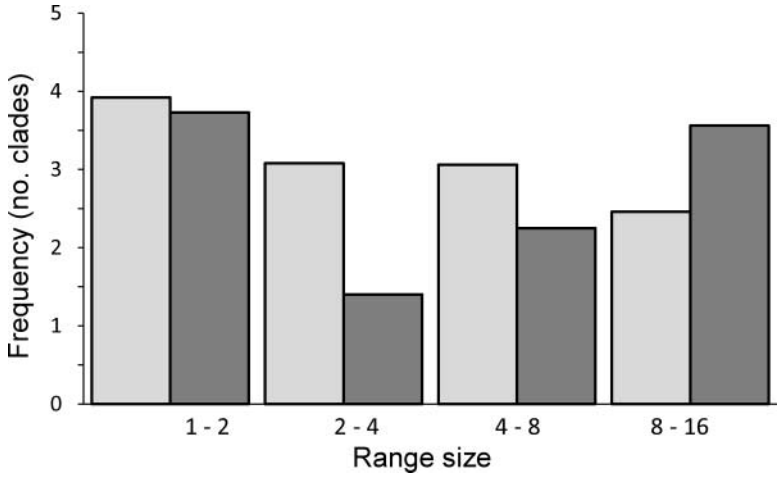

Fig. 3. Frequency histogram of all species' range sizes. Light grey = absolute ranges; dark grey = relative ranges. Relative ranges (% clade range interval) are scaled from 1 to 16 to allow direct comparison with absolute ranges. If ancestors are randomly sampled with respect to range size, then the ancestral histogram should echo this one. Thus the deviation of the ancestral histogram (Fig. 2) with respect to this plot represents how range size influences the chance of being an ancestor – that is, the range-size dependence of speciation probability.

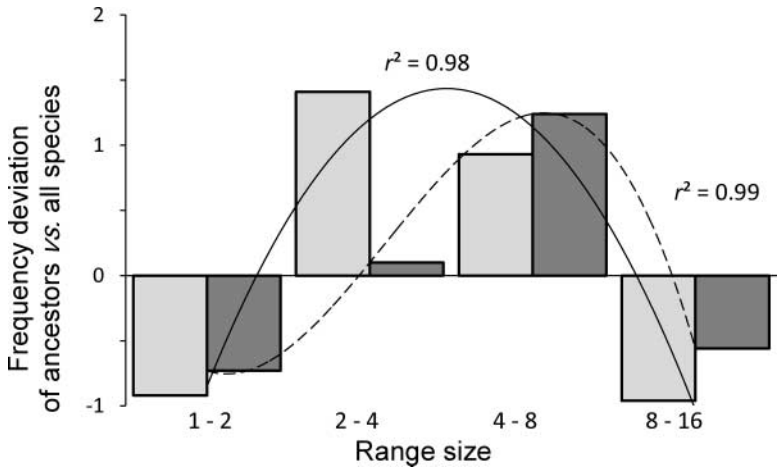

Fig. 4. The frequency deviation (number of clades) of ancestors is a surrogate of the speciation/range-size curve (see Step 5 of Method). The probability of speciation fits unimodal curves with respect to range-size classes. The best model for absolute range (light grey) happens to be a parabola (solid line), and that for relative range (dark grey) a cubic curve (dotted line). Relative ranges (% clade range interval) are scaled from 1 to 16 to allow direct comparison with absolute ranges.

DISCUSSION

The method described here presents two notable advances on previous methods dealing with speciation–range size relationships. First, the focus is not on fossils but on extant species, thus freeing the subject from the sampling problems inherent to the fossil record. Second, the outcome is not a speciation rate but the probability of speciation per species. That probability is the most direct measurement of the influence of range size on speciation.

The fact that the speciation-probability/range-size relationship is unimodal suggests that speciation probability results from a combination of processes that lead to a trade-off with respect to range size. So let us focus on the pattern from the perspectives of the four different processes examined in the Introduction.

