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Sympatry, syntopy, and species age: disentangling drivers of signal evolution in a large radiation of passerine birds (Meliphagides)

Hélène Leroy[1] [ORCID], Lenka Harmáčková[1,2], Nicholas R. Friedman[3], Vladimír Remeš[1,2,*]

[1]Department of Ecology, Charles University, Prague, Czech Republic
[2]Department of Zoology, Palacky University, Olomouc, Czech Republic
[3]Zoological Museum Hamburg, Leibniz Institute for the Analysis of Biodiversity Change, Hamburg, Germany

[*]Corresponding author. Department of Zoology, Faculty of Science, Palacky University, 17. listopadu 50, 77146 Olomouc, Czech Republic. E-mail: vladimir.remes@upol.cz

ABSTRACT

The evolution of signalling traits is crucial in species diversification, because they can become effective barriers to interspecific hybridization. Among various selection pressures acting on signal evolution, species interactions can reinforce signal divergence via reproductive character displacement, especially during secondary sympatry. Although previous evidence suggests that sympatry promotes signal divergence, methods using large-scale geographical range overlap fail to capture local co-occurrence (syntopy), an essential prerequisite of species interactions. In this study, we used 116 sympatric species pairs of Meliphagides, a large radiation of Australasian passerines, to test simultaneously the effects of node age, range sympatry, and, for the first time, local syntopy on colour and song divergence. Signal divergence increased with node age (although not consistently). However, we did not find conclusive evidence that sympatry was driving signal evolution, probably owing to a necessary exclusion of allopatric pairs from our analyses. Furthermore, we did not demonstrate any significant effect of syntopy on signal evolution. This could suggest that reinforcement of signal divergence in sympatry (and syntopy) is not as common as previously thought, with neutral trait drift potentially being a more dominant driver. Alternatively, constraints on signal evolution might prevent trait divergence.

Keywords: song evolution; colour evolution; species interactions; reproductive character displacement; convergence

INTRODUCTION

Signalling traits, also referred to as sexual or communication signals (Höbel and Gerhardt 2003, Simpson *et al.* 2021), play a crucial role in lineage diversification because they can form effective barriers to interspecific hybridization (Liou and Price 1994, Martin *et al.* 2010, Lipshutz 2018). Signal evolution is influenced by a multitude of selection pressures, which can drive signal divergence among closely related species. Specifically, signals can diverge in allopatry via neutral trait drift, whereby trait differences accumulate with time spent in geographical isolation, resulting in a positive correlation between trait divergence and genetic distance between species (Freeman *et al.* 2023). Moreover, when distinct environments provide contrasting conditions for signal transmission, divergent selection pressures can strengthen signal divergence (Marchetti 1993, Baldassarre *et al.* 2013, Hulse *et al.* 2020). Crucially, signalling traits contribute to species recognition. When sufficiently divergent, they act as a mechanism of reproductive isolation, thus limiting hybridization

and competitive interactions between closely related sympatric species (Losin *et al.* 2016, Cowen *et al.* 2020, Drury *et al.* 2020). Once incipient species come into secondary contact, or secondary sympatry, species interactions can reinforce signal divergence via reproductive character displacement (Grether *et al.* 2009, Lemmon 2009).

The effect of sympatry (i.e. breeding range overlap) on signal divergence has been investigated across taxa including fishes, frogs, and birds, with evidence from both visual and acoustic signals suggesting that sympatry can promote signal divergence between closely related species (Höbel and Gerhardt 2003, Seddon 2005, Kirschel *et al.* 2009, Lemmon 2009, Martin *et al.* 2010, Hemingson *et al.* 2019, Simpson *et al.* 2021). Alternatively, signalling traits can converge in sympatry, possibly as an adaptation to enhance signal transmission within shared habitats (Boncoraglio and Saino 2007, Ey and Fischer 2009, Tobias *et al.* 2010), implying an ecological constraint on signal evolution; or as a result of a convergent agonistic character displacement,

