Phylogenetic biome conservatism as a key concept for an integrative understanding of evolutionary history: Galliformes and Falconiformes as study cases

JONATHAN S. PELEGRIN[1,2,*], JUAN L. CANTALAPIEDRA[3], SARA GAMBOA[4,5], IRIS MENÉNDEZ[4,5] and MANUEL HERNÁNDEZ FERNÁNDEZ[4,5]

[1]*Grupo de Investigación en Ecología y Conservación de la Biodiversidad (EcoBio), Área de Biología y Programa de Maestría en Educación Ambiental y Desarrollo Sostenible, Facultades de Ciencias Básicas y Educación, Universidad Santiago de Cali, Colombia*
[2]*Departamento de Biología, Facultad de Ciencias Naturales y Exactas, Universidad del Valle, Colombia*
[3]*GloCEE – Global Change Ecology and Evolution Research Group, Departamento de Ciencias de la Vida, Universidad de Alcalá, 28805, Alcalá de Henares (Madrid), Spain*
[4]*Departamento de Estratigrafía, Geodinámica y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, C/ José Antonio Novais 2, 28040, Madrid, Spain*
[5]*Departamento de Cambio Medio Ambiental, Instituto de Geociencias (UCM, CSIC), C/ José Antonio Novais 2, 28040, Madrid, Spain*

Biomes are climatically and biotically distinctive macroecological units that formed over geological time scales. Their features consolidate them as 'evolutionary scenarios', with their own diversification dynamics. Under the concept of phylogenetic niche conservatism, we assessed, for the first time, the evolution of biome occupation in birds. We aimed to analyse patterns of adaptation to different climatic regimes and the determinant factors for colonization of emerging biomes by clades from different ancestral biomes. In this work, we reconstructed the biome occupation history of two clades of birds (Galliformes and Falconiformes) under an integrative perspective through a comprehensive review of ecological, phylogenetic, palaeontological and biogeographical evidence. Our findings for both groups are consistent with a scenario of phylogenetic biome conservatism and highlight the importance of changes in climate during the Miocene in the adaptation and evolution of climatic niches. In particular, our results indicate high biome conservatism associated with biomes situated in some of the extremes of the global climate gradient (evergreen tropical rainforest, steppe and tundra) for both bird taxa. Finally, the historical dynamics of tropical seasonal biomes, such as tropical deciduous woodlands and savannas, appear to have played a preponderant role during the diversification processes of these bird lineages.

ADDITIONAL KEYWORDS: biome occupation – birds – Cenozoic – climatic niche – falcons – landfowl macroecology – macroevolution – phylogenetics.

INTRODUCTION

Biomes have acquired broad relevance as analytical units in macroecological and macroevolutionary studies (Crisp *et al.*, 2009; Moncrieff *et al.*, 2016; Mucina, 2019; Landis *et al.*, 2021). The biome concept integrates information on both biotic and abiotic conditions (Walter, 1970; Whittaker, 1975; Moncrieff *et al.*, 2016; Mucina, 2019), describing environments not only as a set of different climatic variables, but also considering the specific plant physiognomy that these variables determine (Walter, 1970; Whittaker, 1975; Donoghue & Edwards, 2014; Ringelberg *et al.*, 2020). The use of biomes in macroecological studies might provide a new understanding of the relationship between

*Corresponding author. E-mail: jonathan.pelegrin00@usc.edu. co

historical climatic dynamics and the configuration of evolutionary processes, patterns of diversification and colonization of new environments at the global scale (Guerrero *et al.*, 2013; Cantalapiedra *et al.*, 2014; Ringelberg *et al.*, 2020; Menéndez *et al.*, 2021; Gamboa *et al.*, 2022; Hernández Fernández *et al.*, 2022).

Global climatic changes during the Cenozoic have affected biome geographical dynamics (Potts & Behrensmeyer, 1992; Flower & Kennett, 1994; Jaramillo *et al.*, 2010; Pound *et al.*, 2012; Landis *et al.*, 2021), as inferred from global climate models and from palaeobotanical and stable isotopic data (Salzmann *et al.*, 2008; Domingo *et al.*, 2013; Barbolini *et al.*, 2020; Steinthorsdottir *et al.*, 2021). According to such sources, terrestrial biomes changed consistently, with a global cooling and drying trend during Neogene (Zachos *et al.*, 2001; Salzmann *et al.*, 2008; Pound *et al.*, 2012; Steinthorsdottir *et al.*, 2021). In this context, different biomes exhibited different geographical dynamics (contraction–expansion, fragmentation and generation of new environments), which created diverse evolutionary scenarios and allowed processes of vicariance (Vrba, 1992, 1995; Hernández Fernández & Vrba, 2005; Brennan & Keogh, 2018; Menéndez *et al.*, 2021).

According to the environmental niche conservatism hypothesis, species tend to preserve and share ancestral adaptive and ecological traits adjusted by phylogenetic constraints (Wiens, 2004; Wiens *et al.*, 2010; Peterson, 2011). Niche conservatism has been studied at different time scales, from short-term shifts of species ranges to deeper comparisons across species (Peterson, 2011). Specifically, the study of the effects of niche conservatism on evolutionary trends across taxa requires phylogenetic hypotheses for the species involved (Eaton *et al.*, 2008; Peixoto *et al.*, 2017). The growing development of phylogenetic hypotheses for diverse clades has allowed the production of evidence that speciation processes are not typically linked to ecological and adaptive innovations (Olalla-Tárraga *et al.*, 2016; Dorey *et al.*, 2020). However, the prevalence of niche conservatism is still a debated issue. Disagreement arises from confusion over its precise definition, the application at different taxonomic and time scales and the approaches to measure its prevalence in order to explain macroevolutionary processes (Hadly, *et al.*, 2009; De Santis *et al.*, 2012; Münkemüller *et al.*, 2015; Peixoto *et al.*, 2017).

Despite phylogenetic niche conservatism, many clades succeeded in the colonization of newly available habitats as new biomes evolved (Guerrero *et al.*, 2013). Specific environmental conditions might promote the development of physiological traits to cope with adverse conditions in different climatic regimes, although they might also require highly specialized functional features (Ghalambor *et al.*, 2006; Bonetti & Wiens,

2014). Conversely, high versatility in relationship to resources and climatic conditions could, theoretically, enable a prominent capacity to colonize and occupy diverse habitat types (Jocque *et al.*, 2010; Salisbury *et al.*, 2012; Pigot & Tobias, 2013, 2015; Lv *et al.*, 2016; Fargallo *et al.*, 2022). In many cases, palaeoclimatic changes might have promoted environmental flexibility by expanding climatic tolerance (Guerrero *et al.*, 2013; Jara-Arancio *et al.*, 2014; Ringelberg *et al.*, 2020), a process that depends on the genetic variation of species populations (Somero, 2010; Pauls *et al.*, 2013; Razgour *et al.*, 2013).

The integration of niche conservatism theory and the biome concept generates a macroevolutionary context in which biome conservatism might have an important role in explaining, in more detail, some global patterns of species richness (Crisp *et al.*, 2009). This conceptual framework is also key to recognizing the tempo and mode of climatic niche evolution, associated with the development of adaptations for the occupation of novel environments (Crisp *et al.*, 2009; Guerrero *et al.*, 2013; Donoghue & Edwards, 2014; Jara-Arancio *et al.*, 2014). The process of biome colonization might contribute valuable information about possible morphophysiological constraints, functional traits or the ecological and climatic versatility that might provide some taxa with exceptions (*sensu* Gould & Vrba, 1982) to adverse biomes, such as desert or tundra. Additionally, it would allow us to gain a better understanding of the potential response of different taxa in the context of the current climatic crisis and threats to biodiversity (Tucker *et al.*, 2019). However, the research addressing adaptation to climatic regimes at the macroevolutionary scale, considering the climatic niche concept, has focused mainly on plant taxa (e.g. Crisp *et al.*, 2009; Donoghue & Edwards, 2014; Jara-Arancio *et al.*, 2014; Gagnon *et al.*, 2019; Ringelberg *et al.*, 2020), while studies of animal taxa have been limited to a few taxonomic groups, such as spiders (Magalhaes *et al.*, 2019), lizards (Wiens *et al.*, 2013; Tejero-Cicuéndez *et al.*, 2022) and mammals (Lv *et al.*, 2016; Peixoto *et al.*, 2017).

Birds are good indicators for macroevolutionary and macroecological studies owing to their well-known biogeography, great diversity and relatively well-established phylogenies (Jetz *et al.*, 2012; Jarvis *et al.*, 2014; Prum *et al.*, 2015; Kimball *et al.*, 2019). Considering an extensive review of the phylogenetic biome conservatism concept, we analysed, for the first time, the patterns of biome occupation and conservatism in landfowl (Galliformes) and falcons (Falconiformes) in relationship to past climatic changes and geological processes. Both groups were selected because these bird orders present a broad global distribution and inhabit all terrestrial biomes. In addition, there is an important amount of ecological information in

both groups, and they are associated with different trophic positions in the ecosystem dynamics (fowl are mainly herbivorous, whereas falcons are faunivorous), which is a trait that might influence the pattern of biome occupation and its conservatism across their evolutionary history (Hernández Fernández & Vrba, 2005; Moreno-Bofarull *et al.*, 2008). Therefore, the aim of this work was to evaluate biome conservatism, differential macroevolutionary trajectories across biomes and the historical dynamics of colonization of emerging biomes in these bird taxa.

MATERIAL AND METHODS

Studied taxa and phylogenetic information

Galliformes

The order Galliformes (landfowl and allies) contains 289 extant species, all of them with predominantly herbivorous diets (Del Hoyo *et al.*, 1994). In addition to their environmental variability, Galliformes exhibit a broad body size range, from the relatively small common quail, *Coturnix coturnix* Linnaeus, 1758, weighing ~35 g, to the wild turkey, *Meleagris gallopavo* Linnaeus, 1758, weighing ~5 kg. The phylogenetic relationships of Galliformes are among the best known within birds (Braun *et al.*, 2019). Phylogenetic hypotheses for the group were based initially on morphological data and have been revised and updated constantly with the implementation of molecular techniques (Eo *et al.*, 2009; Kimball *et al.*, 2011; Hugall & Stuart-Fox, 2012; Wang *et al.*, 2013, 2017; Hosner *et al.*, 2015b, 2017; Stein *et al.*, 2015; Braun *et al.*, 2019; Mandiwana-Neudani *et al.*, 2019; Hosner *et al.*, 2020). All these studies have a broad consensus that establishes Galliformes as a monophyletic group divided into five families: Megapodidae (brush-turkeys and scrubfowl), Cracidae (curassows and guans), Numididae (guineafowl), Odontophoridae (New World quails) and Phasianidae (pheasants, Old World quails, grouse and turkeys). Nevertheless, there is not yet a complete phylogeny at the species level for this order (Braun *et al.*, 2019). For this reason, we used the software Mesquite (Maddisson & Maddison, 2015) to build an informal supertree that integrates 77.8% of the species (225 species), taking into account the most complete calibrated phylogeny published at the moment (Hugall & Stuart-Fox, 2012) complemented by information from later works (Wang *et al.*, 2013; Stein *et al.*, 2015; Hosner *et al.*, 2017).

We used fossil data to calibrate this Galliformes phylogenetic supertree. Palaeontological reports from Asia support the possible origin of crown Galliformes during the Late Eocene (Mayr, 2009, 2017; Hwang

et al., 2010), with subsequent dispersal to Europe, as evidenced by *Sobniogallus* Tomek *et al.*, 2014 from the Early Oligocene of Poland (Tomek *et al.*, 2014). The earliest record of Megapodidae is *Ngawupodius* Boles & Ivison, 1999 from the Late Oligocene of Australia (Boles & Ivison, 1999), although indisputable fossils are from Australian Plio-Pleistocene localities (Mayr, 2017). Cracidae presents its oldest records in the Miocene of North America, as evidenced by *Palaeonossax* Wetmore, 1956, although their recent distribution is constrained to the Neotropics. *Palaeortyx* Milne-Edwards, 1869, from the Early Oligocene of Europe, evidences the presence of stem Phasianoidea at this time. Possibly, Phasianidae diversified throughout Asia during much of the Middle and Late Miocene, with the ancestors of Tetraonini colonizing North America during the Early Miocene, as attested by *Rhegminornis* Wetmore, 1943 from Florida (Mayr, 2017). Finally, for taxonomic consistency, the nomenclature for the consensus tree was adapted according to Del Hoyo & Collar (2014).

Falconiformes

The order Falconiformes (falcons and allies) includes 66 species classified within the family Falconidae (Fuchs *et al.*, 2012, 2015; Del Hoyo & Collar, 2014). Overall, falcons are faunivorous, with a body size spectrum that varies from small species, such as the black-thighed falconet, *Microhierax fringillarius* Drapiez, 1824, near 35 g, to the gyrfalcon, *Falco rusticolus* Linnaeus, 1758, weighing ~1.7 kg (Ferguson-Lees & Christie, 2001). Ecologically, falcons dwell in a great variety of habitats, including forest, savanna, desert and steppes, with many species showing a wide spectrum of environmental occupation, as is the case for the peregrine falcon, *Falco peregrinus* Tunstall, 1771, with a worldwide distribution (Wilcox *et al.*, 2019). The evolutionary relationships of falcons are well established on molecular evidence (Jarvis *et al.*, 2014; Fuchs *et al.*, 2015; Prum *et al.*, 2015; Kimball *et al.*, 2019; Wilcox *et al.*, 2019). Only one family is recognized in the order (Falconidae), and two subfamilies are well established: Herpetotherinae (laughing and forest falcons) and Falconinae (caracaras, falconets, falcons and kestrels). For our purposes, we used the complete falcon phylogeny published by Fuchs *et al.* (2015), which includes all the species. This phylogeny was calibrated with the Early Miocene *Thegornis* F. Ameghino, 1895 from Argentina, which is considered a sister taxon of Herpetotherinae (Noriega *et al.*, 2011), and the Middle Miocene *Pediohierax* Becker, 1987, an early North American member of Falconinae (Becker, 1987). Finally, we followed Del Hoyo & Collar (2014) for taxonomic consistency in all scientific names and the nomenclature of avian clades.

