

The Evolution of Local Co-occurrence in Birds in Relation to Latitude, Degree of Sympatry, and Range Symmetry

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ABSTRACT: Recent speciation rates and the degree of range-wide sympatry are usually higher farther from the equator. Is there also a higher degree of secondary sympatry (coexistence in local assemblages in sympatry) at higher latitudes and, subsequently, an increase in local species richness? We studied the evolution of sympatry in passerine birds using worldwide species distribution data. We chose recently diverged species pairs from subclades not older than 5 or 7 million years, range-wide degree of sympatry not lower than 5% or 25%, and three definitions of the breeding season. We related their sympatry to latitude, the degree of sympatry (breeding range overlap), range symmetry, and the age of split. Sympatry was positively related to latitude, but it did not differ between tropical and temperate regions, instead increasing from the Southern to the Northern Hemisphere. Sympatry was also higher in species pairs with a higher degree of sympatry and more symmetric ranges, but it did not predict local species richness. Following speciation, species in the Northern Hemisphere presumably achieve positive local co-occurrence faster than elsewhere, which could facilitate their higher speciation rates. However, this does not seem to be linked to local species richness, which is probably governed by other processes.

Keywords: sympatry, coexistence, speciation, range overlap, species richness.

Introduction

Biological diversity exhibits a pronounced latitudinal gradient, increasing toward the equator in most groups of organisms (Hillebrand 2004). Several hypotheses have been proposed to explain the evolution of this diversity gradient. For instance, higher diversity in the tropics has been suggested to result from the older age of tropical biomes and subsequent availability of more time for speciation (Mittelbach et al. 2007; Marin and Hedges 2016). Additionally, higher resource availability leading to higher species carrying capacity (Currie 1991; Hawkins et al. 2003; Pigot et al.

2016; Etienne et al. 2019), lower extinction rates (Rolland et al. 2014; Pulido-Santacruz and Weir 2016), and higher diversification rates (Cardillo 1999; Cardillo et al. 2005) could also be contributing factors. Yet despite extensive research, relative support for these theories has not been firmly established. For example, the idea that species originated in the tropics at a faster rate than in the temperate regions was prevalent in the field for a long time and found support in several clades (Martin and McKay 2004; Allen and Gillooly 2006; Jablonski et al. 2006; Ricklefs 2006; Martin and Tewksbury 2008; Kiessling et al. 2010; reviewed in Mittelbach et al. 2007). However, later studies have shown great variation in speciation rates across the tree of life (Rabosky et al. 2015; Rabosky 2016), with recent speciation rates not necessarily differing between temperate and tropical regions (Rabosky et al. 2015; Marin and Hedges 2016). Most recently, compelling evidence has emerged indicating that recent speciation rates are, in fact, higher in species-poor temperate regions (Weir and Schluter 2007; Rabosky et al. 2018; Harvey et al. 2020; Machac 2020; reviewed in Schluter and Pennell 2017; meta-analysis in Freeman et al. 2022b).

Fast speciation rates, with constant extinction rates and other factors, should generate comparatively higher diversity (Cutter and Gray 2016). However, this is conditioned by the successful transition of incipient species into secondary sympatry to complete the speciation cycle (Tobias et al. 2020). Typically, speciation begins after the division of a species' range into several allopatric segments. The ranges of resulting daughter species are less likely to subdivide in the future because of their smaller sizes. For further allopatric speciation to occur, daughter lineages must first expand geographically, often leading to some mutual range overlap (fig. 1; Weir and Price 2011). This scenario obviously assumes that species typically originate in allopatry, where ranges spatially subdivide and then

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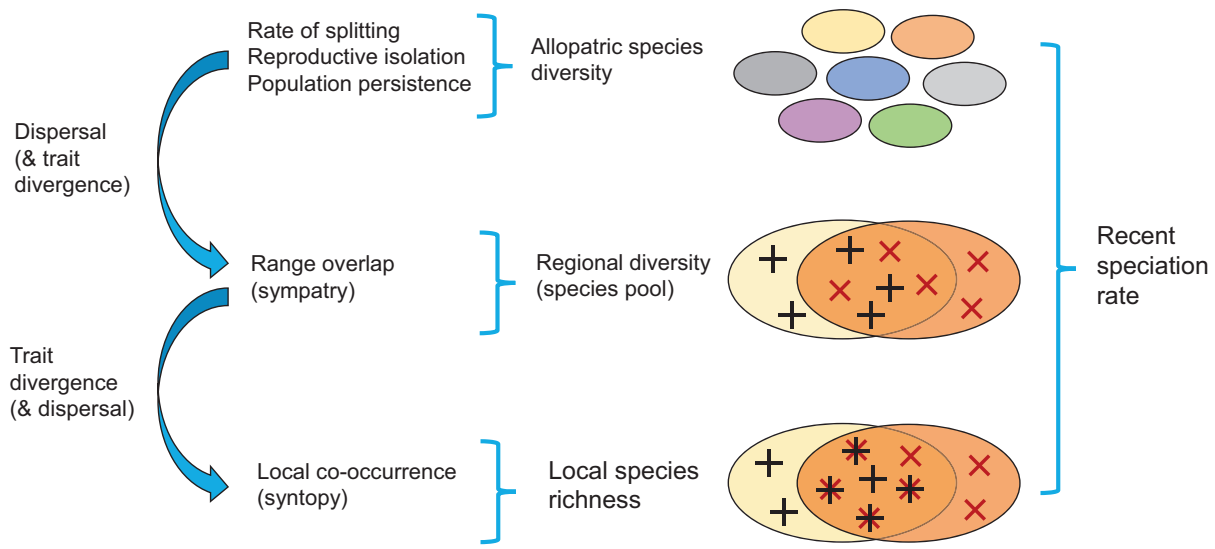


