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Completing the Speciation Cycle: Ecological Niches and Traits Predict Local Species Coexistence in Birds Across the Globe

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ABSTRACT

Aim: The build-up of local species diversity requires completing the transition from allopatry to sympatry to local coexistence (syntopy). However, understanding processes than enable species arising in allopatry to become syntopic remains an unsolved challenge. Potential explanations include niche conservatism, niche divergence, and energy availability. To gauge their importance, we modelled the effects of species split age, the divergence in beta and alpha niches, specialisation, and resource availability to reveal factors driving the evolution of local species coexistence upon speciation.

Location: Global.

Time Period: Miocene to the present.

Major Taxa Studied: Passerine birds.

Methods: We collated a dataset of 206 passerine sister species pairs, each with their age of divergence; range sympatry; degree of syntopy (derived from 7,257,312 complete eBird checklists falling within the area of range overlap); beta niche divergence (habitats and environmental characteristics); alpha niche divergence (morphology, diet, and foraging stratum); species ecological specialisation (diet and foraging stratum); resource availability; and body mass. We used phylogeny-informed models to infer which of these factors best explained local species coexistence upon speciation.

Results: There was a major effect of niche conservatism as species with more similar beta niches (canopy height, vegetation greenness, moisture availability, and habitat affinities) exhibited higher degree of syntopy. Small species with similarly sized beaks and high specialisation on diet were also more likely to coexist locally. In contrast, the divergence or overlap in alpha niches (diet and foraging stratum) did not predict the degree of syntopy. Confirming previous studies, the degree of syntopy strongly increased with increasing range sympatry, while only weakly in older species pairs.

Main Conclusions: The evolution of secondary syntopy is driven by niche conservatism, ecological specialisation, and body mass-related energy requirements. Consequently, the accumulation of local species richness is facilitated by both conservatism and differentiation along various ecological niche dimensions.

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1 | Introduction

In clades speciating allopatrically, periods of range splitting and mutually exclusive geographic occurrence of incipient species alternate with the evolution of range overlap (Price 2008; Tobias, Ottenburghs, and Pigot 2020). This is particularly true in birds, where most speciation events are inferred to occur via allopatric speciation (Barraclough and Vogler 2000; Linck, Freeman, and Dumbacher 2020; Phillimore et al. 2008; Pigot and Tobias 2015; Smith et al. 2014). The subdivision of ranges cannot continue indefinitely due to an ultimate lower limit on range size. Therefore, the geographic expansion of daughter lineages is necessary for further allopatric speciation to occur, inevitably leading to some degree of mutual range overlap (called secondary sympatry, Table 1; Weir and Price 2011). This process has been extensively studied in terms of how secondary sympatry evolves over time (age-range correlations; Barraclough, Vogler, and Harvey 1998) and the environmental and trait predictors of the degree of secondary sympatry (Alencar and Quental 2023; Davies et al. 2007; Pigot et al. 2018; Pigot, Tobias, and Jetz 2016).

However, when ranges are defined as the extent of occurrence maps, they do not fully predict where species actually occur (Lu and Jetz 2023). This phenomenon is evident in local gaps in species occurrence, termed incomplete range filling (Hurlbert and White 2007). Consequently, the degree to which species occupy the same study site (called local co-occurrence or syntopy, Table 1) within the broad area of range overlap varies widely. Note that this degree of local co-occurrence will depend on the definition of "local" and on the spatial grain of study. For instance, the percentage of 2–6 ha study sites occupied by both species from a species pair varied from 0% to 52% in Australian passerine birds (Remeš and Harmáčková 2023). Thus, even in fully sympatric species (i.e., species with completely overlapping ranges), individuals of these species may not necessarily encounter each other due to mutually exclusive spatial occurrence (referred to variously as negative co-occurrence, species segregation, allotopy, mosaic sympatry, or checkerboard distribution; Connor, Collins, and Simberloff 2013). Simultaneously, the degree of syntopy has carryover effects on the potential for species interactions, selection on trait divergence, reproductive interference, and interspecific territoriality (Dorková et al. 2020; Drury, Cowen, and Grether 2020; Grether et al. 2017). Consequently, an important question arises: What factors predict the degree of syntopy within the area of range overlap? So far, only few studies have addressed this essential question within an explicitly phylogenetic framework tied to the speciation cycle (Fehér et al. 2018; Remeš and Harmáčková 2023; Harmáčková and Remeš 2024).

The evolution of syntopy upon speciation may depend on species habitat selection. More specifically, the similarity of daughter species in their beta niches, which refer to the macrohabitat and spatial components of species niches (e.g., preferences for certain habitat types and environmental characteristics; Pigot and Tobias 2013), can in principle facilitate positive species co-occurrence. The reason is that species with the same habitat preferences might be more likely to occupy the same study site as compared to species with different habitat preferences, with the strength of this effect depending on relative size of study sites in

TABLE 1 | Glossary of key terms as used in this work.

Term	Explanation
Alpha niche	Key traits linked to resource use (e.g., beak and body dimensions, diet, and foraging stratum). Alpha niche has been quantified using published measurements and information
Beta niche	Macrohabitat and spatial components of the species niche (e.g., preferences for certain habitat types and environmental characteristics). Beta niche has been quantified by extracting environmental characteristics from the whole range of a given species using global raster grids
Range	The extent of occurrence of a species defined by an expert map and depicted by a polygon
Range overlap	Situation when the ranges of two species spatially overlap. Its degree is quantified by a number called an *index of range overlap*
Secondary sympatry	Situation when two daughter species evolve range overlap upon speciation
Syntopy (= co-occurrence)	The phenomenon of individuals of two species occupying the same study site, without specifying whether the two species tend to be spatially associated (positive co-occurrence) or segregated (negative co-occurrence). This concept is not to be confused with the difference in the beta niche between species, because beta niche is quantified using the whole range of a given species, not only the area of range overlap between two species in a species pair
The degree of syntopy (= degree of co-occurrence)	Quantifying syntopy (= co-occurrence) by any of many indexes of species association available. Here, we use *log Odds Ratio*, where 0 means independent occurrence of species, positive values mean positive co-occurrence (species association), while negative values mean negative co-occurrence (species segregation)

relation to the grain of habitat mosaic. On the other hand, even species with the same beta niches can display mutually exclusive spatial occurrence, for example if they actively avoid each other spatially. Consequently, a higher degree of syntopy may or may not be associated with similar beta niches of species, and this relationship must be empirically tested rather than assumed a priori.

Similar beta niches may stem from two different evolutionary processes. First, when the parental species is geographically split, daughter species can retain ancestral habitat affinities, a phenomenon known as niche conservatism (Anderson and Weir 2022; Freeman et al. 2023). Similar habitat affinities then can allow for both range overlap and positive co-occurrence to evolve (Royan et al. 2016; Sottas et al. 2018). Second, when speciation takes place on an environmental gradient, daughter species can evolve different habitat and environmental preferences (Reif et al. 2018). Then, convergence in these preferences facilitates the evolution of range sympatry and positive co-occurrence in sister species (Remeš and Harmáčková 2023). Insights into relative importance of these two scenarios can be gained by studying how the degree of sympatry and syntopy evolve over time since a species pair diverged.

