Evolutionary patterns and processes of migratory behaviour in Palearctic-Paleotropical birds

Patrones y procesos evolutivos del comportamiento migratorio en aves del Paleártico-Paleotrópico

Raquel Ponti de la Iglesia

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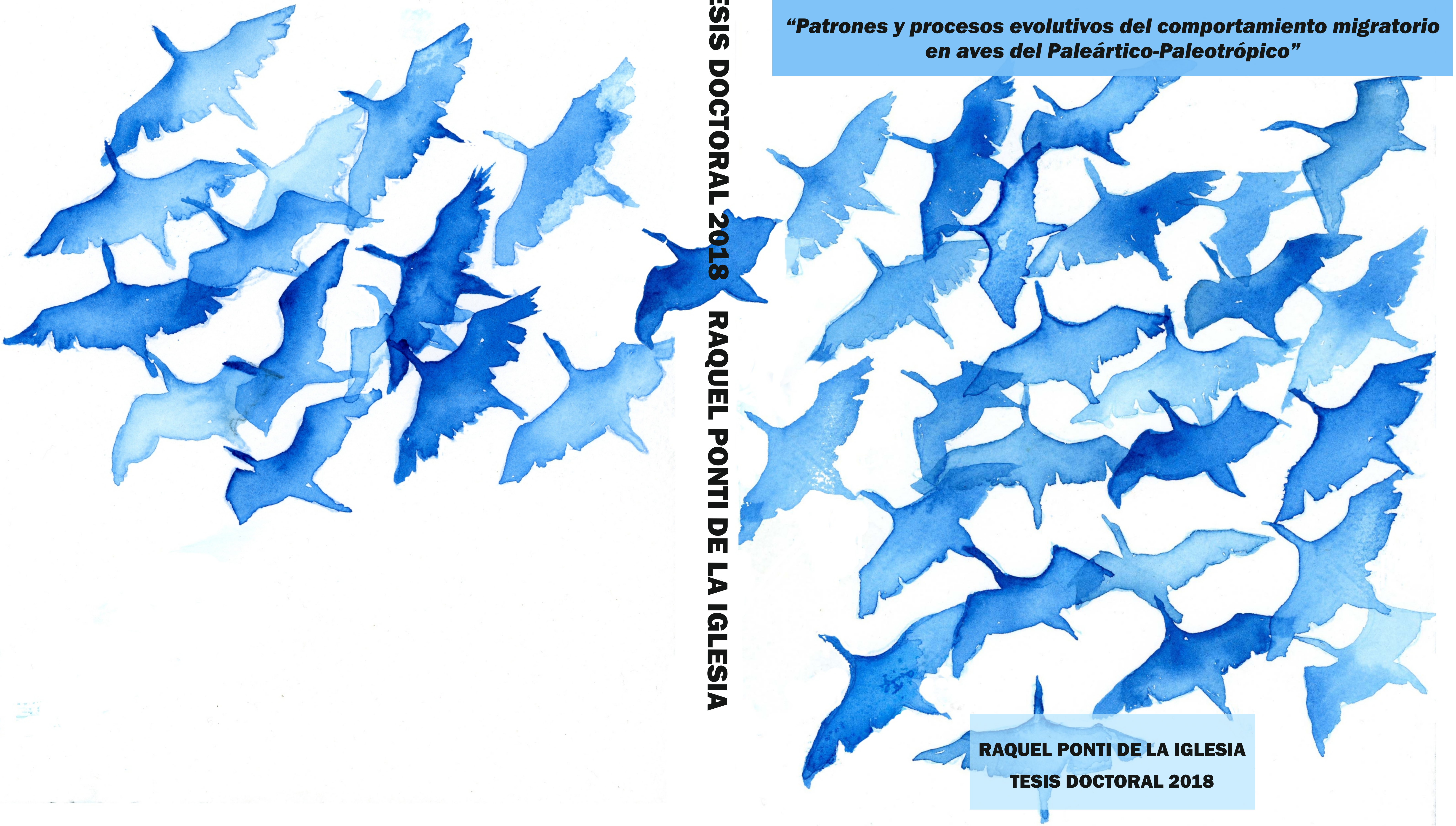

RAQUEL PONTI DE LA IGLESIA

TESIS DOCTORAL 2018

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Departamento de Biología Evolutiva, Ecología y Ciencias Ambientales. Programa de Doctorado en BIODIVERSIDAD.

Museo Nacional de Ciencias Naturales (MNCN). Consejo Superior de Investigaciones Científicas (CSIC)

“Evolutionary patterns and processes of migratory behaviour in Palearctic-Paleotropical birds.”

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Memoria presentada por **Raquel Ponti de la Iglesia** para optar al título de Doctora por la Universidad de Barcelona.

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Se ha asomado una cigüeña a lo alto del campanario.
Girando en torno a la torre y al caserón solitario,
ya las golondrinas chillan. Pasaron del blanco invierno,
de nevadas y ventiscas los crudos soplos del infierno.

Antonio Machado, Primavera 1907

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GENERAL INTRODUCTION

One of the most fascinating aspects of birds is their ability to migrate, or move seasonally from one place to another. In ancient times, where some bird species spent the winter was a mystery, and some people even thought that they could hibernate like the bears, as suggested by Aristoteles. An unlucky stork was the key to the discovery of the bird migration, when in 1822 it was shot in Germany and it had superficially pierced an African spear (Newton, 2010). Other 29 *"Pfeilstorch"* (storks pierced with arrows) were found in Germany after that episode that left no doubt about the migration of this species to Africa. From then until now, migration has been a reiterated subject of study for the scientific community which is reflected in an extensive literature (e.g. Alerstam, 1990; Berthold, 2001; Newton, 2010), and different tools and methodologies have been developed over the past 120 years to study the migratory behaviour of birds.

There are around 2000 migratory bird species of different families and from different biogeographic regions in the world (around 20% of the bird species) that fly hundreds to thousands of kilometres from their breeding to their wintering ranges (Sekercioglu, 2007). The traditional idea of bird migration is related to the most common migratory dynamics that imply long journeys from the Northern hemisphere in Arctic to temperate latitudes to the Southern hemisphere in Equatorial and tropical latitudes, strategy shown by the so-called long-distance (LD) migrants. However, not all species migrate far from their breeding grounds, as many species present local seasonal movement strategies at a population level, including few species with migratory, partial migratory and sedentary populations (Morganti *et al.*, 2015). In fact, animal migration can be defined simply as the "act of moving from one spatial unit to another" (Baker, 1978). Short distance migrants, such as altitudinal migrants, are common in tropical areas and normally are related to dry and wet seasonality [e.g. some African species spend their breeding season at higher altitudes in the Eastern Arc Mountains moving downslope during the non-breeding season (Burgess & Mlingwa, 2000)]. Other bird species move profiting from the temporal availability of resources but without a phylopatric component. Those birds are called vagabonds or nomadic species and are common in arid or savannah areas, as some Australian land-birds (Chan, 2001; Reside *et al.*, 2010; Eyres *et al.*, 2017). Among birds, apart from sedentary and migratory species, hundreds of species are partially migratory, in which some individuals of the same species can be migratory or sedentary. One of the cases in the Palearctic is the Eurasian blackcap (*Sylvia atricapilla*) with migratory and non-migratory individuals living in sympatry in the South of Spain (Pérez-Tris & Tellería, 2002).

Most small or medium size migratory birds migrate by flapping, while large-bodied species they do it by soaring or gliding. The latter entails a much lower energetic cost, as they profit from thermal currents, rising up and gliding with the loss of height to the next thermal current in a regular cycle (Newton, 2011). During flapping flights, instead, the movement is made through an active and continuous self-propulsion by wing muscle power (Pennycuick, 1969). The amount of energy spent in flapping flight hampers heavier birds to migrate in this manner. Indeed, large birds, as geese or storks, further minimise fuel cost by flying in V formation, saving up to 12 to 20% of the energy compared with birds that fly alone (Alerstam, 1990).

Birds can migrate during the day or night, but nocturnal migrations are not exclusive for nocturnal species as owls, being also a widespread behaviour in diurnal species. This strategy has been explained as a way to avoid predators, gain time and feed during the day (Berthold, 2001; Stresemann, 1934) or profiting from colder temperatures, save energy and reducing dehydration (Berthold, 1996).

Birds have developed all those different migratory strategies allowing migrating to bird families with very different biology and morphology.

Ecophysiology and adaptations of migratory birds

Migratory birds require morphological, physiological and behavioural adaptations that allow them to overcome the difficulties that entail such long journeys. Those adaptations are related to the physiological plasticity, the orientation skills and timing mechanisms that allow species depart and return in the appropriate time of the year from their breeding to their wintering ranges and vice versa (Newton, 2010). In fact, before carrying out their migration, birds experiment some changes in their body, as the accumulation of fat (Alerstam & Lindström, 1990), the reduction of the digestive organs (in shorebirds) (Piersma & Gill, 1998) and changes in mass of flight muscles (Piersma, 1988), that revert after migration. This physiological plasticity allows a reduction in flight costs, especially in long-distance migratory birds.

Apart from temporal morphological changes due to the plasticity, some morphological features differ from migratory to non-migratory closely-related species or populations of the same species. One of the most obvious is the wing shape. Normally, migratory individuals show more pointed and longer wings, as opposed to non-migratory individuals that show rounded and shorter ones. This has been shown in blackcap *Sylvia atricapilla* populations (Lo Valvo *et al.*, 1988; Pérez-Tris & Tellería, 2003) or in the common reed bunting *Emberiza schoeniclus* (Copete *et al.*, 1999). Furthermore, migratory bird species tend to have more squared and shorter tails than non-migratory ones (Leisler & Winkler, 2003). Another difference found between migratory and sedentary birds is the size of the brain and the development of the hippocampus. It has been observed that resident individuals have larger and rounded skulls compared to migratory ones (Winkler & Leisler, 2005), but in compensation migratory birds have a more developed hippocampus that gives greater spatial memory skills to migratory individuals (Cristol *et al.*, 2003; Fuchs *et al.*, 2015).

The differences between migratory and non-migratory populations are not irreversible. There are evidences that the shape of the wing or other adaptations can change in few generations, as it has been shown in studies where bird species shift their morphology and their niche after the colonization in islands (Alström *et al.*, 2015). This suggests that the adaptations linked to the migratory behaviour do not evolve independently every time a linage becomes migratory, but that all birds have the potential to further develop or modify already existing features to become migratory or non-migratory. However, the transitions to migratory to non-migratory or the other way around is not equally probable and the loss of migration could be easier than its gain.

Evolution of migration

One of the most interesting topics in the study of migratory behaviour is how it has evolved and when did it originated. Migratory species and clades are interspersed in the phylogeny of birds, hence it has been suggested that migration has independently evolved multiple times along the evolutionary history of birds (Zink, 2011). The transition from a migratory state to another, gaining or losing migratory behaviour can happen rapidly in evolutionary time (Berthold *et al.*, 1992; Kondo & Omland, 2007; Zink, 2011). This suggests that the genetic machinery related to the capability of migrating is old and it is present in most species, probably switching on and off according to the environmental conditions (Berthold, 1999; Helbig, 2003; Salewski & Bruderer, 2007). Indeed, recent studies related to climate change have shown that some species, such as blackcaps (Pulido & Berthold, 2010) or storks *Ciconia ciconia* (Aguirre, 2012), have reduced their migratory activity due to Global Change in very few generations.

Some genes were described as candidate loci related to migration (Delmore *et al.*, 2015; Mueller *et al.*, 2011), linked, for example to phenology (Chakarov *et al.*, 2013; Saino *et al.*, 2015, 2017) and breeding time (Bourret & Garant, 2015). Most of them are located in the chromosome Z (sexual chromosome) that could also play a role in the divergence of birds (Ruegg *et al.*, 2014). This supports the idea that migration is controlled by different genes as suggested Berthold and Helbig (1992), given the variety of migratory movements and the physiological and morphological demands associated with migratory behaviour.

Several biogeographical hypotheses have been proposed to explain the origin of migration in birds. Among them, the classic and most popular debate confronted the “Northern-home-theory” with the “Southern-home theory”. The former one assumed that the birds' original ranges were placed in the preglacial Northern areas. Climatic changes, like the Pleistocene alternation of glacial and interglacial periods, would have forced birds to move southwards during the winter, as their survivorship would have become more difficult in their Northern ranges throughout the year, followed by the return to the areas of origin (Gauthreaux, 1982; Winger *et al.*, 2014). The “Southern-home theory” assumed instead, that the ancestors of migratory birds resided in tropical areas and started to migrate to higher latitudes to spend there their breeding season (Helbig, 2003; Joseph *et al.*, 2003; Rappole, 1995; Safriel, 1995). These two hypotheses, nevertheless, did not need to be exclusive. Several studies such as Pulgarín *et al.* (2013) and Joseph *et al.* (1999) have supported both Northern and Southern origin of migration in *Pheucticus* and *Charadrius* genera respectively. However, those classic hypothesis are thought in a context where the geography is static, but most species of birds are older than the Pleistocene, and the whole Order originated between 70 MYA (Prum *et al.*, 2015) and 100 MYA (Jarvis *et al.* 2014). Hence, it is likely that migration evolved when the continents where in other positions and the Earth's climate was different. Given that, Louchart (2008) proposed a new theory, the “shifting home model”, that takes into account the paleoclimate and the fossil record, suggesting a dynamic perspective in the origin of bird migration, focused in the Palearctic and Paleotropical regions. Generally, a great part of the modern bird families originated during the Oligocene, or even earlier (Prum *et al.*, 2015) and possibly the events of appearance and disappearance or change of migratory behaviour happened within some of the modern genera from the Miocene until now, with support of the fossil record (Louchart, 2008; Olson, 1985). Louchart (2008) suggested that possibly non-migrant African tropical bird taxa occupied current European latitudes during the part of the Cenozoic and given the climate changes and the cooling of the continents the distribution limits moved southwards until the current African tropical latitudes. These dynamics probably induced the origin of short migratory behaviour up to a progressive development of long distance migration.

BOX 1: Ecological niche

There are several definitions of what an ecological niche is. The niche is defined as ecological (biotic and abiotic) conditions that a species requires to survive and maintain its populations in a particular space (Colwell & Rangel, 2009; Hutchinson, 1957). Depending on the emphasis given to a component or another, two principal perspectives can be described. The Grinnellian niche focused on the environmental conditions that determine the large-scale distribution of species, while Eltonian niche is based more on species interactions and local scale (Peterson *et al.*, 2011). In this thesis, we talk about niche in the Grinnellian sense, as it is described by Hutchinson (1957): a multidimensional space determined by characteristics were a species can survive. The environmental niche is used to determine the potential distribution of species and is broadly used for performing Species Distribution Models (SDMs). This potential distribution is called fundamental niche. Furthermore, Hutchinson (1957) differentiates the fundamental niche from the realized niche, which is a subset of the fundamental niche where species are the main competitors and can survive and maintain their populations.

A partial migratory condition has been proposed as the first step in the evolution of long migrant species by other authors too (Berthold, 1999; Berthold *et al.*, 1990). When resident birds, under a change in the climatic conditions, a demographic expansion or by chance, started to move to unexplored areas in the limit of their distribution ranges and found favourable conditions, the migratory behaviour could be selected starting with short distance migrants. The conversion from sedentary to migratory behaviour would be the consequence of an extension of the ecological niche **[BOX 1]** of the bird species (Cox, 1985). Unlike the idea of an obligate partial migratory step, several authors have shown that the gain or loss of migratory behaviour can happen very fast in evolutionary time and without an intermediate step (Kondo & Omland, 2007; Kondo *et al.*, 2008). One of the most notable situations of shift in migratory behaviour entails island species, where the colonization of isolated lands promotes the loss of migration, as exemplified by the Greenland populations of *Turdus pilaris* that became sedentary in 1937 after a single colonization event (Salomonsen, 1950).

Why migrate?

The reason why, when considering the Southern origin theory, a sedentary tropical species started such journeys to breed in temperate latitudes has been discussed very broadly. Reducing intraspecific competition during the breeding season has been suggested as the main reason for the beginning of migratory behaviour (Cox, 1968). In tropical areas, despite the high productivity, the great density of bird species and individuals with similar niches in terms of trophic categories or habitats may be disadvantageous for reproduction, driving some of those species or populations to temperate areas where there are parts of the niche to be occupied.

However, other factors have also been contemplated. The reduced load of parasites in the Northern latitudes compared with the tropical ones could play an important role in bird migrations. In shorebirds it has been noted that they tend to select breeding arctic and marine environments with poor parasite concentrations, allowing them to less invest in their immune system (Piersma, 1997). The same has been found in the Southern hemisphere, where bird species from Southern and colder latitudes presented less prevalence of parasites (Merino *et al.*, 2008). As equivalent, the honeycreepers in Hawaii colonized montane habitats due to the reduced parasite load. In lowlands, the introduction of mosquitoes provoked the extinction of honeycreepers due to the diseases and remained confined to higher altitudes were mosquitoes are not present (Van Riper *et al.*, 1986; Warner, 1968).

The different predation risks depending on latitude have also been related with migratory behaviour. McKinnon *et al.* (2010) showed that considering a gradient of latitudes from around 55º to 85º, the predation risk in nesting Arctic birds declined towards higher latitudes. This could compensate the cost of the further distance movement northwards with a greater reproductive success.

The rhythms of migratory activities (phenology), furthermore, have been related with the circannual variations in environmental conditions (McNamara & Houston, 2008), as the temperature or the photoperiod (the day-length). The increase of the photoperiod in

Northern latitudes during spring could be advantageous for breeding and feeding nestlings, as the available hours in which birds can develop activities increase. Moreover, it has been shown that birds respond to changes in the photoperiod (Coppack *et al.*, 2001) and it has been suggested that the photoperiod acts as a cue to initiate migrations. However, the changes in the photoperiod are pronounced in Northern latitudes (if considering the Northern Hemisphere) but not closer to the equator, being only a good hint when birds return to tropical areas after breeding. This suggests the existence of endogenous circannual rhythms that control the migration (Gwinner, 1977) and probably the main clue before departing from the tropics and subtropics are the climatic conditions, as the higher temperature and precipitations in the Sahel (Saino & Ambrosini, 2008).

The high availability of resources during spring/summer in temperate latitudes has been identified as one of the main factors driving the annual movements in birds (Aharon-Rotman *et al.*, 1990; La Sorte *et al.*, 2014; Thorup *et al.*, 2017). Some studies using tracking technologies or dated occurrence data on bird species, indicated that birds migrate according to the increase in greenness or primary productivity of the areas where they move to (Aharon-Rotman *et al.*, 2016; La Sorte *et al.*, 2014; Thorup *et al.*, 2017).

The reason why birds migrate can be a combination of all factors mentioned above, as all provide advantages for the breeding and survival compensating the high cost of such migratory journeys.

Migratory flyways and Palearctic-Paleotropical migratory birds

Migratory birds tend to follow particular routes during their migratory travelling from Northern to Southern latitudes and vice versa. Usually, those routes also known as flyways, follow certain terrain and landscape features such as rivers, mountain ranges or coastlines that help navigate birds, although there are many examples where birds directly cross oceans or deserts (Egevang *et al.*, 2010; Strandberg *et al.*, 2010). There are around seven main flyways over the world (Fig.1). Migratory bird species use these flyways differently, performing long-distance movements between continents or much shorter displacements within continents. Furthermore, within the same species, populations can take different migratory routes, even if breeding ranges are geographically close, in what is called migratory divides caused by barriers (Møller *et al.*, 2011; Ruegg *et al.*, 2014) or secondary contact (Berthold, 2001; Chamberlain *et al.*, 2000; Delmore *et al.*, 2015; Delmore & Irwin, 2014; Hobson *et al.*, 2015).

These flyways show distinctive features regarding their geography. In the North-South American system, migratory birds have to choice between the Central American land corridor, crossing the Caribbean Sea overflying Caribbean islands, or even the Atlantic Americas flyway that crosses from the Arctic to South America directly through the sea, as it has been shown in the Hudsonian godwit *Limosa haemastica* (Senner *et al.,* 2014). In the Central Asia flyway, birds have to face barriers as the Himalayas Mountains and in Eastern Asia/Australasia flyways crossing the Yellow sea suppose a great challenge. In the Black Sea/Mediterranean, East Atlantic and East Asian/East African flyways the big barrier from the breeding to the wintering range is the Sahara Desert (Strandberg *et al.*, 2010).

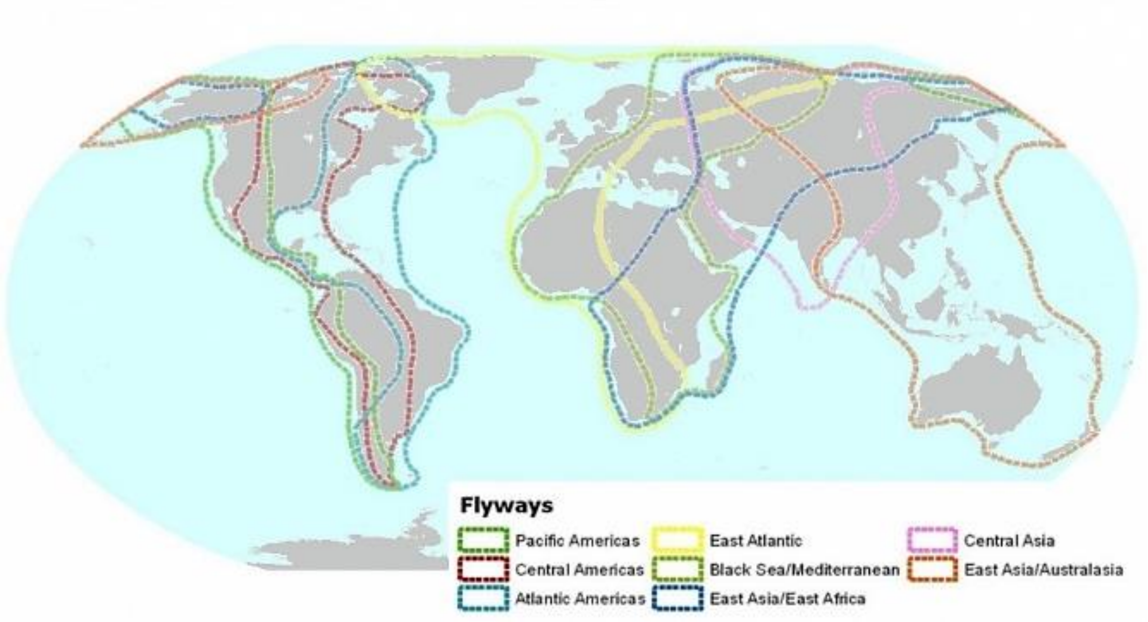

Figure 1 Bird flyways over the world. Figure modified from http://www.birdlife.org/worldwide/programme-additional-info/migratory-birds-and-flyways

The Sahara Desert is a large arid land devoid of resources and with an extreme climate that becomes a great barrier to many migratory birds with few possible stopovers (Hahn *et al.*, 2009), as it divides the African continent in two. Nonetheless, more than 2 billion birds cross this desert every year (Hahn *et al.*, 2009). The Sahara Desert has not been as arid as nowadays, as a great aridification happened during the Plio Pleistocene (DeMenocal, 1995; Trauth *et al*., 2009) and also humid periods such as in the mid-Holocene (~6000 years ago) took place also in this region, contracting and shaping the extent of the desert (Schuster *et al.*, 2006). These events could have affected migratory birds as their migratory distances would have changed, increasing with its aridification.

The spring and the autumn migratory routes are not necessarily the same for a certain species (Egevang *et al.*, 2010). In fact, there are some cases in which the same species uses different flyways depending on the migration, as the red-backed shrike L*anius collurio* that uses the Black Sea/Mediterranean flyway during the autumn migration and the East Asian/East African flyway in the spring when returning to their breeding quarters (Bäckman *et al.,* 2016).

