

A late burst of colour evolution in a radiation of songbirds (Passeriformes: Parulidae) suggests secondary contact drives signal divergence

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Abstract

Evolutionary radiations provide important insights into species diversification, which is especially true of adaptive radiations. New World wood warblers (Parulidae) are a family of small, insectivorous, forest-dwelling passerine birds, often considered an exemplar of adaptive radiation due to their rapid diversification followed by a slowdown. However, they deviate from the expectations of an adaptive radiation scenario due to the lack of conspicuous morphological and ecological differentiation. We fitted several macroevolutionary models to trait data in 105 species of wood warblers. We tested whether morphological traits underwent an early burst of evolution (suggesting adaptation to new ecological niches in adaptive radiations) and whether song and colour underwent a diversity-dependent acceleration of trait evolutionary rate (consistent with reproductive interference driving signal evolution). Morphology and song evolved gradually under stabilizing selection, suggesting niche conservatism, with morphology possibly acting as a constraint on song evolution. In contrast, many feather colour traits underwent a diversity-dependent burst of evolution occurring late in the clade's history. We suggest that a two-step process has led to the remarkable diversification of wood warblers. First, their early diversification probably proceeded by allopatric speciation. Second, feather colour divergence likely occurred during secondary contact after range expansion. This diversification of signalling traits might have facilitated species coexistence, in combination with behavioural niche partitioning. Wood warblers seem to present characteristics of both adaptive and non-adaptive radiations.

Keywords: adaptive radiation, evolutionary radiation, macroevolutionary models, song evolution, trait evolution

Introduction

Evolutionary radiations, broadly defined as a significant increase in the diversity of a clade within a relatively short time span, have given rise to an important part of species diversity on Earth (Wiens, 2017). They represent spectacular phenomena of biological evolution, providing unique insights into evolutionary processes (Cerca et al., 2023; Naciri & Linder, 2020). The relative importance of biotic and abiotic factors in driving evolutionary radiations enables the delimitation of several types of radiations (Simões et al., 2016). Out of these, adaptive radiations have received the most attention (Glor, 2010; Martin & Richards, 2019; Simpson, 1953; Tobias et al., 2014). Here, an increase in diversification is coupled with adaptive divergence of traits (Vinciguerra & Burns, 2021), that enable the utilization of new ecological opportunities and facilitate long-term species coexistence (Glor, 2010; Schluter, 2000; Stroud & Losos, 2016). However, many clades have undergone rapid diversification without a concomitant increase of morphological and ecological divergence (e.g., Crouch & Ricklefs, 2019; Imfeld & Barker, 2022), a sign of non-adaptive radiations (Czekanski-Moir & Rundell, 2019; Rundell & Price, 2009).

Non-adaptive radiations have recently begun to receive increasing attention (Czekanski-Moir & Rundell, 2019;

Rundell & Price, 2009). Two types of non-adaptive radiations in particular can explain the diversity of many groups of organisms. First, diversification in geographic radiations is facilitated by higher opportunities for allopatric speciation due to the presence of plentiful geographic barriers (Simões et al., 2016). Indeed, geographic barriers played a significant role in several adaptive radiations, including Darwin's finches on the Galapagos islands (Abzhanov, 2010), anoles in the Neotropics (Poe et al., 2017), and threespine sticklebacks in North American lakes (Bell & Foster, 1995). Consequently, besides an undisputed role of morphological and ecological divergence in these radiations, geographic barriers might have acted additively to accelerate the diversification of these clades. Second, sexual selection is a driving force behind sexual radiations, where a significant divergence in signalling traits, for example, coloration or song, is observed (Martin & Richards, 2019). Species coexistence in sexual radiations can be facilitated by reproductive interference (Gómez-Llano et al., 2021), leading often to interspecific territoriality (Cowen et al., 2020; Losin et al., 2016).

Wood warblers (Parulidae) provide a unique opportunity to evaluate these different scenarios of evolutionary radiations. They are a family of 109–113 species of passerine birds (Barker et al., 2015; Fjeldså et al., 2020; Lovette et al., 2010)

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inhabiting exclusively the New World (del Hoyo et al., 2010). Wood warblers have often been presented as a typical example of an adaptive radiation (Price et al., 1998) unfolding over the past 6 million years (Fjelds  et al., 2020; Oliveros et al., 2019). One line of evidence suggesting that wood warblers could be classified as an adaptive radiation was that they underwent rapid diversification from a common ancestor (Barker et al., 2015; Oliveros et al., 2019), followed by a diversification slowdown (Figure 1A). The rationale is that these slowdowns have been suggested to indicate that available ecological niches became saturated (Lovette & Bermingham, 1999; Phillimore & Price, 2008; Rabosky & Lovette, 2008), although alternative hypotheses to explain diversification slowdowns have been suggested (Moen & Morlon, 2014). Moreover, wood warblers provide a classic example of foraging niche divergence, which has been hypothesized to facilitate species coexistence in local communities (MacArthur, 1958; Sherry & Kent, 2022) that may remarkably harbour up to 20 wood warbler species (Lovette & Hochachka, 2006).

On the other hand, several observations seem to be at odds with the scenario of an adaptive radiation. First, wood warblers are not exceptionally morphologically diverse, at least in comparison with similarly-sized-related families (Figure 1B; Fjelds  et al., 2020; Lovette & Bermingham, 1999;

Rosamond et al., 2020). Second, the breadth of habitats they occupy is quite narrow, with most species living in forests and woodlands (Figure 1C; del Hoyo et al., 2010; Fjelds  et al., 2020). Third, they display diverse plumage colours (Shutler & Weatherhead, 1990), which is especially true in northern temperate, migratory species living in high local co-occurrence (del Hoyo et al., 2010). Moreover, they often exhibit interspecific aggression and territoriality, especially in young species with similar plumage coloration and song (Losin et al., 2016). Thus, there is an alternative to adaptive radiation when explaining the diversification of this bird lineage. Wood warblers might have first undergone a geographic radiation (Kennedy et al., 2018), followed by a burst of sexual radiation (Martin & Richards, 2019; Streebman & Danley, 2003). The latter would include the evolution of interspecific territoriality and signal divergence (Losin et al., 2016), at least in areas with many young species living in high local co-occurrence (Lovette & Hochachka, 2006).