Figure 1: Constituent processes of speciation lead to an emergent characteristic of recent speciation rates that can be identified from molecular phylogenies (Rabosky 2016). Each of these constituent processes can be a rate-limiting step in the accumulation of species. However, under allopatric speciation, without the transition to secondary sympatry, speciation generates diversity of allopatric species (geographic radiation *sensu* Simões et al. 2016). The transition to secondary sympatry allows the buildup of regional diversity in species pools (Weir and Price 2011), while the transition to secondary syntopy allows the buildup of local species diversity (Remeš and Harmáčková 2023). Although it is possible to close the speciation cycle (Tobias et al. 2020) by the evolution of sympatry and without developing syntopy, there is ultimately an upper limit on how many species can accumulate regionally without developing syntopy because microallopatry has its spatial limit. The evolution of syntopy and local species richness is obviously conditioned by the evolution of range overlap and the buildup of regional species pools. Transitions to secondary sympatry and syntopy are conditioned by successful dispersal and can be facilitated by niche divergence between species. Dispersal is more important than trait divergence for the evolution of secondary sympatry, and vice versa for secondary syntopy (Tobias et al. 2020; Remeš and Harmáčková 2023). Species ranges are depicted schematically by ovals of different colors, and two species sampled at different localities are illustrated by black and red crosses.

expand, which is generally true in birds (Barraclough and Vogler 2000; Phillimore et al. 2008; Smith et al. 2014; Pigot and Tobias 2015).

In a typical case, the evolution of sympatry (range overlap) requires, at minimum, incipient species to develop reproductive isolation and ecological divergence, enabling their long-term coexistence (Weber and Strauss 2016; Germain et al. 2021; Irwin and Schluter 2022; reviewed in Tobias et al. 2020). Divergence in traits related to the evolution of the premating reproductive barriers occurs more rapidly in temperate regions than in the tropics (e.g., bird song and its discrimination [Weir and Wheatcroft 2011; Weir and Price 2019; but see Freeman et al. 2022a], coloration [Martin et al. 2010]). Furthermore, divergence of ecological traits among incipient species, even while still in allopatry, and higher dispersal propensity might facilitate earlier transitions to secondary sympatry via species sorting (Tobias et al. 2020). Alternatively, acceleration in trait divergence might be promoted by the transition to secondary sympatry itself (Anderson and Weir 2021, 2022), which is

expected to proceed faster in temperate regions (Martin et al. 2010; Weir and Price 2011; Martin et al. 2015). In sum, the evolution of secondary sympatry might be faster in temperate regions due to a combination of higher rates of trait divergence (Martin et al. 2010; Freeman et al. 2022b) and higher dispersal rates (Sheard et al. 2020), which could facilitate faster contact between species after the removal of the geographical barrier (Price 2008). This accelerated evolution of secondary sympatry, in turn, can lead to a faster closure of the speciation cycle (Tobias et al. 2020), faster speciation rates, and faster accumulation of diversity in temperate regions (Weir and Schluter 2007; Rabosky et al. 2018; Harvey et al. 2020; Machac 2020; Freeman et al. 2022b).

Previous studies of the evolution of secondary sympatry have been conducted at the regional scale, using species ranges as proxies for species occurrence (e.g., Pigot et al. 2016; Pigot et al. 2018; reviewed in Remeš and Harmáčková 2023). This is relevant for the evolution of species pools and regional diversity, including their latitudinal

gradient. However, when studying the buildup of local species diversity, we must downscale to a correspondingly small spatial grain, using local assemblages (fig. 1; Remeš and Harmáčková 2023). There are at least two reasons. First, even species living in sympatry might not necessarily meet locally inside the area of range overlap (“mosaic sympatry” or allotopy) because of incomplete range filling (Hurlbert and White 2005, 2007). This can be caused by differences in ecology, especially in microhabitat use (Rivas 1964; Dorková et al. 2020). Second, the intensity of species interactions might change with latitude and thus affect local species co-occurrences (e.g., via competitive or predator-mediated exclusion; Martin 1988; Schemske et al. 2009; Matysioková and Remeš 2022). To at least indirectly account for species interactions, we must work at spatial scales local enough to allow for interactions among individuals. Then, two critical questions arise. First, is the degree of syntopy (local species co-occurrence inside the range overlap) higher farther from the equator when controlled for the age of species split? We believe it should be, because divergence in species recognition-related and ecological traits is faster farther from the equator (as mentioned above), and trait divergence seems to facilitate species syntopy (Remeš and Harmáčková 2023). Second, does the degree of syntopy between closely related species predict local species richness? We believe it should, because all else being equal, higher syntopy means more species can accumulate locally and thus increase local species richness.

In sum, due to differences in trait divergence rates, dispersal propensity, and the intensity of interspecific interactions between the tropics and temperate regions, the degree of syntopy might vary across latitudes. Moreover, secondary syntopy might be a precondition for the buildup of local species richness, similar to how secondary sympatry is a prerequisite for the buildup of regional species richness (fig. 1). These two conjectures lead to our two primary objectives. First, to illuminate the geographical trends in the evolution of local species co-occurrence, we examine the latitudinal gradient in the degree of secondary syntopy while controlling for the age of species split. To achieve robust results, we analyze a large sample of occurrence records (7,834,063 checklists from the eBird project) covering 887 passerine bird species distributed globally. Given that trait divergence rates are indeed faster in temperate areas and that trait divergence promotes syntopy of newly evolved species, we expect a higher degree of syntopy (when controlled for the age of species split) farther from the equator. Second, we study the relationship between the degree of syntopy and local species richness derived from the same eBird checklists. Under the assumption that syntopy is a prerequisite for the buildup of local diversity, we expect a positive relationship between these variables.

Methods

When preparing our dataset and selecting the analytical methods, we encountered several decisions summarized in table S1 (tables S1–S4 are available online).

Phylogenetic and Distributional Data

We obtained data on species relatedness from <https://birdtree.org> (Jetz et al. 2012). We downloaded 1,000 time-calibrated phylogenetic trees based on genetic data and built using the Ericson backbone (6,670 species). Because of uncertainty in exact divergence times and species relationships, we randomly selected 100 trees and replicated all analyses across these trees. We pruned the trees to contain only songbirds (order Passeriformes), resulting in phylogenies with 4,032 species.