Migration and climatic changes in the evolutionary history of migratory birds

The distribution of species has been contingent on the variation of climatic conditions and environment along the Earth history and species have been changing their geographical ranges according to their ecological niche **[BOX 1]**. Migratory routes were likely shaped by past climatic changes, changing through time (Winger *et al.*, 2014; Zink & Gardner, 2017). In fact, the origin of some of the current migratory divides has been related to post-glacial colonisations from Southern refugia (Irwin *et al.*, 2005; Ruegg & Smith, 2002; Ruegg *et al.*, 2006). In the Pleistocene, a great part of the Northern hemisphere was covered by ice (Ehlers & Gibbard, 2004), hampering the occupancy of birds, other animals and plants at higher latitudes. Thus, migratory bird species that currently occur in Arctic areas during the breeding season must have bred at lower latitudes during glaciations. As a consequence, those migratory species could stop migrating becoming sedentary in their wintering ranges (Zink & Gardner, 2017), back to a migratory strategy again during postglacial periods resulting in a Northern expansion of bird populations (Milá *et al.*, 2006). An alternative scenario is that migratory distances could have been reduced during those glacial periods and increased again in the interglacial periods without becoming sedentary; hence migration persisted reducing only the migratory distance.

Shifts in migratory behaviour could have not only happened in the past under cold climates, but also in the present as the conditions change as a consequence of Global Change. In the last decades, several long-distance migratory species have become nearly sedentary, staying close to their breeding areas, profiting from warmer winters and food availability (Aguirre, 2012). In other cases, the breeding range would shift northwards, potentially increasing migratory distances (Doswald *et al.*, 2009), as long as the cost of migration does not become too high, preventing the colonization of Northern latitudes with potential suitable habitats (Toews, 2017).

Many studies have shown that the present climate change has also affected the times (phenology) in the life-cycle of species (Parmesan & Yohe, 2003; Root *et al.*, 2003; Walther *et al.*, 2002). However, not all organisms may respond in the same way to global warming, causing a mismatch in ecological communities. For example, the higher temperatures during the spring in temperate latitudes have advanced the vegetation phenology (e.g. flowering times) (Menzel *et al.*, 2006; Schwartz *et al.*, 2006), which is linked to an earlier development of the insects (Visser & Both, 2005). This situation forces migratory birds to advance their spring arrival date to the breeding ranges in order to profit from the peak of the available resources during the breeding season (Pulido, 2007), or otherwise provokes a decline in the populations that lag behind (Saino *et al.*, 2011). Consequently, the change in climate along the Earth history, possibly not only have shifted the spatial distribution of migratory birds but also the time in which these movements took place.

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The number of aspects that can be studied of migratory behaviour in birds is countless. In the previous paragraphs I introduced some of the main ones in order to introduce the following work. Despite the large amount of work on migratory behaviour, there are still some aspects that are not well studied. In this thesis I aimed to unravel how migration evolves throughout evolutionary time and which are the potential drivers that act in the change of migratory behaviour in birds. Some studies focused on the evolution of migratory behaviour in some groups (Kondo & Omland, 2007). However, there is not an integrative study, which consider both morphologic and environmental factors or explore the migration as a discrete (migrate or not migrate) and continuous character (migratory distance). On the other hand, several works have been made using Nearctic-Neotropical bird species about the change in migratory bird distribution in the past (Winger *et al.*, 2014; Zink & Gardner, 2017); and the characteristics of their climatic niche (Marínez-Meyer *et al.* 2004; Nakazawa *et al.*, 2004). However, those aspects are underexplored in Euro-African trans-Saharan migratory birds. Here we tried to contribute to a better understanding of the evolution of migration and we asked ourselves some questions that we want to respond in this thesis: Are the environmental factors, as climate or resource availability essential in the evolution of bird migration? Is the morphology important and determinant in its evolution? How fast can birds shift their migratory behaviour? Do all trans-Saharan passerines and large-size birds respond in the same manner to environmental changes and in consequence their migratory behaviour evolved in the same way?

To answer the question of how migration evolves through the history of birds (Section I, see **Structure of the Thesis and Objectives**) I selected one Passerine genus with available phylogenetic information for all species and including species with both migratory and sedentary behaviour. In the Section II, I selected long distance trans-Saharan migratory birds to unravell general patterns in migratory birds in a biogeographic and macro-ecological perspective including several orders of birds. All those birds, although belonging to different orders, have in common that have to cross the great barrier of Sahara desert and that perform long migrations In the following I introduce the group used in the first section and their taxonomy.

Taxonomy of the superfamily Sylvioidea and the group of study

The taxonomy of Old World warblers and related taxa has been debated until now. In the past, most of the denominated Old World warblers were englobed in a single family Sylviidae. Recent studies done by Alström *et al.* (2006) and Fregin *et al.* (2012) have shed some light on the matter. However, the relationships between and within some families are still unresolved.

The Sylvioidea superfamily belongs to the order Passeriformes and is one of the three superfamilies of the parvorder Passerida (Sibley & Ahlquist, 1990) along with Muscicapoidea and Passeroidea. This superfamily is composed by 22 families with more than 1200 species, including: Panuridae, Nicatoridae, Alaudidae, Pycnonotidae, Hirundinidae, Pnoepygidae, Macrosphenidae, Cettiidae, Aegithalidae, Phylloscopidae, Acrocephalidae, Locustellidae, Donacobiidae, Bernieridae, Cisticolidae, Timaliidae, Pellorneidae, Leiothrichidae, Sylviidae, Zosteropidae, Scotocercidae and Erythrocercidae, based in a multilocus phylogeny using both mitochondrial and nuclear markers (Fig. 2 taken from Fregin *et al.*, 2012).

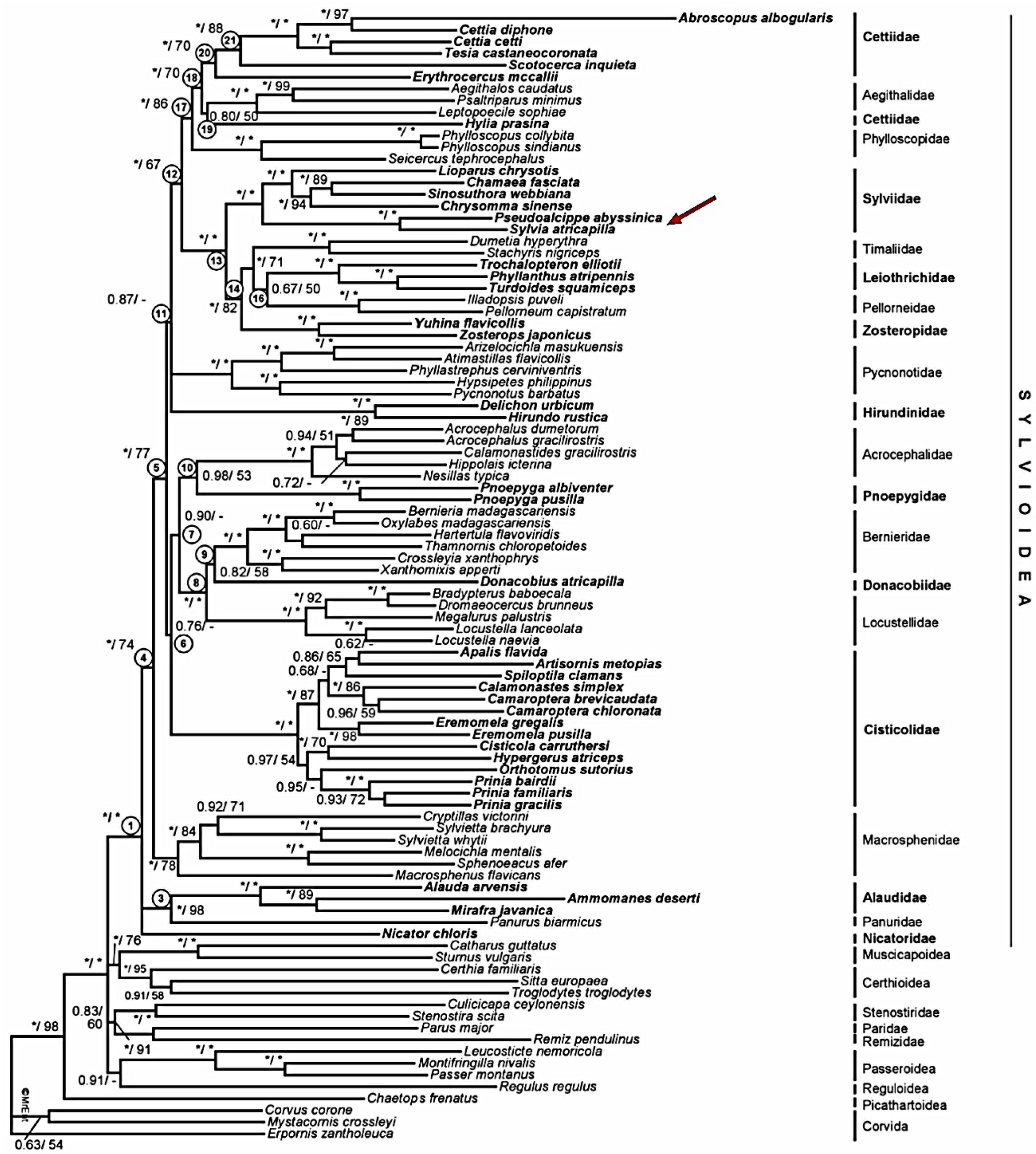

Figure 2. Phylogeny of Sylvioidea based on Cytb, FGB, GAPDH, LDHB, MB, OCD1, RAG1 genes, analysed by Bayesian Inference and Maximum Likelihood, modified from Fregin *et al.* (2012). The red arrow points out the group of study.

In my thesis I will use the genus *Sylvia* belonging to the family Sylviidae [Sylviinae: *Sylvia* (Cibois, 2003)], as a case study to explore the evolution of bird migration in a phylogenetic context and to determine the factors involved in it. The variety of migratory behaviours of the species of this group makes it interesting for the study the evolution of migration.

Sylvia warblers

Sylvia warblers compound an Old World passerine genus with 26 currently described species (Shirihai *et al.*, 2010). They are distributed in Eurasia and Africa, with most of the diversity gathered around the Mediterranean basin (Fig. 3).

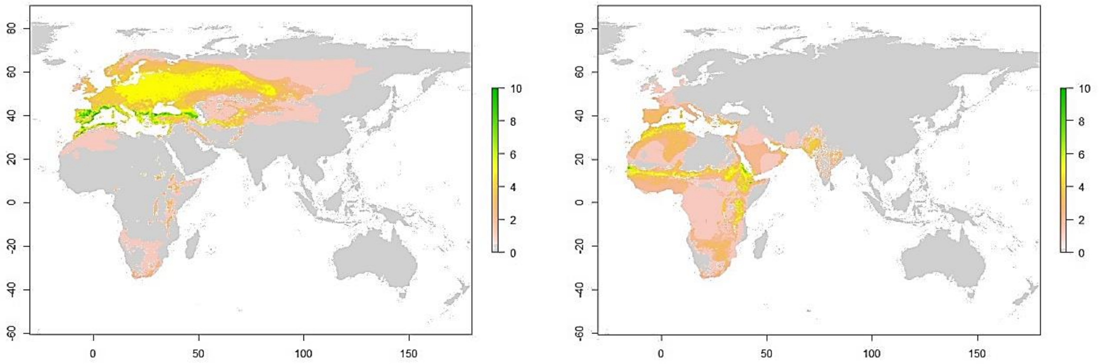

Figure 3. On the left, species richness of *Sylvia* warblers during their breeding season. On the right, species richness of *Sylvia* warblers during their wintering season. Birdlife maps were summed (BirdLife International and NatureServe, 2011).

Those birds are fundamentally insectivorous, although fruits, seeds and vegetal material become an important component of their diet especially during the wintering season (del Hoyo *et al.*, 2006). Species within the genus *Sylvia* show a great variety of migratory behaviours, with sedentary and migratory species interspersed in the phylogeny (Fig. 4).

Sylvia atricapilla is exceptional as different populations show divergent migratory behaviours, including non-migratory, partial migratory and long-distance migratory populations (Pérez-Tris & Tellería, 2002). There are long-distance migratory species that travel from Europe to Africa, as *Sylvia borin*; and other species with sedentary habits, primarily island species such as *Sylvia balearica* ,with their distribution in tropical or subtropical Africa such as *Sylvia boehmi*, or some that are resident in the Mediterranean as *Sylvia undata* or in Arabia as *Sylvia bury* (Shirihai *et al.*, 2010).

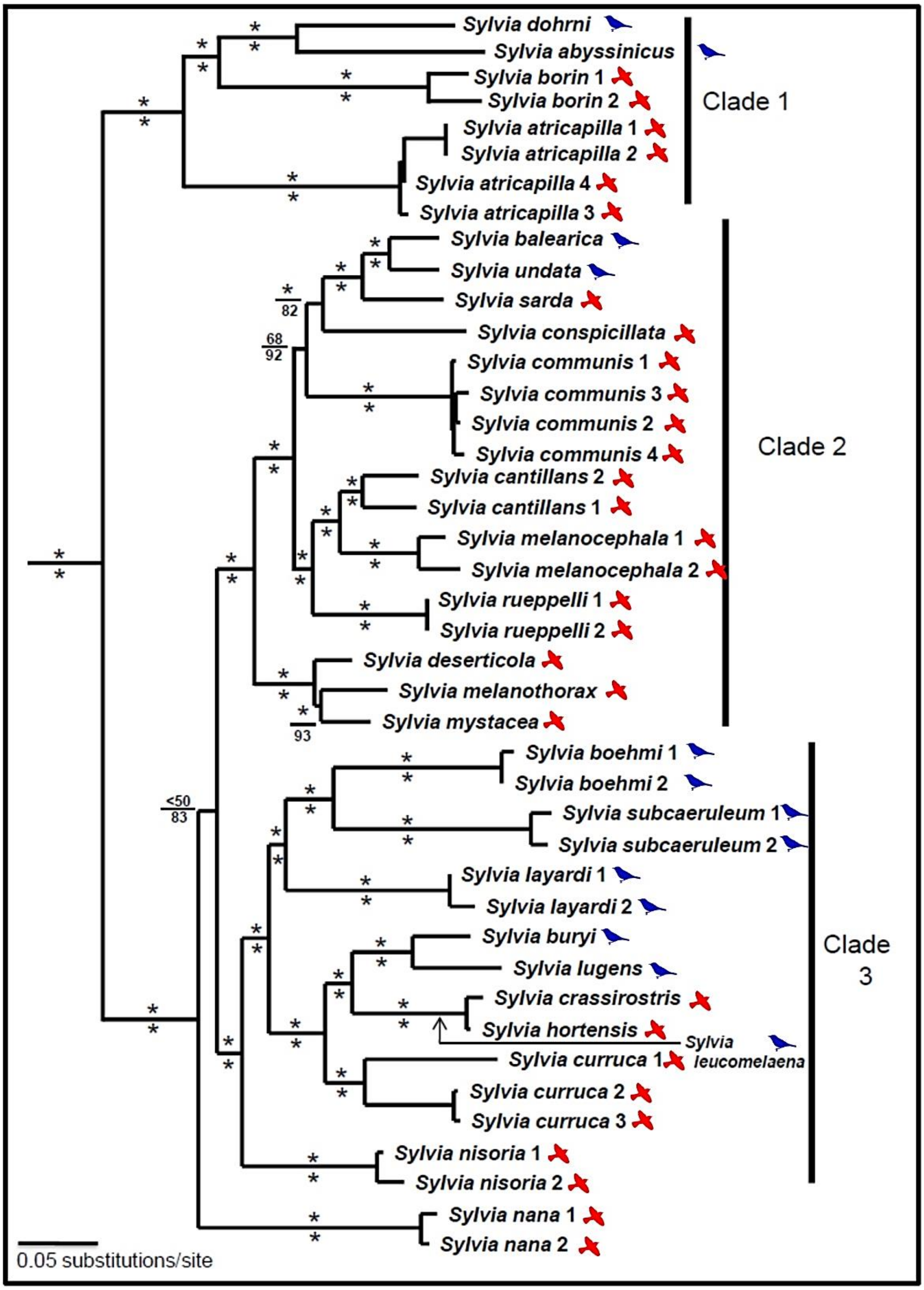

Figure 4. Phylogeny of *Sylvia* warblers based on Bayesian and Maximum Likelihood approaches using Cytb and ND2 mitochondrial genes, modified from Voelker and Light (2011). Birds in red represent migratory taxa while birds in blue represent sedentary taxa.

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OBJECTIVES

STRUCTURE OF THE THESIS AND OBJECTIVES

In the present thesis I want to unravel the patterns and processes that are involved in bird migration in a phylogenetic and historical context. This thesis explores this main issue by performing phylogenetic comparative analyses and including evolutionary, ecological and biogeographical approaches.

The particular issues and objectives explored in this thesis are described below:

SECTION I: The evolution of the migratory behaviour in *Sylvia* warblers and the factors involved

Chapter 1: We aimed to disentangle the evolutionary pattern of bird migration by reconstructing migration using phylogenetic comparative methods. To do this we used *Sylvia* warblers as case of study. We explored this by performing a set of ancestral state reconstruction analyses (ASRs), covering all of the available methodologies, and evaluating how different ASR parameters affect the results of character evolution. We assessed the degree of variation of these approaches using different combinations of model of evolution, branch lengths, character coding and software, and their consequences in determining how bird migration may have evolved in an evolutionary context. Additionally, we want to review the phylogenetic relationships of *Sylvia* warblers.

Chapter 2: In this chapter, we explored which factors are related to the evolution of migration in *Sylvia* warblers, to test the hypothesis that migratory behaviour appeared in order to reach areas with higher availability of resources or better conditions during the breeding season. We investigated whether several morphological, climatic or productivity variables correlate with the pattern of appearance or disappearance of migratory behaviour in this genus in a phylogenetic context.

SECTION II: Climatic niche and Paleo-distribution of trans-Saharan migratory birds

Chapter 3: It is unclear if birds select the same climatic conditions in breeding and non-breeding periods, which may imply a reduced niche breadth than if the conditions are different between these periods. In this chapter we explored this issue using all long-distance migratory birds from Africa to Europe as study group. We wanted to assess if their breeding and the wintering climatic niches are similar, as well as if climate is one of the main drivers of migratory behaviour. We also explored if climatic niches of breeding and wintering ranges are conserved between sisters species.

Chapter 4: It has been suggested that migration disappeared during Pleistocene glacial cycles in some North American bird species, being regained during interglacial periods, a controversial hypothesis. Considering the different historical biogeographic setting of the Palearctic and African regions from the Nearctic, we wanted to test the hypothesis that migratory distances were reduced during the LGM due to the ice cover in the Northern Hemisphere, but migration did not disappear in the Eurasian-African flyways. For that we combined hindcasting modelling into the past (Last Glacial Maximum climate) to compare to present distributions, and a revision of the fossil record from the Pleistocene. We also wanted to assess the potential role as a barrier of the Sahara during its increasing aridification.

GENERAL METHODS

Correction of bird distribution maps and data extraction

All bird distribution maps were taken from BirdLife International and NatureServe (2011). Birdlife distribution maps show raw distribution ranges, including habitats where species are not likely to occur. Hence, we corrected all bird distribution maps maintaining only the areas where suitable habitats are present for each species. To do that we collected habitat information for each species from Birdlife International (2012), for both the breeding and non-breeding periods, keeping with the level 1 of the habitat categories present in the Birdlife International Data Zone (habitat and altitude of each species). We used the landcover layer from GLOBCOVER (Bontemps *et al.*, 2011), the altitude layer from WorldClim 1.4. (Hijmans *et al.*, 2005) and the water layers from the Global Land Cover Facility (GLCF) (Carroll *et al.*, 2009). The altitude layer has 30 arc-seconds (~1km) resolution. The water and landcover layers were re-scaled to the same grid cell size as the altitudinal layer, and re-classified to represent the Birdlife habitat categories available for all species (Birdlife International, 2012). In total, nine categories were used: coastal, terrestrial artificial lands, aquatic artificial lands, forests, grasslands, shrublands, savannah, wetlands and deserts. We created new potential habitat maps with the sum of the suitable habitat categories for each species. All Birdlife species distribution shapefiles were converted to raster format files with the same resolution of the altitudinal layer (30 arc-seconds ~1km). The process of correction consisted on creating new occurrence bird maps by overlapping raster layers with the habitat information from each species and their area of occurrence (resolution:1km) both for breeding and non-breeding ranges (Fig. 5). ArcGis 10 (ESRI, 2011) was used for GIS analyses. By doing this step we increased the accuracy of bird distributions by eliminating areas where species do not occur.

From these corrected bird distribution maps, we randomly sampled 10,000 occurrence points both in the breeding and the non-breeding ranges, with the ArcGIS package GME (Beyer, 2012). We used those points to extract latitude and longitude coordinates, climatic and productivity variables from each seasonal range.

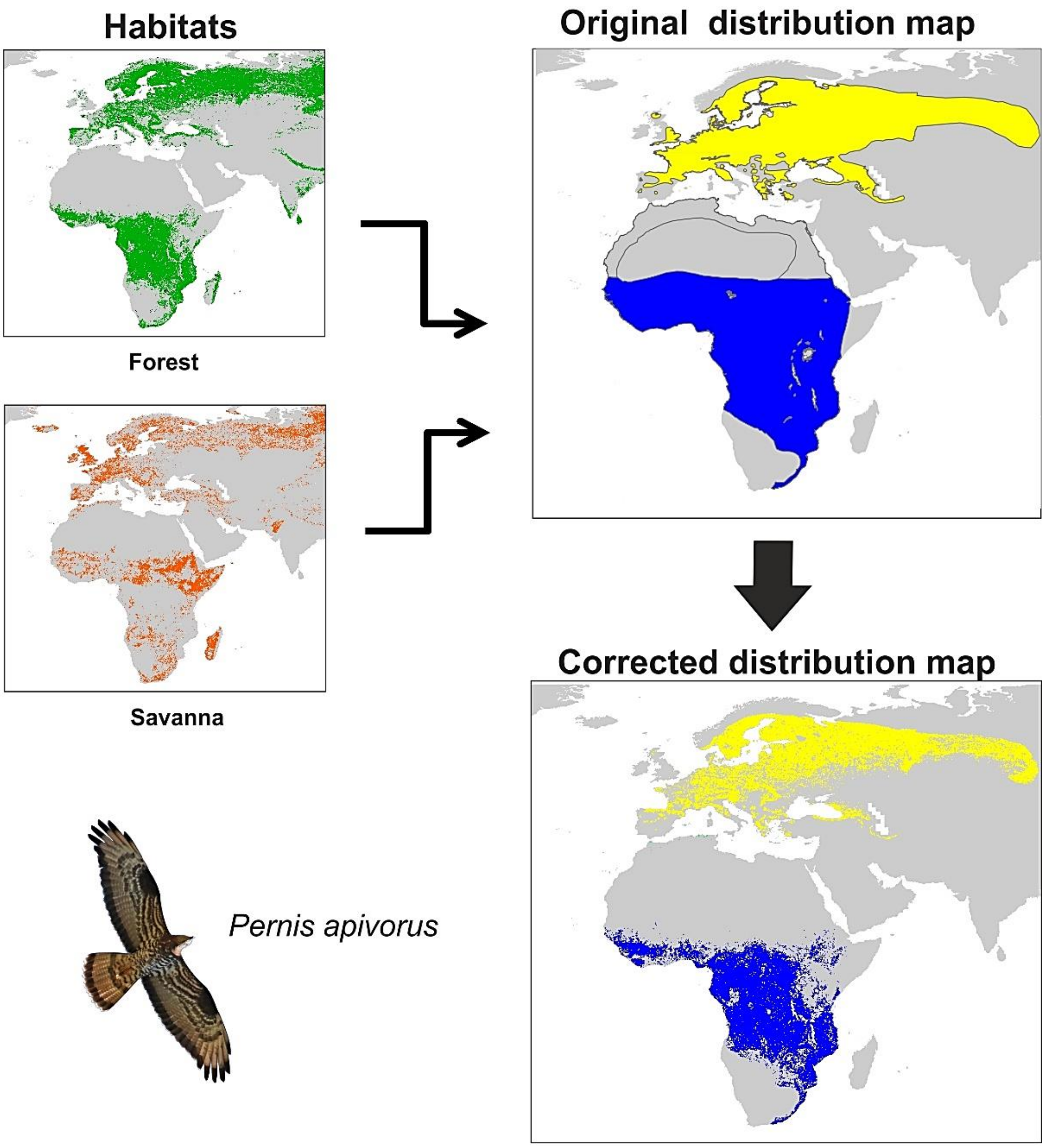
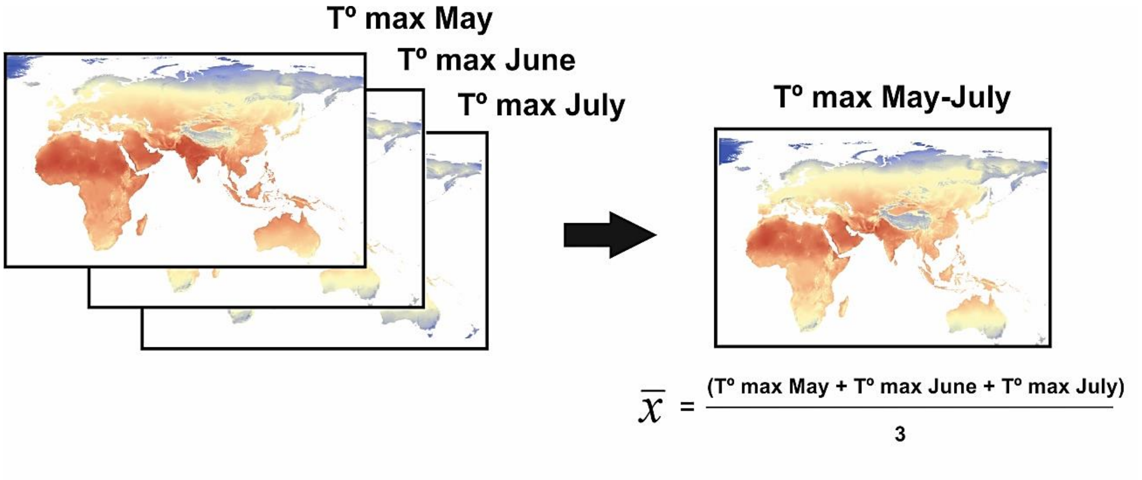


Figure 5. Diagram of the correction process of bird distribution maps. Example of the distribution of the honey buzzard *Pernis apivoris*: in yellow the breeding range and in blue the wintering range. Habitat maps (in this case Savanna and Forest) are overlapped with the original distribution map, resulting in a corrected distribution map were non suitable habitats are gone. Photograph of *Pernis apivorus* modified from Michael Sveikutis.