Syntopy may be facilitated by resource partitioning (Schoener 1974), which may, in turn, enable long-term species coexistence (Abrams 1983). One way to achieve resource partitioning is the divergence in key traits linked to resource use, a concept known as alpha niche divergence (Pigot and Tobias 2013). Avian morphological traits, which include characteristics of beaks, legs, and wings, have been associated with microhabitat and resource use, as well as foraging behaviour (Friedman et al. 2019; Miles and Ricklefs 1984; Pigot et al. 2020; Remeš et al. 2021b). Divergence in these morphological traits can facilitate effective resource partitioning among co-occurring species (Schoener 1974). Community-wide patterns of trait overdispersion support this view (Dayan and Simberloff 2005). Similarly, evolutionary studies of morphospace filling suggest that divergence facilitates species coexistence and the accumulation of species richness (Price et al. 2014).

On top of morphology, ecological traits, including diet and foraging behaviour, have been subject to detailed examination (Holmes and Recher 1986; MacArthur 1958; Remeš et al. 2021b). Studies indicate that species specialised in habitat, diet, and foraging strata may coexist due to more effective resource partitioning (Belmaker, Sekercioglu, and Jetz 2012; Harmáčková, Remešová, and Remeš 2019; Norman et al. 2007). Moreover, the probability of species coexistence increases with increasing divergence in vegetation stratum where birds forage, probably due to weakened competition for resources (Remeš and Harmáčková 2023). These two factors may interact, such that resource partitioning and species coexistence might be especially apparent in specialists with low overlap of niches (Harmáčková, Remešová, and Remeš 2019). Taken together, the partitioning of ecological space within habitats facilitates species coexistence, and it has evolved repeatedly and convergently across bioregions and continents (Holmes and Recher 1986; Korňan et al. 2013; Miller et al. 2017; Remeš et al. 2021b, 2021a). However, studies examining how alpha niche divergence predicts the degree of syntopy upon speciation are largely lacking (Remeš and Harmáčková 2023).

Species co-occurrence may be additionally facilitated by high availability of energy. The underlying rationale is that increased availability of resources enables the coexistence of a larger number of individuals, and subsequently, a higher number of species (Wright 1983). Resource availability is influenced by environmental characteristics such as moisture, rainfall, and vegetation complexity (Bohdalková et al. 2021; Remeš et al. 2022). Moreover, when controlled for average productivity, in highly seasonal environments relatively more resources become available due to a larger proportion of the population dying out during the lean season. Survivors are then left with surplus resources per capita, a phenomenon known as Ashmole's effect (Ricklefs 1980). Accordingly, relatively high seasonality is associated with higher individual fecundity (Hořák, Tószögyová, and Storch 2015). We propose that it may also lead to higher degree of syntopy of species, analogously to higher range sympatry found in more productive environments (Pigot, Tobias, and Jetz 2016). In addition, body mass may also predict the degree of syntopy because larger species require more energy, have larger home ranges and territories (Schoener 1968; Tamburello, Côté, and Dulvy 2015), and thus reach lower densities (Santini et al. 2018). Consequently, there might be a lower chance of finding individuals of larger species together in the same area, simply because they are widely spaced.

In this study, we examined the evolution of the degree of syntopy, or local co-occurrence of species, in passerine birds following speciation. We analysed 206 passerine sister species pairs, utilising occurrence data from the global citizen science program eBird, which included 7,257,312 checklists. To quantify and analyse the degree of syntopy, we calculated the $\log_e$ odds ratio (logOR), a convenient species association index, for each species pair. As outlined and justified above, we envision that the main drivers of the degree of syntopy are habitat selection, resource partitioning, and energy. More specifically, we predict that high degree of syntopy will be apparent in species pairs with similar habitat preferences (low beta niche divergence), high resource partitioning (high alpha niche divergence and high specialisation), and high supply and low demand of energy (many resources available in species with small body mass). We tested these predictions within five main hypotheses, including proxies of (1) beta niche divergence (habitats and environmental characteristics); (2) alpha niche divergence (morphology, diet, and foraging stratum); (3) species ecological specialisation (diet and foraging stratum); (4) resource availability (moisture, vegetation complexity and greenness, plus their seasonality); and (5) resource demand (body mass; Table 2). Based on previous studies (Remeš and Harmáčková 2023; Harmáčková and Remeš 2024), we also accounted for secondary sympatry (range overlap) and the age of species split. Our study offers a comprehensive understanding of the evolution of the degree of syntopy following speciation in passerine birds on a global scale.

2 | Methods

2.1 | Sister Species Pairs

We sourced our data on the phylogenetic relatedness of species from birdtree.org (BT; Jetz et al. 2012). We downloaded all 10,000 trees based on genetic data and structured around the

Ericson backbone (6670 species). We then pruned each tree to include only songbirds (order Passeriformes; 4032 species). Utilising all the pruned trees, we constructed a single Maximum Clade Credibility (MCC) tree using TreeAnnotator v2.7.5, with parameters set to 0% burnin percentage, 0.0 posterior probability limit, and node heights kept at target heights (Bouckaert et al. 2019). Finally, we extracted sister species pairs from this MCC tree, yielding a total of 1317 pairs. We made sure that phylogenetic uncertainty did not bias our conclusions (Text S1.1 in Appendix S1 in Supporting Information).

To consolidate data on species phylogenetic relationships, distributions, and traits from various sources, we needed to align our BT taxonomy with other sources. To achieve this alignment, we devised a single taxonomic crosswalk table for names in BT, eBird Basic Dataset Version EBD_relFeb-2021 (EB; Sullivan et al. 2014), and BirdLife species ranges (BL; BirdLife International and NatureServe 2020; Text S1.1 in Appendix S1). Once we have matched species names across all sources, we began to refine BL shapefiles to include only areas where species' presence was categorised as “extant,” “probably extant,” or “possibly extant,” origin was identified as “native” or “reintroduced,” and the season was marked as “resident” or “breeding season.” These categorisations of parts of BL shapefiles are available in the attribute table associated with each shapefile. If no part of a shapefile remained after this refinement, we eliminated the entire species pair. Subsequently, we calculated the range area (in m^2) and the longitude and latitude coordinates of the range centroid for each species using these refined versions of BL shapefiles.

For each sister pair, we overlapped the ranges of the two species and computed their degree of sympatry based on the area of the smaller range (area of range overlap/area of a smaller range × 100), their degree of sympatry based on the union of their ranges (area of range overlap/(sum of areas of both ranges – area of range overlap) × 100), and range symmetry (area of the smaller range/sum of areas of both ranges). Previous studies have utilised the degree of sympatry based on the smaller range in conjunction with range symmetry (Barraclough and Vogler 2000; Harmáčková and Remeš 2024; Hemingson et al. 2019; Remeš and Harmáčková 2023). However, we found that range sympatry based on the union of ranges incorporates both the traditional range sympatry index and range symmetry (Figure S2.1 in Appendix S2) and thus we adopt it here as a single metric of range sympatry. We further computed the area of range overlap (in m^2) and longitude and latitude coordinates of the range overlap centroid. All these procedures yielded 722 species pairs with non-zero range sympatry. We could retain only species pairs with non-zero range sympatry, because syntopy is calculated from sites falling within the area of range overlap (otherwise, it is biased towards negative values, see Remeš and Harmáčková 2023).