BIOME DATA

We selected the biome classification system developed by Walter (1970) and modified by Hernández Fernández (2001), which establishes ten biomes, considering the annual relative distribution of temperature and precipitation (Table 1). We reviewed diverse palaeoclimatic studies that reveal variation in the age and spatial dynamics of the biomes (Pennington *et al.*, 2004a; Jetz & Fine, 2012; Mucina, 2019; Landis *et al.*, 2021). The oldest biomes, such as evergreen tropical rainforest, have been reported since the Cretaceous and the Palaeocene (Davis *et al.*, 2005; Jaramillo *et al.*, 2010; Jaramillo & Cárdenas, 2013; Eiserhardt *et al.*, 2017; Carvalho *et al.*, 2021). During the Eocene, owing to climatic fluctuations, areas of tropical deciduous woodland appeared (Bredenkamp *et al.*, 2002; Jacobs, 2004; Pennington *et al.*, 2004a; Jaramillo & Cárdenas, 2013), which extended widely during the Oligocene and Late Miocene (Pennington *et al.*, 2004b; Edwards *et al.*, 2010; Charles-Dominique *et al.*, 2016). Likewise, during the Eocene, temperate evergreen forest and broadleaf deciduous forest biomes in high-latitude zones emerged (Axelrod, 1966; Markgraf *et al.*, 1995; DeVore & Pigg, 2013; Landis *et al.*, 2021). After the Mid-Miocene Climatic Optimum, the reduction in global temperature triggered the increase of arid conditions in different areas (Zachos *et al.*, 2001; Charles-Dominique *et al.*, 2016; Harzhauser *et al.*, 2016; Hurka *et al.*, 2019). These factors promoted the origin of boreal coniferous forests in the highest latitudes (Pound *et al.*, 2011; Popova *et al.*, 2012, 2017). Meanwhile, open biomes, such as savannas, steppes and deserts, began to expand in the arid and semi-arid regions (Axelrod, 1985; Bredenkamp *et al.*, 2002; van Dam, 2006; Byrne

Table 1. Structure, age and development of world biomes after Walter (1970) and Hernández Fernández (2001)

Biome	Biome type	Age of origin	References
Evergreen tropical rainforest (I)	(F)	Late Cretaceous–Palaeocene	(Davis *et al.*, 2005; Jaramillo *et al.*, 2006; Jaramillo *et al.*, 2010; Jaramillo, 2012; Eiserhardt *et al.*, 2017; Carvalho *et al.*, 2021)
Tropical deciduous woodland (II)	(F)	Early Eocene (small areas) Early Oligocene (covering large areas)	(Jacobs, 2004; Pennington *et al.*, 2004b; Werneck *et al.*, 2011; Charles-Dominique *et al.*, 2016)
Savanna (II/III)	(O)	Early Eocene (small areas) Late Miocene (covering large areas)	(Jacobs, 2004; Pennington *et al.*, 2004b; Beerling & Osborne, 2006)
Subtropical desert (III)	(O)	Early Oligocene (small areas) Pliocene (covering large areas)	(Bobe, 2006; Senut *et al.*, 2009; Guerrero *et al.*, 2013)
Sclerophyllous woodland–shrubland (IV)	(F)	Late Miocene (small areas) Plio-Pleistocene (covering large areas)	(Hernández Fernández *et al.*, 2007; Buerki *et al.*, 2012)
Temperate evergreen forest (V)	(F)	Early Eocene	(Markgraf *et al.*, 1995; Fine & Ree, 2006; DeVore & Pigg, 2013; Landis *et al.*, 2021)
Broadleaf deciduous forest (VI)	(F)	Early Eocene	(Markgraf *et al.*, 1995; Fine & Ree, 2006; DeVore & Pigg, 2013)
Steppe to cold desert (VII)	(O)	Early Miocene (small areas) Plio-Pleistocene (covering large areas)	(Axelrod, 1985; Janis, 1993; Zimov *et al.*, 1995; Franzke *et al.*, 2004; Wang, 2004; Kahlke, 2014; Hurka *et al.*, 2019)
Boreal coniferous forest (VIII)	(F)	Middle–Late Miocene	(Fine & Ree, 2006; Pound *et al.*, 2011; DeVore & Pigg, 2013; Popova *et al.*, 2017)
Tundra (IX)	(O)	Plio-Pleistocene	(Zimov *et al.*, 1995; Hewitt, 2003; Kahlke, 2014)

Abbreviations: F, forest environments; O, open environments.

et al., 2008; Senut *et al.*, 2009; Guerrero *et al.*, 2013; Charles-Dominique *et al.*, 2016; Hurka *et al.*, 2019). Pliocene and Pleistocene geological and climatic events caused phases of icehouse and subsequent glaciations, which made possible the emergence of biomes such as the sclerophyllous woodland–shrubland in subtropical latitudes (Hernández Fernández *et al.*, 2007; Buerki *et al.*, 2012) and the tundra near the poles (Zimov *et al.*, 1995; Hewitt, 2003). Moreover, this period implied the prominent expansion of steppes in high latitudes (Franzke *et al.*, 2004; Kahlke, 2014) and deserts in the subtropical belts (Bobe, 2006; Senut *et al.*, 2009), with the opposite effect of contractions in the area of tropical and wet biomes (Pennington *et al.*, 2000; Hooghiemstra & Van der Hammen, 2004; Jaramillo & Cárdenas, 2013; Raes *et al.*, 2014; Dexter *et al.*, 2018; Table 1).

The biome occupation of each species was determined following the methodology developed by Hernández Fernández (2001). According to the geographical distribution of each species, we codified the presence or absence of the species in each biome, considering the overlapping and relative size of its reported geographical range (Del Hoyo & Collar, 2014; Birdlife International, 2019). If ≥ 15% of the geographical range of the species was situated within a specific biome, the species was considered to occupy that biome. For the case of biomes with relatively small areas in relationship to the geographical range of the species, we also recorded the presence of species when the species inhabited ≥ 50% of one climatic dominion, that is, the south-eastern coastal forests of South Africa for *Numida meleagris* Linnaeus, 1758. Species with presence in mountain environments were also recorded as present in the analogous biome, considering the elevational climatic gradient (Hernández Fernández & Vrba, 2005).

ANCESTRAL BIOME RECONSTRUCTION

In order to trace ancestral biome occupation, we modelled the occurrence of species in the ten biomes along the evolutionary history of Galliformes and Falconiformes, taking a phylogenetic approach. The ancestral biome occupation for all lineages was estimated through maximum likelihood analysis of geographical range evolution using the package BIOGEOBEARS (BioGeography with Bayesian and Likelihood Evolutionary Analysis) implemented in R (Matzke, 2015). This analysis allowed us to model the dynamics of biome occupation in relationship to the timing of cladogenesis based on the splitting times of the phylogenetic trees. Although it was designed originally for the study of biogeographical evolution, BIOGEOBEARS is an analytical approximation that allows probabilistic inference of ecological characters, biome occupation in our case, integrating different

models onto a time-calibrated phylogenetic tree (Batalha-Filho *et al.*, 2014; Lynch Alfaro *et al.*, 2015; Buckner *et al.*, 2015; de Medeiros & Lohmann, 2015). This tool enabled us to infer the ancestral biome in each node along the phylogeny by considering biomes as geographical areas with their own connectivity dynamics according to the climatic history of the Earth (Cardillo *et al.*, 2017; Landis *et al.*, 2021). BIOGEOBEARS estimates maximum likelihood for ancestral states during speciation events, modelling the transitions between different states (biomes occupied) along the phylogenetic branches as a function of time. The analyses were conducted using the dispersal–extinction–cladogenesis (DEC) model (Ree & Smith, 2008), modified in BIOGEOBEARS with the +J parameter (for *jump*), which models the process of founder-event speciation (Matzke, 2014a, b, 2015). We performed the DEC model a priori because it includes all biogeographical processes available in the DIVALIKE and BAYAREALIKE models. We conducted a BIOGEOBEARS model considering founder events (parameter +J) because of the long-distance dispersal capacities expected in birds (Price & Clague, 2002; Pigot & Tobias, 2015; Hosner *et al.*, 2017), which are expected to be important in the context of an island system, such as the one studied here, based on multiple climatic dominions. This is especially so, considering the relevance of transcontinental colonization events for avian diversification. Specifically, the DEC and DEC+J models have been consistent to explain colonization processes in biogeographical and macroevolutionary studies carried out in various lineages of birds, including Megapodidae (Harris *et al.*, 2014), Motacillidae (van Els *et al.*, 2019), Coraciiformes (McCullough *et al.*, 2019), Trogoniformes (Oliveros *et al.*, 2020), Rallidae (García-R & Matzke, 2021) and Sphenisciformes (Pelegrin & Acosta Hospitaleche, 2022). According to these studies, we consider that the +J parameter could be relevant in the evolution of Falconiformes and Galliformes because many lineages have achieved remarkable dispersion (e.g. *Falco eleonorae* Gene, 1839 has colonized Madagascar; several *Megapodius* Gaimard, 1823 species are distributed across islands of Micronesia), sometimes associated with long-distance migration (e.g. *Falco naumanni* Fleischer, 1818 or *Coturnix coturnix* Linnaeus, 1758). Finally, although Ree & Sanmartín (2018) criticized the conceptual basis of the DEC/DEC+J model, Klaus & Matzke (2020) rejected their claims based on standard, widely accepted principles of model evaluation and comparison (for details, see Klaus & Matzke, 2020).

Processes of climate change have altered the ecological conditions of the Earth over geological time. This has led to different biomes having particular histories in relationship to their origin and processes of geographical

fluctuation. Therefore, in our reconstruction we incorporated information about the availability of each biome along the Cenozoic by implementing 'biome existence–connection matrices' (Supporting Information, Table S1). These matrices were established according to an extensive review of palaeoecological and palaeoclimatic literature (for references, see Table 1) and allowed us to reflect the presence or absence of biomes since the Eocene/Oligocene (time of origin of the study groups, according to the phylogenies) until the Pleistocene–Holocene. These matrices also reflect the connectivity among biomes, hence their potential colonization pathways. For example, there is extensive documentation on the climatic and geographical relationship between the evergreen tropical rainforest and tropical deciduous woodland biomes (Dexter *et al.*, 2018) that supports the plausibility of colonization processes between them, whereas the rainforest and tundra have never had direct connections. This methodological approach allows us to introduce temporal constraints related to the geological, climatic and ecological history of biomes in the analysis. Likewise, there is some uncertainty regarding the timing of the onset of the biomes (Jetz & Fine, 2012). For this reason, we constructed two biome existence–connection matrices based on geological and fossil evidence in a broad time interval (see references in Table 1). These biome matrices were established as follows, one for the Oligocene–Miocene (in which biomes III, IV, VII and IX were not yet present) and a second one for the Pliocene–Pleistocene (with all extant ten biomes). The connectivity between two biomes was coded with '1' and the absence of connectivity among biomes or non-existence was coded as '0' (Supporting Information, Table S1).

To avoid the computational intractability of the analysis with all 1023 potential biome combinations (Hernández Fernández & Vrba, 2005) in two phylogenies with a high number of species, we complemented the biome existence–connection matrices with information on biome occupation in recent birds. To some extent, extant avifauna shows potential biome occupation in birds, considering biological clade properties such as flight capability and migratory behaviour, which have an influence on dispersal ability (Rolland *et al.*, 2014). Thus, we reduced these 1023 potential biome combinations to a set of only 239 biome combinations, which represented the observed combined biome occupations in all extant non-passerine birds (3951 spp.; Supporting Information, Table S2).

The process to reconstruct the ancestral biome occupation of Galliformes and Falconiformes combined the information on living species biome occupation, tree topology, availability and connections among biomes through time, at the same time yielding the likelihood values for each biome combination in each node. The BIOGEOBEARS output for a ten-area analysis was complex. In order to organize the results and obtain general patterns of historical biome occupation, we established a criterion based on selection of the biome combinations with the highest probabilities for each node, which were organized in a decreasing fashion according to their likelihood value. The probability scores for these biome combinations were cumulative until a value of 0.5 was reached. The relative likelihood scores of each biome within the selected combinations were summed, and all biomes with a cumulative likelihood of > 0.25 were retained for each node (Supporting Information, Tables S3 and S4). For example, if, for a given node, the most probable biome combinations were III–IV (presence in desert and sclerophyllous woodland), with a likelihood value of 0.4, and IV–VII (presence in sclerophyllous woodland and steppe), with a likelihood value of 0.12, this would imply that the values of relative probability for each biome were defined as follows: III = 0.4, IV = 0.52 and VII = 0.12. We would then consider that only biomes III and IV were reconstructed robustly for that particular node.

NICHE CONSERVATISM AND BIOME COLONIZATION

To assess the phylogenetic biome conservatism patterns for both Galliformes and Falconiformes, we counted the transitions between biomes from each node to its descendant nodes. In this sense, the transition was defined, for each biome, as the path between an ancient node with respect to its descendant node. The transitions could be conservative (i.e. the biome state was preserved between ancestor and descendent), contributing to phylogenetic biome conservatism, or non-conservative, implying the colonization of a biome different from those occupied by its ancestor (Fig. 1). Also, we counted the cases of biome loss between the biome occupation state of the ancestor and descendent. The reconstruction of biome occupation for each node of the phylogeny allowed us to describe the occupation trends of the ten different biomes through time. We counted the transitions, comparing the state in an ancestral node with respect to its descendants, and codified whether a specific biome was conserved or not (implying change or loss) between ancestor and descendent nodes. This approach to conservatism quantification was similar to the one proposed by Duchêne & Cardillo (2015) based on latitudinal zones.

Numerous works have focused on the related hypothesis of tropical conservatism, which aims to explain the observed imbalance in diversity richness in tropical latitudes compared with temperate zones. This hypothesis proposes that the great species richness found in tropical environments is attributable to the niche conservatism of the lineages linked in their origin to these environments, which expanded across the Palaeogene (Wiens & Donoghue, 2004). However, the tropical conservatism hypothesis has
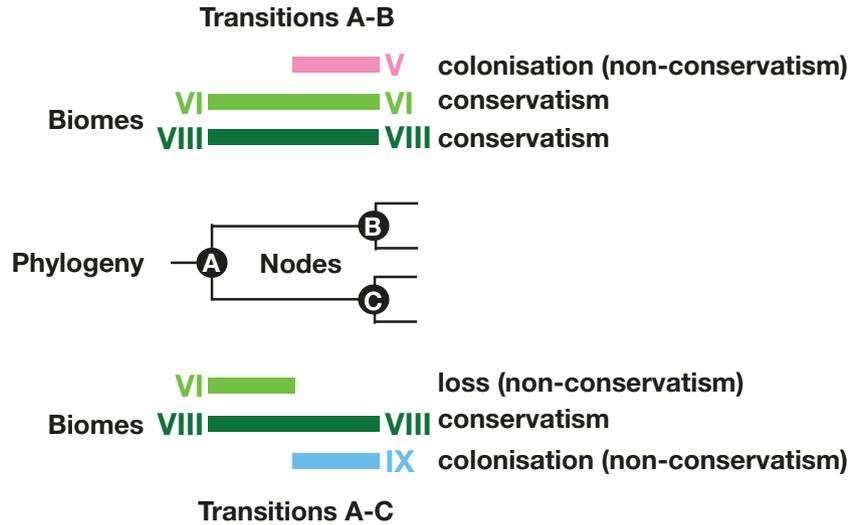
Figure 1. Schematic explanatory example for transition categories considered in this study: transition with biome conservatism; transition with colonization; and transition with loss of ancestral biome occupation. Note that ancestral biome occupation (for node A) is the same above and below, whereas biome occupations for derived nodes B (above) and C (below) differ.

been explored from a purely latitudinal approach for plant and bird taxa (Kerkhoff *et al.*, 2014; Duchêne & Cardillo, 2015).

Finally, we explored the colonization dynamics of each biome, considering the colonization events inferred across the phylogeny. However, these colonization events have a temporal uncertainty that is proportional to the branch length. Likewise, the phylogenies present a trend to increase the number of branches over time, producing a bias towards the present. To solve these issues, we analysed the biome colonizations through time using a sliding window method. This approach was taken to calculate the proportion and mean of colonization rates in each biome, considering time intervals of 1 Myr, and smoothed with a 5 Myr sliding window that included a correction factor taking into account the number of branches during each time bin (Vieites *et al.*, 2007; Meredith *et al.*, 2011).

RESULTS

ANCESTRAL BIOME OCCUPATION RECONSTRUCTION IN GALLIFORMES

Our analysis reconstructed the ancestral biome occupation for 220 nodes (98.21%); the remaining four nodes presented low statistical support for any of the ten biomes (Supporting Information, Table S3). The common ancestor of the Galliformes was associated during the latest Eocene with tropical rainforest, tropical deciduous forest, savanna and temperate evergreen forest biomes (Fig. 2). According to the results

for biome occupation patterns in Galliformes, this group presented three main moments of diversification. First, during the Early/Middle Miocene, Phasianidae presented an important radiation associated mainly with tropical deciduous woodlands. Likewise, during this epoch there was an important colonization of broadleaf deciduous forests, which favoured the subsequent colonization of temperate and cold biomes. Second, throughout the Late Miocene several tropical families experimented with a prominent process of diversification in Australasia (Megapodiidae), the Afrotropics (Numididae) and Neotropics (Cracidae and Odonthophoridae), where they showed a close relationship with tropical deciduous woodland, savanna and temperate evergreen forest. Conversely, some phasianid lineages (Tetraonini) radiated after colonizing new cold biomes, such as the taiga. Third, during the Plio-Pleistocene, Galliformes reached important levels of diversification and, especially, during glaciation periods Phasianidae lineages colonized new emerging and expanding biomes, such as sclerophyllous woodland–shrubland, desert, steppe and tundra (Zimov *et al.*, 1995; Douglas *et al.*, 2006; Senut *et al.*, 2009).