Long-distance Eurasian migrants spend some months of the year breeding in temperate and Arctic latitudes, and the non-breeding months in Southern, usually tropical, latitudes, hence being subject to potentially different climatic conditions in these periods. As a consequence, annual climatic variables seem not to be appropriate for studying the climatic conditions experienced by these species in each of these periods. For example, an Arctic breeding shorebird, which reproduces between May and July, experiences a climate that is radically different in the same spot than the winter climate in that place when the bird is absent. Because of that, we compiled the information of the months that each species spend in the breeding and wintering ranges from the literature (Brown *et al.*, 1982-2004; Cramp *et al.*, 1977-1994; del Hoyo *et al.*, 1992-2009). We gathered current climatic variables from the WorldClim dataset (~1950-2000, Hijmans *et al.*, 2005). We used monthly: total precipitation, mean precipitation, mean temperature, maximum temperature and minimum temperature with 30 arc-seconds (~1km) resolution. Then we generated new spatio-temporal climatic layers by calculating the mean temperatures of the months that each species spends in each territory, as well as the accumulated and mean precipitation of those months (Fig. 6).



$$\bar{x} = \frac{(\text{T° max May} + \text{T° max June} + \text{T° max July})}{3}$$

Figure 6. Example of new climatic map of maximum temperature corresponding to the period from May to July. The new layer is created by doing the mean with the monthly maximum temperature of May, June and July.

We gathered Net Primary Productivity (NPP) spatial data from NASA layers (http://neo.sci.gsfc.nasa.gov/view.php?datasetId= MOD17A2_E_PSN). The Net Primary Productivity is defined as the amount of carbon dioxide that the vegetation takes during photosynthesis minus the amount of carbon dioxide the plants release during respiration. It is measured in grams of carbon per square meter per day, and it provides an estimate of the productivity of the plants. Monthly data for more than 10 years are available in the NASA database. However, some months corresponding to several years lack information in most of tropical areas probably due to the cloud coverage. Because of that, we selected the years 2001, 2002 and 2003, which present accurate NPP information for all months and the whole planet, and we created new NPP monthly layers by calculating the mean of each month for all the three years, and an annual NPP layer.

To estimate which months show higher or lower values in NPP with respect to the average, we extracted NPP data for all months and annual NPP for each breeding and wintering point locations. Then, we divided each monthly NPP value by the yearly mean NPP value. We calculated the monthly mean of those values considering all breeding or wintering points. By doing this, we got a value for each month and for each season that could be higher or less than 1 corresponding to a positive or negative balance of NPP in each season compared to the mean global NPP, allowing assessing the monthly peaks of productivity in each area. We counted the number of months with NPP greater than the annual mean NPP, to estimate how long the season could be considering the peak of productivity in each area.

To estimate migratory distances, we determined the distance between breeding and wintering areas measured as median, minimum and maximum values. The median migratory distance was defined as the difference between the median latitude of breeding points expressed in degrees and the median latitude of the wintering points. The maximum migratory distances were calculated as the difference between the maximum latitude of the breeding range and the minimum latitude of the wintering range. The minimum migratory distances were defined as the difference between the minimum latitude of the breeding range and the maximum latitude of the wintering range. To convert the degrees into kilometres we used the equation, being 1: breeding and 2: wintering areas.

$$\begin{aligned} &Migratory\ distance\ (MD) \\ &= \sin(latitude\ 1) \times \sin(latitude\ 2) + \cos(latitude\ 1) \\ &\times \cos(latitude\ 2) \times \cos(longitude\ 1 - longitude\ 2) \end{aligned}$$

$$km = \operatorname{acos}(MD) \times 111.194$$

We are aware that migratory distances are highly variable within and among species, including latitudinal and longitudinal migratory routes. However, we considered only the linear distance between latitudes of breeding and wintering areas as a proxy to estimate the separation of both areas in the evolution or change of migratory distance in the past.

Spatial distribution models and ecological niche comparisons

Many authors assume that with the breeding climate they can infer the non-breeding distribution range, but this implies that that species show similar climatic niches both in the breeding and the wintering ranges, being the climate one of the main driver of the birds' movement, hypothesis that needs to be formally tested (**Chapter 3**). To explore this, we compared the climatic niches of breeding and wintering ranges of 355 migratory bird species that migrate from Africa to Europe and Asia. We used the statistical framework proposed by Broennimann *et al.* (2012), which compares environmental niches using occurrence and spatial environmental data (Fig. 7). This framework allows the comparison of the environmental niche of two species or two entities (populations, or even the same species in different times) and quantifies the degree of similarity by calculating the amount of niche overlap between them. In our case, the entities are the breeding and wintering climatic niches of the same species. We also tested whether the breeding climatic niches of sister species and the wintering climatic niche of sister species are highly conserved as expected by the niche conservatism hypothesis or not (**Chapter 3**).

The Broennimann *et al.* (2012) framework involves different steps. In the **first step** we calculated the density of occurrence and environmental factors along the global environmental space defined by the axis of a multivariate analysis. For each species, we performed a principal component analysis (PCA) including the climatic variables of both breeding and wintering periods (see **General Methods**: "Correction of bird distribution maps and data extraction", Fig. 7) of all the study extent (Palearctic, Afrotropical, Indo-Malayan and Australian regions). Given the high resolution of climatic layers we used a subset of 200.000 random points for each climatic variable for each season separately and for all the study extent, data that were used in the PCA. The climatic space defined by the two main principal components was divided in a grid of 100 x 100 cells, with each cell containing a unique vector of climatic conditions (v_{ij}). For each species, 10.000 random points per season were used as occurrence data. A kernel function (Worton, 1989) was used to determinate the smoothed density of occurrences of the species (o_{ij}), and the density of available climatic conditions in the background (e_{ij}) (Broennimann *et al.*, 2012). The occupancy of each entity (z_{ij}) (in our case, each season per species) is calculated by dividing (o_{ij}) into (e_{ij}). The **second step** involves the comparison of both season occupancies (z_{ij}), and calculating the degree of overlap. Niche overlap was calculated using the D metric (Schoener, 1970; Warren *et al.*, 2008) that varies from 0 (no overlap) to 1 (totally overlap):

$$D = 1 - \frac{1}{2}\left(\sum_{ij}\left|z_{1ij} - z_{2ij}\right|\right)$$

To interpret the degree of overlap given the D metric, we used the categories proposed by Rödder and Engler (2011): (0–0.2 = no or very limited overlap, 0.2–0.4 = low overlap, 0.4–0.6 = moderate overlap, 0.6–0.8 = high overlap, 0.8–1.0 = very high overlap).

The **third step** consists on the performance of the similarity and equivalency tests. The test of equivalency consists on performing the D metrics a hundred times by randomly reallocating occurrence points to the two compared ranges. This test determines if the observed niche overlap is similar to the expected niche overlap. If the observed value of niche overlap falls outside the 95% of the simulated values of niche overlap, it can be concluded that the two niches are not equivalent. The test of similarity differs from the test of equivalency because in the former the total observed occurrence density of a range is shifted randomly and the niche overlap is calculated with the other observed range. If the observed value of niche overlap is greater than 95% of the simulated values means that the two niches are more similar to each other that expected by chance.

We also determined the climatic niche breadth of each species, by calculating the breeding, wintering and total niche breadths. To do this we used the coordinates of the points of occurrence from the PCA and computed the minimum convex polygon (MCP) for each species. To calculate each seasonal niche breadth, we took only the breeding or the wintering points and performed the MCP. To calculate the total niche breadth instead, we took breeding and wintering points all together and computed an MCP as well. Pracma and adehabitatHR (Calenge, 2006) packages for R were used to do those analyses.

Species distribution models (SDMs) were used in **Chapter 4**. SDMs use statistical models to predict the potential distribution of a species using occurrence information and environmental data as predictors (Guisan & Zimmermann, 2000, Fig. 7). In SDMs, the environmental conditions of the points of presence are compared with the environmental conditions of the points of absence, a random background or pseudo-absences if there is not real absence data available. If the predictors respond to a spatial gradient, we can assess the probability of occurrence in a particular area given this environmental information by projecting the SDM.

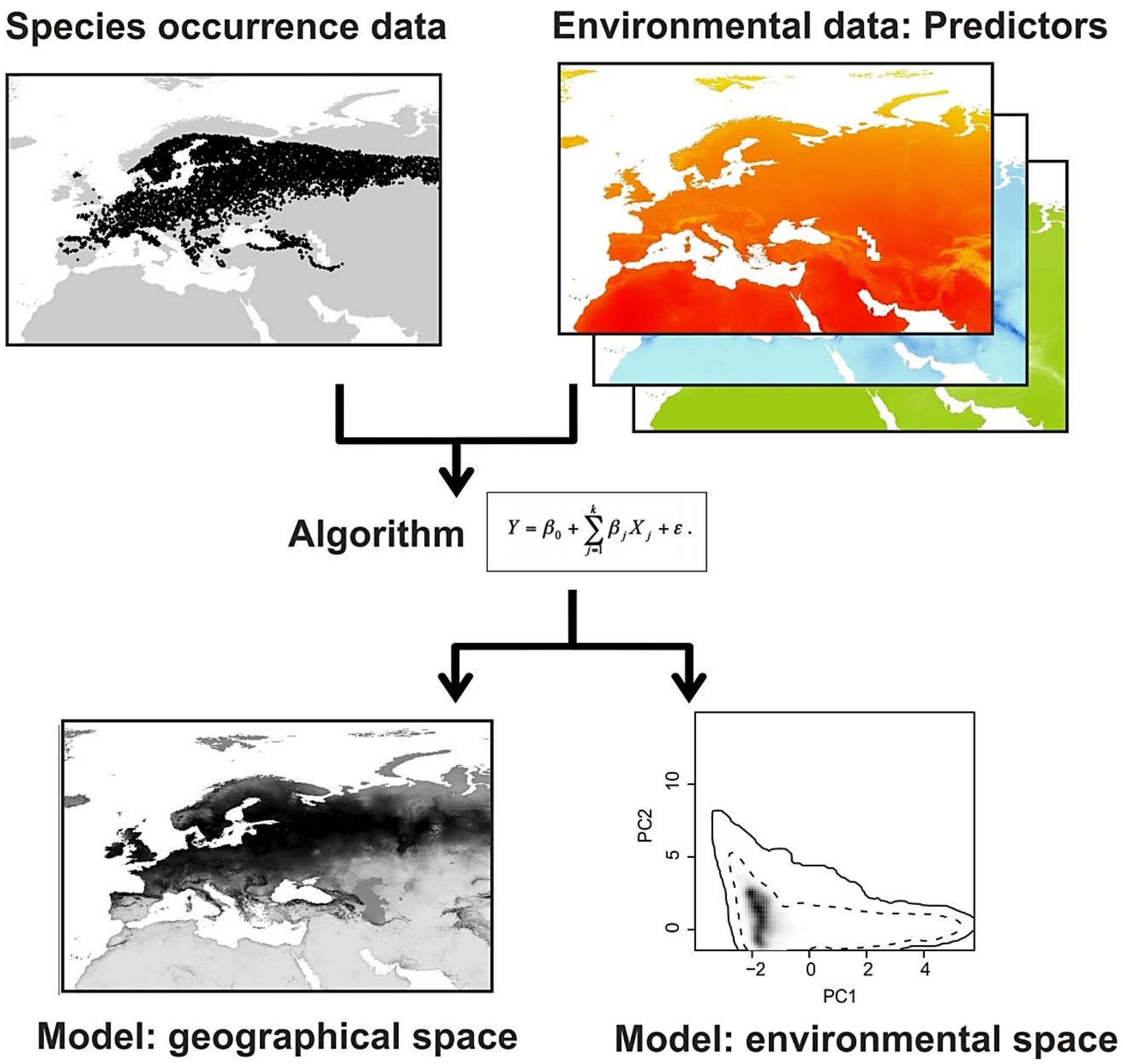


Figure 7. Diagram of the computation of Species Distribution Models (SDMs). Species occurrence data and environmental data linked with an algorithm predict models such as geographical space models or environmental space models.

The performance of SDMs had different steps. We performed SDMs for the breeding and the wintering ranges for each species separately. First, as we describe above, we randomly generated 10,000 points from the corrected species distribution maps for both breeding and wintering ranges, which are our points of presence for the species. We selected Africa, Eurasia and Australasia as maximum extent for the projections for our models and then generated 20,000 random points as background. Depending on the original distribution of each species, we reduced the extent for the projection of our models. For example, if we modelled a species which its current distribution is in a part of Africa, we only maintain Africa as extent where the model is projected. As predictors we used the climate corresponding to the period that each species spend in their breeding or wintering ranges (see **General Methods**: “Correction of bird distribution maps and data extraction”, Fig 7). Maximum, mean and minimum temperature of each period and mean precipitation of each period were calculated from WorldClim V.2 (Fick & Hijmans, 2017) maps with a 2.5 minutes resolution.

There are several methods to perform SDMs (Elith *et al.*, 2006). Considering the variation observed between models, we followed an ensemble approach running four different methods for each species and each season. The methods used where: GAM, GLM, GLM polynomial and BIOCLIM. All those methods were evaluated using the Area Under the Curve ROC (AUC) and COR (correlation) approaches to assess the agreement between presence and absence records and the predictors (Elith *et al.*, 2006). To avoid possible bias linked to each model (Araujo & New, 2006), we created an ensemble model from the four approaches performed and we re-evaluated it. The resulted projections showed a gradient of probability of occurrence for each species in each season. To make easier the operation with the projection maps created, we converted them to a presence-absence (0/1) map applying a threshold. As threshold we used the point at which the sensibility and specificity diverge in the model (Liu *et al.*, 2005).

In **Chapter 4**, we aimed to hindcast the past distributions of migratory species during the Last Glacial Maximum (LGM) and compare them with their present distributions. Given that it is unknown which and how many months the species spent in their breeding and non-breeding quarters in the Pleistocene, we selected the central ones of the current breeding and wintering season, to avoid variable months from the initial and final breeding seasons. Given the climatic variability along the year during the LGM, we assumed that the breeding and wintering seasons did not differ excessively from the present ones. All species selected to model present a breeding season from March to September and a non-breeding season from September to March, so we selected the interval from May to August as a homogenous breeding season, and from October to March as a homogenous wintering season to be projected in the past and in the present. Each model was computed as described above, with the climatic conditions of the period that each species spend in the breeding or the non-breeding ranges as predictors. Then, the projections were computed using the May-August or October-Match climatic maps for current and past climates. We projected our models to both the present and past climatic conditions with the homogenous seasons since it makes them comparable. All those steps were computed using R packages raster (Hijmans & van Etten, 2014), dismo (Hijmans *et al.*, 2017), rgeos (Bivand & Rundel, 2014), rgdal (Keitt, 2010), plotmo (Milborrow, 2015) and mgcv (Wood & Wood, 2015).

Phylogenetic analyses: phylogeny and divergence time estimation

To explore the evolution of migration in the study group described in the **General Introduction**, we assembled phylogenies and time calibrated trees. The phylogenies reconstruct the evolutionary history of a taxonomic group using DNA, morphology or proteins. Maximum Likelihood or Bayesian Inference approaches are the more often used frameworks to reconstruct phylogenies by using DNA as trait. There are different available models of DNA evolution to reconstruct phylogenies that assume different or equal nucleotide frequencies, transitions and transversions, or substitution rates between pairs of nucleotides. Among them the most common are: Jukes and Cantor model (JC69), Kimura model (K80), Tamura-Nei (TrN), Hasegawa-Kishino-Yano (HKY) or General Time Reversible (GTR).

Phylogenetic analyses were performed in **Chapters 1** and **2**. We selected the genes that where available in every or nearly all species and some subspecies of *Sylvia* warblers. In general, there is a lack of available genetic data in birds due to the difficulty of getting fresh tissues from the breeding ranges, as if individuals are caught during passage or in wintering ranges it is impossible to know their provenance. For *Sylvia* warblers the NADH dehydrogenase subunit 2 (ND2) and Cytochrome b (Cytb) genes were available in GenBank for all species and many subspecies, as other loci had unequal or fragmented taxonomic coverage. For each species and subspecies we selected one sequence for each gene, and more than one when the individuals came from very distant localities. Subspecies were assigned when the localities were specified in GenBank information. For specimens in which this information were not available, we assigned subspecific status when the specimens were collected in their breeding range and the locality was not shared between more than one subspecies of the same species. When the specimens were collected in their wintering range or in passage, we only maintained the species status, to avoid errors.

All sequences were aligned by the Clustal W algorithm (Thompson *et al.*, 1994) using BIOEDIT (Hall, 1999), followed by a correction by eye. We used select the best model of sequence evolution by using PartitionFinder (Lanfear *et al.*, 2012). Both Maximum Likelihood (ML) and Bayesian Inference (BI) were used to infer phylogenies. MrBayes 3.2.2 (Ronquist *et al.*, 2012) was used to perform Bayesian analyses, using as priors the parameters given by PartitionFinder. For each partition scheme, we ran two independent analyses consisting on four Markov-chain Monte Carlo (MCMC) chains for

20 million generations and sampling every 1000 generations. The option “prest ratepr” was set as variable to ensure that branch lengths were estimated separately for each codon partition. The temperature was fixed in 0.03. Stationarity and convergence between runs were assessed by using the “sump” command in MrBayes and checked in Tracer (Rambaut *et al.*, 2014). We discarded about the 25% of the generations in each analysis as burnin and we calculated a 50% majority rule consensus tree with the remaining trees. We reconstructed phylogenies under maximum likelihood implemented in RAxML v7.3.2 (Stamatakis, 2006). We used the same partition schemes and models as in the Bayesian analyses. Node support was evaluated with 1000 bootstrap repetitions.

We performed time calibrated trees for *Sylvia* warblers. Normally, geographical events and the fossil record are used to infer the age of the nodes of a tree. However, in birds the fossil record for Passeriformes is scarce and fossils are difficult to assign to a particular genus, because of the similarity of the bones. Some studies have estimated the age of bird groups including most Orders (Jetz *et al.*, 2012; Nabholz *et al.*, 2016; Prum *et al.*, 2015) and substitution rates in bird mitochondrial DNA have been proposed. Despite of the amount of studies, there are some discrepancies about substitution rates in mitochondrial DNA among birds. Given that, we explored different substitution rates and their impact on divergence time estimation. In **Chapter 1** for *Sylvia* warblers, we used the standard molecular clock for mitochondrial genomes in birds (Weir & Schluter, 2008). Then, we repeated the analyses using the rates from Pereira and Baker (2006), using the corresponding to the genus *Vidua* which is the closest phylogenetic relative to *Sylvia* available in their study.

Phylogenetic comparative methods and ancestral state reconstruction methods

In this thesis we used various phylogenetic comparative methods and ancestral state reconstruction methods (ASR) to respond different questions about the evolution of migratory behaviour in some passerine birds.

Ancestral State Reconstructions

The goal of ASR methods is to estimate the ancestral condition of a character in a group. For estimating ancestral states, Parsimony, Maximum Likelihood (ML) and Bayesian Inference (BI) frameworks can be used. Here we explored all of them. We reconstructed the migratory behaviour coded as a discrete character (migratory vs sedentary) and as a continuous character (migratory distance measured in km) in the **Chapters 1** and **2**. We also reconstructed ecological niches and morphological characters in **Chapter 2.** The first chapter aimed to unravel the possible differences in ASR methods by using different character coding, tree shape, taxon sampling, models of evolution and software. To explore the effect on ASR of branch lengths of the tree, we reconstructed migratory distance as a proxy for migration as discrete character using both a time calibrated tree and a phylogram. All ASR analyses were performed also using a complete phylogeny with all taxa included and another without some taxa. In the **Chapter 2** we included only the approaches that differ the most to explore the possible bias linked to the different parameters found in **Chapter 1**. In the following, all software, models and parameters used are detailed.

Mesquite

Mesquite software (Maddison & Maddison, 2015) allowed us to reconstruct discrete and continuous characters under the parsimony method. ML was available only for discrete characters. Two models of evolution were used: Mk1 ("Markov k-state 1 parameter model"($q01=q10$)) and Mk2 ("Asymmetrical Markov k-state 2 parameter model" ($q01\neq q10$)). Mk1 model uses a single change rate where both forward and reverse transitions are equally probable, Mk2 instead calculates a rate for each transition sense (a forward rate from 0 to 1, and a backward rate from 1 to 0).

Package Ape for R

Parsimony and ML approaches are implemented in the Ape package for R (Paradis *et al.*, 2004). Parsimony was used for both continuous and discrete characters. For discrete characters there is a script for doing parsimony (MPR), while for continuous traits we used the ML script, which transforms all branch lengths to 1. The evolution of migration as a discrete character was analysed with Mk1 and Mk2 models. Other three methods, apart from ML, are implemented in APE for continuous characters: REML (Residual Maximum Likelihood), PIC (Phylogenetic Independent Contrast) and GLS (Generalized Least Square), all of which we used in our analyses.

BayesTraits

Before reconstructing ancestral character states, we estimated the model parameters both coding migration as a discrete and as a continuous character. BayesTraits-multistate

(Pagel & Meade, 2007) was used to assess the ML evolution model for discrete coding and to compute ASR. We used both the Mk2 (q01≠q10) and Mk1 (q01=q10) models. The Kappa parameter was estimated by ML and compared to a null model where κ =0. These parameters referred to a punctuated (κ =0) or a graduated (κ =1) mode of change. The Bayesian approach was performed to assess the models described before. The parameter values obtained from the ML analyses gave an approximation of average values that can be used to define the prior's distribution for the MCMC analyses. Prior distributions have to be chosen carefully to strengthen as more as possible the sampling rate. We ran different analyses with uniform, exponential and gamma distribution priors for Mk1 and Mk2, including the Reverse Jump exponential Hyperprior, to assess which prior distribution performed better. The Reverse Jump exponential Hyperprior performed well, and we used it with a uniform distribution between 0 and 10 values for ASR. The analysis consisted on 1 million generations and a burnin of 100.000 generations.