We used the extent of occurrence maps of birds (BirdLife International and NatureServe 2011) to quantify species ranges. We utilized range maps available for BirdLife taxonomy version 4.0 to align species between phylogenetic and spatial datasets. In cases of discrepancies, we (i) merged ranges when a species in the phylogenies was split into multiple species in range data and (ii) removed a species from phylogenies when no range information was available. We were interested in ecological and evolutionary processes occurring during the time of breeding, as we expect that interspecific interactions would be strongest during this time (i.e., resource competition). Therefore, we filtered the ranges so that they included only areas where species presence was described as “extant,” “probably extant,” or “possibly extant,” and season was characterized as “resident” or “breeding season.” This filtering resulted in 3,999 species available across both datasets.

For the calculation of species co-occurrences in local assemblages, we obtained observational data on species occurrences from a community science project (monitoring done by volunteers, also widely known as “citizen science”), the eBird Basic Dataset (downloaded version: February 2021). We linked eBird taxonomic names to species names in phylogenetic and geographic datasets. Then we filtered the eBird data so that they included only complete checklists (all observed species recorded) with observation duration of 20–60 min, distance traveled up to 1 km, and the type of protocol being “traveling,” “stationary,” or “random.” These criteria were chosen to ensure that all species occurrences were recorded under standardized observation conditions and at relatively local spatial scales. Subsequently, for every species pair from all phylogenies (see “Subclades and Species Pairs”), we further spatially filtered this set of checklists so that it included only checklists occurring within the overlap of the ranges (intersection

of the BirdLife shapefiles) of the two species (Remeš and Harmáčková 2023).

Although we used only “resident and breeding” parts of species ranges for spatially filtering the eBird checklists, they still contained observations from months outside the breeding season. Here, we were interested in the events occurring during the breeding season only, as they are most critical for reproductive fitness (e.g., high demand and competition for resources). Thus, we aimed to further filter the eBird data to contain only checklists recorded during the breeding season. However, determining the timing of the breeding season for a large number of species worldwide is challenging. Therefore, we employed three different approaches to achieve this. First, we divided species pairs into three categories based on the mean latitude of the checklists occurring within their range overlap (a method hereafter referred to as “Breeding”). For species pairs with a mean checklist latitude higher than 23°N (the Tropic of Cancer), we retained only checklists recorded from April to July (i.e., those falling into the typical breeding season in the Northern Hemisphere). In pairs with a mean checklist latitude lower than 23°S (the Tropic of Capricorn), we retained only checklists from September to December (the usual breeding season in the Southern Hemisphere). For pairs with a mean checklist latitude falling between 23°N and 23°S, we included checklists from all months. Second, for every species pair, we selected only checklists falling within months when both species were observed (at least one observation of each species in each month, possibly in different checklists; a method hereafter referred to as “Months”). This method did not strictly limit observations to the breeding season but ensured that we used only months in which both species had a chance to co-occur. Third, we divided the checklists of every species pair into 10°-wide latitudinal bands and retained only checklists falling within the months of the breeding season in a particular band, as defined by Cazalis et al. (2021; a method hereafter referred to as “Bands”).

Subsequently, using the checklist data, we created a presence-absence matrix for each species pair. Based on these matrices, we calculated an index of syntopy for each species pair. This index should not require randomizations (for calculating *Z*-scores or standardized effect sizes; Keil 2019; Keil et al. 2021), which would be computationally prohibitive given the millions of checklists and hundreds of species pairs involved. Furthermore, it should not be sensitive to sample size. There are numerous association indices for presence-absence data, but only some of them do not require randomizations (Hubalek 1982; Keil 2019; Keil et al. 2021). We chose to use odds ratio (also known as the cross-product ratio) because it is a widely used and well-understood index for quantifying associations in 2 × 2 contingency tables (e.g., Koricheva et al. 2013, chaps. 6

and 13; Agresti 2018, chap. 8; 2019; see text 1, available online). To improve statistical properties, it is advisable to use a log_e transformation to obtain the log odds ratio (logOR; Koricheva et al. 2013, chaps. 6 and 13). For independently occurring species, the logOR equals 0, positive values indicate positive co-occurrence (species association), and negative values indicate negative co-occurrence (species segregation). It ranges from minus infinity to plus infinity. We excluded species pairs with expected co-occurrence at fewer than one site (as recommended by Veech 2013) and with fewer than 50 checklists within the range overlap. The latter was our own ad hoc criterion with the aim of excluding observations with substantial sampling variance in the estimates of syntopy (fig. S1; figs. S1–S24 are available online). We did not impose a maximum limit on the number of checklists because we wanted to utilize as much information as possible, and logOR is unbiased with respect to sample size (fig. S1).

Subclades and Species Pairs

We were interested in the evolution of secondary syntopy as a prerequisite for the buildup of local species diversity. Thus, we focused on relatively recent postspeciation events instead of working across the whole phylogeny. However, working exclusively with sister species pairs is made difficult by two factors. First, most sister pairs are allopatric (Barraclough and Vogler 2000; Phillimore et al. 2008; Smith et al. 2014; Pigot and Tobias 2015), which precludes the calculation of syntopy. Moreover, species pairs identified on our phylogenies were not necessarily true sister pairs. The reason was that the phylogenetic trees we used contained only species whose phylogenetic relations were based on genetic data (4,032 species out of 5,966 passerine species in total), making it impossible to identify true sister pairs. As a compromise, in each of the 100 phylogenies we identified groups of species forming subclades with the maximum age of the oldest node being either 5 or 7 million years. The species pairs were then selected as all pairwise combinations of species in each subclade (fig. S2A).