In sum, wood warblers have been recognized as a prime example of an adaptive radiation (Price et al., 1998; Rosamond et al., 2020) due to a pronounced diversification slowdown (Rabosky & Lovette, 2008) and adaptive divergence in foraging niche and behaviour (MacArthur, 1958; Sherry & Kent, 2022). However, quantitative tests rigorously

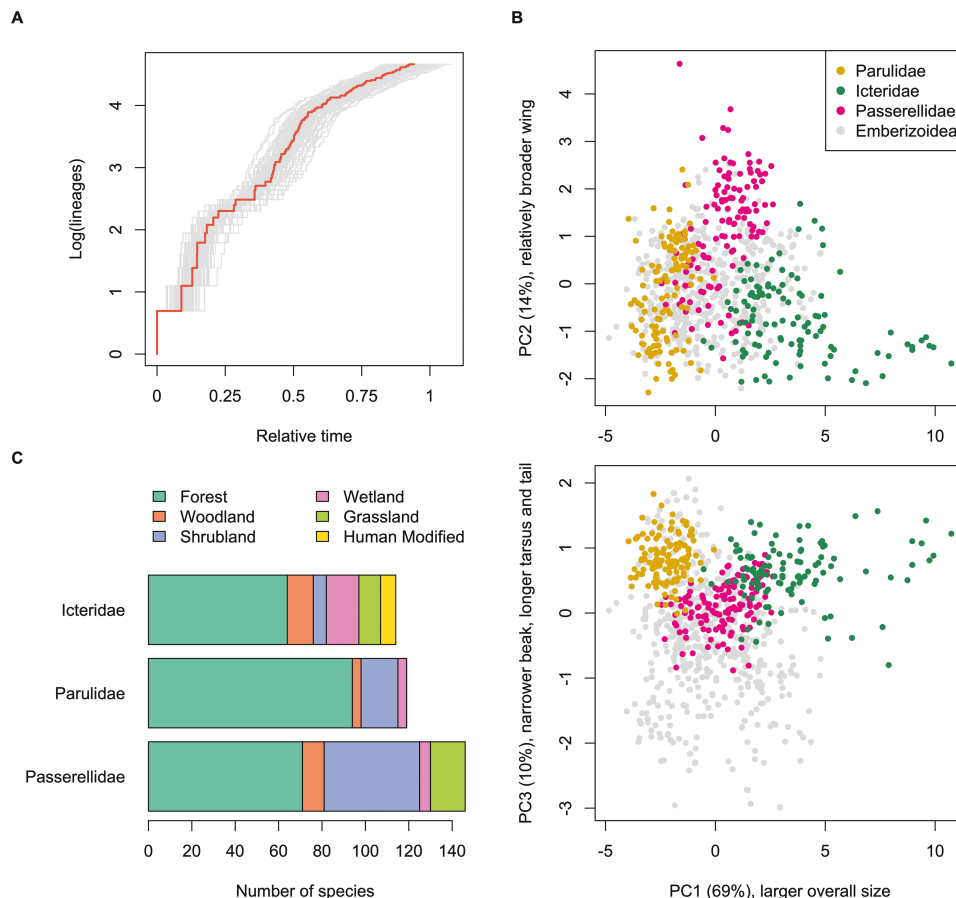


Figure 1. Diversification and trait diversity in New World wood warblers (Parulidae). (A) Lineage-through-time plots (LTT) obtained from a hundred randomly selected trees from the Barker et al. (2015) sample (grey lines) and the maximum clade credibility tree (red line). This LTT illustrates the diversification slowdown within the wood warbler clade (see *Methods* for a full explanation of LTT plots). The time axis runs from 0 (root) to 1 (tips) and depicts relative age of the clade. (B) The projection of wood warblers and two most closely related families with a similar number of species into a PCA-reduced morphological space of eight traits, calculated for 886 species of Emberizoidea songbirds. (C) The distribution of species among habitats in the same three families as for morphology. Data on morphology and habitats were taken from Tobias et al. (2022).

examining large-scale trait macroevolution are lacking in this important clade. Yet, one way to test different scenarios of an evolutionary radiation is to study the tempo and mode of trait divergence. Here, we examined: (a) the mode of trait evolution by fitting different macroevolutionary models to morphological, song and colour traits across the wood warbler phylogeny; (b) evolutionary patterns of phenotypic disparity through time (dtt); and (c) the rate of phenotypic evolution through time. More specifically, we tested whether morphological traits underwent an early burst (EB) of evolution, which would be indicative of adaptation to new ecological niches in an adaptive radiation. Furthermore, we tested for diversity-dependent acceleration of trait evolutionary rate in song and colour, which would be consistent with reproductive interference driving trait evolution once local species co-occurrence is common. Taken together, we test alternative evolutionary scenarios of trait diversification to better understand the drivers that underlie the remarkable wood warbler radiation.

Methods

Wood warblers and their phylogeny

Wood warblers (Parulidae) are a New World family of 109–113 species of passerine birds (depending on the authority, see [Barker et al., 2015](#); [Fjeldså et al., 2020](#); [Lovette et al., 2010](#)). They originated most probably in North America ([Barker et al., 2015](#)) some 6 million years ago ([Fjeldså et al., 2020](#); [Oliveros et al., 2019](#)). Species inhabiting North America migrate to the south for the extended period of cold winter with food shortages, most often to the Caribbean, Central America, and northern South America, while tropical and southern Hemisphere species are mostly permanent residents that do not migrate ([del Hoyo et al., 2010](#)). Wood warblers reach their highest species richness in North America, where up to 20 species might co-occur locally ([Lovette & Hochachka, 2006](#)). They might exhibit interspecific aggression and territoriality, which is especially true in recently split species with similar plumage coloration and song ([Losin et al., 2016](#)). Sympatric occurrence, in turn, leads to the evolutionary divergence in plumage coloration, but to the convergence of male song ([Simpson et al., 2021](#)).

Most of the wood warbler species are confined to forests and woodlands, although some species occur in shrublands and wetlands ([Figure 1C](#); [del Hoyo et al., 2010](#)). They are morphologically quite uniform ([Figure 1B](#)), exhibiting a warbler-like design similar to the Old World warblers ([Fjeldså et al., 2020](#)). Almost all species are insectivores ([Tobias et al., 2022](#)), but show differentiation in foraging behaviour and substrate selection, which is hypothesized to facilitate their local coexistence ([Kent & Sherry, 2020](#); [MacArthur, 1958](#); [Sherry & Kent, 2022](#)). In contrast to their conserved gross morphology, wood warblers are famous for widely varied plumage colours, ranging from browns and blacks to yellows and reds (see colour tables in [del Hoyo et al., 2010](#)). Many species display profound sexual dichromatism with males being more colourful than females, which is especially true in northern temperate migratory species ([Simpson et al., 2015](#)).

We used the wood warbler phylogeny ($n = 106$ species) published by [Barker et al. \(2015\)](#). These authors used two mitochondrial and four nuclear genes to generate a near-species-level phylogeny of the New World Emberizoidea

passerine clade that includes wood warblers. They made available a sample of 7,500 trees derived from the 95% posterior density sampling of Bayesian phylogenetic analysis of wood warblers, from which we randomly extracted a hundred trees to fit models of trait evolution (details below). Using the full sample of trees from [Barker et al. \(2015\)](#), we also constructed a maximum clade credibility tree (mcc tree) for additional analyses. To generate the mcc tree we used the software TreeAnnotator (v. 2.0.2; [Drummond & Rambaut, 2007](#)) with default options (node heights kept as “Common Ancestor heights”).

