

Research article

Resource use divergence facilitates the evolution of secondary syntopy in a continental radiation of songbirds (Meliphagoidea): insights from unbiased co-occurrence analyses

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Allopatric speciation followed by the evolution of range overlap (sympatry) allows the build-up of regional diversity. However, local species richness requires that species co-occur locally (syntopy). Importantly, correct estimates of syntopy must be available to identify ecological traits facilitating it. We thus provide a method to correctly estimate local co-occurrence and demonstrate it on the evolution of secondary syntopy. First, we performed probabilistic co-occurrence analyses on simulated data across a sympatry gradient from 0 to 100%. Second, we extracted 116 species pairs younger than 10 My from a dated phylogeny of Meliphagoidea songbirds. We constructed a presence–absence matrix of 58 species across 470 sites based on 37 250 censuses in Australia and Tasmania from 1989 to 1995. We also constructed a spatial mask based on species ranges, identifying sites within versus outside the area of sympatry. We ran both unconstrained and range mask-constrained co-occurrence analyses. We compared the resulting syntopy and predicted it by species ecology. Simulations and exact analyses showed that co-occurrence analyses must be limited to sites in the area of sympatry between species. Without this spatial limit, syntopy was negatively biased, especially in common species. Accordingly, syntopy was negatively biased in Meliphagoidea when data from all sites were used, but this bias decreased with increasing sympatry, in agreement with numerical and exact analyses. When using correct estimates, syntopy increased with increasing divergence in the use of foraging stratum (ground, shrub, subcanopy and canopy) and with decreasing divergence in diet. In conclusion, we introduced a general method for calculating local species co-occurrence and confirmed its validity by simulations. We illustrated its use by analyzing the evolution of secondary syntopy in a phylogenetic framework. We found support for both niche divergence (foraging stratum) and niche conservatism (diet) in facilitating evolutionary transitions to secondary syntopy, allowing the build-up of local species richness.

Keywords: co-occurrence, niche divergence, speciation, species richness, sympatry



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Introduction

Understanding the coexistence of species is a fundamental task in ecology and evolutionary biology due to its link to the evolution of species richness. Cycles of allopatric speciation followed by the evolution of secondary sympatry (Box 1) allow the build-up of species richness (Mayr 1963, Barraclough and Vogler 2000, Phillimore et al. 2008). Therefore, understanding the drivers of secondary sympatry is fundamental to our understanding of the evolution of species diversity (Pigot et al. 2016). The evolution of secondary sympatry after allopatric speciation is conditional upon the evolution of reproductive isolation (Cooney et al. 2017) and the cessation of the geographic barrier that caused speciation in the first place (Kisel and Barraclough 2010). However, once the barrier is absent, both historical (dispersal limitation) and ecological factors (niche divergence, resource availability, species interactions) can impede the development of sympatry (Louthan et al. 2015, Pigot et al. 2018). Given enough time, range drift can bring species into contact, thus overcoming dispersal limitation (Warren et al. 2014). The development of sympatry then depends on the completion of reproductive isolation (Cowles and Uy 2019), the availability of resources and the evolution of niche differences (Pigot et al. 2016, 2018, McEntee et al. 2018).

In general, the distinction between sympatry and syntopy is in part needed due to data deficiencies. Imagine a perfect

world where we knew precise spatial position of all individuals of all species. Then we could analyze segregation versus association between species spatially explicitly and across all individuals, calculating a quantitative index of pairwise species co-occurrence usable in a multitude of ecological and evolutionary studies. However, we live in a world where the distribution of a great majority of species is poorly known. In such a situation, we find making a distinction between sympatry and syntopy a useful improvement on previous work allowing novel insights into many ecological issues.

Most previous multi-species, large-scale studies of secondary sympatry were conducted at the level of species ranges (Barraclough and Vogler 2000, Weir and Price 2011, Pigot et al. 2016; Fig. 1a–b), which bear no information on the fine-grained spatial distribution of individuals within ranges. However, the ecological theory of species co-existence is predicated on the possibility of individuals interacting locally (Araújo and Rozenfeld 2014). By local interaction we mean the potential for individuals to literally interact (scramble competition, interference competition, predation) because they are in the same physical place at the same time. Local interactions between individuals of different species are hypothesized to generate nonrandom patterns of co-existence and resource use (Schoener 1974, Diamond 1975, Holmes and Recher 1986, Weiher and Keddy 1999), and lead to ecological and reproductive character displacement and

Box 1: Sympatry and syntopy – definitions

Mayr (1963, p. 672) defined sympatry as ‘the existence of a population in breeding condition within the cruising range of individuals of another population’, clearly implying the existence of spatial contact between individuals of different species. The ‘cruising range’ condition has been mostly neglected by previous studies using the extent-of-occurrence expert maps (see Introduction for examples). Some studies relied on habitat associations to approximate breeding contact among individuals of different species (Schoener 1965). However, here we make a clear distinction between the physical location of individuals of a given species in space (think of spatial coordinates) and its position in an abstract environmental space whose axes are defined by ecological factors, referring to so called Hutchinson’s duality (Colwell and Rangel 2009). Thus, a term to define the local physical co-occurrence of individuals irrespective of their ecological preferences, namely syntopy (Rivas 1964), is needed. A great advantage of this distinction is that we can study which ecological traits of species predict their syntopy without confounding physical and ecological, niche spaces. We used following definitions.

- 1) Range-wide sympatry was defined as range overlap (%) between species 1 (*SP1*) and species 2 (*SP2*) and calculated as (Eq. 1) $100 \times \frac{\text{area of overlap}}{\min\{\text{areaSP1}, \text{areaSP2}\}}$ (Barraclough and Vogler 2000, Pigot et al. 2016, 2018; Fig. 1). Ranges are

here defined as extent-of-occurrence maps, traditionally used in macroecological analyses, which are agnostic in terms of the fine-grained spatial distribution of individuals within the borders of the range (i.e. range filling; Diamond 1980). As such, they should not be used as predictors of the physical contact between individuals of different species in the area of sympatry, as has been done by many previous studies.

