


## LETTER

Nest architecture is linked with ecological success in songbirds 

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## Abstract

Nests are essential constructions that determine fitness, yet their structure can vary substantially across bird species. While there is evidence supporting a link between nest architecture and the habitat a species occupies, we still ignore what ecological and evolutionary processes are linked to different nest types. Using information on 3175 species of songbirds, we show that—after controlling for latitude and body size—species that build domed nests (i.e. nests with a roof) have smaller ranges, are less likely to colonise urban environments and have potentially higher extinction rates compared to species with open and cavity nests. Domed nests could be a costly specialisation, and we show that these nests take more time to be built, which could restrict breeding opportunities. These diverse strands of evidence suggest that the transition from domed to open nests in passerines could represent an important evolutionary innovation behind the success of the largest bird radiation.

## KEYWORDS

bird macroevolution, nest evolution, parental care, range size

## INTRODUCTION

Nests are fundamental structures for avian reproduction that determine egg survival and development (Deeming et al., 1991; Deeming & Mainwaring, 2015). The thermal environment inside these natural incubators influences an individual's fitness, and therefore, nest traits that affect internal conditions are expected to be under strong selection (Heenan, 2013; Mainwaring et al., 2014). Songbirds (suborder Passeri) and their more than 4500 species represent the largest extant bird radiation and are known to build a variety of nest types. Most species in this clade build 'open nests', that is, cups or platforms where nest contents are exposed. In contrast, some species like Australian lyrebirds, African weavers and penduline tits, build domed nests, which are structures characterised by an enclosing roof and a side entrance.

Domed nests have often been suggested to reduce predation and offer thermal insulation, protecting nest contents better than open nests (Collias, 1997; Hall et al., 2015; Lamprecht & Schmolz, 2004; Martin et al., 2017). Recent evidence highlights their thermoregulatory advantages in colder environments by enabling parents to spend more time away from their nests (Lamprecht & Schmolz, 2004; Martin et al., 2017; Matysioková & Remeš, 2018), and in extremely hot environments by shielding nests from solar radiation (Griffith et al., 2016). Given the presumed advantages of domed nests over open nests, it remains a mystery why most birds in the world (~70% of all avian families, (Fang et al., 2018)) build open nests.

For years, it was thought that selection imposed by temperature or predation rates would have favoured the transition from open to domed nests in some clades

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(Collias, 1997; Hansell, 2000; Price & Griffith, 2017). The evolutionary history of nests in passerines, however, suggests the opposite: the common trait of building an open nest is a derived condition. In 2017, Price and Griffith found evidence that the ancestral type of nest in passerines is domed, and this result is further supported by other comparative analyses (Fang et al., 2018; Medina, 2019). Thus, rather than selection favouring the occurrence of domed nests throughout the evolution of passerines, this trait has been repeatedly lost. Furthermore, the transition from domed to open nests in passerines has been hypothesised to be a key innovation, given the subsequent diversification, colonisation and expansion of open nest building lineages (Fang et al., 2018; Price & Griffith, 2017). Although the evolutionary history of nests in passerines has been explored previously (e.g. Fang et al., 2018; Price & Griffith, 2017) and there is evidence that transitions from domed to open nests occurred, we currently ignore why these transitions occurred, and whether such transitions had macroevolutionary consequences. For instance, it is possible that costs associated with nest building could have led to the loss of domed nests. While we lack information on whether building domed nests represents a higher energetic cost over building open nests, nest building is considered a costly activity and domed nests are heavier relative to the size of the builder when compared to open nests (Hansell, 2000; Mouton & Martin, 2019).

The type of nest a species builds could also be tightly linked with its ability to live across different habitats or environments. For instance, if domed nests offer greater protection across a wider range of environments, then we would expect species with domed nests to sustain broader climatic tolerances, thereby enabling them to inhabit a wider range of habitats. On the other hand, if domed nests are a costly ancestral adaptation to specific habitats, then domed-nest lineages might exhibit narrower and more specialised environmental tolerances than their open-nest counterparts. Indeed, Australian species with domed nests tend to have smaller ranges, smaller climatic niches and are more likely to be under an IUCN threat category compared with species that build open nests (Medina, 2019).

Our main aim is to understand the evolutionary success of open nests by studying the potential ecological and evolutionary trade-offs associated with different nest types. First, we compare the building costs between domed and open nests using published information on time taken to construct a nest. We then test whether the evolution of different nest types in passerines is associated with differences in range size, climatic niche breadth, colonisation of novel environments and variation in speciation or extinction rates. We examine a comprehensive dataset under a macroevolutionary lens to explore the evolution and ecology of a critical component of the extended phenotype of birds.

