

# Seasonal migration and the evolution of an inverse latitudinal diversity gradient in shorebirds

Paul Dufour<sup>1,2</sup>  | Pierre-André Crochet<sup>1</sup> | Fabien L. Condamine<sup>3</sup>  | Sébastien Lavergne<sup>4</sup>

<sup>1</sup>CEFE, CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France

<sup>2</sup>Gothenburg Global Biodiversity Centre, Göteborg, Sweden

<sup>3</sup>Institut des Sciences de l'Évolution de Montpellier, UMR 5554, CNRS, Université de Montpellier, IRD, EPHE, Montpellier, France

<sup>4</sup>Laboratoire d'Écologie Alpine, Univ. Grenoble Alpes, CNRS, Univ. Savoie Mont Blanc, CNRS, LECA, Grenoble, France

## Correspondence

Paul Dufour, CEFE, CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France.

Email: [paul.dufour80@gmail.com](mailto:paul.dufour80@gmail.com)

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## Abstract

**Aim:** While the evolution of seasonal migration and its association with biogeography have been the subject of numerous studies, its influence on species diversification has rarely been examined. The aim of this study is to explain the atypical latitudinal diversity gradient in shorebirds: did seasonal migration influence diversification and did the gradient evolve from higher in situ diversification or repeated transitions?

**Location:** Global.

**Time Period:** Palaeogene to present.

**Major Taxa Studied:** Order Charadriiformes (shorebirds and allies). Shorebirds include the species with the longest annual migrations in birds and exhibit an inverse latitudinal diversity gradient, with more species breeding toward higher latitudes.

**Methods:** We first assessed the temporal and geographical framework of the evolution of migration using a newly reconstructed time-calibrated phylogeny, and using the fossil record as a complementary source of information. We then used hidden state speciation and extinction models to test whether diversification and thus the latitudinal diversity gradient has been shaped by migratory behaviour or species latitudinal distribution.

**Results:** We found that the ancestor of Charadriiformes was likely a tropical year-round resident and that the current clade's distribution of diversity was not shaped by dispersal events out of the tropics but rather by higher in situ diversification in temperate biomes compared to tropical biomes. Seasonal migration did not affect diversification rate in our models. However, the evolution of seasonal migration seems to be a prerequisite to breed in temperate biomes, indirectly enabling the higher diversification observed in temperate biomes.

**Main Conclusions:** Our results bring original insights into how the migratory behaviour acted as a precursor in the diversification and biogeographical history of a large bird clade, ultimately shaping an atypical latitudinal diversity gradient.

## KEYWORDS

biogeography, Charadriiformes, diversity gradient, latitude, phylogeny, seasonal migration

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## 1 | INTRODUCTION

One of the most conspicuous biogeographical patterns on Earth is the decrease of species diversity in most groups of organisms from low to high latitudes (Hillebrand, 2004; Mannion et al., 2014). The origins of this latitudinal diversity gradient (LDG) have been the subject of much research and debate over the last 50 years (Jablonski et al., 2017; Pianka, 1966; Willig et al., 2003) but no consensus has emerged so far (see Pontarp et al., 2019). The avian class is no exception to this rule (Pulido-Santacruz & Weir, 2016; Rabosky et al., 2015), as most birds are year-round tropical resident species (Somveille et al., 2013). However, some avian orders, for example, Procellariiformes or Anseriformes (Cerezer et al., 2022), exhibit an inverse latitudinal diversity gradient, meaning their diversity is highest towards temperate zones (Kindlmann et al., 2007). These two avian orders share a common property: they both have a high proportion of seasonal migratory species.

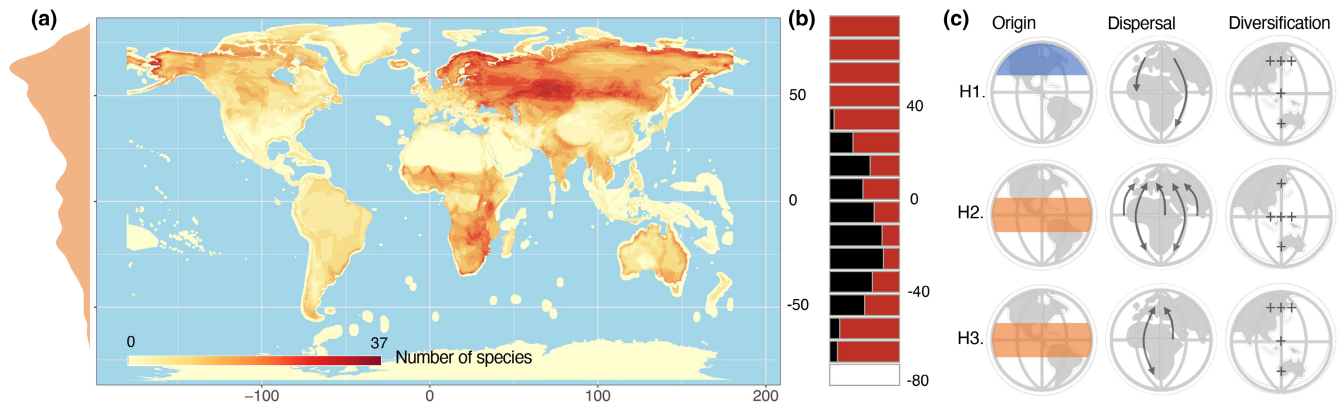
How seasonal migration influences diversification processes remains poorly understood (Fudickar et al., 2021) and seasonal migration has mostly been regarded as a barrier to speciation because it may prevent genetic divergence between populations (Claramunt et al., 2012; de Freitas et al., 2022; Helbig, 2003). In the context of the inverse latitudinal diversity gradient, the emergence of long-distance seasonal migration might have influenced the diversification dynamics of different clades. First, the emergence of seasonal migration might have indirectly facilitated species to breed in high latitudes, thus promoting the colonization of novel biogeographical regions, eventually creating ecological opportunities, and boosting species diversification (Liedvogel & Delmore, 2018). Second, the seasonal migration might have directly spurred species divergence by favouring dispersal or by allowing long-distance colonization events (e.g. through migratory drop-off, meaning shifts towards sedentariness), thus fostering speciation (Gómez-Bahamón et al., 2020; Rolland et al., 2014).