improving the efficiency of aggressive signals in the context of interspecific territoriality (Grether *et al.* 2009, 2017, Tobias and Seddon 2009, Tobias *et al.* 2014, Losin *et al.* 2016, Drury *et al.* 2020). For instance, this convergence was observed in several characteristics of song in wood warblers (Parulidae; Simpson *et al.* 2021), antbirds (Thamnophilidae; Tobias and Seddon 2009), ovenbirds (Furnariidae; Tobias *et al.* 2014) and larks (Alaudidae; Laiolo 2012). Moreover, signal convergence can also result from introgressive hybridization, as observed in the song of *Hippolais* warblers (Acrocephalidae; Secondi *et al.* 2011), or from heterospecific copying of song in hybrid zones, which, in turn, can facilitate hybridization, as seen in *Ficedula* flycatchers (Muscicapidae; Haavie *et al.* 2004, Qvarnström *et al.* 2006). Ultimately, investigating how sympatry influences signal divergence or convergence can provide insights into mechanisms driving species diversification in shared habitats (Anderson and Weir 2021, 2022).

Sympatry has traditionally been quantified using large-scale geographical range overlap (Seddon 2005, Lemmon 2009, Martin *et al.* 2010, Simpson *et al.* 2021). However, this does not seem sufficient, because species must interact locally to have the potential to exert selection on traits. At the same time, local interactions are possible only if species co-occur on appropriate spatial scales that enable individuals to meet (syntopy; Losin *et al.* 2016, Drury *et al.* 2020, Remeš and Harmáčková 2023, Harmáčková and Remeš 2024). We thus hypothesize that both sympatry and syntopy are necessary if species interactions are to promote signal evolution. First, high sympatry brings into

contact potentially large shares of the populations of two species. Second, high syntopy increases the probability of a regular interspecific contact. Moreover, species must coexist in sufficient numbers for interspecific interactions to be common (Kirschel *et al.* 2009). Yet, few studies have included this scale of interaction (Höbel and Gerhardt 2003, Kirschel *et al.* 2009), and none has teased apart independent effects of range-wide sympatry and local syntopy on trait evolution in multiple species pairs.

In this study, we aim to investigate how node age (used as an indicator of the time elapsed since speciation), sympatry, and syntopy predict the divergence of visual and acoustic signals within Meliphagides, a large radiation of Australasian passerines that emerged in the Oligocene, ~23–34 Mya (Marki *et al.* 2017, Oliveros *et al.* 2019). These songbirds exhibit a noteworthy range of colours and songs and are represented in a wide variety of habitats, from arid scrubland to tropical rainforest (Winkler *et al.* 2020). Secondary contact is common among closely related species (Ford 1981, Sardell and Uy 2016). Using 116 Meliphagides species pairs, we test additive effects of node age, sympatry, and syntopy on the divergence of colour and song traits within the framework of five working hypotheses (Fig. 1): (i) under the constraint model, signalling traits do not diverge with node age, sympatry, or syntopy, which could suggest that constraints on signal evolution are preventing divergence; (ii) under the neutral model, signalling traits diverge with node age only owing to neutral trait drift, meaning that changes in traits would accumulate gradually with time since speciation; (iii) under the sympatry model, signalling traits diverge with node age and sympatry;

Figure 1. A conceptual figure showing expectations under the following five hypotheses: constraint model, in which signalling traits do not diverge with node age, sympatry, or syntopy; neutral model, in which signalling traits diverge with node age only; sympatry model, in which signalling traits diverge with node age and sympatry; syntopy model, in which signalling traits diverge with node age and syntopy; and integrated model, in which signalling traits diverge with node age, sympatry, and syntopy. Please note that in case of convergent signal evolution, the direction of trait evolution would be reversed.