(a) The sampling effect of dispersal barriers by range size is the only mechanism that predicted unimodal curves (Rosenzweig, 1975, 1978, 1995). However, the prediction requires that some dispersal barriers are engulfed by large ranges, and Rosenzweig (1975), in the light of theoretical simulations, doubted the importance of this effect for land biotas. Nevertheless, the engulfing effect could explain the speciation-probability/range-size curve obtained here because the largest Mediterranean bird ranges are clearly large enough to engulf all the dispersal barriers in the region (see Svensson *et al.*, 2010). We can imagine wide-ranged birds from the Mediterranean region engulfing mountain ranges by crossing mountain passes, or by expanding around mountainsides, or both. Similarly, many Mediterranean bird species cross the Mediterranean Basin between Europe and Africa during their annual migrations (Blondel and Aronson, 1999), and so they are engulfing sea 'passes' each year. Thus the situation of the Mediterranean bird fauna allows for the sampling of dispersal barriers by range size, including the engulfing effect.

(b) A second process mentioned in the Introduction is dispersal ability: high dispersal should lead to large geographical ranges and so interfere with the long-term isolation required for allopatric speciation. Hence increased dispersal ability would produce decreasing speciation-probability/range-size curves, not unimodal ones. So dispersal ability cannot be the sole explanation of the unimodal curve. But it might contribute to the loss of speciation probability over large range sizes.

(c) Species with large ranges tend to be abundant, and this abundance would increase the appearance of mutations thus enhancing speciation. This process might lead to the rising probabilities over smaller range sizes (Fig. 4), but cannot account for the declining probabilities over larger range sizes.

(d) The time-for-speciation effect conflates speciation and extinction. Yes, larger ranges may well reduce species extinction probabilities. But lower extinction is not higher speciation. Theory and this paper try to measure speciation separately from extinction. So, to the extent that the method of this paper succeeds in teasing out the effect of range size on speciation probability, species survival time cannot be responsible for the speciation pattern of Fig. 4.

In summary, the pattern of Fig. 4 may result from barrier sampling alone, or a combination of mutation rates and dispersal, or the first with either of the other two, or even all three processes. Moreover, if the engulfing aspect of barrier sampling is in part responsible for the results, then the results contradict the previous suggestion for land biotas (Rosenzweig, 1978, 1995). And the actual biogeography of the Mediterranean and its avifauna does suggest the inadequacy of the simulations that called the engulfing effect into question.

All mechanisms discussed in this paper are based on allopatric speciation as the main speciation process, and allopatric speciation fits our current knowledge of the origin of Mediterranean endemic bird species (Covas and Blondel, 1998; Blondel and Aronson, 1999). There is only one example of another speciation process in the dataset, namely speciation by hybridization: *Passer italiae* from *P. domesticus* and *P. hispaniolensis*. Both of the latter two species have very large geographic ranges in the region. Perhaps large ranges could favour speciation by hybridization simply because the larger the ranges, the higher the probability that they overlap, thus allowing species to hybridize. Anyway, if it exists, this effect of large range size is probably unusual, as suggested by the reduced probability of speciation over the large ranges of Fig. 4.

The possible interaction between dispersal ability and the sampling of dispersal barriers demands further attention. Low dispersal ability in an ancestral species may result from a low environmental tolerance that prevents the crossing of dispersal barriers. This could intensify its sensitivity to dispersal barriers, thus facilitating allopatric speciation. In this case, poor dispersal ability would reinforce the sampling of dispersal barriers by range size (the species would 'see' a barrier where a better disperser would not). Anyway, poor dispersal ability may act against range size expansion, thus reducing opportunities of finding dispersal barriers and so decreasing speciation. Little more can be said on this subject because the dispersal–range size relationship has not received the attention it deserves. However, in the Mediterranean region, this relationship seems to be negative, since endemics tend to be more sensitive to elevational barriers in snails, amphibians, reptiles, and small mammals (López-Villalta, 2011). These considerations reveal the interest in and complexity of the interaction between dispersal, range size, and speciation.