Considering families (Fig. 2), Megapodidae showed an ancestral biome occupation within tropical deciduous forest and savanna biomes, whereas Cracidae presented an ancestral occupation associated with tropical deciduous woodlands and temperate evergreen forests, from which there was a differential evolutionary trend in the climatic niche evolution towards temperate evergreen forests in the case of the subfamily Penelopinae and tropical deciduous forest
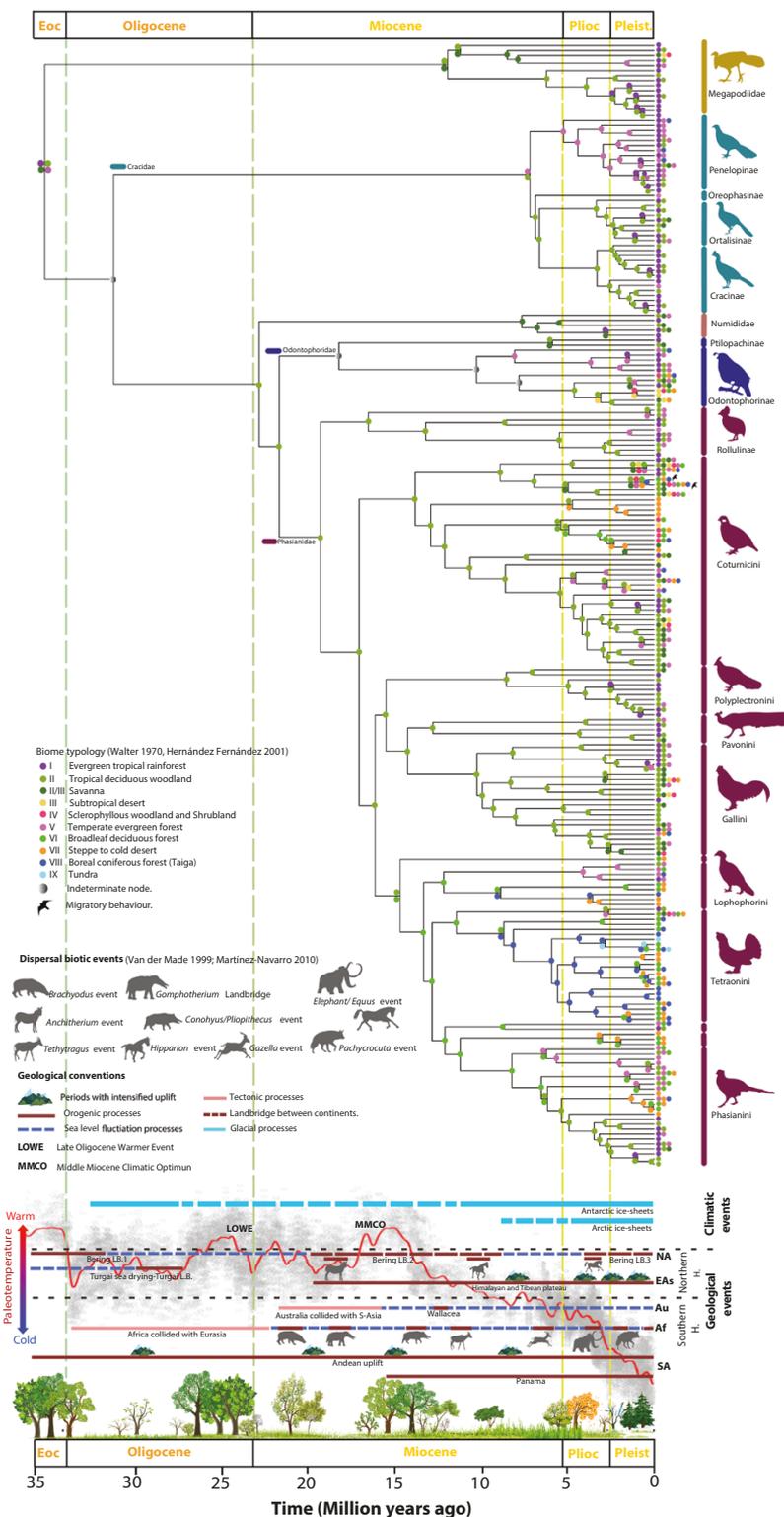
Figure 2. Ancestral biome reconstruction for Galliformes. Coloured circles represent the ten different biomes implemented in the model (Walter, 1970; Hernández Fernández, 2001); those at the nodes represent the inferred ancestral biome(s) occupancy; those at the tips correspond to the recent biome distribution of species. Along the time scale, geological and climatic histories are shown, in addition to intercontinental biotic interchanges. Abbreviations: Af, Africa; Au, Australia; EAs, Eurasia; LB, land bridge; NA, North America; SA, South America.

in the rest of the subfamilies. Megapodidae probably originated from Eurasian ancestors that colonized Australia during the Oligocene–Miocene (Mayr, 2017). In contrast, it is likely that Cracidae originally had a North American distribution, but later contracted latitudinally towards the tropics, with a relatively recent diversification in South America after the Great American Biotic Interchange (GABI) (Pelegrin *et al.*, 2018). These processes could generate diversification patterns such as those evidenced by the phylogenies, with a gap remaining with respect to stem lineages. Thus, it appears necessary to improve the sampling of the early fossil record for these families.

The ancestral biome reconstructed for Numididae was savanna. In contrast, the ancestral biome occupation for Odontophoridae showed an uncertain state, which was probably attributable to the incomplete knowledge of phylogenetic relationships within this family, especially in its most species-rich genus, *Odontophorus* Vieillot, 1826 (Hosner *et al.*, 2015a). As a result, inclusion of climatic information for all known species was impeded in the phylogenetic reconstruction. However, our results showed a clear differentiation among its main lineages, whose radiations were mostly associated with tropical deciduous woodlands or temperate evergreen forest biomes. Finally, for the most species-rich Phasianidae, we found an ancestral biome occupation of tropical deciduous woodland and early diversification during the Middle–Late Miocene associated with this biome (Fig. 2). The tropical deciduous woodland was the ancestral biome of the subfamily Rollulinae from Southeast Asia. Several tribes of Phasianinae with an important geographical distribution in Africa and Southeast Asia (Coturnicini, Polyplectronini, Pavonini and Gallini) also diversified while conserving the occupation in tropical deciduous woodland. The lineage of phasianids ancestral to Lophophorini, Tetraonini and Phasianini colonized the temperate broadleaf deciduous forests during the Middle Miocene. Within this lineage, basal Lophophorini and Tetraonini occupied the boreal coniferous forests independently during the Middle–Late Miocene. In contrast, the diversification of Phasianini during the Late Miocene showed a trend to the conservation of biome occupation associated with broadleaf deciduous forest, with subsequent Plio-Pleistocene colonization events of temperate evergreen forest and tropical deciduous forest (Fig. 2).

Our results showed different phases of biome colonization in Galliformes (Fig. 3). During the Oligocene–Miocene boundary, there was an outstanding increase in the colonization rate of tropical deciduous woodlands. In the Middle Miocene, the broadleaf deciduous forest registered an important increase of colonization. Later, during the Late Miocene, the

rates of colonization in tropical deciduous woodlands, savanna, temperate evergreen forests and taiga increased during the same time interval. Throughout the Pliocene, we evidenced a marked growth in the colonization rates for hot and cold deserts. Finally, during the Plio-Pleistocene, there was an increase of colonization in tropical evergreen rainforest, sclerophyllous woodland, broadleaf deciduous forest and tundra.

We found important support for phylogenetic biome conservatism (%BC in Table 2) in the evolution of Galliformes. Biome colonization was represented by 292 events (38.07%; Fig. 4), while conservative biome occupation was observed along the phylogeny in 475 of 767 transitions, which reflects a relatively high signal of biome conservatism (61.92%). Nevertheless, biome conservatism was not homogeneously distributed across biomes. All biomes, except the savanna and sclerophyllous woodland–shrubland, presented values for biome conservatism > 50% (Table 2). The highest values of biome conservatism (> 75%) were associated with biomes occupying the extremes of the climate gradient: evergreen tropical rainforest (82.93%), steppe (83.78%) and tundra (100%). Despite being another extreme biome, however, the desert showed only 55.6% biome conservatism. The tropical deciduous woodland, broadleaf deciduous forest and boreal coniferous forest presented relatively high biome conservatism values (> 60%). Transition patterns among biomes (Fig. 3) showed an important directional bias; the tropical deciduous woodland appeared to be the main net species source for other biomes in tropical and subtropical latitudes.

ANCESTRAL BIOME OCCUPATION RECONSTRUCTION IN FALCONIFORMES

We reconstructed the ancestral biome occupation for 60 of 65 (92.31%) nodes in the phylogenetic tree of Falconiformes (Fig. 5; Supporting Information, Table S4). Only five nodes showed uncertainty estimation of biome occupancy. Our findings showed that the Early Oligocene ancestor of falcons was probably a biome generalist, occupying environments associated with tropical biomes, such as evergreen tropical rainforest, tropical deciduous woodland and savanna (Fig. 5). During the Early and Middle Miocene, Herpetotherinae extended towards temperate evergreen forests but conserved the association with tropical ancestral biomes. In contrast, Poliborini and Falconini diverged during the Middle Miocene, while conserving their ancestral biome occupation. Our results indicated an initial colonization from tropical biomes to temperate environments by Poliborini ancestors during the Late Miocene, with a subsequent specialization towards tropical drier
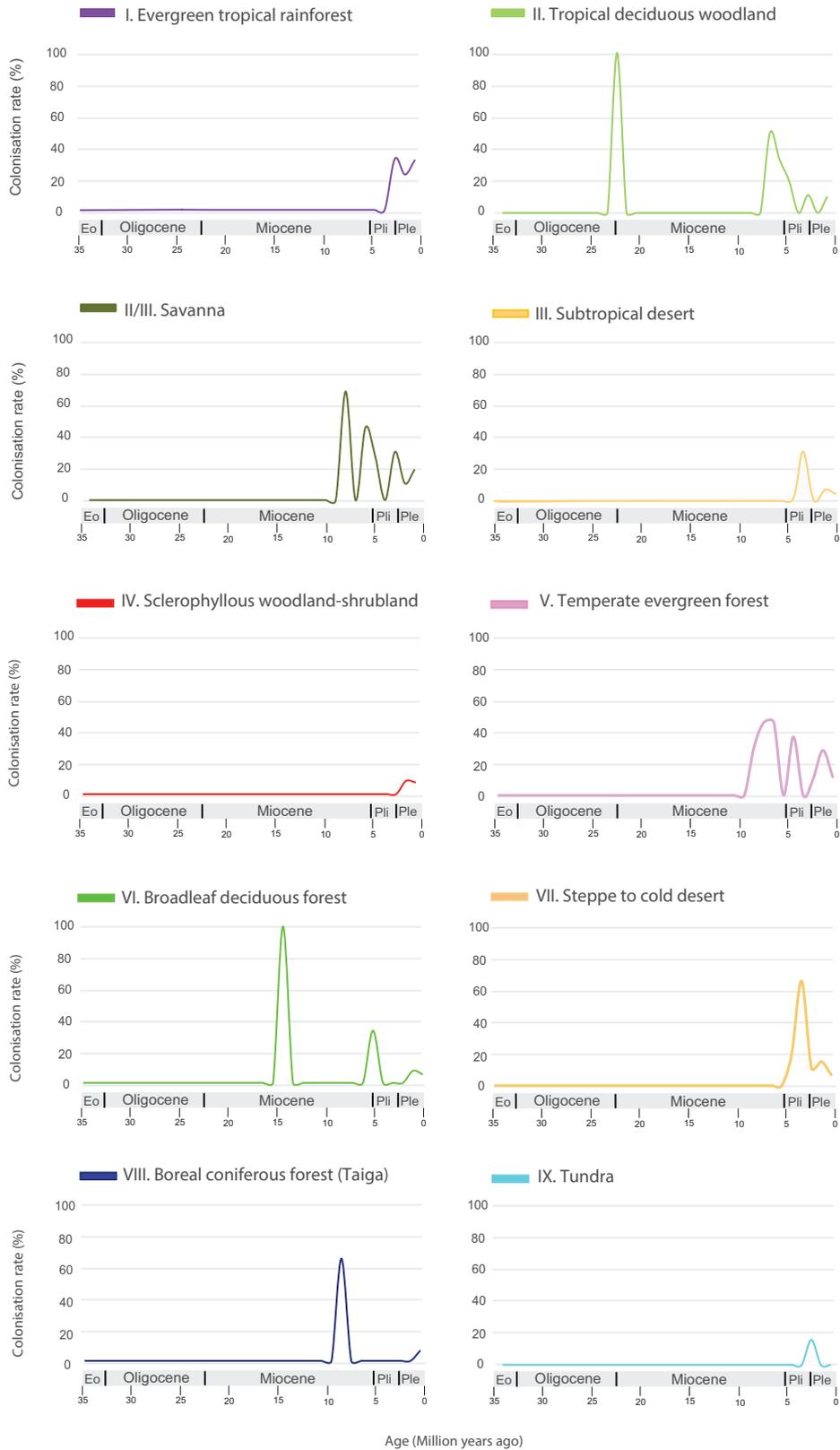
Figure 3. Colonization dynamics of Galliformes. Each graph represents the rate of colonization by new lineages for each biome throughout the Cenozoic.

Table 2. Biome transitions in Galliformes

Biome	Destination											
Source	Loss	I	II	II/III	III	IV	V	VI	VII	VIII	IX	Total col.	%BC
Evergreen tropical rainforest (I)	1	**34**	4	1	–	–	2	–	–	–	–	7	**82.9**
Tropical deciduous woodland (II)	8	55	**225**	34	10	7	29	7	7	–	–	149	**60.2**
Savanna (II/III)	–	7	5	**23**	2	4	3	2	4	–	–	27	**46.0**
Subtropical desert (III)	–	–	–	–	**5**	1	–	1	2	–	–	4	**55.6**
Sclerophyllous woodland–shrubland (IV)	–	–	–	–	–	**3**	–	1	3	1	–	5	**37.5**
Temperate evergreen forest (V)	1	20	13	3	–	1	**67**	5	–	10	–	52	**56.3**
Broadleaf deciduous forest (VI)	–	–	3	–	1	4	4	**54**	10	6	–	28	**65.9**
Steppe cold desert (VII)	–	–	–	–	–	1	–	1	**31**	4	–	6	**83.8**
Boreal coniferous forest (taiga) (VIII)	–	–	–	–	–	–	–	7	6	**30**	1	14	**68.2**
Tundra (IX)	–	–	–	–	–	–	–	–	–	–	**3**	0	**100.0**

The number of biome transitions is given for each biome, considering the source (rows) and destination (columns). Bold numbers along the diagonal show conservative transitions (total, 475). 'Total col.' indicates the non-conservative transitions that imply colonization (total, 292). '%BC' represents the proportion of biome conservatism for each biome according to colonization events. Biome non-conservative transitions that implied loss of the ancestral biome are also shown. The total number of transitions (767) is the sum of conservative transitions (475) and non-conservative transitions (292).

and more seasonal environments (savannas and tropical deciduous woodlands) during the latest Miocene and Pliocene. Finally, during the Pleistocene, Poliborini developed an extreme generalist spectrum in some lineages, with broad biome occupation. The divergence within Falconini could be related to the dynamics between tropical deciduous woodlands and savannas. Thus, the common ancestor of *Microhierax* Sharpe, 1874 and *Polihierax* Kaup, 1847 was probably specialized in savanna environments, whereas the late Neogene *Microhierax* ancestors colonized tropical forest biomes (I and II) and developed a less specialized condition during their Plio-Pleistocene diversification. On the contrary, the *Falco* Linnaeus, 1758 lineage expanded from tropical woodland and savanna environments towards temperate biomes from the Early Pliocene onwards (Fig. 5), first in the broadleaf deciduous forest biome and later in many other biomes, including the novel and emerging biomes produced by the Northern Hemisphere Pleistocene glaciations.

In general terms, during the Oligocene and Early Miocene evolution of Falconiformes their patterns of biome colonization showed relatively few events, only related to the temperate evergreen forest (Fig. 6). The late Miocene witnessed the colonization of evergreen tropical rainforest and temperate evergreen forest by some falconid lineages. Nevertheless, during the Pliocene, they began an outstanding process of colonization of some tropical and temperate dry biomes, such as tropical deciduous woodland, savanna, desert, steppe and sclerophyllous woodland. Finally,

taiga and tundra environments were colonized during the Pleistocene.

Biome transitions in Falconiformes (Table 3; Fig. 7) showed similar trends for biome conservatism with respect to Galliformes. The biome was conserved in 273 of 436 (62.61%) biome transitions. Meanwhile, there were 163 (37.39%) transition events with new biome colonization. All biomes presented values of biome conservatism > 50% (Table 3). The highest scores were registered for biomes such as evergreen tropical rainforest (82.5%), steppe (77.8%), taiga (93.8%) and tundra (87.5%). There was also a prominent directional bias in the transitions among biomes, with an important role of tropical deciduous woodlands and, secondarily, savannas as net sources of species, while the evergreen tropical rainforest, temperate evergreen forest and steppe biomes would have acted as evolutionary receptors of colonizing species (Table 3; Fig. 7).