(iv) under the syntopy model, signalling traits diverge with node age and syntopy; and (v) under the integrated model, signalling traits diverge with node age, sympatry, and syntopy.
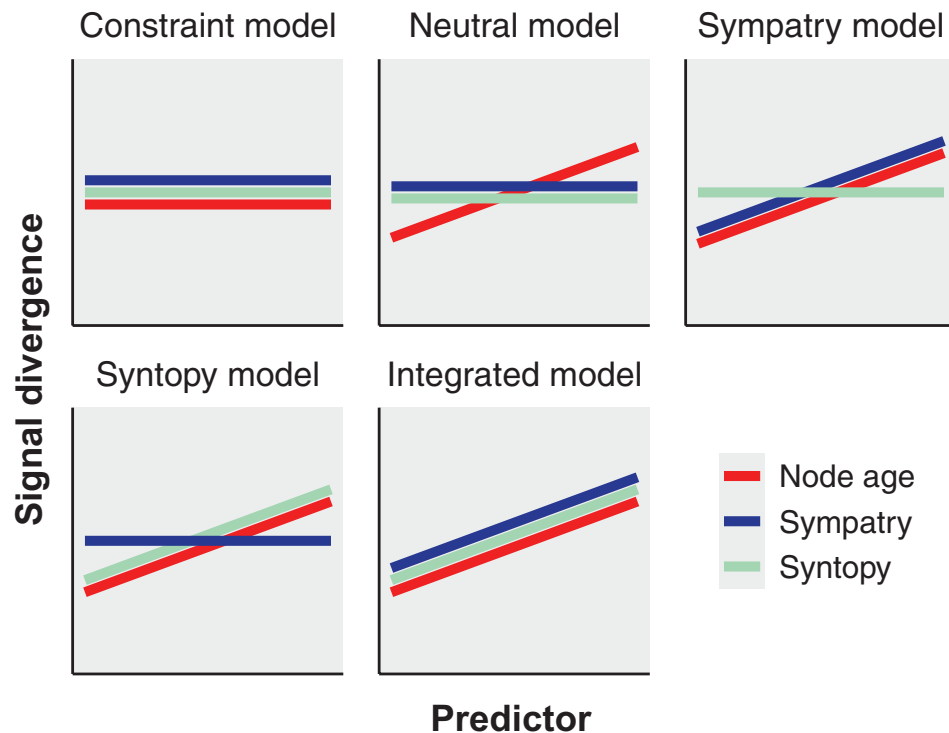
MATERIALS AND METHODS

Species pairs

Meliphagides are the largest radiation of Australasian passerines, comprising 289 recognized species composed of thornbills and allies (Acanthizidae), bristlebirds (Dasyornithidae), fairywrens (Maluridae), honeyeaters (Meliphagidae), and pardalotes (Pardalotidae; Marki *et al.* 2017, Oliveros *et al.* 2019). We used 116 sympatric species pairs (in 58 species; see Supporting Information, Table S1) of Meliphagides identified by Remeš and Harmáčková (2023) from a recent time-calibrated phylogeny (Marki *et al.* 2017), from which we obtained the node age for each species pair. Only sympatric species pairs were selected, because syntopy can be calculated exclusively in species pairs with at least some degree of range overlap. These species pairs diverged in relatively recent times within Australia and Tasmania, with the oldest node dating back to 10 Mya (Remeš and Harmáčková 2023). This approach focuses on groups of related species instead of using only sister-species pairs (Weber and Strauss 2016). This also means that one species can be found in more than one species pair, which is the case for 42 species (more specifically, 39 species belonged to two to four species pairs, and three species belonged to 11 species pairs). This overlap in species identities among species pairs was, however, controlled for in statistical analyses (see Statistical analyses, below).

