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Predation, Climate and Species Traits Interact to Shape Global Patterns of Avian Nest Architecture

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ABSTRACT

Aim: Bird nest structures are critical for reproductive success and vary widely across species. However, the ecological and evolutionary drivers behind enclosed nests (domes and cavities) remain unclear, with previous studies yielding conflicting results. Leveraging recently available comprehensive nest trait data, we aim to clarify whether enclosed nests primarily function as protection from predation or for regulation of microclimate.

Location: Global.

Time Period: Contemporary (environmental data from 1981 to 2010).

Major Taxa Studied: Birds (Aves).

Methods: Using phylogenetic logistic regression models for 7427 bird species, we examined whether the observed relationships between nest structure and potential environmental drivers and species traits were consistent with the predictions of the two functional hypotheses. To explore potential variations in the function, we built separate models for domes and cavities, as well as for passerines and non-passerines.

Results: Predation risk increases the likelihood of dome use, especially in passerines, where a stronger increase is among the species that are more susceptible to nest predation such as ground-nesting, non-cooperative and larger clutch size species. Climatic effects are more pronounced in cavity nesters, with aridity promoting cavity use among passerines, and both cold and hot temperatures increasing cavity use among small non-passerine species.

Main Conclusions: Different types of enclosed nests correspond to distinct environmental challenges, with dome nests primarily associated with predation pressure and cavities with adverse climatic conditions. These findings contribute to resolving long-standing debates about the functional significance of enclosed nests and offer insights into the evolution of avian nest structures.

1 | Introduction

Breeding in birds involves careful allocation of limited resources across diverse activities, such as searching and competing for nest sites, building nests, incubating eggs, foraging, feeding and caring for nestlings and defending against predators and intruders. All of these activities revolve around the nest, which serves as a central hub that shapes how breeding birds interact with their surroundings. Although nest types are typically highly conserved within species, they vary widely across species, from laying eggs directly on the ground (Cairns 1982; Ingels et al. 1984), competing for and utilizing pre-existing cavities (Aitken and Martin 2008; Botero-Delgadillo et al. 2017; Dhondt 2012; Wiebe et al. 2007), to spending weeks excavating new cavities or constructing complex domed nests (Asokan et al. 2008; Mainwaring and Hartley 2013; Medina et al. 2022; Ritchison 2023). This variation in nesting efforts likely reflects evolutionary trade-offs made to optimize reproductive success (Badyaev and Ghalambor 2001; Reid et al. 2000; Taylor et al. 2024). Therefore, the extra costs required for constructing and occupying enclosed nests, such as domes and cavities, imply that these structures provide breeding benefits that justify the investment.

Two primary hypotheses have been proposed to explain the evolutionary advantage of enclosed nests: protection from predation and regulation of microclimate. Enclosed nests may reduce predation by preventing visual detection and intruder access. Field experiments have found lower predation rates for enclosed nesters relative to open nesters in some systems (Fontaine et al. 2007; Linder and Bollinger 1995; Noske et al. 2008; Okada et al. 2017). Moreover, species with enclosed nests often have larger clutch sizes and longer developmental periods, which collectively imply lower predation risk that allows for extended nesting periods, more frequent feeding visits and reduced opportunities for renesting (Jetz et al. 2008; Remeŝ and Martin 2002; Skutch 1985; Vanadzina et al. 2024).

Enclosed nests may also buffer nests from extreme or variable microclimates. Experimental and comparative studies have shown that enclosed nests can enhance egg warming and embryo growth rates (Martin et al. 2017), enabling small species to breed in colder environments (Mainwaring and Street 2021). Conversely, enclosed nests may shelter eggs from solar radiation, preventing overheating and water loss in hot, dry locations (Colombo et al. 2024; Englert Duursma et al. 2018).

However, existing studies on the functions of enclosed nests vary widely in geographic scope and taxonomic coverage, providing inconsistent support for different hypotheses (Colombo et al. 2024; Englert Duursma et al. 2018; Fontaine et al. 2007; Jezierski et al. 2025; Mainwaring and Street 2021; Martin et al. 2017; Mouton and Martin 2019; Noske et al. 2008; Ocampo et al. 2023; Sheard et al. 2024). While some studies have achieved broad geographic or taxonomic coverage, differences in study design, definitions of nest types and the extent to which species traits and environmental interactions are considered may contribute to the lack of consensus. Absence of a unified comparative framework has hindered a holistic understanding of the key drivers of nest structure evolution and the factors contributing to discrepancies among previous findings. Multiple, newly available comprehensive datasets on extant bird species (Chia et al. 2023; Lumbierres et al. 2022; Rotenberry and Balasubramaniam 2023; Tobias et al. 2022; Tobias and Pigot 2019) have enabled us to revisit the long-standing debate on the function of enclosed nests at a global scale.

In this study, we test two non-mutually exclusive hypotheses regarding the use of enclosed nests—protection from predation and regulation of microclimate—each with specific predictions (Table 1; Figure 1). Under the predation hypothesis, we expect enclosed nests to be more prevalent in environments with high predation risk (Prediction P_A). Furthermore, species more susceptible to predation should exhibit a stronger response to predation risk and thus have a higher tendency to adopt enclosed nests in response to increasing risk than less susceptible species (P_B, P_C, P_D). Specifically, ground nesters are expected to face higher risk due to their exposure to terrestrial predators (Hall et al. 2015; Matysioková and Remeš 2024) (P_B), whereas cooperative breeders should experience lower predation risks due to enhanced ability in detection and defense (Shen et al. 2017) (P_C). Species with larger clutch sizes are likely at a greater disadvantage under high predation risk because they tend to produce fewer broods per season, making the loss of a single brood to predation relatively more costly (Kopsová-Storchová et al. 2017; Skutch 1985; Slagsvold 1984) (P_D).

Under the microclimate hypothesis, enclosed nests should be more common in arid environments with large daily temperature fluctuations and high wind speeds, wherein enclosed nests would stabilize temperature and prevent water loss (Hilton et al. 2004) ($M1_A$). Such nests may also be more prevalent in habitats with more extreme mean temperatures, where they would maintain warmth (Mainwaring and Street 2021; Martin et al. 2017), coolness (Colombo et al. 2024; Englert Duursma et al. 2018) or both ($M2_A$). Furthermore, we expect smaller species, which are less tolerant of harsh climates (Classen et al. 2017; Weathers 1981), to exhibit stronger responses to each adverse climate condition ($M1_B$ and $M2_B$).

