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## The causes and ecological context of rapid morphological evolution in birds

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#### Abstract

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Episodic pulses in morphological diversification are a prominent feature of evolutionary history, driven by factors that remain widely disputed. Resolving this question has proved challenging because comprehensive species-level data are generally unavailable at sufficient scale. Combining global phylogenetic and morphological data for birds, we show that pulses of diversification in lineages and traits tend to occur independently and in different contexts. Speciation pulses are preceded by greater differentiation in overall morphology and habitat niche, then followed by increased rates of beak evolution. Contrary to standard hypotheses, pulses of morphological diversification tend to be associated with habitat niche stability rather than adaptation to different diets and habitat types. These patterns suggest that the timing of diversification varies across traits according to their ecological function, and that pulses of morphological evolution may occur when successful lineages subdivide niche space within particular habitat types. Our results highlight the growing potential of functional trait data sets to refine macroevolutionary models.

#### **KEYWORDS**

adaptation, birds, diversification, habitat, macroevolution, morphology, phylogeny

### INTRODUCTION

A longstanding goal of evolutionary biology is to explain the discrepancy in diversity between lineages (Alfaro et al., 2009; Rabosky, 2009; Slowinski & Guyer, 1993; Tank et al., 2015). One of the main hypotheses proposed to explain these asymmetries involves pulses of diversification restricted to particular lineages (Barker et al., 2013). These pulses can involve diversification in either lineages or ecomorphological traits, with rapid and simultaneous increases in both these factors often viewed as the hallmark of adaptive radiations (Gavrilets & Losos, 2009; Glor, 2010; Schluter, 2000; Simpson, 1953). Previous research has identified multiple processes that can stimulate bursts of phenotypic evolution, including transitions between ecological niches (Sheratt et al., 2017), ecological opportunity (Losos, 2010; Stroud & Losos, 2016) and competition (Rosenzweig, 1978; Winkelmann

et al., 2014). However, the drivers of diversification, and the extent to which rates of ecomorphological evolution are correlated with speciation rates, remains disputed (Adams et al., 2009; Cooney & Thomas, 2021; Crouch & Ricklefs, 2019; Folk et al., 2019; Rabosky et al., 2013).

When pulses of lineage and ecomorphological diversification occur independently this can result in two widely different outcomes. On the one hand, lineages may diversify rapidly without notable ecological differentiation, producing so-called 'non-adaptive radiations' wherein lineage diversification outpaces morphological diversification (Gittenberger, 1991; Rundell & Price, 2009). Alternatively, phenotypic evolution may proceed rapidly without elevated lineage diversification, a pattern sometimes dubbed 'adaptive non-radiation' (Moen et al., 2021). Few studies have attempted to quantify the predominance or likely context of these outcomes over deeper timescales (Burns & Sidlauskas, 2018).

Consequently, little is known about the drivers of rapid phenotypic diversification in the absence of lineage diversification, and vice versa (Elmer et al., 2014; Losos & Ricklefs, 2009; Stroud & Losos, 2016; Yoder et al., 2010). Pulses of morphological differentiation are generally thought to reflect ecological adaptation to widely divergent niches, such as the evolution of beak morphology in Darwin's finches to a wide range of diets, including nectar, seeds and invertebrates (Grant, 1986). However, similar bursts of morphological differentiation may occur if lineages diversify within a single ecological niche, for example if a novel evolutionary innovation or adaptation leads to one lineage 'cornering the market' then specialising further so that diversification explores the limits of available niche space (Gillespie et al., 2020; Schluter et al., 2000).

While the inclusion of extinct species can undoubtedly provide important insights into the evolution of anatomical features (Clarke & Middleton, 2008; Goswami et al., 2014; Parins-Fukuchi, 2020), the sampling of their ecological traits is generally too sparse for macroevolutionary studies reliant on estimates of species differences. In particular, key features such as bird beaks and flight adaptations are poorly preserved in the fossil record, which is also rarely accompanied by accurate information on species ecology. Assessing rates of morphological and lineage diversification in the context of ecology is therefore best achieved by focusing on the richer sampling of extant species. Nonetheless, generating comprehensive species-level trait and phylogenetic data at macroevolutionary scales for extant species is so time-intensive that such resources are lacking for most groups and have only recently been completed for birds (Tobias et al., 2020).