Several theories are still debated to explain the evolution of seasonal migration (Louchart, 2008; Salewski & Bruderer, 2007; Winger et al., 2019). The most widely accepted 'southern-home' theory proposes that long-distance migrants evolved from resident tropical species through the poleward shift of breeding ranges (Cox, 1968; Gauthreaux, 1982; Levey & Stiles, 1992; Rappole, 1995). The 'northern-home' theory proposes that migration evolved from resident species in temperate climate, shifting their non-breeding grounds to lower latitudes as a response to seasonality of climate and resources (Bell, 2000; Gauthreaux, 1982). This latter view was refined by Louchart (2008) as 'shifting-home' to integrate the dynamism of the palaeoclimate history such as the southward retraction of the tropical biomes. More recently, Salewski and Bruderer (2007) and Winger et al. (2019) insisted that the mechanisms of migration evolution and the biogeographical origin of migratory lineages should be distinguished; they summarized that migration could evolve either (1) following increased seasonality in geographically stable breeding areas, or (2) after breeding range shifts into more seasonal environments (Bruderer & Salewski, 2008). While it is important to examine separately the biogeography and the evolution

of migration, we can expect an association between mechanisms and biogeography (Dufour et al., 2020). As thermal stability decreases from the equator to the poles, dispersal into more seasonal habitats has mainly occurred when tropical lineages shifted their range into higher latitudes ('southern-home'; although tropical biomes begun to retreat from high latitudes after the mid-Eocene climatic optimum). Shifts in non-breeding areas must have disproportionately affected species from temperate latitudes via the progressive increase in seasonality in higher latitudes throughout the Cenozoic (Mosbrugger et al., 2005; Zachos et al., 2001) initiated by the tropical biome retreat ('shifting-home') or later ('northern-home'). If these scenarios are more complex than initially suggested, the general distinction between a shift in breeding range or a shift in non-breeding range, from tropical or temperate biomes, remains valid to explain the evolution of migration.

In this paper, we investigated the possible links between seasonal migration and latitudinal diversity patterns in birds using the order Charadriiformes. This diverse (375 species) avian clade exhibits a very high diversity in the temperate and Arctic latitudes and an unusually high proportion of migratory species (Figure 1a), including some of the avian species with the most extreme strategies of seasonal migration (*Limosa lapponica* in Gill et al., 2009; *Sterna paradisaea* in Egevang et al., 2010). We examined three non-exclusive biogeographical scenarios to explain the latitudinal diversity patterns of Charadriiformes which constitutes another example of an inverse LDG (see Figure 1b). Firstly, the clade could have a temperate or Arctic origin followed by in situ diversification and secondary colonization of the tropics in some clades. Secondly, the clade could have a tropical origin and the atypical LDG could result from repeated dispersal events outside the tropics. Thirdly, the diversity pattern could result from a tropical origin with few events of breeding range shifts outside the tropics followed by increased diversification in temperate or Arctic biomes. It is, therefore, essential to understand the temporal concordance between the colonization of seasonal environments and the emergence of migratory behaviour to understand the evolution of the LDG.

To do so, we examined the various hypotheses on the evolution of migration as a general conceptual framework for tracing and dating the biogeographical history of Charadriiformes to understand how seasonal migration may have influenced the evolution of their inverse LDG. We first estimated the evolution of migration across a species-level phylogeny that we reconstructed using available molecular data and dated with recent fossil discoveries. We then determined how the evolution of migration relates to the evolution of breeding latitudes, using the fossil record as a complementary source of information to validate that some lineages were present in temperate areas when our dated phylogeny suggested so. Finally, we used hidden state speciation and extinction models (HiSSE; Beaulieu & O'Meara, 2016), to test whether diversification and thus the LDG have been shaped by migratory behaviour or species latitudinal distribution. Overall, we found evidence that migration enabled the colonization of temperate and Arctic areas which in turn favoured the diversification of this clade, ultimately shaping this atypical LDG.



**FIGURE 1** Inverse latitudinal diversity gradient in Charadriiformes and hypothetical scenarios to explain its origin. (a) World map showing the species richness of Charadriiformes during the breeding period. Species richness was calculated from distribution maps (IUCN Red List for Birds, 2020) gridded at a 10-min resolution. A density plot of cell richness against latitude is indicated on the left to depict the inverse latitudinal diversity gradient. (b) Bar plots representing the proportion of migratory (red) versus non-migratory (black) species breeding per band of 10 degrees of latitude. The white colour indicates the absence of breeding species in the band. (c) Hypothetical evolutionary scenarios for the inverse latitudinal diversity gradient of Charadriiformes. H1: temperate or Arctic origin followed by in situ diversification and secondary colonizations of the tropics in some clades. H2: tropical origin with diversification mainly resulting from repeated and frequent dispersal events outside the tropics. H3: tropical origin, with few events of breeding range shifts outside the tropics followed by increased diversification in temperate or Arctic biomes. In the three scenarios, seasonal migration and breeding latitudes, which are closely linked, may have both directly and indirectly influenced diversification dynamics.

## 2 | MATERIALS AND METHODS

### 2.1 | Species, spatial and movement data

Our study follows the taxonomic reference of BirdLife International and the Handbook of the Birds of the World (HBW; del Hoyo & Collar, 2014). We collected a total of 375 distribution maps of extant Charadriiformes species from BirdLife International (IUCN Red List for Birds, 2020) and gridded them at a 10-min resolution. We separated breeding ranges by grouping *native resident* and *native breeding* areas and non-breeding ranges by grouping *native resident* and *native non-breeding* areas according to the BirdLife International categorization. We categorized species as *migratory* or *non-migratory* (i.e. resident) based on information provided by reference handbooks (see Dufour et al., 2020). For partial migrant species (i.e. when not all populations perform seasonal movements), we used published information to classify them as *migratory* when they have mostly migratory populations and as *non-migratory* when they have mostly resident populations (see Supplementary Data).

We also collected fossil occurrences of Charadriiformes between the Eocene and Miocene to assess the clade's distribution during these periods. For this purpose, we performed an exhaustive review of the literature, relying on several reviews for specific clades (Bochenski et al., 2019; De Pietri, Mayr, et al., 2020; Smith & Clarke, 2015), while being careful not to include fossils with uncertainty regarding their taxonomic assignment (e.g. †*Jiliniornis huadianensis*, Hou & Ericson, 2002; Mayr, 2009).

### 2.2 | Phylogenetic reconstructions and fossil calibrations

We used DNA sequences from GenBank and palaeontological information to reconstruct and calibrate the most complete species-level

global phylogeny of Charadriiformes (see also Černý & Natale, 2022). We collected DNA sequences for six nuclear genes and ten mitochondrial genes covering 300 of the 375 species (80%) recognized by the BirdLife/HBW taxonomy (see Supplementary Data). Sequences were aligned using MAFFT (Katoh, 2005) and alignments were run through Gblocks (Castresana, 2000) to remove poorly aligned positions, then concatenated using FASconCAT (Kück & Meusemann, 2010). The common crane *Grus grus* (Aves: Gruiformes; sister clade of the Charadriiformes) was used as an outgroup in phylogenetic reconstructions. The final concatenated supermatrix included a total of 12,838 sites, with on average, each species having 5.8 genes and 4865 sites in the alignment (only 16 species out of 300 were represented by a single gene).