2.2 | Occurrence Data and Syntopy

We utilised the eBird Basic Dataset (version February 2021) to gather local species occurrences from complete checklists. Checklist is a list of species that an observer records during a birdwatching trip and submits to the eBird database. It is designated as complete if *all* observed species are recorded and submitted. To standardise EB checklists used, we applied filters to include only observation dates after 1 January 1960, checklist types designed as “stationary,” “travelling,” “random,” “historical,” and “area,” duration between 20 and 60 min, and distance travelled < 1 km. Importantly, this selection defines local grain as used here, defining individuals of two species occurring up to 1 km apart in space as co-occurring locally. We merged checklists within groups (i.e., checklists from the same birding trip shared between several observers and thus duplicated). Subsequently, we overlaid coordinates of these checklists with sympatry areas of each sister pair to generate a list of checklists and species observations inside sympatry for each sister pair. We kept all checklists inside sympatry irrespective of the presence of either species from a given species pair, as checklists where both species are absent are needed for the calculation of a quantitative index of the degree of syntopy (see Text S1.1 in Appendix S1).

We further refined EB checklists to include only those from the breeding season. Due to the difficulty of defining breeding seasons of birds across the whole globe, we defined three types of the breeding season: “Breeding,” “Months,” and “Bands.” For the Breeding type, we retained only checklists from April to July for latitudes above 23°, checklists from September to December for latitudes below −23°, and all checklists from latitudes in between. For the month type, we retained only checklists from months in which both species were observed, either separately or together in any checklist in a given month. For the Bands type, we retained only checklists whose observation date fell between starting and ending Julian days defined for the breeding season in individual latitudinal bands, as outlined in Cazalis et al. (2021).

Given the differences in a list of checklists retained for different breeding season definitions, we calculated the degree of syntopy individually for each breeding season type. For all checklists associated with each species pair, we determined the presence or absence of each species in a checklist and calculated the degree of syntopy as the logOR index (Koricheva, Gurevitch, and Mengersen 2013). This index eliminates the need for randomisations and is unbiased in relation to sample size (Figure S2.2 in Appendix S2). Its values range from minus infinity (indicating species segregation or negative co-occurrence) to plus infinity (indicating species association or positive co-occurrence), with zero representing independently occurring species (details in Text S1.1 in Appendix S1). As it is impossible to work with infinite values in analyses, we kept only finite logOR values (excluding 9–10 species pairs with infinite logOR, depending on the breeding season definition). In the final step, we calculated the expected number of checklists in which both species were expected to be found together if they occurred independently (calculated as the proportion of checklists with sp1 × proportion with sp2 × number of checklists; Remeš and Harmáčková 2023), and excluded sister pairs with values lower than one checklist. We also excluded species pairs with < 50 checklists available (Table S3.1 in Appendix S3).

2.3 | Trait Data

We sourced data from multiple references to acquire species trait information. Specifically, we obtained measurements

TABLE 2 | Summary of the main hypothesised drivers of syntopy, together with the five specific hypotheses tested, their justification and predictions, and proxy variables used to quantify beta niches, alpha niches, ecological specialisation, and resource availability and demand.

Driver	Hypothesis	Justification and predictions	Proxy variables	Model specification (all models included these terms: Sympatry + pair age)
Habitat selection	(1) Beta niche divergence	Similar beta niches can facilitate the evolution of syntopy because species with the same habitat preferences might be more likely to occupy the same study site as compared to species with different habitat preferences (Pigot and Tobias 2013), with the strength of this effect depending on the relative size of study sites in relation to the grain of habitat mosaic (see Figure S2.12 in Appendix S2)	*Beta niche* (*difference between species*): Canopy height, moisture availability, NDVI, habitat	Sqrt (Canopy difference) + Habitat difference Sqrt (Moisture difference) + Habitat difference Sqrt (NDVI difference) + Habitat difference
Resource partitioning	(2) Alpha niche divergence	Species differing in key traits linked to resource use (alpha niche) should be more likely to co-occur because they are more likely to partition available resources (Schoener 1974)	*Alpha niche*: Beak dimensions, hand-wing index, body mass, diet, and stratum preferences	Log_{10} (Beak PPCA distance) + sqrt (Hand-wing index difference) + sqrt (Body mass difference) + Diet overlap + Stratum overlap Sqrt (Beak PPCA1 difference) + sqrt (Beak PPCA2 difference) + sqrt (Beak PPCA3 difference) + sqrt (Hand-wing index difference) + sqrt (Body mass difference) + Diet overlap + Stratum overlap
	(3) Ecological specialisation	Specialists can more effectively partition the resources, which facilitate their local coexistence (Belmaker, Sekercioglu, and Jetz 2012)	*Specialisation*: Diet and stratum specialisation	Mean diet specialisation + Mean stratum specialisation
	(2 + 3) Alpha niche divergence and specialisation	Specialisation can facilitate local co-occurrence especially when alpha niches differ, implying their interactive effect on co-occurrence (Harmáčková, Remešová, and Remeš 2019)	*Alpha niche*: Diet and stratum preferences *Specialisation*: Diet and stratum specialisation	Diet overlap + Mean diet specialisation + Diet overlap: Mean diet specialisation Stratum overlap + Mean stratum specialisation + Stratum overlap: Mean stratum specialisation

(Continues)

TABLE 2 | (Continued)

Driver	Hypothesis	Justification and predictions	Proxy variables	Model specification (all models included these terms: Sympatry + pair age)
Energy	(4) Resource availability	More energy can support more individuals, which can, in turn, allow the coexistence of more species (Wright 1983). Seasonal environments provide more resources, because many individuals die during the lean season and the remaining individuals have a lot of resources per capita (Ricklefs 1980)	*Resource availability (within range overlap)*: Moisture availability and its seasonality, NDVI and its seasonality, Canopy height	Mean moisture + Mean moisture seasonality Mean NDVI + Mean NDVI seasonality Sqrt (Mean Canopy height)
	(5) Resource demand	Large species require more energy per day, and consequently need larger territories (Tamburello, Côté, and Dulvy 2015) and reach lower densities (Santini et al. 2018)	*Resource demand*: Body mass	Log_{10}(Mean body mass)

Note: The last column specifies multi-predictor models with the degree of syntopy as a dependent variable, structured according to our five main hypotheses. All variables were scaled (i.e., centred around 0 and divided by one standard deviation) to enable comparison among regression coefficients. Sqrt denotes a square-root transformation, PPCA means phylogenetic principal component analysis, and NDVI denotes the normalised difference vegetation index (index of vegetation greenness). We avoided fitting Canopy difference, Moisture difference, and NDVI difference in one model under the "beta niche divergence" hypothesis because they are alternative metrics of the beta niche and are highly mutually correlated (Figure S2.4 in Appendix S2). Due to the same two reasons, we avoided including Moisture, NDVI, and Canopy height into one model under the "Resource availability" hypothesis (Figure S2.6 in Appendix S2). Besides overall Beak PPCA distance, we also fitted a model with the three PPCA axes separately to find which aspect of beak size and shape predicted syntopy (Figure S2.5 in Appendix 2 and Table S3.2 in Appendix 3).