For every species pair in all subclades in all phylogenies, we first obtained its age as the age of the most recent split between the two species. Note that this age could be different for the same species pair in different phylogenies because of uncertainty in the estimates of divergences times. Second, we obtained geographic latitude for each species pair as the average latitude of all checklists that were used to calculate syntopy for the respective pair. To ensure that there was no bias in the estimate of latitude, we also calculated it as the geographic centroid of the range overlap of the respective species pair. These two estimates were highly correlated (Pearson correlation coefficient $r = 0.99$; major

axis regression slope = 0.99), and we used the mean checklist latitude in further analyses. Third, we computed the degree of range sympatry (%) as $\text{area of range overlap} / \min(\text{area of species 1, area of species 2}) \times 100$ (Barraclough and Vogler 2000; Pigot et al. 2016, 2018). The value of the degree of sympatry spans from 0% (ranges of the two species do not intersect) to 100% (complete overlap, whereby the smaller range lies completely within the larger range). Fourth, we computed range symmetry (%) as $\min(\text{area of species 1, area of species 2}) / \sum(\text{area of species 1, area of species 2}) \times 100$ (Barraclough and Vogler 2000; Hemingson et al. 2019). Symmetry spans from close to 0% (highly asymmetric ranges; the value of 0% can never be observed in real data) to 50% (perfect symmetry; i.e., the ranges with the same area). Finally, for all subclades we created two alternative datasets by keeping only species pairs with the degree of sympatry of at least 5% or 25% (fig. S2B). We did so to obtain robust estimates of syntopy (i.e., range overlap will contain enough checklists) and to also obtain datasets where species pairs analyzed were reasonably sympatric and not only parapatric (for a similar approach, see, e.g., Pigot et al. 2016). In the end, we obtained 1,200 datasets coming from 100 phylogenies with species pairs filtered according to 12 combinations of the two age thresholds (5 and 7 million years), two degree of sympatry thresholds (5% and 25%), and three breeding season definitions (Breeding Month, Bands). In this way, we accounted for both phylogenetic uncertainty and uncertainty stemming from using different criteria to subsample data.

To account for data nonindependence, we wanted to use only one species pair from each subclade. At the same time, we aimed at minimizing the variation introduced by species split ages. Thus, our intention was to further use only the youngest species pair from each subclade passing the threshold criterion for the degree of sympatry. However, because of data limitations, sometimes the youngest pair could not be used. We thus applied the following procedure. First, we ranked all species pairs in a subclade according to their split age, with the youngest pair being assigned rank 1, the second youngest rank 2, and the third youngest rank 3 (fig. S2C). If there were more species pairs with the same age (and thus the same rank), we kept them as well. All other, older pairs were removed. Finally, in each subclade we selected species pairs for the analysis as follows: if the species pair ranked 1 was deemed usable (i.e., expected co-occurrence was higher than 1 and there were more than 50 checklists within the range overlap of the two species in the pair), we kept it for further analyses and removed all remaining pairs with higher ranks. If there were several pairs ranked 1 and all of them were usable, we selected one of them at random. If there were no usable pairs ranked 1, pairs ranked 2 were evaluated using the previous steps (fig. S2D). If needed, pairs ranked 3

followed. If none of the pairs in a subclade was usable, the whole subclade was removed from further analyses.

Assemblage-Level Syntopy and Species Richness

For geographical analyses, we prepared two datasets, each pertinent to one of our two major questions. The common principle was to calculate an aggregated characteristic for each regional assemblage to be used as a data point in spatial analyses and mapping (so-called assemblage-wide means). To delimit regional assemblages, we used a global hexagonal grid (ISEA3H, resolution 7) with 21,860 cells, each with an area of approximately 23,323 km² (Mocnik 2019).

First, for assemblage-level analyses of syntopy, we calculated mean syntopy, degree of range sympatry, range symmetry, and pair age for all unique species pairs across all 1,200 datasets (see table S2). Next, we determined which species pairs fall into every hexagon. For this, we overlapped spatial positions of all unique checklists of all species pairs with our global hexagonal grid. The assemblage of every hexagon was defined as a list of species pairs with at least one checklist falling into that hexagon. Finally, we calculated assemblage-wide means of our variables. We retained only hexagons containing at least 20 checklists.

Second, for assemblage-level analyses of species richness, we calculated the assemblage-wide mean of species richness per eBird checklist, while we used the assemblage-wide mean of syntopy as defined in the previous step. We overlapped spatial positions of all unique checklists of all species pairs with our hexagonal grid. Thus, we obtained lists of eBird checklists falling within every hexagonal cell. We calculated the number of passerine species in each checklist as our estimate of local species richness. Then we computed the assemblage-wide mean of local species richness as an average of local species richness of all checklists falling into a hexagonal cell. Ultimately, we used 7,834,098 checklists within 2,497 hexagon cells.

Statistical Analyses

We fitted several regression models with the logOR index of syntopy as a dependent variable and latitude, degree of sympatry, range symmetry, and species pair age (time since species divergence) as predictors (table S2). In all models, we included quadratic effects of all predictors to test their nonlinearity. This was important, especially in the case of latitude, because we expected similar trends from the equator toward both poles, and the quadratic effect would allow for such a pattern in the fit. An alternative approach would have been splitting the data by hemisphere and fitting a

model with absolute latitude, hemisphere, and their interaction. However, we felt that such a model would be unnecessarily complicated and would not provide additional insight compared with a simple quadratic effect of latitude. However, quadratic effects were never statistically significant, and thus we excluded them from the final models.

First, we fitted univariate models with each of the predictors separately. Then we fitted a multipredictor model with latitude, degree of sympatry, range symmetry, and pair age together as predictors (table S2). We accounted for phylogenetic relatedness among species pairs by using the phylogenetic generalized least squares (PGLS) models. The phylogenetic variance-covariance matrix for these models was created using phylogenies with one member of each species pair randomly deleted. We also weighted each estimate by the $\log_{10}(\text{number of checklists})$ used to calculate syntopy, because the variance of syntopy estimates typically increases with decreasing sample size (fig. S1). We fitted all PGLS models (table S2) to all 1,200 datasets. For presentation, for each model we computed mean parameter estimates from 100 model fits run on our 100 phylogenies within each of the 12 combinations of subclade age threshold, degree of sympatry threshold, and breeding season definition (hereafter referred to as “mean-model estimates”). In this way, we averaged across the phylogenetic uncertainty (a nuisance factor for us) but retained the apparent variation in parameter estimates caused by different data subsampling.