## MATERIALS AND METHODS

### Nest type and other species traits

We extracted species-level nest information from the website Birds of the World (BW) (Beruldsen, 1980; Billerman et al., 2020). We searched for information on all species of songbirds (suborder Passeri), following the taxonomy from Jetz et al. (2012) phylogenies (4685 species), with manual resolution of taxonomic names between BW and Jetz et al. (2012). For each species, we collected information on nest type, which was classified into two broad categories: domed (defined as having a side entrance or a roof, or as being globular) or open (defined as a cup or a platform, or cases where there is only a mat of leaves, or vegetable material). Additionally, we recorded whether the species used cavities to nest or not, whether the species built both domed and open nests, or whether the nest was described as a pouch. With these variables, we generated a fine-scale classification: open ( $n = 1656$ ), domed ( $n = 790$ ), deep cup ( $n = 187$ ), both ( $n = 60$ ), dome in cavity ( $n = 81$ ) and open nest in cavity ( $n = 401$ ). Based on results, we further merged data into broader categories, to increase sample size in each category. For analyses that tested associations between variables, the nest categories used in the analyses presented in the main text were domed ( $n = 790$ ), open ( $n = 1903$ ) or cavity nesters ( $n = 482$ ), which allowed us to test if, besides differences between open and domed nests, placing the nest in a cavity could lead to any changes. Other classifications were used as well (domed vs. open, and the fine-scale classification described above). For those analyses that invoked evolutionary mechanisms (e.g. diversification and ancestral reconstruction), we only considered domed versus open nests, because the trait of interest is the construction behaviour, and whether a domed or an open nest was built (not where it was placed). Classifications used in analyses and their rationale are explained in more detail in the supplementary material. Our final dataset included 3175 species with nest information (68% of all Passeri).

Given that response variables like range size can be associated with body size and species latitude, we also collected information on body size for each of the species from Wilman et al. (2014), who collated this information mainly from Dunning Jr (2007); and information on the mean latitude from their distribution range from Sheard et al. (2020). As a measure of colonisation of novel habitats, we also collated information of species' presence in urban environments, which was extracted from the IUCN habitat scheme (data from IUCN, collated in Ducatez et al. (2020)). This was recorded as 1 (presence in urban areas) or 0 (no presence).

To test whether there are differences in the costs of nest building across nest types, we used the time spent building nests as proxy of the energetic cost. We searched for information on the average number of days that takes

a species to construct a nest (details in supplementary material). We also collected information on who builds the nest (females, males or both), given this could affect the time of nest construction.

## Environmental variables

To test whether there are differences in niche width and range size between species with different nest types, we used geographical distribution information from BirdLife International and HBW (2019). We used a published dataset (Cally et al., 2021) of bioclimatic variables from Worldclim (Fick & Hijmans, 2017) (details of extraction in Cally et al., 2021, and 14 variables used in Table S1). These variables were sampled in 1000 random points across the distribution of each species, and provide information on temperature and rainfall across the range. We also extracted information on range size from Cally et al. (2021) ( $n = 3175$ ), who used shapefiles from Birdlife (BirdLife International and HBW, 2019). For a smaller set of species for which breeding range information was available ( $n = 3049$ ), we extracted information on the same 14 bioclimatic variables following the protocol in Cally et al. (2021), but this time we used a more recently developed dataset (CHELSA) resulting from an algorithm that predicts current precipitation patterns at high spatial resolution (Karger & Zimmermann, 2019). For each climatic variable, and each species, we calculated the standard deviation across the 1000 points sampled, to estimate climatic variability across the species range (and breeding range). Since species restricted to islands are limited both in the extent of their range and the niche width, we performed analyses using both the whole dataset and only continental species. Finally, we also performed additional analyses on elevational ranges of species to test whether wider elevational ranges—associated with higher climatic variation—are linked with nest type. Details of this approach can be found in the supplementary material.

To summarise information on variation in temperature and variation in precipitation across a species range, we performed two principal component analyses, one for temperature and one for precipitation variables. We split precipitation from temperature because we expected that nest types would be more linked to temperature than precipitation variables, given the proposed thermoregulatory capabilities of domed nests (Martin et al., 2017). The same was done for the breeding range, leading to four principal component analyses that summarise information on how variable temperature and precipitation are, both within total and only within breeding ranges. We report the PC loadings and percentage of variance explained for PCs. We refer to the first principal component from temperature variables as  $PC_{TEMP}$  (for breeding and total range) and to the first principal component based on precipitation variables as  $PC_{PRE}$ . These

four PCs were used each as a different response variable in statistical analyses, but some of them were highly correlated (e.g.  $PC_{TEMP\ breeding}$  and  $PC_{TEMP\ total}$ ,  $r^2 = 0.90$ , Figure S1). To ensure that the measures of variation used (PCs) were also capturing variation in conditions during breeding times, we also repeated analyses using variables from the wettest season (three wettest months of the year for each location) in the breeding range of each species, given that rainfall is linked to productivity and many species start breeding during the wet season (Hau et al., 2008).

## Tip-level regression analyses

Information on days taken to build a nest was available for 277 species in HBW (69 domed, 208 open), and to test whether there are differences in the time taken to build a nest we used linear models that account for evolutionary history (PGLS, description of approach below). We used the time taken to build in days as response variable (log transformed) and we used log body size, the sex of the builder (female, male or both), latitude (absolute) and the type of nest built (domed/open) as predictors. We provide details on the data employed for this analysis in the supplementary material.

To test whether building different nest types is associated with current range size and niche width, we used linear models that account for evolutionary history, with climatic niche width ( $PC_{TEMP}$  or  $PC_{PRE}$ ), range size or presence in urban environments (yes/no) as response variables. As predictors, we used the species nest type and body size (log), because body size is known to explain variation in range size in birds (Gaston & Blackburn, 1996). In the case of range size, we also accounted for the absolute mid-latitude of the species range, since tropical species are expected to have smaller ranges (Gaston et al., 1998). We did not incorporate latitude or range size to regressions with niche width (PCs) as response variable, because we were interested in the link between nest type and the width of the niche experienced by the species, even if such is a combination of range size and location. For PGLS analyses, we focused on using the predictor of nest category with three levels: ‘open’, ‘domed’ and ‘cavity’, but we also report results on alternative nest classifications, which rendered similar results. We used the R package ‘performance’ and the command *check\_model* to detect outliers, and assess whether there were any collinearity issues in our set of predictors (Lüdecke et al., 2019).