We simultaneously inferred the tree topology and divergence times through Bayesian inference as implemented in BEAST 2.7.5 (Suchard et al., 2018) using an relaxed molecular clock model, which allows variation in the rate of molecular evolution among lineages (Drummond et al., 2006). To calibrate the molecular clock, we used seven calibration points and generated the empirical calibration information from the fossil record with the package CladeDate (Claramunt, 2022). First, we carefully selected the oldest fossils for each calibration point following the latest palaeontological discoveries and recommendations of De Pietri, Worthy, et al. (2020) and Smith (2015). Then, for each calibration point, we searched the literature for the first fossil occurrence of each clade in each major geographic regions of the world (South America, North America, Europe, Africa, Asia, Australia, Zealandia) to complete the set of fossil occurrences and estimate the choice of the calibration function and its parameters (see also Claramunt & Cracraft, 2015; details about the choice of the oldest fossils and the set of fossil occurrences can be found in Table S1 and Supplementary Materials). We performed a run of 400 million generations for the Markov chain

Monte Carlo (MCMC), sampling trees every 50,000 generations assuming a birth–death speciation process as the tree prior. We set a uniform prior between 0 and 10 with starting value of 0.1 for the birth rate, a uniform prior between 0 and 2 with starting value of 0.1 for the relative extinction rate and we kept default values for the other priors. We checked the estimated parameters using Tracer (Rambaut et al., 2018), determining convergence success based on the shapes of the MCMC traces (likelihood parameter), and their effective sample sizes (ESS > 200 representing an acceptable effective sample size). We discarded the first 30% generations as a burn-in and summarized the trees with TreeAnnotator (BEAST tool) to compute a maximum clade credibility (MCC) tree with posterior probabilities (PP) and median ages as well as their 95% credibility intervals (CI). We also performed a prior-only run analysis in BEAST without considering the genetic data to evaluate how the marginal prior distribution of the calibrated nodes may differ from the calibration density used to construct the tree prior (Heled & Drummond, 2012). Prior and posterior distributions with and without considering the genetic data were compared to evaluate how posterior estimates differ from the designed prior distribution.

To minimize effects of sampling bias related to missing species and missing data in our biogeographical and diversification analyses, we added the species for which no DNA data were available (75 species). Most missing species were added as sister species of other species present in the tree (or as sister species of a group of species) based on information found in the published literature (i.e. published phylogeny or morphological, plumage or acoustical similarities discussed in literature). They were added with a divergence time randomly chosen between 0 and the length of the branch. For species for which we had no information, they were randomly added within their respective genus (*Turnix*, *Vanellus*, some *Sterna* and *Gallinago*). They were first added as polytomies (the polytomy was randomly placed at a node within this group), and we used the *bifurcatr* function in the package PDcalc (Faith, 2013) to randomly resolve the polytomies once all the species had been added. Codes and information regarding the addition of missing species can be found in Supplementary Data. We built 500 different complete phylogenies to explore the range of potential solutions for the addition of missing species and also computed a least-squares consensus tree of the 500 trees with the *ls.consensus* function in the package phytools (Revell, 2012).

### 2.3 | Ancestral migratory and breeding latitude estimations

To determine how migration (coded as a binary character, see above) evolved in Charadriiformes, we used the *fitDiscrete* function in the package geiger (Pennell et al., 2014) to test for equal rates and different rate models using the consensus tree. We compared corrected Akaike Information Criterion values (AICc) to select the best fitting model and then performed ancestral states estimations across the 500 topologies of the shorebird phylogeny. We performed stochastic

character mapping using the *make.simmap* function in package phytools with 1000 simulations, employing the evolutionary model with the lowest AICc (Revell, 2012). We estimated the number of transitions between migratory and non-migratory with transition being defined as instances where the PP cut the 0.5 threshold. Again, transitions were estimated from ancestral states estimations performed across the 500 phylogenetic trees.

To determine the most likely breeding latitudes of the ancestor of Charadriiformes, we divided the globe into four latitudinal sections following the approximate latitudinal distribution of the major terrestrial biomes, which also roughly correspond to the major type of breeding habitats used by shorebirds and their allies. The different latitudinal bands considered are: Boreo-Arctic zone (>55°N; boreal forests, taiga, tundra), northern temperate zone (30°/55°N; temperate grasslands), tropical zone (30°N/–30°S; savannah, deserts) and southern temperate zone (–30°S/–55°S; temperate grasslands, alpine zone). We assigned each species to one or several sections if at least 20% of its breeding distribution overlaps with it. We used the package BioGeoBEARS (Matzke, 2014) to fit four models of ancestral areas estimation: the Dispersal–Extinction–Cladogenesis (DEC; Ree & Smith, 2008), the DEC+J (Matzke, 2014) models as well as the DIVALIKE and the DIVALIKE+J models as widespread vicariance may be common in birds. The J parameter allows for founder-event speciation which seems relevant in the case of a bird group that has very high dispersal capacities (here potentially enhanced by migration behaviour), and where we expect that geographical ranges can have evolved in a jump-like manner. We estimated transitions between latitudinal bands as change of state between two consecutive nodes in the phylogeny. We estimated transitions: (i) towards the poles (i.e. out of the tropics, from the tropical zone towards Arctic and temperate zones), (ii) towards the tropics (from Arctic and temperate towards the tropical zone) and (iii) between non-adjacent areas (from the Arctic towards tropical and southern temperate zones or from the northern temperate towards the southern temperate; and vice-versa).

We acknowledge that in the case of predominantly migratory clades, it may be more appropriate to use a model that reconstructs the evolution of breeding and non-breeding areas in parallel (Winger et al., 2014). Nonetheless, we would like to emphasize that such models remain complex to use. Indeed, the ability of Charadriiformes to make very long-distance dispersal movements would require extensive parameterization. Furthermore, due to the contrasting distribution of Charadriiformes between breeding (highly variable) and non-breeding (stable) areas, we do not expect such a model to produce fundamentally different results (see Discussion).

### 2.4 | Analyses of diversification dynamics

Because it is notoriously challenging to estimate speciation and extinction dynamics separately from contemporary data (Kubo & Iwasa, 1995; Louca & Pennell, 2020), we examined variation in

diversification rates and used external information on ecological patterns and processes to interpret them in terms of speciation or extinction rates. To determine if seasonal migration directly influences diversification dynamics of different clades or rather allowed the colonization of novel biogeographical regions, in turn opening new ecological opportunities, we investigated if diversification rates differ between migratory behaviour and between breeding habitats. For breeding latitudes, we used latitudinal cut-offs that broadly encompass the different types of breeding habitat and biomes of Charadriiformes. We separated species breeding in temperate and Arctic biomes (absolute mean breeding latitudes  $>30^\circ$ ) and species breeding in tropical biomes (absolute mean breeding latitudes  $<30^\circ$ ).