- 2) Range symmetry was defined as the range of the smaller species divided by the total area of both species and calculated as (Eq. 2) $\frac{\min\{\text{areaSP1}, \text{areaSP2}\}}{\text{sum}\{\text{areaSP1}, \text{areaSP2}\}}$ (Barraclough and Vogler 2000, Hemingson et al. 2019). This value spans from approaching 0 where ranges are vastly different in size to 0.5 where ranges are equal in size.

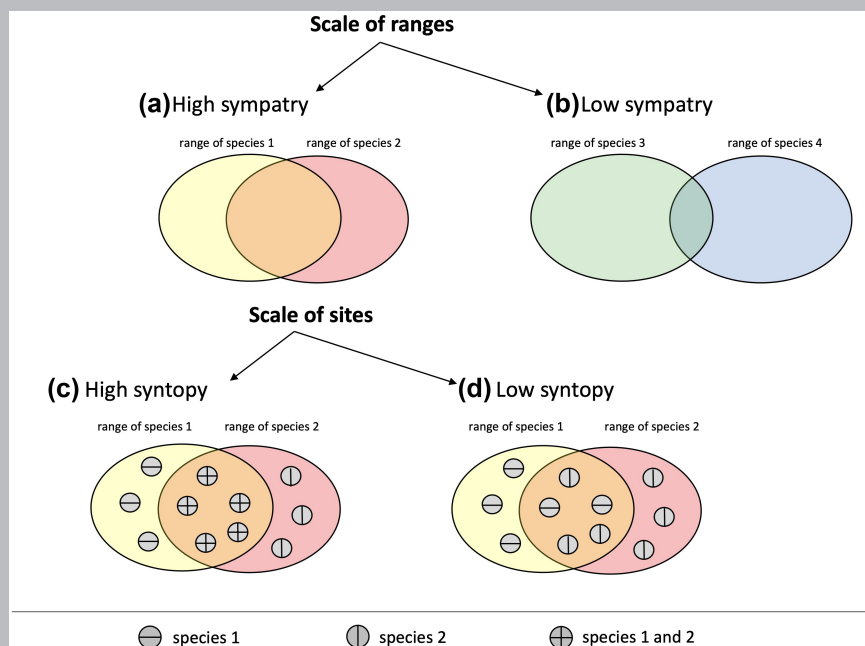


Figure 1. Scale dependence of species co-occurrence. Species differ in the degree of sympatry (range overlap) and this variation has been used to test hypotheses on the causes and consequences of secondary sympatry (panel a versus b). However, species pairs with the same degree of sympatry can have a different degree of syntopy across localities (panel c versus d). Specifically, species 1 and 2 have the same sympatry (50%), but in panel (c) they have 100% syntopy, while in panel (d) they have 0% syntopy. We show that syntopy must be quantified in the limited area of sympatry, where both species can, in principle, co-occur (here sites inside the orange-colored sympatry zone). Including sites outside the sympatry zone (yellow and pink-colored parts of the ranges) leads to negative bias when estimating syntopy.

- 3) Syntopy was defined as the physical proximity of individuals of different species such that these individuals can behaviorally interact. It was calculated as the co-occurrence of *SP1* and *SP2* in local assemblages laying inside the range overlap of the two species (Fig. 1). We chose to use only the area of range overlap to quantify syntopy (considered best practice by Veech 2014), because we were interested in ecological traits predicting syntopy and the build-up of local species richness. However, there might be other situations when it could be appropriate to estimate syntopy across all sites irrespective of spatial arrangement of ranges, and the choice rests with aims of each individual study. To quantify syntopy, we used a probabilistic model (Veech 2013, 2014) formulated using the hypergeometric distribution (Arita 2016, Griffith et al. 2016). In particular, we calculated a standardized effect size (SES, also known as Z-score) as the deviation of the observed co-occurrence (observed number of sites with both species, N_{obs}) from the expected co-occurrence (expected number of sites with both species, N_{exp}) divided by the standard deviation of the hypergeometric distribution (Carmona and Pärtel 2021; see Supporting information for complete formulas). A big advantage of this formulation of SES is that it conveys information on the strength of the association between two species in standard deviation units (Keil 2019). Zero syntopy index means that species occur independently, while negative values denote negative co-occurrence (species segregation) and positive values denote positive co-occurrence (species association). N_{exp} was calculated under the assumption of species independence as (Eq. 3) $\frac{N_{Sp1}}{N_{\text{tot}}} \times \frac{N_{Sp2}}{N_{\text{tot}}} \times N_{\text{tot}}$, where

N_{Sp1} is the number of sites with species 1 and N_{Sp2} is the same for species 2. The most difficult problem rests in correctly estimating N_{tot} , because it should typically include only those sites where both species of the analyzed species pair could potentially occur (Veech 2013, Griffith et al. 2016).

interspecific territoriality (Grether et al. 2009, Drury et al. 2020). However, range overlap does not necessarily predict local-scale syntopy (Rivas 1964; Box 1, Fig. 1c–d, 2), because species might differ in habitat use. On the other hand, this depends on the spatial grain of a habitat mosaic: if it is fine

in relation to typical home ranges of the studied species, true syntopy may indeed occur. On the contrary, if the spatial grain is relatively coarse, interactions between individuals of different species might be precluded (allotopy sensu Rivas 1964; sometimes called ‘mosaic sympatry’ or ‘microallopatry’;