Song distances

We obtained recordings from three databases (Xeno-Canto, Macaulay Library at the Cornell Lab of Ornithology, and the Australian National Wildlife Collection), with an average pairwise geographical distance between recording locations of 739.7 km. We analysed 300 song recordings with RAVEN software (RAVEN PRO v.1.6.5; K. Lisa Yang Center for Conservation Bioacoustics 2023), with an average of 5.2 songs per species (ranging from 1 to 17). Following established protocols from prior studies on song evolution (Price *et al.* 2007, Tobias *et al.* 2014, Friedman *et al.* 2019), we measured 27 song traits, previously used in evolutionary research in Meliphagides (Friedman *et al.* 2019). We sorted these traits into the following four categories: (i) frequency (song level); (ii) frequency (note level); (iii) tempo; and (iv) note variation (for song traits definitions and transformations, see Supporting Information, Table S2).

We ran a phylogenetic principal component analysis (PPCA) on each group of song traits, using the 'phyl.pca' function from the 'phytools' package (Revell 2012) for the language R (R Core Team 2024). Variables were highly correlated within frequency (song level) and frequency (note level), and PPCAs did not converge when retaining all variables. Therefore, from each group we removed variables that had the highest correlation with other variables, namely 'song bandwidth' [based on a correlation coefficient (r) = 0.93 with 'song maximum frequency'] and 'note minimum frequency' (r = 0.96 with 'note peak frequency'), and re-ran the PPCAs. We then selected the number of phylogenetic principal component axes based on their cumulative proportion of explained variance (>0.95) to calculate Euclidean distances

with the 'dist' function from the 'stats' package (R Core Team 2024). Additionally, we ran non-phylogenetic principal component analyses (PCAs), which converged and thus did not require removal of any variables. Distances derived from PPCA and PCA were highly correlated (Supporting Information, Fig. S1), ensuring the reliability of our estimates.

Colour distances

We performed spectrophotometric measurements on specimens from the bird collections of the Australian National Wildlife Collection (ACT, Australia) and the American Museum of Natural History (NY, USA) using the Jaz-PX spectrophotometer (Ocean Optics, USA). Measurements were taken while holding the probe, enclosed in non-reflective black sheathing, perpendicular to the surface of the feather. Eleven body patches were measured for each specimen: crown, throat, breast, belly, cheek, flanks, back, rump, tail, wing coverts, and primaries. Each patch was measured three times, and the resulting data were averaged to obtain representative values. We recalibrated the device with a white standard (WS-2) after each specimen was measured. In total, 310 specimens from the 58 selected species were measured, with an average of 5.3 specimens per species (ranging from 3 to 9). We measured males exclusively, because Meliphagides species can exhibit significant sexual dichromatism, with male colour traits potentially experiencing stronger sexual selection pressure (Johnson *et al.* 2013, Friedman and Remeš 2015, 2024). If needed (owing to the small number of male specimens available), we additionally selected specimens (N = 3) for which sex was unknown in species without sexual dichromatism (i.e. for *Acanthiza inornata*, *Melithreptus brevirostris* and *Manorina melanophrys*).

Processing of reflectance spectra was done in the 'PAVO' package (Maia *et al.* 2019) for R. Negative values were set to zero, and spectra were smoothed by a span of 0.16. We calculated an average spectral measurement per species, separately for each patch (measurements were missing for bare parts, such as *Philemon corniculatus* crown and cheek and *Entomyzon cyanotis* cheek).

Colour distances were calculated using two methods. First, we calculated just-noticeable differences (JNDs) for each patch between species in each of the 116 species pairs. For each patch, spectra were run in an avian visual model based on the avian visual system with the ultraviolet-sensitive cone, as implemented in the 'PAVO' package (Maia *et al.* 2019). The JNDs were obtained for each patch, then averaged across patches within body regions defined by Simpson *et al.* (2021) as follows: (i) head, including crown, throat, and cheek; (ii) upper-body, including back and rump; (iii) under-body, including breast, belly, and flanks; and (iv) flight feathers, including tail, wing coverts, and primaries. We also calculated JNDs using visual models based on the avian visual system with the violet-sensitive cone. Both JND estimates were highly correlated (Supporting Information, Fig. S2), hence we opted to use JNDs calculated using the ultraviolet-sensitive cone visual system for subsequent analyses, hereafter referred to simply as 'JNDs'. Second, we calculated unweighted Euclidean distances by projecting reflectance spectra into a tetrachromatic colour space before calculating Euclidean colour distances. The JNDs and unweighted Euclidean distances of the four body regions were again highly correlated (Supporting Information, Fig. S3), hence we used only JNDs for downstream analyses.

