



Ecological divergence among young lineages favours sympatry, but convergence among old ones allows coexistence in syntopy

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ABSTRACT

Aim We analyse when and why closely related species start to coexist in sympatry at the range (continental) scale, and in syntopy at the local (community) scale. We contrast the idea that limiting similarity and time constrain the transition to sympatry of sister lineages after their initial allopatric split, with the hypothesis of ecological convergence, leading to the coexistence of species with similar ecological attributes in similar environments.

Location European continent, north-west Italy and north-west Spain.

Methods With a comparative framework we test whether the spatial overlap of bird ranges within Europe, at the continental scale, and in two European regions at the community scale, vary with their degree of ecological similarity (trophic niche, body size, elevational preferences), when accounting for the evolutionary time available for range expansion.

Results A larger number of sister species with recent common ancestors are found in the continent than within communities, a likely consequence of the allopatric mode of divergence of lineages. Divergence in elevational preferences and niche breadth favoured a way back to secondary sympatry of European sister species, which took place *c.* 2 Myr after their split. Once in sympatry, the coexistence of species at the local scale took almost twice as long and was instead favoured by ecological convergence.

Main conclusions Ecological similarity poses a fundamental constraint to species coexistence, but whether it hampers or favours it depends on the scale, both spatial (sympatry versus syntopy) and temporal (young versus old lineages). Scaling issues are not independent – the reduction of the spatial scale expands the temporal one – generating mismatches between ecological patterns (within communities) and macroecological ones (within ranges).

Keywords

Alps, Cantabrian Mountains, character displacement, convergent evolution, ecological niche, environmental filtering, scaling.

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INTRODUCTION

Processes affecting species distribution act across a broad continuum of temporal and spatial scales (Brown *et al.*, 1996). At the smallest spatial scale, vagility and micro-habitat selection of individuals are the most relevant (ecological

underlying mechanisms (Turchin, 1998). However, as the scale increases to embrace local communities, the number of species sharing spatial patterns also increases, together with the partitioning of environmental space due to interactions (MacArthur, 1972; Case & Taper, 2000). Since most species

split allopatrically from their closest relatives, groups of closely related species and different biota become the main biological actors at even larger scales, such as continental ones (Tobias *et al.*, 2014). Here, physical processes (e.g. climate, geology), phylogenetic relationships (niche conservatism) or evolutionary processes (character displacement) tend to dominate and dissipate ecological processes (Brooks, 1988; Wiens, 1989). The temporal dimension also varies with the scale, because large areas have more chances to embrace the allopatric ranges of young lineages (Kisel & Barraclough, 2010; Bergsten *et al.*, 2012). As a result, larger numbers of young species are found with increasing geographical scale of sampling. The opposite occurs at small scales, because local species pools assemble components that had time to expand their ranges, cross geographical barriers and pass coarse environmental filters (Silvertown *et al.*, 2006). Emerging from these considerations is the realization that evolutionary and ecological processes must be viewed at the appropriate scale to put them into context, and multiscale approaches may make a significant contribution to this understanding (Willis & Whittaker, 2002). These approaches have permitted key controversies, about the roles of evolution, biotic and abiotic forces in structuring assemblages (Price *et al.*, 2014) or about the degree of divergence that allows species coexistence in sympatry (Pigot & Tobias, 2013), to be tackled.