In this study, we make use of ecological and morphological trait data for >99% of bird species (Tobias et al., 2014, 2022) in combination with a global phylogeny (Jetz et al., 2012). We use these resources to perform phylogenetic analyses estimating rate shift locations for speciation and phenotypic evolution. Focusing on a sample of ten morphological traits describing the overall body plan of each species and reflecting variation in trophic niches (Pigot et al., 2020), we assess (1) whether macroevolutionary shifts in speciation rate coincide with bursts of phenotypic evolution (i.e. adaptive radiations), (2) how rates of morphological evolution vary before and after speciation rate-shift nodes and (3) whether morphological diversification is associated with high rates of ecological evolution (i.e. habitat and diet). We perform these analyses on a diverse set of avian taxa such that our results describe patterns of diversification over the entire Cenozoic.

Previous models have investigated the underlying relationship between rates of lineage diversification and phenotypic evolution in birds (Crouch & Ricklefs, 2019). Here, we apply new approaches to a much larger sample of species and traits to address different questions about episodic bursts of diversification and their link with ecology, while also accounting for temporal variation in rates. The continued absence of extinct species from the sample no doubt impairs our ability to accurately pinpoint shifts in evolutionary rates, meaning that caution is required when interpreting the results. Nonetheless, by focusing on rates of phenotypic evolution upstream and downstream of speciation pulses, as well as the link between phenotypic evolution and ecological states, our analyses offer new insight into the dynamics and drivers of rapid morphological evolution.

### MATERIALS AND METHODS

#### Phylogenetic data and speciation rate

We extracted phylogenetic trees from Jetz et al. (2012), re-running the placement of species lacking molecular data using TACT (Taxonomic Addition for Complete Trees, Chang et al., 2020; see Supplementary Material). We identified putative locations of speciation rate shifts in two ways. First, we analysed the resulting phylogenetic data of 9993 species using Bayesian analysis of macroevolutionary mixtures (BAMM: Rabosky, 2013, 2014), identifying nodes that most likely represent shifts in speciation rate using the getBestShiftConfiguration function in BAMMtools (Rabosky et al., 2014). This is considered best practices for evaluating a single set of rate shifts, although other configurations may have similar likelihoods, given the large number of rate shift configurations produce by a BAMM analysis (14,242 in this study). Second, we identified shifts using MEDUSA (Alfaro et al., 2009), implemented in the R package geiger (Harmon et al., 2008; Pennell et al., 2014).

#### Morphology, ecology and rates of trait evolution

Morphological data for this study are sampled from Tobias et al. (2022). These data consist of 10 external measurements commonly used to quantify ecological differences between bird species (Miles et al., 1987; Pigot et al., 2020; Sheard et al., 2020). The measurements include four trophic traits (beak width and depth, and two estimates of beak length), and six traits associated with dispersal and locomotion (leg length, tail length and four measures of wing shape, including hand-wing index). Although direct or inferred morphological data are available for all species (n = 9963) included in the global bird phylogeny, the analysis including all possible species failed to reach stable convergence. To resolve this, we extracted data on 7524 species from the 11 monophyletic 'landbird' orders (Telluraves), which have diversified into a wide range of ecological niches. For each of the species, we extracted habitat data from Tobias et al. (2014) and diet data from Pigot et al. (2020).

We estimated rates of evolution for morphological and habitat data using a variable rates model in *BayesTraits* (Pagel et al., 2004; additional information in Supplementary Material). This is a model of correlated evolution, with all traits analysed simultaneously under a Brownian Motion model of evolution, including parameters for the rate of evolution ( $\sigma$ ) and phylogenetic mean ( $\alpha$ ) equal to the number of traits. The variable rates model allows automatic detection of shifts in rates of evolution, estimating their location on single branches or for entire clades. We also ran a separate analysis for beak traits (n = 4), because the beak is tightly coupled with the trophic niche, providing clear examples of rapid morphological evolution (Cooney et al., 2017; Lerner et al., 2011; Reddy et al., 2012; Tokita et al., 2016).