DISCUSSION

TRENDS IN PHYLOGENETIC BIOME CONSERVATISM

The biome occupation patterns throughout the evolutionary history of Galliformes and Falconiformes (Figs 2, 5) revealed high levels of phylogenetic biome conservatism. On average, biomes were conserved in > 50% of the potential biome transitions in landfowl and falcons. Interestingly, most biomes at the extremes of the climatic gradient consistently presented biome conservatism values > 75% (evergreen tropical
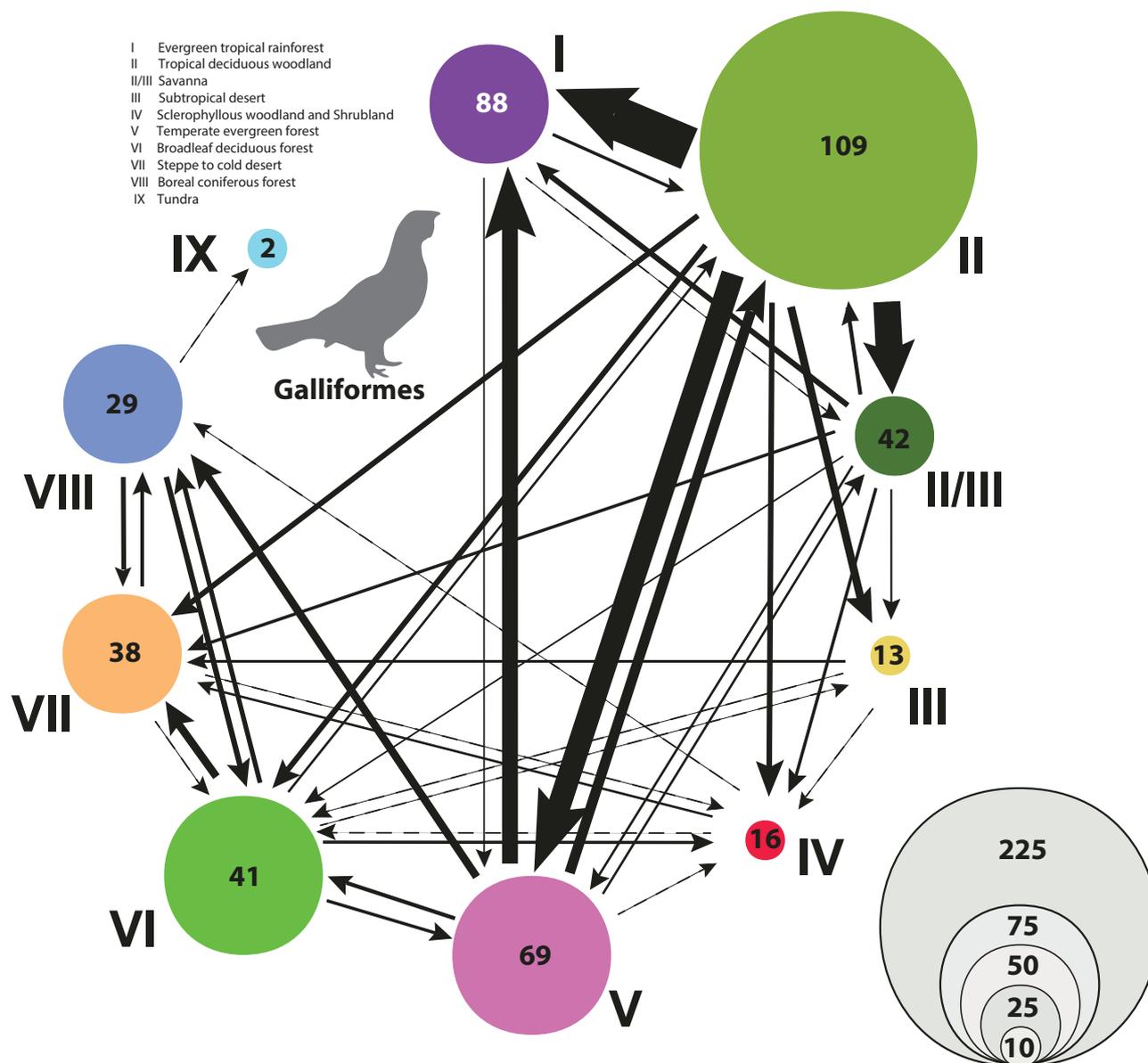
Figure 4. Biome transitions in Galliformes. The number of recent species is indicated inside the circles. Arrow thickness is proportional to the number of colonizations. The dashed lines indicate only one colonization event. The number of transitions that did not imply colonization (niche conservatism) is indicated as different areas of the circles, classified in five categories. For more details about absolute scores, see Table 2.

rainforest, steppe and tundra, but not desert). The high degree of biome conservatism in these extreme biomes is compatible with the observed prevalence of specialized lineages associated with them (Hernández Fernández & Vrba, 2005; Moreno-Bofarull *et al.*, 2008; Cantalapiedra *et al.*, 2011; Menéndez *et al.*, 2021; Hernández Fernández *et al.*, 2022; Gamboa *et al.*, 2022), which has been related to the incidence of global climatic changes associated with the recurrent environmental extremes of the astronomical cycles (also called Milankovitch cycles) as direct promoters

of vicariance and speciation, particularly among biome specialists from extreme biomes (Vrba, 1980, 1987, 1992; Hernández Fernández & Vrba, 2005).

Nevertheless, the desert (which is also an extreme climatic biome) did not present a high percentage of conservatism in either Galliformes or Falconiformes. This finding is probably related to the fact that some morphophysiological traits might determine constraints for colonization and specialization in desert environments (Hill, 2004; Williams & Tieleman, 2005). For instance, some traits in birds, such as presence of
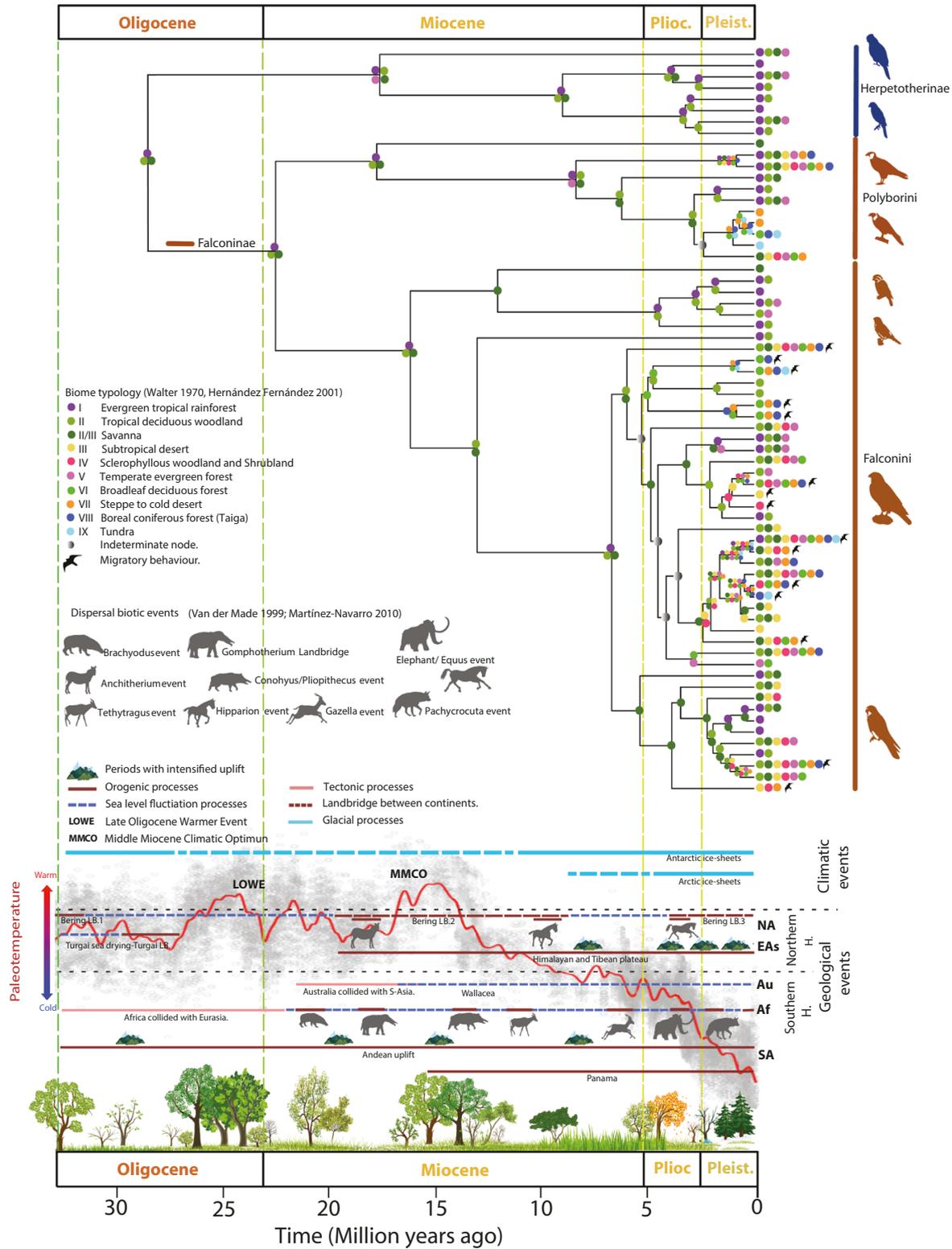
Figure 5. Ancestral biome reconstruction for Falconiformes. Coloured circles represent the ten different biomes implemented in the model (Walter, 1970; Hernández Fernández, 2001); those at the nodes represent the inferred ancestral biome(s); those at the tips correspond to the recent biome distribution of species. Along the time scale, geological and climatic histories are shown, in addition to intercontinental biotic interchanges. Abbreviations: Af, Africa; Au, Australia; EAs, Eurasia; LB, land bridge; NA, North America; SA, South America.
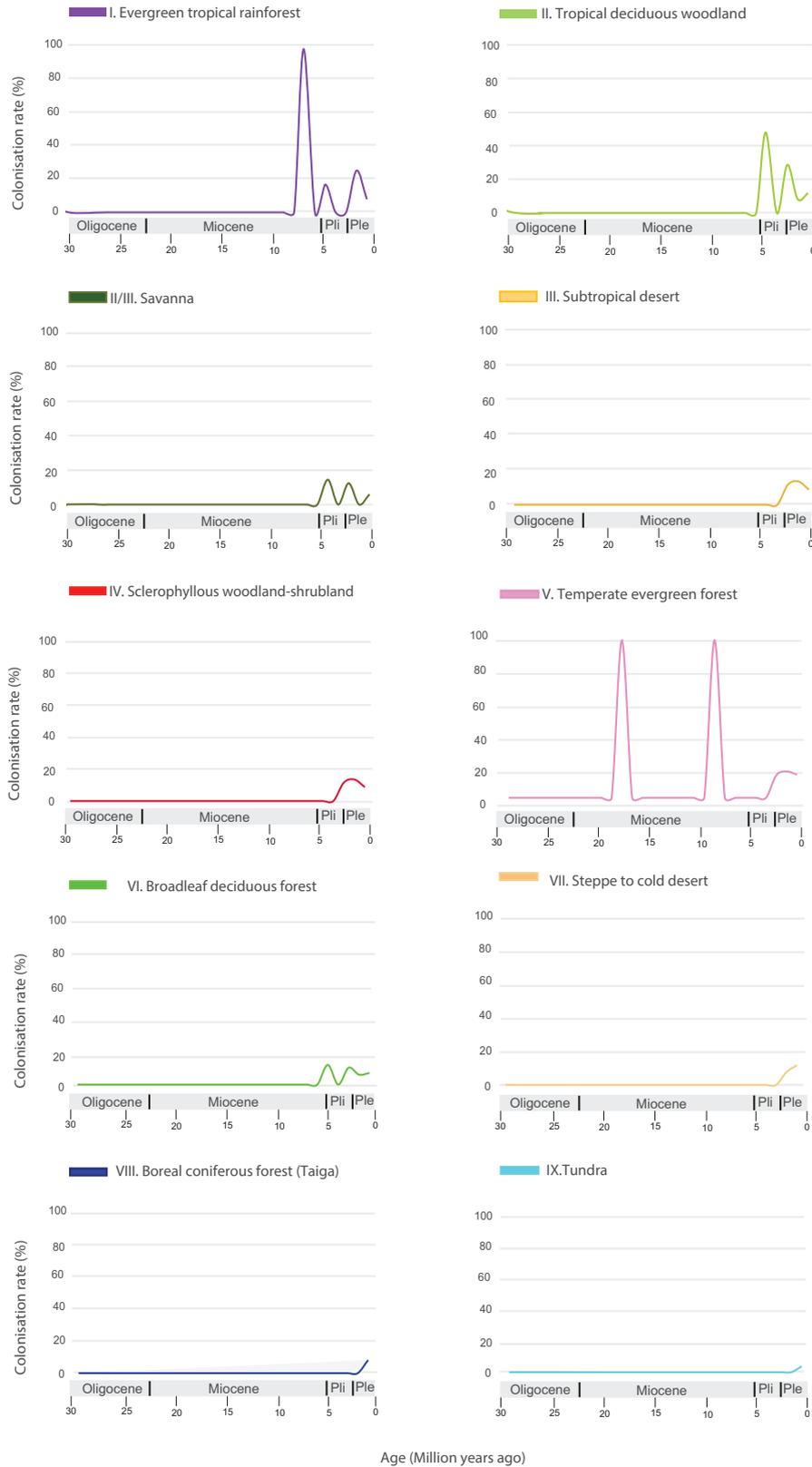
Figure 6. Colonization dynamics of Falconiformes. Each graph represents the rate of colonization by new lineages for each biome throughout the Cenozoic.

Table 3. Biome transitions in Falconiformes

Biome	Destination												
Source	Loss	I	II	II/III	III	IV	V	VI	VII	VIII	IX	Total col.	%BC
Evergreen tropical rainforest (I)	2	**33**	3	2	–	–	2	–	–	–	–	7	**82.5**
Tropical deciduous woodland (II)	–	11	**61**	4	4	5	12	5	1	–	–	42	**59.2**
Savanna (II/III)	1	8	10	**57**	8	7	7	4	6	–	–	50	**53.3**
Subtropical desert (III)	–	–	3	–	**20**	1	–	4	4	–	–	12	**62.5**
Sclerophyllous woodland–shrubland (IV)	–	–	1	–	1	**18**	2	3	3		–	10	**64.3**
Temperate evergreen forest (V)	–	1	3	1	–	1	**18**	1	–	6	–	13	**58.1**
Broadleaf deciduous forest (VI)	–	–	2	1	1	2	1	**23**	4	8	2	21	**52.3**
Steppe cold desert (VII)	–	–	–		–	–	–	–	**21**	5	1	6	**77.8**
Boreal coniferous forest (taiga) (VIII)	1		–	–	–	–	–	–	–	**15**	1	1	**93.8**
Tundra (IX)	–	–	–	–	–	–	–	–	–	1	**7**	1	**87.5**

The number of biome transitions is given for each biome, considering the source (rows) and destination (columns). Bold numbers along the diagonal show conservative transitions (with no change of biome) (total, 273). 'Total col.' indicates the non-conservative transitions, which implies colonization (total, 163). '%BC' represents the proportion of biome conservatism for each biome according to colonization events. Biome non-conservative transitions that implied loss of the ancestral biome are also shown. The total number of transitions (436) is the sum of conservative transitions (273) and non-conservative transitions (163).

feathered extremities, lack of sweat glands and high metabolic rates, would be exaptations for colder rather than arid environments. In this way, Bartholomew & Cade (1963) and Maclean (1996) suggested that once some bird lineages develop special adaptations to survive in the desert (e.g., sandgrouse, Pteroclidae), this might favour the subsequent specialization in this biome despite their limitations (Williams & Tieleman, 2002, 2005).