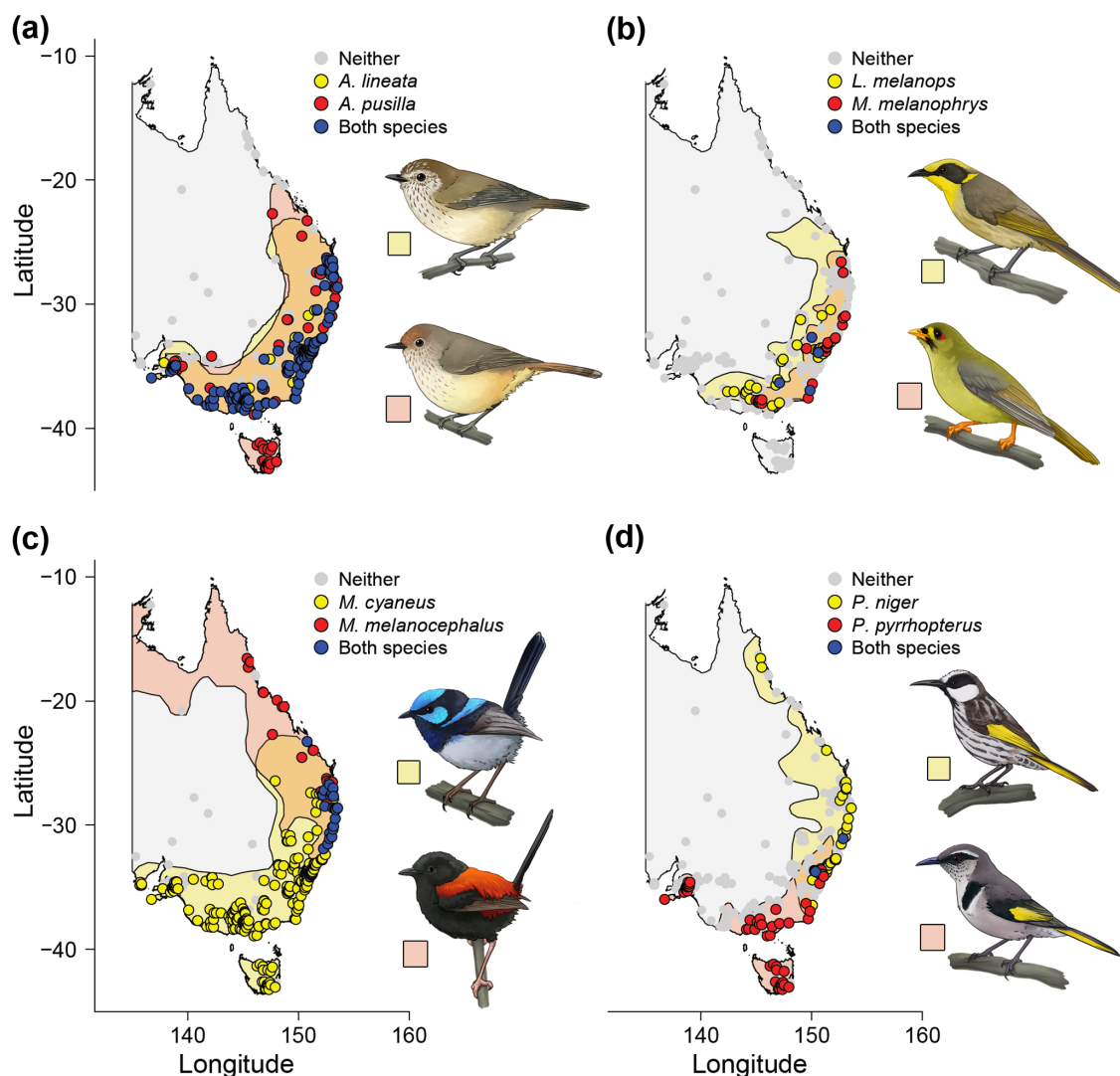


Figure 2. Examples of scale-dependent co-occurrence in Australian birds (Meliphagoidea). In species pairs with high range sympatry (a, b), local syntopy might be either high (a, species co-occur on 43.1% of sites within the sympatry zone) or low (b, 1.8%). Similarly, in species pairs with low sympatry (c, d), syntopy might be comparatively high (c, 35.7%) or low (d, 1.6%). In all panels, the absence of both species on a site is indicated by gray color. If such a site is within the range of at least one species, it might indicate either a false negative (a species was present but was not detected during sampling) or an unsuitable habitat. Ranges are colored yellow and pink in case only one of the two species can occur there, or orange in case of range overlap where both species can occur. The genera depicted are (a) *Acanthiza*, (b) *Lichenostomus* and *Manorina*, (c) *Malurus* and (d) *Phylidonyris*. Bird art by Jana Růžičková.

Dorková et al. 2020). Thus, analyzing the development of secondary sympatry based on ranges is, at best, ambiguously related to the existing theory. Moreover, only syntopy predicts reliably local interspecific encounters of individuals, which in turn drive selection on trait and behavioral divergence (Drury et al. 2020). Yet, previous studies focusing on divergence in morphology, songs and color typically relied on range-wide scale of analysis (Martin et al. 2010, 2015, Weir and Wheatcroft 2011, Freshwater et al. 2014, Tobias et al. 2014, Bothwell et al. 2015, Laiolo 2017, Drury et al. 2018, Hemingson et al. 2019, Anderson and Weir 2021; but see McEntee et al. 2018). Therefore, studies examining the development of sympatry and syntopy after speciation are clearly needed to link speciation, co-existence and trait divergence.

Although studies of these topics have been conducted in individual species pairs (Reif et al. 2018), these are not easily generalizable to large sets of species.

Allopatric speciation seems to prevail in birds (Barraclough and Vogler 2000, Phillimore et al. 2008, Pigot and Tobias 2015). Two scenarios might then explain how secondary sympatry and syntopy evolve (Fig. 3). First, once a geographic barrier is gone or overcome, ranges might start overlapping due to range drift and climate niche tracking (Warren et al. 2014). This might be facilitated if the new species retain their ecological characteristics (niche conservatism). Therefore, higher species similarity should be correlated with higher sympatry and syntopy (Fig. 3). Second, the hypothesis of ecological isolation postulates that secondary

