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

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1 **ABSTRACT**

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

8 **Location:** European Continent, north-west Italy and north-west Spain.

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

14 **Results:** A larger number of sister species with recent common ancestors is found in the
15 continent than within communities, a likely consequence of the allopatric mode of
16 divergence of lineages. Divergence in elevational preferences and niche breadth favored
17 the way back to secondary sympatry of European sister species, which took place ca. 2
18 million years after their split. Once in sympatry, the coexistence of species at the local
19 scale took almost twice as long and was instead favored by ecological convergence.

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

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 increasing the geographical scale of sampling. The opposite occurs at small scales, because local species pools assemble components that had time to expand their ranges, cross geographic 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 in context, and multiscale approaches may significantly contribute to this understanding (Willis and Whittaker, 2002). These approaches have permitted to tackle 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).

In this study, we assess whether ecological similarity and evolutionary time constrains species coexistence and distribution. We combine bird distributions, phylogenetic relationships and degree of ecological similarity to address co-occurrence patterns at different extents, continent vs. regions of a narrow latitudinal and longitudinal span, and at different grains, range vs. 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 (Hagemeijer & Blair, 1997), as well as our own extensive data on regional assemblages in the Alpine (NW Italy) and the Cantabrian regions (NW 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 ground) or environmental filtering (in the ecological ground) (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 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, introduced or with most of their range outside the continent. A multigene phylogeny was built by downloading 10,000 time-calibrated relaxed molecular clock trees from www.bird.tree.org (Jetz *et al.*, 2012) using the Hackett backbone of species (Hackett *et al.*, 2008). For all selected species, sequence data were available. 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 (Appendix S1 and S2 in 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 species evolutionary age, 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 ($r^2 = 0.91$; $t_{16} = 8.23$; $P < 0.001$) that confirms that multigene phylogeny provides a robust estimate of sister species age. The number of sister taxa dramatically dropped when downscaling to the regional assemblages, in spite these includes over 130 species. There were only four pairs in the Cantabrian Mountains and five in the Alps if we consider two pairs that were not included in multigene phylogeny (Appendix S1). These were *Phylloscopus collybita* and *P.*

ibericus, and *Corvus corone* and *C. cornix*, the evolutionary age of which was alternatively derived from Price (2010) and Jönsson *et al.* (2016), respectively. *Corvus* 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 it.

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 sister (hereafter, non-sister congeners) when the region missed their true sisters. These species share habitat and aspects of their phenotype and niche, 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 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 scale

To analyse species distribution at the continental scale, we downloaded the presence/absence dataset of European birds within 30 arc-minute grids (ca. 50×50 km) available from the EBCC Atlas of European Breeding Birds (Hagemeijer & 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 areas covered similar elevations and size, roughly corresponding to six cells of the European dataset (16,000 km², 120 – 2,770 m a.s.l., in the Alps, and 17,000 km², 1 – 2,615 m, in the Cantabrian

Mountains). We surveyed both open and forested habitats, establishing almost 4000 survey plots - 1,390 in the Alps and 2,539 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 a proxy of the climatic niche of populations and species. From 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 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 of 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 (6 pairs if we consider both sites). Thus, by assuming that 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 multi-state 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 6 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 correspond to 20% overlap in the smaller range or regional plot occupancy, as done by 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 overparameterization 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 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 95% CI do 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. Multi-state models were run in R with the package *mcn* (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. We were however able to test whether phenotypic and ecological dissimilarities influenced their present degree of segregation (C-score) when controlling for species evolutionary age (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 less 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 million years ± 0.56 SE) than the subsets found in the Alps (5.47 ± 1.7) or Cantabrian Mountains (5.86 ± 1.87). The oldest lineages are however non-sister congeners (Alps: 10.0 ± 2.1 with multigene phylogeny and 7.1 ± 1.3 with literature data; Cantabrian Mountains: 10.6 ± 2.0 and 6.3 ± 0.52 , respectively). The simplest model of transition to sympatry, including just time, indicates that it took 2.73 myrs ± 0.66 SE to 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: $\chi^2_3 = 11.52$, $P < 0.001$) (see Appendix S6 for the performance of the rest of 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 in 2.12 myrs ± 0.70 SE. The transition to syntopy of the few sister species of regional assemblages took more than twice as long to occur, 6.51 ± 3.93 SE 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 covariate, the addition of which speeded up coexistence in syntopy (3.41 myrs ± 3.14 SE; AIC_c = 6.57 vs. 13.42 of the simplest model, Likelihood ratio-test: $\chi^2_1 = 8.86$, $P = 0.003$; Fig. 1;

Appendix S6). However, contrarily 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 modeled the continuous variation in the C-score, thus positive regression slopes indicate that divergence facilitates segregation, not aggregation as above (Tab. 1). In non-sister congeners from both the Alps and the Cantabrian Mountains, differences in elevational preferences or body mass (or both) lead to high levels of spatial segregation. Results varied slightly among regions and depended on the source of information used for estimating evolutionary age (Tab. 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 (Tab. 1, Appendix S7).