related to beak morphology (beak length to culmen, beak width, and beak height); wing shape (the hand-wing index); adult body mass; and habitat type from the AVONET database (Tobias et al. 2022). Beak morphology, body mass, and hand-wing index are linked to resource and habitat use (Friedman et al. 2019; Miles and Ricklefs 1984; Pigot et al. 2020; Remeš et al. 2021a; Sheard et al. 2020; White 2016) and have been commonly used in studies of avian ecology and ecomorphology (Crouch and Ricklefs 2019; Imfeld and Barker 2022; Tobias et al. 2022). For assessing beak size, body mass, and hand-wing index, we focused on differences between species within a species pair. In the case of beak measurements, we initially conducted a phylogenetic principal component analysis (PPCA) with $\log_{10}$-transformed traits, using the "phyl.pca" function from the "phytools" library for R (Revell 2024). Subsequently, we calculated the Euclidean distance between sister species in the PPCA space (Table S1 in Appendix S3) to be used in subsequent analyses. To quantify differences, we considered the absolute value of the difference in $\log_{10}$-transformed body mass (referred to as body mass difference) and the absolute value of the difference in hand-wing index values (HWI difference). To see which aspect of beak size and shape predicted syntopy, we also used absolute values of differences along the three PPCA axes as predictors. Additionally, for body mass, we utilised the mean value of the two species within a species pair (body mass mean). The 10 habitat categories in the AVONET database (Tobias et al. 2022) include desert, rock, grassland, shrubland, woodland, forest, human-modified, wetland, riverine, and coastal. We transformed them into a binary variable: a value of 0 indicated identical categories between the two species in a pair, while a value of 1 indicated differing categories.

We sourced data related to diet preferences from the comprehensive SAviTraits database (Murphy et al. 2023). Initially, this dataset provided species-level information on percentage use of 10 distinct dietary categories: ectotherms, endotherms, fish, fruit, invertebrates, nectar, other, scavenger, seed, and unknown. Notably, these preferences were given separately for each month. To establish a consistent framework, we determined the breeding season for each species based on the latitude coordinate of their breeding range centroid by categorising species into three groups. These included (1) high-latitude species (latitude $> 23°$) where we exclusively utilised data from the months of April–July, (2) low-latitude species (latitude $< -23°$) where we considered data from the months of September to December, and 3) intermediate-latitude species (latitude between $-23°$ and $23°$) where we retained data for all 12 months. For each dietary category, we calculated the mean value of its percentage use across all included months. We used these average percentage use values for the dietary categories to calculate specialisation and niche overlap. We computed two commonly used indices to assess dietary specialisation and niche overlap (Harmáčková, Remešová, and Remeš 2019): (1) Levins' specialisation index, which quantifies the degree of intraspecific specialisation on different dietary resources. It ranges from 0 (indicating generalists) to 1 (representing specialists). In our analyses, we used the mean Levins' index for the two species in each species pair. (2) Pianka's niche overlap index, which captures the extent of dietary overlap between species. It spans from 0 (exclusive niches) to 1 (identical niches; see Text S1.1 in Appendix S1 for more details).

We sourced information on foraging stratum use from the EltonTraits database (Wilman et al. 2014). This database provides species-level data on the percentage use of seven distinct stratum categories: below water surface, around water surface, ground, understory, mid-high, canopy, and aerial. To quantify species' foraging ecology, we calculated mean pair-level Levins' specialisation index based on all stratum categories and Pianka' niche overlap index based on all stratum categories of both species in each species pair.

We acquired data on canopy height (Simard et al. 2011), soil moisture availability (Hersbach et al. 2018), and the Normalised Difference Vegetation Index (NDVI; Modis-based MOD13C2.006 version from https://search.earthdata.nasa.gov) in the form of global raster grids with varying resolutions (1 × 1 km for canopy height, 0.25° × 0.25° for moisture, and 0.05° × 0.05° for NDVI). These variables are expected to predict the amount of available resources for birds: canopy height (meters) predicts overall vegetation volume and available resources (Remeš et al. 2021b, 2022), moisture availability (volume of water in soil layer 0–7 cm deep) predicts ecosystem productivity (Remeš and Harmáčková 2018), and NDVI (spectral reflectance) is an index of vegetation greenness, thus vegetation volume and productivity (Pettorelli et al. 2011). Moisture and NDVI data were available for each month, enabling the calculation of breeding season values and seasonality. We calculated breeding season values of Moisture and NDVI separately for high-latitude (April–July), low-latitude (September–December), and intermediate-latitude species (all months; see above for definitions). We calculated seasonality of Moisture and NDVI as the coefficient of variation (CV) of the monthly values across all 12 months.

We overlaid these grids with geographic ranges and sympatry areas for each species pair and extracted the grid cells falling inside all these areas. More specifically, we extracted the values from grid cells falling inside the whole range of species 1, the whole range of species 2, and the area of range overlap between species 1 and 2, doing this for each species pair. We then calculated the mean Canopy height, breeding season Moisture, and breeding season NDVI as the mean of the grid values falling within sympatry areas of each species pair. Additionally, we calculated Moisture seasonality and NDVI seasonality as the mean CV value of the grid values within sympatry areas. These environmental characteristics obtained from the areas of range overlap were used as proxies of energy availability (Model 4 in Table 2). Furthermore, we calculated species-specific Canopy height, breeding season Moisture, and breeding season NDVI as the mean value of all the grid cells falling within the whole range of a given species. For each species pair, we then calculated the absolute difference between these Canopy height, Moisture, and NDVI values. These differences in species-specific environmental characteristics were used as proxies of beta niche divergence between species in species pairs (Model 1 in Table 2).

Finally, we excluded species pairs that had missing values in trait data for any of the breeding season types. This process led to 193, 204, and 200 sister species pairs remaining for the Breeding, Months, and Bands breeding season definitions, respectively. There were 206 unique species pairs across all three definitions distributed throughout the world (Figure S2.3 in Appendix S2). The mean number of checklists per species pair was 80,371 (ranging from 54 to 1.95 million checklists).

2.4 | Statistical Analyses

To evaluate the hypothesised drivers of the degree of syntopy, we constructed a set of models structured according to the five main hypotheses we tested: (1) beta niche divergence, (2) alpha niche divergence, (3) ecological specialisation, (2 + 3) interaction between alpha niche divergence and ecological specialisation, (4) resource availability, and (5) resource demand (Table 1). Within each of these five main hypotheses, we had either one model or several models (up to three) with different proxy variables (Table 1). We did not include several proxy variables of the same factor (e.g., beta niche or resource availability) into a single model. This would not make sense and, of course, these alternative proxies were mutually correlated and thus would lead to models with high predictor multicollinearity (mutual correlations of predictors are depicted in Figures S2.4–S2.6 in Appendix S2). All models were fit with the degree of syntopy (logOR) as a dependent variable, and the degree of sympatry derived from the union of species ranges and the age of species pair split as explanatory variables (both these predictors were thus included in all models).