By integrating ecological, life-history and environmental predictors into broad-scale models covering over 7400 extant bird species, we aim to identify the key factors associated with the distribution and prevalence of enclosed nest types and to infer their potential functional significance. We perform separate analyses for passerine and non-passerine species, as well as for dome nests and cavities, to uncover potentially distinct mechanisms influencing the adoption of different nest structures. The results can provide insight into how nesting strategies may have diversified and evolved across environments and avian lineages.

2 | Methods

2.1 | Nest Traits and Associated Species Traits

Nest structure and nest site data were sourced from Chia et al. (2023). The seven nest structures defined in the original dataset were grouped into *open* nests (scrapes, platforms and cups), *domes* (dome and dome with tunnel) and *cavities* (including nests excavated by the nesters themselves, termed primary cavities, as well as those placed in naturally formed niches such as rock crevices or burrows dug by other animals, termed secondary cavities), where both domes and cavities are considered as *enclosed* nests. We analyzed primary and secondary cavity nesters together to achieve broader phylogenetic representation and because their nests share similar physical properties that are likely to provide comparable functional benefits. The seven nest sites were grouped into *ground* (on the ground and underground) and *off-ground* (tree, non-tree vegetation, cliff or bank, waterbody and ant or termite nest) locations, indicating higher and lower nest predation risk,

TABLE 1 | Detailed descriptions of the predictions associated with the two hypotheses on the use of enclosed nests.

Code	Prediction for the probability of species using enclosed nests	Rationale
Predation hypothesis		
P_A	Positive effect of predation risk	Species breeding in environments with high predation risk are more likely to use enclosed nests to avoid predators.
P_B	Stronger positive effect of predation risk on ground nesters	Ground-nesting species are more exposed to predators. Therefore, the trend described in P_A should be stronger among ground-nesters than among off-ground nesters.
P_C	Stronger positive effect of predation risk on non-cooperative species	Non-cooperative breeders may exhibit weaker defence capabilities against predators. Therefore, the trend described in P_A should be stronger among non-cooperative breeders than among cooperative breeders.
P_D	Stronger positive effect of predation risk on species with larger clutch sizes	Species with large clutch sizes are more vulnerable to predation due to the relatively high cost of losing a brood. Therefore, the trend described in P_A should be stronger among species with larger clutch sizes than among species with smaller clutch sizes.
Microclimate hypothesis		
$M1_A$	Positive effect of aridity and climate instability	Species breeding in arid and unstable climates are more likely to use enclosed nests to reduce water loss, stabilize daily temperature fluctuation, or reduce exposure to sun and/or wind.
$M1_B$	Stronger positive effect of aridity and climate instability on species with smaller eggs	Smaller eggs and nestlings are more susceptible to water loss and temperature fluctuations. Therefore, the trend described in $M1_A$ should be stronger among species with smaller eggs than among species with larger eggs.
$M2_A$	Negative/positive/U-shaped effect of temperature	Species are more likely to use enclosed nests either in cold conditions to keep warm (negative effect), in hot conditions to keep cool (positive effect), or both (U-shaped effect), leading to linear or U-shaped relationships with mean temperature.
$M2_B$	Stronger negative/positive/U-shaped effect of temperature on species with smaller eggs	Smaller eggs and nestlings are more susceptible to extreme temperatures. Therefore, the relationship found in $M2_A$ should be more pronounced among species with smaller eggs than among species with larger eggs.

respectively. Obligate brood parasites were excluded from the analyses.

We use egg mass, obtained from Rotenberry and Balasubramaniam (2023), rather than adult body mass to reflect the egg and nestling sizes because the latter two are potentially more relevant to nest thermoregulation. Mean clutch size data were obtained from Tobias and Pigot (2019). Cooperative breeding information is binary and was obtained from Jetz and Rubenstein (2011). Due to the time and energy tradeoffs between migration and nest building, as well as the disadvantages migratory species may face in cavity competition due to later arrival at breeding grounds (Kokko 1999; Vanadzina et al. 2024), we include migratory status as a control variable, anticipating a potential negative relationship between migration and the use of enclosed nests. Migratory status is ordinal, with 3 for migratory, 2 for partially migratory and 1 for sedentary and was obtained from the AVONET dataset (Tobias et al. 2022). Egg mass and clutch size were log-transformed before analysis. All traits were matched to the HBW-BirdLife v5 taxonomy.

2.2 | Biotic and Abiotic Environmental Variables

We compiled global layers of predation risk and climatic conditions during the breeding season to test the predation and microclimate hypotheses, respectively. All variables were prepared at 10 × 10 km resolution in the Mollweide equal-area projection and summarized at the species level.

We used predator species richness as a proxy for predation risk. To identify the main predator groups, we used over 3900 global avian nest predation records with predator identities from de Framond et al. (2025). The main predator taxa include mammalian carnivores (Carnivora), rodents (Rodentia), snakes (Serpentes) and bird species with nest predation potential. Avian predators were identified based on taxa with documented nest predation (de Framond et al. 2025), including corvids (Corvidae), birds of prey (hawks and owls), gulls (Laridae) and cowbirds (genus *Molothrus*), as well as species classified as vertivores based on their trophic niches (Tobias et al. 2022). We obtained the breeding range for these predators from the Area of Habitat Maps (Lumbierres et al. 2022)

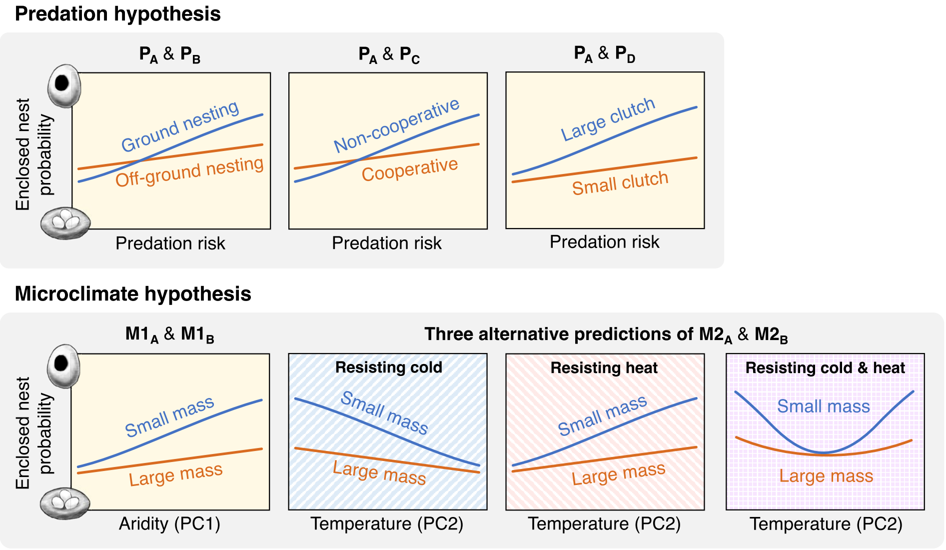

FIGURE 1 | Predictions of the relationships between environmental factors and the probability of using enclosed nests for the predation and microclimate hypotheses. Predator species richness is used as a proxy for predation risk. Aridity and temperature represent the first and second principal components derived from seven climatic variables. These diagrams depict the likelihood of species using enclosed nests across traits and environmental gradients, with the term 'probability' here referring to interspecific trends rather than within-species variation. Codes above each panel correspond to the predictions listed in Table 1. Blue lines indicate traits expected to be more sensitive to predation risk or climatic conditions, whereas orange lines represent less sensitive traits. Clutch size and body mass have been previously identified as being positively and negatively correlated, respectively, with the use of enclosed nests. Therefore, large-clutch and small birds are expected to have a higher probability of using enclosed nests than small-clutch and large birds, respectively, across environmental gradients.