In this study we assess whether ecological similarity and evolutionary time constrain the coexistence and distribution of species. We combine bird distributions, phylogenetic relationships and the degree of ecological similarity to address co-occurrence patterns at different extents (continents versus regions with a narrow latitudinal and longitudinal span) and at different grains (range versus territorial neighbourhood). We centre on pairs of congeneric species that are each other's closest relatives at different scales, i.e. on species that display the broadest biological similarity (e.g. life styles, niche attributes) and are thus exposed to the greatest constraints to coexistence (Laiolo *et al.*, 2015; Pigot *et al.*, 2016). We analyse: (1) when and why species ranges start to overlap in secondary sympatry (i.e. within the same broad region of a continent), and (2) when and why species start to occur in syntopy (within the same habitat plot). We used published data on the distribution of European birds (Hagemeyer & Blair, 1997) as well as our own extensive data on regional assemblages in the Alpine (north-west Italy) and the Cantabrian regions (north-west Spain). The former data encompass an area of over 10,000,000 km² with a grain of 2500 km²; the latter encompass 16,000 km² with a grain of 0.0134 km². We tested the ideas that limiting similarity and time constrain the transition to secondary sympatry (MacArthur & Levins, 1967; Ricklefs, 2006; Pigot & Tobias, 2013) by using several proxies for ecological divergence (elevational preferences, niche breadth and overlap, and morphology) and estimates of divergence time between species. We contrasted these hypotheses with the alternative of convergence (in the evolutionary background) or environmental filtering (in the ecological background) (Nekola & White, 1999;

Cavender-Bares *et al.*, 2006; Tobias *et al.*, 2014), which should lead instead to the coexistence of species with similar phenotypic or ecological attributes. This will permit us to scrutinize the temporal and spatial scale at which competitive exclusion and convergent evolution of traits involved in environmental filtering operate.

METHODS

Phylogenetic information

We initially identified 283 congeneric European species that were not sea or coastal birds and were not introduced or had most of their range outside the continent. A multigene phylogeny was built by downloading 10,000 time-calibrated relaxed molecular clock trees from <http://www.bird.tree.org> (Jetz *et al.*, 2012) using the Hackett backbone of species (Hackett *et al.*, 2008). Sequence data were available for all selected species. A maximum credibility clade tree was constructed with TreeAnnotator of BEAST 1.8.2 (Drummond *et al.*, 2002) in which we identified non-nested pairs of species. For each of these pairs, we identified sister species (i.e. pairs of species that are each other's closest extant relatives) by using the genus phylogeny from the same source and alternative published phylogenies (Appendices S1 & S2 in the Supporting Information). Species were considered as true sister lineages only when multigene and literature phylogenies agreed in their status, which was the case for 32 pairs. In order to quantify the evolutionary age of species, we calculated the length of the branch that connects the terminal tip to the node and compared this value with that available from literature. We found a high and significant correlation ($r^2 = 0.91$, $t_{16} = 8.23$, $P < 0.001$), confirming that multigene phylogeny provides a robust estimate of the age of sister species. The number of sister taxa dropped dramatically with downscaling to the regional assemblages; even so, over 130 species were included. There were only four pairs in the Cantabrian Mountains and five in the Alps if we consider two pairs that were not included in the multigene phylogeny (Appendix S1). These were *Phylloscopus collybita* and *Phylloscopus ibericus* and *Corvus corone* and *Corvus cornix*, the evolutionary age of which was alternatively derived from Price (2010) and Jönsson *et al.* (2016), respectively. The *Corvus* species pair was also added to the list of sister species of the European sample, given that the parapatric distribution of its species is well known, while for *Phylloscopus* the lack of information at large scales prevented this.

To allow a larger sample of species for tests of limiting similarity at the regional scale, we also considered patterns among the closest members of a genus that are not sisters (hereafter, non-sister congeners) when the region missed their true sisters. These species share habitat and aspects of their phenotype and niche, and thus may well compete for space and resources (Laiolo *et al.*, 2015), but display a much lower potential for hybridization (Gholamhosseini *et al.*, 2013). Their evolutionary age was estimated in the multigene phylogeny of the regional species pools, as done at the

continental scale. For these deepest branches, however, the agreement between ages estimated in multigene phylogeny and the literature (Appendix S3) was low (Alps, $r^2 = 0.25$, $t_{10} = 0.76$, $P = 0.46$; Cantabrian Mountains, $r^2 = 0.29$, $t_{10} = 0.9$, $P = 0.37$), thus statistical analyses were run accounting for both sources (see below).