We fit our models using the phylogenetic generalised least squares (PGLS) method. All models were fit on three sets of data delimited by the three different definitions of the breeding season. We used the MCC phylogenetic tree to define an initial variance–covariance structure of residuals and optimised it by using the Pagel's lambda statistic that flexibly adjusts the analysis for the degree of phylogenetic autocorrelation in model residuals. Models were weighted by $\log_{10}$ number of checklists. Prior to analyses, all variables were scaled so that their mean was equal to 0 and SD equalled 1. We fit the models in the “gls” function of the “nlme” package (Pinheiro et al. 2021) using the restricted maximum likelihood optimisation. To make sure our results were not biased by a particular computational approach, we fit all the models also in the “brm” function of the "brms" package (Bürkner 2017) in a Bayesian framework. We quantified phylogenetic signal in logOR using Pagel's lambda statistic, which varies from 0 to 1. The value of 0 means that traits evolve independently of phylogeny and resemble random evolution, while the value of 1 means that traits evolve in a way strongly consistent with the structure of the phylogenetic tree. We did so in the “phylosig” function of the “phytools” package (Revell 2024). We used the “nagelkerke” function from the “rcompanion” package to obtain the proportion of variation explained by the PGLS models (Nagelkerke pseudo R^2). All analyses were conducted in R 4.3.0.

3 | Results

We found that species on average positively co-occurred, as evidenced by the mean degree of syntopy (logOR) being > 0 across the three breeding season definitions (mean = 1.09, SD = 1.3). LogOR was weakly predictable based on the knowledge of phylogenetic relationships among sister species pairs, as evidenced by low phylogenetic signal of logOR that was not significantly different from zero (Pagel's lambda = 0.08, $p = 0.2$; Figure 1). LogOR increased with the degree of range sympatry in all models (Figure 2a), with a mean standardised regression coefficient of 0.28 (SD = 0.058, $N = 27$ gls models; mean = 0.28, SD = 0.054, $N = 27$ brm models; Table S3.3 in Appendix S3). Furthermore, logOR increased significantly with pair age in some, but not all, analyses (Figure 2b; Table S3.3 in Appendix S3). LogOR values were widely spread around regression lines, including the youngest species pairs (Figure 2b) and pairs with very low degree of range sympatry (Figure 2a). Considering that the degree of range sympatry increased with the age of species split (Figure S2.7 in Appendix S2), this wide spread of logOR values suggests that some species pairs started overlapping their ranges in positive co-occurrence, while others in negative co-occurrence.

LogOR was positively correlated with the similarity of beta niches between species in a species pair. Specifically, species occupying ranges with similar canopy heights, NDVI values, and moisture index values exhibited higher logOR values (Figures 3a and 4a). Similarly, species preferring the same primary habitat type demonstrated higher logOR values compared to those preferring different habitat types (Figures 3b and 4a; Figure S2.8a in Appendix S2; and Table S3.3 in Appendix S3).

Surprisingly, there was a tendency for *smaller* distance in beak PPCA space being positively correlated with logOR, meaning that species more similar in beak size and shape tended to co-occur positively, although the significance of this effect depended on the definition of the breeding season (Figure 4b; Figure S2.8b in Appendix S2). When broken down, the relatively strongest effect was that of an overall beak size (PPCA2, but not different from zero in some breeding season definitions), with effects of beak shape (PPCA1, PPCA3) being negligible and not statistically significant (Figure S2.9 in Appendix S2, Tables S3.2 and S3.3 in Appendix S3). No other proxy of alpha niche divergence predicted logOR (Figure 4b; Figure S2.8b in Appendix S2; and Table S3.3 in Appendix S3). Diet specialists exhibited greater logOR compared to diet generalists, while specialisation on foraging stratum had no significant effect (Figures 3c and 4b; Figure S2.8b in Appendix S2). The effect of diet specialisation was independent of diet overlap because the statistical interaction between these two variables was not significant (Figure S2.10 in Appendix S2; Table S3.3 in Appendix S3). Resource demand predicted logOR; more specifically, large species displayed lower logOR (Figures 3d and 4c; Figure S2.8c in Appendix S2). In contrast, no index of resource availability (moisture availability, vegetation complexity estimated by canopy height and NDVI, and seasonality of moisture and NDVI) was found to have a significant explanatory effect on logOR (Figure 4c; Figure S2.8c in Appendix S2; and Table S3.3 in Appendix S3).

The proportion of variation in data explained by our models was highest in models of beta niche divergence (pseudo-$R^2 = 0.20–0.23$ in gls models; $R^2 = 0.35–0.39$ in brm models), followed by models of ecological specialisation (pseudo-$R^2 = 0.17–0.19$ in gls models; $R^2 = 0.28–0.29$ in brm models), alpha niche divergence (pseudo-$R^2 = 0.15–0.16$ in gls models; $R^2 = 0.29–0.32$ in brm models), resource demand (pseudo-$R^2 = 0.14–0.16$ in gls models; $R^2 = 0.24–0.27$ in brm models), and resource availability (pseudo-$R^2 = 0.12–0.13$ in gls models; $R^2 = 0.26–0.28$ in brm models; see Table S3.3 in Appendix S3). All results were consistent across the three definitions of the breeding season (Figure 4; Figure S2.8 in Appendix S2), which agreed with estimates of the degree of syntopy being highly similar across these definitions (Figure S2.11 in Appendix S2).

4 | Discussion

Our study contributes significantly to the understanding of the ecological and evolutionary processes governing local co-occurrence patterns among passerine species pairs globally. Our results indicated that the degree of syntopy, a measure of the degree of positive co-occurrence between species, increased with time elapsed since species split. However, the wide spread of the degree of syntopy observed in young species pairs with low range sympatry suggested that species pairs enter sympatry in both positive and negative co-occurrence. Confirming previous results (Remeš and Harmáčková 2023; Harmáčková and Remeš 2024), we also showed that the degree of syntopy was strongly positively correlated with range sympatry, demonstrating that the evolution of positive local co-occurrence is closely tied to the evolution of overlapping ranges. Furthermore, the similarity of beta niches was the strongest predictor of the degree of syntopy among ecological factors. In contrast, the effects of alpha niche divergence and resource availability were relatively weak, except for the degree of syntopy increasing with higher diet specialisation and smaller body size, and a tendency of species with beaks of similar size to display positive local co-occurrence. These findings collectively suggest that both alpha and beta niche evolution during and following allopatric speciation play critical roles in shaping local species coexistence and diversity dynamics.

One of the most significant predictors of the degree of syntopy was range sympatry, which is consistent with previous findings using data from the Australian Bird Count (Remeš and Harmáčková 2023) and eBird (Harmáčková and Remeš 2024) programs. Interspecific behavioural interactions, including territorial and mating interactions, can significantly impact the spatial distributions of species and hinder their range expansion (Patterson and Drury 2023). Furthermore, agonistic behavioural interactions are more likely to occur among related and phenotypically similar species (plumage colour and song) that overlap in resource and habitat use (Drury, Cowen, and Grether 2020; Losin et al. 2016). For example, the collared flycatcher (*Ficedula albicollis*) exhibits aggressive behaviour towards its sister species, the pied flycatcher (*Ficedula hypoleuca*), which leads to the latter species occupying suboptimal habitats. As a result, pied flycatchers nesting in these low-quality habitats are less likely to hybridise with collared flycatchers, thereby strengthening the habitat segregation of these two species (Rybinski et al. 2016; Vallin et al. 2012). The cumulative evidence suggests that morphological and ecological similarity can preclude species from evolving syntopy and sympatry alike. In this context, the mutual diffusion of two ranges and the evolution of sympatry might be slowed down or impeded by agonistic behavioural interactions due to similar ecological requirements (Patterson and Drury 2023).