for mammals and birds and from Roll et al. (2017) for reptiles. We then overlaid and summed these data to derive a global nest predator species richness (hereafter predator diversity) map, representing global variation of nest predation risk. To validate that predator diversity can serve as a proxy for predation risk, we compiled published estimates of daily nest predation rates (Kubelka et al. 2018; Smart et al. 2024), totaling 962 species-site records across 550 species, and examined the relationship between predation rate and predator diversity using beta regression (Figure S1). Because observed predation rates already reflect interactions with nest defences, we analysed open- and enclosed-nesting species separately to partially account for the influence of nest structure. Predator diversity was positively associated with predation rate for open-nesting species ($\beta = 0.004$, $p < 0.001$), whereas the relationship was weak for enclosed-nesting species ($\beta = 0.001$, $p = 0.088$), consistent with the presumably protective function of enclosed nests. These results support the use of predator diversity as a coarse proxy for predation risk at a broad spatial scale.

We considered seven climatic variables relevant to nest microclimate regulation, including mean temperature, diurnal temperature range, precipitation, relative humidity, surface solar radiation, vapour pressure deficit and wind speed. All climate data were obtained from CHELSA v2.1, averaged over the years 1981–2010 (Karger et al. 2017). Diurnal temperature range was calculated as the difference between mean maximum daily temperature and mean minimum daily temperature. We computed the mean values of these climatic variables across the breeding season, which was defined as March to June in the northern hemisphere above 23.5° N, September to December in the southern hemisphere below 23.5° S, and year-round in the tropics (between 23.5° N and 23.5° S) (Vanadzina et al. 2023). To validate this definition, we examined over 212,000 georeferenced egg collection records from open databases (iDigBio, https://www.idigbio.org/; GBIF, https://www.gbif.org/; Atlas of Living Australia, https://www.ala.org.au, extracted between July 2024 and April 2025) and confirmed that the timing of egg collections broadly aligns with our breeding season definition (Figure S2).

For each environmental layer (predator diversity and climatic variables), we extracted mean values associated with each bird species' breeding range (Lumbierres et al. 2022) to obtain species-level data, using only resident and breeding season distribution ranges for migratory species. We then performed principal component analysis (PCA) to extract the first two principal components (PCs) of the climatic variables, which together explain 84.7% of the variance (Table S1; Figure S3). PC1, hereafter 'aridity', is positively correlated with diurnal temperature range, solar radiation and wind speed and is negatively correlated with precipitation and relative humidity. PC2, hereafter 'temperature', is strongly correlated with mean temperature (Pearson's correlation coefficient $r = 0.96$).

2.3 | Phylogenetic Regression Models

To analyse the effect of traits and environmental factors on nest structure while accounting for the phylogenetic closeness among bird species, we built phylogenetic logistic regression models (Ives and Garland 2010). To examine potential functional differences between domes and cavities, we built three sets of models with different definitions of the response variable (Y). In the *Enclosed* models, $Y = 1$ if the species can build either domes or cavities. In the *Dome* models, $Y = 1$ if the species can build domes. In the *Cavity* models, $Y = 1$ if the species can build cavities. In all models, $Y = 0$ if the species only builds open nests. We also built three sets of models for different subsets of species to examine potential distinct strategies employed by the passerine clade. The *All Species* models include all species with available data, the *Passerine* models include only species in the order Passeriformes and the *Non-Passerine* models include all species except passerines. For each of the resulting nine model sets (3 response variables x 3 species subsets), we built two separate models: one to test the predation hypothesis and the other to test the microclimate regulation hypothesis. The predation model included predator species richness and its interactions with three species traits, which are ground-nesting status, cooperative breeding status and clutch size. The microclimate regulation model includes aridity, mean temperature and its quadratic term (to capture the potential non-linear, including U-shaped, relationships) and their interactions with egg mass. Migratory status was included as a covariate in both models as a control factor.

We constructed a consensus phylogenetic tree from 1000 trees of the Hackett backbone obtained from Birdtree.org (Jetz et al. 2012), using the majority rule for tree topology and the least squares method for edge length estimation with R package *phytools* (Revell 2012). We built phylogenetic logistic regression models using R package *phyloglm* (Ho and Ané 2014) with the method 'logistic_MPLE'. For each model, we bootstrapped 1000 times to derive 95% confidence intervals. To reduce the risk of convergence failures or convergence on local minima, we generated 300 random sets of initial model coefficients (βs) using ranges informed by model fits initialized with zero valued coefficients and selected the coefficient sets yielding the lowest Akaike information criteria (AIC) scores as starting points for subsequent bootstrap procedures. The initial phylogenetic correlation parameter α was set as 1/Tmax where Tmax represents the age of the root in the phylogenetic tree. To address phylogenetic uncertainty, we also built separate models using 1000 different phylogenetic trees of the Hackett backbone to derive 95% confidence intervals, using the same selected sets of initial coefficients. We excluded models that did not converge, which were less than 10% for each model set.

All independent variables were standardized to a mean of zero and a standard deviation of one. The BirdLife-BirdTree crosswalk data (Tobias et al. 2022) was used to match all species-level datasets prepared in HBW-BirdLife v5 taxonomy to BirdTree taxonomy. When multiple BirdLife species were associated with one BirdTree species, the values of each independent variable, including binary and ordinal traits, were averaged across the BirdLife species. For the response variable (nest structure), species were coded as 1 when at least one matched species used the target nest type (enclosed nest, dome, or cavity, depending on the model) and coded as 0 when only open nests were observed among the matched taxa. All analyses were performed in R version 4.3 (R Core Team 2023).