In spatial analyses across grid cells, we first fitted a model with mean logOR as a dependent variable and linear and quadratic effects of latitude (grid cell coordinate), the degree of sympatry, range symmetry, and pair age as predictors. Then we fitted a spatial model with local species richness as a dependent variable and mean logOR as a predictor. In both models, we fitted a simple generalized least squares (GLS) model without spatial autocorrelation and 10 spatial GLS models with different spatial autocorrelation structures (see table S2). We then selected the best model with the lowest Akaike information criterion. To calculate the relative importance of the four predictors in multipredictor models, we used the *relaimpo* package (Grömping 2006). Since this method does not work on GLS models and, as far as we know, no effective method exists to allow quantifying the relative importance of predictors in GLS models, we refitted all our multipredictor models using linear regression without phylogenetic effects. All predictors were centered and scaled so that their mean = 0 and SD = 1 prior to analyses. Models were fitted in R version 4.3.0 (R Core Team 2023) using the *gls* function from the *nlme* package (Pinheiro and Bates 2022). The R code to fully reproduce all our analyses is available on Zenodo (<https://doi.org/10.5281/zenodo.8421492>; Harmáčková and Remeš 2023), and the

distributions of all variables across selection criteria are depicted in figures S3–S10.

Results

The total number of unique species pairs in all 1,200 datasets was 545 (mean = 166 species pairs per one dataset). Syntopy (\log_e odds ratio) of species pairs ranged from -4.1 to 5.1 (mean = 1.0, median = 1.1; all datasets considered; fig. S10). The mean \log_e odds ratio of 1.0 translates into an odds ratio of $\exp(1.0) = 2.7$. Both of these values demonstrate that, on average, species occurrences were positively associated: the odds of one species occurring in a checklist when the other species also occurred were on average 2.7 times higher than if the other species was absent. Note that the odds ratio is a symmetric index, so it does not matter which species from the species pair we take as a reference when calculating syntopy.

Latitude predicted syntopy statistically significantly in just one out of the 12 mean-model estimates in the univariate analyses (figs. 2, S11–S13; table S3). However, in the multipredictor analyses, a significantly positive effect of latitude on syntopy was found in all mean-model estimates with the combination of 5 million years and 25% thresholds. In threshold combinations of 5 million years with 5% and 7 million years with 25%, it was significant only for one breeding season definition (Months), and it was never significant in the combination of 7 million years with 5% (figs. 3, S14, S15; table S4). The effect of latitude was stronger in mean-model estimates with the age threshold of 5 million years compared with 7 million years. Overall, relationships between syntopy and latitude were stronger in mean-model estimates based on the breeding season definition using Months.

Syntopy was significantly positively related to the degree of range sympatry only in mean-model estimates with a sympatry threshold of 5% in univariate analyses (figs. 2, S11–S13; table S3) but in all multipredictor mean-model estimates (figs. 3, S16, S17; table S4). Syntopy was positively correlated with range symmetry in all univariate and multipredictor mean-model estimates (figs. 2, 3, S11–S13, S18, S19; tables S3, S4). On the other hand, syntopy showed no relation to pair age in any of the mean-model estimates (figs. 2, 3, S11–S13, S20, S21; tables S3, S4).

Standardized effect sizes were consistently higher in the multipredictor models than in the univariate models. The overall increase was from 0.108 to 0.147 for latitude, from 0.187 to 0.247 for the degree of sympatry, and from 0.277 to 0.339 for range symmetry (we do not give these figures for pair age, which was never statistically significant). Multipredictor models thus captured more residual variation, leading to higher estimates of standardized regression coefficients. At the same time, correlations between