Lineage-through-time plots

We constructed lineage-through-time (LTT) plots using the hundred randomly sampled trees and the mcc tree, using the “litt” function from the “phytools” package ([Revell, 2012](#)). This is a way of visualizing the diversification pattern of a clade. A constant rate of diversification leads to a linear LTT plot. An acceleration of diversification is apparent from the slope of the LTT becoming steeper, whereas a slowdown is apparent from a gradually decreasing slope.

Morphological traits

We took morphological measurements on specimens from the bird collections of the Museum of Vertebrate Zoology (CA, USA), the Carnegie Museum of Natural History (PA, USA), the Natural History Museum of Los Angeles County (CA, USA), the American Museum of Natural History (NY, USA), the Field Museum of Natural History (IL, USA), the Louisiana Museum of Natural History (LA, USA), the Harvard Museum of Natural History (MA, USA), the Smithsonian National Museum of Natural History (DC, USA), and the Natural History Museum at Tring (UK). In total, we took measurements from 659 individuals of 105 species (morphological data were missing for *Myiothlypis leucophrys*), with an average of 6.3 individuals per species (range from 2 to 12). We measured on average 3.0 females (range 0–6) and 3.2 males (range 0–7). Five individuals in total were of unknown sex.

We measured six morphological traits commonly used in ecomorphological studies due to their link to habitat and resource use (e.g., [Crouch & Ricklefs, 2019](#); [Imfeld & Barker, 2022](#); [Tobias et al., 2022](#)): tarsus length, beak length, beak width, and beak depth taken with digital callipers to the nearest 0.1 mm. Tarsus length was measured as the distance between the tibia–tarsus notch and an estimated point at which the tarsus ends at the foot (often referred to as the first undivided scute). Beak length was measured from its tip to the base of the skull along the culmen, and beak width and depth were measured at the distal edge of the nostrils. We measured tail length with a paper ruler to the nearest 0.5 mm by inserting the ruler between tail feathers and undertail coverts and reading the length of the tail at its tip. We measured wing length using a ruler with a perpendicular stop fixed at zero to the nearest 0.5 mm. The ruler was slipped under the folded wing and the measurement was taken from the bend of the wing to the tip of the longest primary, while gently flattening the wing along the ruler. All morphological measurements were taken by V.R. Morphological measurements were averaged per species and \log_{10} -transformed.

Song traits

We obtained 488 unique song recordings from publicly available databases (Xeno-canto and Macaulay Library at the

Cornell Lab of Ornithology), with 1,891 songs in total and an average of 18.7 songs per species ($n = 101$ species). We transformed the recordings into spectrograms and measured song traits in the Avisoft-SASLab software. We measured the following song traits: lowest frequency, highest frequency, peak frequency (the frequency at which the maximum energy occurs in a song), peak time (the time at which peak frequency occurs), delta frequency (highest frequency minus lowest frequency), song duration, frequency slope (delta frequency divided by song duration), number of different notes, number of different note types, transitions (the number of switches between syllable types within a song), versatility (the number of transitions divided by the maximal potential number of transitions in a song of a given length), and diversity (the number of syllables per song divided by the number of syllable types per song; see [Supplementary Appendix S1](#)). Measurements were averaged per species (song data were missing for *Setophaga pharetra*, *Geothlypis beldingi*, *Leucopoeza semperi*, *Myioborus albifacies*, and *Myioborus cardonai*). When necessary, measurements were transformed so that their distribution was closer to a normal distribution (see [Supplementary Appendix S1](#)). It was not possible to much improve the distribution of the traits' versatility and diversity (see [Supplementary Appendix S2](#)).

Colour traits

We used spectrophotometry to obtain reflectance spectra of bird feathers from 320 to 700 nm (all measurements were taken with the Ocean Optics Jaz-PX spectrophotometer). The probe, covered with black, non-reflective sheathing, was held perpendicularly to the surface of the feather. We recalibrated the device using a white standard (WS-2) after each specimen. We used the same specimens that were used for morphological measurements. We measured 11 feather patches: crown, throat, breast, belly, face, flanks, back, rump, tail, wing coverts, and primaries. Each patch on each specimen was measured 3 times and we obtained an average from these three repeated measurements. Here we present analyses of male coloration only ($n = 293$ individuals, with 2.8 individuals per species and ranging from 1 to 5). For each of the 11 patches, we averaged the spectral measurements per species ($n = 104$ species; measurements were missing for *M. leucophrys* and *L. semperi*). The reflectance spectra were processed using the pavo package ([Maia et al., 2019](#)). Negative values were removed from spectra, and they were smoothed by a span of 0.2.

Colour is a complex, multidimensional trait that cannot be captured by a single measure. We wanted to reduce the dimensionality of spectral measurements to a few axes that could be used in comparative analyses. At the same time, we wanted to avoid visual modelling, as cone sensitivities for wood warblers are not available. To achieve our goal of reducing the complexity of colour, we followed standard methodological approaches ([Montgomerie, 2006](#)) and previous bird feather colour research ([Friedman & Remeš, 2015](#); [Matysioková et al., 2017a](#); [Price-Waldman et al., 2020](#)). Consequently, we used the following two approaches.

First, we extracted long-medium wavelength (LM) hue and medium-short wavelength (MS) hue. The calculation of these traits is based on chroma, hue and brightness and therefore these traits capture most of the variation in the colour spectra ([Endler, 1990](#)). More specifically, LM hue is the relative difference in reflectance and chroma between long- and medium-wavelength segments, while MS hue is the difference

between medium- and short-wavelength segments ([Endler, 1990](#)). We also calculated chroma and carotenoid chroma to capture the distinct signal contents emitted by melanins and carotenoids ([Badyaev & Hill, 2000](#)). Chroma was calculated as $(R_{\max} - R_{\min})/\text{mean brightness}$, where R_{\max} is the maximum reflectance, R_{\min} is the minimum reflectance, and mean brightness is the mean reflectance across the whole spectral range used. Carotenoid chroma was calculated as $(R_{700} - R_{450})/R_{700}$, where R_{700} is reflectance at 700 nm while R_{450} is reflectance at 450 nm ([Montgomerie, 2006](#); [Supplementary Appendix S3](#)). In addition, we calculated colour volume and colour span as traits to capture the complexity of the whole plumage. Colour volume is the total volume occupied by spectral points in the tetrahedral colour space computed with a 3D convex hull, while colour span is a mean Euclidean distance among all plumage patches in the tetrahedral colour space ([Stoddard & Prum, 2008](#)).