For the continuous response variables (time spent building nest,  $PC_{TEMP}$ ,  $PC_{PRE}$  and range size—breeding and whole), we used a phylogenetic generalised least squares regression (PGLS), using maximum likelihood to estimate lambda, implemented in the R package ‘caper’ (Orme, 2013). To control for phylogenetic relatedness among species, we obtained a maximum clade

credibility tree (MCC, across 10,000 trees) using the package ‘Phangorn’ (Schliep, 2011) and a set of 10,000 phylogenies from birdtree.org (Jetz et al., 2012). For models with significant results using the MCC tree, we also performed PGLS analyses across a set of 100 trees. For each model using the MCC tree, we report the estimates and p-values calculated, and for the analysis on 100 trees we generated 95% highest posterior density intervals (HPD) for the estimates using the R package ‘coda’ (Plummer et al., 2006).

For the binary response variable (urban or not), we used a Bayesian approach in the R package MCMCglmm (Hadfield, 2010) using nest type (open, domed, cavity) and log body size as predictors. We run one model using the MCC tree as a random effect until convergence was reached. To account for phylogenetic uncertainty, we followed Ross et al. (2013). Briefly, we run the model using 1300 different trees and for each tree used 100,000 iterations and saved the last iteration before going into the next tree. We used the first 300 saved iterations (e.g. 300 trees) as burn-in and assessed model convergence, ensuring that the effective sample size was above 900. We report the credibility intervals for each predictor in each model.

## Diversification analyses and evolutionary models

We estimated speciation rates across a range of phylogenetic trees using the cladogenetic diversification rate shift (CladS) Bayesian model (Maliot et al., 2019) that infers branch-specific diversification rates. CladS allows for gradual variation in diversification rates and was shown to perform well in identifying both small and large rate shifts (Maliot et al., 2019). We used the model that accounts for a scenario with a constant turnover rate (CladS2 model) and the faster implementation in Julia (v.1.1.0, Bezanson et al., 2017) that uses data augmentation (Maliot & Morlon, 2020), setting the sampling probability to 0.63. To test whether nest type is associated with variation in speciation rates, we used the tip-rate estimates (estimates for each terminal branch at present) extracted from CladS as response variable in a PGLS model, with nest type and log(range size) as predictors, since range size has been shown to be associated with speciation (Cally et al., 2021). The nest type category used for this model was open versus domed, given that we are interested in the actual nest structure built, not where the nest is placed. A main model was run using the MCC tree and we also performed the same analysis in a sample of 20 phylogenetic trees to account for phylogenetic uncertainty.

To gain a more mechanistic understanding on the feedback between species traits and their influence on diversification, we used the Multiple State Speciation Extinction (MuSSE) model to jointly estimate state dependent speciation and extinction rates (FitzJohn,

2012). Modelling trait evolution while accounting for the diversification process results in more appropriate estimates of trait transition rates and ancestral estimates, while accounting for uncertainty in the species for which we do not have state information (FitzJohn, 2012; Maddison et al., 2007). We modelled the correlated evolution of *niche width* and *nest type* data by aggregating them into four different states: narrow niche and domed nest, narrow niche and open nest, wide niche and domed nest and wide niche and open nest. We assigned a species as having a wide or narrow niche based on whether the  $PC_{TEMP}$  was below or above the median value of the whole dataset ( $PC_{TEMP} = -0.639$ ). Species with narrow niches also had smaller ranges and were more likely to be tropical. Since we are interested in the interaction among these states, we disallowed transition rates between states that effectively would represent simultaneous changes in nest type and niche width (e.g. going from wide niche and domed nest directly to narrow niche and open nest is not allowed). Finally, to examine whether nest type provides a mechanistic transition route between niche breadths, we performed a direct test on the evolutionary association between nest type and niche width category (same binary classification as described above), using the software BayesTraits (V3.0.1) (Pagel & Meade, 2006) which implements Reversible Jump Markov Chain Monte Carlo (RJ MCMC). We compared the dependent model (a model where the rates of change between nest type and niche breadth are interdependent) against a model of independent evolution (where nest type and niche breadth evolved independently) while accounting for phylogenetic uncertainty; details are presented in the supplementary material.

Additionally, to allow for unobserved taxonomic variance in the diversification process, thereby not forcing the model to explain all the heterogeneity in diversification, we ran HiSSE (Hidden State Speciation Extinction) with two concealed states (Beaulieu & O’Meara, 2016). Both analyses were performed using the MCC tree within a Bayesian Framework using RevBayes (Höhna et al., 2016), including ancestral state estimation (details in supplementary material). To evaluate the effect of phylogenetic uncertainty, we ran the Maximum Likelihood approach MuSSE implemented in the R package ‘castor’ (Louca & Doebeli, 2018) across 100 phylogenetic trees. Because results were consistent across methods, we present the castor analyses in the main text and RevBayes (MuSSE and HiSSE) results in the supplementary material. Finally, given that the uncertainty of species position in the phylogeny might be higher for some states, potentially biasing transition rates, we implemented an additional analysis that specifically accounted for missing data per character state (details in supplementary material). All analyses were carried out in R except where specified that another software was employed (V4.0.4, R Core Team, 2021).