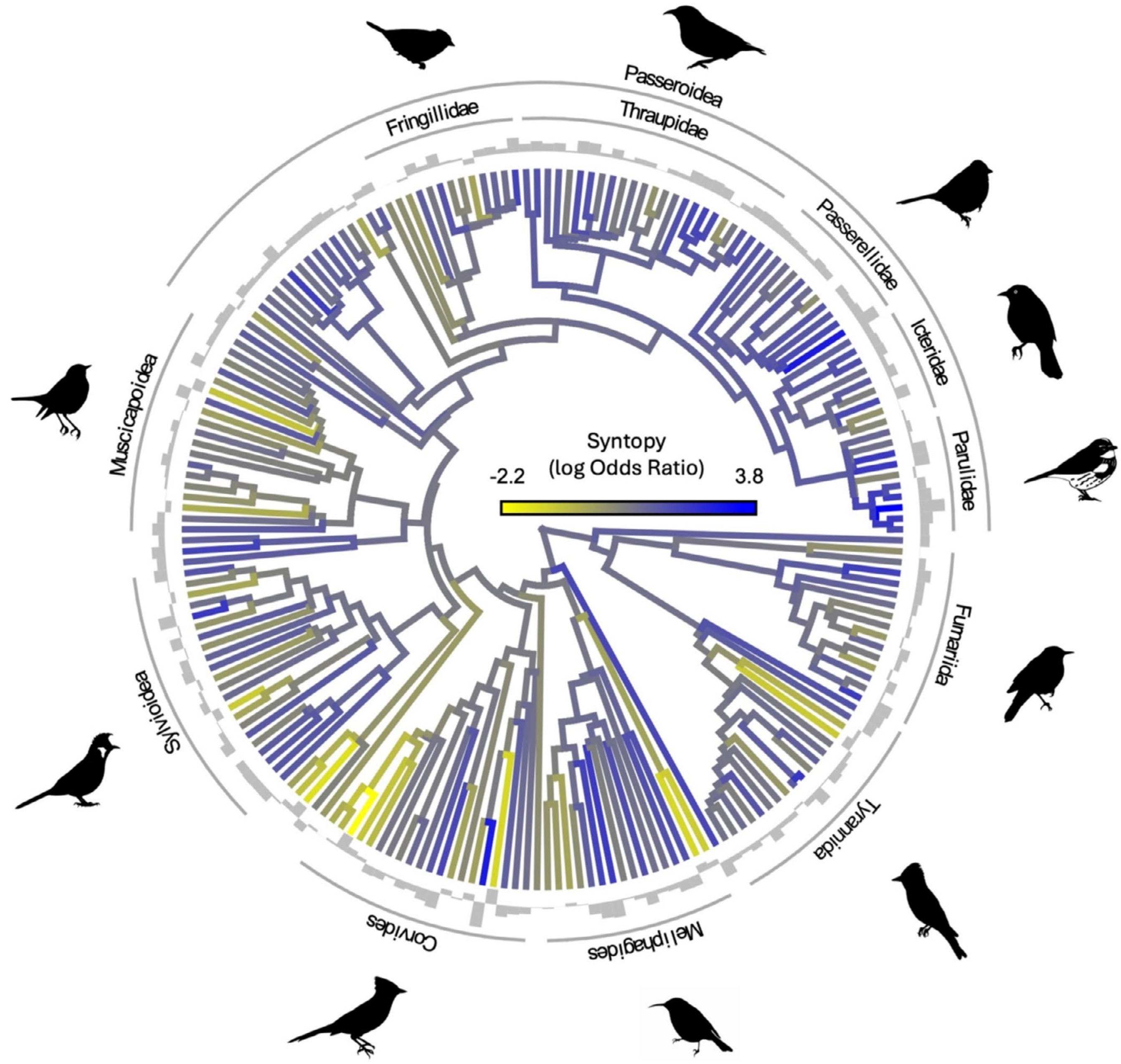

FIGURE 1 | The phylogenetic distribution of syntopy across passerine birds ($n = 206$ species pairs). The degree of syntopy ($\log_e$ odds ratio) is plotted at branch tips as grey bars, with each species pair represented by one tip only. Ancestral reconstruction is shown along branches of the tree by yellow to blue colour palette for illustrative purposes (using the 'plotBranchbyTrait' function from the 'phytools' package for R; Revell 2024). Licence information for the PhyloPics (www.phylopic.org) is available in Text S1.2 in Appendix S1.

After controlling for range sympatry, the degree of syntopy exhibited a weak positive correlation with species split age. Notably, a wide range of the degree of syntopy, encompassing both positive and negative species co-occurrence, was observed even in young species pairs with limited range overlap. This observation suggests that some species pairs underwent limited divergence and retained ancestral niches, while others evolved characteristics allowing them to coexist in mutually exclusive occurrence (see below). This finding has significant implications for a long-standing evolutionary debate: how much do species diverge during the allopatric phase of the speciation cycle (Tobias, Ottenburghs, and Pigot 2020)? Limited ecological divergence has been found in pairs of bird taxa living in allopatry across similar rainforest habitats in South America (Freeman et al. 2023). Additionally, vertebrate species pairs have been found to share evolutionary optima during allopatry (Anderson and Weir 2022). However, habitat differences were not considered in the latter study. Therefore, it remains unclear whether initial niche divergence or conservatism during the allopatric phase of speciation can be predicted by the habitats of incipient species. While individual species pairs have demonstrated these patterns (Reif et al. 2018; Sottas et al. 2018), broader studies are

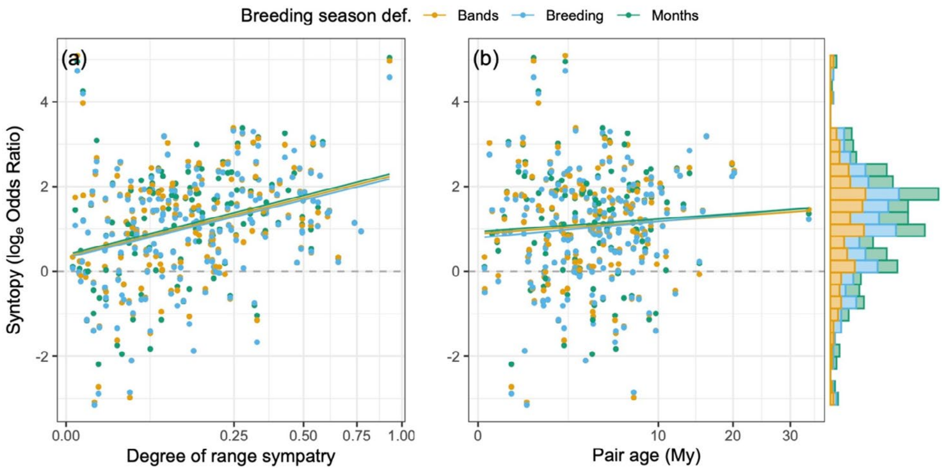

FIGURE 2 | Relationships between the degree of syntopy and (a) the degree of range sympatry (square-root transformed; 0—no sympatry, 1—complete sympatry) and (b) pair age (square-root transformed), depicted separately for the three different definitions of the breeding season. Ordinary linear least squares regression lines are included for illustrative purposes only. The distribution of the degree of syntopy across all species pairs is depicted by a histogram on the right.

needed to fully understand the relationship between habitat and the allopatric phase of speciation.