3 | Results

3.1 | Nest Traits and Associated Species Traits Across Bird Phylogeny

A total of 7427 species are included in the analysis, covering 74.3% of species according to the BirdTree taxonomy. Of these, 44.2% are capable of building or using enclosed nests; more specifically, 24.8% can build domes and 32.7% can build or use cavities (see Table S2 for detailed species counts by model). The nest type and other species traits generally show strong phylogenetic signals but exhibit considerable variation within clades (Figure 2). Both open and enclosed nests, as well as both ground and off-ground nests and cooperative breeding, have emerged multiple times across the phylogeny. Correlations among all traits and the environmental predictors are reasonably low (Table S3).

3.2 | Enclosed Nests for Reducing Predation Risk

Across all species, we found support for three of the four predictions of the predation hypothesis (black bars in Figure 3a; partial effect plots in Figures S4–S6), where species breeding in locations with higher predator diversity are more likely to use enclosed nests (P_A), with stronger effects among ground nesters (P_B, Figure S5a) and non-cooperative breeders (P_C, marginal effect, Figure S5b). Further examination of submodels revealed that the support for the predation hypothesis is most evident in passerines building dome nests. Among passerines, dome nest use increased much more strongly with predator diversity among ground nesters than off-ground nesters, well aligning with Prediction P_B (Figure 4b). Similar interactions were observed for non-cooperative breeders and species with larger clutches, in line with Prediction P_C and P_D (Figure 4c,d), though with smaller effect sizes and greater uncertainty. These patterns among dome-nesting passerines are generally consistent across alternative model specifications (Figure S7). Overall, other than dome nests among passerines, no clear patterns support the predation hypothesis in the use of cavities or among non-passerine lineages (Figure 4a).

3.3 | Enclosed Nests for Regulating Microclimates

The effects of climatic variables are inconsistent across species groups, providing little overall support for the microclimate hypothesis. Submodel analyses indicate that the climatic effects are more evident in cavity use than in dome nests (Figure 4a), with different climatic factors influencing nest use in different ways across species groups. For temperature, cavity nests become more common at both low and high thermal extremes among species with smaller eggs (Figure S6e), particularly at low temperatures, but not among those with larger eggs. This is partially consistent with the $M2_B$ prediction. Although both passerine and non-passerine models show partial support (Figure 4a), the effect is more evident in non-passerines (Figure 4f) than in passerines (Figure S6o). For aridity, cavity use also increases under drier conditions, again most prominently among species with smaller eggs (Figure 4e), aligning with predictions $M1_A$ and $M1_B$. This pattern persists in the passerine model but not the non-passerine model, suggesting that aridity effects may be more evident in passerines (green bars in Figure 3c). The temperature and aridity trends are retained in the alternative models fitted with 1000 candidate trees (Figures S7 and S8).

3.4 | Effects of Species Traits and Phylogenetic Uncertainty

Several traits previously identified as correlating with the use of enclosed nests show significant effects in our models (Figure 3).

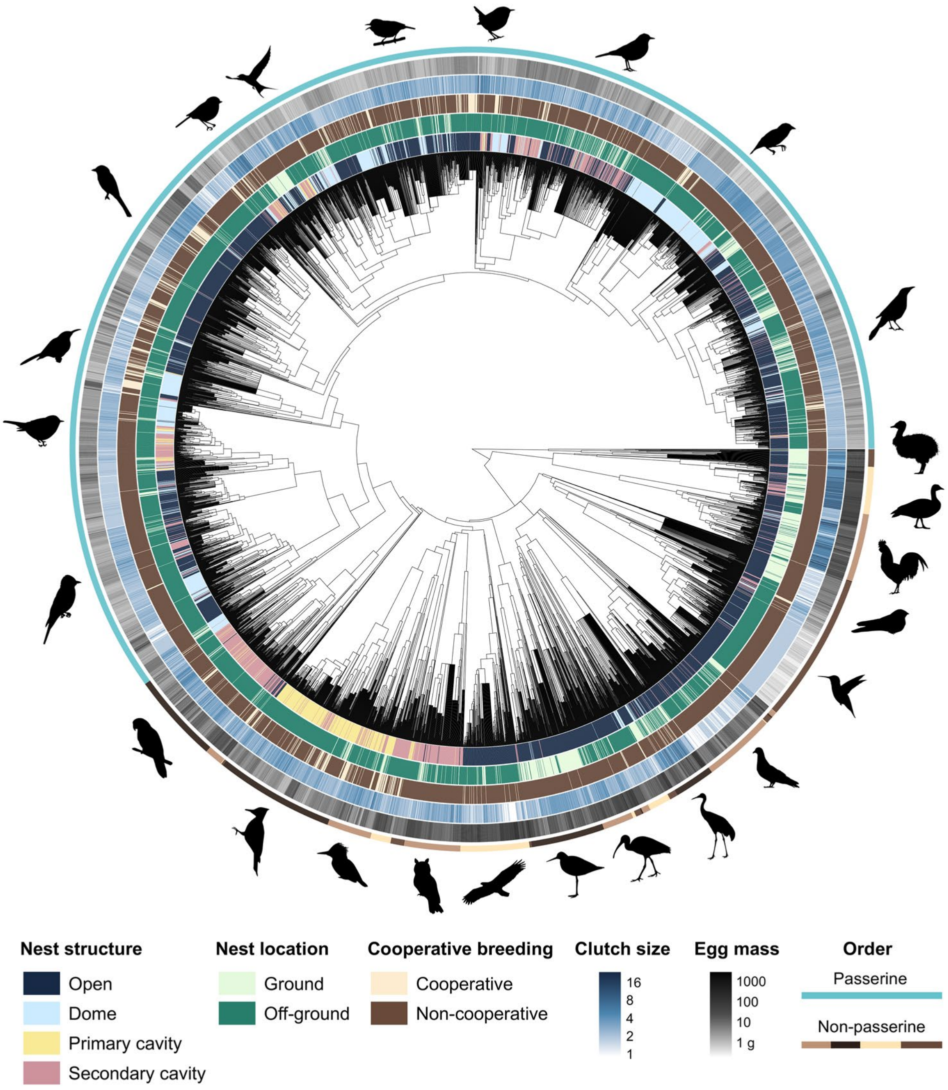

FIGURE 2 | Distribution of species traits across the phylogenetic tree. Each of the 7427 species in the analysis is represented by a tip of the tree. The coloured rings illustrate different traits, from inner to outer: nest structure, nest location, cooperative breeding behaviour, clutch size and egg mass. The outermost narrow ring denotes the classification of species to taxonomic orders, with alternating shades differentiating adjacent orders. All silhouette images are from the public domain and obtained from PhyloPic.org.