## RESULTS

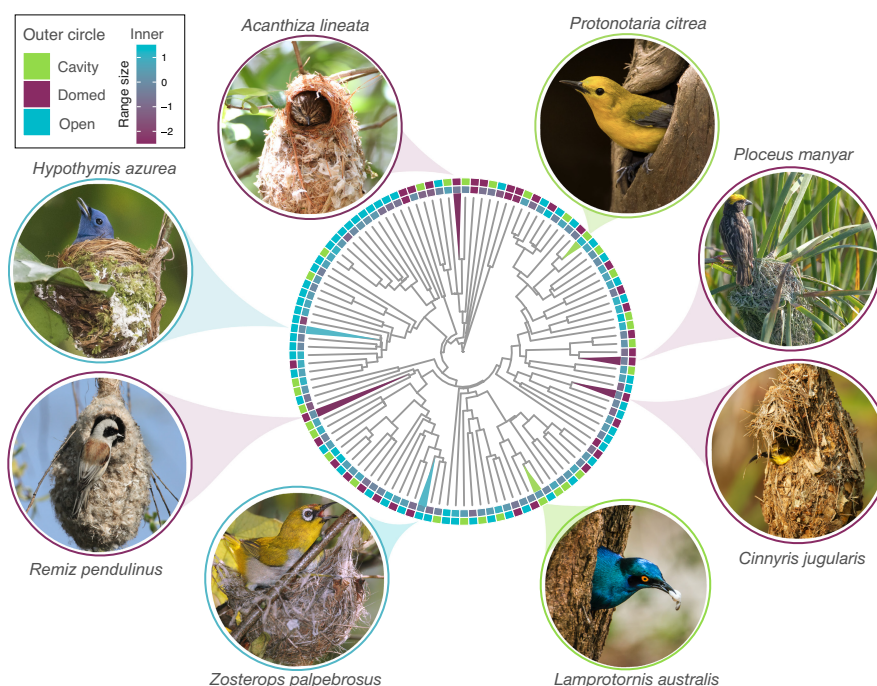
From all species considered in this study ( $n = 3175$ , Figure 1), 60% (1903 spp.) were classified as having an open nest, 25% (790 spp.) were classified as domed nesters and 15% (482 spp.) were classified as cavity nesters. Only 1.8% of the species (60 spp.) build both types of nests. From the cavity nesters, 17% build domed nests inside the cavities and 83% build cups. Most species were classified as continental (81.7%).

Species that build domed nests spend more time building their nests than species with open nests ( $\beta_{\text{MCC}} = 0.36$  [HPD 95% across 100 trees: 0.35, 0.39],  $t$ -value = 3.15,  $p = 0.002$ , Figure 2). Larger species take longer to build nests ( $\beta_{\text{MCC}} = 0.13$  [0.11, 0.13],  $t$ -value = 2.55,  $p = 0.01$ ) and there is no effect of latitude ( $\beta_{\text{MCC}} = -0.004$  [-0.004, -0.003],  $t$ -value = -1.51,  $p = 0.13$ ) or who builds the nest ( $\beta = 0.14$  [0.14, 0.16],  $t$ -value = 1.63,  $p = 0.10$ ).

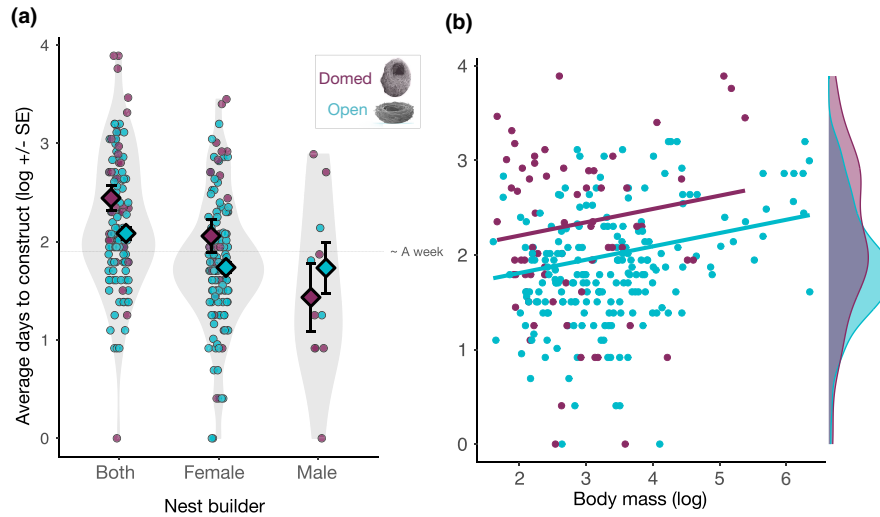
Species with domed nests tend to have a tropical distribution, but there was no link between nest type and body size in our dataset (Figure S2), so there was enough variation in these predictors across species to avoid multicollinearity issues, and all variance inflation factors were low (max 2.18), and well below the recommended threshold of five (Gareth et al., 2013). The area of geographic and breeding ranges was predicted by nest type, and species with domed nests had significantly smaller ranges compared to both, species that build open nests and those that use cavities, after controlling for the significant effects of latitude and body size on range size