Migratory distance as a continuous character was analysed with BayesTraits-continuous. Like with discrete characters, both ML and BI approaches were used. Brownian motion model is defined with values of scaling parameters (λ, σ, κ) equal to 1, which is the default model in BayesTraits. We compared this model with the models calculated with the ML values of the parameters with LR tests. We also took into account models A (random walk) or B (directional) of change in trait evolution. Those parameters were estimated again with MCMC, using a uniform prior for the alpha parameter (with the minimum and the maximum value of each character for delimitating the range of the prior), and also for the beta parameter for the directional model. Internal nodes were reconstructed with the AddMRCA command using models estimated with MCMC. Continuous characters can only be reconstructed with MCMC.

Continuous characters were analysed with Bayestraits-continuous. Like with discrete characters, both maximum likelihood and Bayesian approaches were used. Brownian motion model is defined with values of scaling parameters (λ, σ, κ) equal to 1, which is the default model in BayesTraits. We compared this model with the models calculated with the maximum-likelihood values of the parameters with LR tests. We also fixed λ=0 that means that trait evolution is independent from the phylogeny, and compared it with the most likely value of λ estimated. The most likely value of κ was also assessed with the null model defined with κ =0 (referred to a punctuation mode of change of traits' states, whereas κ =1 refers to a gradual evolution of traits). The parameter σ, indicates an adaptive radiation when values are lower than one, or species-specific adaptation when values are higher than one. Again, we tested the most likely value of σ with the null model σ=0. We also took into account models A (random walk) or B (directional) of change in trait evolution. Those parameters were estimated again with MCMC, using an uniform prior for the alpha parameter (with the minimum and the maximum value of each character for delimitating the range of the prior), and also for the beta parameter for the directional model. Internal nodes were reconstructed with the AddMRCA command using models estimated with MCMC (in continuous data Ancestral state reconstruction is not available with maximum likelihood models). All of these parameter options were estimated using both ML and MCMC. Continuous characters can only be used with MCMC.

Diversitree BiSSE

Diversitree package in R (Fitzjohn, 2012) only offers the estimation of ancestral state reconstruction by BISSE (Binary State Speciation and Extinction) or Mk2, hence we only performed ASRs with migration as a discrete character. BiSSE computes the probability of a phylogenetic tree and the observed distribution of a binary character state within the tree, given a model of trait evolution, speciation and extinction (Maddison *et al.*, 2007). This method estimates six parameters: two speciation rates ($\lambda 0$, $\lambda 1$), two extinction rates ($\mu 0$, $\mu 1$) and two transition rates (q10, q01). We could compare those estimated parameters with our tree and data with fixed models, restricting parameters to be equal: one with $\lambda 0= \lambda 1$, other with $\mu 0= \mu 1$, other with q10= q01; and four more possible combinations between all of them. The best fit model was selected by likelihood or the Akaike information criterion (AIC).

Phylogenetic comparative methods

Phylogenetic comparative methods used relationship information between species to test evolutionary hypotheses. In this thesis we used PGLS (Phylogenetic Generalized Least Squares) and PIC (Phylogenetic Independent Contrast) to test the correlation of some morphological and ecological traits with the migratory behaviour in *Sylvia* warblers (see **General Introduction** and **Chapter 2**). PGLS analyses were performed with the package Caper for R (Orme, 2013) and PIC analyses were performed with APE package for R (Paradis *et al.*, 2004).

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SECTION I:

The evolution of the migratory behaviour in *Sylvia* warblers and the factors involved

Chapter 1:

Understanding the evolution of migratory behaviour in warblers: controversial hypotheses using ancestral state reconstructions

This chapter reproduce entirely the manuscript:

Ponti. R., Arcones, A., Ferrer, X. and Vieites D. Understanding the evolution of migratory behaviour in warblers: controversial hypotheses using ancestral state reconstructions. Under Review

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Understanding the evolution of migratory behaviour in warblers: controversial hypotheses using ancestral state reconstructions

Abstract

Bird migration has been described as a labile behaviour that evolved multiple times in a phylogenetic context. Some hypotheses have been proposed for the origin and the mechanism of the evolution of bird migratory behaviour, including the tropical sedentary status of the ancestor. Here we explored the evolution of migration in *Sylvia* warblers as discrete and continuous character using ancestral state reconstruction methods. As there are different elements involved in those analyses with different levels of uncertainty (i.e. phylogenetic reconstruction, branch length estimation, trait coding, statistical framework, taxon sampling or software) that could affect in the interpretation of trait evolution, we performed a set of analyses including all possible combinations of such elements. We recovered the basal node as migratory in most analyses, suggesting seven independent losses of migratory behaviour in *Sylvia* warblers. Both analyses performed with migration as discrete or continuous character recovered different probabilities of sedentariness or migratoriness in some conflicting nodes depending of the ASR elements used. This forced as to consider controversial hypotheses of evolution of migration in some clades that could evolved from migratory to sedentary in a very short period of time or going through a partial migratory status instead. Those discrepancies in our results suggest that performing a single method analysis, as most studies did, could drive to an erroneous interpretation of the evolution of a trait, or at least to a non-consideration of an alternative hypothesis equally probable.

Keywords: evolution of migration, *Sylvia* warblers, Ancestral State Reconstruction.

INTRODUCTION

Bird migratory behaviour has evolved multiple times in birds (Zink, 2011), but how it evolves is still a subject of debate. It is not clear how fast changes from migratory to non-migratory states, or vice versa, can happen in evolutionary time. Many clades of birds are fully migratory or sedentary, going far back in the evolutionary tree of birds, suggesting that migration could be a conserved character in the evolution of birds. Traditional views suggested an ancestral partial migratory condition that derived into a full migratory or sedentary behaviour (Berthold, 1988; Berthold & Helbig, 1992), or that migration arose from sedentary species that moved to new areas as a consequence of competition and profit from food resources (Cox, 1985). These scenarios imply a gradual change from one condition to another, and a certain degree of conservation of the migratory or non-migratory states.

However, it also has been shown that the change from being sedentary to migratory, or vice versa, can be fast in evolutionary time (Kondo & Omland, 2007; Outlaw *et al.*, 2003; Pulido & Berthold, 2010). This hypothesis implies that the genes switching on and off the genetic machinery related to migration must be relatively conserved (Berthold, 1999; Helbig, 2003; Salewski & Bruderer, 2007), although an alternative scenario pictures the independent origins of migratory genes, loci that can be expressed by environmental requirements (Shaw & Couzin, 2013). There are key examples of species with migratory, partial migratory and sedentary populations like the blackcap (*Sylvia atricapilla*) (Lo Valvo *et al.*, 1988; Pérez-Tris & Tellería, 2002; Pulido & Berthold, 2010), although it is unclear how common this scenario of multiple migratory strategies in birds is.

If migratory behaviour is a conserved character, it would be possible to reconstruct its evolutionary history in a phylogenetic context using ancestral state reconstruction methods (ASRs). This would allow inferring the ancestral state (root of the tree) and confirm or reject traditional hypotheses on the gradual or sudden changes from one sate to another. If the evolution of migration is a gradual process, we can expect that most nodes in a phylogeny will show intermediate probabilities between sedentary and migratory behaviour, especially the most recent common ancestors (MRCAs) of non-migratory lineages. On the contrary, if the change from migratory to sedentary or vice versa happens rapidly, we could expect that the reconstructed probability of being migratory or sedentary of MRCAs will be high. If migratory behaviour is a labile character, then changes between states will happen multiple times in a single branch, making unreliable the reconstruction of such characters in old lineages.

There is another potential source of error that could challenge the interpretation of the results, related to ancestral state reconstruction analyses. ASRs have allowed inferring how species' traits, like bird migration, evolve through time (e.g Odom *et al.*, 2014; Struck *et al.*, 2011; Vieites *et al.*, 2009; Watts *et al.*, 2016), as well as testing hypotheses in a phylogenetic framework (Harvey & Pagel, 1991). ASRs aim to reconstruct the tempo, mode and the sequence of change of a species’ trait using phylogenetic trees as observations. The reconstruction of ancestral states is inferred from trait states of extant terminal taxa represented in the tree, and can be informed by fossil or biological data whenever available. Like most comparative phylogenetic methods, ASRs can be done under different statistical frameworks and software packages (Parsimony, ML or Bayesian) using different evolutionary models (Fitzjohn, 2012; Maddison & Maddison, 2015; Pagel & Meade, 2007; Paradis *et al.*, 2004). Likelihood and Bayesian methods lay on probability distributions where the probability of change is a function of time or length of branches between ancestral and descendant nodes, while in parsimony ASR methods branch lengths are generally ignored. This results in an underestimation of change between trait states in longer branches, which can be positively misleading if the trait in question influences diversification rates (Goldberg & Igić, 2008; Maddison *et al.*, 2007). Conflicting results related to the different elements involved in ASRs have been reported, including the use of different methods (Cohen, 2012; Ekman *et al.*, 2008; Stireman, 2005), branch lengths (Cusimano & Renner, 2014; Litsios & Salamin, 2012), taxon sampling and tree shapes (Gascuel & Steel, 2014; Maddison *et al.*, 2007; Mooers, 2004; Salisbury & Kim, 2001), phylogenetic uncertainty (Goldberg & Igić, 2008), rate heterogeneity (Skinner, 2010) or trait coding (Cohen, 2012). However, it remains unclear the extent and direction the different combinations of these ASR elements have on the inference of trait evolution, which is the basis to our understanding on how species evolve through time. These potential conflicts between the results of ASR analyses will not likely affect all nodes in a phylogenetic tree in the same way; For example, if all extant species of a clade share the same trait state (e.g. migratory lineages), the internal nodes within this clade will likely be reconstructed with the similar trait state as the terminal taxa. Hence, the critical nodes likely affected by discrepancies will be the ones corresponding to the most recent common ancestor (MRCA) of a clade constituted by species with similar trait values, as well as the nodes where lineages with different character states coalesce.

Here, we want to study how bird migratory behaviour evolves in passerines in a phylogenetic context, using the Afro-Palearctic *Sylvia* warbler radiation as a case study. This genus is particularly interesting as it comprises migratory and non-migratory lineages intercalated in the phylogeny, also including several sedentary island lineages with close fully-migratory relatives. Also, it has been a model system for studies related to the evolution of migratory behaviour, mainly focused on the blackcap (*Sylvia atricapilla*) (e.g Berthold *et al.*, 1990; Berthold, 1973; Berthold *et al.*, 1992; Pulido *et al.*, 1996; Pulido & Berthold, 2010; Voelker & Light, 2011). Considering the conflicting results reported using different ASR approaches, we performed a comprehensive analysis including all elements involved in ASR together. Hence, here we explored these potential discrepancies by testing the effect of all possible combinations of several elements on bird migration ASRs, including software, statistical frameworks, branch lengths, taxon sampling and trait coding. By doing this we aim to explore if conflicting hypotheses on the evolution of bird migration can be supported depending on the methodological approach.

MATHERIAL AND METHODS

Phylogeny reconstruction

We assembled a phylogeny for the genus *Sylvia* from previously available genetic data, increasing the most comprehensive published dataset available so far (Voelker & Light, 2011). We included all species, and from the 78 currently recognized subspecies (Shirihai *et al.*, 2010) mitochondrial DNA sequences were available for 26 of them. The lack of availability of fresh tissues for most species prevented us to generate a comprehensive nuclear-level phylogeny for the group. Novel available data sometimes lack explicit subspecific status. In such cases, we assigned sequences to subspecies only when the capture place and collecting time were clearly within the breeding range and capture period of a particular subspecies, discarding wintering or passage captures as well as samples from areas where several subspecies may coexist. We chose more than one sequence per taxon when localities were very distant from each other, as in the case of *Sylvia atricapilla*. We also included species from the genera *Parophasma* and *Lioptilus* to explore their phylogenetic position in relation to *Sylvia* (full dataset phylogeny). We also performed another phylogenetic hypothesis of *Sylvia* not including these genera, sensu Shirihai *et al.* (2010), to evaluate their potential impact on ancestral state reconstruction (partial dataset phylogeny).

Two mitochondrial genes were used to reconstruct the phylogeny of the genus *Sylvia*: NADH dehydrogenase subunit 2 (ND2) and Cytochrome b (Cytb) as in previous works (Böhning-Gaese *et al.*, 2003; Voelker & Light, 2011) (Genbank accession numbers available in **Appendix Chapter 1**, Section A1.1). Cytb sequences were available for all species except *Sylvia galinieri*, whereas ND2 were only available for 40 out of 67 lineages. As outgroups for the phylogenetic analyses, we included *Paradoxornis guttaticollis*, recognized as one of the closest relatives to *Sylvia* in a previous work (Johansson *et al.*, 2008), and *Phylloscopus collybita*. Sequences were aligned in BIOEDIT (Hall, 1999) by the Clustal W algorithm (Thompson *et al.*, 1994), followed by a correction by eye. Phylogenies were reconstructed under Maximum Likelihood (ML) and Bayesian Inference (BI) approaches. For both, we explored different partition strategies, by gene, by codon and gene, and concatenated, with linked and unlinked branch-lengths. We used PartitionFinder (Lanfear *et al.*, 2012) to select the best model of sequence evolution.

Bayesian analyses were performed for each partition scheme using MrBayes 3.2.2 (Ronquist *et al.*, 2012), using as priors the parameters given by PartitionFinder. For each partition scheme, we ran two independent analyses consisting on four Markov-chain Monte Carlo (MCMC) chains for 20 million generations, sampling every 1000 generations, and the option "prest ratepr" set as variable to ensure that branch lengths were estimated separately for each codon partition. The temperature was fixed in 0.03. Stationarity and convergence between runs were assessed by using the "sump" command in MrBayes and checked in Tracer (Rambaut *et al.*, 2014); based on this, we discarded the first three million generations and with the remaining trees we calculated a 50% majority rule consensus tree. The harmonic means of likelihood scores from the posterior distribution were compared with Bayes Factors to choose the best fit partitioning scheme. We reconstructed phylogenies under ML implemented in RAxML v7.3.2 (Stamatakis, 2006). We used the same partition schemes as in the Bayesian analyses using the model GTR+I. Node support was analysed using the model GTR+I. Node support were evaluated with 1000 bootstrap repetitions (See **General Methods**, Section "Phylogenetic analyses: phylogeny and molecular clocks").

Divergence time estimates

We used BEAST v1.8.0 (Drummond *et al.*, 2012) to infer the divergence time for the whole *Sylvia* complex. As there are some discrepancies in the literature about the substitution rates in bird mitochondrial DNA, we carried out molecular clock analyses to explore different substitutions rates and their impact on divergence time estimation. First, we employed the widely-used standard molecular clock for mitochondrial genomes in birds (Weir & Schluter, 2008), of 0.0105 substitutions/site/lineage/My, and we applied it to both loci. We then repeated the analysis with the rates from Pereira & Baker (2006), from which we used the corresponding to *Vidua*, being the closest phylogenetic relative to *Sylvia* available in their analysis. In this case, we ran the analysis using the mean value for each gene independently (0.01227 s/s/l/My for Cytb, 0.0086 s/s/l/My for ND2) and the top of the 95% credible interval (0.02007 s/s/l/My for Cytb, 0.01394 s/s/l/My for ND2). We set a Log-normal relaxed molecular clock, using a normally distributed prior for the standard deviation prior, with mean values of 0.00359 for Cytb and 0.0025 for ND2. Best-fit substitution models selected were TrN+I+G (for positions 1 and 2) and GTR+G (for position 3) on each gene. Each analysis ran for 100 million generations, sampling every 1000 steps, and using the first 10% generations as burn-in. Tree topologies were obtained using the Maximum credibility clade (MCC) method, as implemented in Tree annotator v1.8.0 (Rambaut & Drummond, 2013) (See **General Methods**, Section “Phylogenetic analyses: phylogeny and molecular clocks”).

Migratory behaviour trait as discrete and continuous variable

Bird migratory behaviour can be modelled either continuously by using migratory distance, or discretely by considering it as a two-state trait (migratory/sedentary). Hence, we performed ASR using both approaches. Migratory behaviour was coded as a discrete character using 0 (sedentary) and 1 (migratory), based in del Hoyo *et al.* (2006) and Shirihai *et al.* (2010) information. As a continuous character, median migratory distances were used for the analyses. These distances correspond to the linear separation in kilometres between the median point of the breeding range and the median point of the wintering range (See **General Methods**, Section “Correction of bird distribution maps and data extraction”). We are aware that migratory distances are highly variable within and among species. However, we considered only the linear distance between median latitudes to assess the evolution of separation of breeding and non-breeding areas as a proxy. In species with complex migratory strategies, which include sedentary, partial migratory and long-distance migratory populations like the blackcap, we considered overall breeding and wintering areas, as it is not possible to account for intraspecific variation without samples from all those populations.

Modelling trait evolution and ancestral state reconstructions

To compare the different statistical frameworks available for ASR of characters, we used maximum parsimony, maximum likelihood (ML) and Bayesian inference (BI) frameworks. We aimed to determine potential differences in the results of ancestral state reconstruction software; hence we repeated all analyses with different parameter settings in each program. As tree shape may have an impact on phylogenetic reconstruction, we performed all analyses with the phylogram and the recovered chronogram, having different branch lengths. In the following, we specify the different software packages and settings used in the comparative analyses. Analyses were performed with both partial and full datasets.

Mesquite

Mesquite software (Maddison & Maddison, 2015) allowed us to reconstruct discrete and continuous characters with the parsimony method. ML was available only for discrete characters. Two models of evolution were used: Mk1 ("Markov k-state 1 parameter model"($q01=q10$)) and Mk2 ("Asymmetrical Markov k-state 2 parameter model" ($q01\neq q10$)). Mk1 model uses a single change rate where both forward and reverse transitions are equally probable, Mk2 instead calculate a rate for each transition sense (a forward rate from 0 to 1, and a backward rate from 1 to 0).

Package Ape for R.

Parsimony and ML approaches are implemented in the Ape package for R (Paradis *et al.*, 2004). Parsimony was used for both continuous and discrete characters. For discrete characters there is a script for doing parsimony (MPR), while for continuous traits we used the ML script but it transforms all branch lengths to 1. The evolution of migration as a discrete character was analysed with Mk1 and Mk2 models. Other three methods, apart from ML, are implemented in APE for continuous characters: REML (Residual Maximum Likelihood), PIC (Phylogenetic Independent Contrast) and GLS (Generalized Least Square), all of which we used in our analyses.

BayesTraits.

Before reconstructing ancestral character states, we estimated the model parameters both coding migration as a discrete and a continuous character. BayesTraits-multistate (Pagel & Meade, 2007) was used to assess the ML evolution model for discrete coding and to compute ASR. We used both the Mk2 ($q01 \neq q10$) and Mk1 ($q01=q10$) models. The Kappa parameter was estimated by ML and compared to a null model where $\kappa = 0$. The Bayesian approach was performed to assess the models described before. The parameter values obtained from the ML analyses gave an approximation of average values that can be used to define the prior's distribution for the MCMC analyses. We ran different analyses with uniform, exponential and gamma distribution priors for Mk1 and Mk2, including the Reverse Jump exponential Hyperprior, to assess which prior distribution performed better. The Reverse Jump exponential Hyperprior performed well, and we used it with a uniform distribution between 0 and 10 values for ASR. The analysis consisted on 1 million generations and a burnin of 100.000 generations.

Migratory distance as a continuous character was analysed with BayesTraits-continuous. Like with discrete characters, both ML and BI approaches were used. Brownian motion model is defined with values of scaling parameters (λ, σ, κ) equal to 1, which is the default model in BayesTraits. We compared this model with the models calculated with the ML values of the parameters with LR tests. We also took into account models A (random walk) or B (directional) of change in trait evolution. Those parameters were estimated again with MCMC, using a uniform prior for the alpha parameter (with the minimum and the maximum value of each character for delimitating the range of the prior), and also for the beta parameter for the directional model. Internal nodes were reconstructed with the AddMRCA command using models estimated with MCMC. Continuous characters can only be reconstructed with MCMC.

Diversitree BiSSE.

Diversitree package in R (Fitzjohn, 2012) only offers the estimation of ASR by BiSSE (Binary State Speciation and Extinction) or Mk2 for discrete character. BiSSE computes the probability of a phylogenetic tree and the observed distribution of a binary character state within the tree, given a model of trait evolution, speciation and extinction (Maddison *et al.*, 2007). This method estimates six parameters: two speciation rates ($\lambda0$, $\lambda1$), two extinction rates ($\mu0$, $\mu1$) and two transition rates ($q10$, $q01$). We compared those estimated parameters with our tree and data with fixed models, restricting parameters to be equal: one with λ0= λ1, other with μ0= μ1, other with q10= q01; and four more possible combinations between all of them. The best fit model was selected by likelihood or the Akaike information criterion (AIC).

Phylogenetic signal

We used Picante package in R (Kembel *et al.*, 2010) to estimate the phylogenetic signal as K of Blomberg parameter (Blomberg *et al.*, 2003) of migratory behaviour.

Ordination of ASR analyses

We performed a cluster analysis using Euclidean distance with all results of ASR analyses made with discrete characters, in SPSS v23. For this, we gathered the values of each node, assembled a matrix for each analysis, and those were used as input for the analysis. The phylogenetic reconstructions made with the complete dataset and the partial dataset have different number of nodes; hence we pruned the nodes from the tree corresponding to the full dataset, in order to make both datasets comparable, using only the common and comparable nodes to perform the cluster analysis.

We performed a non-metric multidimensional scaling analysis (nMDS) to test if the grouping of these five subgroups was random or not, we permutated the original matrix 999 times and performed an ANOSIM R (Clarke, 1993) that supports a non-random grouping (R = 0.989, alpha = 0.1 %.). All ANOSIM paired tests between pairs results in R>0.9 and alpha between 0 and 1.8% suggesting that in none of the paired test the grouping is hazardous, supporting those five subgroups. We also performed a similarity profile (SIMPROF) test (Clarke *et al.*, 2008), that orders similarities from a group of a prior unstructured samples from smallest to largest, plotted against their rank, and compared this profile against the one expected under a simple null hypotheses of no meaningful structure within that group. This test also supported five subgroups with pi group values between 0.01 and 0.27 (p=0.01).

RESULTS

Sylvia phylogeny

We assembled the most complete phylogenetic hypothesis so far for the genus *Sylvia*, including all *Sylvia* species and many subspecies, as well as some taxa that until now were not considered to belong to this group. In this phylogenetic hypothesis, most nodes were fully supported with both ML and Bayesian inference (Fig. 1.1). In the full dataset, we recovered *Parophasma galinieri* and *Lioptilus nigricapillus* nested within *Sylvia* with high statistical support, and we treat them here as *Sylvia* species (see Taxonomic section). We recovered two main clades with high statistical support. The subgenus *Sylvia* (Fig. 1.1) includes a group of non-migratory sub-Saharan resident species (*S. dorhni, S. abyssinica, S. atriceps, S. galinieri, S. nigricapilla*, node 56) which is the sister group to the fully migratory *S. borin*. The relationships within this group are not fully resolved with this dataset, although they form a monophyletic group (ML probability of 90, and Bayesian probability of 1). The *S. atricapilla* complex also belongs to this clade, not showing much genetic variation. It includes the Macaronesian subspecies *S. a. gularis* and *S. a. heineken*, which are sedentary.