Species with larger clutches are more likely to use enclosed nests, whereas migratory species are less likely to do so, both aligning with expectations. Egg mass has distinct effects on the use of domes and cavities: domes tend to be built by species with smaller eggs, whereas cavities are used by species with larger eggs. Moreover, cavity nests are less common among ground nesters compared to those nesting off-ground, likely due to differences in the availability of cavity sites. All model coefficients, including the supplementary models, can be found in Tables S4–S11; Figures S8–S10.

4 | Discussion

Using data from over 74% of the world's bird species, we examined two key hypotheses regarding the function of enclosed nests: protection from predation and regulation of microclimate. Overall, no single function consistently explains variation across phylogeny or across different enclosed nest structures. Rather, domes and cavities serve distinct adaptive roles. The use of domes is primarily related to predation risk, particularly for passerines, whereas the use of cavities appears to help adapt to harsh climates, especially among smaller species with limited thermoregulatory capacity.

Previous studies testing the functional significance of enclosed nests have reported varying support for predation and thermoregulation hypotheses, with evidence differing across nest structures, taxa, geographic regions and ecological contexts (e.g., Colombo et al. 2024; Duursma et al. 2018; Fontaine et al. 2007; Mainwaring and Street 2021; Martin et al. 2017; Mouton and Martin 2019; Noske et al. 2008). By jointly modelling species traits, environmental variables and their interactions across broad phylogenetic coverage and different enclosed nest categories, our study reveals context-dependent associations suggesting that the use of enclosed nests depends on life-history characteristics, breeding environments and the specific enclosed nest structures considered. These findings

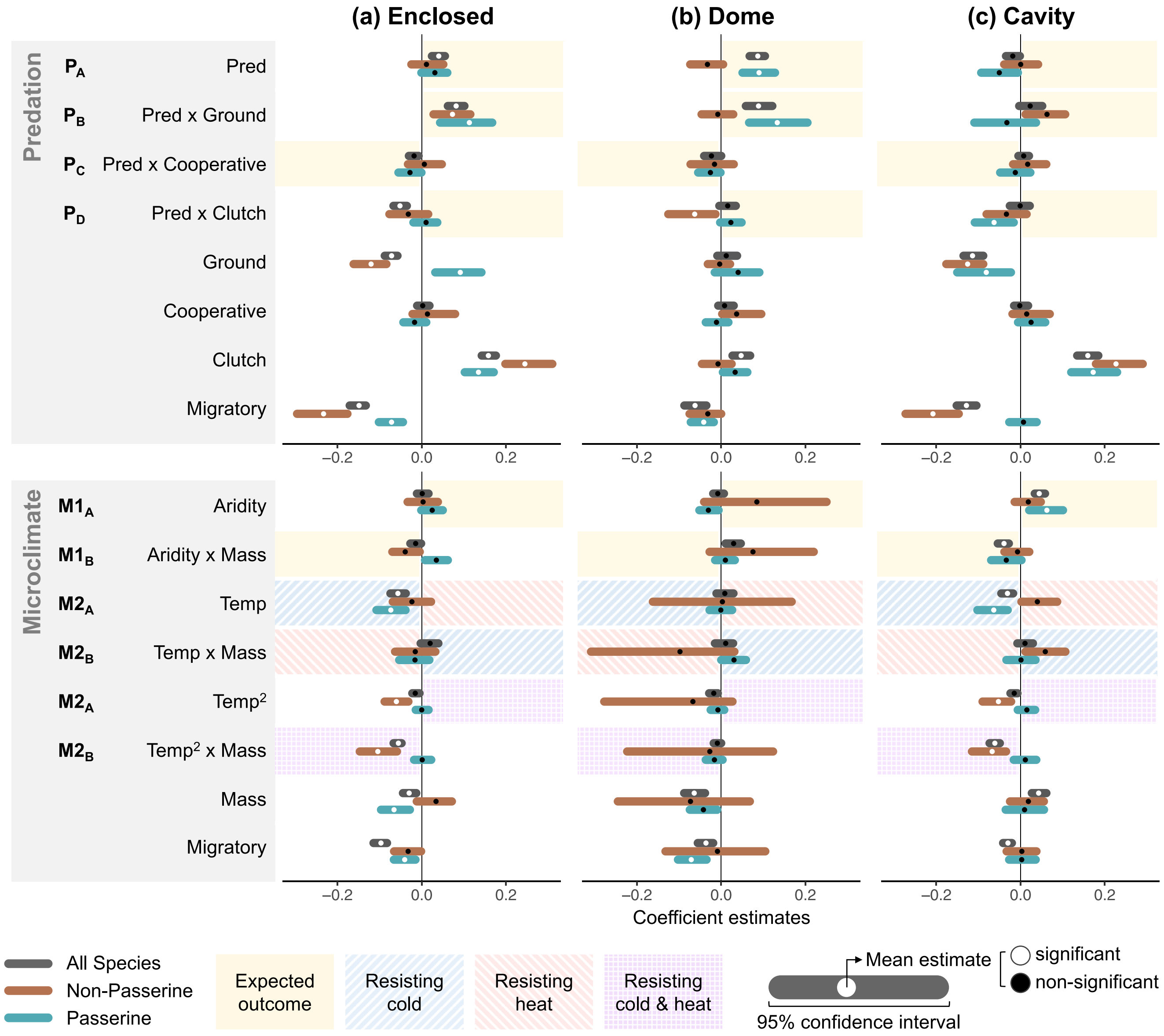

FIGURE 3 | Coefficient estimates for the predictor variables in the predation and microclimate models for nine model sets for the use of enclosed, dome and cavity nests by all bird species, non-passerines and passerines. All predictors were standardized so the coefficients represent effect sizes. The mean estimate of effect sizes with significant effects (95% confidence intervals not crossing zero) are marked in white, whereas nonsignificant effects are marked in black. Yellow shades indicate expected outcomes. The three alternative expectations for Prediction M2 are presented as blue right-leaning stripes, red left-leaning stripes and purple grids, indicating that enclosed nests are used for resisting cold, heat, or both, respectively (as in Figure 1).

broadly align with recent large-scale comparative studies highlighting differing ecological associations and evolutionary trade-offs among enclosed nest types (Jezierski et al. 2025; Sheard et al. 2024; Vanadzina et al. 2024). Through an integrative framework, our study further improves our understanding of how multiple evolutionary solutions shape the macroevolution of enclosed nests.