(Figure 3). Models that included nest type were more than 50 times better at predicting range size than those including only latitude and body size (Tables S6a–d), and the link between range size and nest type was also evident when including only tropical species in the analysis, or within body size categories (Table S10). Species with domed nests also have narrower temperature niches ( $\text{PC}_{\text{TEMP}}$ ), but not precipitation niches ( $\text{PC}_{\text{PRE}}$ ), when compared with species with open or cavity nests (Table 1, Figure 3, Figure S3). This pattern was similar when comparing domed and open nests built within cavities ( $n = 482$ , Figure S3). Importantly, the link between nest type and  $\text{PC}_{\text{TEMP}}$  does not seem to be independent of latitude and range size (Table S11) so dome-nesting species have narrower thermal niches because they are tropical and have smaller ranges. Similar trends were found when using either continental or all species, when using whole range or breeding range information, when using alternative classifications of nest type (Tables S2–S5, Figure S3) and when using elevation data (Table S6). However, patterns were slightly weaker when using breeding versus total geographic range. Species that build domed nests are also less likely to live in urban environments ( $\beta = -1.858$ ,  $p = 0.001$ , Table S8, Figure S4, domed  $n = 693$ , open  $n = 1760$ , cavity  $n = 435$ ), but there were no differences between open and cavity nesters (Table S8).

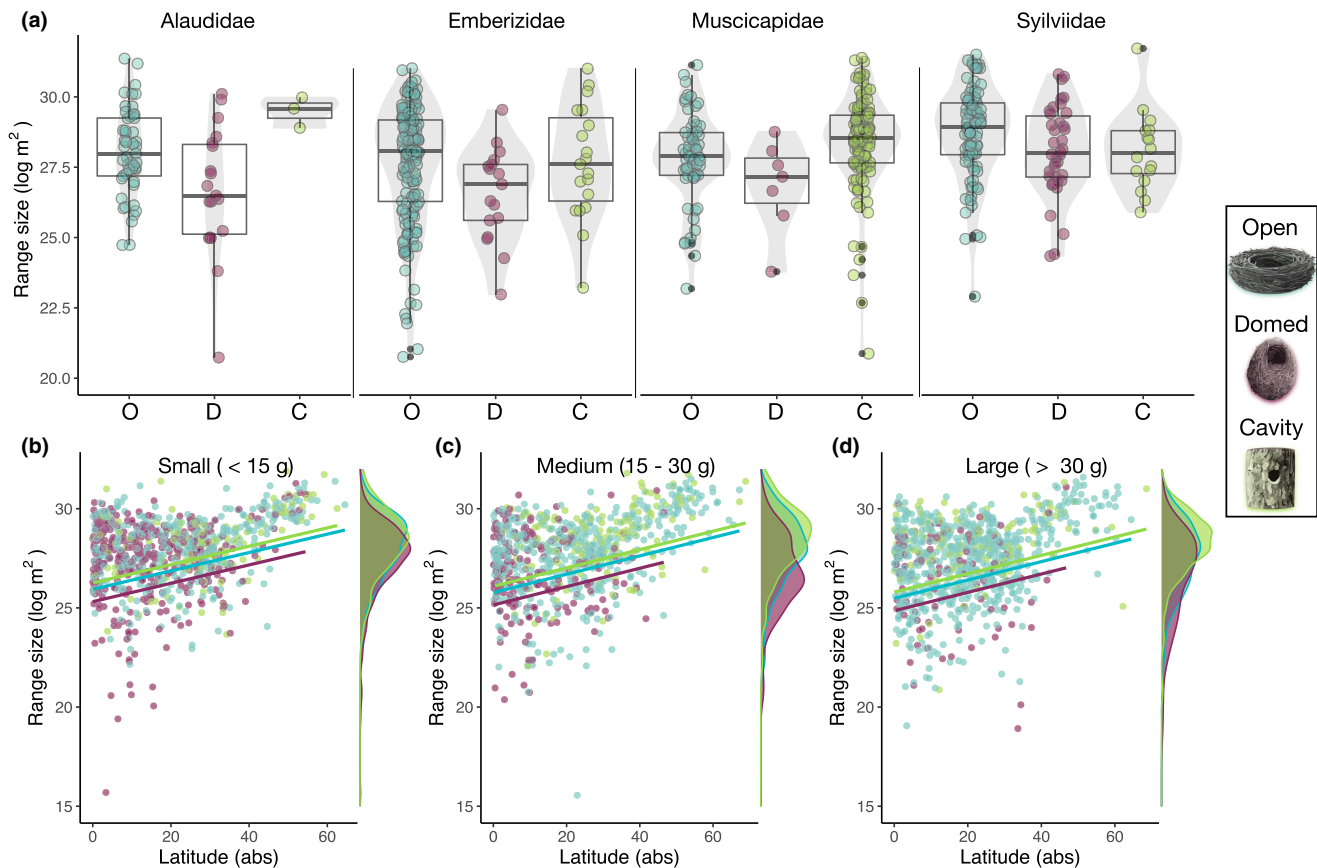
There were no differences in speciation rates between species with different nest types when using tip rates derived from the ClaDS model. Although when using



**FIGURE 1** Phylogenetic distribution of nest types and association with range size across 3175 species of songbirds. Purple represents domed nests ( $n = 790$ ), green represents cavities ( $n = 482$ ) and blue represents open nests ( $n = 1903$ ). Tips represent families in most cases, except when there is more than one nest type per family, in which case the tip is divided. Pictures purchased from iStockphoto.com, except for *Hypothymis azurea* and *Ploceus manyar*, taken by Damien Esquerré. Figure prepared using R package ggtree (Yu et al., 2017)