The results support the idea that species with moderate-sized ranges are the main producers of new species. But understanding the shape of the range size distribution of species also requires consideration of how extinction risk affects that distribution. Small-ranged species tend to face a high extinction risk, which usually decreases with range size (Raup, 1994; Pimm *et al.*, 1995). This is relevant for theoretical macroecology because speciation and extinction rates, together with changes in range size, combine to produce the range size distribution (Gaston, 1998). Since the speciation–range size curve presented here resembles a lognormal distribution (Fig. 3), we should not be surprised by the fact that most range size distributions resemble a lognormal one (Gaston, 1998; Gaston and Blackburn, 2000). Such a shape would be more surprising if new species tended to originate from the largest ranges; in this case, a strong effect caused by extinction, range transformation, or both would be required for lognormality. Thus the curve shown in Fig. 3 suggests a simple explanation for this macroecological pattern: it may be largely determined by the range-size dependence of speciation rate.

Today, small-ranged species face dramatic conservation problems: in the current biodiversity extinction event, endangered species tend to have narrow geographic ranges (Pimm *et al.*, 1995). The largest ranges within these narrow-ranged species could fall in the intermediate range-size class, where speciation is most likely (see Fig. 4). Then, we will be not only eroding our biodiversity heritage, but also severely impeding its turnover and eventual recovery in evolutionary time.

Could wide-ranged species substitute for species with intermediate range size as the principal speciators of the future, when many large geographic ranges will shrink and become smaller, as is happening today (Pimm *et al.*, 1995; Gaston and Spicer, 2004)? It is doubtful that shrunken ranges will become the principal species producers. First, most surviving species

in the future might not experience shrunken ranges at all; they might instead have large geographic ranges simply because a preponderance of small-ranged species had disappeared due to their intrinsically high risks of extinction. Second, today's wide-ranged species may occupy their large ranges due to a high dispersal ability. That would translate into a higher gene flow than that of modern intermediate-ranged species across the same dispersal barriers. Thus wide-ranged species might remain worse at genetic isolation (and allopatric speciation) even were they reduced to the same ranges as modern species with intermediate ranges. These and other possibilities demand further attention to help us understand and conserve such a key evolutionary process as speciation.

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Comment: A new approach to relative speciation rates

Sometimes we need to remind ourselves of the simplest basics as we struggle to understand the most complex of evolutionary and ecological processes. I believe that López-Villalta (2011: *Evol. Ecol. Res.*, **13**: 665–679) should serve to remind us of that. The issue? The generation and maintenance of S, the number of species that exist on the Earth.

López-Villalta does not concern why S is at equilibrium, because S is not at equilibrium. Evolutionary ecology has long realized that S fluctuates considerably. The question instead is what keeps S within bounds? What processes lead to S-dynamics looking like steady-state dynamics?

For S to remain within bounds, the differential equation that summarizes its creative (speciation) and destructive (extinction) processes must be regulated by negative feedback.

Feedback characterizes a dynamic system if (and only if) the rate at which a state variable changes depends on the size of the state variable itself. In cases of negative feedback, the larger the variable, the slower its net rate of production. Of course, negative feedback may be inadequate to keep a state variable in bounds; the variable's net rate of production may decline to a positive asymptote, resulting in continual explosive growth. But that is a different issue – one, I might add, that the fossil record suggests is not very likely to require our concern.

By definition, the creative rate in S-dynamics must be rate-of-speciation. But from a mathematical perspective, keeping S in bounds does not require negative feedback in the rate-of-speciation. The negative feedback could reside solely in the negative process, i.e. extinction rates. Is speciation rate subject to negative feedback?

Certainly, speciation has a large and interesting set of causes. I personally doubt that we have even been able to list them all, let alone close the books on how each one works. So how can we determine whether speciation rate is subject to negative feedback if we cannot even make a list of all the equations that we need to model speciation rate? It would seem hopeless.

The answer may be empiricism. Go to the fossil record. Measure the response of speciation rate to S. If it is negative, then speciation rate is subject to negative feedback. Otherwise it is not.