We quantified the most likely locations of shifts in the rates of morphological evolution using the standalone version of VarRatesPP (provided by the authors of BayesTraits, available for download from http://www. evolution.reading.ac.uk/VarRatesWebPP/) and custom R scripts. Specifically, we quantified the probability of a node being the location of a shift in the rate of evolution as the proportion of samples in which it was identified as a rate shift location. We repeated this procedure for the analysis of all morphological traits and beak traits separately, and compared the results against nodes identified as speciation rate shifts.

# Testing for elevated rates of morphological evolution across shifts in speciation rate

To test whether evolutionary rates were elevated across speciation rate shifts, we compared the rates of morphological and habitat evolution on branches either side of putative speciation-rate shift nodes. Specifically, we defined the branch immediately preceding as the 'parent' branch and the two branches below as the 'daughters' (Figure 1). We compared their evolutionary rates to a 'base' rate of trait evolution (i.e. all morphology, beak and habitat), which we defined in two ways. First, we defined the base rate as all branches within the phylogeny that were not a parent or daughter (Figure 1a). Second, we restricted branches in the base rate to contemporary branches, that is those present at the same geological time as the rate shift node (Figure 1b). We included this second definition as rates may show a temporal trend, which we determined by generating rate-through-time plots from the posterior distributions using a custom R function. Restricting comparisons to same-age nodes helps to ensure that our results are not influenced by comparing between nodes of widely different ages, which likely differ in detectability (Louca & Pennell, 2020; Rabosky, 2010; Rabosky & Lovette, 2008a; Stadler, 2012).

For both definitions of the base rate, we re-ran analyses with different numbers of branches in the daughter category: two (the two branches derived from the rate shift node, see Figure 1), up to six (including the daughter branches from the nodes descendant from the rate shift node), and up to 14 (including the 'grand-daughter' branches from the second set of nodes descendent from the rate-shift node). The analyses including more descendant nodes might not have the full number of branches (i.e. 6 and 14 respectively) depending on the depth of the target node in the phylogeny.

We conducted two sets of sensitivity analyses to assess whether our results were influenced either by inaccurate placement of species by taxonomy in the Jetz et al. (2012) tree or potential biases introduced by using BAMM. We also ran our models on 'classic adaptive radiations'—Darwin's finches, Hawaiian honeycreepers and Madagascan vangas—to evaluate its performance. Finally, we ran all the main analyses with and without log-transforming the linear trait measurements to



**FIGURE 1** Location of parent and daughter branches in relation to a hypothetical node identified as the location of a shift in speciation rate. In both examples shown, only the immediate branches descendant from the rate shift node are included in the daughter partition (sometimes extended to include further descendant branches towards the present) Panel (a) shows the base rate defined using all branches not treated as either a parent or daughter branch, whereas in panel (b) the base rate is defined using the rate of evolution on contemporary branches (i.e. all branches present at the same time as the rate shift node) Under this latter definition, some branches are not treated as parent, daughter, or 'base' and are therefore excluded from analysis

explore how different treatments of the data affected the results. Methods and additional analyses are described in Supplementary Material.

# Testing whether shifts in phenotypic evolution are associated with ecological lability

We determined whether shifts in the rate of morphological evolution are associated with ecological lability by quantifying the mean rate of ecological evolution (habitat and diet) in clades. We assessed whether these rates deviated from a null expectation by comparing the results against all nodes of approximately the same age (±2 Myr). Taking the difference between the null and the empirical values for each node therefore reflects ecological stability (positive values) and ecological lability (negative values) respectively. All analyses and manipulations were implemented in R (R Core Team, 2018), with the full analytical workflow provided in the supplementary material. All custom R functions used in this study are provided on Dryad along with data generated here.