We applied the HiSSE model as implemented in the package *hisse* (Beaulieu & O'Meara, 2016), which represents an extension of the Binary State Speciation and Extinction (BiSSE) model (Maddison et al., 2007) by including a second hidden binary trait that can impact diversification in addition to (or instead of) the observed focal trait (Beaulieu & O'Meara, 2016). We used, for both variables, four different models to test the effect of the character: a BiSSE model, a HiSSE model, a character-independent diversification model with two hidden states (CID-2) and a character-independent diversification model with four hidden states (CID-4). We applied these diversification models to 100 complete tree topologies (375 species), randomly selected among the 500 tree topologies generated. For each topology, Akaike weights of the four models were used in the weighted average of model parameters to obtain model-averaged diversification rates for all tips of the phylogeny. We also investigated the consequences of grafting species lacking genetic data in trait-dependent models (Rabosky, 2015) by repeating HiSSE analyses for the MCC tree containing only species with molecular data (300 species).

To test the sensitivity of the analyses to type I error, we generated 100 data sets with species' states randomly distributed across the Charadriiformes phylogeny and performed HiSSE analyses as with the real data (only for HiSSE and CID4 models to reduce computing time). We then compared the distribution of the differences of AICc scores between HiSSE and CID-4 models obtained from these randomized data with the difference of AICc scores between the same models with the original data. We performed this test for both variables on 100 tree topologies randomly selected among the 500 tree topologies generated.

### 3 | RESULTS

#### 3.1 | Timetree of Charadriiformes

The Bayesian inferences of BEAST converged as supported by ESS  $\gg 200$  for all parameters, stable, random fluctuations in the trace plots, stable distribution of the posterior distributions over time, etc. The Bayesian chains were used to generate a MCC tree (see Figure S1). Overall, the tree was well resolved (72% of nodes

have PP  $\geq 0.95$ ) and all families (except the Charadriidae; see Baker et al., 2012) were recovered as monophyletic with strong node supports. The backbone of the tree was nearly identical to the latest global avian phylogenies based on genomic data (Figure S1; see Prum et al., 2015; Kuhl et al., 2021) and to a recently published phylogeny of the clade (Černý & Natale, 2022).

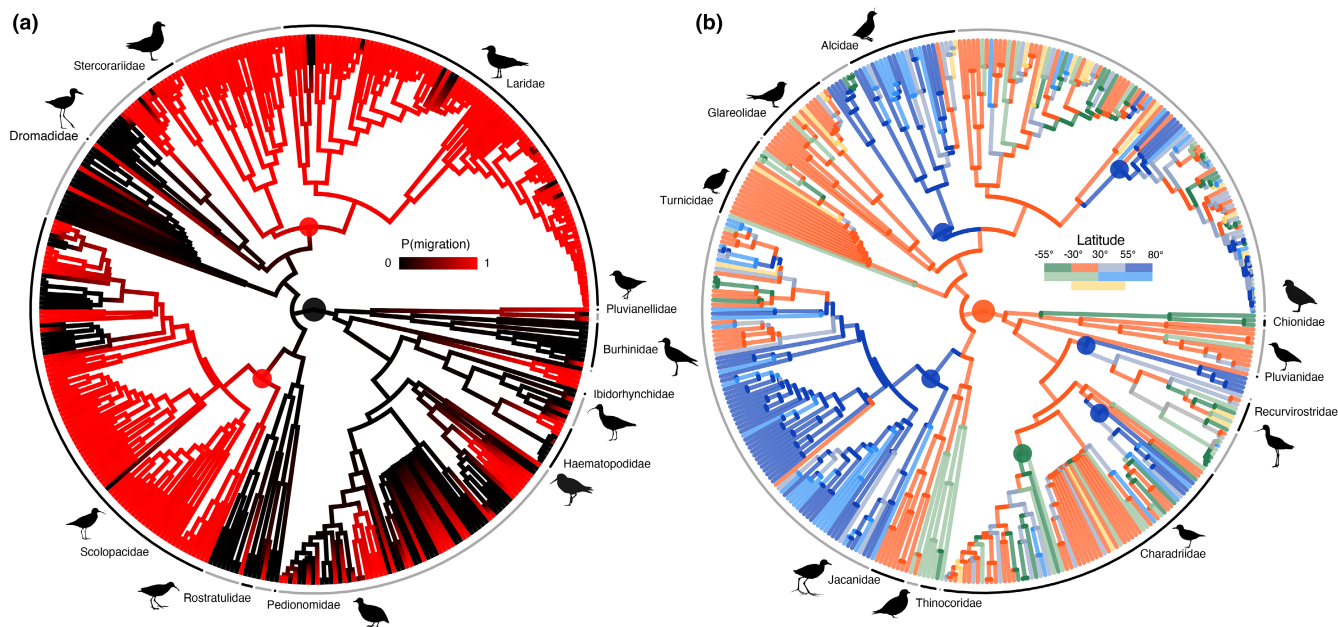
Comparisons of the prior distributions for the seven calibrated nodes, together with the posterior distributions from the prior-only run and the posterior distributions showed perfect match or reasonable deviations from the calibration priors (Figure S2). Calibration points representing the split between *Limosa* and the other Scolopacidae (fossil 4: †*Mirolia brevirostrata*), and to a lesser extent the split between *Gallinago* and *Limnodromus* (fossil 5: †*Gallinago azovica*), were the two points that were the most shifted towards the distribution tail of their prior. At the opposite, the node of the split between Stercorariidae and Alcidae calibrated with †*Pan-Alcidae incertae sedis* (fossil 7) exhibited a posterior distribution close to the lower bound of the prior.