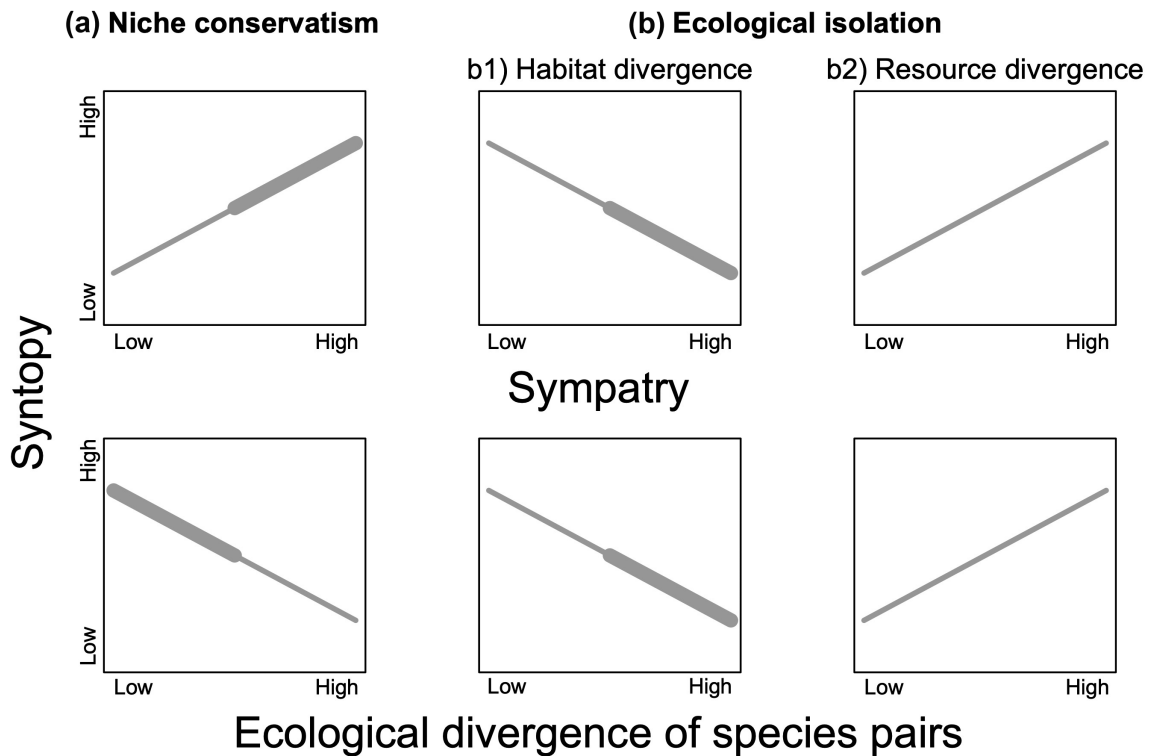


Figure 3. Different scenarios of the development of secondary sympatry and syntopy. Lines show hypothesized relationships between variables, with thick parts denoting areas where most species are predicted to reside. Under the niche conservatism hypothesis (a), sympatry and syntopy develop due to similar habitat preferences of the two species. Species pairs should be clustered towards higher sympatry and syntopy, and lower habitat divergence (thick part of trend lines). Under the ecological isolation hypothesis (b), two scenarios are possible. If habitat divergence was important (b1), high sympatry would be facilitated by low syntopy, which would in turn be driven by high divergence in habitat preferences. Species pairs should be clustered towards higher sympatry, lower syntopy and higher habitat divergence (thick part of trend lines). If divergence in resource use was important (b2), high sympatry would be correlated with high syntopy, and high divergence in resource use would promote high syntopy. In both niche conservatism and habitat divergence scenarios, the development of sympatry depends on habitat preferences. However, while in the former similar habitat preferences lead to sympatry and syntopy, in the latter divergent habitat preferences allow higher sympatry via allotopy.

sympatry is facilitated by ecological and behavioral divergence, allowing species to either avoid local contact (allotopy; Fig. 1d) or to truly coexist in local syntopy (Fig. 1c; Lack 1971). In the former case, ranges might start overlapping once a geographic barrier is gone, but only if species diverge in habitat associations, which allows allotopy (habitat-based avoidance). In the latter case, ranges can overlap only if species diverge in resource use, which allows syntopy (resource partitioning-based local coexistence; Fig. 3). Avian species can partition resources, for example, in terms of foraging behavior, substrates or vegetation layers (Holmes and Recher 1986, Terborgh and Robinson 1986, Korňan et al. 2013, Remeš et al. 2021a, b). The hypothesis of ecological isolation thus assumes niche divergence during speciation and post-speciation processes (Germain et al. 2021).

Here, we test the above-mentioned scenarios by studying the development of secondary sympatry and syntopy in Meliphagoidea, the largest endemic radiation of Australasian songbirds. We address the following two questions. First, do sympatry and syntopy develop in parallel? Second, does ecological conservatism or divergence between species predict

syntopy? To answer these questions, we developed a method to calculate syntopy inspired by the concept of the biogeographic species pool (Carstensen et al. 2013). We show that syntopy should be calculated using only assemblages included in the range overlap of the two species (Stone et al. 1996, Connor et al. 2013). Otherwise, a negative bias in syntopy is introduced. Taken together, our study is the first methodologically valid estimate of the post-speciation transition to sympatry and syntopy, and ecological correlates of the latter. It paves the way for large-scale studies of this phenomenon in a multitude of taxa, which would clarify the role of ecology in post-speciation processes and the resulting build-up of regional and local species diversity.

Material and methods

Meliphagoidea is a large radiation of Australasian passerines that originated between 28 and 35 million years ago (Marki et al. 2017, Fjeldså et al. 2020) and includes honeyeaters (Meliphagidae), thornbills and allies (Acanthizidae),