#### RESULTS

#### Lineage diversification

We detected patterns of speciation rates concordant with previous large-scale analyses. For example we found that the genus Zosterops has elevated speciation rates, in line with previous results (Cai et al., 2020; Moyle et al., 2009). In total, we identified 34 nodes distributed throughout the phylogeny as likely shifts in speciation rate by BAMM (Figure 2). The ages of these nodes were rightskewed, ranging between 1.5 Ma and 78 Ma, with a mean of 22.6 Ma and median of 14.6 Ma. Most of our BAMM analyses exclude the root node which has no parent branch to compare with daughter branches (see below). When we used MEDUSA as an alternative approach, the nodes identified were completely distinct from those identified by BAMM (i.e. no nodes were identified as speciation rate-shifts in both analyses), consistent with previous comparisons highlighting the different assumptions of each method (Rabosky, 2014). Despite these differences, the number of nodes identified by MEDUSA was similar (28), with a similar distribution of ages (minimum 1.5 Ma, mean 27.4 Ma, maximum 78 Ma, Figure 2).

#### Trait diversification

Rates of trait evolution varied significantly among study orders when trait data were not log-transformed (Figure S1). In this analysis, the diverse passerines (Passeriformes, n = 5966) exhibit the lowest mean rate of morphological evolution while the phylogenetic signal of traits is similar in passerines and non-passerines (Figure S2). However, when the data were log-transformed there were no significant differences in trait evolution between orders (Figure S3) suggesting that rate differences among orders detected with unlogged data can be explained by scaling artifacts. In other words, the smaller size of passerines manifests in relatively reduced morphological differences between species in comparison with non-passerines, most of which have much larger absolute trait values.

Using untransformed data, low background rates for passerines help explain why shifts in the rate of evolution were also mainly found in passerines (Figure 2), since any clades with high trait diversity—such as the exceptional radiation in beak morphology in Madagascan vangas (Reddy et al., 2012)—are more likely to be identified as shifts in the overall rate of evolution. For transformed data, shifts were more evenly distributed across the phylogeny (Figure S4). There was no strong correlation between order richness and mean rate of morphological evolution, regardless of data treatment (all traits r = -0.01/0.40, beak traits r = 0.16/0.26, n = 11). Conversely, for the analyses of habitat data, there was a strong positive correlation between the species richness of orders and their mean rate of evolution (r = 0.73, n = 11).

Analyses of all morphological traits and only beak traits produce a similar distribution of probabilities for nodes being the locations of node shifts (Figure 2a, Figure S4), but with a larger number of shifts with probability  $\ge 0.95$  in the analysis of all traits (26 vs. 5, Figure 2b). This disparity was even more pronounced after logtransformation of trait data (33 vs. 3, Figure S4). For all analyses, the locations of shifts in the rate of trait evolution show no concordance with speciation rate shift nodes identified by BAMM or MEDUSA (Figure 2b, S4, S5). Trait shifts are considerably younger than speciation rate shifts for both analyses (mean = 7.0 Ma younger for all traits; 4.2 Ma younger for beak traits). These age differences were similar after log-transformation of the trait data (6.7 Ma and 2.6 Ma younger, respectively). The relatively recent bursts of trait evolution differ from a previous analysis of beak morphology by Cooney et al. (2017) who found shifts in rate distributed throughout the tree (see their Figure 3).

We identified a strong temporal component to all estimated rates of trait evolution. Morphological traits show a decline in rates through time (Figure 3, Figure S6) despite lineage-through-time plots for the same phylogenetic data show an increased rate of diversification towards the present (Figure S7). As branch lengths affect estimated rates of character evolution (Chira & Thomas, 2016; Pagel, 1999a,b; Revell et al., 2008), the shorter branch lengths near the present should theoretically favour an overall increase in rate as morphological changes are occurring over shorter timescales. Our result instead suggests a substantial slowdown in the generation of morphological novelty towards the present, with minor variations, including an increase in



**FIGURE 2** (a) Distribution of probabilities for each node in the phylogeny being the location of a shift in the rate of morphological evolution. (b) Distribution of nodes identified as being the location of shifts in the speciation rate and rates of morphological evolution (estimated using two different subsets of morphological traits). Coloured branches indicate those with the fastest overall rates of evolution (i.e. those in the top 1%) split between the two analyses of morphological traits

the mean rate of beak evolution in the late Oligocene/ early Miocene (25–20 Ma). When we visualised taxonomic orders independently, the predominant pattern was again of declining rates of morphological trait evolution (Figure S8, S9). The analysis of habitat data showed a contrasting pattern to the morphological data, with the rate increasing through time until approximately 5 My, then dropping markedly (Figure 3), and the analysis of diet remaining largely consistent through time except for a marked drop towards the present (Figure 3).