#### 3.2 | Emergence of migratory behaviour

For the evolution of migratory behaviour, the different rate model was a better fit (AICc=392.6) than the equal rates model (AICc=400.5). We found a likely resident ancestor for all 500 tree topologies (PP at the root of being non-migratory, mean=0.98, CI $\pm$ 0.04) and showed that migratory behaviour emerged early in the history of Charadriiformes (Figure 2a). The first nodes showing strict migratory behaviour were consistently the most recent common ancestor (MRCA) of Laridae, Alcidae and Stercorariidae (mean PP=0.81, CI $\pm$ 0.12) or the MRCA of the Scolopacidae (mean PP=0.73, CI $\pm$ 0.14), which are, respectively, dated to 37.3Ma and 36.6Ma (late Eocene). The first emergence events of migratory behaviour occurred during the global cooling from the late Eocene onwards. Then, from the mid-Miocene temperate cooling that preceded the global expansion of C4 grasslands, the accumulation of migratory lineages seems to be roughly constant over time with a slight deviation from the linear trend (i.e. from constant rates) for the Oligocene and the late Miocene (Figure 3a). On average, we found more frequent gain of migratory behaviour (mean=57.73, CI $\pm$ 2.47) than loss (mean=29.68, CI $\pm$ 2.28) in our estimations and a transition rate from non-migratory to migratory higher (mean=0.03, CI $\pm$ 0.002) than the converse (mean=0.01, CI $\pm$ 0.001).

#### 3.3 | Past distribution of Charadriiformes

Ancestral area estimations suggested that Charadriiformes diversified from an equatorial tropical ancestor (Figure 2a, probability at the root=0.55 [DEC+J]). Among the four models tested, the model DEC+J was a better fit (AIC=1357.8) than the others (AIC=[DEC]: 1475; [DIVALIKE]: 1507.3; [DIVALIKE+J]: 1392.1). We found a large evolutionary lability of breeding distributions with several



**FIGURE 2** Phylogenetic tree of the Charadriiformes showing the evolution of migratory behaviour (a) and breeding latitude (b). The evolution of migratory behaviour was estimated using stochastic character mapping and the evolution of breeding latitudes was reconstructed using the DEC+J model of BioGeoBEARS. For breeding latitudes, colours represent the four latitudinal areas (see Materials and Methods) or combinations of several areas (combinations of more than three areas are represented in grey). In (a), P represents the posterior probability of being migratory along the branch. Coloured points indicate major events of emergence of migratory behaviour or of shifts out of the tropics, as described in the results. The names of the 19 families are indicated with several silhouettes (© HBW Alive/Lynx Edicions).

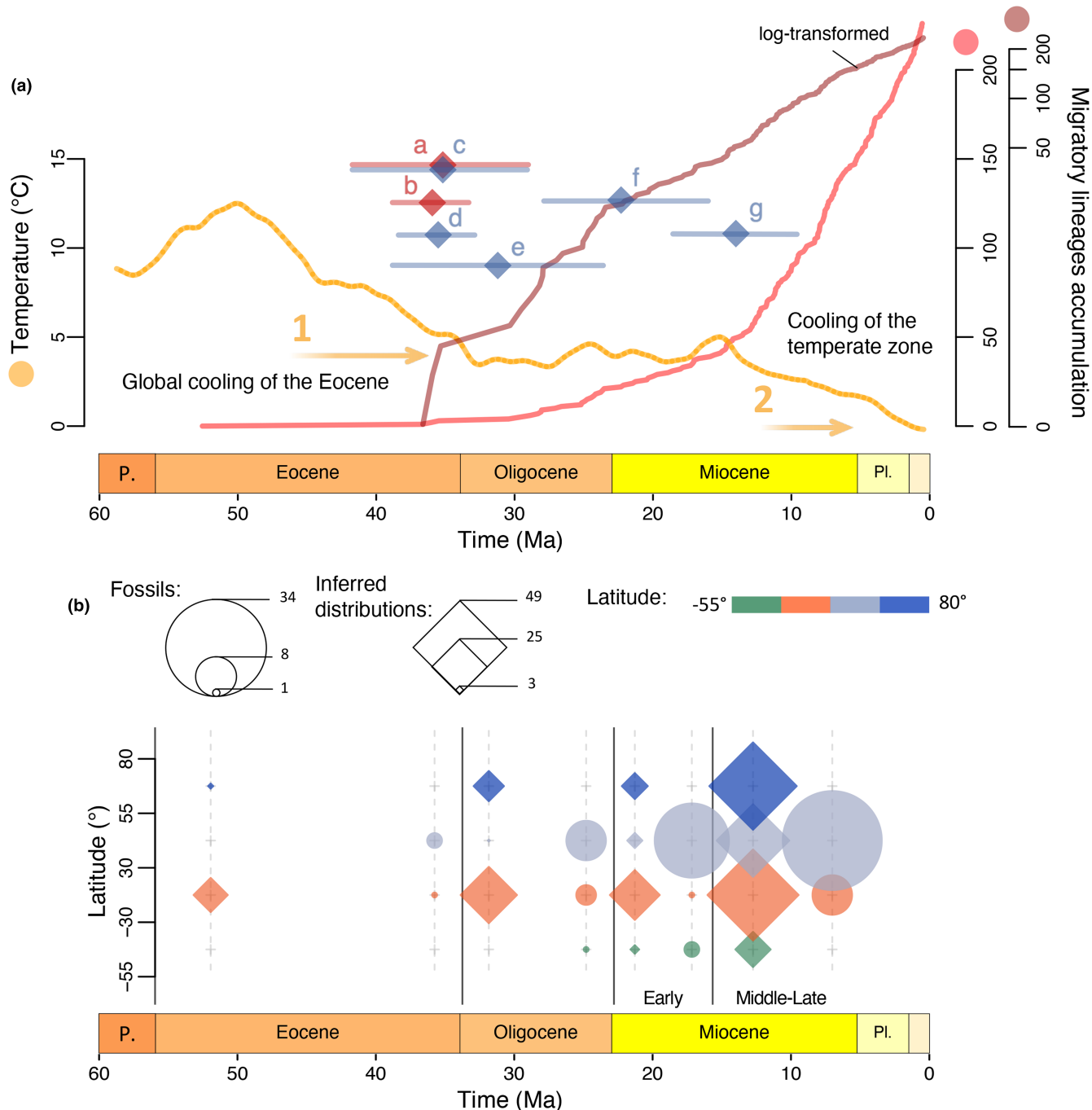
independent transitions out of the tropics at different time periods (Figure 2b), which contrast with the more stable distribution of Charadriiformes in tropical latitudes during the non-breeding period (Figure S3). For Scolopacidae, Alcidae and Stercorariidae, we found that some early shifts out of the tropics to higher latitudes probably preceded in situ diversification within higher latitudes, followed by subsequent reverse colonizations to lower latitudes (e.g. *Coenocorypha*, *Gallinago* in Scolopacidae, some *Sterna* in Laridae and *Catharacta* in Stercorariidae). Note that we found the same results of a tropical ancestor and early shifts out of the tropics for the crown of Scolopacidae and for the ancestor of the Alcidae and Stercorariidae for all the 500 tree topologies. Within the suborder Charadrii, early diverging families (Chionidae, Haematopodidae and Recurvirostridae) came out of the tropics towards higher (northern or southern hemispheres) temperate latitudes, while Charadriidae may have first started to diversify in the tropical latitudes before reaching the temperate zones. Accordingly, we estimated, over the 500 topologies, more transitions towards the tropical latitudes than transitions outside the tropics (63.70,  $CI \pm 3.99$  versus 60.02,  $CI \pm 3.39$ ). We also estimated 38.71 ( $CI \pm 3.34$ ) transitions between non-adjacent areas including 19.13 ( $CI \pm 2.17$ ) transitions towards southern latitudes, suggesting that several long-distance, possibly permitted by migratory movements, shaped the diversity of Charadriiformes.