Second, we ran a principal component analysis (PCA) on the spectral data ([Burns et al., 2017](#); [Montgomerie, 2006](#)). Principal component (PC)1 represented brightness (81.3% of the variance explained), because it had positive loadings across the whole spectral range from 320 to 700 nm. PC2 represented hue (15.9%), because it had positive loadings between 400 and 500 nm (violet and blue colours) and negative loadings above 500 nm (yellow, orange, and red colours). PC3 represented the UV part of the light spectrum (2.1%), because it had positive loadings below 400 nm (see [Supplementary Appendix S4](#) for loadings). To characterize whole plumage complexity, we calculated PCA span. PCA span is an analogue of colour span, but it is derived from the PCA analysis ([Friedman & Remeš, 2015](#)).

The selection of patches for downstream analyses was done as follows. We first separated the 11 patches into two categories: Front (i.e., crown, throat, breast, belly, face, and flanks) and Back (i.e., back, rump, tail, wing coverts, and primaries) of the body. To reduce the number of patches analysed, we then selected patches for analysis by performing a phylogenetic principal component analysis, using the function “`phyl.pca`” from the “`phytools`” package (pPCA; [Revell, 2009, 2012](#)). From each cluster of patches, we selected only several representative patches. Among the Front patches, we selected belly and crown because of their constantly high loadings on pPC1 and pPC2, respectively. All Back patches had high loadings on pPC1, thus only back was selected as a representative for all Back colour traits. Colour volume was \log_{10} -transformed to approach the normal distribution, while other colour traits remained untransformed ([Supplementary Appendix S3](#)).

Mode and tempo of evolution

Mode of evolution

The mode of phenotypic evolution was investigated by fitting several models of evolution to the distribution of traits across the phylogeny. The logic of this approach is that different evolutionary processes leave distinctive marks on the distribution of traits across the phylogeny. However, as always, caution is needed when drawing conclusions about processes from fitting models to patterns in data, because different underlying processes can lead to the same patterns in data. The baseline model we use is the Brownian motion (BM) random walk, where the rate of evolution is constant, leading to a linear accumulation of trait variance with time ([Felsenstein, 1973](#); [Figure 2](#)). Under an Ornstein–Uhlenbeck (OU) model

(Hansen, 1997), stabilizing selection towards an optimum trait value is added on top of the BM model. This leads to the expectation that there is slightly more within-clade than among-clade disparity later on in the history of the clade (Figure 2). The reason is that stabilizing selection has had comparatively less time to work within recent clades than among older clades, which also leads to a slightly increasing overall rate of evolution with time (Figure 2).

The EB model represents an adaptive radiation scenario, where the exploitation of new ecological opportunity translates to a burst of trait evolution early in the history of the clade (EB, Blomberg et al., 2003; Harmon et al., 2010). This translates into a slowdown of the evolutionary rate with time and the expectation of much larger among-clade disparity compared to within-clade disparity (Figure 2). The diversity-dependent model considers trait evolutionary rates as a function of the number of species. Evolutionary rates either decline or increase linearly (DDLin) or exponentially (DDexp) with the accumulation of species diversity in the clade (Weir and Mursleen, 2013). In case of the evolutionary rate increasing exponentially with the number of species (DDexp with a positive coefficient), this translates into an increasing evolutionary rate with time and much higher within-clade disparity compared to among-clade disparity (Figure 2).

We compared the fit of the models presented above on 100 randomly selected phylogenetic trees from Barker et al. (2015). These analyses were performed using the

“fitContinuous” function from the “geiger” package (Harmon et al., 2008; Pennell et al., 2014) for the BM, OU, and EB models, and the “fit_t_comp” function from the “RPANDA” package (Morlon et al., 2016) for the DDLin and DDexp models, respectively. We evaluated model fit in two ways. First, for each phylogenetic tree, we calculated each model’s Akaike weight using its Akaike information criterion adjusted for small sample size (AICc). We then calculated the average Akaike weight for each model and for each trait. Second, in each of the 100 model fits of each trait, we identified the model with the lowest AICc value. If this value was lower by more than 2 points than the second lowest AICc value (i.e., $\Delta AICc > 2$), we considered this model as best supported (Chira et al., 2020). For each trait, we then tallied the number of times each alternative model was supported (out of 100 fits). For $\Delta AICc < 2$, none of the models was considered as best supported.

Besides model support, parameter interpretation is key for understanding evolutionary processes (Grabowski et al., 2023). For example, even if the OU model receives the most support, alpha values might be so small that the process does not differ substantially from the BM process (Cooper et al., 2016). One easy way to address this problem is by calculating the phylogenetic half-life (Hansen, 1997). However, a more intuitive metric is rho, a decrease in trait variance caused by the pull towards an optimum, when compared to trait variance expected under a pure BM random walk. It is calculated