# Are speciation rate shifts associated with elevated rates of morphological evolution?

We found that rates of morphological evolution before (parent) and after (daughter) both sets of speciation rate



**FIGURE 3** Rates of evolution through time for morphology, habitat and diet calculated across 11 orders containing a total of 7524 bird species. Solid line denotes the mean rate of all branches in the phylogeny, and shaded region the 95% confidence interval. Rates of morphological evolution show decreasing rates through time (a–b), despite the overall pattern of lineage accumulation trending up towards the present

shift nodes were not significantly different to a either definition of the base rate (Figure 4, S10, S11). Therefore, the identified speciation rate shifts can be considered diversification events (Simões et al., 2016), consistent with the concept of non-adaptive radiations (Folk et al., 2019; Reaney et al., 2020; Rundell & Price, 2009). These analyses recovered some families with exceptionally high rates of morphological and habitat evolution which were largely consistent between analyses; for example the genera *Falco* (falcons, Falconidae) and *Corvus* (crows and allies, Corvidae) showed comparatively greater morphological evolution on their parent branch, indicating diversification in overall body plan before the corresponding speciation rate shift. The genus *Zosterops* ('white-eyes', Zosteropidae), as well as the families Strigidae (true owls) and Picidae (woodpeckers), have greater rates of habitat evolution. Changing the number of daughter branches from two to fourteen did not affect these results (Figure S12, S13), nor did using MEDUSA-identified speciation rate shift nodes (Figure S14, S15). We also found no correlation between rates of phenotypic evolution and speciation rate for either data



**FIGURE 4** Evolutionary rates estimated for branches situated before and after speciation rate-shifts. For 34 rate-shift nodes identified across 7524 bird species in 11 landbird orders (Telluraves), panels compare parent and daughter rates of evolution against base rate defined using all branches not included in a partition (top row) and base rate defined using only those lineages present at the time of the rate shift node (bottom row). With this latter definition, no base rate is plotted as the difference between the base and parent and daughter branches is taken to account for temporal changes in rate of evolution. See Figure 1 for explanation of partitions used for base rate calculations. Distributions show rates of evolution on phylogenetic branches within the respective partitions. Relative evolutionary rate is calculated as within-partition rate minus mean base rate. *Zosterops* and Emberizidae were non-monophyletic, containing members of other clades because of taxonomic error; Emberizidae was removed from the figure because it was an extreme outlier (Supplementary Material). Colours follow the notation for parent and daughter branches in Figure 1

treatment when visualising the trend through time except for a slight negative relationship 20–45 Ma (Figure S16).

Despite finding that the rates of trait evolution on parent and daughter lineages were not different from either base definition, we did find a temporal trend to the difference between parent and daughter rates (Figure 5, Figure S17). For the analyses of all morphological traits and habitat category, there is a negative relationship between the age of speciation rate shift node and the difference between parent and daughter rate, indicating that fastest rates of evolution precede the speciation rate shift. The reverse pattern occurs in beak traits, where we find that younger nodes have a faster rate of evolution following the speciation rate shift (all slopes p < 0.01).