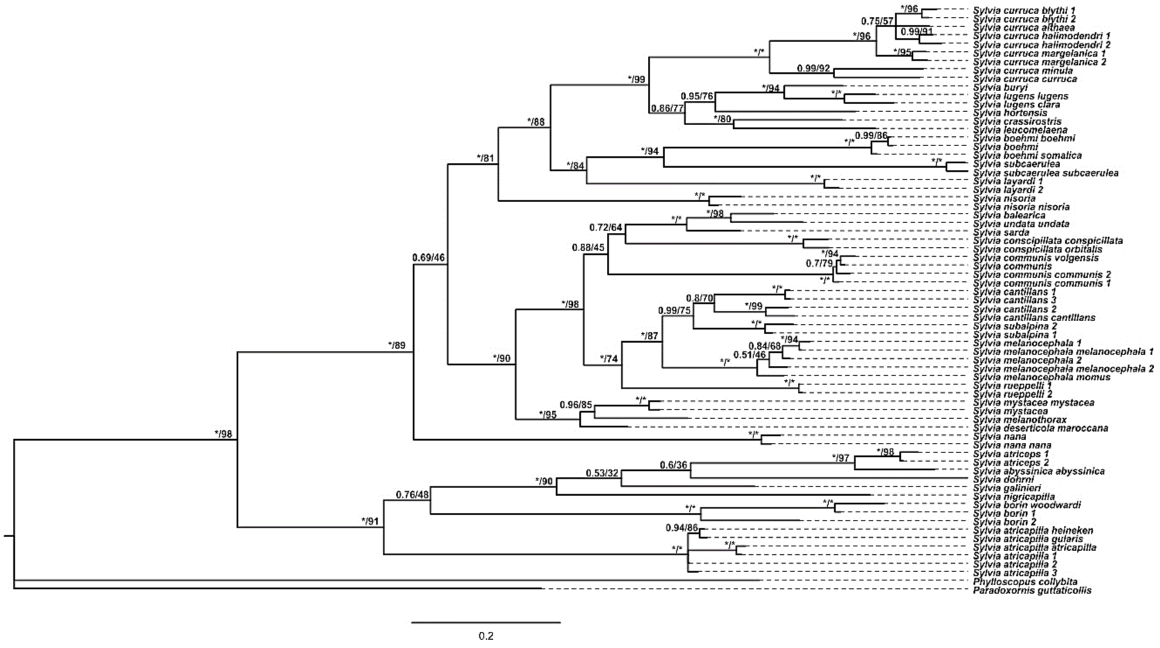


Figure 1.1. Complete phylogeny of the genus *Sylvia*. Support values correspond to posterior probability (Bayesian inference) and bootstrap (RAxML), Asterisk indicate Bayesian posterior probability of 1 and ML bootstrap support of 100%.

In the subgenus *Curruca*, we recovered three main groups, being *Sylvia nana* very divergent from the rest. Within the subgenus *Curruca*, most species are fully migratory with some exceptions. We recovered a non-migratory sub-Saharan African well-supported monophyletic group constituted by *S. boehmi, S. layardi and S. subcaerulea* (node 20 in Fig. 1.3). The fully migratory *S. hortensis* is the sister taxon to the sedentary Arabian Peninsula's *S. buryi* and the African *S. lugens* (node 10). The sedentary Arabian *S. leucomelaena* is the sister taxon to the fully migratory *S. crassirostris* (node 12). The partially migratory *Sylvia sarda* is the sister taxon to the mostly sedentary *S. undata* and the non-migratory island endemic *S. balearica* (node 24). Within the European migratory *S. conspicillata*, *S. c. orbitalis* is resident to the Macaronesia (node 26).

Divergence time estimation

Divergence time estimates from the BEAST analysis based on the complete dataset are shown in Figure 1.2. We recovered the origin of the genus *Sylvia* at the beginning of the Miocene (ca. 23 million years ago (MYA), 17-32 MYA), and the initial split between the two subgenera around 18 MYA (14-23 MYA). The divergences within the subgenus *Sylvia* are old, with a split of *S. atricapilla* complex around 14 MYA (11-18 MYA). Within *S. atricapilla*, the sedentary island subspecies *S. a. gularis* and *S. a. heineken* diverged from migratory populations in the Pleistocene, around 270000 YA (0.05-0.69 YA). Within *Sylvia borin*, the two lineages recovered are very old, splitting in the early Pliocene around 4 MYA, which is older than any split between recognized pairs of sister species within the *Sylvia* complex. The rest of African species of this clade diverged from *S. borin* around 13 MYA (10-17.0 MYA).

Within the subgenus *Curruca*, the basal splits between the three main clades recovered happened around 11-12 MYA. The non-migratory sub-Saharian African group constituted by *S. boehmi, S. layardi and S. subcaerulea* arose about 8.8 MYA (6.5-12.5 MYA). The split between the migratory *S. hortensis* and the sedentary (*S. buryi* + *S. lugens*) happened in the early Pliocene (4.6 MYA, 3-7 MYA). The split between the sedentary Arabian *S. leucomelaena* and the fully migratory *S. crassirostris* happened also in the early Pliocene (4 MYA, 2-6.5 MYA). The split between the migratory *S. conspicillata* and the clade constituted by *Sylvia sarda* + (*S. undata* + *S. balearica*) occurred at the beginning of the Pliocene (5.3 MYA, 3.5-7.5 MYA), with the split between *S. sarda* and the sedentary (*S. undata* + *S. balearica*) around 2.7 MYA (1.7-4.3 MYA). Within *S. conspicillata*, the

Macaronesian sedentary subspecies *S.c. orbitalis* diverged in the Pleistocene around 750000 YA (0.8-2 MYA). Within the *S. curruca* complex, the early split between (*S. c. curruca* + *S. c. minula*) and the rest of subspecies is rather old as it happened in the early Pliocene (4.5 MYA, 2.7-7 MYA), showing a within species genetic divergence older than any pair of recognized sister species within this genus.

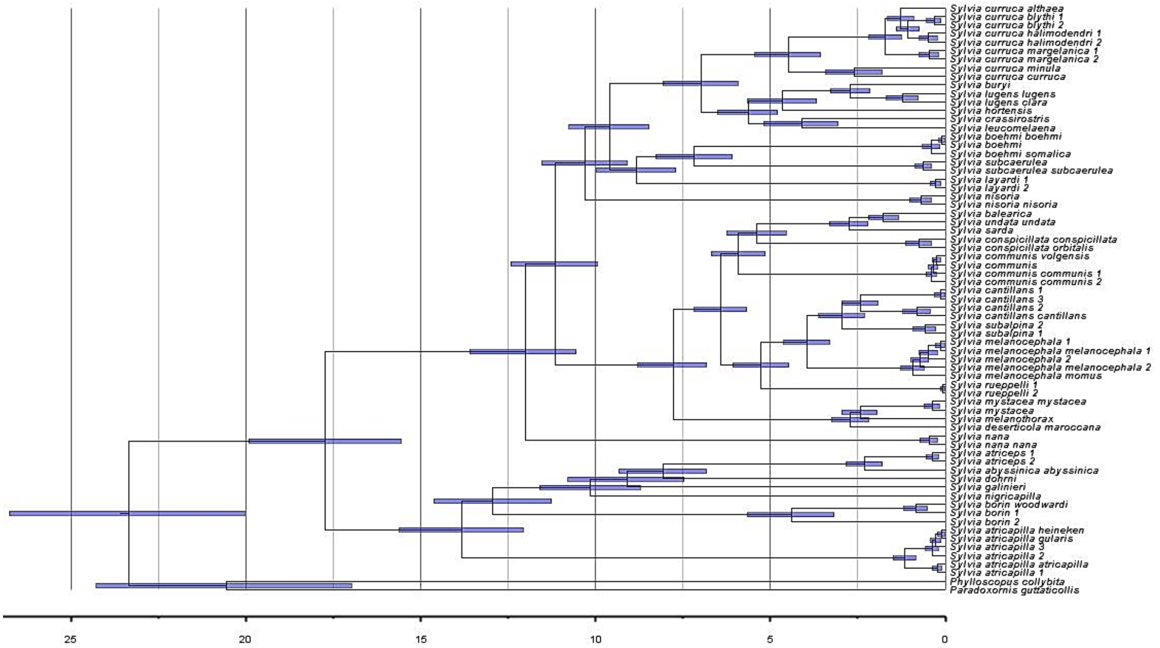


Figure 1.2. Chronogram using the full dataset for the genus *Sylvia*. Scale in millions of years.

ASR results using discrete character-coding

The phylogenetic signal of migration was statistically significant (Blomberg's K > 1, p-value < 0,001). We observed that using different combinations of dataset, branch length, statistical framework and software in ASRs, most often resulted in different results using discrete traits. Those differences between ASR analyses mainly affected a set of twenty one nodes, including the ones where migratory and non-migratory lineages coalesce as well as the MRCAs of non-migratory clades. The nodes within clades where all species are migratory showed no differences between analyses (e.g. Fig. 1.3), while there is a set of nodes showing variation between analyses (hereafter considered conflicting nodes).

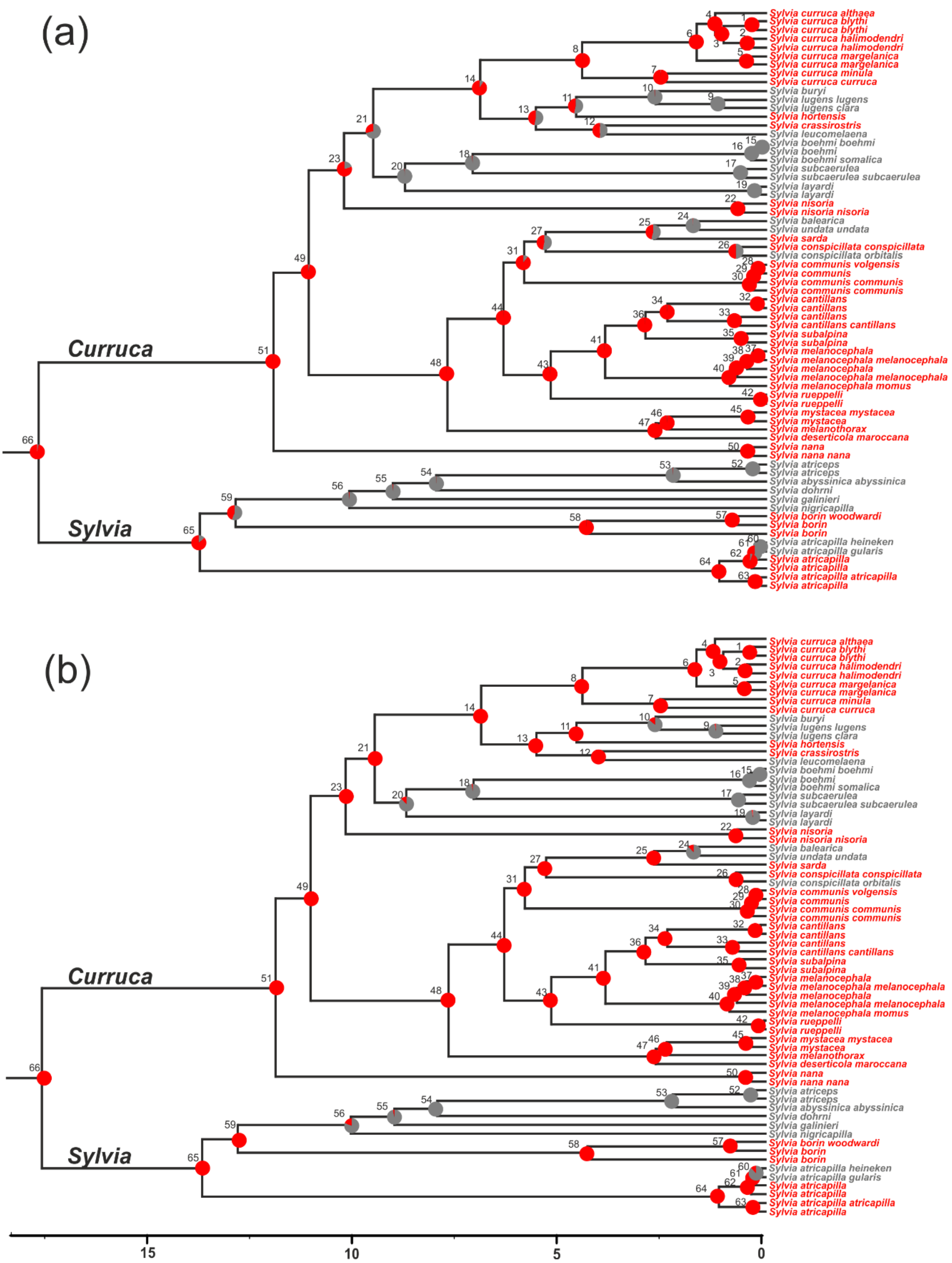


Figure 1.3. ASRs examples with uncertain (a) and certain (b) nodes in the evolution of migration in *Sylvia*. 1.3a tree shows a Mk1 analysis in BayesTraits, and 1.3b shows a Mk2 in Diversitree, both using a chronogram and the full dataset. Red and grey colours indicate migratory and sedentary states, respectively. Circles in nodes represent the percentage of the probability of each reconstructed character state. Scale is in Millions of Years Ago.

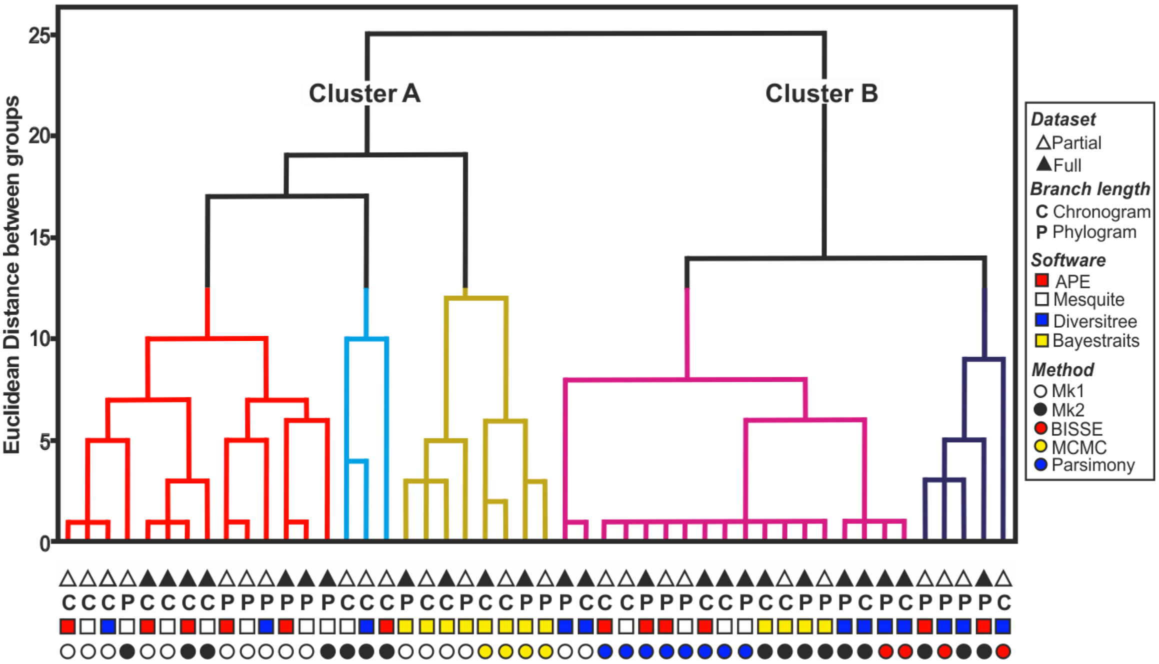


Figure 1.4. UPGMA clustering of all discrete ASR analyses based on Euclidean distances with all results of ASR made with discrete characters. Two main clusters are shown, and within them a non-metric multidimensional scaling analysis supports five subgroups (subgroup branch colours correspond to Figure 1.5). Pair-wise ANOSIM tests support non-random groupings (R >0.9, α= 0.1-1.8%), and a SIMPROF test supported the five subgroups (pi values between 0.01 y 0.27, p=0.01). The different combinations of elements for each analysis are shown at the bottom of the figure, where symbols and letters correspond to the ones in the legend. For example, the first branch corresponds to an analysis using the partial dataset, a chronogram, implemented in the software APE under a Mk1 model.

A cluster analysis based on all node values obtained in each combination of ASR analyses (N=48) recovers two main clusters (Fig. 1.4):25 analyses constitute a cluster where the probabilities of these conflicting nodes are around 50%, hence not supporting a migratory or sedentary value (Fig. 1.4, cluster A); while 23 analyses cluster together and are mainly characterized by showing very high probabilities in most or all these conflicting nodes (nearly or 100%) supporting a single character state (Fig. 1.4, cluster B).

Figure 1.3a and 1.3b provide examples of ASR analyses from both the cluster A and B respectively (see **Appendix Chapter 1**, Figures A1.1-A1.63 for the results of all the set of analyses). Stem nodes of non-migratory clades (nodes 10, 20, 24, 56), are recovered as fully sedentary in 1.3a, as well as with more than 70% of probability of being sedentary in 1.3b. However, the MRCAs of non-migratory clades are not resolved, with probabilities near 50% of being sedentary in 1.3a (nodes 11-13, 21, 25, 27, 59), while in 1.3b those nodes are recovered as fully migratory. Among island species and subspecies, the MRCA of *S. atricapilla heineken* and *S. a. gularis* is recovered as 100% sedentary in 13a and 80%

sedentary in 1.3b (node 60), but their sister lineage is 52% sedentary in 1a and fully migratory in 1.3b (node 61). Island subspecies *S. conspicillata orbitalis* MRCA, as well as the splits of *S. sarda* (*S. undata* + *S. balearica*) (nodes 25-26) are unresolved in 1.3a (recovered with 50% probability) but recovered as fully migratory in 1b. The root of these two examples is recovered as fully migratory, but some analyses the probability of the root node being sedentary can reach up to 48% (see **Appendix Chapter 1**, Figures A1.1-A1.63).

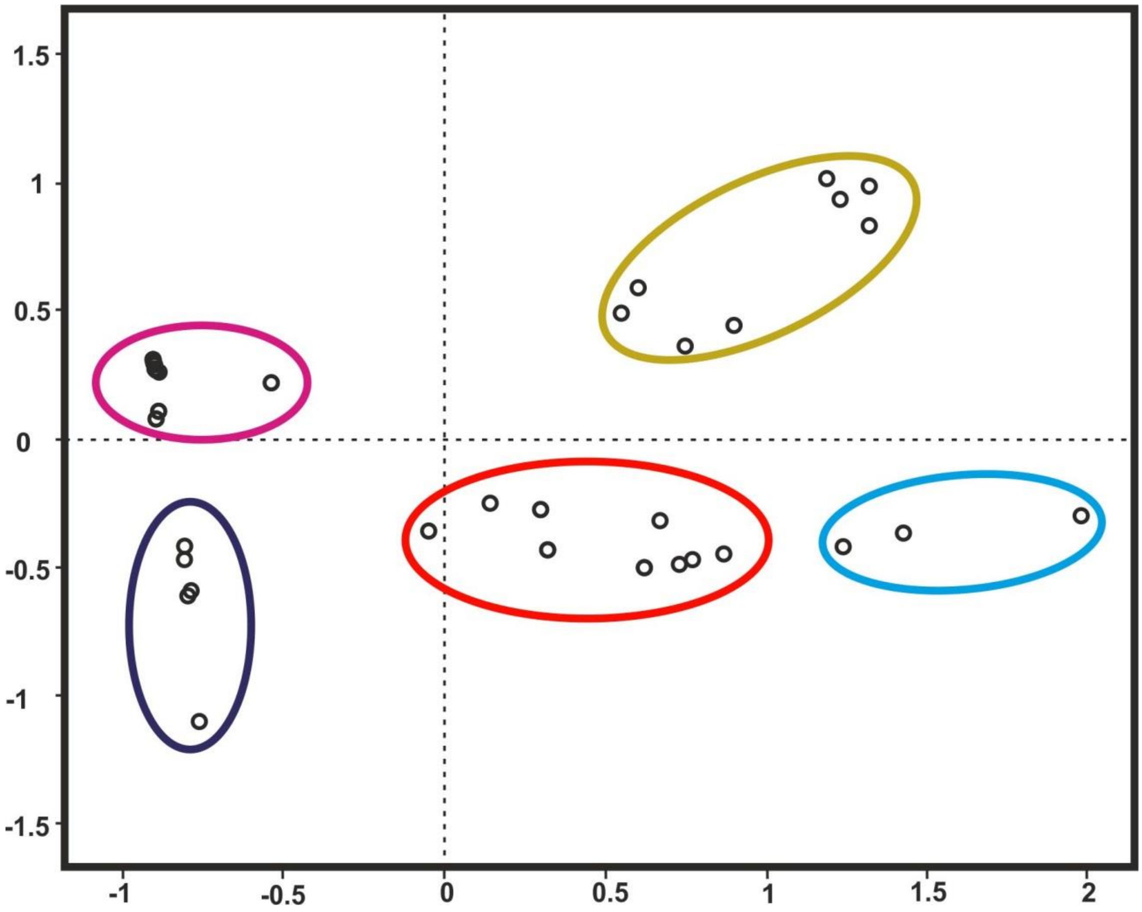
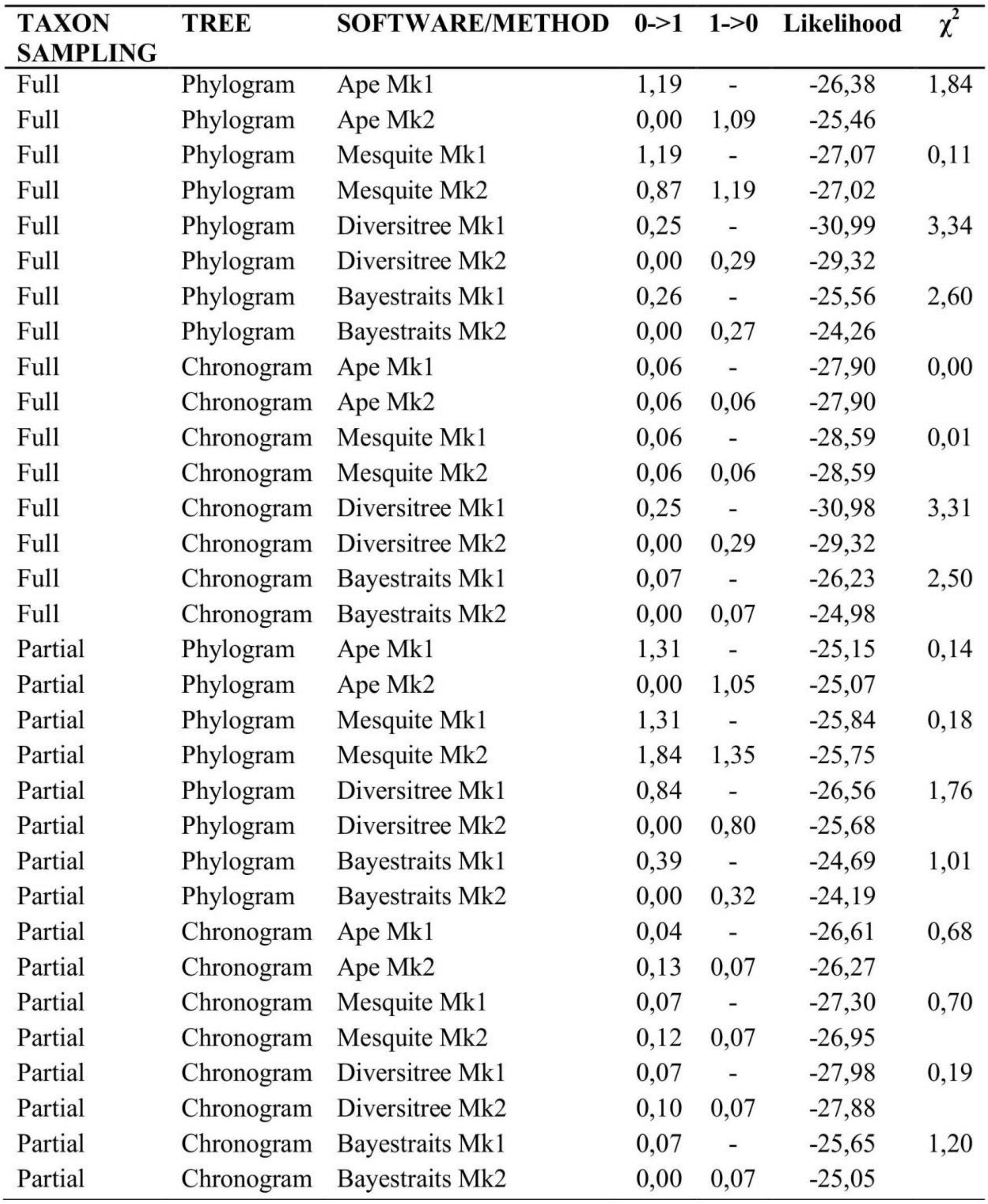


Figure 1.5. Non-metric multidimensional scaling analysis of cluster groups. Colours correspond to the five subgroups supported by the analysis.