But the fossil record has problems of its own, which I will explore below. Meanwhile, in the spirit of Richard Levins (1966: *Am. Sci*, **54**: 421–431), who cautioned that scientific truth is the intersection of independent lies, I am delighted to point out that López-Villalta has opened a new empirical door. By using the tools of modern phylogeny, he seeks to examine the evidence that links speciation rates to the area occupied by species.

Why single out area? Because area is the parameter that offers a mechanistic prediction of the negative feedback itself (Rosenzweig, 1975: pp. 121–140 in M.L. Cody and J.M. Diamond, eds., *Ecology and Evolution of Communities*. Cambridge, MA: Harvard University Press; Rosenzweig, 1995: *Species Diversity in Space and Time*. Cambridge: Cambridge University Press). Although many variables are implicated in setting speciation rates, area alone (so far) explains why rates should change as a function of S itself. As S increases, the average area occupied by a species should decline. With that decline, the

average species should face an increase in its chances of extinction. And as *S* increases, speciation rates should change in some regular fashion – albeit a debatable one.

The bare theory of species' geographical area and speciation rates is clear enough. It is derived from thinking about geographical speciation. It personifies geographical barriers, imagining them trying to transect ranges, although the personification is a mere mathematical formalism, a way to speak about random encounters between geology and biology. No-one actually imagines barriers with any neurological capacity to seek out any range or any range border. (In fact, one could equally well transfer the personification to the ranges themselves.) Using our personification, we may say that finite geographical barriers will encounter larger ranges with higher probability than smaller ones. But we may also say that, once a range is discovered by a finite barrier, it will entirely transect a larger range with less probability than a smaller one. Keeping in mind that encounter and transection must both happen to produce the isolates that initiate speciation, we conclude that the probability of isolate formation will be the joint probability, i.e. the multiple of the two separate probabilities.

If a range is very small, most barriers will miss it and the joint probability will be very small. If a range is very large, most barriers will find it but fail to cut all the way through it so, again, the joint probability will be very small. Thus, the joint probability may well be unimodal, peaking over some intermediate range size. But the unimodal relationship may not be real if the actual distributions of values of range-encounter and range-transection carry the mode beyond the largest ranges. Modelling the curve with some very simplistic assumptions (such as a uniform distribution of barrier lengths), I suggested that the entire terrestrial surface of the Earth is too small to allow the problem of transection ever to reduce the joint probability of isolate formation (Rosenzweig, 1978: pp. 172–194 in D. Wollkind, ed., *Proc. Wash. State Univ. Conference on Biomathematics and Biostatistics*). Thus the mode would be hidden over impossibly large range areas. What we could then expect (from terrestrial species) would be a monotonically declining probability: the smaller the range, the less the probability of isolate formation. Because average range sizes decline with increasing *S*, so would speciation rates decline with increasing *S*. Speciation rate should indeed be subject to negative feedback.

López-Villalta tests the relationship of speciation rates to *S* using real data. His data are not barrier-size distributions and the like, but ranges of real bird species and their real daughters in a real biogeographical theatre, the Mediterranean Basin. His is a sophisticated and difficult step but it shows the likelihood that unimodality in speciation probability does exist. Although he concludes that I was wrong to predict no chance of unimodality, his step delights me personally.

Why trouble with this new step? One straightforward answer is that his work shows that my simplistic assumptions of range-size distributions and the conclusion I drew from them must be discarded. But a second answer is that data from the fossil record are fraught with at least two problems of their own. First, the record often conflates speciation and extinction, making it quite difficult to separate the two (Jablonski *et al.*, 2006: *Science*, **314**(5796): 102–106). Liow *et al.* (2008: *Proc. Natl. Acad. Sci. USA*, **105**: 6097–6102) wrestle with this problem in addressing the effect of small mammal body size on speciation and extinction rates, but statistical significance largely eludes them at the species level. Studies of the fossil record are not alone in conflating speciation and extinction. For example, Condamine *et al.* (2012: *Ecol. Lett.*, **15**: 267–277), who also enlist phylogenetic rather than paleobiological techniques, nevertheless focus on diversification rates. Indeed, studying diversification rates using

phylogenetic information is hardly a new idea (Ricklefs, 2007: *Trends Ecol. Evol.*, **22**: 601–610). What makes López-Villalta's approach truly novel is that it applies the methods of phylogeny to the feedback between S and the parameter that causes that feedback at the species level.