# Effects of ecological stability on rates of phenotypic evolution

Using both definitions of 'base' rates, we did not identify a clear signal between rates of diet evolution and bursts of phenotypic evolution (Figure 6, S18). We found that bursts of phenotypic evolution are consistently recovered at nodes with significantly lower rates of habitat niche evolution (i.e. habitat stability). Additionally, this pattern was stronger for beak traits, as indicated by higher effect size (mean<sub>null</sub>-mean<sub>obs</sub>, 12438 for beak compared to 4049 for all traits) and higher standardised effect size (mean<sub>null</sub>-mean<sub>obs</sub>/sd<sub>null</sub>, 0.05 and 0.03 respectively). In total, 21 of 26 rate-shift nodes were



**FIGURE 5** Comparison between age of nodes identified as speciation rate shifts and the difference between the parent and daughter rate of morphological and habitat niche evolution (n = 32). One extreme outlier (Emberizidae) was removed from all panels because taxonomic error resulted in a miscalculation of evolutionary rates (Supplementary Material)



**FIGURE 6** Estimates of ecological stability for 11 avian clades identified as the location of shifts in the rate of evolution of all morphological traits (left column) and only beak traits (rate column). Observed ecological stability is calculated from data on habitat and diet preferences for all species (n = 7524); null expectation is calculated using the rate of ecological evolution of clades of similar age ( $\pm 2$  Myr). Results show that rate-shift clades are uncorrelated with rates of dietary evolution but show greater habitat stability than expected given their age

associated with habitat stability when pooling all morphological traits, with the proportion increasing to five of five nodes in the analysis of beak traits. Given that most shifts in the rate of phenotypic evolution are comparatively young, an association between these rate-shifts and habitat stability may occur if the rate of habitat evolution declines through time; however, this does not appear to be the case as we only found a weak negative relationship between node age and degree of habitat stability (Figure S19).

#### Taxonomic uncertainty

Most nodes associated with the fastest rates of trait evolution and that subtend two sister species had at least one species placed using taxonomic data for morphology (0.87, all morphological traits; 0.80, beak morphological traits) but not habitat niche (0.44). For the remaining nodes, that is those nodes subtending three or more species, the mean proportion of descendant taxa in the genetic backbone was 0.32 (all morphological traits), 0.31 (beak morphological traits) and 0.44 (habitat). In addition, we detected faster rates of evolution for sister species pairs containing at least one species placed using taxonomy (Figure S20). Nonetheless, there is no correlation between the proportion of species in a family with genetic data and the mean rate of trait evolution (Figure S21), suggesting that taxonomic data inflates evolutionary rate estimates for terminal branches but not for the entire clade.

#### Sensitivity analyses

Restricting analyses to species with genetic data in Jetz et al. (2012) did not change the relative magnitude of parent or daughter rates or the ages of branches with the fastest rates of evolution. We also found no effect on our results caused by the way BAMM estimates the position of speciation rate shifts on parent or daughter rates. Finally, when we tested our method on beak data from 'classic' avian adaptive radiations, we found that it detected them successfully, potentially because the confounding effect of extinction is reduced closer to the tips of the phylogeny. Full details of these sensitivity analyses are presented in Supplementary Material.

### DISCUSSION

Our analyses show that bursts of lineage and phenotypic evolution are decoupled in birds, with bursts of phenotypic evolution being notably younger, mainly concentrated within the last 3 million years. We also show that rates of morphological evolution are not greater than a base rate of evolution across shifts in speciation rate. However, by comparing evolutionary rates before and after these events, we find that rates of differentiation in overall morphology and habitat niche peak before speciation rate-shifts, whereas rates of beak evolution peak afterwards. Across our sample, bursts of morphological evolution are not predicted by high rates of dietary or habitat niche evolution and instead by the opposite pattern of stability in habitat niches. These findings imply that drivers of rapid evolution differ for lineages and morphological traits, and even vary across different subunits of morphology depending on ecological function and context.

The absence of simultaneous evolutionary bursts in our data set is consistent with a growing number of studies reporting a similar decoupling (Folk et al., 2019; Simões et al., 2020). The current analysis builds on these earlier studies by focusing on shifts in speciation rate across over 7000 bird species, as well as integrating ecology to understand bursts of phenotypic evolution. That we find bursts of speciation and phenotypic evolution being asynchronous, despite improvements in method and sampling, provides little support for the widespread view that rapid evolution in lineages and phenotypes are likely driven by the same processes (Givnish, 2015; Glor, 2010; Stroud & Losos, 2016). Instead, our results suggest that much of extant bird diversity has arisen through slower processes of diversification, or bursts limited to either lineages or phenotype alone (i.e. non-adaptive radiation and adaptive non-radiation; Gittenberger, 1991; Rundell & Price, 2009; Moen et al., 2021).