**FIGURE 2** (a) Differences in time to build a nest for songbird species with domed and open nests ( $n = 277$ ). (b) Relationship between body mass and time spent nest building for species with different nest types. Lines represent estimates and intercepts obtained from PGLS model



**FIGURE 3** (a) Variation in range size for different nest types across four songbird families that build different nest types. (b)–(d). Association between latitude and range size for different nest types and different body size categories (small, medium and large species), for continental species ( $n = 2583$ ). Lines represent prediction from model presented in Table 1

the MCC tree we found significantly higher rates for open nests (Domed vs. Open,  $\beta = 0.051$ ,  $t$ -value = 2.36,  $p = 0.017$ ), when we sampled 20 random trees there was no association (HPD interval  $\beta = -0.065$  to 0.030,  $p$ -value = 0.03 to 0.83). The MuSSE analysis showed

similar trends in both Castor and RevBayes (Table S9, Figure S5), and there were no differences in speciation rates between categories of different nest types. There were differences, however, between range sizes, and species with smaller ranges had higher speciation rates in 99

**TABLE 1** Results of PGLS models testing the association between nest type and (a) range size (log), (b) Temperature niche width (PCI) and (c) Precipitation niche width (PCI), for continental species. Estimate, *t*-value and *p*-value from model with MCC tree as phylogenetic control. In case where the MCC model showed significant results, we also present the 95% HPD interval of the estimate across 100 phylogenetic trees

Predictor	Range size ( <i>n</i> = 2583)				Temperature ( <i>n</i> = 2596)				Precipitation ( <i>n</i> = 2596)			
	Estimate	<i>t</i> -value	<i>p</i> -value	Interval	Estimate	<i>t</i> -value	<i>p</i> -value	Interval	Estimate	<i>t</i> -value	<i>p</i> -value	
	mcc				mcc				mcc			
Open versus Domed	-0.624	-4.744	< 0.001	-0.64 to -0.577	-0.439	-2.507	0.012	-0.545 to -0.376	0.054	0.351	0.725	
Open versus Cavity	0.317	2.528	0.012	0.311–0.351	0.483	3.041	0.002	0.426–0.567	0.059	0.417	0.676	
log(body mass)	-0.242	-3.471	0.001	-0.273 to -0.235	-0.244	-2.431	0.015	-0.302 to -0.211	-0.035	-0.412	0.681	
Latitude (abs)	0.046	17.012	< 0.001	0.046–0.047	–	–	–	–	–	–	–	

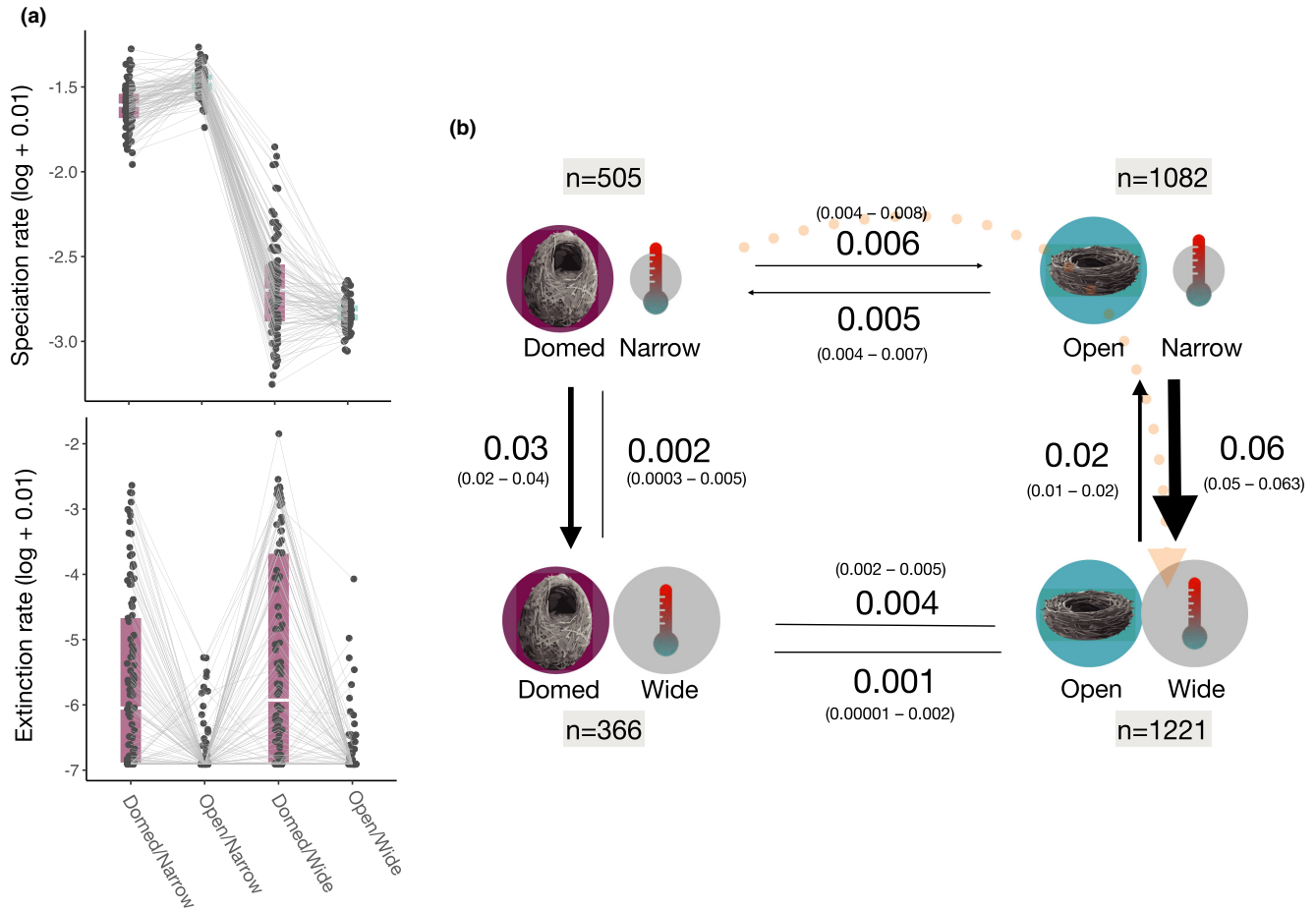
out of 100 trees. In terms of extinction rates, we found that the average rate for dome-nesting categories (wide and narrow niche) was higher than that of the open nest categories in 90% of the trees (Figure 4a). The HiSSE analysis showed similar patterns (Figure S5, Table S9). A similar pattern was also detected in the analyses that employed only species with genetic data (for extinction at least, Table S9), but the effect was less strong.