Similarly to previous studies on trait evolution and range overlap (Seddon 2005, Martin *et al.* 2010, Tobias *et al.* 2014, Hemingson *et al.* 2019, Simpson *et al.* 2021), signalling traits were measured on specimens regardless of whether they originated from allopatric or sympatric populations, relying on the assumption that if trait divergence or convergence occurs in sympatry, the changes also spread to allopatric parts of species ranges.

Sympatry and syntopy

To characterize sympatry, we used a range overlap index commonly used in previous studies (Chesser and Zink 1994, Barraclough and Vogler 2000, Pigot *et al.* 2016, Hemingson *et al.* 2019). It was calculated as range overlap between species 1 (SP1) and species 2 (SP2) according to the formula: 100 × {area of overlap/[min(area SP1, area SP2)]}, using breeding ranges obtained from BirdLife International (BirdLife International and NatureServe 2014). This sympatry index shows what percentage of the smaller range is covered by the larger range.

Syntopy was defined as the physical proximity of individuals of different species allowing for interactions between these individuals. To calculate syntopy, we used data on local assemblages from the Australian Bird Count (Clarke *et al.* 1999, Harmáčková *et al.* 2019). To ensure high data quality, 470 localities (Supporting Information, Fig. S4) and 37 250 censuses (median of 56 censuses per locality) from years 1989–1995 were selected based on stringent criteria. The census duration had to be between 20 and 30 min, and the area of each locality had to range from 2 to 6 ha. Only localities with ≥20 censuses and with a minimum of 90% sample coverage were included. Strongly human-modified, urban, and rural habitats were excluded, as were species observations that were made >100 km away from the species range (Remeš and Harmáčková 2023).

We then calculated a syntopy index as the co-occurrence of SP1 and SP2 in local assemblages positioned inside the area of range overlap of the two species. We used a probabilistic model developed and extensively tested for reliability by Veech (2013, 2014; see also Arita 2016). Specifically, we calculated a standardized effect size (SES, also known as *Z*-score) as the deviation of the observed co-occurrence (i.e. the observed number of sites with both species) from the expected co-occurrence (i.e. the number of sites where both species would co-occur if they occurred independently of each other) divided by one standard deviation (Carmona and Pärtel 2021, Remeš and Harmáčková 2023). 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). A syntopy index of zero means that species occur independently; negative values denote negative co-occurrence (species segregation), and positive values denote positive co-occurrence (species association).

Statistical analyses

All statistical analyses were conducted using the language R (R Core Team 2024). To test whether node age, sympatry, and syntopy predicted divergence in song and colour traits, we fitted phylogenetic general linear mixed models using the function 'pglmm' from the 'PHYR' package in R (Li *et al.* 2020). We predicted trait divergence by node age, sympatry, and syntopy.

Predictors were centred and scaled by their standard deviation. We always included random effects of phylogeny (phylogenetic variance–covariance matrix) and the identity of a subclade from which a particular species pair originated. Units of analysis were thus individual species pairs. We used the following distances (expressing trait divergence between species in a species pair) as response variables: frequency (song level), frequency (note level), tempo, note variation, JND head, JND upper body, JND under-body, and JND flight feathers. We assessed the quality of each model by visualizing the distribution of its residuals. To enhance model quality, we log₁₀-transformed response variables when necessary (i.e. all colour distances).

RESULTS

Divergence with node age

Among song distance traits, frequency-related distances significantly increase with node age at both the song ($P < .01$) and the note ($P < .001$) levels, whereas no significant effects are observed for distances in song tempo and note variation ($P > .1$; Fig. 2; for detailed results, see Supporting Information, Table S3). Regarding distances in colour traits, no significant effect of node age is observed on colour distances ($P > .05$; Fig. 2; for detailed results, see Supporting Information, Table S3).