To appraise differences between ASR results, we performed pairwise comparisons between analyses assessing their membership to similar or different five cluster subgroups supported within the main two clusters (Fig. 1.4 and 1.5). ANOSIM analyses supports a non-random grouping (R = 0.989, alpha = 0.1 %.). All ANOSIM paired tests between pairs results in R>0.9 and alpha between 0 and 1.8% suggesting that in none of the paired test the grouping is hazardous, supporting those five subgroups Also SIMPROF analysis supported five subgroups with pi group values between 0.01 and 0.27 (p=0.01) (Fig. 1.5).

Table 1.1: Likelihood values for MK1 and MK2 using the same taxon sampling, branch lengths, software and methods. χ2 calculated with 1 d.f.. 0>1 and 1>0 indicate the rate of change of character evolution from sedentariness (0) to migratoriness (1).



TAXON SAMPLING	TREE	SOFTWARE/METHOD	0->1	1->0	Likelihood	χ^2
Full	Phylogram	Ape Mk1	1,19	-	-26,38	1,84
Full	Phylogram	Ape Mk2	0,00	1,09	-25,46	
Full	Phylogram	Mesquite Mk1	1,19	-	-27,07	0,11
Full	Phylogram	Mesquite Mk2	0,87	1,19	-27,02	
Full	Phylogram	Diversitree Mk1	0,25	-	-30,99	3,34
Full	Phylogram	Diversitree Mk2	0,00	0,29	-29,32	
Full	Phylogram	Bayestraits Mk1	0,26	-	-25,56	2,60
Full	Phylogram	Bayestraits Mk2	0,00	0,27	-24,26	
Full	Chronogram	Ape Mk1	0,06	-	-27,90	0,00
Full	Chronogram	Ape Mk2	0,06	0,06	-27,90	
Full	Chronogram	Mesquite Mk1	0,06	-	-28,59	0,01
Full	Chronogram	Mesquite Mk2	0,06	0,06	-28,59	
Full	Chronogram	Diversitree Mk1	0,25	-	-30,98	3,31
Full	Chronogram	Diversitree Mk2	0,00	0,29	-29,32	
Full	Chronogram	Bayestraits Mk1	0,07	-	-26,23	2,50
Full	Chronogram	Bayestraits Mk2	0,00	0,07	-24,98	
Partial	Phylogram	Ape Mk1	1,31	-	-25,15	0,14
Partial	Phylogram	Ape Mk2	0,00	1,05	-25,07	
Partial	Phylogram	Mesquite Mk1	1,31	-	-25,84	0,18
Partial	Phylogram	Mesquite Mk2	1,84	1,35	-25,75	
Partial	Phylogram	Diversitree Mk1	0,84	-	-26,56	1,76
Partial	Phylogram	Diversitree Mk2	0,00	0,80	-25,68	
Partial	Phylogram	Bayestraits Mk1	0,39	-	-24,69	1,01
Partial	Phylogram	Bayestraits Mk2	0,00	0,32	-24,19	
Partial	Chronogram	Ape Mk1	0,04	-	-26,61	0,68
Partial	Chronogram	Ape Mk2	0,13	0,07	-26,27	
Partial	Chronogram	Mesquite Mk1	0,07	-	-27,30	0,70
Partial	Chronogram	Mesquite Mk2	0,12	0,07	-26,95	
Partial	Chronogram	Diversitree Mk1	0,07	-	-27,98	0,19
Partial	Chronogram	Diversitree Mk2	0,10	0,07	-27,88	
Partial	Chronogram	Bayestraits Mk1	0,07	-	-25,65	1,20
Partial	Chronogram	Bayestraits Mk2	0,00	0,07	-25,05	

We found that all ASR elements analysed have an impact on ASR results. When considering only taxon sampling, despite that the full topology includes only three more species previously belonging to other genera (*Parophasma* and *Lioptilus*), in 8 comparisons the partial dataset present uncertain nodes and the full dataset certain nodes or vice versa (Fig. 1.4). Only analyses performed with BayesTraits showed no differences between datasets (see **Appendix Chapter 1**, Figures A1.1-A1.63). Using a chronogram or a phylogram affects 4 pairwise comparisons, all using MK2 models and all software except BayesTraits. Surprisingly, being all elements equal and just changing the software package, results place them in different groups in 33 pairwise comparisons, raising the question about the different performance of software packages. Comparisons between statistical frameworks show a similar pattern, with 33 pairwise comparisons placing them into different groups, 20 of them involving MK1. In 7 pairwise comparisons using MK1 or MK2 models, being the rest of elements equal, results were classified in different cluster groups, despite that the MK1 and MK2 models had similar likelihoods (Table 1.1). In Mk2 models 10 to 16 analyses present a rate of change higher of loss of migration than the gain of it, 2 to 16 present the same probability of gain and loss, and the other 4 present higher rate of change from sedentary to migratory (Table 1.1). These results suggest that the loss of migratory behaviour is more probable than the gain in *Sylvia* genus.

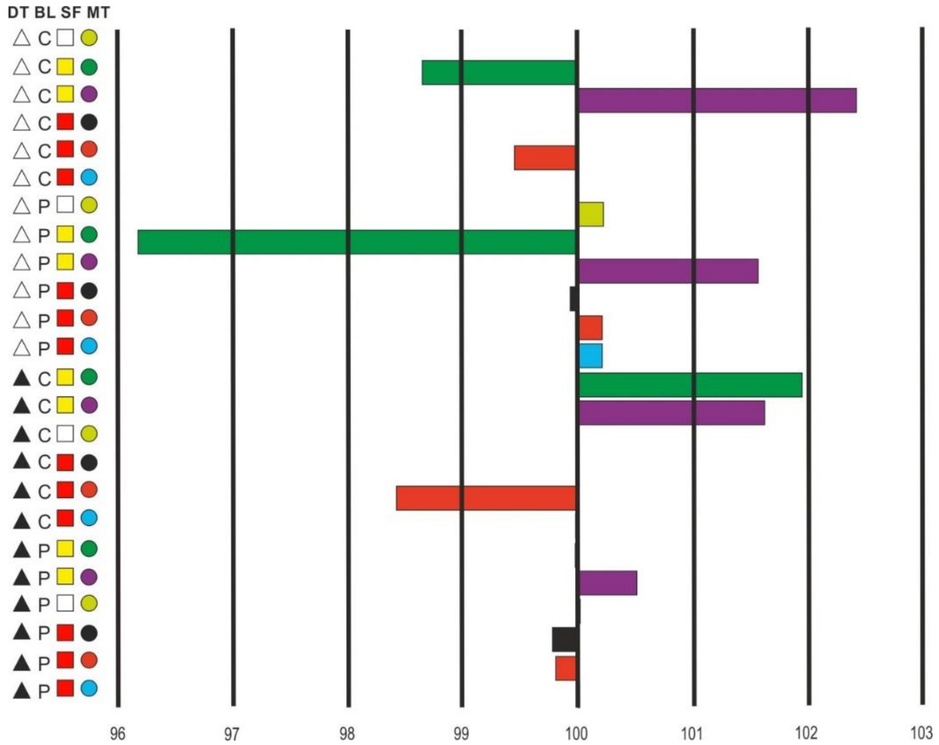


Figure 1.6. Histogram showing the median deviation of each continuous analysis from the median of all of them. Symbols mean: Triangles (dataset type): white=partial, black=full dataset; Letters (branch length): C=chronogram, B=phylogram; Squares (software): red=APE, white=Mesquite, yellow=Bayestraits; Circles (method): light green=Parsimony, dark green=MCMCb, purple=MCMCa, black=GLS, red=PIC, light blue=REML.

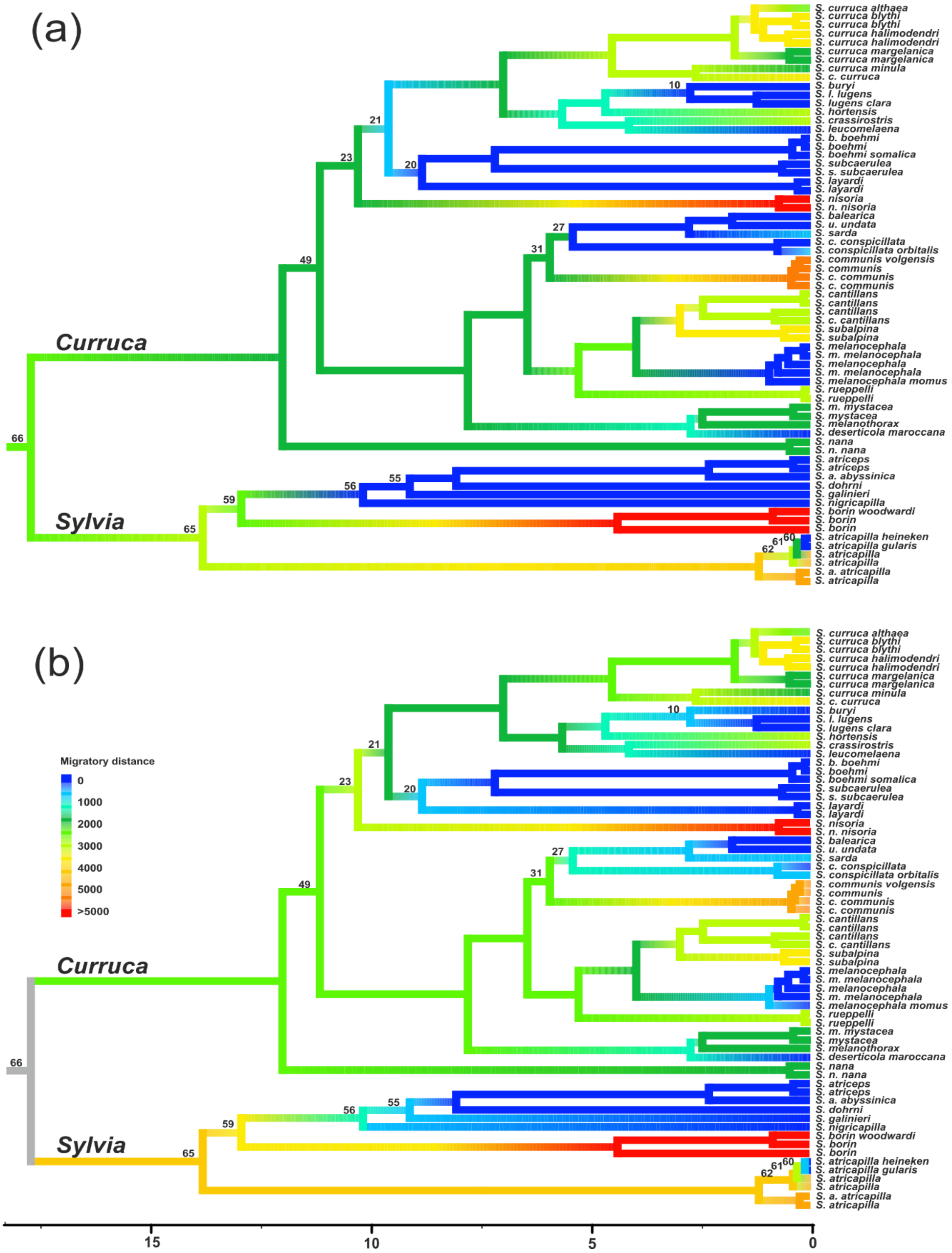


Figure 1.7. ASRs examples of migration as a continuous character in *Sylvia* warblers. (a) The Tree represents a PIC reconstruction, and (b) represents a MCMCa reconstruction, both using a chronogram and the full dataset. Branch colours represent median migratory distances, from zero km (dark blue) to higher than 5000 km (red). Grey colour represents a non-valid reconstruction in (b). Nodes showing important differences between analyses are numbered. Scale is in Millions of Years Ago. Subgenera *Sylvia* and *Curruca* are indicated in the trees (see the full set of analyses in **Appendix Chapter 1**, Figures A1.1-A1.63).

ASR results using continuous character-coding

For ASR analyses considering migration as a continuous trait (by using median migratory distances), the differences in reconstructed values involve the magnitude of change in migratory distance and include antagonistic results for some critical nodes. After discarding APE Parsimony and ML, as they reconstructed the same migratory distance for all nodes, we estimated the median value for each node across all analyses, and the overall deviation for each analysis. Most analyses lay within the confidence interval of the median, although four analyses tended to overestimate migratory distances compared to the median, and two tended to underestimate them (Fig. 1.6). All analyses that lay outside the confidence interval of the median are Bayesian analyses except one PIC analysis. However, considering individual nodes, reconstructed distances can vary from none or few to thousands of km for the same nodes (Fig. 1.7), challenging the interpretation of the evolution of this trait. When comparing analyses (e.g. Fig. 1.7), critical nodes to interpret how migration or sedentariness evolve show clear antagonistic results. For example, in Fig.1.7a nodes 10, 20, 55, 56 and 60 have a reconstructed migratory distance equal to zero, while in the analysis represented in Fig. 1.7b those nodes are recovered as fully migratory with median migratory distances of 591, 823, 552, 1228 and 864 km respectively, similar to extant fully migratory species. Those nodes correspond to the base of clades constituted by fully sedentary species, hence they are very relevant for evaluating if sedentariness arose from migratory ancestors or their ancestor was sedentary too, which also has important biogeographic implications.

DISCUSSION

We have found striking differences between ancestral state reconstruction approaches when reconstructing the evolution of *Sylvia* migratory behaviour. Overall we found a large degree of uncertainty when performing ASRs with discrete and continuous traits, to the point that, surprisingly, opposite hypotheses of trait evolution can be supported depending on the elements involved. Either individual elements alone or their combinations influence results, being more relevant the impact of the combinations of elements on the observed discrepancies. If we consider the two main clusters found in discrete analyses, cluster A could be interpreted as a gradual evolution pattern, where MRCAs show intermediate probabilities between sedentary or migratory states, although from a statistical perspective such nodes are unresolved. Cluster B, however supports sudden changes from migratory to sedentary states in most conflicting nodes with high recovered probabilities, and we never recovered the root node as fully sedentary but in most analyses as fully migratory instead, like in other bird genera (Winger *et al.*, 2012). Considering both, cluster B results suggest at least seven independent losses of migratory behaviour into sedentariness within *Sylvia*, and those may have happened in a very short evolutionary time. Partial migratory nodes are never recovered, and all island sedentary lineages arise from a fully migratory ancestor.

A modern view proposes migratory switching where migration can evolve multiple times in a lineage, and species can have migratory and non-migratory populations with thresholds on migratory activity, shaped by genetics and the environment, as it happens in the blackcap (Pulido *et al.*, 1996). There is biological evidence that the expression of migratory behaviour can change in less than ten generations in *Sylvia* (Berthold *et al.*, 1990; Berthold & Helbig, 1992; Pulido & Berthold, 2010), involving in some cases novel migratory routes (Plummer *et al.*, 2015), which fits better with our cluster B ASRs results (Fig. 1.3b). Those scenarios suggest that sedentariness on islands can happen fast in birds, which has been observed in *Turdus pilaris* after a single colonization event of Greenland in 1937 (Salomonsen, 1950) and in several *Sylvia* non-migratory island subspecies.

The antagonistic results found between some continuous analyses have major implications on how the evolution of migratory behaviour can be interpreted, having also an important biogeographic component. Node 10 on Fig. 1.7 corresponds to the MRCA of *Sylvia buryi* and *S. lugens*, both sedentary species from high mountains in the Arabian Peninsula and eastern Africa, respectively. Under the scenario shown in Fig. 1.7a, their MRCA was non-migratory, so this ancestral species should have been widely distributed from eastern Africa to the Arabian Peninsula until the last 3-5 million years, when Arabian and African populations split leading to speciation. This scenario is compatible with two key events in the region. From one side, Miocene climatic changes supposed an aridification of mid-latitude continental regions (Flower & Kennett, 1994), contributing to the expansion of the Sahara and Arabian deserts, and restricting many species to high elevations where these two warblers occur. From the other side, the end of post-Miocene Red Sea land bridges around 6 Ma across the southern Red Sea (Fernandes *et al.*, 2006; Orszag-Sperber *et al.*, 2001) would have supposed the interruption of gene flow and subsequent isolation between Arabian and African populations. Under the alternative scenario shown in Fig. 1.7b, the MRCA was fully migratory and sedentariness arose more recently from this migratory ancestor. Under this scenario a hypothesis is that migration between mountainous areas from Africa and Arabia happened until it disappeared in the Pliocene – Quaternary.

In the case of node 20 (Fig. 1.7), it represents the MRCA of three sub-Saharan sedentary species: *Sylvia boehmi* + *S. subcaerulea* and *S. layardi* that diverged in the Miocene (ca. 9 Ma). Under a non-migratory scenario (Fig. 1.7a), the ancestor could have been widespread across Africa, and the Miocene climatic changes (Flower & Kennett, 1994) may have led to split into different species, may be involving mountain regions, with a secondary contact in more recent times. The alternative scenario of a fully migratory ancestor (Fig. 1.7b) would have involved migration within Africa from and to unknown areas, with subsequent sedentariness, an impossible to test hypothesis. A similar scenario can be applied to nodes 55 and 56 in figure 1.7, which involve a clade of species from sub-Saharan Africa, clade that originated around 10 Ma and likely exposed to the same biogeographic events than node 20. Node 60 represents a much more recent biogeographic event, involving the recent colonization of oceanic islands by *Sylvia atricapilla heineken* and *S. a. gularis* subspecies, and again two antagonistic scenarios were recovered for their MRCA. In some analyses the MRCA was sedentary (Fig. 1.7a), while in others was fully migratory (Fig. 1.7b). *S. a. heineken* occurs in Madeira, Canary Islands, southern Iberian Peninsula and north-western Africa, while *S. a. gularis* is known from Cabo Verde and Azores islands. Considering their young age and current distribution, the most likely scenario is a fully migratory ancestor that became sedentary on islands, discarding a non-migratory MRCA which could not have colonized the islands. If we consider this recent node 60, the scenario shown in Figure 1.7b is the most likely, although the biogeographic hypotheses presented above for the scenario 1.7a are plausible and cannot totally be ruled out.

Our results suggest that bird species, or in particularly *Sylvia* warblers, lose migratory behaviour more easily than gaining it. All *Sylvia* sedentary species occur in tropical areas or in islands, with the only exception of *Sylvia undata* that remains in Mediterranean areas as well as some populations of *Sylvia atricapilla* (Shirihai *et al.*, 2010). The high productivity available in the tropics throughout the year could explain the loss of migratory behaviour in some species, remaining in their wintering ranges all the year. However, resources and productivity in the islands (as most of the species remain in temperate or subtropical island) do not differed strongly with the yearly dynamic found in mainland at the same latitude. Nevertheless, island species lose totally the ability of migrate, suggesting that islands could act as geographic tramps that it is difficult to leave. The alternative would be that the colonization of those new islands become the opportunity to avoid competition (Cox, 1968), as long as there is a minimum of resources available all year round.

The high degree of uncertainty observed here with ASRs using discrete or continuous traits surpass previous expectations. Most traits of interest in evolutionary ecology, like migratory behaviour, evolve rapidly relative to speciation rate and with high levels of convergence that preclude being certain about the accuracy of the reconstruction (Frumhoff & Reeve, 1994). Hence without a clear biological or fossil evidence to support ASRs, results need to be interpreted with caution, and in many cases would not be possible to discard opposite hypotheses. Our results coding migration as a discrete character are in agreement with recent theories of rapid evolution of migration that consider it as a labile character, which it has implications on how reliable reconstructions are for old nodes with fast evolving characters. Even if cluster B results are correct, differences between ASR approaches are evident and raise a warning of using a single method or approach for any ancestral state reconstruction that could be simply biased by the method. Pruning datasets and repeating analyses has been proposed to test the repeatability of an ASR method (Watts *et al.*, 2016), and a consensus of results of ASRs suggested when there are discrepancies obtained by different methods (Sachs *et al.*, 2014). However, we discourage these considering our observed antagonistic results. Several disturbing issues, as getting different results using the same elements but implemented in different software packages, or the impact of tree topology, method and branch lengths, discourage the use of single method approaches for ASR, which is the common practice in most published works from several fields. Indeed, the lack of the phylogenetic coverage can affect broadly ASRs, as discrepancies have been shown in our case study when including two new sedentary taxa in the phylogeny. To overcome these problems, we propose avoiding relying on single analyses and instead performing multiple ASRs, and whenever possible to incorporate independent biological or fossil evidence (Albert *et al.*, 2009) about the evolution of the traits of interest.

II Taxonomic remarks on *Sylvia* warblers.

We recovered two main clades within *Sylvia* as in previous works (Voelker & Light, 2011). One is constituted by the Western Palearctic *Sylvia atricapilla*, *Sylvia borin* and several African species. Within this clade, Voelker *et al.* (2009) recovered the former *Horizorhinus dohrni* (Dohrn's Thrush-Babbler) and *Pseudoalcippe abyssinica* (African Hill Babbler) nested within *Sylvia*. This relationship was recovered again by Voelker and Light (2011) and the subsequent taxonomic change to *Sylvia dohrni* and *Sylvia abyssinica* is well accepted (Dickinson & Christidis, 2014). We included those species, as well as three more. *Pseudoalcippe atriceps* is the sister taxon to *Sylvia abyssinica* and should be considered a *Sylvia* warbler as well. We also included for the first time the monotypic genera *Parophasma* and *Lioptilus,* represented by *Parophasma galinieri* and *Lioptilus nigricapillus*, together with all *Sylvia* species. Our results indicate that they are deeply nested within this clade with high statistical support. This implies that they belong to the genus *Sylvia* as well, and they should be named *Sylvia galinieri* and *Sylvia nigricapilla*.

The other main clade harbours the rest of species currently known for the genus *Sylvia*. These two main clades have recently been considered as separate genera by Dickinson & Christidis (2014), who kept the genus *Sylvia* for the first clade and suggested the generic name *Curruca* for the second one. According to our phylogeny, as *S. atricapilla* is the sister taxon to (*S. borin* + the rest of taxa), it would suppose a high taxonomic cost to keep the former genera *Parophasma, Lioptilus or Pseudoalcippe,* compared to sinking them all to *Sylvia*. Raising the genus *Curruca* is not informed by integrative taxonomic evidence (morphology + DNA + other characters), just by a phylogenetic split at the base of *Sylvia*, hence raising this genus will not suppose a significant increase in taxonomic information. Both clades are always recovered as monophyletic in molecular studies and share several morphological synapomorphies; accordingly, we acknowledge this split but suggest that *Sylvia* and *Curruca* can be used as subgenera instead, as it retains more phylogenetic information than does recognizing more genera. A previous work (Shirihai *et al.*, 2010) proposed six subgenera within *Sylvia* warblers, one for each main branch in their phylogenetic tree. Naming every basal phylogenetic split as subgenera contributes to taxonomic inflation, and it would imply creating more subgenera for more branches if we consider *Parophasma, Lioptilus, Pseudoalcippe* or *Horizorhinus*, which were not included in their phylogeny. Hence, we suggest a classification with two subgenera instead.

Within the subgenus *Sylvia*, it is interesting that we recovered a deep divergence between two lineages of the Garden warbler (*Sylvia borin*). The divergence between them is larger than between splits of most sister species pairs in the whole genus, suggesting that there is a cryptic species of *Sylvia* which was never detected before. Two subspecies of Garden warbler are currently recognized: *S. b. borin* and *S. b. woodwardi*, and it is likely that *woodwardi* deserves full specific status. Ongoing taxonomic work will help to elucidate this issue. Within the subgenus *Curruca*, most relationships are recovered as in previous phylogenies.