The most likely ancestral state according to all analyses for the clade Passeri was having a small niche and a domed nest, although as usual, reconstruction based only on extant species should be taken with precaution. The pattern reported was evident from the HiSSE analysis but was more ambiguous in the MuSSE analyses, where probabilities of state 1 (small niche and domed nest) and state 3 (large niche and domed nest) were very similar (Table S9). The BayesTraits analyses strongly supported a correlated model of evolution, with log bayes factor values well above 20 (details in supplementary material, Table S12). The transition rate matrix in all analyses (including the one using only species with genetic data) showed that transitions between niche widths (small/large) are more common than transitions between nest types (Figure 4b, Figures S6–S8), and that the most likely route to the association between open nests and wide niches (the most common and derived state) would have occurred from domed nest/narrow niche, to open nest/narrow niche, and then open nest/wide niche (Figure 4b). This path is over 10 times more frequent than evolving a wider niche and then transitioning to an open nest, and suggests that a transition in nest type, from domed to open, is the first step to then support a wider niche.

## DISCUSSION

Nest construction is suggested to be an important innovation that facilitated the radiation of modern birds, specially passerines (Collias, 1997; Collias & Collias, 2014). Our results support the idea that nests could be important in the ecological success of birds and further suggest that the transition from domed to open nests in songbirds could have contributed to the expansion and success of this radiation in the world. We found that species with open nests take less days to build their nests when compared to species with domed nests. Species with open nests also have larger ranges with broader thermal niches, are more likely to colonise urban environments and potentially have lower extinction rates than species with domed nests.

Collias (1964, 1997) suggested several benefits of building open nests. First, they are often made of fewer materials. Second, because they are smaller, they can be hidden from predators and can also allow a quicker escape from predator attack—although see Nice (1957) or Hall et al. (2015) for opposite argument. Third, because



**FIGURE 4** (a) Estimates of speciation and extinction rates from MuSSE analysis (castor) across 100 trees. Gray lines connect estimates for the same tree across categories. (b) Transition rates between the four states presented in panel A, from the analysis on the MCC tree using RevBayes (MuSSE). Numbers in parentheses represent the 95% HPD intervals of the rates. Orange arrow in the back represents most likely path, from the most probable ancestral state (domed nest/narrow niche) to the derived and most common condition (open/wide)

they are relatively smaller (Mouton & Martin, 2019), they should take less time and energy to build, which would make re-nesting during the breeding season more likely. Our results support the hypothesis that building open nests reduces time expenditure; we found that species take significantly less days to build open nests, especially when the nest is built by females or a couple (see extended discussion). This pattern could be explained by the large size of domed nests relative to the size of the builder (Hansell, 2000; Mouton & Martin, 2019). Evolutionary transitions from domed to open nests, hence, could be favoured given the higher costs associated with building domed nests.

Our regression results show that species with open and cavity nests have wider ranges with broader thermal niches compared to species with domed nests, a pattern previously reported for Australian passerines (Medina, 2019). Crucially, this effect seems to be independent of links between nest type and latitude or body mass, as models including nest type are much better at explaining variation in range size compared to models without this variable. These findings support the idea that the type of nest built by a species may have been important in the

radiation of passerines, as explicitly suggested by Price and Griffith (2017) and Fang et al. (2018). A transition to less costly nests could have allowed further expansion of a clade into novel environments, and their evolutionary success. Given trends were slightly stronger when using total rather than breeding range, and given there is no link with niche width that is independent of range size, we do not think that open or cavity nests necessarily allow breeding in a wider range of environments, instead we think that nest type could be linked to species range size through other paths (discussed below). Also, the link between range size (or climatic niche) and nest type that we report in the tip-level analyses is not evidence of causation. Another explanation for such link is that the change in nest type occurred *after* a transition in range size. As species colonised new environments that are less thermally demanding, selection could have favoured another type of nest (i.e. an open nest). Our results, however, do not support this latter hypothesis, since transition rates consistently suggest that changes in niche width (and range size) were preceded by changes in nest type. The likely route to the most common combination of characters—broad niches and open nests—is



from ancestors with narrow niches and open nests, indicating first a change in nest type (to open) and a subsequent expansion in range (and hence niche). Thus, our findings suggest that building open nests or using cavities could be important in the geographical expansion and the success of modern Passeri. This idea is further supported by our analysis on extinction rates, which we discuss below.