High degree of syntopy was observed in species pairs with similar beta niches characterised by primary habitat types, canopy height, vegetation greenness (NDVI index), and moisture availability. This finding is probably a consequence of the spatial arrangement of habitats, where in a mosaic of habitat and vegetation types, species that share the same beta niche preferences might be more likely to co-occur locally (Royan et al. 2016). However, the validity of this simple explanation depends on the spatial grain of the habitat mosaic relative to the grain at which syntopy is defined (i.e., size of the sampling unit; Figure S2.12 in Appendix S2). For instance, theory predicts that the degree of spatial autocorrelation in environmental conditions drives the shape of the coexistence-area relationship, which quantifies how the number of coexisting species increases with sampled area (Hart, Usinowicz, and Levine 2017). Similarly, species segregation was expected to be hump-shaped in relation to sampling plot resolution, with a peak at an intermediate spatial grain, a pattern empirically confirmed in three out of four vegetation types studied (McNickle et al. 2018). In this study, we quantified the degree of syntopy in complete eBird checklists varying in distance an observer walked from 0 to 1 km. Different processes might explain species co-occurrence defined at finer spatial grains. For example, mutually exclusive occurrence due to divergence in habitat preferences can evolve to reduce interspecific interference competition for resources (McEachin, Drury, and Grether 2024) or to reduce costly interspecific hybridisation (Vallin et al. 2012), processes occurring at comparatively fine spatial grains of animal territories. Therefore, further work should concentrate on revealing whether predictors of the degree of syntopy differ when the spatial delimitation of local co-occurrence is changed.

Diet specialists exhibited greater degree of syntopy compared to diet generalists, whereas foraging stratum specialisation and diet and foraging niche overlap did not significantly influence the degree of syntopy. The effect of diet specialisation was independent of diet niche overlap, because the interaction between these two variables was not statistically significant. These findings partially support previous research indicating that specialisation (Belmaker, Sekercioglu, and Jetz 2012; Harmáčková, Remešová, and Remeš 2019; Norman et al. 2007) and divergence in foraging ecology (Remeš and Harmáčková 2023) facilitate species coexistence. Mixed results might be attributed to differences in niche resolution. For instance, a study on Australian passerines found that a link between vegetation complexity and trait diversity was only recoverable when a fine resolution of substrate use was applied, specifically 17–24 categories compared to 8 categories (Remeš et al. 2021b). Similarly, a simulation study demonstrated that the role of biotic interactions in community assembly can be underestimated when using coarse trait categories (Kohli and Jarzyna 2021). This sampling bias presents a significant problem for worldwide-scale analyses of local patterns, because it is very difficult to obtain fine-resolution ecological data for a global set of species, and at the same time local partitioning of ecological space among related species can be very subtle (Brosset 1996).

Consistent with previous studies, (multivariate) divergence in morphology was a weak predictor of syntopy (called breeding contact in McEntee et al. 2018). Species with similar beak size tended to display positive local co-occurrence, but the strength and significance of this effect depended on the definition of the breeding season. However, overall effects of alpha niche divergence were weak in this study. Two factors might have contributed to weak alpha niche effects. First, other interacting species might have prevented divergence in the focal species pair. Adding other species into broad-scale analyses is difficult but should be attempted by future studies (Wilcox, Schwartz, and Lowe 2018). Second, there has been an attempt to divide the ecological niche into (i) its individual component that reflects organismal adaptations and is expressed at the level of an individual (e.g., foraging substrate selection) and (ii) its population component that reflects species persistence over its geographic range (Ricklefs 2010). The latter component, expressed for example in local species densities, range

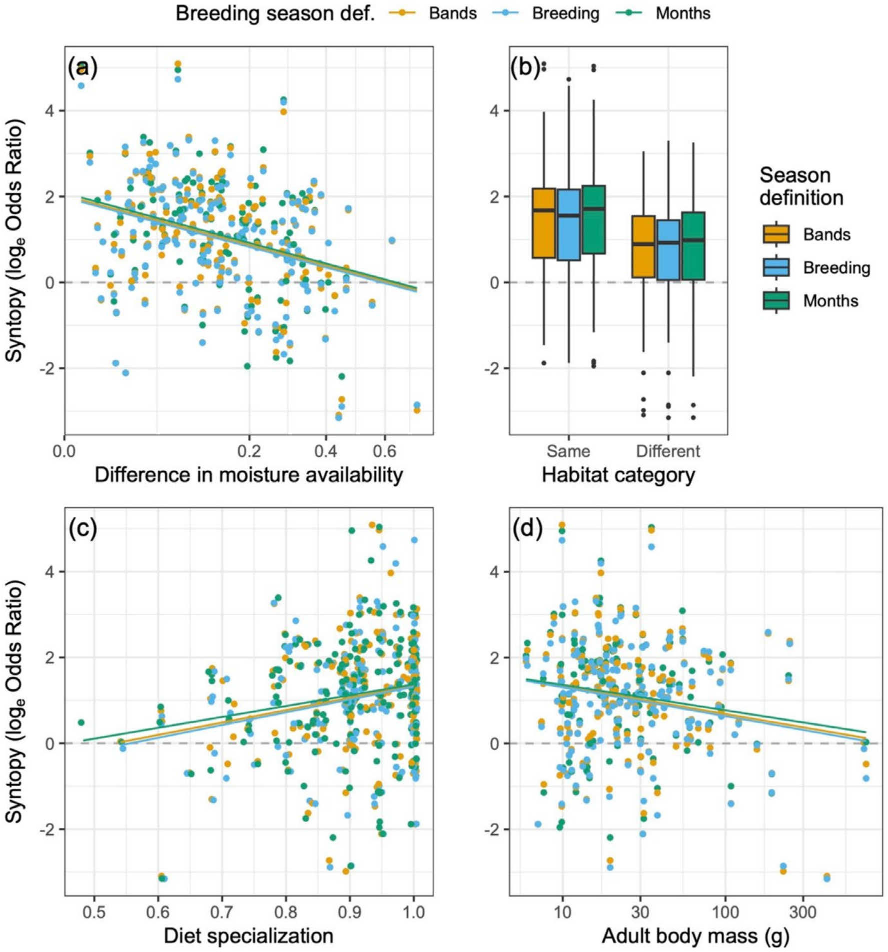

FIGURE 3 | Relationships between the degree of syntopy and four important predictors: (a) the difference in moisture availability (square-root transformed; volume of water in soil layer 0–7 cm deep) between species within species pairs, (b) the difference in breeding habitats between species within species pairs, (c) the mean diet specialisation of the two species quantified using the Levins' index (0—generalists, 1—specialists), and (d) the mean adult body mass ($\log_{10}$-transformed) of the two species.

filling, or occupancy, is envisioned to be labile especially due to interactions with species-specific pathogens (Ricklefs 2011). Then, any link between the individual component and the population component of the niche would be noisy. This noisiness could impair our ability to detect the correlation between alpha niche divergence and syntopy. On the other hand, the link between the individual component of the niche and range-wide sympatry could be much stronger due to its emergence from diffuse interactions integrated across large spatial and temporal scales.