4.1 | Domes for Reducing Predation Risk

Dome nests in passerines seem to serve as a strategy against predation, as they are more prevalent in regions with higher predator diversity, and this effect is more pronounced among species that are more susceptible to nest predation (P_A-P_D in Figure 4b–d). This finding aligns with previous local-scale empirical and experimental studies in North America (Linder and Bollinger 1995) and Australia (Noske et al. 2008; Okada et al. 2017), which reported lowered predation rates for dome nesters compared to open cup nesters in similar environments. Additional evidence at the intraspecific level was found in magpies (*Pica pica*), one of the few well-studied bird species to build both cup (open) and dome (enclosed) nests. Magpies with dome nests experienced significantly less disturbance from predators than did magpies with cup nests (Baeyens 1981). Moreover, magpies constructed denser dome roofs during periods of greater predation risk (Quesada 2007), further supporting the protective role of domes. Our results extend these findings by presenting macroecological patterns that reaffirm the predation hypothesis from a global biogeographic perspective.

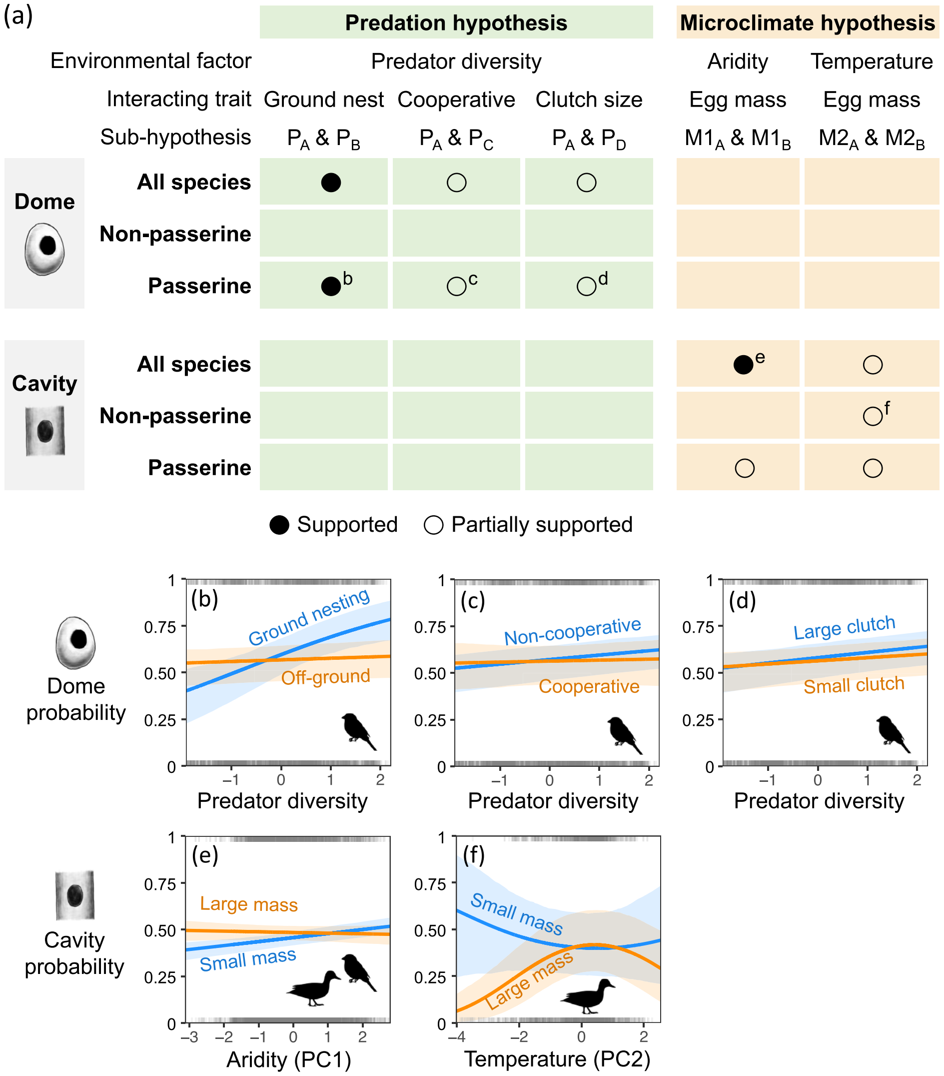

FIGURE 4 | Summary of hypothesis evaluations and partial effects of environmental variables on the probability of using enclosed nests. (a) Summary of model support for each sub-hypothesis. A hypothesis is considered supported when both the main environmental effect and its interaction with the focal species trait show significant results consistent with predictions, and partially supported when one of the effects is significant and consistent with predictions. Superscript letters refer to panels b–f, which visualize the corresponding effects. (b–f) Partial effects of selected environmental variables on dome- and cavity-nesting probability for birds with contrasting traits. Shaded areas represent 95% confidence intervals, derived from 1000 bootstrapped models. Large and small clutch sizes or egg masses correspond to the 90th and 10th percentiles of the trait values. Rugged marks along the top and the bottom of each panel indicate observed data points. Environmental variables are presented in standardized values. Partial effect plots for all global consensus tree models can be found in Figures S4–S6. Expected outcomes are depicted in Figure 1. Silhouette bird images are from the public domain and obtained from PhyloPic.org.

In particular, the predation-related increase in dome use is especially evident among ground-nesting passerines, which face greater exposure to terrestrial predators. These species are more likely to use domes compared to off-ground nesters (Ground in Figure 3b), consistent with previous findings from Old World Babblers (Hall et al. 2015). This tendency is further strengthened in environments with higher predator diversity (Figure 4b), suggesting the use of domes as a protective measure in response to the higher susceptibility of ground nests. In contrast, off-ground nesters do not show increased dome use in high-predator environments, likely because elevated nesting sites already reduce predation risk (Matysioková and Remeš 2024; Piper and Catterall 2004). For these species, the additional investment in domes may be unnecessary or even detrimental, as the increased size of domes compared to cup nests could increase visual detectability in trees (Mouton and Martin 2019).

We recognize that the observed correlation between predator diversity and dome use may reflect confounding environmental effects. For example, regions with high predator diversity may also have denser vegetation, increasing nesting material availability, which is important for building a dome. We compared models using a more general environmental predictor, i.e., latitude, as an alternative proxy of predation risk, and found that predator diversity provided a better model fit than latitude, especially for those models supporting the predation hypothesis (Table S12), suggesting that predator diversity likely captures meaningful variations beyond broad environmental gradients. Furthermore, while such environmental correlations could influence nest structure independently of predation risk, the interaction effect we observed—where the predation signal is amplified specifically among ground-nesting species—is less likely to be driven by these broad environmental gradients alone. Similarly, we observed weaker but generally consistent trends suggesting that non-cooperative breeders and species with larger clutch sizes are more likely to use dome nests in areas of high predator diversity (Figure 4c–d, Figures S7 and S11). These patterns align with predictions that species with fewer anti-predator defences or greater reproductive investment per brood would favour nest structures offering greater protection. Together, these multiple lines of evidence strengthen the inference that domes serve a predation protection function, even in the presence of potential confounding effects.