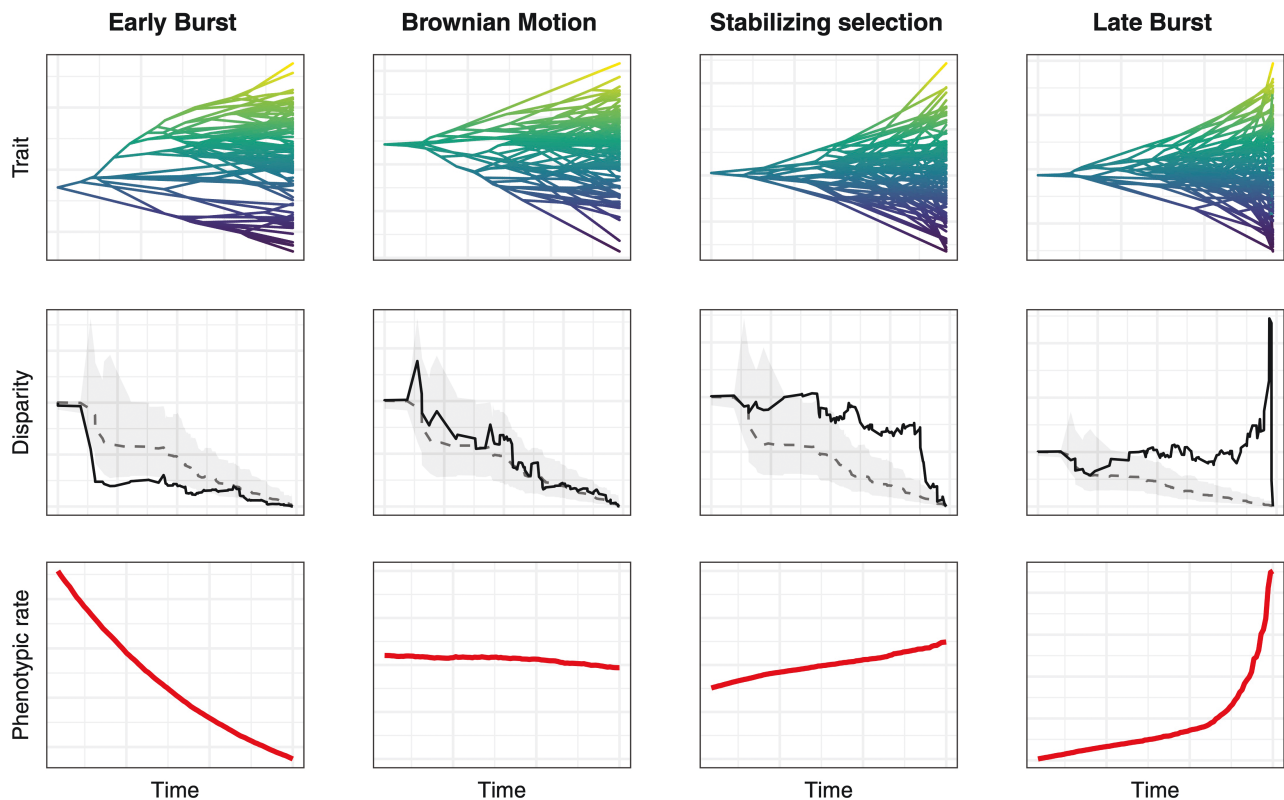


Figure 2. A conceptual figure showing phenograms, disparity-through-time plots, and phenotypic rate-through-time plots according to four different models of evolution: early burst (EB: a time-dependent model with an exponential decrease of evolutionary rate), Brownian motion (BM), stabilizing selection (OU), and late burst (DDexp: a diversity-dependent model with an exponential increase of evolutionary rate). Phenograms (top row) show trait values in lineages versus clade age (time). A false colour gradient from low (blue) to high trait values (yellow) was added for clarity. Disparity-through-time plots (middle row) show the ratio of among-clade to within-clade disparity in traits (full line) in comparison to the expectations of a BM model of trait evolution (mean expectation depicted by a dotted line, with the 95% confidence interval depicted by a grey envelope). Phenotypic rate-through-time plots show the rate of trait evolution versus clade age (time). The maximum clade credibility wood warbler tree was used for all simulations.

as $\rho = 1 - \frac{1 - \exp(-2\alpha T)}{2\alpha T}$, where α is the alpha parameter of the OU process and T is clade age (Cornuault, 2022).

Accounting for potential biases

Macroevolutionary models were fitted with trait values averaged for each species. However, it has been suggested that the OU model can be incorrectly favoured over simpler models when not accounting for intra-specific trait variation (Cooper et al., 2016; Grabowski et al., 2023). We thus re-fitted the models for traits showing overwhelming support for the OU model with species-averaged trait values (i.e., all morphological and song traits), but using within-species standard error as an estimate of within-species trait variation. We fitted the BM, OU, and EB models using the “fitContinuous” function. We showed that the support for the OU model remained the same, or was even stronger, compared to the main analyses using species-specific trait means without the standard error (Supplementary Appendix S5).

Different processes can give rise to similar distributions of traits across species. For example, the OU model could be falsely supported over the BM model, even when data were produced by a pure BM random walk (Cooper et al., 2016). Moreover, the DDexp model could be falsely supported over the OU model, even if traits underwent the OU process (Chira et al., 2020). We thus checked the effectiveness of recovering true evolutionary processes from the data using simulations. We ran the BM or OU process with different parameter values on the mcc wood warbler tree 100 times and fitted BM, OU, EB, and DDexp models. We did not fit the DDlin model, because it was never supported in empirical data (see Results) and its fitting would have doubled the simulation time. We checked the rate of false positives and the effectiveness of recovering true parameter estimates (Supplementary Appendix S6 and below).

Disparity through time

We visually depicted the pattern of disparity accumulating in morphological, song, and colour traits. We used relative subclade disparity-through-time plots (Harmon et al., 2003) fit with the “dtt” function from the “geiger” package. This method depicts patterns of phenotypic disparity in relation to what is expected under a BM model. The BM expectation was generated on the mcc phylogenetic tree using 1,000 simulations. A dtt curve below the 95% expectation (depicted by a grey envelope) shows a larger among-clade disparity compared to within-clade disparity, and it is consistent with an early accumulation of trait disparity. A dtt curve above the expectation shows a larger within-clade disparity compared to among-clade disparity, and it is consistent with a delayed accumulation of disparity. If disparity accumulates according to the BM model, the empirical line falls within the expectation envelope (Figure 2).

Rates of trait evolution through time

To compare rates of phenotypic evolution through time between morphological, song, and colour traits, we used the Bayesian Analysis of Macroevolutionary Mixtures (BAMM v.2.5.0, Rabosky et al., 2014a). For each trait, we used the “setBAMMprior” function from the “BAMMtools” package (Rabosky et al., 2014b) to generate priors. For each Markov chain Monte Carlo analysis, four Metropolis coupled Markov chains were run, with a temperature increment parameter of 0.01, and a swap period of 1,000. We used 10^7 simulation

steps. The outputs were analysed with the “BAMMtools” package. All analyses were run in the R environment (R Core Team, 2022).

Results

Mode of evolution

Out of the five macroevolutionary models compared, the OU was the best model for the diversification of morphological and song traits (Figure 3; parameter estimates in Supplementary Appendix S7). Only tarsus length and note rate were an exception with the BM and DDexp models providing a better fit for these traits, respectively. The estimates of alpha in the OU model were on average 5.2 in morphological traits (without tarsus length) and 6.9 in song traits (without note rate). The corresponding rho values were 0.69 and 0.76, respectively. This shows that the variance of these traits was reduced by ca. 70%–75% compared to traits that evolved according to a pure BM random walk.

Fourteen colour traits were best fitted by the OU model, nine traits were best fitted by the DDexp model, while no model was decisively supported in one trait (PC3 belly, see Figure 3). Alpha values were on average 9.5 for traits evolving according to the OU process, which translated into the rho value of 0.83. So, the variance of these traits was also substantially reduced compared to the BM process. Positive exponent values of the DDexp model (mean $r = 2.6$) in traits evolving according to this process indicated that the rates of trait evolution were exponentially increasing with the number of wood warbler species accumulating over time.

Accounting for potential biases

Our simulations showed that the OU model can be mistakenly identified as the best one even when traits evolve according to the BM process (Supplementary Appendix S6). However, in such cases, the alpha parameter estimated from the data had a low value (from 0.34 to 0.41), translating into low values of rho (from 0.28 to 0.32; see Supplementary Appendix S6). In empirical data, traits evolving according to the OU process had comparatively higher alpha values, which translated to a substantial reduction of trait variance as compared to the BM random walk (i.e., higher rho values; see above). Thus, we conclude that the OU model was most likely identified correctly in our data.