fairywrens (Maluridae), pardalotes (Pardalotidae) and bristlebirds (Dasyornithidae). We used a recent Meliphagoidea phylogeny that included almost all species (286 out of 289 recognized; Marki et al. 2017). We were interested in evolutionary transitions to secondary syntopy and thus focused on relatively recent speciation and post-speciation events instead of working across the whole phylogeny. An ideal approach would be to analyze independent pairs of sister species (pairs of species with a unique most recent common ancestor) identified on the full phylogeny of Meliphagoidea. However, due to methodological and data limitations, we had to adjust our workflow in the following ways. First, we had to prune the phylogeny to include only the 111 species occurring in our data set from Australia and Tasmania because we had data on local assemblages from that region only (altogether 142 species occur in Australia and Tasmania, but 31 of them did not occur at our study sites, see below). This decreased our ability to identify true sister species pairs. Second, most pairs of sister species are typically allopatric (Pigot et al. 2016), and syntopy cannot be calculated in pairs of allopatric species. We thus had to include pairs of nonsister species. As an attempt at a solution, we delimited independent subclades with the oldest node at most 10 million years old ($n=20$ subclades; Supporting information). We worked with all species pairs within these subclades (i.e. with all combinations of species present in a subclade) and consequently some species were part of more than one species pair analyzed. We ended up analyzing 116 species pairs composed of 58 species and belonging to 10 subclades (out of 263 possible species pairs composed of 91 species within 20 subclades). Fifteen species belonged to only one species pair, while three species belonged to 11 species pairs (39 species belonged to four or fewer species pairs). If we used a more stringent subclade age criterion to focus on more recent post-speciation events, we would end up with fewer species pairs. For example, for 5 million years, only 15 species pairs would remain if other data filtering procedures remained as described above. Similarly, if only pairs of sister species were used, only six would remain, both of which would preclude any reasonable analysis. Taken together, we see our approach as an acceptable resolution of a trade-off between sampling enough species pairs for the analysis and focusing on relatively recent post-speciation processes. However, we stress that our methodological approach and resulting compromises were shaped by our research questions. Other approaches will be more convenient for different questions.

Ranges were defined as expert-verified maps of the extent of occurrence of each species. For this purpose, we used digital range maps of Meliphagoidea obtained from BirdLife International (BirdLife-International and NatureServe 2014) to quantify range overlap and symmetry (Box 1). We include range symmetry because it can have consequences for trait evolution of related species (Hemingson et al. 2019), and thus its correlation with syntopy is important. We used local assemblage data to calculate syntopy (Box 1). We define the spatial scale as local when it allows interactions between individuals of passerine species. These interactions include competition for resources (i.e. mutually depleting common

resource pool) and behavioral encounters (agonistic, sexual, etc.). We obtained data on local assemblages from the Australian Bird Count (ABC; Clarke 1999), which originally consisted of 1962 localities and 77 383 censuses. We used several criteria to ensure standardization and comprehensive sampling of species on localities. In terms of standardization, we included only censuses with a duration between 20 and 30 minutes, localities with an area between 2 and 6 ha, and at least 20 censuses. We excluded strongly human-modified, urban and rural habitats. Next, in terms of sampling, we applied rarefaction based on sample coverage (Chao and Jost 2012) using iNEXT (Hsieh et al. 2016) and included only localities with at least 90% coverage. We also performed a final check on the quality of ABC data by removing observations of species on an ABC locality if they were found more than 100 km away from a border of their range, ending up with 470 localities (Supporting information) with 37 250 censuses (median number of censuses per locality was 56) from years 1989 to 1995.

Many species association indexes are available. Fortunately, they provide very similar information (Keil 2019). We quantified syntopy using a pairwise co-occurrence index based on a simple probabilistic algorithm (Veech 2013, 2014). Although it is formally identical to matrix-based approaches (Arita 2016), its advantage is that it can be easily applied to individual species pairs. This is critical to our approach, because we applied the co-occurrence analysis only on assemblages within the range overlap of the two species. When analyzing many species pairs whose ranges do not overlap completely, the occurrence of individual species is impossible on at least some study sites (those outside of a given species' range). Thus, it is impossible to construct a rectangular species occurrence matrix across all study sites that would be valid for all studied species. Consequently, whole matrix randomization approaches are ruled out and a pairwise method is needed. We expressed syntopy as a standardized effect size from the co-occurrence analysis run in the 'cooccur' package (Griffith et al. 2016) for the R software (Box 1). We excluded species pairs with expected co-occurrence at less than 1 site (as recommended by Veech 2013) and with fewer than 20 ABC sites within the range overlap (our own ad hoc criterion).

Including all assemblages within the union of the two ranges should lead to a negative bias in syntopy, because many sites do not contain one of the two species due to its position out of the range of that species (Fig. 1, Supporting information). However, little attention has been paid to this problem in the otherwise rich literature on species co-occurrence, with Stone et al. (1996) and Connor et al. (2013) being notable exceptions. However, no previous study has actually quantified the extent of this problem. Therefore, we quantified it using simulated species ranges with varying degrees of overlap (Supporting information). We created a linear space with 1000 sites and simulated scenarios with sympatry ranging from 100% (complete sympatry) to 0% (complete allopatry) with increments of 10%. We ran 100 replications for each level of sympatry (11 levels in total). Besides simulations, we also provide exact analysis based on

expected values of random variables to support our numerical results (Supporting information). In simulations, we set the baseline probability of occurrence of each of the two species at 0.1, 0.3, 0.5, 0.7 and 0.9. Species occurrences were independent, so the expected syntopy (standardized effect size, Box 1) was zero. We calculated syntopy using either all sites in the union of the two ranges or selecting only sites in the overlap of the ranges and showed that the former method introduced a negative bias in syntopy. We then applied both analyses to real data for Meliphagoidea and showed that the negative bias in syntopy was present also in real data. Thus, for downstream analyses of syntopy, we used only the unbiased calculation from overlaps of ranges.

We obtained data on Meliphagoidea ecology and foraging behavior from the Handbook of Australian, New Zealand and Antarctic Birds (HANZAB; Higgins et al. 2006). We extracted data on five ecological traits (for details, see Harmáčková et al. 2019). Each trait was divided into several categories, and each category of each trait received a value corresponding to the proportional use (percentage) of that category by a given species based on the information in HANZAB. The sum of all categories of a given trait for a given species was always 100. The traits and their categories were as follows: habitat (ten categories: rainforest, forest, woodland, shrub, grassland, heaths, marshes, marine mangrove, bare ground and human settlements), diet (eight categories: leaves, fruit, nectar and pollen, seeds, insects, other invertebrates, vertebrates and carrion), foraging method (nine categories: gleaning, hang-gleaning, snatching, hover-snatching, probing, manipulating, pouncing, flycatching and flush chasing; see Remešová et al. 2020