Divergence with sympatry and syntopy

No significant effect of either sympatry or syntopy is observed on song divergence ($P > .05$; Fig. 2; for detailed results, see Supporting Information, Table S3) or on colour divergence ($P > .05$; Fig. 2; for details, see Supporting Information, Table S3).

DISCUSSION

Although previous research has suggested that sympatry promotes signal divergence between closely related species (Höbel and Gerhardt 2003, Seddon 2005, Kirschel *et al.* 2009, Lemmon 2009, Martin *et al.* 2010, Hemingson *et al.* 2019, Simpson *et al.* 2021), our analyses of sympatric species pairs of Meliphagides contradict this expectation. Although we reveal significant effects of node age on the divergence of several song traits, no significant effects of sympatry or syntopy were apparent.

Divergence with node age

The increased divergence with node age of frequency-related song traits supports our neutral model, whereby trait divergence accumulates with node age only (Fig. 1). This finding agrees with the evolution of song frequency being comparatively rapid (Friis *et al.* 2021), potentially leading to the accumulation of evolutionary changes over time, as envisioned by our neutral model.

In contrast, colour traits of Meliphagides species pairs did not diverge with node age. Both natural selection and sexual selection influence the evolution of feather coloration, and their effects might vary across body patches (Matysioková *et al.* 2017, Simpson *et al.* 2020). On the one hand, feather patches in the upper body region are constrained by the colour of the environment inhabited by honeyeater species (Friedman and Remeš 2024). Thus, if species diverge in their ecological niche, we
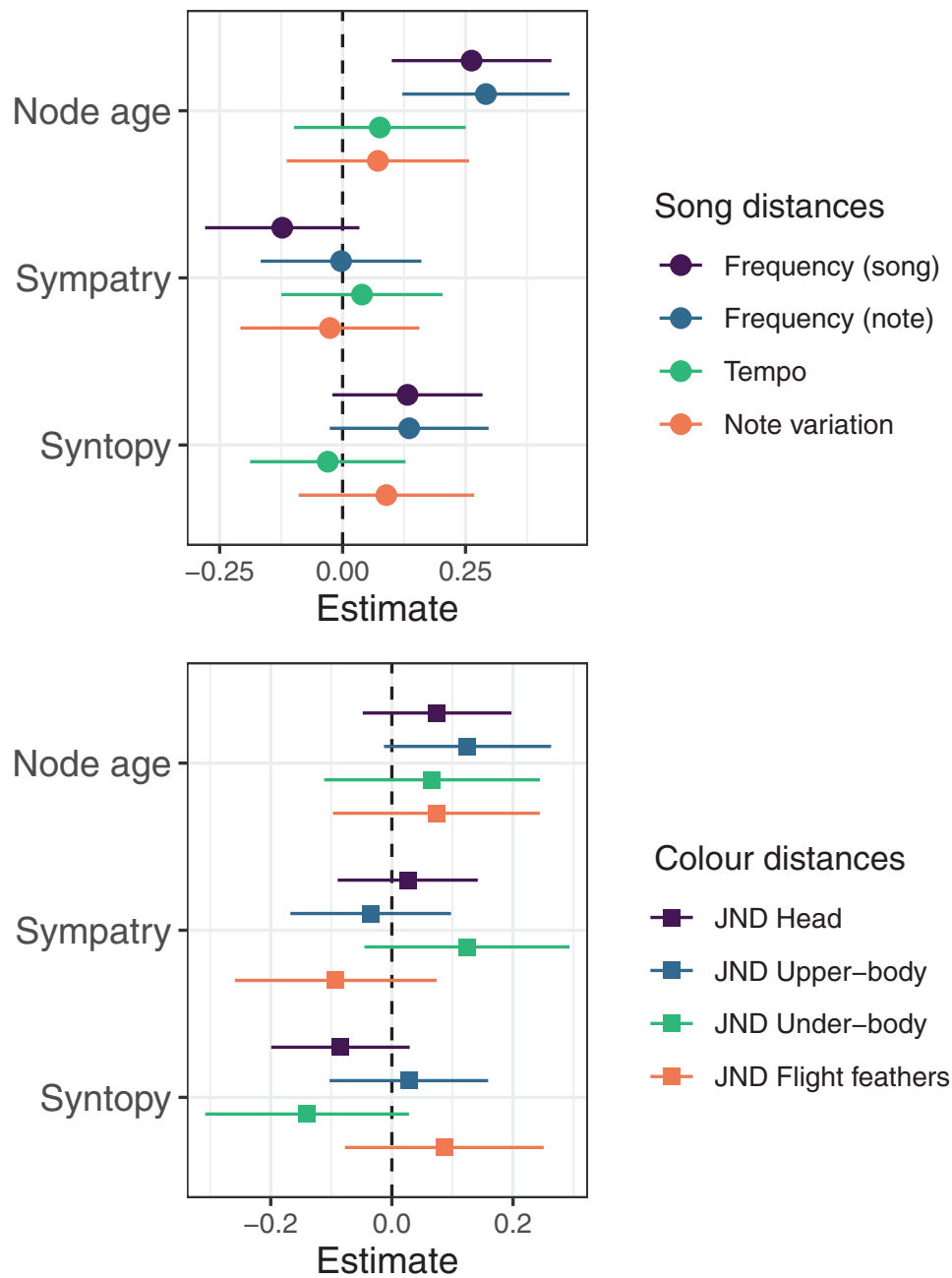
Figure 2. Forest plots presenting the results of phylogenetic generalized linear mixed models assessing the effect of node age, sympatry, and syntopy on the divergence in signalling traits. Error bars show 1.96SE (for detailed results, see Supporting Information, Table S2).