Species co-occurrence at the continental and regional scales

To analyse species distribution at the continental scale, we downloaded the presence/absence dataset of European birds within 30 arcmin grids (*c.* 50 km × 50 km) available from the EBCC Atlas of European Breeding Birds (Hagemeyer & Blair, 1997; <http://ipt.sovon.nl/>). At the regional scale, we studied the spatial distribution of birds from the uplands of the Alps and Cantabrian Mountains down to the respective sea levels during the breeding season (Appendix S4). The study regions covered similar elevations and areas, roughly corresponding to six cells of the European dataset (16,000 km², 120–2770 m a.s.l., in the Alps, and 17,000 km², 1–2615 m, in the Cantabrian Mountains). We surveyed both open and forested habitats, establishing almost 4000 survey plots (1390 in the Alps and 2539 in the Cantabrian Mountains). Each sample plot covered 3.14 ha, an area that may include few territories of a typical medium-size passerine species. Birds were monitored with the standard methodology described in Appendix S4. Continental and regional datasets were used to calculate an index of co-occurrence, the scaled ‘checkerboard’ *C*-score, for sister species in European cells, and for sister and non-sister species in regional plots. This was calculated from the presence/absence matrices, as $C_{ij} = (R_i - D) \times (R_j - D) / R_i \times R_j$, where C_{ij} is the *C*-score for species *i* and *j*, R_i and R_j are the number of occurrences of species *i* and *j*, respectively, and D is the number of cells or plots where species *i* and *j* co-occur. This index was scaled to range from zero, i.e. sympatry at the continental scale and syntopy at the regional scale, to 1, i.e. allopatry and segregation, respectively. The *C*-score was calculated with R package *bipartite* (Dormann *et al.*, 2008).

Phenotypic and ecological divergence

The average elevation of species occurrence plots within each study site was calculated as a proxy of the elevational preferences of species at the regional scale; the average elevation of species within their ranges was instead derived from literature (Appendix S5). These estimates can be considered as a proxy of the climatic niche of populations and species. From the literature we also derived measures of body size (adult mass) and an index of niche breadth, intended as the diversity of foraging items, substrates and techniques used by a species. It was quantified as the natural logarithm of the sum of occurrences of 26 foraging categories (Appendix S5). For each species, we used the same body mass and dietary specialization values at the continental and regional scales, given the low intraspecific variability of these traits (Laiolo *et al.*,

2015; Burin *et al.*, 2016). To quantify the major biological differences between species of a pair, we calculated their absolute differences (contrasts) in niche breadth and elevation (average plot elevation for the regional scale, average range elevation at the continental scale). In the case of body mass, we standardized differences (pairwise differences/species means) to allow contrasts to be phylogenetically independent and normally distributed as for the rest of the contrasts ($0 < \text{Pagel's } \lambda < 0.44$, $P > 0.05$). As a measure of ecological similarity, we also estimated niche overlap as Pianka's (1973) index calculated from the same dataset of niche breadth (Appendix S5).

Statistical analyses

Prior to running statistical tests, we tested for the phylogenetic dependence of our response variable, species segregation (*C*-score). We used the phylogeny of internal nodes as a phylogenetic control in least-square regressions performed with the R package *caper* (Orme, 2013). We quantified the phylogenetic signal (Pagel's λ) in the residuals of the regressions of the *C*-score on predictors (all contrasts and time). We found no phylogenetic signal in sister and non-sister congeners of European, Cantabrian and Alpine datasets (all $\lambda = 0$, $P = 1$). This result indicates that closely related genera do not share patterns of segregation, thus no phylogenetic control was necessary in further analyses.