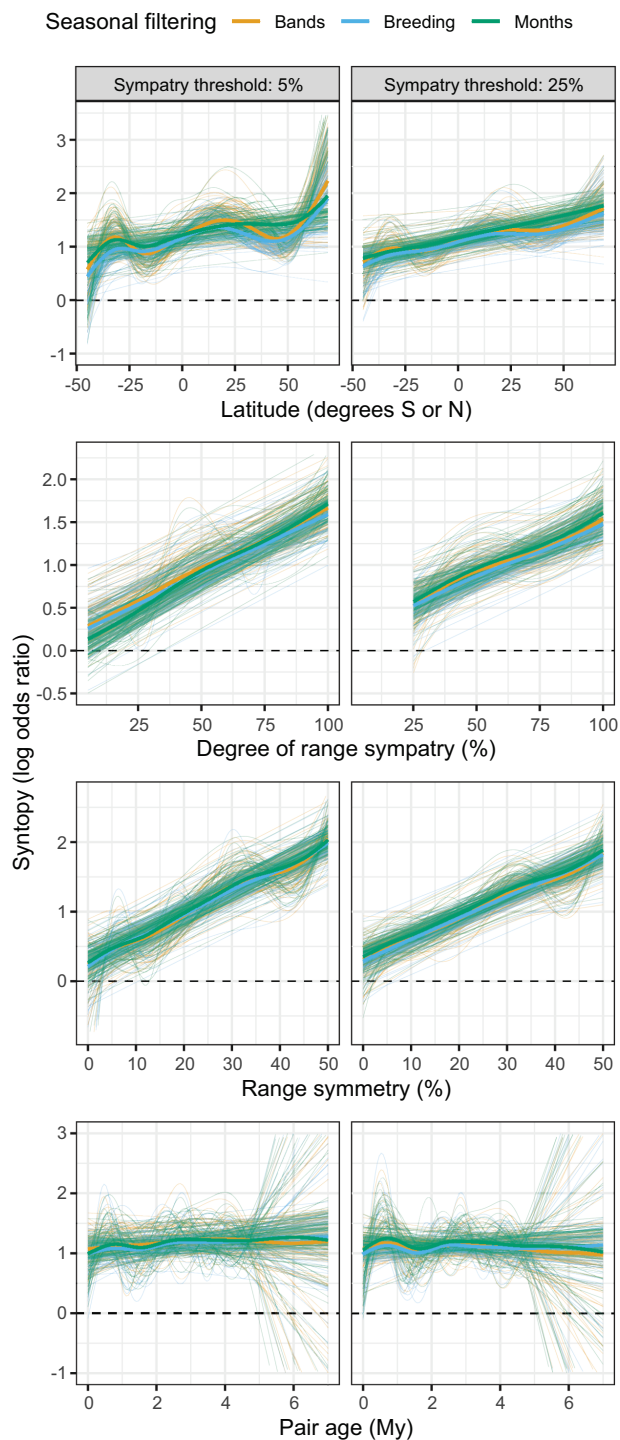


Figure 2: Relationships between syntopy (log odds ratio) and our four predictors using the 5-million-year age criterion for the delimitation of subclades on phylogenies. Thin lines represent model fits on individual phylogenies (100 phylogenies altogether), while thick lines depict mean trends, thus averaging across phylogenetic uncertainty. Relationships are displayed using predicted values from multipredictor generalized additive model (GAM) fits. The

predictors were weak. The median Pearson correlation coefficients across our 1,200 datasets were 0.024 between latitude and the degree of sympatry, -0.131 between latitude and range symmetry, and -0.181 between the degree of sympatry and range symmetry (fig. S22). These low correlations show that multicollinearity among predictors was not a problem in our multipredictor models. The comparison of the relative importance of predictors in multipredictor models showed that range symmetry explained by far the most amount of variation in syntopy (median = 59.8% of model R^2), followed by the degree of sympatry (31.5%), latitude (3.7%), and pair age (0.3%; fig. S23). The median R^2 across all 1,200 models was 0.17.

Geographically, relatively high syntopy was found in assemblages in eastern North America and northwest India, while syntopy lower than zero occurred in only a few cells, mainly in the Bahamas and southeast China (fig. 4). In the spatial analysis, both the linear (est. 0.31 ± 0.08 SE, $t = 3.9$, $P < .001$) and the quadratic effect of latitude (est. 0.28 ± 0.07 SE, $t = 3.9$, $P < .001$; table S2) significantly predicted syntopy, showing a marked increase in syntopy in the northern temperate regions (fig. 5A). Similarly, the degree of range overlap (est. 0.23 ± 0.02 SE, $t = 12.8$, $P < .001$) and range symmetry (est. 0.24 ± 0.02 SE, $t = 11.3$, $P < .001$) significantly positively predicted syntopy, while pair age negatively predicted it but with low effect size (est. -0.06 ± 0.02 SE, $t = -3.4$, $P < .001$). Latitudinal trends were surprisingly consistent across zoogeographic realms, despite quite pronounced regional effects (fig. 5B). On the other hand, the relationship between local species richness and syntopy was not statistically significant (est. -0.03 ± 0.03 SE, $t = -0.9$, $P = .343$; fig. 5C; table S2).

Discussion

Species occurrences were, in general, positively associated: the odds of one species occurring in a checklist when the other species also occurred were on average almost three times higher than if the other species was absent. In terms of predictors of syntopy, it was higher in the Northern Hemisphere, in species pairs with a high degree of sympatry (range overlap), and in species pairs with high symmetry of geographic ranges, while it did not change with the age of species pair split. Range symmetry had the strongest effect, followed by the degree of sympatry and latitude. On the other hand, local species richness was not predicted by syntopy across the globe.

GAM models were used to illustrate that there was not much pattern in the data beyond the linear trends identified by the phylogenetic generalized least squares models used in the main text. My = million years.

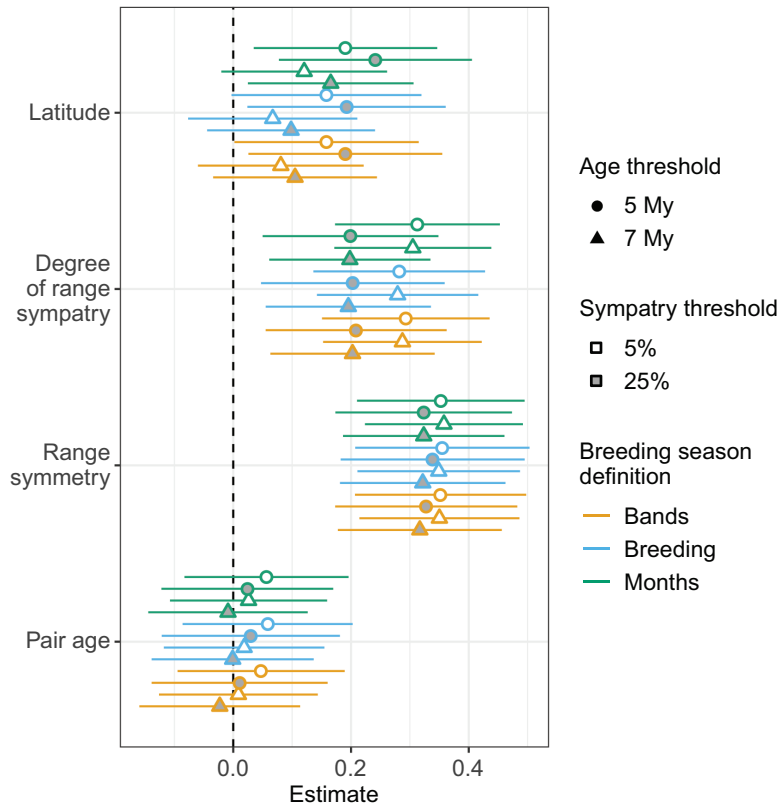


Figure 3: Forest plot displaying the results of multipredictor models with sympatry (log odds ratio) related to latitude, degree of range sympatry, range symmetry, and pair age. Symbols represent mean standardized regression coefficients obtained from model fits conducted across 100 phylogenies, while lines depict 95% confidence intervals. Symbol shape indicates the age threshold, symbol color represents the degree of sympatry threshold, and line color indicates the breeding season definition. Full results of the analyses are available in table S4. My = million years.