In parallel, we collected 87 fossil occurrences of Charadriiformes mostly discovered in the Northern Hemisphere (in Europe and North America) between the Eocene and Miocene, with 24 fossils

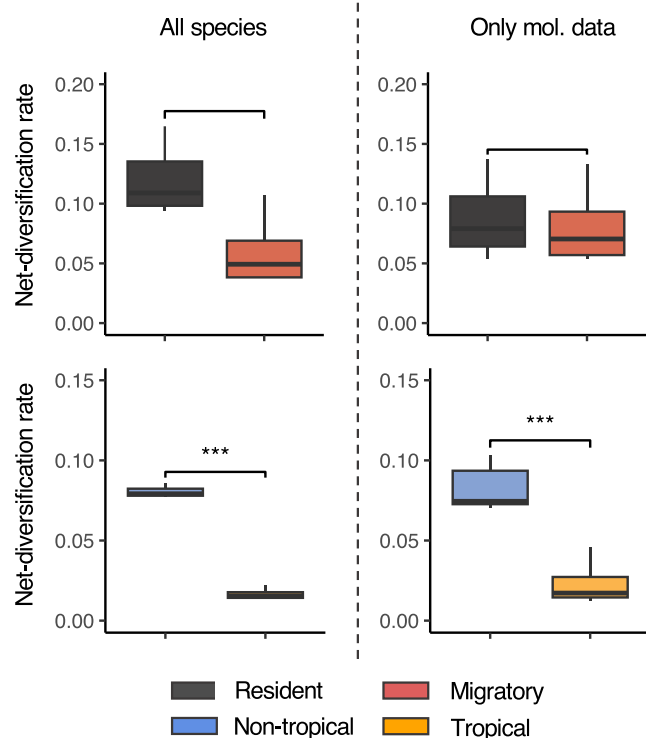
assigned to the suborder Scolopaci, 47 to Lari and 16 to Charadrii (see Supplementary Data). The oldest Lari fossils are dated from the mid-Eocene, whereas the first Scolopaci and Charadrii fossils occurred in the late Eocene (see Figure 3b).

### 3.4 | Diversification dynamics

For the Charadriiformes as a whole, we found higher diversification rates for non-tropical (temperate and Arctic species) than for tropical species (Figure 4). Out of the 100 replicate trees, the HiSSE model was a better fit than other models in 100% of cases (Table S2, Figure S4). This suggests that breeding distribution (non-tropical versus tropical) significantly impacted shorebird diversification. On the contrary, for migration, we found that the model CID4 was a better fit than the other models (Table S2, Figure S4). Because the model CID4 differs from the HiSSE model in having its diversification parameters independent of the observed character state, the results suggest no significant effect of migration on diversification dynamics even if diversification rates are higher on average for resident than migratory species (Figure 4). Using 100 randomized data sets, we always found a difference of AIC values between the HiSSE and CID4 models much lower than with the true data (Figure S5b), discarding the risk of false positive for the HiSSE analysis and confirming an effect of the breeding habitats on speciation (but see Figure S5a for migration). Note that analyses performed on Charadriiformes without the species grafted on the phylogeny (300 species) yielded similar results (Figure 4, Table S2).



**FIGURE 3** Geological context of the emergence and evolution of migratory behaviour (a) and support for the biogeographical scenarios from fossil distributions (b). In (a), a cumulative lineage through time plot represents the accumulation of migratory species through time (both with and without log-transformation). The global deep ocean temperature evolution (orange line, data from Hansen et al., 2013) highlights the global cooling initiated after the mid-Eocene (1; see Zachos et al., 2001) and intensified after the mid-Miocene, which preceded the global expansion of C4 grasslands (2; see Pound et al., 2012). The red diamonds represent the major events of emergence of migratory behaviour highlighted in Figure 2 for Scolopacidae [a] and for the MRCA of Laridae, Alcidae and Stercorariidae [b]. Similarly, the blue diamonds also represent the major events of transitions out of tropics for Scolopacidae [c], the MRCA of Alcidae and Stercorariidae [d], the MRCA of *Pluvialis*, Ibidorhynchidae, Haematopodidae and Recurvirostridae [e], Laridae [f] and the MRCA of the two Charadrius lineages (without the genus *Vanellus*) [g]. The bars indicate the uncertainty around the age of the node. In (b), diamonds represent the number of lineages present in a given latitudinal band at a given geological epoch as inferred from the ancestral area reconstructions. Circles represent the number of fossils in the same latitudinal bands and same geological epochs. Four geological epochs are represented: Eocene, Oligocene, Early Miocene and Middle/Late Miocene. The size of the circles and diamonds is proportional to, respectively, the number of fossils and the number inferred lineages (see legend). A complete list of fossil data can be found in Supplementary Data. A geological timescale is depicted at the bottom of each panel, spanning time since 60 Ma (P., Palaeocene, Pl., Pliocene; Pleistocene are not indicated).



**FIGURE 4** Diversification rates estimated from the model averaged HiSSE analyses, testing both the influence of migratory behaviour (migratory versus non-migratory) and breeding habitats (tropical and non-tropical) on diversification rates. Diversification analyses were performed on the consensus tree containing all grafted species and a tree without grafted species (only molecular data). For the breeding distribution, the HiSSE model was a better fit suggesting that breeding distribution (non-tropical versus tropical) significantly impacted shorebird diversification. The CID4 model was a better fit for migration, implying no significant effect of migration on diversification dynamics even if diversification rates are higher on average for resident than migratory species (see Methods and Results for more details). The upper panels show diversification rates for migratory (red) versus resident (i.e. non-migratory; dark grey) species, the lower panels show diversification for tropical (orange) versus non-tropical (blue) species. Asterisks indicates the significance levels of t-test comparisons between groups (\* indicates  $p < 0.05$ , \*\*\* indicates  $p < 0.001$ ).