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Chapter 2:

Productivity as the main factor correlating with migratory behaviour in the evolutionary history of warblers

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Productivity as the main factor correlating with migratory behaviour in the evolutionary history of warblers

Abstract:

The evolution of migration in birds and its causes are still subject of debate. Recent studies tracking current bird migration have identified peaks in net primary productivity (NPP) as a main driver of bird migratory behaviour. However, it is unclear which variables may have played a major role in the evolution of bird migration at deeper phylogenetic levels. Here, we used phylogenetic comparative methods to assess whether the evolutionary patterns of migratory distances, as a proxy for migratory behaviour, are correlated with several biometric, climatic and productivity variables in a phylogenetic context, using *Sylvia* warblers as a case study. Our results recover NPP in the breeding range and during the breeding season as the variable with stronger positive correlation with migratory distances, being always included in the best models considering all potential variables. Several climatic variables show a correlation with the evolution of migration, but those are also tightly correlated with NPP. Among morphological variables, migratory lineages tend to have longer wings than sedentary ones. Although NPP has been identified as a driver of migratory behaviour in current species, in a phylogenetic scale it is not possible to disentangle if it was a main driver in the evolution of bird migratory behaviour or a consequence of it, yet migration and NPP seem to be tightly related today and along the long evolutionary history of these passerines.

Keywords: bird migration, evolution, Net Primary Productivity, *Sylvia*, warblers.

INTRODUCTION

Bird migration is a common phenomenon that typically entails long distance movements between breeding and wintering grounds. Among migratory birds there are species with the longest migratory distances known in the animal kingdom, like many seabirds (Egevang *et al.*, 2010). Migratory behaviour has independently evolved multiple times both between and within taxonomic groups (Zink, 2011), and even different migratory strategies can be observed between populations of the same species (e.g. Pérez-Tris & Tellería, 2002; Pulido & Berthold, 2010).

How migratory behaviour evolves is still not fully understood, as well as the potential drivers and historical factors that may be involved at different evolutionary scales. In a phylogenetic framework, there are examples of fully migratory as well as non-migratory lineages within clades, species or even populations (Milá *et al.*, 2008). A partial migratory condition has been proposed as the ancestral state of fully sedentary or migratory lineages (Berthold *et al.*, 1992), although recent studies suggest that switches from a state to another can be fast in evolutionary time, without going through an intermediate step (Pulido & Berthold, 2010). This second scenario would imply an early origin and conservation of the genetic architecture related to migratory behaviour in birds (Berthold *et al.*, 1992; Helbig, 2003; Salewski & Bruderer, 2007), which can be differentially expressed as a response to changes in environmental conditions (Plummer *et al.*, 2015). A reconstruction of the ancestral Last Glacial Maximum ranges of 56 species of North American birds suggest switches between sedentary and migratory states during glaciations (Zink & Gardner, 2017), but it is unclear if this pattern holds true for other groups and other regions that harbour migratory species and that were not affected by ice sheets. Such uncertainty raises a complex scenario for the evolution of migratory behaviour, since it is not clear if the same drivers act at different temporal scales, regions and in different clades.

Besides the environment, other ecological, morphological or physiological factors have been proposed as potential drivers of bird migratory behaviour. Some authors consider migration as a mechanism to reach a better body condition that promotes survival and reproduction (Berthold, 2001), linked to peaks in productivity in northern latitude breeding grounds. Other hypotheses involve diminishing parasite loads (Piersma, 1997) or predation risks (McKinnon *et al.*, 2010), or avoiding competition in southern latitudes (Cox, 1968). In parallel to such external factors, migration usually involves phenotypic changes, mainly related to differences in wing length between migratory and non-migratory populations (Pérez-Tris & Tellería, 2003), physiological adjustments for the energetic requirements of such journeys (Piersma *et al.*, 1999), and behavioural changes. However, only a few studies tested if these morphological (Voelker, 2001) and physiological or niche traits (Böhning-Gaese *et al.*, 2003; Laube *et al.*, 2015) are correlated with migratory behaviour in a phylogenetic context and there are no studies involving all variables together to test the comparative relevance of each one in bird migration.

Here, we want to test the hypothesis that the temporal availability of resources (i.e. peaks in NPP) is a key factor related to species' migration. Although productivity has been identified as a main factor driving migration in studies tracking current bird migration (Alerstam & Lindström, 1990; La Sorte *et al.*, 2014; Lindström, 2003; Thorup *et al.*, 2017), it is unclear if it was also a driver of migratory behaviour in the evolutionary history of these birds or a consequence of it.

We also explored several other factors that may be correlated with migratory behaviour in birds, either alone or by interaction, focusing on several ecological, climatic and phenotypic traits. We used *Sylvia* warblers as a case study, as this genus has been a model system for studies on different aspects of migration (Berthold, 2001; Laube *et al.*, 2015; Voelker & Light, 2011). It comprises closely related sedentary and migratory lineages, both at the species, subspecies and population levels, showing different migratory strategies. This genus is also widely distributed including the Palaearctic, Afro-Palaearctic, African, and Mediterranean regions, having colonized many islands. *Sylvia* is a relatively old genus (Voelker & Light, 2011), with species that mostly occur below the major extent of the ice sheets during the last glacial maximum. Hence, we can expect that the glaciations had less effect than in other bird clades occurring far north, and differences in migratory strategies between species may predate the Pleistocene as species are older than that period (Voelker & Light, 2011). There are no fossil or other evidence of the potential effects that the northern hemisphere glaciations may have caused in their migratory behaviour, although part of the observed intraspecific variation may be linked to postglacial expansions.

MATERIALS AND METHODS

Phylogenetic data

We used the most complete phylogeny of *Sylvia* warblers available so far (phylogeny from the **Chapter 1**), that includes an updated taxonomy of *Sylvia* with species from genera not previously considered *Sylvia* (eg. *Parophasma* and *Lioptilus*), as well as subspecies not included in previous works.

Environmental data

We obtained macroclimatic data for every species by interpolating climatic maps with species distribution maps (BirdLife International and NatureServe, 2011). As Birdlife distribution maps provide raw distribution ranges, we refined all species maps by overlapping them with layers of suitable habitats for each species (Birdlife International, 2012), pruning all unsuitable areas and increasing their accuracy (Ocampo-Peñuela *et al.*, 2016) (See **General Methods**, Section "Correction of bird distribution maps and data extraction"). We explored GBIF and eBIRD data for determining birds' distribution, but the coverage was uneven, with most wintering areas in Africa being poorly covered, so we discarded them and worked with BirdLife data. We used the landcover layer from GLOBCOVER (Bontemps *et al.*, 2011), altitude from WordClim 1.4. (Hijmans *et al.*, 2005) and water layers from the Global Land Cover Facility (GLCF) (Carroll *et al.*, 2009). The water and landcover layers were re-scaled to the same grid cell size as the altitudinal layer, and re-classified to represent the Birdlife habitat categories available for all species (Birdlife International, 2012), using ArcGis 10 (ESRI, 2011). All resulting maps have a resolution of 30 arc-seconds (~1km), both for breeding and wintering regions per species. From the corrected occurrence bird maps, we randomly generated 10.000 points each from the breeding and wintering ranges, using the ArcGIS GME package (Beyer, 2012). We interpolated those localities with current climate layers (~1950-2000) from WordClim 1.4. (Hijmans *et al.*, 2005), and NPP data (http://neo.sci.gsfc.nasa.gov/view.php?datasetId=MOD17A2_E_PSN), and extracted those values. We included total and mean precipitation; and mean, maximum and minimum temperature. To account for the climatic conditions during the breeding period in the breeding areas and the conditions during the wintering period and regions, we generated separated spatio-temporal climatic datasets. New climatic layers were constructed for each species considering the months they spend in each territory, calculating the mean temperatures during the breeding and non-breeding months, and the accumulated and mean precipitation. To do that, we revised the literature for each species to determine the months they spend in each area (Cramp & Brooks, 1992; Urban *et al.*, 1997).We also calculated other climatic variables like the differences between breeding and wintering temperature and precipitation, and the temperature range. We here consider the temperature range as the difference between the minimum temperature in the breeding area during the breeding period, and the maximum temperature in the wintering area during the non-breeding period (See **General Methods**, Section "Correction of bird distribution maps and data extraction").

We used the mean monthly NASA's global Net Primary Productivity data layers for the years 2001 to 2003, as other available years have a significant amount of missing NPP data for most tropical areas, mainly caused by clouds. We calculated the positive or negative balance of NPP in each season compared to the global NPP (Thorup *et al.*, 2017). By doing this, we can assess NPP peaks above or below the yearly NPP mean. Hence, we divided monthly NPP by the yearly NPP mean, and then calculated the mean of the breeding and/or non-breeding months. We also calculated the number of months with positive balance of NPP in each territory (See **General Methods**, Section "Correction of bird distribution maps and data extraction").

Median migratory distances were calculated as in **Chapter 1** and **General Methods**, Section "Correction of bird distribution maps and data extraction". We calculated also the maximum and minimum migratory distances as the difference between the maximum latitude of the breeding range and the minimum latitude of the wintering range, and the difference between the minimum latitude of the breeding range and the maximum latitude of the wintering range respectively and then converted to kilometres.

Phenotypic data

Biometric data for *Sylvia* warblers were compiled from primary literature using the mean of all measurements found (mainly Birdlife International, 2012; Cramp & Brooks, 1992; Dunning, 2008; Urban *et al.*, 1997). For each taxa we gathered ten variables, including maximum and minimum of body mass, wing length, tail length, total length and wing-load calculated as: Mass (g)/ 2* Wing length (cm)*Tail length (cm). The full phenotypic dataset is available as supplementary material, **Appendix Chapter 2**, Table A2.1.

Ancestral state reconstructions (ASRs)

ASRs were performed using ML (REML and PIC methods) in the Ape package for R (Paradis *et al.*, 2004), and BI approaches in the BayesTraits software (Pagel & Meade, 2007). We chose these three methods to explore if there are differences in the reconstructions using different approaches (see **Chapter 1**). In BayesTraits, we calculated the values of scaling parameters (lambda (λ), delta (σ) and kappa (κ)) and compared them with the default Brownian model (values =1) and with values equal to 0. We also accounted for random walk and directional models of trait evolution change. Internal nodes were reconstructed with AddMRCA command in BayesTraits using models estimated with MCMC. All these parameter options were estimated using both ML and MCMC. We estimated the phylogenetic signal for all variables with the Pagel´s lambda (λ) parameter (Pagel, 1999).

Phylogenetic Independent Contrasts (PIC) and PGLS

PIC analyses were calculated with the APE R package (Paradis *et al.*, 2004), relating median, maximum and minimum migratory distances with all climatic, biometric and productivity variables. To analyse the total effect of all variables in the migratory distance, we calculated Phylogenetic Generalized Least Squares (PGLS) models in the Caper R package (Orme, 2013). Variance Inflation Factor (VIF) was calculated for all the variables to detect the multicollinearity between them, and variables were reduced to six having values of VIF<5. Those six variables were used to calculate models, considering as a dependent variable the median, minimum or maximum migratory distances. PGLS analyses were performed using the calculated values of λ, σ, κ parameters with more likelihood for each model. For exploring the best model for each dependent variable, we used the AICc criterion (Hurvich & Tsai, 1989).

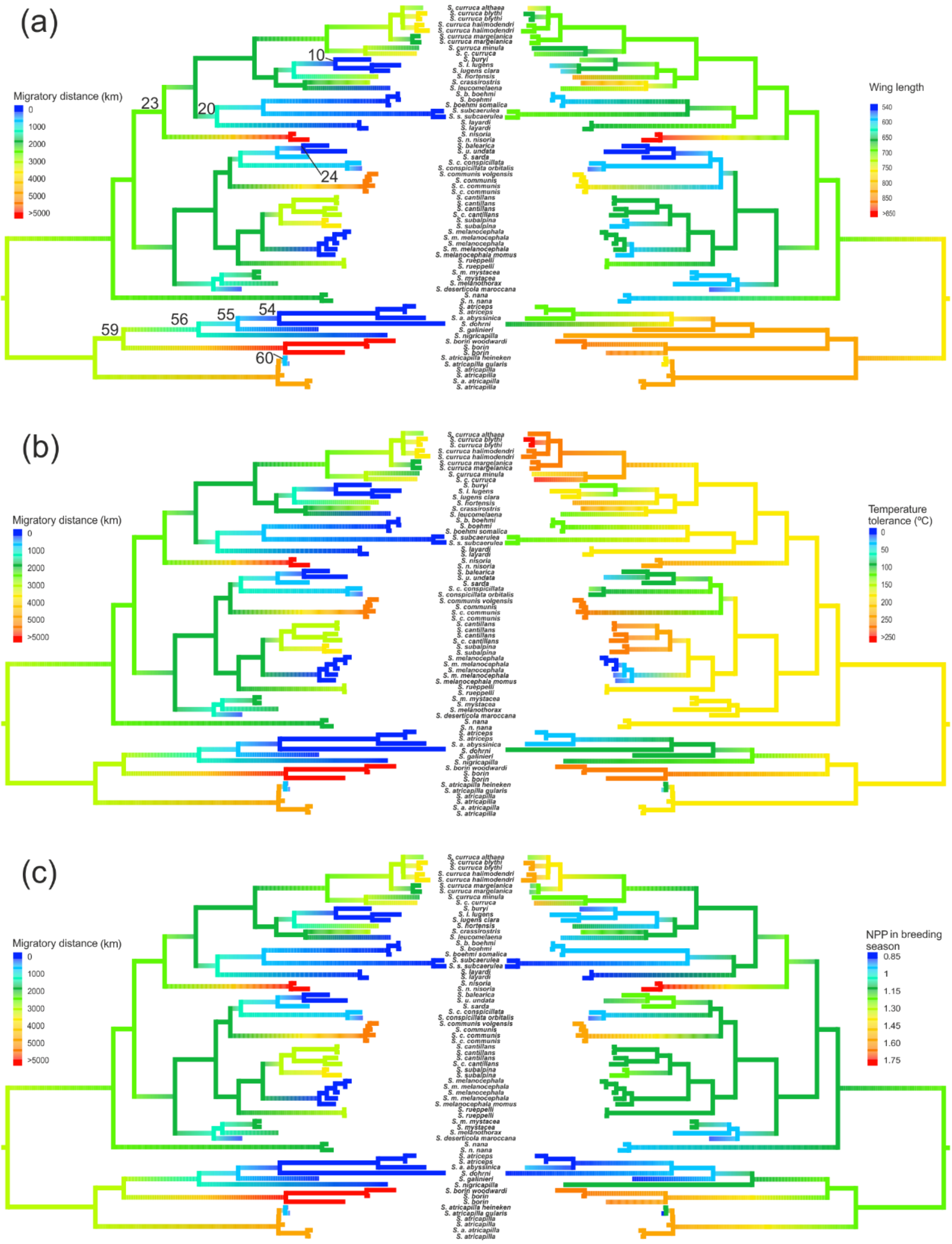

Figure 2.1. REML ancestral state reconstruction of median migratory distance (on the left of (a), (b), (c)) and the REML ancestral state reconstruction of maximum wing length (a), range of temperature (b) and NPP in breeding season (c). Critical nodes showing large differences in reconstructed values and supporting opposite states of bird migration (see text) are numbered in the reconstruction of median migratory distance in (a).

RESULTS

Ancestral State Reconstructions

The models with higher likelihood in MCMC analyses are the ones with the parameters λ, σ, κ estimated. All variables, besides the mean temperature in the breeding range and minimum wing length, recover the MCMCb (directional) as the model with the highest likelihood. However, there is no statistical difference between directional and random walk models in any variables. Hence, we used the directional models to perform the reconstructions. All models show a lambda near 1 suggesting a strong phylogenetic signal.

There are disagreements in the results obtained among ASR methods, as REML, PIC and MCMC reconstructions reconstruct differences of several orders of magnitude in migratory distances for some critical nodes. We consider here critical nodes as the ones reconstructed with a value of 0 km with one method (no migration) and more than 500 km with another (fully migratory; e.g. nodes 10, 20, 55, 56 and 60, highlighted in Fig. 2.1a). The differences in migratory distances between MCMCb and REML reconstructions are narrower than between PIC and the other two reconstructions for these critical nodes. If we consider nodes 20 and 56, they are reconstructed in REML as 1282 and 1279 km. MCMCb reconstructed the same nodes as 801 and 989 km; PIC instead, reconstructed those nodes as 0 km, implying no migration. In the reconstructions of maximum migratory distances, the critical nodes include also nodes 24 and 54, see Fig. 2.1a), showing larger differences in kilometres than with the median migratory distance reconstructions. For example, the node 20 was reconstructed as 0 km with PIC and more than 2000 km with REML. Nodes 24 and 54 are also reconstructed as 0 km with PIC reconstructions, while with REML were 549 km and 591 km, and with MCMCb were 527 and 123 km. When reconstructing the minimum migratory distance, the differences are reduced, recovering only two nodes with differences higher than 500 km (nodes 59 and 23) between PIC and REML-MCMCb.

We recover the ancestral state of the root as migratory in all analyses. The most basal nodes show that ancestral *Sylvia* warblers were migratory with a median migratory distance of 3000 km (Fig. 2.1), with many events of sedentariness. The origin of sedentariness is recovered in the most recent ancestors of tropical species (*S. galinieri*, *S. dohrni*, *S. nigricapilla*, *S. abyssinica* and *S. atriceps*), or insular European species (*S.*

undata, *S. balearica*), and insular subspecies (*S. atricapilla heineken* and *S. atricapilla gularis*).

Table 2.1. Results of Phylogenetic Independent Contrasts between median, maximum (max) and minimum (min) migratory distances and the phenotypic, productivity and climatic variables. In bold the significant correlations with p-values <0.01

	Median distance		**Max distance**		**Min distance**	
	R^2	**p-value**	**R^2**	**p-value**	**R^2**	**p-value**
Minimum mass (Min mass)	0.01	0.45	0.01	0.36	0.02	0.21
Maximum mass (Max mass)	0.05	0.08	0.04	0.11	**0.12**	**0.00**
Minimum wing length (Min wing)	0.00	0.62	0.03	0.15	0.03	0.18
Maximum wing length (Max wing)	**0.37**	**0.00**	**0.32**	**0.00**	**0.24**	**0.00**
Minimum tail length (Min tail)	0.00	0.75	0.00	0.61	0.00	0.99
Maxumum tail length (Max tail)	0.00	0.87	0.00	0.98	0.01	0.34
Minimum wing load (Min w-load)	0.00	0.88	0.00	0.81	**0.13**	**0.00**
Maximum wing load (Max w-load)	0.04	0.13	0.04	0.11	0.00	0.75
Minimum total length (Min total)	0.00	0.82	0.00	0.74	0.04	0.10
Maximum total length (Max total)	0.00	0.83	0.00	0.80	0.02	0.28
NPP breeding (NPPb)	**0.74**	**0.00**	**0.72**	**0.00**	0.05	0.07
NPP wintering (NPPw)	0.08	0.02	0.09	0.02	0.00	0.95
Nº months >1 NPP breeding (nNNPb)	**0.50**	**0.00**	**0.57**	**0.00**	0.07	0.03
Nº months >1 NPP wintering (nNPPw)	0.00	0.94	0.00	0.60	0.00	0.73
Accumulate precipitation breeding (APb)	**0.22**	**0.00**	**0.25**	**0.00**	0.00	0.60
Mean precipitation breeding (MeanPb)	**0.52**	**0.00**	**0.58**	**0.00**	0.00	0.91
Mean temperature breeding (MeanTb)	**0.38**	**0.00**	**0.36**	**0.00**	0.01	0.52
Maximum temperature breeding (MaxTb)	**0.12**	**0.00**	0.08	0.02	0.04	0.13
Minimum temperature breeding (MinTb)	**0.65**	**0.00**	**0.69**	**0.00**	0.00	0.88
Accumulate precipitation wintering (APw)	0.02	0.27	0.02	0.22	0.01	0.57
Mean precipitation wintering (MeanPw)	0.00	0.92	**0.58**	**0.00**	0.00	0.70
Mean temperature wintering (MeanTw)	0.03	0.14	0.00	0.67	0.07	0.03
Maximum temperature wintering (MaxTw)	**0.52**	**0.00**	**0.37**	**0.00**	**0.11**	**0.01**
Minimum temperature wintering (MinTw)	0.01	0.47	0.01	0.53	0.10	0.01
Difference in mean precipitation (DiffMeanP)	**0.51**	**0.00**	**0.55**	**0.00**	0.00	0.90
Difference in maximum temperature (DiffMaxT)	**0.20**	**0.00**	**0.14**	**0.00**	**0.14**	**0.00**
Difference in mean temperature (DiffMeanT)	**0.15**	**0.00**	0.10	0.01	0.08	0.02
Difference in minimum temperature (DiffMinT)	**0.18**	**0.00**	**0.13**	**0.00**	0.08	0.02
Temperature range (Trange)	**0.55**	**0.00**	**0.43**	**0.00**	0.07	0.03

Phylogenetic Independent Contrasts (PIC)

PIC analyses show statistically significant positive relationships between reconstructed median migratory distances and a half of the variables analysed (Table 2.1). Results obtained using maximum and median migratory distances were similar except in the variables: maximum temperature in the breeding season, difference in mean temperatures, and mean precipitation in the wintering areas. Using the minimum migratory distance, there are five significant relationships, but with low R^2 values (<0.24, Table 2.1). The variable with the highest R^2 with the median and maximum migratory distances is the NPP during the breeding season (R^2=0.74, and 0.72 respectively), followed by the minimum temperature in the breeding season. The temperature range, the mean precipitation in the breeding season and the difference in mean precipitations show significant positive relationships with migratory distance but with lower R^2 values (R^2 ~0.5). The only biometric variable showing a significant relationship with migratory distance is the maximum wing length but with even lower R^2 values (median migratory distance R^2=0.37, maximum R^2=0.32). Fig. 2.1 compares the ASR of the median migratory distance with the reconstructions of the variables showing higher R^2, including NPP in the breeding range, temperature range and the maximum wing length.

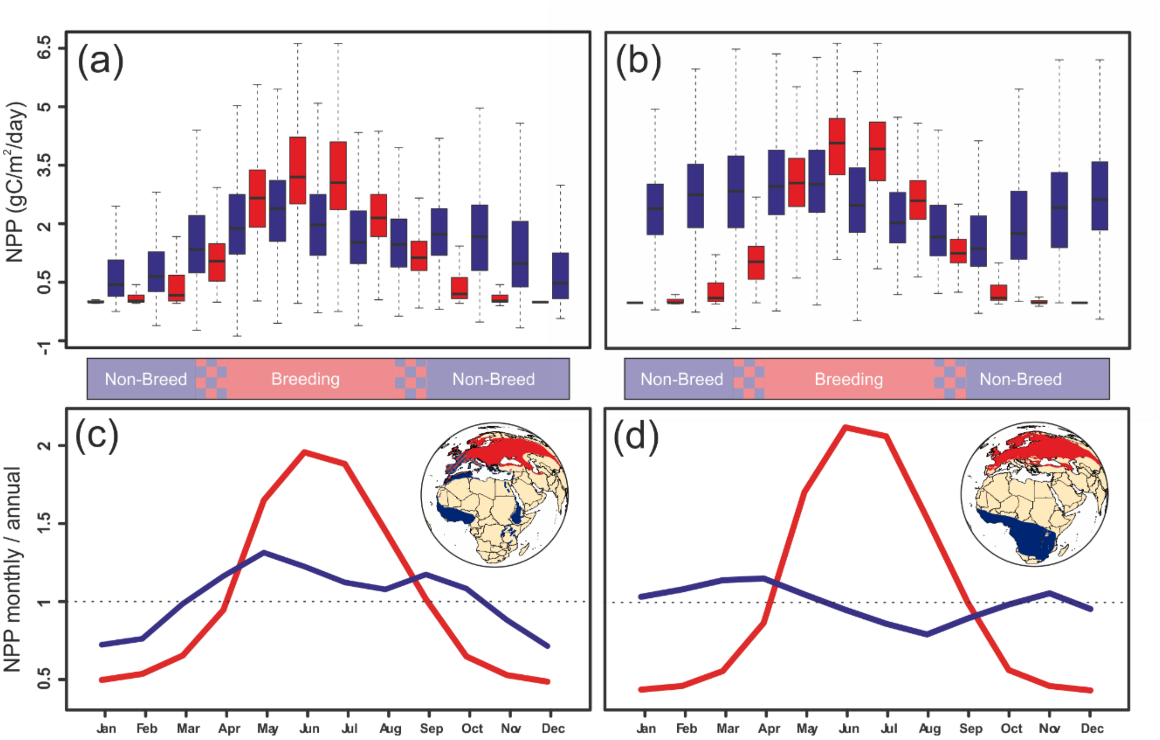

Figure 2.2. Plot representing the yearly variation in net primary productivity (NPP) in breeding areas (red) and non-breeding areas (blue) of two migratory *Sylvia* species. (a) and (b) show box plots of yearly dynamics of NPP from areas where the blackcap (*Sylvia atricapilla*) (a) and the garden warbler (*Sylvia borin*) (b) occur. The middle strip shows the breeding period (in red) and the wintering period (in blue) of both species. Sections (c) and (d) show the median deviation of each month from the yearly mean of the NPP (dashed line, considered as 1) for the areas where the blackcap (c) and the garden warbler (d) occur. Inserted maps represent the global breeding and non-breeding ranges for both species.