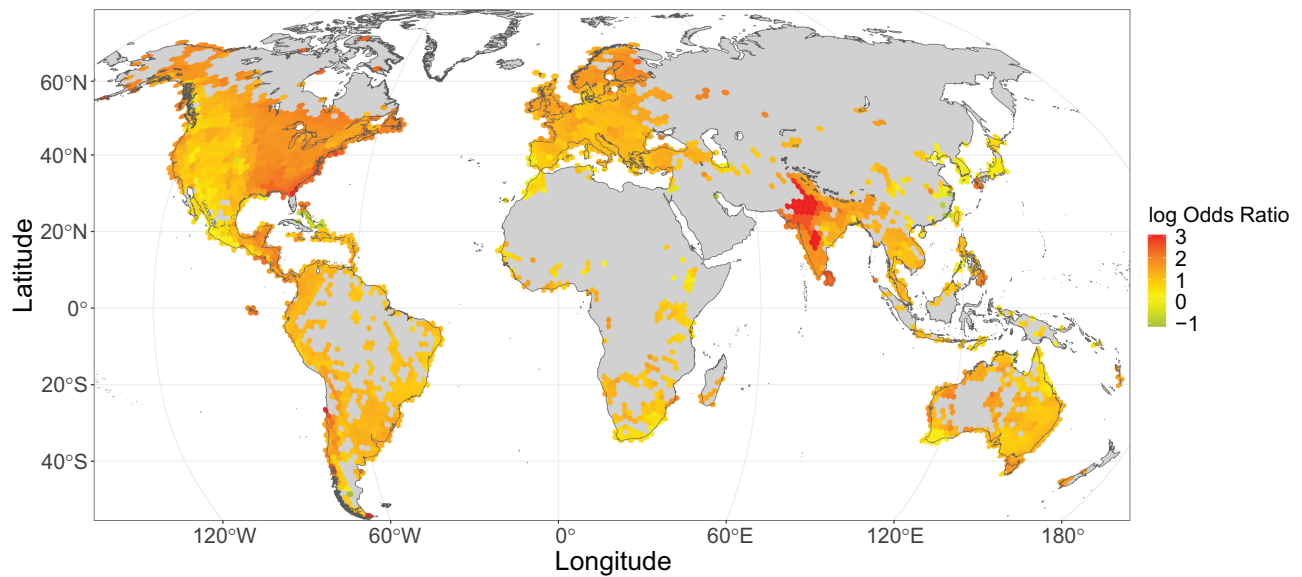


Figure 4: Global distribution of sympatry. It was calculated as the mean sympatry values (log odds ratio [logOR]) of all unique species pairs in the eBird checklists in our data that fell into a given hexagonal grid cell. The yellow-to-red color scale indicates mean grid cell logOR values higher than zero, while green color represents mean cell logOR values lower than zero.

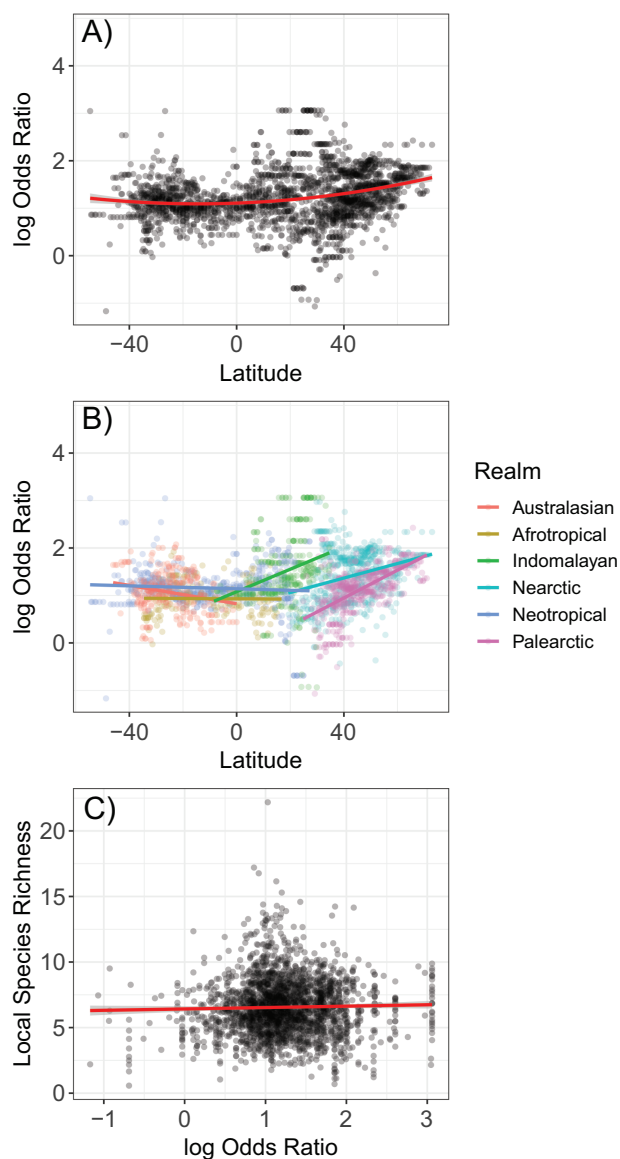


Figure 5: Geographic patterns in syntopy and local species richness. A, Relationship between mean syntopy (log odds ratio [logOR]) and latitude across all grid cells fitted with a quadratic regression line. B, Relationships between syntopy (mean logOR) and latitude in zoogeographic realms (see fig. S24 for the definition of realms). Linear regression lines are shown for visualization purposes only, as we did not fit statistical models to realm-restricted datasets. C, Relationship between local species richness (mean number of passerine species in eBird checklists falling into a given hexagonal grid cell) and syntopy (mean logOR). A linear regression line is shown.