for definitions), foraging stratum (four categories: ground, shrub, subcanopy and canopy) and foraging substrate (eight categories: ground, bark, leaves, buds, fruit, flowers, air and other). Previous work showed that resource partitioning in terms of foraging substrates and methods is important for species co-existence on a local scale in Australian passerines (Harmáčková et al. 2019, Remešová et al. 2020, Remeš et al. 2021a, b), and in passerines in general (MacArthur 1958, Holmes and Recher 1986, Terborgh and Robinson 1986, Korňan et al. 2013). We calculated distance matrices using the Bray–Curtis metric to express species differences along several niche dimensions: habitats, diet, foraging method, stratum, substrate and overall resource use (i.e. all ecological traits except habitat use). Bray–Curtis metric was calculated based directly on quantitative data on ecological trait categories. We used pairwise distances between species in these distance matrices as our index of ecological divergence to test hypotheses depicted in Fig. 3. We used linear mixed models fit in the *pglmm* function of the 'phyr' package (Ives et al. 2020) for R software. We fitted three multiple regression models with syntopy as a response variable. First, we predicted syntopy with range sympatry, symmetry and the age of the split. Second, we predicted it with the divergence in habitat and resource use. Third, we predicted it with the divergence of the four resource use traits, because they represent independent axes of ecological divergence (Supporting information). Random effects included a phylogenetic variance–covariance (VCV) matrix among species pairs, species ID and subclade ID. The VCV matrix was identical to the one constructed among constituent species of species pairs. We scaled all predictor variables

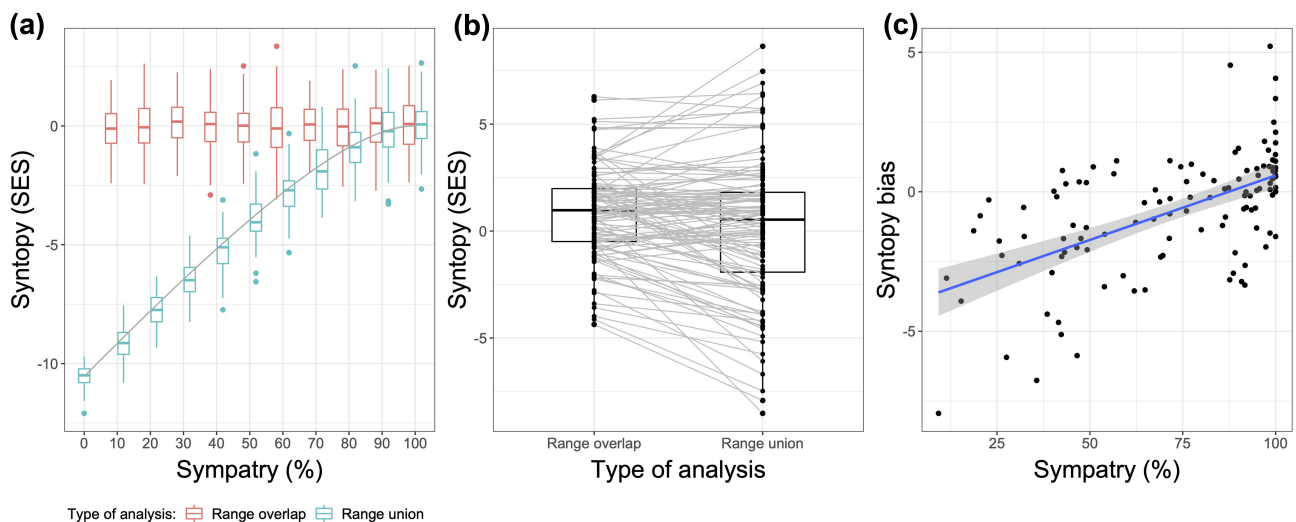


Figure 4. Bias in the estimation of syntopy in simulated and empirical data. We simulated a linear space with 1000 study sites, different levels of range sympatry (100 replications for each level of sympatry), and the baseline probability of occurrence of each of the two species of 0.5. The species were independent, so the expected syntopy (standardized effect size, SES, Box 1) was zero. Syntopy was correctly estimated only when considering exclusively the area of range overlap of the two species, while it was negatively biased when all sites across both ranges were considered (range union); this bias increased with decreasing sympatry of ranges. Boxplots show results of numerical simulations, while the grey line depicts exact expectations (derived in Supporting information) (a). In Australian Meliphagoidea, syntopy was on average lower when considering all sites within both ranges (range union) than when only sites within range overlap were used ($n = 116$ species pairs connected by grey lines; b). This bias increased with decreasing sympatry, mirroring the pattern found in simulated data ($n = 116$ species pairs; c).

to have mean=0 and SD=1. We did so before fitting the models to obtain standardized parameter estimates allowing comparisons between predictors. We used appropriate transformations of variables to achieve normal model residuals.

Results

Simulations showed that when using all sites within the union of both ranges, syntopy was negatively biased when range overlap was low (Fig. 4a). The magnitude of the bias increased with increasing baseline species occurrence probability in a sense that 1) it started to show up already under higher range sympatry values, and 2) it achieved higher absolute values in standard deviation units under the same sympatry (Fig. 4a, Supporting information). Thus, syntopy bias was especially strong in common species, where under low sympatry its magnitude might have reached up to -15 to -20 standard deviation units (Supporting information). Results of numerical simulations were fully supported by exact analyses using probability theory (Fig. 4a, Supporting information).

In Australian Meliphagoidea, syntopy was on average lower when all sites within the union of ranges were used than when only the region of range overlap was considered (estimate (SE) = -0.65 (0.24), $Z = -2.7$, $p = 0.007$; random effects of phylogeny and species and subclade identity together accounted for 17.3% of variance in the data); this bias decreased with increasing sympatry (estimate (SE) = 1.19 (0.16), $Z = 7.4$, $p < 0.001$; random effects explained 12.9% of variance in the data; Fig. 4b–c). Thus, in the following we used only syntopy calculated from the area of range overlap between species. Syntopy increased with both range sympatry and symmetry, while it was not significantly related to the age of the species split (Table 1, Fig. 5). Syntopy was related to neither divergence in habitat use nor divergence in resource use calculated using all four traits (Table 1). However, syntopy increased significantly with divergence in stratum use

while it decreased with divergence in diet (Table 1, Fig. 5). Neither foraging methods nor substrates predicted syntopy significantly (Table 1).