Since trait dissimilarity can favour the way back to sympatry of closely related species after allopatric splitting, we tested whether phenotypic and ecological divergence may have influenced the probability of transition from allopatry to sympatry of sister species, within Europe (33 pairs) and the study regions (six pairs if we consider both sites). Thus, by assuming that the species initial state was allopatric, we modelled the transition to an irreversible state of secondary sympatry as an exponential function of time by means of continuous multistate Markov models (Pigot & Tobias, 2013). Due to the limited number of true sister species co-occurring regionally, at this scale we clumped the Alpine and Cantabrian datasets to achieve a sample of six pairs, and when a pair occurred in both areas the average difference in elevation was considered (elevational divergence was conserved among regions; Appendix S5). In models, each pair of sister species contributed two observations: the state at time zero, established as allopatric, and that at present (e.g. at node age). The present state was categorized as allopatric for *C*-scores > 0.8 and sympatric for *C*-scores ≤ 0.8 , which roughly corresponds to 20% overlap in the smaller range or regional plot occupancy, as in Pigot & Tobias (2013). After running a constant-rate model entering exclusively node age, we included as covariates niche overlap and differences in elevation, niche breadth and (standardized) body mass. To avoid over-parameterization with a limited sample of pairs, the rate of change was kept constant rather than assuming a decline over time, which is plausible for sister species of relatively young age (see Results). We assessed the fit of models

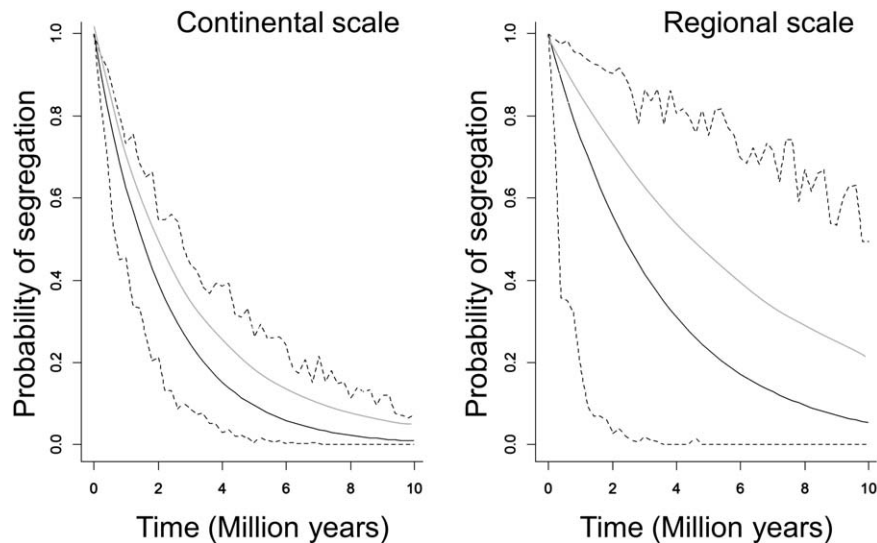


Figure 1 Estimated curves of time-dependent transitions to sympatry (continental scale, left) and syntopy (regional scale, right) of sister species from Europe and from two regional assemblages (the Alps and the Cantabrian Mountains), respectively. Black continuous and dotted lines represent curves and 90% CIs for the best models, including covariates. These were represented, at the continental scale, by differences in niche breadth and elevation and their interaction, and, at the regional scale, by differences in niche breadth. The grey lines represent constant-rate models that only account for species evolutionary age, with no covariate.

including covariates over the model including time by means of the Akaike information criterion corrected for small sample size (AIC_c) and likelihood ratio tests. The effect of covariates and their interactions was assessed by hazard ratios, which are significant when the 95% CI does not include 1. If the transition to sympatry is hampered by dissimilarities, hazard ratios should be < 1 , while they should be > 1 when divergence facilitates the transition. Multistate models were run in R with the package *msm* (Jackson, 2011).