In addition, it is crucial to understand that the ability to survive in arid environments involves several aspects related to physiological mechanisms associated with water balance and thermoregulation. Some adaptations studied in desert birds are a reduction of basal metabolic rate, which allows birds to cope with low food and water availability, regulation of water loss by evaporation or reduction of loss water by renal mechanisms (Williams & Tieleman, 2002, 2005). In particular, tolerance of dehydration (measured as mass loss) is near 50% in the California quail (*Callipepla californica* Shaw, 1798), which may use saline water of marine origin (Bartholomew & MacMillen, 1961). Another example is the partridge (*Alectoris chukar* Gray, 1830), which uses evaporative and behavioural mechanisms in thermoregulation processes, minimizing cutaneous water loss (Marder & Bernstein, 1983). In Falconiformes, the grey falcon (*Falco hypoleucos* Gould, 1841) shows behavioural adaptations related to low activity levels, regulating endogenous heat production. Compared with other *Falco* species, this species also presents developmental delay and feeding dependency of chicks, which are mechanisms that have been proposed as adaptive

for arid environments (Schoenjahn *et al.*, 2022a, b). Nevertheless, our results suggest a relatively recent colonization of the deserts, associated with their Plio-Pleistocene expansion, from a previous generalist biomic condition with presence in biomes such as savanna, tropical dry woodland and sclerophyllous woodland-shrubland, which could enable specific colonizations from these environments during certain periods, as has been suggested for predators such as falcons (Maclean, 1996).

Falconiformes also showed remarkable biome conservatism in the taiga (93.8%), a finding associated with several independent colonization events of this biome during the Pleistocene. At this time, glacial and interglacial cycles generated alternating expansion and contraction in the taiga biome, triggering evolutionary processes (Weir & Schluter, 2004). The ecology of predators is linked to larger home ranges for hunting, which is associated with large geographical distributions and promotes a biome generalist condition according to evidence in carnivorous mammals (Hernández Fernández & Vrba, 2005; Hernández Fernández *et al.*, 2022). Such a generalist condition and large distribution areas might have favoured the subsequent origin of migratory capacity in several lineages of *Falco*, allowing movements and colonization of the taiga during favourable seasons (Alerstam *et al.*, 2003).

Biome conservatism is strong in both Galliformes and Falconiformes, which suggests the existence of common triggering processes, such as abiotic changes, particularly associated with extreme biomes. The mandatory development of

I   Evergreen tropical rainforest
II   Tropical deciduous woodland
II/III Savanna
III   Subtropical desert
IV   Sclerophyllous woodland and Shrubland
V   Temperate evergreen forest
VI   Broadleaf deciduous forest
VII   Steppe to cold desert
VIII Boreal coniferous forest
IX   Tundra
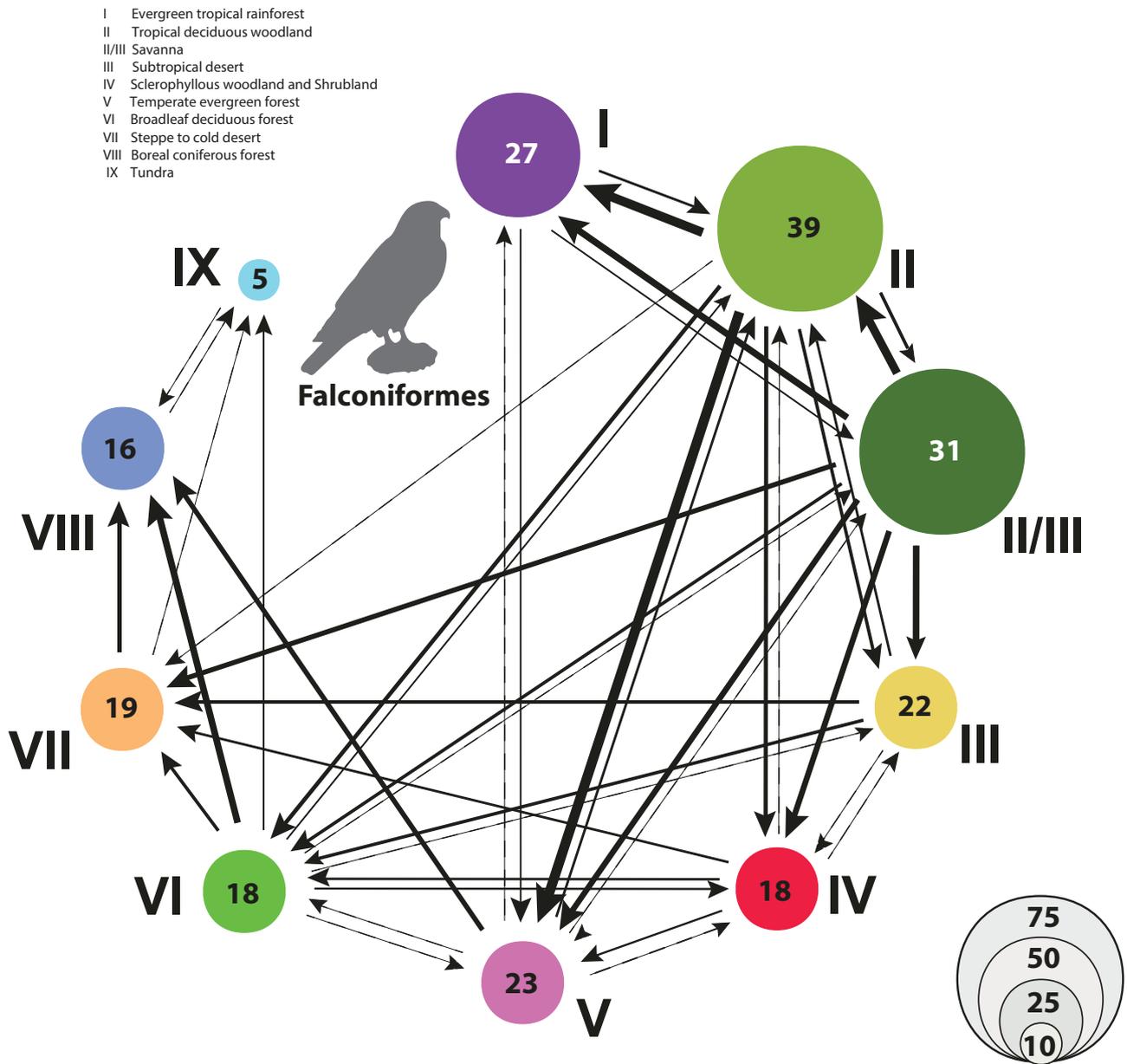
Figure 7. Biome transitions in Falconiformes. The number of recent species is indicated inside the circles. Arrow thickness is proportional to the number of colonizations. The dashed lines indicate only one colonization event. The number of transitions that did not imply colonization (niche conservatism) is indicated as different areas of the circles, classified in four categories. For more details about absolute scores, see Table 3.

physiological adaptations to cold environments (McNab, 2009), such as steppe, taiga and tundra, probably constituted a constraint for subsequent colonizations from these biomes (Hawkins *et al.*, 2007). On the contrary, high resource availability and niche diversity in the tropical rainforest biome might constitute important factors promoting biome conservatism (Wiens, 2004; Peterson & Nyari, 2008), resulting in the existence of lineages occupying this biome since the Palaeogene.

Taken together, our findings depict both the tropical deciduous forests and the savannas as significant evolutionary arenas for Galliformes and Falconiformes (Tables 2 and 3; Figs 4, 7). The patterns of biome occupation and conservatism related to these biomes reveal their important roles as evolutionary cradles and corridors. Owing to their thermal and hydric seasonality (Pennington *et al.*, 2006; Dexter *et al.*, 2018), these biomes present a broad spectrum of environmental variations. Adaptation of species to

such environmental diversity would have promoted the development of a broad physiological spectrum, which allowed these lineages the subsequent colonization and specialization into novel drier and colder climatic conditions brought about by the Late Neogene and Quaternary global cooling trend (Guerrero *et al.*, 2013; Wiens *et al.*, 2013; Jara-Arancio *et al.*, 2014).

The importance of tropical biomes (I, II and II/III) evidenced in the evolutionary patterns of Galliformes and Falconiformes (Tables 2 and 3) is broadly consistent with previous findings for the tropical conservatism hypothesis in birds, studied from a latitudinal perspective (Duchêne & Cardillo, 2015). In this context, evolutionary success might have resulted not from continuous adaptation to new environments but from the development of a broad adaptive physiological spectrum by specific and particular lineages in seasonal biomes. This allowed their expansion and dispersal capacities to colonize new environments during climatic and geological changes (we provide additional discussion and historical details for both bird orders in the Supporting Information: Galliformes and Falconiformes history and biome occupancy patterns).

PATTERNS OF BIOME COLONIZATION

Our results for Galliformes suggest different phases of biome colonization during the Neogene (Fig. 3), when tropical deciduous woodlands, temperate evergreen forests and broadleaf deciduous forest expanded substantially, related to a global cooling (Zachos *et al.*, 2001) that caused the fragmentation and contraction of tropical evergreen rainforest zones. These processes would have promoted the colonization of emerging habitats in drier tropical deciduous woodlands and temperate evergreen forests in northern latitudes (Collinson & Hooker, 2003). In the case of Falconiformes (Fig. 6), during the Early Miocene and probably since the Late Oligocene, the temperate evergreen forest was colonized exclusively by the South American Herpetotherinae lineage, an event probably associated with the initial uplift phases of Andes (Hoorn *et al.*, 2010) and the cooling of southern South America triggered by Oligocene ice-sheet formation in Antarctica (McKay *et al.*, 2016). The observed pattern is consistent with the early evolution of Falconidae in South America as shown by phylogenetic (Fuchs *et al.*, 2015) and fossil (Cenizo *et al.*, 2016) evidence.

During the Early–Middle Miocene, the broadleaf deciduous forest biome presented an increase in colonizations in Phasianidae, which might be related to the ecological gradient established by the initial Himalayan uplift (Shi *et al.*, 1999; Guo *et al.*, 2008; Miao *et al.*, 2012; Hurka *et al.*, 2019). The increase of Galliformes colonization events in the savanna biome

during the Middle–Late Miocene is consistent with an early replacement of forests by grassland biomes (Jacobs, 2004; Edwards *et al.*, 2010; Harzhauser *et al.*, 2016). The generalist ecology of falcons would allow their expansion towards evergreen temperate forest in the rising Andes during the Middle–Late Miocene (Hoorn *et al.*, 2010).

The increase in colonization rates in the Middle and Late Miocene for the majority of biomes could be related to the global decrease in temperatures after the Mid-Miocene Climatic Optimum, which was associated with increasing aridification and the emergence of seasonal biomes (Zachos *et al.*, 2001; van Dam, 2006; Liu *et al.*, 2009). Our results showed an increase during the Late Miocene and Pliocene in the colonization rate for semi-arid biomes, such as tropical deciduous woodland, and for open environments, such as desert, savanna and steppe, when these seasonal biomes expanded their distribution towards high latitudes and when open environments acquired an especial ecological relevance associated with the worldwide expansion of C_4 grasslands (Cerling *et al.*, 1993; Bredenkamp *et al.*, 2002; Edwards *et al.*, 2010; Bouchenak-Khelladi & Hodkinson, 2011; Strömberg, 2011; Charles-Dominique *et al.*, 2016). This global environmental change has been recognized as an important trigger for diversification in *Falco* (Fuchs *et al.*, 2015). Likewise, during the Late Miocene and Pliocene, the falconids (specially *Falco*) and several lineages of landfowl, such as Lophophorini, Tetraonini and Phasianini, also showed an increase in colonization events into temperate and high-latitude biomes, such as broadleaf deciduous forest, taiga and tundra. This colonization pattern is possibly related to previous development of different physiological traits (Klaassen, 1996) and the capacity for long-distance flight (Thorup, 2006), probably linked to the evolution of migration and dispersal across diverse environments (Rolland *et al.*, 2014; Pelegrin *et al.*, 2015; Wilcox *et al.*, 2019). Thus, the Neogene expansion of biomes such as desert (Senut *et al.*, 2009), steppe (Miao *et al.*, 2012; Hurka *et al.*, 2019), taiga (Pound *et al.*, 2011; Popova *et al.*, 2017; Hurka *et al.*, 2019) and sclerophyllous woodland–shrubland (Suc, 1984; Hernández Fernández *et al.*, 2007) might have facilitated the emergence of novel ecological niches for fowl and falcons. Pleistocene glacial–interglacial alternation would also favour adaptation of a few lineages to tundra conditions. Nonetheless, the specific morphophysiological traits required to inhabit these environments meant that these high-latitude biomes were important evolutionary sinks and areas of endemism (Weir & Schluter, 2004; Abellán & Svenning, 2014; An *et al.*, 2015). These factors could explain the observed similarity in the timing of colonization for diverse biomes and the trend towards a significant

presence of basal lineages in warm tropical biomes, whereas higher latitudes (subtropical, temperate and cold) or dry biomes in tropical latitudes were subsequently colonized by later lineages (Hawkins *et al.*, 2006; Duchêne & Cardillo, 2015).

During the Pliocene and Pleistocene, many lineages of landfowl colonized the evergreen tropical rainforest from tropical deciduous woodland. Probably, the close ecological dynamics between both biomes and a relatively broad herbivorous capacity favoured the occupation of rainforests (with a higher diversity of plant-consumer niches), which is reflected in the high number of galliform species inhabiting both biomes. Evergreen tropical rainforests underwent a significant Plio-Pleistocene contraction and fragmentation in successive glacial cycles that probably promoted vicariance events of many tropical lineages, acting as refugia for many biome-specialist lineages during cooler periods (Haffer, 2008; Bennett *et al.*, 2012; Hazzi *et al.*, 2018).

CONCLUSION

The integration of many sources of evidence (phylogeny, ecology, biogeography and the fossil record) provides a general framework for the evolutionary analysis of diverse taxa, which might better explain the relationship and influence of global changes on diversification and turnover patterns. Specifically, biomes and their temporal dynamics have acquired broad importance for understanding macroecological and macroevolutionary processes. The phylogenetic reconstruction of ecological characters provides the opportunity to analyse biome colonization dynamics and processes of adaptation to different climatic regimes from a deep-time perspective.

Our results are broadly consistent with the presence of high levels of phylogenetic niche conservatism for both Galliformes and Falconiformes. The biome conservatism was particularly marked in biomes placed at the extremes of the climatic gradient. Conservatism in the rainforest biome could be favoured by the extraordinary niche diversity and availability of resources, although some lineages developed specific morphophysiological and life-history traits (exaptation in many cases) that allowed them to colonize novel environments (such as tundra and steppe biomes) during the Neogene–Quaternary global cooling. Contrary to expectations, the desert biome did not show a high rate of conservatism, which suggests that the processes of morphophysiological adaptation and specialization to extremely arid conditions might be more limited than to biomes with less hostile conditions. Further studies including morphological and physiological data could shed light on the relationship between phenotypic adaptation and biome colonization.

Diverse changes in climate that occurred during the Miocene triggered the main diversification pulses in Galliformes and Falconiformes. During this epoch, the adaptation and wide occupation of seasonal dry biomes, such as tropical dry woodland and savanna, would have allowed the subsequent colonization of other biomes, in both tropical and temperate latitudes. Our results support the important role of tropical deciduous woodland as a source from which many other biomes are colonized and consolidate its position as an important player in the diversification processes and evolutionary dynamics of landfowl and falcons.

CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ACKNOWLEDGEMENTS

REFERENCES

Abellán P, **Svenning J-C. 2014.** Refugia within refugia – patterns in endemism and genetic divergence are linked to Late Quaternary climate stability in the Iberian Peninsula. *Biological Journal of Linnean Society* **113:** 13–28.

Alerstam T, **Hedenström A**, **Åkesson S. 2003.** Long-distance migration: evolution and determinants. *Oikos* **103:** 247–260.

An B, **Zhang L**, **Liu N**, **Wang Y. 2015.** Refugia persistence of Qinghai-Tibetan Plateau by the cold-tolerant bird *Tetraogallus tibetanus* (Galliformes: Phasianidae). *PLoS One* **10:** e0121118.

Axelrod DI. 1966. Origin of deciduous and evergreen habits in temperate forests. *Evolution* **20:** 1–15.

Axelrod DI. 1985. Rise of the grassland biome, central North America. *The Botanical Review* **51:** 163–201.