Discussion

To estimate syntopy correctly, it is necessary to limit the study sites to the area of sympatry, as shown by our numerical simulations, exact calculations and empirical data. Syntopy was positively correlated with sympatry, range symmetry and divergence in the use of foraging stratum, while negatively correlated with divergence in diet. In terms of sympatry–syntopy correlation, these findings are consistent with both the niche conservatism and resource use divergence scenarios (Fig. 3). In terms of resource use, stratum use patterns were consistent with the resource divergence scenario, while diet use patterns were consistent with the niche conservatism scenario (Fig. 3). Therefore, high syntopy was correlated with similar diet but different use of foraging stratum in 116 pairs of Meliphagoidea species in Australia and Tasmania. Consequently, our results support the critical role of ecological niches in the build-up of local species richness.

Using methodologically valid estimates of syntopy, we showed that Meliphagoidea species pairs with high syntopy tended to have similar diet that was collected in different vegetation strata (ground, shrub, subcanopy and canopy). These observations suggest that both niche conservatism (Laiolo et al. 2017) and the partitioning among species of available resources play a critical role in the build-up of local diversity. Conditioning species co-occurrence on common dietary preferences makes sense in Meliphagoidea, because this clade includes species with diverse beak morphologies (Friedman et al. 2019) linked to feeding preferences ranging from complete insectivory to almost complete nectarivory (Miller et al. 2017, Remešová et al. 2020, Remeš et al. 2021a, b). Then, horizontal patchiness of resources might lead to locally clustered occurrence of species with similar dietary

Table 1. Results of multiple regression mixed models relating syntopy to geographic and ecological predictors. In model 2 and 3, predictors are divergences between species in each species pair. Random effects include phylogeny, and species and subclade identity. Models were fit in the *pglmm* function of the 'phyr' package (Ives et al. 2020) for R software.

Predictors	Estimate	SE	Z	p
Model 1. Geography and time				
Range sympatry	0.767	0.180	4.3	< 0.001
Range symmetry	0.809	0.178	4.5	< 0.001
Split age	-0.080	0.184	-0.4	0.666
Random effects	14.6%			
Model 2. Divergence in habitats and resources				
Habitat use	-0.149	0.194	-0.8	0.442
Resource use	-0.141	0.199	-0.7	0.478
Random effects	10.6%			
Model 3. Divergence in resources (detailed)				
Stratum	0.593	0.193	3.1	0.002
Diet	-0.793	0.227	-3.5	0.001
Foraging methods	-0.301	0.204	-1.5	0.141
Foraging substrates	-0.194	0.193	-1.0	0.316
Random effects	10.3%			

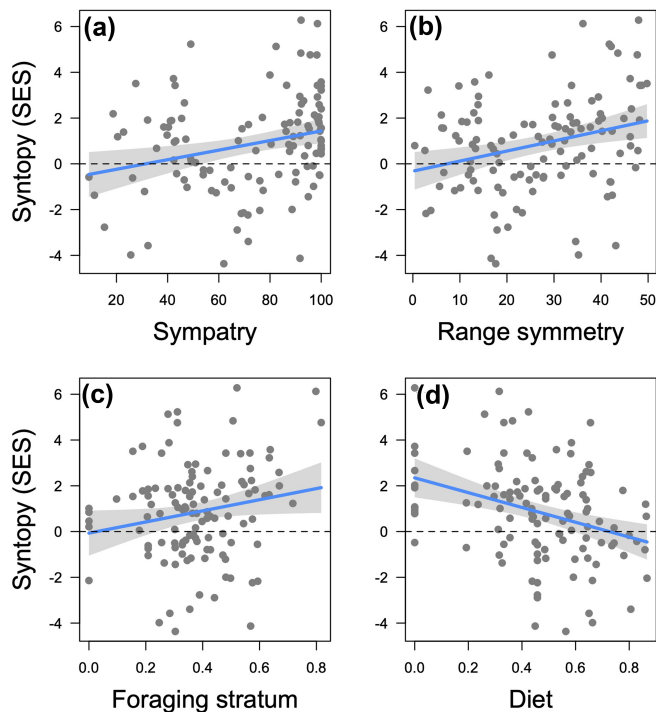


Figure 5. Syntopy in relation to range sympatry, symmetry and ecological divergence. Syntopy (standardized effect size, SES, from the probabilistic co-occurrence model) increased with both range sympatry (%; a) and range symmetry (b; see Box 1 for definitions). Syntopy also increased with divergence in the foraging stratum (c), while it decreased with divergence in the diet (d). Each point represents one species pair. The effect size of zero (hatched horizontal line) depicts an independent occurrence of the two species. The blue lines are linear least-squares regression fits with 95% confidence bands in gray.

preferences, unlike if all species had similar food preferences as in dietarily more conservative clades. In line with our findings, it was previously demonstrated that the use of the foraging stratum was an important predictor of species coexistence in Australian and Tasmanian passerines (Norman et al. 2007, Harmáčková et al. 2019). Similarly, previous studies showed that partitioning of ‘foraging space’ facilitated species coexistence, enabled evolutionary diversifications and happened repeatedly and convergently within and across continents (MacArthur 1958, Holmes and Recher 1986, Terborgh and Robinson 1986, Korňan et al. 2013, Miller et al. 2017, Remeš et al. 2021a, b). Of course, specialization and niche partitioning have been leading explanations for the maintenance of local species diversity for decades (Schoener 1965, 1974, Belmaker et al. 2012, Harmáčková et al. 2019), but here we link them to the evolution of secondary syntopy using an explicit phylogenetic framework.

The evolution of species co-existence following speciation has previously been studied at the level of range sympatry. For example, previous studies showed that secondary range sympatry was facilitated by species dispersal abilities (Pigot and Tobias 2015), energy availability (Pigot et al. 2016, 2018) and ecological divergence between species (Laiolo et al.