It is worth noting that recovering bursts of lineage and phenotypic evolution in disjunct places on the phylogeny does not rule out these instances still being adaptive radiations. Specifically, not all definitions of adaptive radiation require accelerated rates of lineage evolution (see Givnish, 2015). By enforcing rapid speciation as a necessity of adaptive radiations it may make the conditions for identifying them artificially narrow. Moreover, it is plausible that the identified bursts of morphological evolution were adaptive, but our ability to identify them as such has been obscured by subsequent phenotypic evolution.

An alternative interpretation of our results is that bursts of lineage diversification and phenotypic trait evolution are indeed often correlated in birds but not detected in our analyses because of methodological shortcomings. There are three possible reasons for this. First, evidence of past morphological diversification may be removed through subsequent evolutionary change, especially when ecological adaptation drives convergence towards predictable combinations of trait values over millions of years (Pigot et al., 2020; Pincheira-Donoso et al., 2015). Second, the signature of historical processes on phylogenetic structure may also be erased by extinction (Phillimore & Price, 2008; Rabosky & Lovette, 2008a; Slater et al., 2010), thus the number and location of speciation rate shifts may be incorrectly identified here. Finally, as the uncertainty of node ages increases over time, there may be discrepancies of millions of years between events that in reality occurred more or less concurrently. While these factors may make ancient adaptive radiations difficult to detect using phylogenetic and morphometric data, they do not explain why simultaneous pulses of lineage and phenotypic evolution are absent from shallower timescales.

The evidence we show for a decoupling of these events partly contrasts with the findings of Cooney and Thomas (2021), who reported a correlation between the rate of body size evolution and speciation rate in some avian clades but not in others, raising the possibility that such pulses may therefore be overlooked by analyses with broad taxonomic sampling. However, these analyses can be considered clade specific in that a shift in speciation rate at a node affects all the members of the clade it defines. Additionally, visualising our results from different nodes produces similar patterns, suggesting we are not losing signal by pooling the results of multiple clades (Figure S22). Why we find a different result is intriguing because the underlying methods are similar. The most likely explanation is that Cooney and Thomas (2021) focussed exclusively on body size, whereas we identify rate shifts using a set of 10 morphological traits showing a closer relationship with ecological niche differences than body size alone (Pigot et al., 2020; Sheard et al., 2020). Simultaneous bursts of lineage and morphological evolution in birds may therefore be associated with body mass, but rare in the context of niche-related ecomorphological traits.

#### Tempo and timing of rapid trait evolution

Quantifying rates of trait evolution across speciation rate shifts from timetrees of extant taxa may permit some inference of evolutionary processes. For example when analysing all traits or habitat, we found that rates of evolution are greater on the parent branch, that is before estimated speciation rate shifts. This may provide a clue to the way lineages exploit ecological space during radiations. One hypothesis is that lineages gradually fill ecological space as speciation proceeds, ultimately leading to a slowdow in diversification as unoccupied space is depleted (Rabosky & Lovette, 2008b). An alternative sequence of events involves trait disparity peaking early in the radiation as a few divergent lineages dominate the available resources, with speciation peaking later as resources are partitioned ever more finely through specialisation (van Valen, 1985). We suggest that our finding of rapid trait evolution prior to speciation rate-shifts supports the latter view, with subsequent bursts of speciation producing relatively little morphological novelty, perhaps through fine-scale subdivision of available resources (Crouch & Ricklefs, 2019) or 'nonecological speciation' subdividing each dominant morphotype into allospecies (Rundell & Price, 2009).