## 4 | DISCUSSION

### 4.1 | Evolution of an inverse latitudinal diversity gradient

Our study supports a tropical origin of Charadriiformes and links the emergence of migratory behaviour to a few biogeographical shifts of the breeding areas from tropical to temperate biomes (Figure 2), as already reported in Charadriidae (Joseph et al., 1999). We find that the emergence of migration in Charadriiformes may have mostly occurred through dispersal into new seasonal breeding areas, following the idea of 'southern-home' hypothesis (Cox, 1968; Gauthreaux, 1982; Levey & Stiles, 1992). However, because seasonal migration likely emerged early in the history of Charadriiformes (late Eocene), we cannot fully

exclude a scenario where the emergence of migration resulted from the adaptation of high-latitude breeding species in some lineages to increased seasonality. The non-breeding ranges would then have followed the retreat of the tropical (less seasonal) climate, following the 'shifting-home' hypothesis (Louchart, 2008; Winger et al., 2019). The first scenario is well illustrated by several lineages that dispersed into temperate (seasonal) regions after the retreat of the tropical biomes, for example, in Laridae and Charadriidae (e.g. *Vanellus vanellus*, *V. gregarius* among the tropical-adapted genus *Vanellus*). For the second scenario, ancestral reconstructions and fossil occurrences (e.g. Scolopacidae indet. from the early Oligocene of France, Duhamel & Louchart, 2021) suggest that early Scolopacidae already occupied high latitudes where the tropical biome was possibly still present in the late Eocene or early Oligocene (Ziegler et al., 2003), suggesting that this family may have persisted under these latitudes by an adaptive niche shift from a tropical (low seasonality) to a temperate (high seasonality) environment (Louchart, 2008).

Our results also suggest that migratory behaviour has been an evolutionary key innovation that enabled Charadriiformes to breed in temperate environments. Although we interpret deep-time reconstructions with caution, the emergence of seasonal migration in Charadriiformes coincide with the global cooling initiated in the middle Eocene, which is linked to the appearance of markedly latitudinal seasonal climates (Mosbrugger et al., 2005; Zachos et al., 2001). Migratory lineages then increased concomitantly of the progressive retreat of tropical biomes and the global expansion of  $C_4$  grasslands during the Miocene, which corresponds to the habitats used by most of the Holarctic Charadriiformes (tundra, taiga, steppes; Pound et al., 2012; Pound & Salzmann, 2017; Meseguer & Condamine, 2020). We hypothesize that the Neogene expansion of these environments may have created a major novel ecological opportunity that favoured the colonization of high latitudes by several charadriiform clades (Ballmann, 2004; Kraaijeveld & Nieboer, 2000), a biogeographical shift made possible by the emergence of migratory behaviours (as proposed in Louchart, 2008; Winger et al., 2019).

Diversification analyses indicate higher diversification rates under temperate and Arctic latitudes than under tropical latitudes. Such increased diversification rates in high latitudes contrast with the expectation that diversification rates can be higher in the tropics (Hawkins et al., 2007; Meseguer & Condamine, 2020) but are concordant with other studies conducted on large avian clades (Harvey et al., 2020; Kennedy et al., 2014). In the context of the evolution of the latitudinal diversity gradient, the global climate cooling occurring since the middle Eocene has likely allowed the colonization by Charadriiformes lineages of novel (and presumably underexploited) ecological niches in high latitudes, which in turn spurred their diversification rate (Figure 4). In the same perspective, harsh climates and climatic oscillations may have also increased geographic isolation which in turn spurred diversification, as discussed at the population level in Botero et al. (2014) and as an explanation for higher speciation rates during global cooling in birds (Claramunt & Cracraft, 2015). This hypothesis has been investigated by Arcones et al. (2021) in Arctic shorebirds who suggested that the



fragmentation of the breeding ranges during the climatic cycles of the Pleistocene likely determined and promoted the intraspecific diversification. Interestingly they found differences in diversification processes between biogeographic regions across the Arctic, which calls for further research on Charadriiformes as a whole, especially in the different biogeographic regions of the Southern Hemisphere.

It has also been found that the evolution of seasonal migration likely influenced the diversification of breeding systems in Charadriiformes (García-Peña et al., 2009), which in turn may have favoured diversification of this clade (Thomas et al., 2006). In addition, long-distance migratory Charadriiformes seem to be more thermally tolerant than other migratory clades, as long-distance migratory species tend to switch towards warmer climatic niche, between the breeding and the non-breeding period, more than other species (Dufour et al., 2020). We assume that it may have facilitated the colonization of new climatic niches in high-latitude environments. In the same perspective, the HiSSE model further suggests that other trait(s), different from the non-tropical/tropical distribution, affected the diversification of Charadriiformes, suggesting that these biogeographical movements alone cannot explain all the diversification history of Charadriiformes. One could suppose that other traits may have been involved in different families, such as the widespread distribution of Laridae (i.e. their dispersal abilities), the morphological diversity of Scolopacidae (shape and size of the bill and the body), and the diversity of plumage colours in Charadriidae that has been demonstrated to influence diversification rates in other bird clades (Hugall & Stuart-Fox, 2012; Turbek et al., 2021). This would deserve further investigation using multi-trait approaches to depict how traits and niche evolution have jointly spurred the diversification of these clades.

In sum, the evolution of the inverse latitudinal diversity gradient of the Charadriiformes can be attributed to increased diversification rates following the colonization of high latitudes by several lineages of Charadriiformes during climate cooling events, a biogeographical shift made possible by the emergence of seasonal migration. Among the three biogeographical scenarios illustrated in Figure 1b to explain this atypical latitudinal diversity gradient, we found support for the third scenario (H3). The Charadriiformes probably originated from the tropics and their diversity pattern was explained by few dispersal events out of the tropics followed by in situ diversification in high latitudes (higher diversification rates in temperate and Arctic biomes compared to tropical biomes). We did not find any direct effect of the migratory behaviour on diversification rates. However, because all species currently breeding in temperate and Arctic areas are migratory, we suggest that seasonal migration enabled diversification simply by making it possible for shorebirds to breed in temperate and Arctic regions (see Winger et al., 2019).

## 4.2 | Validation of evolutionary scenarios with the fossil record

By comparing the fossil distribution with results of ancestral area estimations, we found support that Charadriiformes may have first occupied tropical latitudes before reaching temperate latitudes in the

early Oligocene where they diversified (e.g. †*Eocliffia primaeva* from the mid-Eocene of Namibia; Mourer-Chauviré et al., 2018). We also found support for an early presence (late Eocene–early Oligocene) of lineages of Scolopaci and Charadrii—that are now mostly migratory—in northern latitudes (Figure 3b; †*Paractitis bardi* from Canada and †*Recurvirostra sanctaenebulae* from France), which is consistent with ancestral state reconstructions. Interestingly, the distribution of fossils shows that clades that are predominantly present within tropical latitudes in present times had a wider distribution in the past (Turnicidae, Burhinidae, Glareolidae; De Pietri, Mayr, et al., 2020; Zelenkov et al., 2016). For example, †*Burhinus lucorum* from the early Miocene of Nebraska (USA) likely occupied various habitats of temperate-latitude environments, while most Burhinidae breeds in dry open habitats under tropical latitudes (but see *Esacus magnirostris*; Bickart, 1981). Such clades may have inhabited higher latitudes when higher latitudes were warm or may have dispersed to high latitudes rapidly during their evolutionary history before specializing to warmer environments in response to the late Neogene aridification of Africa and South Asia (Feakins & de Menocal, 2010).