Furthermore, the DDexp model could be falsely identified as the best one, even if traits were simulated according to the OU process (Supplementary Appendix S6). However, even with very high alpha and rho values, this did not happen in more than 20%–25% of cases when using Akaike weights. When using the fraction of best-supported models, the rate of false positives was always below 5% (Supplementary Appendix S6). Thus, we conclude that the DDexp model was identified correctly in our empirical data, because in cases where it was preferred, it received an overwhelming support in both Akaike weights and in the fraction of best-supported models (Figure 3).

Disparity through time

Disparity through time (dtt) plots were run on the maximum clade credibility (mcc) phylogenetic tree. Morphological disparity overall appeared to conform to a BM model of evolution (Figure 4A). Song trait disparity also seemed to follow the BM model, except for note rate. The dtt curve of this trait strongly

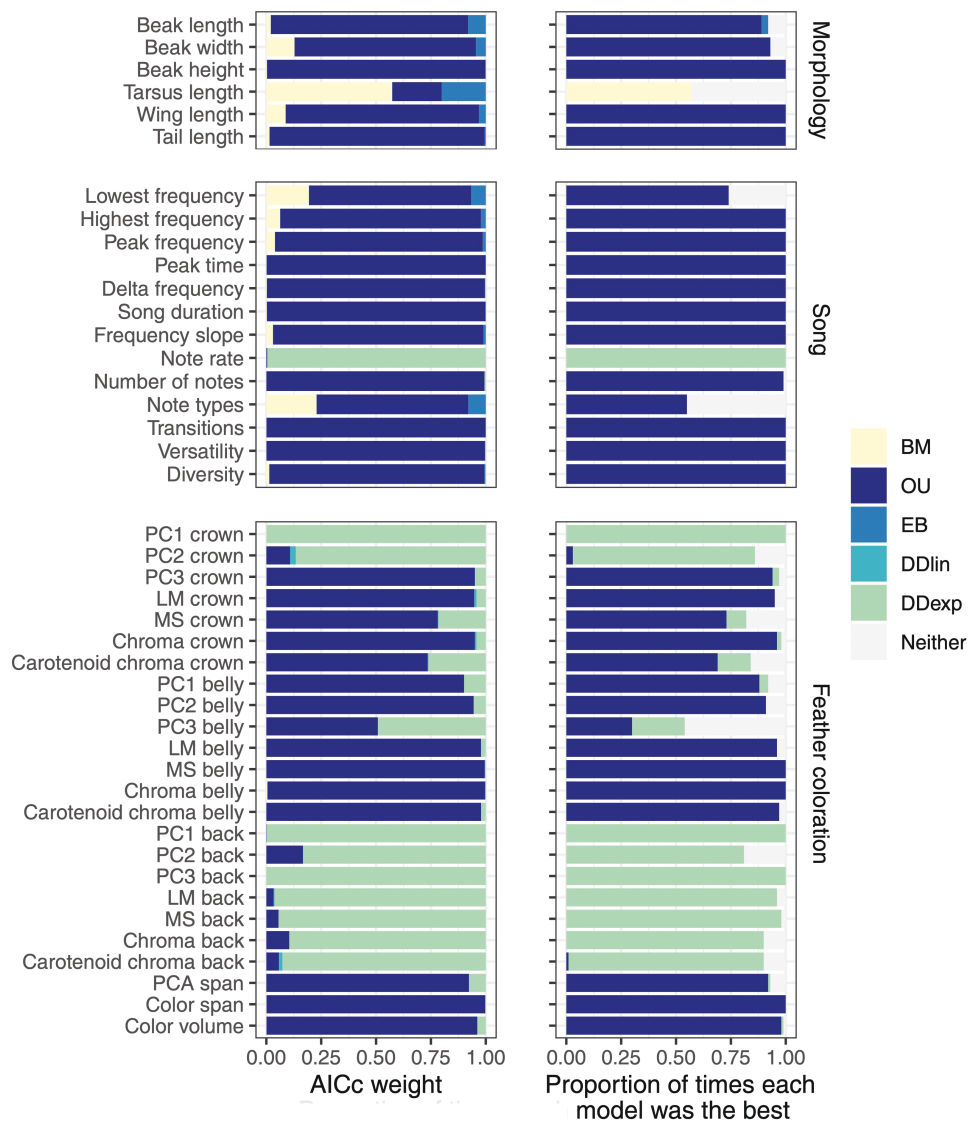


Figure 3. Relative support for different macroevolutionary models in wood warblers (Parulidae) fit to and summarized across 100 phylogenetic trees drawn at random from the Barker et al. (2015) sample. Displayed is the support for BM, OU, EB, DDlin, and DDexp models. Analysed traits included morphology, song, and feather colour. Support is displayed as Akaike weights (left panel) and the number of models (out of 100) that received a decisive support (right panel). Decisive support means delta AICc > 2 for the best model. Delta AICc < 2 was considered an indecisive case (category “Neither”).

increased above the 95% confidence interval of the null BM model simulations, starting slightly before the half age of the clade (the only green line in Figure 4B; compare with Figure 2). Accordingly, this was the only song trait for which the best-supported macroevolutionary model was DDexp (Figure 3).

There was a clear split in colour traits of the back, front, and whole body in their dtt patterns. All back traits and two front traits (PC1 crown and PC2 crown) followed a typical trajectory of traits evolving according to the DDexp model (denoted by green lines in Figure 4C and D). Until approximately half of the clade age, their disparity followed expectations of a BM model. After that time, their dtt curves started rising above the 95% confidence intervals, with their disparity substantially increasing over time (compared with “Late Burst” panels in Figure 2). Other traits mostly followed the expectations of the BM process of trait evolution. Surprisingly, whole body colour traits showed late spikes in disparity (Figure 4E) but their best-supported model was OU (Figure 3).

Rates of trait evolution through time

Rates of trait evolution were quantified using the Bayesian analysis of macroevolutionary mixtures (BAMM) method, run on the mcc phylogenetic tree. Rate through time plots did not reveal any striking temporal bursts of phenotypic evolution (Supplementary Appendix S8). For the morphological and song traits, evolutionary rates seemed to stay constant over time across the entire history of the wood warbler diversification. In several colour traits, the phenotypic rate of evolution increased over time, with an apparent acceleration towards the present (Supplementary Appendix S8), in agreement with the evidence provided by the previous two methods.