DISCUSSION

Contrasting eco-evolutionary processes underlie species coexistence at different spatial scales, involving 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 with European birds are in line with those obtained by Pigot & Tobias (2013) in 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 myrs) matches that proposed for birds in temperate regions (ca. 2 myrs) (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 Myrs) to co-occur in syntopy within regions. This is an extremely long time if we consider that geographic 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 scale. 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 and 2013; Tobias *et al.*, 2014; Losin *et al.*, 2016).

This result, together with that of coexisting non-sister congeners, has also 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 Myrs ago, 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 Myrs), and that is longer than the time required to achieve reproductive isolation at these latitudes (3 Myrs; Price 2008; Martin *et al.*, 2009). 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 as compared to 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 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 the temporal extent, and this may explain the contrasting patterns we found when analyzing 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.

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Supplementary material

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

Appendix S2. Literature sources of phylogenetic information.

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

Appendix S4. Study regions and bird survey methods.

Appendix S5. Dataset of this study.

Appendix S6. Performance of multistate models.

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

Data Accessibility statement

Data are provided in supplementary material

Biosketch

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

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447 Table 1. Results of censored regression models testing for the relationship between C-score in regional assemblages and differences in
448 phenotypic and ecological parameters of congeneric species that are not sister taxa. For each study regions, we run two sets of models, which
449 included among predictors evolutionary ages from multigene phylogeny, and from alternative literature sources. The three models receiving the
450 best support for each subset of data are shown, highlighting in bold the best ranking ones according to AIC_c value. Slope and their SE are also
451 shown, as well as significance levels and the number of species pairs. Positive slopes indicate that the predictor promotes segregation, while
452 negative ones indicate it favours syntopy.
453

Segregation (C-score) in the Alps of non-sister species of the same genus	<i>Evolutionary age derived from multigene phylogeny</i>	<i>Evolutionary age derived from literature sources</i>
	Model 1	Model 1
<i>Predictors</i>	Evolutionary age (-0.004 ± 0.004) Elevation differences (0.0002 ± 0.001)***	Elevation differences (0.0003 ± 0.0001)**
<i>AIC_c</i>	3.00 (<i>n</i> = 14)	4.06 (<i>n</i> = 11)
	Model 2	Model 2
<i>Predictors</i>	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)***
<i>AIC_c</i>	10.00 (<i>n</i> = 14)	11.84 (<i>n</i> = 11)
	Model 3	Model 3
<i>Predictors</i>	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)
<i>AIC_c</i>	13.34 (<i>n</i> = 14)	16.12 (<i>n</i> = 11)

Segregation (C-score) in the
Cantabrian Mountains of non-sister
species of the same genus

*Evolutionary age derived
from multigene phylogeny*

*Evolutionary age derived
from literature sources*

	Model 1	Model 1
<i>Predictors</i>	Evolutionary age (0.008 ± 0.005) Elevation differences (0.0002 ± 0.0001)	Elevation differences (0.0001 ± 0.0000)
<i>AIC_c</i>	6.75 ($n = 14$)	16.84 ($n = 11$)
	Model 2	Model 2
<i>Predictors</i>	Body size differences (0.16 ± 0.04)*	Body size differences (0.13 ± 0.08)
<i>AIC_c</i>	8.70 ($n = 14$)	17.32 ($n = 11$)
	Model 3	Model 3
<i>Predictors</i>	Elevation differences (0.0001 ± 0.0001) Body size differences (0.16 ± 0.08)*	Evolutionary age (0.034 ± 0.018)*
<i>AIC_c</i>	10.02 ($n = 14$)	18.64 ($n = 11$)

* $P < 0.05$

** $P < 0.01$

*** $P < 0.001$

Fig.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 (Alps and Cantabrian Mountains), respectively. Black continuous and dotted lines represent curves and 90% CI 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.