For non-sister taxa we could not assume, as for sister species, the initial state and the number of transitions that pairs faced over their long evolutionary trajectories. Therefore, the above statistical method could not be applied in this sample of species. However, we were able to test whether phenotypic and ecological dissimilarities influenced their present degree of segregation (C -score) when controlling for the evolutionary age of species (from multigene phylogeny or literature data). Censored regression models were run, constrained to the left for C -score = 0 and to the right for C -score = 1, with the R package *censReg* (Henningsen, 2010). Models were ranked on the basis of their AIC_c , and all models separated by fewer than two points from the models with the lowest AIC_c were considered as equally probable.

RESULTS

On average, European sister species are younger ($3.67 \text{ Myr} \pm 0.56 \text{ SE}$) than the subsets found in the Alps ($5.47 \pm 1.7 \text{ Myr}$) or the Cantabrian Mountains ($5.86 \pm 1.87 \text{ Myr}$). However, the oldest lineages are non-sister congeners (Alps, $10.0 \pm 2.1 \text{ Myr}$ with multigene phylogeny and $7.1 \pm 1.3 \text{ Myr}$ with literature data; Cantabrian Mountains, $10.6 \pm 2.0 \text{ Myr}$ and

$6.3 \pm 0.52 \text{ Myr}$, respectively). The simplest model of transition to sympatry, including just time, indicates that it took $2.73 \pm 0.66 \text{ Myr}$ for European sister species to get back to sympatry after their split. However, an alternative model including the interaction between differences in elevation and niche breadth was better supported ($AIC_c = 44.44$ vs. 53.13 , likelihood ratio test: $\chi_3^2 = 11.52$, $P < 0.001$) (see Appendix S6 for the performance of the other models) (Fig. 1). High levels of niche breadth differences associated with diverging elevational preferences (hazard ratios for the interaction $> 1:1.02$; 95% CI 1.001 – 1.042) slightly shortened the times of secondary contact between sister species, estimated as $2.12 \pm 0.70 \text{ Myr}$. The transition to syntopy of the few sister species of regional assemblages took more than twice as long to occur, $6.51 \pm 3.93 \text{ Myr}$ in the simplest model with time alone. This estimate is subject to greater uncertainty due to the small number of species involved (Fig. 1). Again, this model was outperformed by an alternative including differences in niche breadth as a covariate, the addition of which speeded up coexistence in syntopy ($3.41 \pm 3.14 \text{ Myr}$; $AIC_c = 6.57$ vs. 13.42 with the simplest model, likelihood ratio-test $\chi_1^2 = 8.86$, $P = 0.003$; Fig. 1; Appendix S6). However, in contrast to the results at the continental scale, sister species that co-occur in syntopy resemble each other rather than diverge in niche breadth (hazard ratios for differences in niche breadth $< 1:0.00$, 95% CI 0 – 0.09). Also among non-sister congeners, similarity promoted syntopy – although here we modelled the continuous variation in the C -score, so positive regression slopes indicate that divergence facilitates segregation, not aggregation as above (Table 1). In non-sister congeners from both the Alps and the Cantabrian Mountains, differences in elevational preferences or body mass

Table 1 Results of censored regression models testing for the relationship between *C*-score in regional assemblages and differences in phenotypic and ecological parameters of congeneric species that are not sister taxa.