might expect corresponding changes in their dorsal plumage. However, if the ecological niche is highly conserved and changes slowly, any resulting colour divergence might be imperceptible within the time scale of our study. On the other hand, the coloration of feather patches in the anterior body region was hypothesized to be driven by sexual selection in Meliphagides songbirds (Friedman and Remeš 2015, 2024), which could have erased the time dependence of their divergence.

Overall, we detected some significant effects of node age on signalling trait divergence in song traits within sympatric species pairs of Meliphagides. Our findings thus align with previous research documenting similar trends in an allopatric context. For instance, Freeman et al. (2023) found a positive relationship

between sexual trait divergence and genetic distance within allopatric sister pairs of tropical birds and argued that time spent in allopatry is responsible for the divergence in sexual traits (Uy et al. 2009, Freeman et al. 2023), rather than reinforcement during secondary contact (Sætre et al. 1997, Höbel and Gerhardt 2003, Haavie et al. 2004, Dyer et al. 2014). However, another study reported divergent adaptation as a common driver of song trait evolution in allopatric pairs of New World passerines (Anderson and Weir 2022: table 1). Regardless of the underlying process, trait divergence appears to occur consistently over time across numerous taxa, such as birds, mammals, and frogs, as emphasized by Anderson and Weir (2022). For signalling traits specifically, the evidence has been limited and largely confined to

the allopatric context (Anderson and Weir 2022, Freeman *et al.* 2023). Our study contributes to enhancing the evidence base on signal divergence over time, suggesting that this might also extend to sympatric species pairs.