We did not find evidence supporting the thermoregulatory benefit of domes. This aligns with a recent study on the nests of four European songbird species, which reported no significant difference in thermal insulation properties between dome and cup nests (Deeming et al. 2024). However, contrary to our results, previous studies have found that domes are associated with dry and hot climates among tanagers in the Neotropics (Colombo et al. 2024) and passerines in Australia (Duursma et al. 2018). These discrepancies may reflect regional differences in climatic selection pressures or limitations in our ability to capture fine-scale breeding environments. In particular, breeding season variability across regions such as the Neotropics and Australia may weaken the accuracy of our climate predictors, which are based on broad breeding-season definitions. Without detailed global data on temporal breeding patterns, our models may overlook climatic conditions that influence nest function at a local scale. We acknowledge this limitation and encourage future work that incorporates fine-scale phenology and nest microhabitat data to improve understanding of how dome nests function under different environmental pressures.

4.2 | Cavities for Microclimate Regulation

Contrary to dome nests, cavities appear to play a more prominent role in regulating nest microclimate (Figure 3c). The interaction effects between egg mass and both aridity and temperature indicate that cavity use under arid and thermally extreme conditions is especially common among smaller species. This pattern supports the idea that cavities provide thermal insulation, helping buffer nests against cold, heat and large diurnal temperature fluctuations typical of arid environments.

These findings align with previous studies showing that cavity and burrow nests buffer against ambient temperature fluctuations and increase minimum temperatures within the nests (Combrink et al. 2017; Ke and Lu 2009; Maziarz et al. 2017; Michielsen et al. 2019; Sudyka et al. 2023). Biogeographically, the high percentage of cavity-nesting bird species in New Zealand, despite few terrestrial predators, suggests that thermoregulation might be a more important factor than predation in driving the pattern (Rhodes et al. 2009). Structurally, it makes sense that natural cavities and burrows offer better insulation due to thick substrates like tree trunks or soil, outperforming thin structures such as domes or artificial nest boxes (Combrink et al. 2017; Sudyka et al. 2023).

The association between cavity use and climate could partly reflect landscape features that covary with climate. For example, sparse vegetation in harsh environments could increase reliance on cavities for protection against predators. However, this does not explain why the increase in cavity use under harsh conditions occurs mainly among species with smaller eggs. Because body size (strongly correlated with egg mass) shows no consistent relationship with nest predation risk—larger species may face fewer potential predators but can experience higher risk due to more conspicuous nests and longer developmental periods (Mouton and Martin 2019; Unzeta et al. 2020)—predation alone seems insufficient to explain this pattern. Cavity types also vary across landscapes: tree hollows and riverbank burrows are more common in forests and humid regions, whereas rock crevices may be more prevalent in coastal cliffs, rocky deserts, or tundra. Yet, it remains unclear how variation in cavity availability could generate the stronger climatic associations observed among smaller-egged species. Taken together, these considerations suggest that the observed patterns likely reflect, at least in part, the thermoregulatory benefits of cavity nesting in extreme environments.

To clarify whether the observed climatic associations are driven by primary and secondary cavity use, we conducted additional analyses separating these two strategies. Patterns observed in the combined cavity models were largely driven by secondary cavity nesters, which showed consistent associations with climatic variables, whereas primary cavity nesting showed no significant relationships with either climate or predation proxies (Figure S12). This likely reflects the strong phylogenetic clustering of primary cavity nesters (Figure 2), resulting in limited independent evolutionary transitions and reduced statistical power in phylogenetically controlled models. Thus, the climatic signals detected for cavity nesting mainly reflect secondary cavity use. Future work using transition-based approaches may better resolve drivers of such phylogenetically clustered traits.

Several inconsistencies in results warrant further examination. First, given the greater variability of breeding season in the tropics and the Southern Hemisphere, we conducted supplementary analyses restricted to species breeding exclusively in the Northern Hemisphere ($n = 2801$). The effect of aridity on the use of cavities observed in the global dataset disappeared in these biogeographically constrained models (Figures S9–S11), suggesting the global pattern could be largely driven by Southern Hemisphere species. Second, although species with smaller eggs supported the microclimate hypothesis, those with larger eggs exhibit the opposite trend (Figure 4f). This unexpected pattern might reflect environmental or phylogenetic constraints rather than adaptive responses. For example, in alpine or desert landscapes, suitable substrates for constructing large cavities might be limited. Further biome-specific studies are needed to disentangle these potential causes.

While our hypothesis framework did not find strong support for the idea that cavities reduce predation risk, as none of the predation-related predictors or interactions were significant, we did find a strong positive correlation between clutch size and cavity use (Clutch in Figure 3c), a pattern often interpreted as evidence that cavities allow for greater reproductive investment by reducing predation risk (Jetz et al. 2008; Jetz and Rubenstein 2011; Lack 1947; Vanadzina et al. 2024). Within our framework, however, support for the predation hypothesis is evaluated primarily through interaction effects rather than first-order associations; therefore, this result is not treated as direct support. We acknowledge that predation may still play a role in driving cavity nesting, but cannot rule out other mechanisms underlying these correlations. For example, Martin (1993) demonstrated that large clutch sizes in cavity-nesting birds often reflect nest site limitation and unpredictable breeding opportunities, particularly those depending on existing cavities; under this life-history framework, increased clutch size may represent greater reproductive investment per breeding attempt driven by constraints on nesting opportunities rather than a direct response to reduced predation risk.

4.3 | Implications for Nest Structure Evolution

The finding that cavities serve to regulate nest microclimate, whereas domes reduce predation in passerines, sheds light on the potential evolutionary mechanisms driving nest structure development. The common ancestor of modern birds likely made scrapes on the ground (Fang et al. 2018), as seen in several basal bird lineages such as ostriches and tinamous. A clade of cavity nesters (Afroaves) emerged around 63 million years ago (Stiller et al. 2024) during a period of relatively low global temperatures (Scotese et al. 2021), possibly as an adaptation to the harsh climatic conditions. Over time, species that initially relied on pre-existing cavities (secondary cavity nesters) began evolving into cavity excavators (Fang et al. 2018), possibly as a strategy to reduce competition for limited nesting sites. Most of the cavity nesters also nest off ground, likely as a way to avoid predators.