A second caveat in using the fossil record is that we cannot be sure the resolution of the record is sufficient to rely on. That theme is too often brought up in the works of paleobiologists themselves to require review. However, it may matter a lot in solving the problem López-Villalta addresses. Consider that short-lived species are quite likely to be born in a very small region, occupy very small ranges, and disappear without a trace. Yet one cannot assume that the signal of the negative feedback resides in the longer-lived species, likely to occupy a substantial variety of range sizes. So lacking adequate resolution to detect short-lived species might doom any paleobiological attempt to discover the true signal.

The twin issues of resolution and conflation do not imply that we must now give up on the fossil record. For example, one might propose that the conflation does not matter, that speciation rates and extinction rates are correlated. But of course, that is exactly what we would like to know! So assuming that the correlation exists would make the investigation into a tautology.

We can increase our ability to rely on fossil data by being quite picky about which data we use. Instead of throwing it all into the mix and performing a grand meta-analysis, we can seek unusually high resolution records left during periods of marked change in S. Such data do exist, witness the extraordinary record of the late Ordovician muddy benthos in the Nicolet Valley of Quebec unearthed and described by Peter and Sarah Bretsky (Rosenzweig and Taylor, 1980: *Oikos*, **35**: 236–243). And these data do support the hypothesis of negative feedback, i.e. that S tends towards a steady state. But I know of no data adequate to deal with the issue that what we observe are the net changes, changes that both speciation and extinction contributed to.

Rosenzweig and Vetault (1992: *Evol. Ecol.*, **6**: 90–93) approach mathematically the matter of separating speciation rate from extinction rate in the fossil record. But their analyses assume a steady state in S and the estimates they achieve apply to long periods during which there is no capacity to tease out the effect of species range sizes. That promises little value in tracking responses of rates to changes in S. Etienne and Apol (2009: *Evolution*, **63**: 244–255) propose powerful and exciting advances in this method but their improvement does not seem designed to overcome the inadequacy of Rosenzweig and Vetault to assess rate responses to changes in S.

And finally we must face the probability of a lag. Perhaps speciation takes a long time to respond to a pulse of extinction. We might have to add lag terms to our standard correlation studies. In simpler systems, such as population dynamics, the lag could be constant. But in systems involving speciation and extinction, the lags themselves might vary with S in maddening ways. There is nothing simple about the use of the fossil record to reveal feedback by tracking speciation rates as a function of S.

Yes, López-Villalta's phylogenetic analyses present their own difficulties. He faces them openly and suggests ingenious solutions that will surely hearten those wishing to use his approach. But one cannot avoid the observation that he had to bin the bird data into only four categories to reach his conclusions. This binning does reduce the power of his final result. The reader may be assured that the author and I struggled for two months to find a way to preserve the independence of all 16 separate endemic species in the analysis. But we

did not succeed and we both thought it best to let the idea loose into the intellectual swarm, there to inspire others to work on it.

One might imagine another shortcoming of López-Villalta's work. It does not estimate absolute speciation rates, only relative ones. But relative rates are all that we need to assess the hypothesis that speciation rates are involved in the negative feedback. And whereas the existence of the mode in his Figure 4 depends solely on the tenuous significance of the right-hand value being less than the peak values, the increase of relative rate on the left side of his Figure 4 clearly establishes the participation of area in the negative feedback in speciation-rate dynamics.

So we have two lies now, that of the fossil record and that of phylogeny coupled to real ranges. Perhaps one day we will know of a method to achieve a third one and be able to find its intersection with the first two.

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