How could a transition to a different nest type be linked with range and niche expansion? Our study does not offer insights into the precise mechanism, but we propose potential scenarios. One key variable often linked to range size (through abundance) is fecundity (Gaston & Blackburn, 1996; Holt et al., 1997). Higher fecundity can lead to a higher local abundance, and ultimately allow range expansion (Blackburn et al., 2006). Differences in the time taken to build nests could affect the number of nests a species builds in a breeding season (although some birds re-use nests or nesting material), leading to differences in fecundity. Previous studies have reported differences in fecundity between species with open or cavity nests (Barve & Mason, 2015; Böhning-Gaese et al., 2000; Jetz et al., 2008). Testing for differences in fecundity is beyond the scope of our study, but it would be interesting to explore whether the costs of nest building could affect fecundity. An alternative hypothesis for the reduced range of species that build domed nests is that these species have physiologically narrower thermal tolerances, which could result in both, selection for well-insulated nests, and narrower niches. Tropical species are suggested to have narrower thermal tolerances (Linck et al., 2021), and domed nests are common there. However, even within the tropics, species with open and cavity nests have broader ranges than dome-nesting species (Table S10).

Our analyses also suggest that clades with open nests might present lower extinction rates compared to those that build domed nests, offering additional support to the idea of open nests as important in the passerine radiation. We found differences in extinction rates that are consistent across trees, analyses, and linked specifically to nest type. Dome-nesting species (with either small or wide niches/ranges) tend to have higher extinction rates compared to species with open nests. This link cannot be explained through relationships between body size and nest type, since dome-nesting species tend to be smaller and smaller species have been found to have lower (not higher) extinction rates (Bennett & Owens, 1997; Gaston & Blackburn, 1995). We, however, strongly highlight that estimates of extinction rates from molecular phylogenies should be taken with extreme caution (Rabosky, 2010) and differences in rates were small, had high variation and were even smaller when the dataset used included only species with genetic data. In any case, our results do not support the hypothesis of higher speciation rates in species with open nests, and instead show that high

speciation rates are mostly related to small range sizes, which was reported before (Cally et al., 2021). Therefore, the relative success of open-nesting species cannot be attributed to higher speciation rates—supporting Price and Griffith (2017)—but could potentially be linked to a higher risk of extinction of dome-nesting clades.

We also found evidence of higher urban presence for species with open nests, which could potentially be explained by links with range size, since species with open nests tend to have larger ranges, and urban species are also more likely to have large ranges (Reynolds et al., 2019). Our analysis showed, however, that even if range size is controlled for in the model, there is still an independent and significant effect of nest type on urban presence (Table S13). This link could be indirect and explained by selection on variables related to nest type. For instance, previous studies have shown that species living in cities have high rates of annual fecundity (Møller, 2009). If urban habitats constrain the presence of species with low fecundity, that could restrict dome-nesting species. Also, building nests on the ground might be challenging in urban environments (Sol et al., 2014), and species with domed nests more commonly nest on the ground (Hall et al., 2015). On the other hand, the link between urban environments and nest type could be direct: if open/cavity nests require less material than domed nests, then there could be selection against dome nesters in cities. Urban environments could also be more thermally beneficial (e.g. more places with shade or warmer sites—(Lahr et al., 2018)), in which case the thermal benefits of domed nests would not be required. In less harsh environments, species can adjust nest site selection to compensate for the lack of a nest roof (Kauffman et al., 2020; Slagsvold, 1989). Future studies could investigate what is constraining the presence of dome-nesting species in urban environments.

To conclude, our results show an evolutionary link between building certain nest types (open nests) or placing nests in cavities, and traits associated with evolutionary success, such as increased range size, colonisation of urban environments and reduced extinction risk. Our analyses also suggest that transitions between nest types could have enabled such success. Combined, these findings support a scenario explicitly proposed by previous studies (e.g. Fang et al., 2018; Price & Griffith, 2017), where the evolution of open nests is a key innovation in passerines, *sensu* Stroud and Losos (2016) and Rabosky (2017). Namely, although clades with open nests do not present higher speciation rates, having an open nest might be linked with an increase in ecological opportunity, allowing range expansion and the colonisation of novel habitats like cities, and potentially decreasing the risk of extinction. The precise microevolutionary mechanisms that have led to the broad associations reported in this study remain unknown but a fruitful venue for targeted research,

further exploring whether nest building behaviours are linked with fecundity or physiological traits that could affect ecological success. We also highlight the large knowledge gap that still exists about nest-building behaviour, with information lacking for thousands of species and no knowledge on the actual energetic costs of building different nest structures.

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### CONFLICT OF INTEREST

The authors declare no competing interests.

### AUTHOR CONTRIBUTION

IM and IQ designed research; IM, DMP, CL, ACAS and JC collected and extracted data with assistance from OM; IM and IQ performed analyses. IM and IQ drafted the manuscript, and all authors edited and approved the final draft.

### PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13998>.

### OPEN RESEARCH BADGES



This article has earned Open Data Design badge. Data design and analysis plan are available at: <https://doi.org/10.5061/dryad.mpg4f4r25>.

### DATA AVAILABILITY STATEMENT

Data and code used to generate our results have been archived in Dryad (<https://doi.org/10.5061/dryad.mpg4f4r25>).

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