Passerines emerged in the Australian landmass around 50 million years ago (Stiller et al. 2024) during a time of particularly warm climate conditions (Scotese et al. 2021). We postulate that the warm climate relaxed the need for thermoregulation in nests, diminishing the reliance on cavities and facilitating the evolution of domes. Constructing domes allows passerines to nest on the ground while still protecting themselves from predation. Later, cup nests evolved from domes, primarily placed off-ground to mitigate predation risk and became prevalent in passerines as a cost-effective nesting strategy (Medina et al. 2022; Price and Griffith 2017). The transition from open or dome nests to cavities occurred multiple times in both passerine and non-passerine lineages in more recent periods, potentially driven by the decline of global temperature and expansion of the global temperature range (Scotese et al. 2021), or as an adaptation to changes in predation pressure.

4.4 | Limitations

We acknowledge several limitations of this study. First, using predator diversity as a surrogate of nest predation risk provides only a rough approximation of the actual patterns. Important aspects such as predator abundance, foraging strategies like sensory modalities (e.g., visual or olfactory detection) and habitat structure, all affect nest detection and predation but are not captured by our metric. Nonetheless, predator diversity remains the most practical option for global analysis. Throughout the discussion, we have addressed potential confounding effects from correlated environmental variables and explained why these are unlikely to overturn our key findings. As more data become available, future work will be better positioned to refine these models with more accurate representations of predation risk.

Second, although we included several traits relevant to predation risk and energetic costs, other potentially important factors such as colonial breeding behaviour that may enhance collective defence, the position of nests concealed in the surrounding microhabitats that may reduce detection risk and the activity level of adults near the nest that may increase detection, were not accounted for due to a lack of comprehensive data. More broadly, nest function likely emerges from the interaction of multiple co-evolving traits, including behavioural, ecological, life-history and multiple aspects of nest characteristics, rather than from nest structure alone (e.g., Jezierski et al. 2025). Because these traits may jointly shape both predation risk and microclimatic conditions in context-dependent ways, their omission may have weakened contrasts among nesting strategies and thus weakened the detectable influence of predation or climate in our models, making our conclusions conservative.

Third, the fixed breeding periods we used do not fully capture the timing of reproduction for all species, especially in tropical regions and the Southern Hemisphere where breeding seasons are more variable, often in response to precipitation (Duursma et al. 2017; Stouffer et al. 2013). This mismatch could introduce noise into our analysis of climate effects, particularly in the effects of aridity. To assess the potential influence of this limitation, we conducted a sensitivity analysis restricted to species breeding in the Northern Hemisphere, which yielded generally consistent results (Figures S9–S11). Although species-specific breeding phenology data are not currently available at the global scale, future efforts to include that information would greatly improve the precision and interpretability of the current analysis.

Fourth, like most comparative macroecological studies, our models present correlations rather than direct causality, and as such, our findings could be influenced by unmodeled covariates. Despite this limitation, the statistical interaction terms we modelled provide clear additional evidence supporting our conclusions, which were made with careful consideration of potential confounding effects. Considering these interactions alongside first-order effects may help explain why previous studies have reported differing patterns.

Lastly, our focus on interspecific variations across large phylogenetic and geographic scales means that species-specific adaptations or regional nuances may not be fully captured, leaving room for more detailed studies of intraspecific variation and patterns among smaller clades or smaller geographic regions to provide further insights into the diverse adaptive mechanisms underlying bird nest evolution.

5 | Conclusion

This study helps resolve the long-standing debate on the function of enclosed nests and provides insights into the potential drivers behind the evolution of enclosed nests among bird species globally, highlighting the function of domed nests in reducing predation risk and the role of cavities in regulating nest microclimate. Our findings also have important conservation implications. For example, they underscore the importance of considering thermal properties when installing artificial nest boxes, as they often fall short of the insulation provided by natural cavities and can become ecological traps for cavity nesters (Sudyka et al. 2023). Additionally, with predation pressures shifting under climate change (Romero et al. 2018), ground-nesting birds with open nests in regions of heightened risk may be especially vulnerable due to the lack of protective structures. As climate change intensifies aridity and temperature variability (IPCC 2023), non-cavity nesters could be disproportionately impacted. Although further research is necessary to draw species-specific conclusions, this study offers a macroecological view of the potential impact of ongoing global changes on nesting birds.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The compiled dataset and code used in the study are archived at Zenodo (https://doi.org/10.5281/zenodo.20494320).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Loadings of the principal components of seven climatic variables. **Table S2:** Counts and percentages of enclosed- and open-nesting species in each model set. **Table S3:** Pairwise Pearson correlation coefficients between model predictors, including species traits and environmental variables. **Table S4:** Model coefficients for the main predation models fitted using the consensus tree. **Table S5:** Model coefficients for the predation models fitted using 1000 phylogenetic trees. **Table S6:** Model coefficients for the predation models restricted to Northern Hemisphere species fitted using the consensus tree. **Table S7:** Model coefficients for the predation models restricted to Northern Hemisphere species, fitted using 1000 phylogenetic trees. **Table S8:** Model coefficients for the main microclimate models fitted using the consensus tree. **Table S9:** Model coefficients for the microclimate models fitted using 1000 phylogenetic trees. **Table S10:** Model coefficients for the microclimate models restricted to Northern Hemisphere species, fitted using the consensus tree. **Table S11:** Model coefficients for the microclimate models restricted to Northern Hemisphere species, fitted using 1000 phylogenetic trees. **Table S12:** AIC values of the nine fitted models using different proxies of predation risk. **Figure S1:** Relationship between predator species richness and daily nest predation rate across all species, open-nest species and enclosed-nest species. **Figure S2:** Seasonal and latitudinal distribution of global egg collection records. **Figure S3:** PCA biplot of the climatic variables. **Figure S4:** Partial effect plots of the Enclosed models. **Figure S5:** Partial effect plots of the Dome models. **Figure S6:** Partial effect plots of the Cavity models. **Figure S7:** Partial effect of selected environmental variables on the probability of using dome or cavity nests among birds with different species traits. **Figure S8:** Model coefficient estimates for the global models fitted using 1000 phylogenetic trees. **Figure S9:** Coefficient estimates for models restricted to Northern Hemisphere species fitted using the consensus tree. **Figure S10:** Coefficient estimates for the models restricted to Northern Hemisphere species, fitted using 1000 phylogenetic trees. **Figure S11:** Partial effect of selected environmental variables on the probability of using dome or cavity nests among birds with different species traits for models restricted to Northern Hemisphere species, fitted using (a) consensus phylogenetic tree and (b) 1000 individual phylogenetic trees. **Figure S12:** Coefficient estimates for models comparing (a) primary cavity nesters and (b) secondary cavity nesters with open nesters, fitted using the consensus tree.