A leading explanation for large-scale gradients in species richness is that they are controlled by differences in ecological limits to coexistence (Rabosky and Hurlbert 2015). This idea provides a strong motivation to study links between the evolution of sympatry and syntopy on the one hand and resource availability on the other hand. Ecological limits might be released by more available energy and vegetation complexity both regionally and locally (Feng et al. 2020; Remeš and Harmáčková 2018; Remeš et al. 2021b). Surprisingly, we did not find any effect of diverse indices of resource availability (moisture availability, vegetation greenness, canopy height, environmental seasonality) on the degree of local species co-occurrence. Range overlap was previously shown to increase with energy availability indexed by net primary productivity (Pigot, Tobias, and Jetz 2016). However, it also declined as regional assemblages became saturated with species (Pigot et al. 2018), while the degree of local co-occurrence was not related to local species richness (Harmáčková and Remeš 2024). Moreover, no effect of seasonality of productivity was found on range-wide coexistence (Pigot, Tobias, and Jetz 2016). These mixed results suggest that an interplay between resource availability, their exploitation by species-rich communities, and the evolution of syntopy is complex and requires further examination.

Finally, we found a clear negative correlation between the degree of syntopy and average body mass of species in species pairs, whereby small species exhibited higher degree of local co-occurrence. Two explanations are possible. First, small species require less resources per capita, thus they might more easily coexist locally. For instance, two small individuals foraging on the same tree trunk could be equivalent to a single large individual monopolising the same tree trunk due to the latter's comparatively high requirements of energy. Second, small species have smaller territories and higher densities (Santini et al. 2018; Schoener 1968; Tamburello, Côté, and Dulvy 2015), which

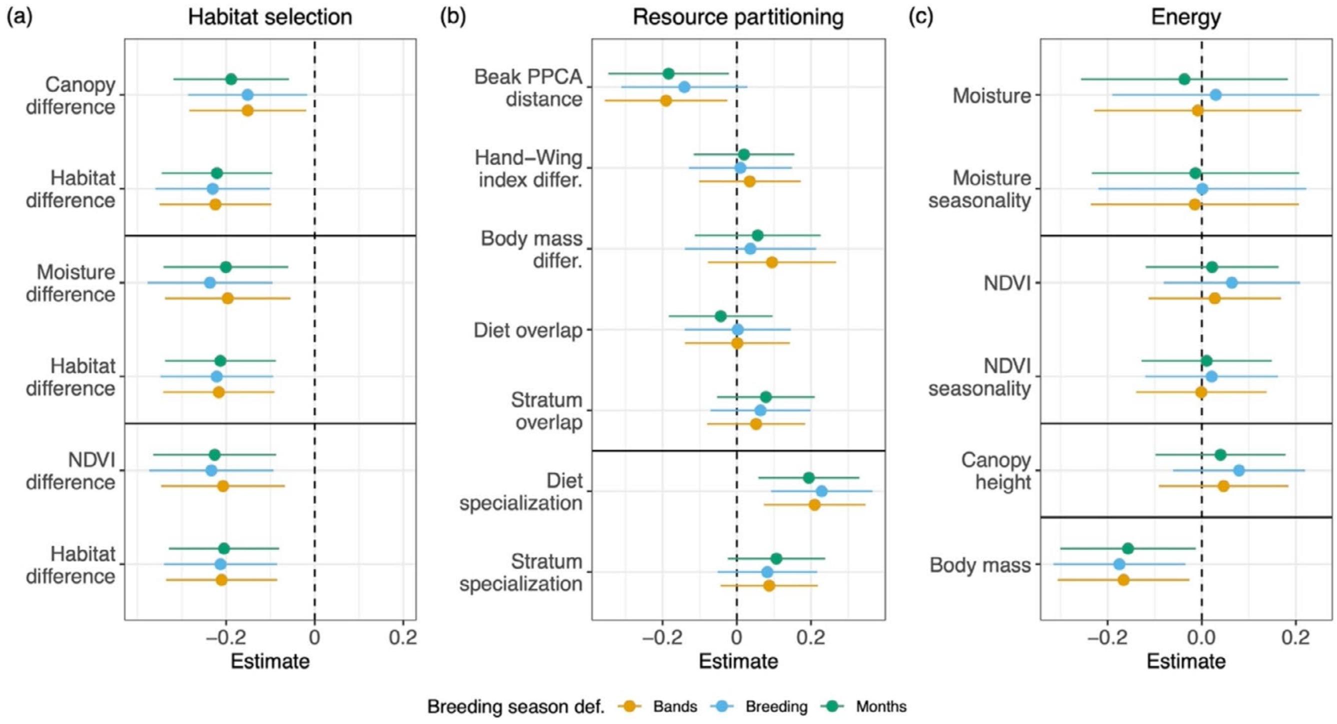

FIGURE 4 | Standardised effect sizes from the phylogenetic generalised least squares regression models of the degree of syntopy in relation to (a) habitat selection, (b) resource partitioning, and (c) energy availability and demand. Depicted are estimates (dots) and 1.96 standard errors as an approximation of 95% confidence intervals (error bars). Maximum likelihood estimates are available in Table S3.3 in Appendix S3, while Bayesian estimates are depicted in Figure S2.8 in Appendix S2 and listed in Table S3.3 in Appendix S3.

should facilitate detection by observers on the same birding route due to their higher numbers per unit area.

Our study provides valuable insights into the interplay of ecological and evolutionary processes that shape local species coexistence and diversity dynamics. Most bird lineages speciate allopatrically (Barraclough and Vogler 2000; Linck, Freeman, and Dumbacher 2020; Phillimore et al. 2008; Smith et al. 2014), although the prevalence of different geographical modes of speciation probably depends on the clades studied (Skeels and Cardillo 2019). Dispersal assembly models, exemplified by hand-wing index as a measure of dispersal abilities, explain best the transition to secondary range contact (Pigot and Tobias 2015; Pigot et al. 2018), with morphology mostly evolving along shared optima in the allopatric phase (Anderson and Weir 2022; Freeman et al. 2023). Subsequent transition to widespread sympatry is better predicted by metrics of competition, especially divergence in beak and body dimensions (McEntee et al. 2018; Pigot et al. 2018), and resource availability (Pigot, Tobias, and Jetz 2016). However, species can exhibit both positive and negative co-occurrence in the area of range overlap, even on a time scale of millions of years (Remeš and Harmáčková 2023; Harmáčková and Remeš 2024; this study). While in sympatry, species usually diverge in preferred microhabitats (Brosset 1996; Reif et al. 2018; Sottas et al. 2018), foraging ecology (Remeš and Harmáčková 2023), and morphology (Anderson and Weir 2021). This divergence enables them to coexist locally (Lack 1971), especially in small and specialised species (this study) and those with interspecific territoriality (Drury, Cowen, and Grether 2020). Greater degree of syntopy evolves alongside widespread range sympatry (Remeš and Harmáčková 2023; Harmáčková and Remeš 2024; this study). Large ranges then allow for the next round of speciation to start, thus completing the speciation cycle (Tobias, Ottenburghs, and Pigot 2020).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All the data and R code are available from the Zenodo Repository: https://zenodo.org/records/12579439.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.