		Evolutionary age derived from multigene phylogeny	Evolutionary age derived from literature sources
Segregation (<i>C</i> -score) in the Alps of non-sister species of the same genus			
Model 1	Predictors	Evolutionary age (-0.004 ± 0.004) Elevation differences (0.0002 ± 0.001)***	Elevation differences (0.0003 ± 0.0001)**
	AIC _c	3.00 ($n = 14$)	4.06 ($n = 11$)
Model 2	Predictors	Elevation differences (0.0002 ± 0.00008)** Body size differences (0.19 ± 0.08)*	Evolutionary age (-0.019 ± 0.008)* Elevation differences (0.0004 ± 0.0001)***
	AIC _c	10.00 ($n = 14$)	11.84 ($n = 11$)
Model 3	Predictors	Evolutionary age (-0.005 ± 0.004) Elevation differences (0.0002 ± 0.00008)** Body size differences (0.19 ± 0.08)*	Evolutionary age (-0.019 ± 0.007)* Elevation differences (0.0003 ± 0.0001)*** Differences in niche breadth (0.19 ± 0.02)
	AIC _c	13.34 ($n = 14$)	16.12 ($n = 11$)
Segregation (<i>C</i> -score) in the Cantabrian Mountains of non-sister species of the same genus			
Model 1	Predictors	Evolutionary age (0.008 ± 0.005) Elevation differences (0.0002 ± 0.0001)	Elevation differences (0.0001 ± 0.0000)
	AIC _c	6.75 ($n = 14$)	16.84 ($n = 11$)
Model 2	Predictors	Body size differences (0.16 ± 0.04)*	Body size differences (0.13 ± 0.08)
	AIC _c	8.70 ($n = 14$)	17.32 ($n = 11$)
Model 3 (for literature source-derived age only)	Predictors	Elevation differences (0.0001 ± 0.0001) Body size differences (0.16 ± 0.08)*	Evolutionary age (0.034 ± 0.018)*
	AIC _c	10.02 ($n = 14$)	18.64 ($n = 11$)

For each study region we ran two sets of models, which included among the predictors evolutionary ages from multigene phylogeny and from alternative literature sources. The three models receiving the best support for each subset of data are shown, highlighting in bold the best ranking ones according to their AIC_c value. Slope and their SE are also shown, as well as significance levels and the number of species pairs. Positive slopes indicate that the predictor promotes segregation, while negative ones indicate it favours syntopy.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

(or both) lead to high levels of spatial segregation. Results varied slightly among regions and depended on the source of information used to estimate evolutionary age (Table 1). The degree of segregation was influenced by species age, but the direction of the relationship varied among regions and with the source of phylogenetic information (Table 1, Appendix S7).

DISCUSSION

Contrasting eco-evolutionary processes underlie the coexistence of species at different spatial scales, and include ecological divergence between young lineages at the continental scale and convergence between old lineages at the local scale. Evolutionary time and, arguably, dispersal limitations, were not the sole constraints to range expansion of European birds after their initial allopatric split. The secondary contact of species ranges was accelerated by dissimilarities in ecological attributes, a pattern that is consistent with limiting similarity in the ecological domain and character divergence in the evolutionary one. Both processes are known to stem from the fitness costs of sharing resources (Brown & Wilson, 1956) or unsuccessful mating (Servedio & Noor, 2003) with close relatives.

Our results for European birds are in line with those obtained by Pigot & Tobias (2013) for species-rich South American avian assemblages with respect to the role played

by trophic divergence. Differences in climatic niche (elevation) have also assisted the way back to secondary sympatry of European lineages. These are likely to have permitted the local spatial segregation of species with otherwise similar biological attributes and overlapping ranges (Cadena, 2007; Laiolo *et al.*, 2015). The time we estimated for secondary contact (2.1 Myr) matches that proposed for birds in temperate regions (*c.* 2 Myr) (Price, 2008; Weir & Price, 2011) and also largely coincides with the major shifts of continental ice driven by Milankovitch cycles during the Quaternary (Bennett, 1997). These climatic fluctuations have been proposed to engender selection for generalized niches and vagility, ultimately promoting large changes in the size and location of species distributions (Dynesius & Jansson, 2000).