Discussion

Wood warblers have been presented as a classic example of adaptive radiation (Price et al., 1998; Rosamond et al., 2020). By testing alternative macroevolutionary scenarios for the diversification of phenotypic traits in the wood warbler

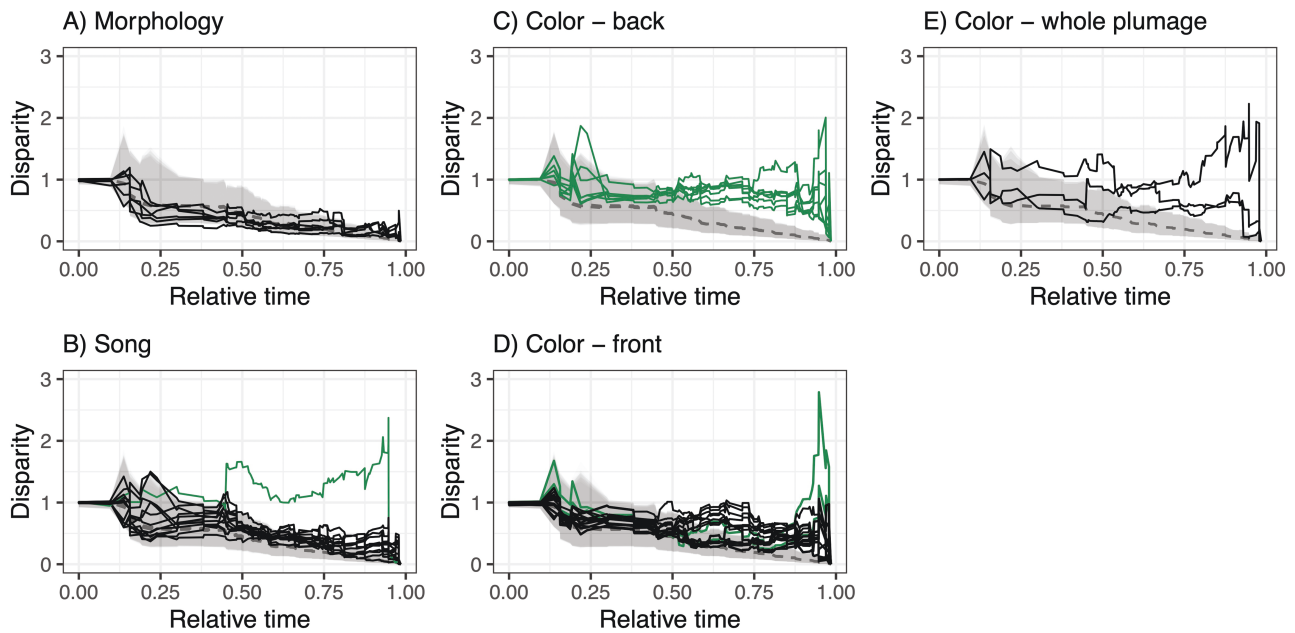


Figure 4. Disparity through time (dtt) plots for all (A) morphological, (B) song, and (C–E) colour traits. Colour traits were separated into three categories: (C) back and (D) front of the body, and (E) whole-plumage parameters (see *Methods* for individual colour metrics). Black lines denote traits which did not differ from expectations under the BM or OU models of trait evolution. The hatched line depicts mean trait disparity values, while the grey envelope depicts the 95% confidence limits of the BM expectation. Traits for which the DDexp model received strong support are coloured in green.

radiation, we unravelled diverse patterns of trait evolution, potentially in conflict with a strict definition of an adaptive radiation. While almost all morphological and song traits evolved under stabilizing selection, many colour traits underwent a diversity-dependent late burst of evolution. Below we outline a potential scenario of wood warbler trait diversification using the framework suggested by [Streelman and Danley \(2003\)](#) for vertebrate evolutionary radiations, whereby the divergence in habitats and trophic morphology is followed by divergence in communication and signalling traits.

Divergence in morphology

Wood warblers are morphologically relatively uniform ([del Hoyo et al., 2010](#); [Lovette & Bermingham, 1999](#); [Rosamond et al., 2020](#)). For example, although a few species evolved ecological and morphological convergence towards thrushes, nuthatches, and flycatchers, most wood warblers have retained a generalized design of small, arboreal insectivores ([Morse, 1989](#)). This morphological uniformity is also in line with trait evolution constrained by a stabilizing attraction towards an optimum value (OU model), as recovered here. Similarly, previous analysis did not find any effect of interspecific competition on beak size and shape evolution in this family ([Chira et al., 2020](#)). These findings are certainly at odds with the predictions of adaptive radiation, where EBs of morphological evolution, usually associated with adaptation to new ecological opportunities, are a crucial aspect of clade diversification.

One explanation could be that we did not have enough statistical power to detect EBs of morphological evolution ([Harmon et al., 2010](#)). However, we do not find this explanation very likely, because there was negligible support for the EB model (with possible exception of tarsus length; see [Figure 3](#)) and rate through time plots did not reveal any temporal bursts of morphological evolution ([Supplementary Appendix S8](#)). Another explanation could be that wood

warblers speciated in ecologically homogeneous environments ([Freeman et al., 2023](#)) and reproductive isolation evolved in allopatry alongside niche conservatism, as is typically the case in non-adaptive radiations ([Czekanski-Moir & Rundell, 2019](#); [Rundell & Price, 2009](#)). For example, [Reaney et al. \(2018\)](#) suggested stabilizing selection as the mechanism driving niche conservatism within a non-adaptive lizard radiation (*Phymaturus*). Indeed, wood warblers showed evidence of ecological conservatism when selecting breeding habitats ([del Hoyo et al., 2010](#); [Lovette & Hochachka, 2006](#)), whereby 83% of species have forests and woodlands as their primary breeding habitats ([Figure 1C](#); [Tobias et al., 2022](#)).

On the other hand, breeding habitat conservatism did not prevent wood warblers from local coexistence, and local co-occurrence of sympatric species increased with time ([Lovette & Hochachka, 2006](#)). Subtle differences in morphology, diet, and foraging behaviour, which can facilitate species coexistence ([Remeš & Harmáčková, 2023](#)), might drive this pattern ([Kent & Sherry, 2020](#); [MacArthur, 1958](#); [Rosamond et al., 2020](#)). Thus, there is a possibility that we did not study the macroevolutionary divergence in key phenotypic traits associated with adaptation for different ecological niches. What remains to be determined is whether local species coexistence arose due to trait divergence resulting from resource competition after secondary contact had been established, or from species-sorting that occurred during secondary contact. Trait divergence induced by resource competition after secondary contact can play a significant role in the evolution of diversity in adaptive as well as non-adaptive radiations ([Anderson & Weir, 2021](#); [Grant & Grant, 2006](#); [Lambert et al., 2019](#)).

In general, morphological evolution in wood warblers seemed to be in contradiction with a scenario of adaptive radiation. Our finding of a decoupled morphological divergence and lineage diversification agrees with previous studies of squamates ([Burbrink et al., 2012](#)), oscines ([Imfeld &](#)

Barker, 2022), terrestrial birds (Crouch & Ricklefs, 2019), and horses (Cantalapiedra et al., 2017). Nevertheless, evolutionary patterns and processes depend on the phylogenetic scale (Graham et al., 2018), and so adaptive trait divergence could have occurred at a broader phylogenetic scale. Presumed sister clades of wood warblers, namely, New World blackbirds (Icteridae) and New World sparrows (Passerellidae; Barker et al., 2015), present more variation in morphology (e.g., beak size, body size) and habitats than wood warblers do (Figure 1B and C; Fjelds  et al., 2020). Moreover, tanagers, another group falling within the Emberizoidea radiation (Barker et al., 2015) showed an EB pattern of beak shape evolution, consistent with adaptive radiation and the filling of morpho-space (Vinciguerra & Burns, 2021). So, it is plausible that other New World oscine passerines had pre-empted diverse ecological niches and parts of morpho-space before the diversification of wood warblers took place.