Divergence with sympatry and syntopy

Neither sympatry nor syntopy appears to drive song divergence in Meliphagides. This finding is in agreement with other studies reporting no increase of song divergence with sympatric overlap within wood warblers (Simpson *et al.* 2021), ovenbirds (Tobias *et al.* 2014), and larks (Laiolo 2012). Although those studies found that sympatric occurrence could instead lead to song convergence, we revealed no such convergence in Meliphagides. This could suggest an interplay of various factors constraining song evolution in this clade. On the one hand, convergence could result from song traits adapting to optimize signal transmission in shared habitats, as suggested by the acoustic adaptation hypothesis (Boncoraglio and Saino 2007, Ey and Fischer 2009, Tobias *et al.* 2010, Simpson *et al.* 2021), although evidence for this hypothesis is mixed (Boncoraglio and Saino 2007, Graham *et al.* 2017, Sebastián-González *et al.* 2018, Hardt and Benedict 2021). Alternatively, song traits related to aggressive interference could converge to reduce the cost of direct physical conflicts in the context of interspecific territoriality (Grether *et al.* 2009, 2017, Tobias and Seddon 2009, Tobias *et al.* 2014, Losin *et al.* 2016, Drury *et al.* 2020). On the other hand, studies of single species pairs found evidence for character displacement of song, for example in tinkerbirds (Kirschel *et al.* 2009) or flycatchers (Haavie *et al.* 2004). Thus, opposing forces causing song convergence (e.g. owing to acoustic adaptation or agonistic character displacement) and divergence (e.g. reproductive character displacement) might balance each other, with no net effect of sympatry and syntopy on song divergence. This balance could explain why sympatry and syntopy have no apparent influence on song evolution in Meliphagides. Likewise, a clade-wise comparative analysis of tanagers found no net effect of species interactions on song evolution (Drury *et al.* 2018).

Previous studies on the divergence of plumage colour in birds and coloration in fish found that sympatry often played a crucial role in driving colour divergence (Martin *et al.* 2010, 2015, Hemingson *et al.* 2019, Simpson *et al.* 2021). Some studies observed this phenomenon only at intermediate levels of sympatry (Martin *et al.* 2015) or in cases where ranges were symmetric between species pairs (Hemingson *et al.* 2019) or during the early stages of the speciation process (Tavera and Wainwright 2019). Sympatry has also been shown to induce colour convergence (Hemingson *et al.* 2019, Miller *et al.* 2019), sometimes in correlation with the asymmetry of ranges (Hemingson *et al.* 2019). The lack of observed effect of sympatry on plumage colour divergence in our study might suggest a need to investigate further the interplay of factors influencing sympatric interactions. It might also stem from excluding allopatric species pairs from the analyses, which might have limited the variation in colour divergence and consequently weakened our ability to detect any effects of the degree of sympatry. However, this exclusion was inevitable because our objective was to evaluate the effect of syntopy, and syntopy can be calculated only for species pairs with at least some sympatry evolved (see Materials and methods). The absence of any effect of syntopy on signal

divergence could suggest that syntopy interacts with other untested factors in influencing signal divergence or that it does not affect the specific signalling traits we examined. Our provisional conclusion here is that syntopy did not predict signal divergence in the Meliphagides clade.

CONCLUSION

Our study examines, for the first time, simultaneous effects of node age, range sympatry, and local syntopy on signal divergence. It provides evidence that the divergence of certain song traits can increase with node age, hence their evolution could be explained mainly by neutral trait drift (neutral model; Fig. 1). However, contrary to previous research (Höbel and Gerhardt 2003, Seddon 2005, Kirschel *et al.* 2009, Lemmon 2009, Martin *et al.* 2010, Hemingson *et al.* 2019, Simpson *et al.* 2021), we found no evidence that sympatry was driving colour and song evolution, possibly owing to the necessary exclusion of allopatric species pairs from our study. We also found no effect of syntopy on signal divergence. Aside from the song traits mentioned previously, the evolution of most signalling traits was not predicted by node age, sympatry, or syntopy (constraint model; Fig. 1). Our results seem to suggest that reinforcement in both sympatry and syntopy is less prevalent than previously thought in driving signal divergence. We suggest that further studies investigate this problem in other taxa.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

None declared.

DATA AVAILABILITY

Data and code are available from the Zenodo repository: https://doi.org/10.5281/zenodo.11077987 (Leroy *et al.* 2024).

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