Once sister species attained sympatry, they took almost twice as long (3.41–6.51 Myr) to co-occur in syntopy within regions. This is an extremely long time if we consider that geographical distances have shrunk and, from this secondary contact on, they should constitute a minor barrier. From an evolutionary perspective, however, this extended interval may be required for convergent evolution to enhance the ecological resemblance of species and, in turn, permit their clustering within communities and habitats (Cavender-Bares *et al.*, 2006). In line with this idea, our result indicates that the local coexistence of sister species is assisted by similarity in

the degree of trophic specialization rather than by its divergence, as occurs at the largest scales. A process of parallel evolution under stabilizing selection is conceivable even after an initial transient state of divergence (Fox & Vasseur, 2008), and has been proposed to explain the interspecific similarities in agonistic behaviours of coexisting birds in both temperate and tropical latitudes (Laiolo, 2012, 2013; Tobias *et al.*, 2014; Losin *et al.*, 2016). This result, together with that of coexisting non-sister congeners, also has an ecological reading. Resemblance may permit species to pass local environmental filters and eventually assemble where their environmental fit is optimal, in a process of niche tracking that ultimately leads to the functional clustering of congeners (Cornwell *et al.*, 2006). These species split from their closest relatives 5–10 Ma, depending on whether they are or not sister lineages, a time lag that agrees with that estimated by Price *et al.* (2014) in Himalayan songbirds (7.5 Myr), and that is longer than the time required to achieve reproductive isolation at these latitudes (3 Myr; Price, 2008; Martin *et al.*, 2010). Therefore, in spite of an enhanced ecological similarity, syntopic congeners are old enough to be sexually divergent and reproductively isolated in nature.

However, alternative explanations for our findings are also plausible and worth acknowledging. The lack of divergence we observed at the regional scale may, for instance, reflect the specific geographical and historical background of our study system. At temperate latitudes, the biotic selective pressures that lead to limiting similarity may be reduced compared with selection stemming from abiotic and energetic constraints (Bothwell *et al.*, 2015; Pigot *et al.*, 2016). In the few cases in which we observed a significant association between species age and segregation in congeneric birds, the relationship spanned from phylogenetic limiting similarity (negative relationship) to the opposite pattern, phylogenetic conservatism (positive relationship). Little *in situ* radiation of avian taxa occurred in Europe (Richman, 1996), a fact that also reduces the chance for limiting similarity among young species, and at the same time enhances that of convergence among old ones (Tobias *et al.*, 2014). Eventually, the small sample of closely related syntopic species available for this study may have conditioned the magnitude of predictor effects. Apart from some regional and taxonomic idiosyncrasies, it should also be acknowledged that the differentiation time from the closest heterospecific inevitably increases when the geographical scale of sampling is shrunk (Bergsten *et al.*, 2012). This side-effect of the frequency of allopatric speciation may end up influencing our appreciation of phylogenetic limiting similarity in natural communities, starting from the fact that phylogenetic similarities may be low at small scales.

In conclusion, this study shows that the reduction of the spatial scale involves a parallel expansion of temporal extent, and this may explain the contrasting patterns we found when analysing limits to coexistence within biomes and within communities. Ecological similarity poses a fundamental constraint on the number of species coexisting at any single

point in space (alpha diversity) as well as the continental scale (gamma diversity), but scaling issues must be carefully scrutinized before any conclusion on underlying mechanisms can be drawn.

ACKNOWLEDGEMENTS

We are grateful to A. Segura for help during fieldwork and to the EBCC for providing raw data on European breeding birds. We also thank G. Thomas and to two anonymous referees for providing insightful comments that substantially improved this paper. This work was funded by 'Fundación Biodiversidad', and grants CGL2011-28177 and CGL2014-53899-P. J.S. belongs to the research network REMEDINAL3-CM (P2013/MAE-2719).

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Phylogenetic relationships among the sister species of European avifauna.

Appendix S2. Literature sources for phylogenetic information.

Appendix S3. Non-sister congener species in the study regions.

Appendix S4. Study regions and bird survey methods.

Appendix S5. Dataset for this study.

Appendix S6. Performance of multistate models.

Appendix S7. Relationships between species evolutionary age and C-score in syntopy.

DATA ACCESSIBILITY

Data are provided in Supporting Information.

BIOSKETCH

The authors study ecological patterns and evolutionary processes that explain species distribution, biotic interactions, and phenotypic variation within and among species.

Editor: Gavin Thomas