Barbolini N, **Woutersen A**, **Dupont-Nivet G**, **Silvestro D**, **Tardif D**, **Coster PMC**, **Meijer N**, **Chang C**, **Zhang H-X**, **Licht A**, **Rydin C**, **Koutsodendris A**, **Han F**, **Rohrmann A**, **Liu X-J**, **Zhang Y**, **Donnadieu Y**, **Fluteau F**, **Ladant J-B**, **Le Hir G**, **Hoorn C. 2020.** Cenozoic evolution of the steppe-desert biome in Central Asia. *Science Advances* **6:** eabb8227.

Bartholomew GA, **Cade TJ. 1963.** The water economy of land birds. *The Auk* **80:** 504–539.

Bartholomew GA, **MacMillen RE. 1961.** Water economy of the California quail and its use of sea water. *The Auk* **78:** 505–514.

Batalha-Filho H, **Pessoa RO**, **Fabre P-H**, **Fjeldså J**, **Irestedt M**, **Ericson PG**, **Silveira LF**, **Miyaki CY. 2014.** Phylogeny and historical biogeography of gnateaters (Passeriformes, Conopophagidae) in the South America forests. *Molecular Phylogenetics and Evolution* **79:** 422–432.

Becker JJ. 1987. Revision of '*Falco*' *ramenta* Wetmore and the Neogene evolution of the Falconidae. *The Auk* **104:** 270–276.

Beerling DJ, **Osborne CP. 2006.** The origin of the savanna biome. *Global Change Biology* **12:** 2023–2031.

Bennett KD, **Bhagwat S**, **Willis K. 2012.** Neotropical refugia. *The Holocene* **22:** 1207–1214.

Birdlife International. **2019.** *IUCN Red List for birds*. Available at: http://www.birdlife.org

Bobe R. 2006. The evolution of arid ecosystems in eastern Africa. *Journal of Arid Environments* **66:** 564–584.

Boles WE, **Ivison TJ. 1999.** A new genus of dwarf megapode (Galliformes: Megapodiidae) from the Late Oligocene of central Australia. *Smithsonian Contributions to Paleobiology* **89:** 199–206.

Bonetti MF, **Wiens JJ. 2014.** Evolution of climatic niche specialization: a phylogenetic analysis in amphibians. *Proceedings of the Royal Society B: Biological Sciences* **281:** 20133229.

Bouchenak-Khelladi Y. Hodkinson T. 2011. Savanna biome evolution, climate change and the ecological expansion of C4 grasses. In: Hodkinson T, ed. *Climate change, ecology and systematics*. Cambridge: Cambridge University Press, 156–175.

Braun EL, **Cracraft J. Houde P. 2019.** Resolving the avian tree of life from top to bottom: the promise and potential boundaries of the phylogenomic era. In: Krause RHS, ed. *Avian genomics in ecology and evolution*. Cham: Springer, 151–210.

Bredenkamp G, **Spada F**, **Kazmierczak E. 2002.** On the origin of northern and southern hemisphere grasslands. *Plant Ecology* **163:** 209–229.

Brennan IG, **Keogh JS. 2018.** Miocene biome turnover drove conservative body size evolution across Australian vertebrates. *Proceedings of the Royal Society B: Biological Sciences* **285:** 20181474.

Buckner JC, **Alfaro JWL**, **Rylands AB**, **Alfaro ME. 2015.** Biogeography of the marmosets and tamarins (Callitrichidae). *Molecular Phylogenetics and Evolution* **82:** 413–425.

Buerki S, **Jose S**, **Yadav SR**, **Goldblatt P**, **Manning JC**, **Forest F. 2012.** Contrasting biogeographic and diversification patterns in two Mediterranean-type ecosystems. *PLoS One* **7:** e39377.

Byrne M, **Yeates DK**, **Joseph L**, **Kearney M**, **Bowler J**, **Williams MAJ**, **Cooper S**, **Donnellan SC**, **Keogh JS**, **Leys R**, **Melville J**, **Porch N**, **Wyrwoll KH. 2008.** Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology* **17:** 4398–4417.

Cantalapiedra JL, **Hernández Fernández M**, **Morales J. 2011.** Biomic specialization and speciation rates in ruminants (Cetartiodactyla, Mammalia): a test of the resource-use hypothesis at global scale. *PLoS One* **6:** e28749.

Cantalapiedra JL, **Hernández Fernández M**, **Morales J. 2014.** The biogeographic history of ruminant faunas determines the phylogenetic structure of their assemblages at different scales. *Ecography* **36:** 1–9.

Carvalho MR, **Jaramillo C**, **de la Parra F**, **Caballero-Rodríguez D**, **Herrera F**, **Wing S**, **Turner B**, **D`Apolito C**, **Romero-Baez M**, **Narvaez P**, **Martínez C**, **Gutierrez M**, **Labandiera C**, **Bayona G**, **Rueda M**, **Paez-Reyes M**, **Cárdenas D**, **Duque Á**, **Crowley JL**, **Santos C**, **Silvestro D. 2021.** Extinction at the end-Cretaceous and the origin of modern Neotropical rainforests. *Science* **372:** 63–68.

Cardillo M, **Weston PH**, **Reynolds ZK**, **Olde PM**, **Mast AR**, **Lemmon EM**, **Lemmon AL**, **Bromham L. 2017.** The phylogeny and biogeography of *Hakea* (Proteaceae) reveals the role of biome shifts in a continental plant radiation. *Evolution* **71:** 1928–1943.

Cenizo M, **Noriega JI**, **Reguero MA. 2016.** A stem falconid bird from the Lower Eocene of Antarctica and the early southern radiation of the falcons. *Journal of Ornithology* **157:** 885–894.

Cerling TE, **Wang Y**, **Quade J. 1993.** Expansion of C4 ecosystems as an indicator of global ecological change in the late Miocene. *Nature* **361:** 344–345.

Charles-Dominique T, **Davies TJ**, **Hempson GP**, **Bezeng BS**, **Daru BH**, **Kabongo RM**, **Maurin O**, **Muthama A**, **van der Bank M**, **Bond WJ. 2016.** Spiny plants, mammal browsers, and the origin of African savannas. *Proceedings of the National Academy of Sciences of the United States of America* **113:** E5572–E5579.

Collinson ME, **Hooker JJ. 2003.** Paleogene vegetation of Eurasia: framework for mammalian faunas. *DEINSEA* **10:** 41–83.

Crisp M, **Arroyo MT**, **Cook LG**, **Gandolfo MA**, **Jordan GJ**, **McGlone MS**, **Weston P**, **Westoby M**, **Wilf P**, **Linder HP. 2009.** Phylogenetic biome conservatism on global scale. *Nature* **458:** 754–756.

van Dam JA. 2006. Geographic and temporal patterns in the late Neogene (12–3 Ma) aridification of Europe: the use of small

mammals as paleoprecipitation proxies. *Palaeogeography, Palaeoclimatology, Palaeoecology* **238:** 190–218.

Davis C, **Webb C**, **Wurdack K**, **Jaramillo C**, **Donoghue MJ. 2005.** Explosive radiation of Malpighiales supports a mid-cretaceous origin of modern tropical rain forests. *American Naturalist* **165:** E36–E65.

De Medeiros M, **Lohmann LG. 2015.** Phylogeny and biogeography of *Tynanthus* Miers (Bignonieae, Bignoniaceae). *Molecular Phylogenetics and Evolution* **85:** 32–40.

Del Hoyo J, **Collar NJ. 2014.** *HBW and BirdLife International illustrated checklist of the birds of the world, Vol. I: non-passerines*. Barcelona: Lynx Edicions.

Del Hoyo J, **Elliott A. Sargatal J. 1994.** *Handbook of the birds of the world. Vol. 2: New World vultures to guineafowl*. Barcelona: Lynx Edicions.

De Santis LRG, **Beavins RA**, **Koontz CS**, **Roseberry JC**, **Velasco MC. 2012.** Mammalian niche conservation through deep time. *PLoS One* **7:** e35624.

DeVore ML, **Pigg KB. 2013.** Paleobotanical evidence for the origins of temperate hardwoods. *International Journal of Plant Science* **174:** 592–601.

Dexter KG, **Pennington RT**, **Oliveira-Filho AT**, **Bueno ML**, **Silva De Miranda PL**, **Neves DM. 2018.** Inserting tropical dry forests into the discussion on biome transitions in the tropics. *Frontiers in Ecology and Evolution* **6:** 1–7. DOI=10.3389/fevo.2018.00104

Domingo L, **Koch PL**, **Hernández Fernández M**, **Fox DL**, **Domingo MS**, **Alberdi MT. 2013.** Late Neogene and Early Quaternary paleoenvironmental and paleoclimatic conditions in southwestern Europe: isotopic analyses on mammalian taxa. *PLoS One* **8:** e63739.

Donoghue MJ, **Edwards EJ. 2014.** Biome shifts and niche evolution in plants. *Annual Review of Ecology, Evolution, and Systematics* **45:** 547–572.

Dorey JB, **Groom SV**, **Freedman EH**, **Matthews CS**, **Davies OK**, **Deans EJ**, **Rebola C**, **Stevens M**, **Lee MS**, **Schwarz MP. 2020.** Radiation of tropical island bees and the role of phylogenetic niche conservatism as an important driver of biodiversity. *Proceedings of the Royal Society B: Biological Sciences* **287:** 20200045.

Douglas ME, **Douglas MR**, **Schuett W**, **Porras LW. 2006.** Evolution of rattlesnakes (Viperidae; *Crotalus*) in the warm deserts of western North America shaped by Neogene vicariance and Quaternary climate change. *Molecular Ecology* **15:** 3353–3374.

Duchêne DA, **Cardillo M. 2015.** Phylogenetic patterns in the geographic distributions of birds support the tropical conservatism hypothesis. *Global Ecology and Biogeography* **24:** 1261–1268.

Eaton MD, **Soberón J**, **Peterson AT. 2008.** Phylogenetic perspective on ecological niche evolution in American blackbirds (family Icteridae). *Biological Journal of the Linnean Society* **94:** 869–878.

Edwards EJ, **Osborne CP**, **Stromberg CAE**, **Smith SA**, **Bond WJ**, **Christin PA**, **Cousins AB**, **Duvall MR**, **Fox DL**, **Freckleton RP**, **Ghanaum O**, **Hartwell J**, **Huang Y**, **Janis C**, **Keeley JE**, **Kellogg E**, **Knapp AK**, **Leakey ADB**, **Nelson DM**, **Saarela JM**, **Sage RF**, **Sala OE**, **Salamín N**, **Still CJ**,

Tipple B. 2010. The origins of C4 grasslands: integrating evolutionary and ecosystem science. *Science* **328:** 587–591.

Eiserhardt WL, **Couvreur TL**, **Baker WJ. 2017.** Plant phylogeny as a window on the evolution of hyperdiversity in the tropical rainforest biome. *New Phytologist* **214:** 1408–1422.

Eo SH, **Bininda-Emonds OP**, **Carroll JP. 2009.** A phylogenetic supertree of the fowls (Galloanserae, Aves). *Zoologica Scripta* **38:** 465–481.

Fargallo JA, **Navarro-López J**, **Cantalapiedra JL**, **Pelegrin JS**, **Hernández Fernández M. 2022.** Trophic niche breadth of Falconidae species predicts biomic specialisation but not range size. *Biology* **11:** 522.

Ferguson-Lees J, **Christie DA. 2001.** *Raptors of the world*. London: Houghton Mifflin Harcourt.

Fine PVA, **Ree RH. 2006.** Evidence for a time-integrated species-area effect on the latitudinal gradient in tree diversity. *American Naturalist* **168**: 796–804.

Flower BP, **Kennett JP. 1994.** The middle Miocene climatic transition: East Antarctic ice sheet development, deep ocean circulation and global carbon cycling. *Palaeogeography, Palaeoclimatology, Palaeoecology* **108:** 537–555.

Franzke A, **Hurka H**, **Janssen D**, **Neuffer B**, **Friesen N**, **Markov M**, **Mummenhoff K. 2004.** Molecular signals for Late Tertiary/Early Quaternary range splits of an Eurasian steppe plant: *Clausia aprica* (Brassicaceae). *Molecular Ecology* **13:** 2789–2795.

Fuchs J, **Johnson JA**, **Mindell DP. 2012.** Molecular systematics of the caracaras and allies (Falconidae: Polyborinae) inferred from mitochondrial and nuclear sequence data. *Ibis* **154:** 520–532.

Fuchs J, **Johnson JA**, **Mindell DP. 2015.** Rapid diversification of falcons (Aves: Falconidae) due to expansion of open habitats in the Late Miocene. *Molecular Phylogenetics and Evolution* **82:** 166–182.

Gagnon E, **Ringelberg JJ**, **Bruneau A**, **Lewis GP**, **Hughes CE. 2019.** Global succulent biome phylogenetic conservatism across the pantropical *Caesalpinia* group (Leguminosae). *New Phytologist* **222:** 1994–2008.

Gamboa S, **Condamine FL**, **Cantalapiedra JL**, **Varela S**, **Pelegrin JS**, **Menéndez I**, **Blanco F**, **Hernández Fernández M. 2022.** A phylogenetic study to assess the link between biome specialization and diversification in swallowtail butterflies. *Global Change Biology* **28:** 1–13. https://doi.org/10.1111/gcb.16344

Garcia-R JC, **Matzke NJ. 2021.** Trait-dependent dispersal in rails (Aves: Rallidae): historical biogeography of a cosmopolitan bird clade. *Molecular Phylogenetics and Evolution* **159:** 107106.

Ghalambor CK, **Huey RB**, **Martin PR**, **Tewksbury JJ**, **Wang G. 2006.** Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology* **46:** 5–17.

Gould SJ, **Vrba E. 1982.** Exaptation—a missing term in the science of form. *Paleobiology* **8:** 4–15.

Guerrero PC, **Rosas M**, **Arroyo MTK**, **Wiens JJ. 2013.** Evolutionary lag times and recent origin of the biota of

an ancient desert (Atacama–Sechura). *Proceedings of the National Academy of Sciences of the United States of America* **110:** 11469–11474.

Guo Z, **Sun B**, **Zhang Z**, **Peng S**, **Xiao G**, **Ge J**, **Hao Q**, **Qiao Y**, **Liang M**, **Liu J. 2008.** A major reorganization of Asian climate by the early Miocene. *Climate of the Past* **4:** 153–174.

Hadly EA, **Spaeth PA**, **Li C. 2009.** Niche conservatism above the species level. *Proceedings of the National Academy of Sciences of the United States of America* **106:** 19707–19714.

Haffer J. 2008. Hypotheses to explain the origin of species in Amazonia. *Brazilian Journal of Biology* **68:** 917–947.

Harris RB, **Birks SM**, **Leaché AD. 2014.** Incubator birds: biogeographical origins and evolution of underground nesting in megapodes (Galliformes: Megapodiidae). *Journal of Biogeography* **41:** 2045–2056.

Harzhauser M, **Daxner-Höck G**, **López-Guerrero P**, **Maridet O**, **Oliver A**, **Piller WE**, **Richoz S**, **Erbajeva M**, **Neubauer T**, **Göhlich UB. 2016.** Stepwise onset of the Icehouse world and its impact on Oligo-Miocene Central Asian mammals. *Scientific Reports* **6:** 36169.

Hawkins B, **Diniz-Filho JAF**, **Jaramillo C**, **Soeller SA. 2006.** Post-Eocene climate change, niche conservatism, and the latitudinal diversity gradient of New World birds. *Journal of Biogeography* **33:** 770–780.

Hawkins B, **Diniz-Filho JAF**, **Jaramillo C**, **Soeller SA. 2007.** Climate, niche conservatism, and the global bird diversity gradient. *The American Naturalist* **170:** S16–S27.

Hazzi NA, **Moreno JS**, **Ortiz-Movliav C**, **Palacio RD. 2018.** Biogeographic regions and events of isolation and diversification of the endemic biota of the tropical Andes. *Proceedings of the National Academy of Sciences of the United States of America* **115:** 7985–7990.

Hernández Fernández M. 2001. Bioclimatic discriminant capacity of terrestrial mammal faunas. *Global Ecology and Biogeography* **10:** 189–204.

Hernández Fernández M, **Alvarez-Sierra M**, **Pelaez-Campomanes P. 2007.** Bioclimatic analysis of rodent palaeofaunas reveals severe climatic changes in southwestern Europe during the Plio-Pleistocene. *Palaeogeography, Palaeoclimatology, Palaeoecology* **251:** 500–526.