Latitudinal differences in syntopy were more apparent between hemispheres rather than between tropical and temperate regions. In particular, syntopy increased from the equator to the north but not to the south (fig. 5A, 5B). The Northern Hemisphere has more land mass,

and the relationship might be asymmetric simply because the checklists we used spanned from 70° in the north to only -45° in the south (figs. 2, S9). However, this is probably not the only explanation, because the climate at the same distance from the equator is colder in the Northern Hemisphere than in the Southern Hemisphere (Chown et al. 2004), causing more environmental stress. Additionally, the Northern Hemisphere was more strongly affected by glaciation during the ice ages than the Southern Hemisphere (Byrne et al. 2011). While environmental drivers of diversity gradients have been well studied (Currie 1991; Hawkins et al. 2003; Pigot et al. 2016; Etienne et al. 2019), understanding their role in shaping secondary sympatry and syntopy is rudimentary. Although the trend of syntopy increasing from the equator to the north was consistent across zoogeographic realms, there were quite pronounced regional effects, as syntopy differed among realms and for the same latitude (e.g., higher in the Indomalayan realm than the Palearctic or Nearctic; fig. 5B). Thus, differences in syntopy might not be driven only by large-scale climatic conditions but also by biome-specific environments (e.g., habitat types). They might facilitate the faster establishment of local species coexistence, for example, due to higher energy availability in a system (Pigot et al. 2016) or more resources available in heterogeneous vegetation (Remeš et al. 2022). Consequently, it would be interesting to see whether any generalities in terms of environmental predictors of syntopy emerge.

Secondary syntopy increased with both the degree of sympatry and range symmetry. This finding confirms a recent study of Australian Meliphagoidea songbirds, which found the same patterns using data from a completely different community science project (Remeš and Harmáčková 2023). Species with a low degree of sympatry might have recently split and avoided each other due to similar ecological requirements carried over from analogous evolution during speciation in allopatry (Anderson and Weir 2021, 2022), leading to microallopatry within (so far small) range overlap. Only the subsequent divergence of traits after secondary contact has been established can then enable both local (higher syntopy) and global (higher range overlap) coexistence. This process can be accelerated when ranges become more sympatric and symmetric because then a large share of populations of both species has a chance to interact locally. This might further promote ecological character displacement (e.g., foraging strategy [Remeš and Harmáčková 2023], beak shape [Anderson and Weir 2021]) and the divergence of traits important for species recognition and the evolution of premating reproductive barriers (e.g., coloration; Hemingson et al. 2019). All of these processes might facilitate species differentiation and long-term coexistence. A hint in this direction is the stronger statistical effect of the degree of range sympatry for the 5% overlap threshold than

for the 25% threshold (fig. 3). In the former case, the analysis includes species pairs with lower sympatry and syntopy (fig. 2), probably leading to the stronger effect size identified. Alternatively, young species usually have a small range size (Webb and Gaston 2000), while their habitat niche breadth tends to be narrower (Laube et al. 2013). This could lead to low species association, whereby a large-ranged generalist species can be found in many localities where the small-ranged specialist species cannot occur because of narrow habitat requirements. Once the small-ranged species starts to expand its range due to the evolution of broader habitat preferences, range overlap, range symmetry, and syntopy can all start to increase, leading to their positive associations identified here.

The evolution of secondary sympatry is a prerequisite for completing the speciation cycle (Tobias et al. 2020) and increasing the regional diversity of species pools, as observed in highly productive areas (Pigot et al. 2016). Following a similar logic, we suggested that on a local scale, the evolution of syntopy could be a prerequisite for the buildup of high local species richness. However, this conjecture was not supported by our findings, as syntopy did not predict local species richness. Thus, it appears that although species evolve positive associations faster in the northern temperate regions, this does not translate into higher local species richness. One possible explanation might be that the evolution of syntopy in recently split species pairs is likely not a rate-limiting step in the buildup of local species richness. In other words, the time available for the accumulation of local species richness is probably longer than the time needed for the evolution of syntopy between recently split species. Local species richness would then be driven by factors other than the evolution of syntopy, such as local resource availability or vegetation complexity (e.g., Thiollay 1990; Hillebrand 2004; Remeš et al. 2022).

Our study demonstrates that the development of large datasets produced by community science might allow novel insights into large-scale macroecological patterns. At the same time, it is important to stress that unstructured, global-scale community science data are not a panacea. The problems involve the nonrandom selection of birding locations (e.g., a preference for urban areas or bird feeders as observation spots), a lack of control over weather conditions during birding, asymmetric coverage of hemispheres, or possible misidentification of species. However, eBird employs quality control over observation submissions as a combination of machine filter checks with regional editors communicating with the contributors (Sullivan et al. 2014). Still, researchers working with these data face a number of decisions to be made. The data are so voluminous that stringent filtration criteria can be applied to ensure a reasonable level of standardization (see table S1). In this way, community science data can be a very useful supplement to data generated by more focused research projects. In particular, the

global coverage of eBird data, when handled properly, offers insights not available using other sources of data.

In conclusion, based on a large sample of passerine species pairs distributed globally, we have shown that the degree of syntopy in closely related species pairs, controlled for the age of species split, is higher in the Northern Hemisphere, increases when their ranges overlap significantly and are similar in size. Since the evolution of secondary syntopy could be a rate-limiting step in the speciation cycle (Rabosky 2016; Tobias et al. 2020), these findings might explain faster recent speciation rates identified in regions farther from the equator. However, we lack a detailed understanding of the ecological and behavioral processes involved in the evolution of secondary syntopy across the tree of life. Further studies involving the effects of environmental conditions, habitats, and traits across lineages are thus needed to gain insight into the processes leading to the buildup of local diversity (Remeš and Harmáčková 2023).

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Statement of Authorship

L.H.: conceptualization (supporting), data curation (lead), data analysis (lead), writing (equal). V.R.: conceptualization (lead), data curation (supporting), data analysis (supporting), writing (equal).

Data and Code Availability

Data and R code to reproduce our data processing, statistical analyses, and main figures are available on Zenodo (<https://doi.org/10.5281/zenodo.8421492>; Harmáčková and Remeš 2023).

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