Divergence in communication

Song

Song traits seem to have primarily evolved under stabilizing selection (OU model), similar to morphological traits. Accordingly, diversification of beak morphology and body size have been found to drive patterns of vocal signal evolution in Darwin's finches (Podos, 2001) and Australasian honeyeaters (Meliphagidae; Friedman et al., 2019). Moreover, phylogenetically conserved morphological traits rather than ecological divergence are thought to have driven the evolution of song in vireos (Vireonidae; Mej as et al., 2020). Additionally, song evolution is directly constrained by physical limits, such as the size of the syrinx, bounded by body size, which impacts the frequency of sounds produced (Martin et al., 2011). Consequently, the finding of a similar mode of evolution in morphological and song traits of wood warblers is consistent with a correlated evolution of morphology and song within this clade.

Given an increasing number of wood warbler species and their expanding range and sympatry over time, one could expect that secondary contact would result in a late burst of song divergence, potentially enhancing species recognition. This was true only in note rate. As song rate might be linked to territorial behaviour (Collins, 2004), one explanation for the late burst pattern of note rate could be that aggressive interactions became more frequent with time. On the contrary, a recent study showed that songs converged among more sympatric wood warbler species, although this was true only in two out of six song traits, namely, song bandwidth and syllable rate (Simpson et al., 2021). Simpson et al. (2021) hypothesized that songs of coexisting species converged as an adaptation to enhance signal transmission in shared habitats (Ey & Fischer, 2009). Therefore, patterns of song evolution in wood warblers most likely resulted from a trade-off between sexual selection (Catchpole, 2000; Price & Lanyon, 2002), ecological constraints (Boncoraglio & Saino, 2007; Weir et al., 2012), and morphological limitations. While sexual selection concerns the strategic aspect of signal design, ecological and morphological constraints impose limitations on its tactical aspect, or signal efficacy (Guilford & Dawkins, 1991). With limitations on song evolution in wood warblers in place, it is possible that other signalling traits could have undergone more divergent evolution (Badyaev et al., 2002; Shutler, 2011; Shutler & Weatherhead, 1990).

Feather coloration

In contrast to morphological and song traits, many feather coloration traits showed a diversity-dependent burst of trait evolution occurring late in the history of the clade. Evolutionary rates of colour traits probably accelerated following the full build-up of wood warbler species richness and subsequent secondary contacts between species, with reproductive interactions promoting colour divergence and reinforcing species recognition (G mez-Llano et al., 2021). Indeed, sympatry can induce divergence of signalling traits (Ord & Martins, 2006). In line with this idea, Simpson et al. (2021) showed that plumage coloration diverged among more sympatric wood warbler species. As wood warblers underwent little ecological divergence, local species coexistence could be stabilized via plumage divergence (Losin et al., 2016) acting as a species recognition signal and a prezygotic reproductive barrier (G mez-Llano et al., 2021). Accordingly, male birds usually respond more strongly to homotypic over heterotypic signals and demonstrate enhanced recognition of conspecific males in sympatry over allopatry (Uy et al., 2018). On the other hand, hybridization occurs frequently in wood warblers (McCarthy, 2006; Ralston et al., 2015; Toews et al., 2018), indicating that the premating barrier is not fully effective in all species (Toews et al., 2021). This suggests that wood warbler species can maintain phenotypic divergence in plumage colour despite significant genetic compatibility (Toews et al., 2016).

However, not all colour traits showed a diversity-dependent burst of evolution. Interestingly, diversity-dependent bursts were almost completely confined to the back of the body, while almost all traits on the front (except the crown) conformed to the stabilizing, OU model of evolution. Different rates of evolution among feather patches have been identified previously in fairywrens (Friedman & Reme , 2015), Old World orioles (Matysiokov  et al., 2017a), and honeyeaters (Friedman & Reme , 2024). Indeed, arguments were made that the strength and direction of natural and sexual selection might differ across feather patches (Matysiokov  et al., 2017b; Simpson et al., 2020). Females may cue on specific colour traits when selecting males, and the same may be true for male aggression. Then, the accelerated evolution of a key subset of feather patches might be enough for reproductive isolation and interspecific territoriality to evolve. However, it is unclear why the key patches should be located on the back side of the body in wood warblers, especially given previous research suggested that key patches for communication are located at the front end of passerine birds (Friedman & Reme , 2015, 2024).

Conclusions

Our study provides a comprehensive insight on trait macroevolution across the wood warbler (Parulidae) radiation. Rapid lineage diversification of wood warblers (Rabosky & Lovette, 2008) most likely occurred allopatrically (Bermingham et al., 1992; Lovette & Bermingham, 1999; Morse, 1989), resulting in weak morphological and ecological divergence (Freeman et al., 2023). This is consistent with the expectations of non-adaptive radiation (Czekanski-Moir & Rundell, 2019; Rundell & Price, 2009). After a period in allopatry, wood warbler species either remained in allopatry or became sympatric due to a spatial movement of their ranges in response to the dynamics of glacial cycles (Bermingham et al., 1992; Lovette, 2005; Morse, 1989). Species coexistence was likely facilitated

by behavioural niche partitioning (MacArthur, 1958; Remeš & Harmáčková, 2023) and signal divergence (so-called “sexual radiation” *sensu* Martin & Richards, 2019). Thus, the evolutionary history of wood warblers bears marks of both adaptive and non-adaptive radiations.

Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

Data are available from the Zenodo repository: <https://doi.org/10.5281/zenodo.10654392>

Author contributions

Helene Leroy (Conceptualization [equal], Data curation [equal], Formal analysis [lead], Investigation [equal], Methodology [lead], Writing—original draft [equal], Writing—review & editing [equal]), Rauri Bowie (Data curation [equal], Writing—original draft [supporting], Writing—review & editing [supporting]), Lucia Turcokova (Data curation [equal], Writing—original draft [supporting], Writing—review & editing [supporting]), Beata Matysiokova (Data curation [equal], Writing—original draft [supporting], Writing—review & editing [supporting]), and Vladimir Remes (Conceptualization [equal], Data curation [equal], Funding acquisition [lead], Investigation [equal], Methodology [supporting], Supervision [lead], Writing—original draft [equal], Writing—review & editing [equal])

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Conflicts of interest

All authors declare that they have no conflict of interest.

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