Hernández Fernández M, **Pelegrin JS**, **Gómez Cano AR**, **García Yelo BA**, **Moreno-Bofarull A**, **Sánchez-Fontela N**, **Rodríguez-Ruiz C**, **Ramiro Camacho A**, **Domingo L**, **Menéndez I**, **Martín-Perea DM**, **Bazán CM**, **Alcalde GM**, **Domingo MS**, **Luna B**, **Peinado Cortés MM**, **Arias A**, **González Couturier G**, **Márquez Villena A**, **Anaya N**, **Blanco F**, **Galli E**, **Gamboa S**, **Quesada A**, **Sanz-Pérez D**, **Varela S**, **Cantalapiedra JL. 2022.** Macroevolution and climate changes: a global multi-family test supports the resource-use hypothesis in terrestrial mammals. *Historical Biology* **34:** 1471–1479.

Hernández Fernández M, **Vrba E. 2005.** Macroevolutionary processes and biomic specialization: testing the resource-use hypothesis. *Evolutionary Ecology* **19:** 199–219.

Hewitt GM. 2003. Ice ages: their impact on species distributions and evolution. In: Rothschild LJ, Lister AM, eds. *Evolution on Planet Earth*. New York: Academic Press. pp 339–361.

Hill RW, **Wyse GA**, **Anderson M. 2004.** *Animal physiology*. Sunderland: Sinauer Associates.

Hooghiemstra H, **Van der Hammen T. 2004.** Quaternary ice-age dynamics in the Colombian Andes: developing an understanding of our legacy. *Philosophical Transactions of the Royal Society B: Biological Sciences* **359:** 173–181.

Hoorn C, **Wesselingh FP**, **Ter Steege H**, **Bermudez MA**, **Mora A**, **Sevink J**, **Sanmartin I**, **Sanchez-Meseguer A**, **Anderson CL**, **Figueiredo JP**, **Jaramillo C**, **Riff D**, **Negri FR**, **Hooghiemstra H**, **Lundberg J**, **Stadler T**, **Särkinen T**, **Antonelli A. 2010.** Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* **330:** 927–931.

Hosner PA, **Braun EL**, **Kimball RT. 2015a.** Land connectivity changes and global cooling shaped the colonization history and diversification of New World quail (Aves: Galliformes: Odontophoridae). *Journal of Biogeography* **42:** 1883–1895.

Hosner PA, **Faircloth BC**, **Glenn TC**, **Braun EL**, **Kimball RT. 2015b.** Avoiding missing data biases in phylogenomic inference: an empirical study in the landfowl (Aves: Galliformes). *Molecular Biology and Evolution* **33:** 1110–1125.

Hosner PA, **Owens HL**, **Braun EL**, **Kimball RT. 2020.** Phylogeny and diversification of the gallopheasants (Aves: Galliformes): testing roles of sexual selection and environmental niche divergence. *Zoologica Scripta* **49:** 549–562.

Hosner PA, **Tobias JA**, **Braun EL**, **Kimball RT. 2017.** How do seemingly non-vagile clades accomplish trans-marine dispersal? Trait and dispersal evolution in the landfowl (Aves: Galliformes). *Proceedings of the Royal Society B: Biological Sciences* **284:** 20170210.

Hugall AF, **Stuart-Fox D. 2012.** Accelerated speciation in colour-polymorphic birds. *Nature* **485:** 631–634.

Hurka H, **Friesen N**, **Bernhardt KG**, **Neuffer B**, **Smirnov S**, **Schmakov A**, **Blattner F. 2019.** The Eurasian steppe belt: status quo, origin and evolutionary history. *Turczaninowia* **22:** 5–71.

Hwang SH, **Mayr G**, **Bolortsetseg M. 2010.** The earliest record of a galliform bird in Asia, from the Late Paleocene–Early Eocene of the Gobi Desert, Mongolia. *Journal of Vertebrate Paleontology* **30:** 1642–1644.

Jacobs BF. 2004. Palaeobotanical studies from tropical Africa: relevance to the evolution of forest, woodland and savannah biomes. *Philosophical Transactions of the Royal Society B: Biological Sciences* **359:** 1573–1583.

Janis CM. 1993. Tertiary mammal evolution in the context of changing climates, vegetation, and tectonic events. *Annual Review of Ecology and Systematics* **24:** 467–500.

Jara-Arancio P, **Arroyo MT**, **Guerrero PC**, **Hinojosa LF**, **Arancio G**, **Méndez MA. 2014.** Phylogenetic perspectives on biome shifts in *Leucocoryne* (Alliaceae) in relation to

climatic niche evolution in western South America. *Journal of Biogeography* **41:** 328–338.

Jaramillo C. 2012. Historia geológica del bosque húmedo neotropical. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales* **36**(138)**:** 57–77.

Jaramillo C, **Cárdenas A. 2013.** Global warming and neotropical rainforests: a historical perspective. *Annual Review of Earth and Planetary Sciences* **41:** 741–766.

Jaramillo C, **Ochoa D**, **Contreras L**, **Pagani M**, **Carvajal-Ortiz H**, **Pratt LM**, **Krishnan S**, **Cardona A**, **Romero M**, **Quiroz L**, **Rodríguez G**, **Rueda MJ**, **De la Parra F**, **Moron S**, **Green W**, **Bayona G**, **Montes C**, **Quintero O**, **Ramirez R**, **Mora G**, **Schouten S**, **Bermudez H**, **Navarrete R**, **Parra F**, **Alvarán M**, **Osorno J**, **Crowley JL**, **Valencia V**, **Vervoort J. 2010.** Effects of rapid global warming at the Paleocene-Eocene boundary on Neotropical vegetation. *Science* **330:** 957–961.

Jaramillo C, **Rueda MJ**, **Mora G. 2006.** Cenozoic plant diversity in the Neotropics. *Science* **311:** 1893–1896.

Jarvis ED, **Mirarab S**, **Aberer AJ**, **Li B**, **Houde P**, **Li C**, **Ho SYW**, **Faircloth BC**, **Nabholz B**, **Howard JT**, **Suh A**, **Weber CC**, **Da Fonseca RR**, **Li J**, **Zhang F**, **Li H**, **Zhou L**, **Narula N**, **Liu L**, **Ganapathy G**, **Boussau B**, **Bayzid MS**, **Zavidovych V**, **Subramanian S**, **Gabaldón T**, **Capella-Gutiérrez S**, **Huerta-Cepas J**, **Rekepalli B**, **Munch K**, **Schierup M**, **Lindow B**, **Warren WC**, **Ray D**, **Green RE**, **Bruford MW**, **Zhan X**, **Dixon A**, **Li S**, **Li N**, **Huang Y**, **Derryberry EP**, **Bertelsen MF**, **Sheldon FH**, **Brumfield RT**, **Mello CV**, **Lovell PV**, **Wirthlin M**, **Schneider MP**, **Prosdocimi F**, **Samaniego JA**, **Vargas Velazquez AM**, **Alfaro-Núñez A**, **Campos PF**, **Petersen B**, **Sicheritz-Ponten T**, **Pas A**, **Bailey T**, **Scofield P**, **Bunce M**, **Lambert DM**, **Zhou Q**, **Perelman P**, **Driskell AC**, **Shapiro B**, **Xiong Z**, **Zeng Y**, **Liu S**, **Li Z**, **Liu B**, **Wu K**, **Xiao J**, **Yinqi X**, **Zheng Q**, **Zhang Y**, **Yang H**, **Wang J**, **Smeds L**, **Rheindt FE**, **Braun M**, **Fjeldsa J**, **Orlando L**, **Barker FK**, **Jønsson KA**, **Johnson W**, **Koepfli KP**, **O'Brien S**, **Haussler D**, **Ryder OA**, **Rahbek C**, **Willerslev E**, **Graves GR**, **Glenn TC**, **McCormack J**, **Burt D**, **Ellegren H**, **Alström P**, **Edwards SV**, **Stamatakis A**, **Mindell DP**, **Cracraft J**, **Braun EL**, **Warnow T**, **Jun W**, **Gilbert MT**, **Zhang G. 2014.** Whole-genome analyses resolve early branches in the tree of life of modern birds. *Science* **346:** 1320–1331.

Jetz W, **Fine PVA. 2012.** Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLoS Biology* **10:** e1001292.

Jetz W, **Thomas HH**, **Joy JB**, **Hartman K**, **Mooers AO. 2012.** The global diversity of birds in space and time. *Nature* **491:** 444–448.

Jocque M, **Field R**, **Brendonck L**, **De Meester L. 2010.** Climatic control of dispersal– ecological specialization trade-offs: a metacommunity process at the heart of the latitudinal diversity gradient? *Global Ecology and Biogeography* **19:** 244–252.

Kahlke R-D. 2014. The origin of Eurasian mammoth faunas (*Mammuthus–Coelodonta* Faunal Complex). *Quaternary Science Reviews* **96:** 32–49.

Kerkhoff AJ, **Moriarty PE**, **Weiser MD. 2014.** The latitudinal species richness gradient in New World woody angiosperms is consistent with the tropical conservatism hypothesis. *Proceedings of the National Academy of Sciences of the United States of America* **111:** 8125–8130.

Kimball RT, **St Mary CM**, **Braun EL. 2011.** A macroevolutionary perspective on multiple sexual traits in the Phasianidae (Galliformes). *International Journal of Evolutionary Biology* **2011:** 423938.

Kimball RT, **Oliveros CH**, **Wang N**, **White ND**, **Barker FK**, **Field DJ**, **Ksepka DT**, **Chesser RT**, **Moyle RG**, **Braun MJ**, **Brumfield RT**, **Faircloth BC**, **Tilston Smith B**, **Braun EL. 2019.** A phylogenomic supertree of birds. *Diversity* **11:** 109.

Klaassen M. 1996. Metabolic constraints on long-distance migration in birds. *The Journal of Experimental Biology* **199:** 57–64.

Klaus KV, **Matzke NJ. 2020.** Statistical comparison of trait-dependent biogeographical models indicates that Podocarpaceae dispersal is influenced by both seed cone traits and geographical distance. *Systematic Biology* **69:** 61–75.

Landis M, **Edwards EJ**, **Donoghue MJ. 2021.** Modeling phylogenetic biome shifts on a planet with a past. *Systematic Biology* **70:** 86–107.

Liu L, **Eronen JT**, **Fortelius M. 2009.** Significant mid-latitude aridity in the middle Miocene of East Asia. *Palaeogeography, Palaeoclimatology, Palaeoecology* **279:** 201–206.

Lv X, **Xia L**, **Ge D**, **Wu Y**, **Yang Q. 2016.** Climatic niche conservatism and ecological opportunity in the explosive radiation of arvicoline rodents (Arvicolinae, Cricetidae). *Evolution* **70:** 1094–1104.

Lynch Alfaro JW, **Boubli JP**, **Paim FP**, **Ribas CC**, **da Silva MNF**, **Messias M**, **Röhe F**, **Mercês MP**, **Silva Júnior JS**, **Silva CR**, **Pinho GM**, **Koshkarian G**, **Nguyen MTT**, **Harada ML**, **Rabelo RM**, **Queiroz HL**, **Alfaro ME**, **Farias IP. 2015.** Biogeography of squirrel monkeys (genus *Saimiri*): south-central Amazon origin and rapid pan-Amazonian diversification of a lowland primate. *Molecular Phylogenetics and Evolution* **82:** 436–454. http://dx.doi.org/10.1016/j.ympev.2014.09.004

Maddison WP, **Maddison DR. 2015.** Mesquite: A modular system for evolutionary analysis. Version 3.04. Retrieved from http://mesquite-project.org

Maclean GL. 1996. Desert avifaunas. In: Maclean GL. *Ecophysiology of desert birds. Adaptations of desert organisms*. Berlin: Heidelberg: Springer. pp 9–21.

Magalhaes ILF, **Neves DM**, **Santos FR**, **Vidigal THDA**, **Brescovit AD**, **Santos AJ. 2019.** Phylogeny of Neotropical *Sicarius* sand spiders suggests frequent transitions from deserts to dry forests despite antique, broad-scale niche conservatism. *Molecular Phylogenetics and Evolution* **140:** 106569.

Mandiwana-Neudani TG, **Little RM**, **Crowe TM**, **Bowie RC. 2019.** Taxonomy, phylogeny and biogeography of African spurfowls Galliformes, Phasianidae, Phasianinae, Coturnicini: *Pternistis* spp. *Ostrich* **90:** 145–172.

Marder J, **Bernstein R. 1983.** Heat balance of the partridge *Alectoris chukar* exposed to moderate, high and extreme

thermal stress. *Comparative Biochemistry and Physiology Part A: Comparative Physiology* **74:** 149–154.

Markgraf V, **McGlone M**, **Hope G. 1995.** Neogene paleoenvironmental and paleoclimatic change in southern temperate ecosystems — a southern perspective. *Trends in Ecology & Evolution* **10:** 143–147.

Matzke NJ. 2014a. Model selection in historical biogeography reveals that founder- event speciation is a crucial process in island clades. *Systematic Biology* **63:** 951–970.

Matzke NJ. 2014b. *Package 'BioGeoBEARS' BioGeography with Bayesian (and likelihood) evolutionary analysis in R scripts. Version 0.2.1.* http://phylo.wikidot.com/biogeobears

Matzke NJ. 2015. *BioGeoBEARS: biogeography with Bayesian (and likelihood) evolutionary analysis in R Scripts.* Berkeley: University of California.

Mayr G. 2009. *Paleogene fossil birds.* Heidelberg: Springer Science & Business Media.

Mayr G. 2017. *Avian evolution: the fossil record of birds and its paleobiological significance.* London: John Wiley & Sons.

McCullough JM, **Moyle RG**, **Smith BT**, **Andersen MJ. 2019.** A Laurasian origin for a pantropical bird radiation is supported by genomic and fossil data (Aves: Coraciiformes). *Proceedings of the Royal Society B: Biological Sciences* **286:** 20190122.

McKay RM, **Barrett PJ**, **Levy RS**, **Naish TR**, **Golledge NR**, **Pyne A. 2016.** Antarctic Cenozoic climate history from sedimentary records: ANDRILL and beyond. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences* **374:** 20140301.

McNab BK. 2009. Ecological factors affect the level and scaling of avian BMR. *Comparative Biochemistry and Physiology Part A: Molecular Integrative Physiology* **152:** 22–45.

Menéndez I, **Gómez Cano AR**, **Cantalapiedra JL**, **Peláez-Campomanes P**, **Álvarez-Sierra MA**, **Hernández Fernández M. 2021.** A multi-layered approach to the diversification of squirrels. *Mammal Review* **51:** 66–81.

Meredith RW, **Janecka JE**, **Gatesy J**, **Ryder OA**, **Fisher CA**, **Teeling EC**, **Goodbla A**, **Eizirik E**, **Simão TL**, **Stadler T**, **Rabosky DL**, **Honeycutt RL**, **Flynn JJ**, **Ingram CM**, **Steiner C**, **Williams TL**, **Robinson TJ**, **Burk-Herrick A**, **Westerman M**, **Ayoub NA**, **Springer MS**, **Murphy WJ. 2011.** Impacts of the Cretaceous terrestrial revolution and KPg extinction on mammal diversification. *Science* **334:** 521–524.

Miao Y, **Herrmann M**, **Wu F**, **Yan X**, **Yang S. 2012.** What controlled Mid–Late Miocene long-term aridification in Central Asia? Global cooling or Tibetan Plateau uplift: a review. *Earth-Science Reviews* **112:** 155–172.

Moncrieff GR, **Bond WJ**, **Higgins S. 2016.** Revising the biome concept for understanding and predicting global change impacts. *Journal of Biogeography* **43:** 863–873.

Moreno-Bofarull A, **Arias A**, **Hernández Fernández M**, **Ortiz-Jaureguizar E**, **Morales J. 2008.** Influence of continental history on the ecological specialization and macroevolutionary processes in the mammalian assemblage of South America: differences between small and large mammals. *BMC Evolutionary Biology* **8:** 97.

Mucina L. 2019. Biome: evolution of a crucial ecological and biogeographical concept. *New Phytologist* **222:** 97–114.

Münkemüller T, **Boucher FC**, **Thuiller W**, **Lavergne S. 2015.** Phylogenetic niche conservatism – common pitfalls and ways forward. *Functional Ecology* **29:** 627–639.