When we restricted our analyses to beak characters the dominant axis of rapid ecomorphological adaptation in birds (Chira et al., 2018; Cooney et al., 2017) and the one most tightly associated with trophic niches (Pigot et al., 2020; Reddy et al., 2012; Tokita et al., 2016)—we found that speciation rate shifts correlated with an increased subsequent rate of morphological evolution (i.e. daughter rates that exceed parent rates). This pattern suggests that lineage diversification can give rise to new ecological opportunities, which in turn drive subsequent pulses of evolution in trophic traits. In addition, this sequence of events potentially occurs when allopatric speciation initially gives rise to non-adaptive radiations, which then undergo trait divergence after secondary contact, for example via character displacement (Tobias et al., 2020).

# Is trait evolution linked to ecological diversification?

We predicted that high rates of evolution in ecological niches would be associated with bursts in morphological evolution given previous work showing how trait diversification can be driven by adaptation to widely different dietary niches (Felice et al., 2019; Grant, 1986) or colonisation of novel, complex habitats (Price et al., 2012; Salvidio et al., 2015). Instead, we found that rapid bursts of morphological evolution were associated with unexceptional rates of dietary evolution, even when focusing on beak characters alone (Figure 6). This result runs counter to expectations for classic adaptive radiations, although taxonomic scale clearly plays a role since the connection between rates of beak and diet evolution is more apparent when these clades are compared with their closest relatives (Figure S23). When we tested the same hypothesis at a global scale using rates of habitat niche evolution, we found that bursts of phenotypic evolution are associated with stable habitat niches, that is pulses of trait evolution correlated with lower rates of habitat niche evolution (Figure 6).

Some caution is required interpreting the results for two main reasons. First, any test of diversification applying evolutionary models to large phylogenetic trees of extant taxa poses widely acknowledged challenges that cannot be avoided without adding data from extinct lineages (Beaulieu & O'Meara, 2018; Louca & Pennell, 2020). Second, the global bird tree (Jetz et al., 2012) has served as a useful phylogenetic framework for nearly a decade but contains many placement errors based on obsolete taxonomy and is in urgent need of an update. We included a series of sensitivity analyses showing that our results are robust to data treatment and taxonomic uncertainty. Future work could expand on our approach by identifying the location of rate shifts using improved phylogenetic data reconstructed incorporating extinct taxa, although in such cases it will remain impossible to quantify morphological and ecological traits that do not fossilise.

### CONCLUSION

Using comprehensive morphological trait data for birds, we detect no correlation between shifts in speciation rate and shifts in phenotypic evolution over the past 66 Myr, suggesting that lineage diversification is only weakly associated with bursts of phenotypic evolution on a macroevolutionary scale. These independent bursts of morphological evolution-termed 'disparification' events by Simões et al. (2016)-are nonetheless widespread. Focusing on the timing and ecological context of these events, we show how rates of dietary evolution, thought to be a major factor in driving the diversification of avian functional traits, appear unrelated to bursts of phenotypic evolution. Rapid trait diversification is instead more often associated with habitat niche stability. Although this finding may seem counter-intuitive, it potentially reflects a common pathway for morphological diversification whereby a lineage diversifies in a broad habitat niche where it has a particular advantage, resulting in ongoing adaptation and morphological innovation so that related species partition resources ever more finely within that habitat. More generally, our analyses highlight the importance of emerging global trait datasets as a template for larger-scale evolutionary models. Continued improvements to these datasets, in conjunction with complete phylogenies and the integration of fossil data where possible, will open a fertile new frontier in the quest to understand how biodiversity evolves.

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#### AUTHORSHIP

NMAC conceived the study and performed the analyses; JAT helped develop the conceptual framework and provided trait data; both authors contributed to writing and revising the manuscript.

#### PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13962.

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This article has earned an Open Data badge for making publicly available the digitally-shareable data necessary to reproduce the reported results. The data is available at https://doi.org/10.5061/dryad.b2rbnzsdp.

#### DATA AVAILABILITY STATEMENT

A number of supporting files for this work will be provided on Dryad. These are the posterior distribution of phylogenetic scaled to represent rates as generated by BayesTraits, and R scripts used in the analysis. A markdown file detailing how the control files were generated, as well as analysis of the BayesTraits results is also provided in the supplementary material (https://doi. org/10.5061/dryad.b2rbnzsdp).

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#### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

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