The predominant distribution of fossils in the Northern Hemisphere or from well monitored sites (e.g. Saint-Gérand-le-Puy, France; De Pietri et al., 2011) indicates large prospection bias and a large incompleteness in the fossil record of Charadriiformes. Hence, only few Palaeogene fossils of Charadriiformes have been discovered in tropical, Arctic and southern temperate areas and it is reasonable to expect that new fossil discoveries could refine the estimation of biogeographical scenarios for several families of Charadriiformes. Our biogeographical analyses focused on extant species for which we could gather genetic data and information on the breeding distribution but did not include the fossil record. Not accounting for the fossil record can bias ancestral estimations (Betancur-R et al., 2015; Crisp et al., 2011; McCullough et al., 2019; Meseguer & Condamine, 2020) but including inherently incomplete fossil knowledge may also generate biases (Cracraft & Claramunt, 2017). Considering a widespread extinct clade as a single representative taxon in biogeographical analyses could substantially influence deep ancestral range estimates; likewise, geographical biases in the fossil record may alter the distribution range of extinct taxa. In addition, in the case of migratory birds, it is important to know whether the species was present on its breeding ground, non-breeding ground or migrating between these areas, making the use of the fossil record even more difficult in such an analytical framework.

## 4.3 | Limitations of our study

The ancestral states of traits such as migratory behaviour or habitat can be difficult to reconstruct accurately on a phylogeny, especially when they depend on the evolution of other factors like climate (Holland et al., 2020). Our historical scenario implies several transitions into and out of the tropics, and between sedentary and migratory species, but many of these transitions appear as strongly supported in our phylogenetic reconstructions and, most importantly, none are

individually crucial to our conclusions. Furthermore, although not visible in reconstructions, it is plausible that additional latitudinal shifts of biomes (Arctic and temperate biomes) have repeatedly taken place during the glacial cycles of the Pleistocene. Naturally, our past biogeographical scenarios estimate species' traits, not distribution per se: "Arctic species" are species that breed in Arctic biomes, not necessarily in the current Arctic latitudes. Pleistocene climate cycles have, thus, not necessarily generated changes in migratory behaviour or shifts between biomes, as migratory lineages may have bred at lower latitudes to track biomes and suitable climates (Buehler et al., 2006; Conklin et al., 2022; Somveille et al., 2020; Thorup et al., 2021). The fossil record of Scolopacidae from the Pliocene of Tanzania (Prassack et al., 2018) shows no specimen with medullary bones (which may indicate local reproduction; Matthiesen, 1990), supporting the idea that long-distance migration did not stop during glacial periods (Louchart, 2008). Likewise, past climatic niche modelling recently revealed the presence of suitable breeding areas for shorebirds throughout the Pleistocene, even in very high latitudes (Arcones et al., 2021; see also Buehler et al., 2006).

Diversification models have been repeatedly questioned for their abilities to estimate speciation and extinction rates separately from phylogenies of extant taxa (from Kubo & Iwasa, 1995 to Louca & Pennell, 2020). Since model identifiability can be flawed in complex evolutionary scenarios, we have used comparative models that are less impacted by these issues (i.e. SSE models; see the Supplementary Materials of Louca & Pennell, 2020). Nevertheless, we remain careful when interpreting our results by referring to net diversification rather than using speciation and extinction rates and found that Charadriiformes have higher diversification rates under temperate, Arctic and austral latitudes. We are tempted to interpret this as higher speciation in the high and temperate latitude, even if we cannot totally exclude higher extinction in the tropics. We believe that the reduced fossil record in the tropics (which is admittedly biased), the widespread occurrence of increased speciation rates following colonization of new niches in other groups (e.g. Garcia-Porta et al., 2022) and the often-accepted paradigm of increased stability of habitats in the tropics (Mac Arthur, 1972), also point towards this direction.

## 5 | CONCLUSION

In this study, we found that migratory behaviour allowed the colonization of highly seasonal areas where diversification was increased compared to the ancestral tropical biomes. Our results corroborate those of Cerezer et al. (2022), who aimed to understand the relative role of time, diversification rates and regional energy in the shaping of inverse latitudinal diversity gradient. For Anseriformes and Procellariiformes, they also found that regional diversification rates contribute most to the formation of such a gradient. Although it is likely that a variety of interactions can shape inverse latitudinal diversity gradients (Pontarp et al., 2019), it would be interesting to test whether seasonal migration has systematically played this precursor role in the evolution of diversity gradients in migratory clades.

Although we did not find a direct effect of migration on diversification rates, we did find several episodes of transitions between non-adjacent biogeographical regions, particularly from Arctic or northern temperate regions to southern temperate regions. These transitions suggest that seasonal migration may have promoted the long-distance colonization of novel areas (through migratory drop-off; Gómez-Bahamón et al., 2020; Rolland et al., 2014). Since most of these transitions correspond to shifts towards sedentariness, the interruption of gene flow between sedentary and migratory populations may have promoted speciation in several groups (e.g. *Sterna*, *Gallinago*, *Prosobonia*, *Coenocorypha* and *Catharacta*). Phylogenomic studies could now help refine the evolutionary history of these groups to understand the role of seasonal migration as a direct driver of diversification.

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## CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

All data used in the analyses and relevant code are archived on a public repository (<https://zenodo.org/records/10604034>). It includes a data file containing information on migration data, position of species without genetic data, GenBank accession numbers and fossil occurrences.

## ORCID

Paul Dufour  <https://orcid.org/0000-0002-7940-9997>

Fabien L. Condamine  <https://orcid.org/0000-0003-1673-9910>

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## BIOSKETCH

Paul Dufour is an experienced field ornithologist with a broad interest in the ecology of birds. His research focuses on the evolution of movement in birds (<https://pauldufour80.wordpress.com/>). The other co-authors are all interested in evolution and ecology with focuses on the evolution of phenotypes, macroevolution and global biodiversity patterns.

PD and SL conceived and designed the study. PD collected the data and ran the analyses. PD wrote the first draft of the paper with later input from P-AC, FC and SL.

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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