Noriega JI, **Areta JI**, **Vizcaíno SF**, **Bargo MS. 2011.** Phylogeny and taxonomy of the Patagonian Miocene falcon *Thegornis musculosus* Ameghino, 1895 (Aves: Falconidae). *Journal of Paleontology* **85:** 1089–1104.

Olalla-Tárraga MA, **González-Suárez M**, **Bernardo-Madrid R**, **Revilla E**, **Villalobos F. 2016.** Contrasting evidence of phylogenetic trophic niche conservatism in mammals worldwide. *Journal of Biogeography* **44:** 99–110.

Oliveros CH, **Andersen MJ**, **Hosner PA**, **Mauck WM III**, **Sheldon FH**, **Cracraft J**, **Moyle RG. 2020.** Rapid Laurasian diversification of a pantropical bird family during the Oligocene–Miocene transition. *Ibis* **162:** 137–152.

Pauls SU, **Nowak C**, **Bálint M**, **Pfenninger M. 2013.** The impact of global climate change on genetic diversity within populations and species. *Molecular Ecology* **22:** 925–946.

Peixoto FP, **Villalobos F**, **Cianciaruso MV. 2017.** Phylogenetic conservatism of climatic niche in bats. *Global Ecology and Biogeography* **26:** 1055–1065.

Pelegrin JS, **Cantalapiedra JL**, **Hernández Fernández M. 2015.** The macroevolutionary role of migration for bird occupation of biomes with adverse climatic conditions. In: Domingo L, Domingo S, Fesharaki O, García Yelo B, Gómez Cano AR, Hernández-Bellarín V, Hontecillas D, Cantalapiedra JL, López Guerrero P, Oliver A, Pelegrin JS, Pérez de los Ríos M, Ríos M, Sanisidro O, Valenciano A. et al., eds. *Current Trends in Paleontology and Evolution.* Madrid: Early-Stage Researchers in Paleontology (EJIP) Editorial. pp. 197–199.

Pelegrin JS, **Gamboa S**, **Menéndez I**, **Hernández Fernández M. 2018.** El gran intercambio biótico Americano: una revisión paleoambiental de evidencias aportadas por mamíferos y aves neotropicales. *Ecosistemas* **27:** 5–17.

Pelegrín JS, **Acosta Hospitaleche C. 2022.** Evolutionary and Biogeographical History of Penguins (Sphenisciformes): Review of the Dispersal Patterns and Adaptations in a Geologic and Paleoecological Context. *Diversity* **14:** 255. https://doi.org/10.3390/d14040255

Pennington RT, **Cronk QC**, **Richardson JA. 2004a.** Introduction and synthesis: plant phylogeny and the origin of major biomes. *Philosophical Transactions of the Royal Society B: Biological Sciences* **359:** 1455–1464.

Pennington RT, **Lavin M**, **Prado DE**, **Pendry CA**, **Pell SK**, **Butterworth CA. 2004b.** Historical climate change and speciation: Neotropical seasonally dry forest plants show patterns of both Tertiary and Quaternary diversification. *Philosophical Transactions of the Royal Society B: Biological Sciences* **359:** 515–538.

Pennington RT, **Lewis G**, **Ratter J. 2006.** An overview of the plant diversity, biogeography and conservation of neotropical savannas and seasonally dry forests. In: Pennington RT, Lewis G, Ratter J, eds. *Neotropical savannas and the seasonally dry forests.* Boca Raton: Taylor and Francis Group, 1–29.

Pennington RT, **Prado DE**, **Pendry CA. 2000.** Neotropical seasonally dry forests and Quaternary vegetation changes. *Journal of Biogeography* **27:** 261–273.

Peterson AT. 2011. Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography* **38:** 817–827.

Peterson AT, **Nyari AS. 2008.** Ecological niche conservatism and Pleistocene refugia in the thrush-like mourner, *Schiffornis* sp., in the Neotropics. *Evolution* **62:** 173–183.

Pigot AL, **Tobias JA. 2013.** Species interactions constrain geographic range expansion over evolutionary time. *Ecology Letters* **16:** 330–338.

Pigot AL, **Tobias JA. 2015.** Dispersal and the transition to sympatry in vertebrates. *Proceedings of the Royal Society B: Biological Sciences* **282:** 20141929.

Popova S, **Utescher T**, **Gromyko D**, **Bruch A**, **Henrot AJ**, **Mosbrugger V. 2017.** Cenozoic vegetation gradients in the mid- and higher latitudes of Central Eurasia and climatic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* **467:** 69–82.

Popova S, **Utescher T**, **Gromyko D**, **Bruch A**, **Mosbrugger V. 2012.** Palaeoclimate evolution in Siberia and the Russian Far East from the Oligocene to Pliocene – evidence from fruit and seed floras. *Turkish Journal of Earth Sciences* **21:** 315–334.

Potts R, **Behrensmeyer AK. 1992.** Late Cenozoic terrestrial ecosystems. In: Behrensmeyer AK, Damuth JD, DiMichelle WA, Potts R, Sues HD, Wing SL, eds. *Terrestrial ecosystems through time: evolutionary paleoecology of terrestrial plants and animals*. Chicago: University of Chicago Press, 419–451.

Pound MJ, **Haywood AM**, **Salzmann U**, **Riding JB. 2012.** Global vegetation dynamics and latitudinal temperature gradients during the Mid to Late Miocene (15.97–5.33 Ma). *Earth-Science Reviews* **112:** 1–22.

Pound MJ, **Haywood AM**, **Salzmann U**, **Riding JB**, **Lunt DJ**, **Hunter SJ. 2011.** A Tortonian (late Miocene, 11.61–7.25 Ma) global vegetation reconstruction. *Palaeogeography, Palaeoclimatology, Palaeoecology* **300:** 29–45.

Price JP, **Clague DA. 2002.** How old is the Hawaiian biota? Geology and phylogeny suggest recent divergence. *Proceedings of the Royal Society B: Biological Sciences* **269:** 2429–2435.

Prum RO, **Berv JS**, **Dornburg A**, **Field DJ**, **Townsend JP**, **Lemmon EM**, **Lemmon AR. 2015.** A comprehensive phylogeny of birds (Aves) using targeted next-generation DNA sequencing. *Nature* **526:** 569–573.

Raes N, **Cannon CH**, **Hijmans RJ**, **Piessens T**, **Saw LG**, **Van Welzen PC**, **Slik JF. 2014.** Historical distribution of Sundaland's dipterocarp rainforests at Quaternary glacial maxima. *Proceedings of the National Academy of Sciences of the United States of America* **111:** 16790–16795.

Razgour O, **Juste J**, **Ibáñez C**, **Kiefer A**, **Rebelo H**, **Puechmaille SJ**, **Arlettaz R**, **Burke T**, **Dawson DA**, **Beaumont M**, **Jones G. 2013.** The shaping of genetic variation in edge-of-range populations under past and future climate change. *Ecology Letters* **16:** 1258–1266.

Ree RH, **Sanmartín I. 2018.** Conceptual and statistical problems with the DEC+J model of founder event speciation and its comparison with DEC via model selection. *Journal of Biogeography* **454:** 741–774.

Ree RH, **Smith SA. 2008.** Maximum likelihood inference of geographic range evolution by dispersal, local extinction and cladogenesis. *Systematic Biology* **57:** 4–14.

Ringelberg JJ, **Zimmermann NE**, **Weeks A**, **Lavin M**, **Hughes CE. 2020.** Biomes as evolutionary arenas: convergence and conservatism in the trans-continental succulent biome. *Global Ecology and Biogeography* **29:** 1100–1113.

Rolland J, **Jiguet F**, **Jønsson KA**, **Condamine FL**, **Morlon H. 2014.** Settling down of seasonal migrants promotes bird diversification. *Proceedings of the Royal Society B: Biological Sciences* **281:** 20140473.

Salisbury CL, **Seddon N**, **Cooney CR**, **Tobias JA. 2012.** The latitudinal gradient in dispersal constraints: ecological specialisation drives diversification in tropical birds. *Ecology Letters* **15:** 847–855.

Salzmann U, **Haywood AM**, **Lunt D**, **Valdes P**, **Hill D. 2008.** A new global biome reconstruction and data-model comparison for the middle Pliocene. *Global Ecology and Biogeography* **17:** 432–447.

Schoenjahn J, **Pavey CR**, **Walter GH. 2022a.** Delayed juvenile behavioural development and prolonged dependence are adaptations to desert life in the grey falcon. *Current Zoology* **1:** 1–9. https://doi.org/10.1093/cz/zoac001

Schoenjahn J, **Pavey CR**, **Walter GH. 2022b.** Low activity levels are an adaptation to desert-living in the grey falcon, an endotherm that specializes in pursuing highly mobile prey. *Journal of Thermal Biology* **103:** 103108.

Senut B, **Pickford M**, **Ségalen L. 2009.** Neogene desertification of Africa. *Comptes Rendus Geoscience* **341:** 591–602.

Shi Y, **Tang M**, **Ma Y. 1999.** Linkage between the second uplifting of the Qinghai-Xizang (Tibetan) Plateau and the initiation of the Asian monsoon system. *Science in China Series D: Earth Sciences* **42:** 303–312.

Somero GN. 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *The Journal of Experimental Biology* **213:** 912–920.

Stein RW, **Brown JW**, **Mooers AO. 2015.** A molecular genetic time scale demonstrates Cretaceous origins and multiple diversification rate shifts within the order Galliformes (Aves). *Molecular Phylogenetics and Evolution* **92:** 155–164.

Steinthorsdottir M, **Coxall HK**, **De Boer AM**, **de Huber M**, **Barbolini N**, **Bradshaw CD**, **Burls NJ**, **Feakins SJ**, **Gasson E**, **Henderiks J**, **Holbourn AE**, **Kiel S**, **Kohn MJ**, **Knorr G**, **Kürschner WM**, **Lear CH**, **Liebrand D**, **Lunt DJ**, **Mörs T**, **Pearson PN**, **Pound MJ**, **Stoll H**, **Strömberg CAE. 2021.** The Miocene: the future of the past. *Paleoceanography and Paleoclimatology* **36:** e2020PA004037.

Strömberg CA. 2011. Evolution of grasses and grassland ecosystems. *Annual Review of Earth and Planetary Sciences* **39:** 517–544.

Suc JP. 1984. Origin and evolution of the Mediterranean vegetation and climate in Europe. *Nature* **307**(5950)**:** 429–432.

Tejero-Cicuéndez H, **Tarroso P**, **Carranza S**, **Rabosky DL. 2022.** Desert lizard diversity worldwide: effects of environment, time, and evolutionary rate. *Global Ecology and Biogeography* **31:** 776–790.

Thorup K. 2006. Does the migration constrain dispersal and range sizes of migratory birds? *Journal of Biogeography* **33:** 1166–1171.

Tomek T, **Bochenski ZM**, **Wertz K**, **Swidnicka E. 2014.** A new genus and species of a galliform bird from the Oligocene of Poland. *Palaeontologia Electronica* **17:** 17.3.38A.

Tucker CM, **Aze T**, **Cadotte MW**, **Cantalapiedra JL**, **Chisholm C**, **Díaz S**, **Grenyer R**, **Huang D**, **Mazel F**, **Pearse W**, **Pennell MW**, **Winter M**, **Mooers AO. 2019.** Assessing the utility of conserving evolutionary history. *Biological Reviews* **94:** 1740–1760.

van Els P, **Norambuena HV**, **Etienne RS. 2019.** From pampa to puna: Biogeography and diversification of a group of Neotropical obligate grassland birds (*Anthus*: Motacillidae). *Journal of Zoological Systematics and Evolutionary Research* **57:** 485–496.

Vieites DR, **Min MS**, **Wake DB. 2007.** Rapid diversification and dispersal during periods of global warming by plethodontid salamanders. *Proceedings of the National Academy of Sciences of the United States of America* **104:** 19903–19907.

Vrba ES. 1980. Evolution, species and fossils: how does life evolve? *South African Journal of Sciences* **76:** 61–84.

Vrba ES. 1987. Ecology in relation to speciation rates: some case histories of Miocene-Recent mammal clades. *Evolutionary Ecology* **1:** 283–300.

Vrba ES. 1992. Mammals as a key to evolutionary theory. *Journal of Mammalogy* **73:** 1–28.

Vrba ES. 1995. On the connections between paleoclimate and evolution. In: Vrba ES, Denton GH, Partridge TC, Burckle LH, eds. *Paleoclimate and evolution, with emphasis of human origins*. New Haven: Yale University Press, 24–45.

Walter H. 1970. *Vegetationszonen und Klima*. Stuttgart: Eugen Ulmer.

Wang WM. 2004. On the origin and development of *Artemisia* (Asteraceae) in the geological past. *Botanical Journal of the Linnean Society* **145:** 331–336.

Wang N, **Kimball RT**, **Braun EL**, **Liang B**, **Zhang Z. 2013.** Assessing phylogenetic relationships among Galliformes: a multigene phylogeny with expanded taxon sampling in Phasianidae. *PLoS One* **8:** e64312.

Wang N, **Kimball RT**, **Braun EL**, **Liang B**, **Zhang Z. 2017.** Ancestral range reconstruction of Galliformes: the effects of topology and taxon sampling. *Journal of Biogeography* **44:** 122–135.

Weir JT, **Schluter D. 2004.** Ice sheets promote speciation in boreal birds. *Proceedings of the Royal Society B: Biological Sciences* **271:** 1881–1887.

Werneck FP, **Costa GC**, **Colli GR**, **Prado D**, **Sites JW. 2011.** Revisiting the historical distribution of seasonally dry tropical forests: new insights based on palaeodistribution modelling and palynological evidence. *Global Ecology and Biogeography* **20:** 272–288.

Whittaker RH. 1975. *Communities and ecosystems*, *2nd edn*. New York: Macmillan.

Wiens JJ. 2004. Speciation and ecology revisited: phylogenetic niche conservatism and the origin of species. *Evolution* **58:** 193–197.

Wiens JJ, **Ackerly D**, **Allen AP**, **Anacker BL**, **Buckley LB**, **Cornell HV**, **Damschen EI**, **Davies TJ**, **Grytnes J-A**, **Harrison SP**, **Hawkins BA**, **Holt RD**, **McCain CM**, **Stephens PR. 2010.** Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13:** 1310–1324.

Wiens JJ, **Donoghue MJ. 2004.** Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution* **19:** 639–644.

Wiens JJ, **Kozak KH**, **Silva N. 2013.** Diversity and niche evolution along aridity gradients in North American lizards (Phrynosomatidae). *Evolution* **67:** 1715–1728.

Wilcox JJ, **Boissinot S**, **Idaghdour Y. 2019.** Falcon genomics in the context of conservation, speciation, and human culture. *Ecology and Evolution* **9:** 14523–14537.

Williams JB, **Tieleman BI. 2002.** Ecological and evolutionary physiology of desert birds: a progress report. *Integrative and Comparative Biology* **42:** 68–75.

Williams JB, **Tieleman BI. 2005.** Physiological adaptation in desert birds. *Bioscience* **55:** 416–425.

Zachos J, **Pagani M**, **Sloan L**, **Thomas E**, **Billups K. 2001.** Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292:** 686–693.

Zimov SA, **Chuprynin VI**, **Oreshko AP**, **Chapin FS III**, **Reynolds JF**, **Chapin MC. 1995.** Steppe-tundra transition: an herbivore-driven biome shift at the end of the Pleistocene. *The American Naturalist* **146:** 765–794.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Biome existence and connection matrices.
Table S2. Two hundred and thirty-nine diverse biome occupations of non-passerine birds.
Table S3. Definition of biomes for each node in Galliformes based on probability values for each node [I = tropical rainforest; II = tropical deciduous woodland; II/III = savanna; III = subtropical desert; IV = sclerophyllous woodland–shrubland; V = temperate evergreen forest; VI = temperate broadleaf deciduous forest; VII = steppe to cold desert; VIII = boreal coniferous forest (taiga); IX = tundra].
Table S4. Definition of biomes for each node in Falconiformes based on probability values for each node [I = tropical rainforest; II = tropical deciduous woodland; II/III = savanna; III = subtropical desert; IV = sclerophyllous woodland–shrubland; V = temperate evergreen forest; VI = temperate broadleaf deciduous forest; VII = steppe to cold desert; VIII = boreal coniferous forest (taiga); IX = tundra].