2017). However, one might argue that linking ecological processes to range sympatry likely compares phenomena at mismatched spatial grains, because range sympatry is defined regionally, while ecological interactions happen locally (Araújo and Rozenfeld 2014). The reason why several previous studies identified ecological correlates of secondary range sympatry could be a positive correlation between syntopy and sympatry ($r=0.26$ in this study, Fig. 5a), which could generate a spurious correlation between ecology and range sympatry. As a hint in this direction, sympatry was positively correlated with divergence in the use of the foraging stratum in our data ($r=0.27$). On the other hand, it is unclear how strong the correlation between syntopy and sympatry is in general, because studies for comparison are lacking. Our analysis is agnostic as to whether syntopy develops by spatial diffusion of species with differences evolved in allopatry or whether secondary sympatry exerts selection on traits (ecological character displacement, Grether et al. 2009). However, the fact that symmetry predicts syntopy suggests that selection might play some role, because more symmetric ranges mean the potential contact of a higher share of the total population of the two species in question.

Unbiased estimates of local species co-occurrence are essential for advancement in key areas of ecology and evolution, including assembly rules (Diamond 1975, Weiher and Keddy 1999), character displacement (Grether et al. 2009), ecological speciation (Germain et al. 2021) and the maintenance of biodiversity (Calatayud et al. 2020). Co-occurrence varies with spatial extent and grain (Araújo and Rozenfeld 2014, Belmaker et al. 2015, McNickle et al. 2018). However, an important aspect of spatial scaling of co-occurrence has been largely neglected, namely the effect of limited species ranges and biogeographic history on the estimates of co-occurrence (Fig. 1). On the other hand, many studies did not suffer from this problem, because the spatial spread of survey sites was much smaller than the size of species ranges. However, when working on large spatial extents, our results from simulations, exact analyses and empirical data showed that without adjusting for limited species ranges, negatively biased estimates of syntopy were produced, and this bias was especially strong in common species (Fig. 4a, Supporting information). Nevertheless, researchers might still want to include sites outside the known range of a species if this is part of the study design, e.g. in some biogeographic analyses (Veech 2013).

It is fair to note that several previous studies pinpointed the problem of limited species distributions in relation to co-occurrence analyses. For example, Gotelli et al. (1997) randomized species occurrences only within species’ habitat types but were not able to account for geographic ranges. Brown and Kurzius (1987) restricted their analyses of desert rodent assemblages to within species ranges. Stone et al. (1996) clearly demonstrated that not accounting for species’ differing geographic ranges can yield unrealistic co-occurrence estimates. Connor et al. (2013) tried to account for the limited distribution of species across archipelagoes in their analysis of island assembly rules (see the discussion in

Diamond et al. 2015 and Connor et al. 2015). Fehér et al. (2018) adjusted for restricted species distributions by limiting their co-occurrence analyses to probabilistically delimited species ranges. Furthermore, Blanchet et al. (2020) showed that a similar problem exists in relation to the width of the environmental gradient sampled: the detected associations between species depended on the portion of the environmental gradient considered.

Despite these pioneering efforts, most studies of species co-occurrence have ignored the problem of limited geographic ranges. At least part of the reason probably is that overcoming this problem is not trivial as in most taxa, we do not have as good data on species ranges, defined as the extent of occurrence, as in birds. Then, when analyzing a set of sampling sites, it is not obvious where a given species can or cannot occur, and running a range-constrained co-occurrence analysis might be impossible. In fact, the problem is even worse, because studies can inadvertently include even sites outside of both ranges. This may easily happen when studying species with poorly known ranges or when working with systems where species ranges are difficult to define (for example, in island systems; see a discussion in Connor et al. 2013, Connor et al. 2015 and Diamond et al. 2015). We think that the problem with range-constrained co-occurrence analysis is more severe than the problem with habitat-constrained analysis (Gotelli et al. 1997, Blanchet et al. 2020) because the habitat associations of many species are known and habitats can be mapped globally, while ranges are known much less, and their size and shape are affected by randomness and historical legacy. On the other hand, habitat-constrained analyses have their own problems, because they automatically preclude investigating habitat as a mechanism that could produce greater than expected positive co-occurrence (shared habitat affinities) or greater than expected negative co-occurrence (habitat divergence).

One solution of the lack of independent information on ranges might be a probabilistic delimitation of ranges that uses presence-absence data. This method assigns occurrence probabilities to all sites based on their distance from all other sites, weighted by whether a given species occurs there or not. Then, data are simulated based on these occurrence probabilities and co-occurrence analyses applied (Fehér et al. 2018). One advantage of this approach is that it can account for incomplete range filling (Diamond 1980). A disadvantage is that one must define a spatial weighting function, which might differ idiosyncratically among taxa, and apply a correction to the occurrence probability matrix, thus potentially biasing results (Fehér et al. 2018). A solution could be to combine strengths of different data types and approaches to infer ranges, including expert maps, habitat associations, species traits related to dispersal, distance-based weights and downscaling of species distributions (Keil et al. 2014, Lasky et al. 2017, Merow et al. 2017). Thus, approximations are available, and we suggest future studies use them. However, the critical question arises of what part of negative co-occurrences reported in the literature (Gotelli and McCabe 2002) are a result of the methodological bias identified previously (Stone et al. 1996) and quantified here. This remains to be determined.

Conclusions

In summary, using methodologically valid estimates of syntopy, we showed that both niche conservatism (diet) and divergence in resource use (foraging stratum) were important predictors of secondary syntopy in species pairs of Australian and Tasmanian Meliphagoidea passerines. In contrast, we found no support for the hypothesis of habitat divergence postulating the facilitation of secondary range sympatry by allotopy. Our results thus give support to Lack's (1971) ecological isolation hypothesis claiming that the evolution of 'foraging space' partitioning among related species is a prerequisite for the development of local species richness. Our study provides a phylogenetically explicit counterpart to previous studies on resource partitioning and species diversity. As a whole, this body of evidence lends strong support to the critical role of ecological niches in the build-up of local species richness.

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Author contributions

Vladimír Remeš: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Funding acquisition (lead); Investigation (lead); Writing – original draft (lead); Writing – review and editing (lead). **Lenka Harmáčková:** Data curation (equal); Investigation (supporting); Writing – review and editing (supporting).

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Data availability statement

Data are available from the Zenodo Repository: <https://doi.org/10.5281/zenodo.7304341> (Remeš and Harmáčková 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

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