PGLS analyses

We included 30 independent variables sorted into climatic, biometric and productivity categories. A first pairwise correlation analysis discarded fourteen variables showing pairwise correlation values higher than 0.75. VIF analyses reduced the remaining variables into six, two per each category. The models performed with biometric variables, climate and productivity separately are all statistically significant using the median or the maximum migratory distances (Table 2.2). According to AICs, the best model is the one including all variables, both for the median and maximum migratory distances; however, a model using only NPP and climate variables performs as well as the best model (as the ΔAICc value is less than 2 between them (Burnham & Anderson, 2004) (Table 2.2), suggesting that those variables contribute the most to the model with all variables. When using minimum migratory distances, the effect of NPP and climate dilutes, recovering the model with morphology only as the best one (Table 2.2), followed by the one with morphology and NPP.

NPP comparison between breeding and wintering areas

The yearly dynamics of NPP in the areas of occurrence of the long range migratory garden warbler (*S. borin*) and the blackcap (*S. atricapilla*) are shown in Fig. 2.2, as examples of migratory species for this clade. In the blackcap (Fig. 2.2a), NPP increases significantly in the breeding areas during the spring-summer when birds are present, showing values much higher than in those regions during the non-breeding period (monthly medians around 2 or 3 gC/m^2/day versus medians below 1 gC/m^2/day, respectively). The NPP in the non-breeding areas does not show such marked pattern and during the spring-summer show lower NPP values compared to the breeding areas. The pattern in the garden warbler (Fig. 2.2b) is similar in the breeding regions, while the NPP pattern in non-breeding areas shows a more constant productivity throughout the year, but again lower than during spring-summer in breeding regions. When considering the deviations from the median NPP (value of 1 in Fig. 2.2c and Fig. 2.2d), the pattern is similar for both species, showing a clear peak and much higher productivity during the breeding period in the breeding areas, and a more stable NPP throughout the year in the non-breeding areas.

Table 2.2. PGLS models for the median, maximum and minimum migratory distances. In grey the best AIC models. Acronyms are the same as in Table 2.1. Biometric variables are only the maximum ones.

	Variables	Lambda	Delta	Kappa	AICc	ΔAICc	w_i
MEDIAN MIGRATORY DISTANCE							
Model 1: Morphology	Tail, Wing	0.94	3.00	1.85	1104.68	149.98	1.87e-33
Model 1.1: Tail	Tail	0.94	3.00	2.36	1140.25	185.55	3.65e-41
Model 1.2: Wing	Wing	0.99	3.00	2.00	1129.96	175.25	6.29e-39
Model 2: Productivity	NPPb, NPPw	1.00	0.16	3.00	1022.10	67.40	1.60e-15
Model 2.1: NPP breeding	NPPb	1.00	0.38	0.60	1069.03	114.32	1.07e-25
Model 2.2: NPP wintering	NPPw	1.00	3.00	2.36	1140.17	185.47	3.81e-41
Model 3: Climate	DiffMeanP, Trange	1.00	2.56	2.07	1079.38	124.68	5.85e-28
Model 3.1: Precipitation	DiffMeanP	1.00	3.00	1.77	1116.12	161.41	6.37e-36
Model 3.2: Temperature	Trange	0.99	3.00	2.37	1092.62	137.91	8.07e-31
Model 4: Morphology and Productivity	Tail, Wing, NPPb, NPPw	1.00	0.49	0.57	1027.52	72.82	9.90e-17
Model 5: Morphology and Climate	Tail, Wing, DiffMeanP, Trange	1.00	0.29	0.41	1054.89	100.19	1.13e-22
Model 6: Climate and Productivity	DiffMeanP, Trange, NPPb, NPPw	1.00	0.12	3.00	955.62	0.92	4.06e-01
Model 7: all variables		1.00	0.11	3.00	954.70	0.00	5.94e-01
MAXIMUM MIGRATORY DISTANCE							
Model 1: Morphology	Tail, Wing	0.93	3.00	2.05	1192.15	108.01	4.09e-24
Model 1.1: Tail	Tail	0.97	3.00	2.20	1216.04	131.90	2.74e-29
Model 1.2: Wing	Wing	0.96	3.00	2.06	1205.93	121.79	4.31e-27
Model 2: Productivity	NPPb, NPPw	1.00	0.17	2.89	1126.51	42.37	7.33e-10
Model 2.1: NPP breeding	NPPb	0.98	2.38	1.97	1161.10	76.95	2.35e-17
Model 2.2: Npp wintering	NPPw	0.98	3.00	2.19	1216.45	132.31	2.24e-29
Model 3: Climate	DiffMeanP, Trange	1.00	0.24	0.34	1179.80	95.66	1.97e-21
Model 3.1: Precipitation	DiffMeanP	1.00	3.00	1.55	1208.12	123.98	1.44e-27
Model 3.2: Temperature	Trange	0.97	3.00	2.18	1197.51	113.37	2.91e-25
Model 4: Morphology and Productivity	Tail, Wing, NPPb, NPPw	1.00	0.16	3.00	1117.39	33.25	6.53e-08
Model 5: Morphology and Climate	Tail, Wing, DiffMeanP, Trange	1.00	0.36	0.22	1172.30	88.15	7.80e-20
Model 6: Climate and Productivity	DiffMeanP, Trange, NPPb, NPPw	1.00	0.22	2.69	1098.92	14.78	6.69e-04
Model 7: all variables		1.00	0.16	3.00	1084.14	0.00	9.99e-01
MINIMUM MIGRATORY DISTANCE							
Model 1: Morphology	Tail, Wing	0.99	0.12	2.80	929.51	0.00	3.99e-01
Model 1.1: Tail	Tail	0.99	0.09	2.94	933.11	3.60	6.82e-02
Model 1.2: Wing	Wing	1.00	0.25	1.12	948.47	18.96	1.91e-05
Model 2: Productivity	NPPb, NPPw	0.99	0.09	2.93	935.15	5.65	2.38e-02
Model 2.1: NPP breeding	NPPb	0.99	0.09	2.98	933.43	3.92	5.83e-02
Model 2.2: Npp wintering	NPPw	0.99	0.09	2.91	933.10	3.59	6.86e-02
Model 3: Climate	DiffMeanP, Trange	0.99	0.10	2.90	934.28	4.77	3.67e-02
Model 3.1: Precipitation	DiffMeanP	0.99	0.09	2.91	933.27	3.76	6.30e-02
Model 3.2: Temperature	Trange	1.00	0.09	3.00	934.15	4.64	1.94e-08
Model 4: Morphology and Productivity	Tail, Wing, NPPb, NPPw	0.99	0.10	2.92	931.40	1.89	1.45e-01
Model 5: Morphology and Climate	Tail, Wing, DiffMeanP, Trange	1.00	0.09	3.00	937.62	8.12	6.43e-03
Model 6: Climate and Productivity	DiffMeanP, Trange, NPPb, NPPw	0.99	0.09	3.00	933.41	3.90	5.27e-02
Model 7: all variables		0.99	0.10	3.00	932.49	2.98	7.74e-02

DISCUSSION

Our results suggest that productivity could have had an important role in the evolution of migration in *Sylvia* warblers. NPP is the variable with the strongest correlation with migratory distances in a phylogenetic context, being as well always included in the best models considering a combination of potential factors related to the evolution of bird migration. There is a growing evidence that extant species profit and track resources during migration (e.g. Helbig, 2003; Hensz, 2015; La Sorte *et al.*, 2014; Thorup *et al.*, 2017). Although productivity itself depends strongly on climate, a recent study tracking cuckos during migration (Thorup *et al.*, 2017) has shown that migratory birds track areas at the peak of productivity compared to the annual mean. Thus, it seems that what matters the most for migratory birds is following this extra productivity that likely translates into assured trophic resources and less competition.

Our data show that sedentary lineages breed in areas with median NPP around the annual mean for those territories, while long distance migrants breed in areas where the median NPP in breeding months is above the annual mean (Fig. 2.2), in agreement with the observations of Thorup *et al.* (2017). Hence, migratory species take clear advantage of the peak of productivity at their breeding grounds, departing to wintering areas when productivity falls below the annual mean. In fact, it has been shown that supplementary feeding in gardens favour overwintering of *Sylvia* warblers (Plummer *et al.*, 2015), supporting the hypothesis that changes in resource availability can drive migratory movements. The strategies of sedentary lineages are different, including for example the increase in the length of their breeding period, involving in some cases several clutches per year (Catchpole & Phillips, 1992).

Apart from the relationship with productivity, our PIC analyses detected significant relationships between migratory distance and climate (mean and minimum precipitation of the breeding period, difference in mean precipitation and temperature range) and morphology (maximum wing length). The best two PGLS models with median migratory distance are the ones with all variables and one with just climate and NPP variables. Both models are equally valid suggesting that productivity and climatic variables have the strongest influence in the model with all variables too. Although NPP builds mostly upon climatic factors, it has been shown that *Sylvia* warblers do not track climatic niches (Laube *et al.*, 2015), but likely resources.

There are several examples showing that other species track NPP during migration. In the marine environment, the arctic tern fall migration routes are driven by the increase in NPP and winds, while the main factor during the spring migration is the decrease of sea surface temperature (Hensz, 2015). However, in both periods, high levels of NPP slow down travelling speeds, suggesting that terns adjust their migratory strategy to profit from available resources. The same happens with continental bird species that track productivity during their migration (Alerstam & Lindström, 1990; Lindström, 2003; Thorup *et al.*, 2017). The relationship between NPP and migration has been found in other taxonomic groups, like fish, as terrestrial NPP drives migratory behaviour and anadromy in the arctic char (Finstad & Hein, 2012). Here, we show that productivity has likely played an important role in the migratory behaviour of *Sylvia* warblers.

Regarding wing morphology, changes have been reported before in relation to migratory/non-migratory species and populations (Pérez-Tris & Tellería, 2003). Wing length morphology in *Sylvia* warblers is a well-known good proxy for migratory states in some species, where migratory populations show longer and pointed wings, while non-migratory populations have rounded and shorter wings (Böhning-Gaese *et al.*, 2003; Pérez-Tris & Tellería, 2003). We found a significant positive correlation between the evolution of migratory distance and wing morphology, as expected, where sedentary species or subspecies show shorter wing lengths (Table 2.1). Only *Sylvia atricapilla* shows complex migratory strategies, with some fully migratory, partial migratory and sedentary populations. We were unable to include this variation in our analyses, as there are no data on migratory distances or genetic data for all populations, but this species exemplifies that switches between strategies can happen fast.

Although sedentary island subspecies are very recent in evolutionary time, they show shorter wing lengths than their migratory sister taxa (Fig. 2.1a). This happens for example in *Sylvia conspicillata orbitalis* (Madeira, Canarias and Cabo Verde islands), *S. atricapilla heineken* (Canarias and Madeira islands) or *S. a. gularis* (Cabo Verde and Azores islands). This supports the hypothesis of fast switching between migratory to non-migratory phenotypes (Helbig, 2003; Pulido & Berthold, 2010), which may be regulated by epigenetic or differential expression of genes related to feather development. In older sedentary species (longer branches in the tree), the relationship between shorter migratory distances and shorter wing lengths is stronger, as expected.

Considering that *Sylvia* warblers are evolutionary old and the divergences between species predate the Pleistocene (Voelker & Light, 2011); together with the clear phylogenetic signal found in our dataset; and that the breeding distribution ranges of most species were not highly affected by the expansion and contraction of ice sheets during the Pleistocene, the relationship between NPP and migration has likely been occurring at deeper phylogenetic levels. A recent study postulated that several long-range North American migratory species switched from migratory to non-migratory strategies during glaciations based on hindcasting species distribution modelling (Zink & Gardner, 2017), but it is unclear if the ice acted in the same way in other areas and with species with distribution ranges outside the areas affected by ice sheets, like *Sylvia* warblers, which also retained their wintering areas separated in the glaciations. In fact, in this genus most species and subspecies that are either migratory or sedentary likely retain their ancestral strategy, with very few others that clearly have suffered fast reversals from migratory to sedentary states, mainly linked to island colonisations (Voelker & Light, 2011). All our ASR analyses show that several events of sedentariness evolved from migratory ancestors, including the ones reported on islands, and that such switches happened fast in evolutionary time. *Sylvia atricapilla heineken* and *Sylvia a. gularis* represent a good example of sedentary insular subspecies from a fully migratory ancestor, in contradiction with the hypothesis of Lomolino *et al.* (2017) that insular sedentary birds derive from sedentary or short-migratory ancestors.

Our results cannot disentangle if NPP has been one of the main drivers of bird migration or it is a consequence of bird migratory behaviour, but it seems clear that there is and has been a tight relationship between migratory behaviour and productivity in birds. There is a growing evidence that nor present or past climates but productivity peaks drive bird migratory movements (Helbig, 2003; Hensz, 2015; La Sorte *et al.*, 2014; Thorup *et al.*, 2017), and this relationship seems to be at the root of the rise of bird migratiory strategies. The relationship between NPP and migration at deeper temporal scales needs to be further explored in other bird clades, both subject to past glaciations and from areas with low exposure to ice, as different factors may be acting, alone or in interaction, in different geographic regions.

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SECTION II:

Climatic niche and Paleo-distribution of trans-Saharan migratory birds

Chapter 3:

Seasonal climatic niches diverge in migratory birds

This chapter reproduce entirely the manuscript:

Ponti. R., Arcones, A., Ferrer, X. and Vieites D. Seasonal climatic niches diverge in migratory birds. Under Review

Seasonal climatic niches diverge in migratory birds

Abstract:

Species distributions reflect their realised niche, composed by biotic and abiotic factors that allow their survival and reproduction. Identifying those factors is essential to understand and predict present and past potential species distributions. Migratory birds occupy different geographic areas during breeding and non-breeding periods, which may entail different factors determining the range limits depending on the season. One of those factors is the climatic component of the niche which is widely used to model species distributions; however the temporal component is often neglected. In this work, we tested if migratory birds display similar climatic conditions in both breeding and non-breeding areas, using 355 bird migratory species from Eurasian to Africa flyways. We performed niche overlap analyses to test this hypothesis and compared niche differences between sister species, as well as linking them to migratory distances. For more than 80% of the species, there is no overlap or very little between their breeding and non-breeding climatic niches. Sister species display a larger climatic niche overlap between their breeding areas or their non-breeding areas, than the climatic overlap within species. Finally, there is a clear negative relationship between migratory distances and climatic niche overlap for each species. Our results suggest that the climatic niche of most Euro-African migratory species is larger than the climatic niche inferred from their breeding distributions, showing a higher climatic tolerance than expected. Given these results, both breeding and non-breeding climatic data need to be considered when performing species distribution models, to incorporate the total width of the climatic niche.

Keywords: migration, climate, niche overlap

INTRODUCTION

Identifying the factors that had determined current species distributions is of paramount importance to understand and predict their potential shifts due to present or past climatic changes. Among these factors, there are both intrinsic ones like physiological tolerance, phenotypic plasticity or behaviour; and extrinsic ones, such as present and past climatic conditions experienced by species, historical contingency, barriers to dispersal, habitat availability, or ecological ones like competition or predation. Current species distributions are the result of the combination of several of these biotic and abiotic factors that determine species survival and reproduction in space and time, which are also linked to the ecological niche concepts (e.g. Grinnell, 1917; Hutchinson, 1957). Also, the historical combination of these factors determines that most species do not occur where their fundamental niche predicts, but their realised distributions being smaller than their potential ones (Hutchinson, 1957).

Migratory species experience an extra challenge as, throughout the annual cycle, migratory populations use different geographic regions during breeding and non-breeding periods. This behavioural strategy is common in birds, having evolved multiple times (Zink, 2011), with many long-distance migratory species that perform some of the greatest annual movements in the animal kingdom (Alerstam *et al.*, 2003). In this context, the factors that determine the distribution range limits of these long-distance migrants may be different between breeding and non-breeding areas, as they usually move from arctic or temperate regions to tropical ones. However, for most long-range migratory species there is a general lack of data from their non-breeding grounds as well as for the degree of migratory connectivity between populations (Kramer *et al.*, 2018; Webster *et al.*, 2002). Populations trend seem to be partly determined by non-breeding factors like habitat quality and loss (Goss- Custard *et al.*, 1995; Kramer *et al.*, 2018; Marra, 1998), climate (Peach *et al.*, 1995; Saino *et al.*, 2011) or accessibility to food resources (van Gils *et al.*, 2016), that may influence physical condition at departure and changes in departure time (Gordo, 2006). Those factors have also been linked to reproductive success, recruitment and survival (Gill *et al.*, 2001; Peach *et al.*, 1995; Saino *et al.*, 2011; Sillett *et al.*, 2000). Among those, climate and habitat availability are likely the better predictors for forecasting species future distributions under Global Change scenarios.

The climatic component of the niche has been extensively used to model current species distributions in space, which might approximate the real occupancy area of species (Colwell & Rangel, 2009), as well to forecast (e.g. Araújo *et al.*, 2011) or hindcast their potential ranges (Nogués-Bravo, 2009), based on the localities where species are present. However, in most cases, for migratory birds, only the climate from their breeding distribution range is regularly used in models and macroecological works, and the seasonal environmental variability, as well as the dynamic behaviour of species, have rarely been considered (Eyres *et al.*, 2017; Laube *et al.*, 2015). This implicitly assumes that the climatic conditions that species experience during their non-breeding period should be similar or overlap with the ones during their breeding period, yet if there is a pattern where long-range migratory species migrate to areas with similar environmental conditions or not it needs to be tested.

Migratory birds leave their breeding areas when environmental conditions turn inadequate for their survival (Berthold, 2001). There are examples where some species track their breeding climatic conditions to non-breeding ranges, while others switch climates in non-breeding ranges (Gómez *et al.*, 2016; Laube *et al.*, 2015; Martínez-Meyer *et al.*, 2004; Nakazawa *et al.*, 2004). If the climate that migratory species experience in the breeding and non-breeding areas is different (i.e. there is no climatic overlap), we can hypothesise that species climatic tolerance, and their climatic niche, is much wider than expected considering the breeding period only. This has important implications when forecasting possible species responses to future climate change, as the climatic component of their niche has been broadly used in species distribution models (SDM). However, breeding and non-breeding climatic conditions have not usually been considered separately. In most cases, models have been performed with annual climatic variables (Doswald *et al.*, 2009; Hu *et al.*, 2010; Zink & Gardner, 2017).

Here, we want to test if migratory bird species show similar climatic conditions in breeding and non-breeding ranges, using short and long-range migratory bird species from the Eurasian to Africa flyway as a case study. As null hypothesis, we expect that migratory species occupy similar climatic conditions in both seasonal distributions (Fig. 3.1a; H0). Alternatively, the climatic niches of migratory species are wider than expected by only considering their breeding or non-breeding ranges (Fig. 3.1a; H1). Given the diversity of bird groups with migratory behaviours, we want to explore whether small-bodied species (i.e. Passeriformes) show the same pattern as large-sized birds, as storks or raptors.

Differences in seasonal climatic conditions would be linked to different bird families, or conversely, there might be a general pattern common for all migratory birds. To explore this, we included all migratory bird species from Africa and Europe, encompassing species that migrate within each continent or species which part of their breeding or non-breeding range also occur in Asia.

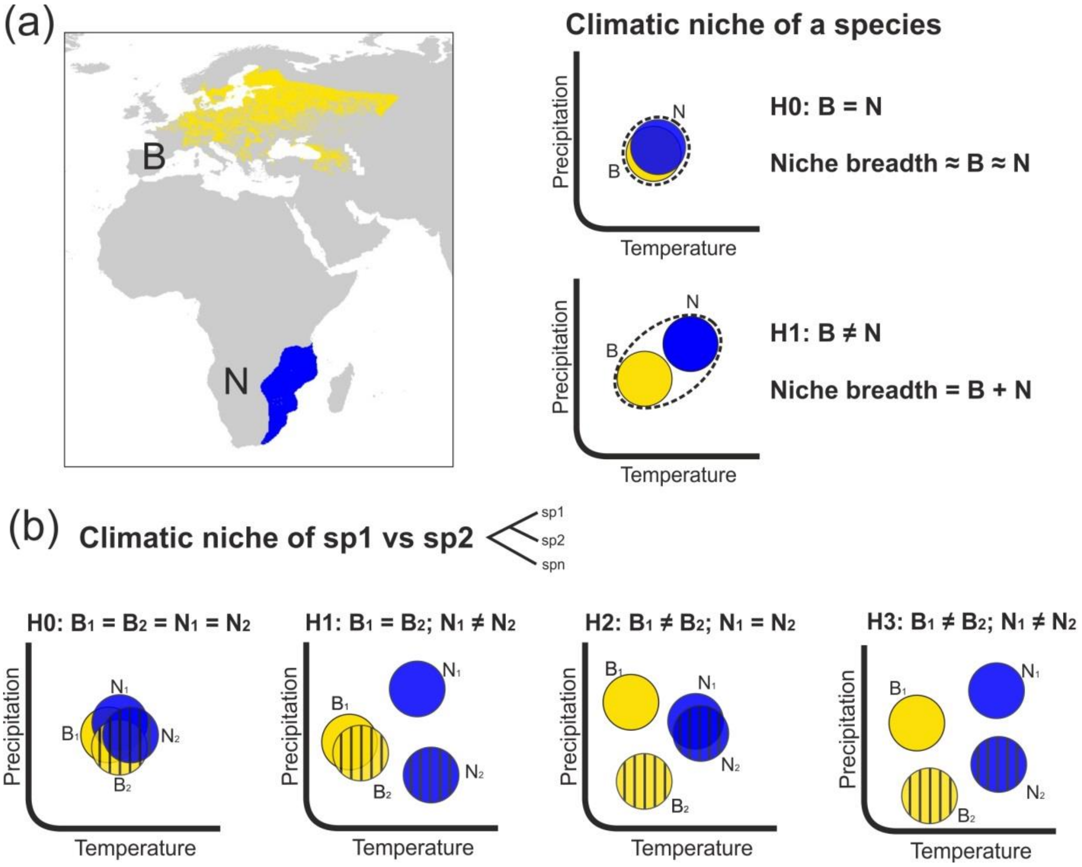

Figure 3.1. Alternative hypotheses when comparing both seasonal climatic niches of one species and two sister species. (a) On the left, the distribution range of a migratory bird species, being in yellow the breeding range [B] and in blue the non-breeding range [N]. On the right, two alternative hypotheses of the climatic niche of a migratory bird species, represented in the climatic space. The yellow and blue circles correspond to the climatic niche of the breeding and non-breeding range respectively. Hypothesis 0 (H0) represents similar seasonal climatic niches and hypothesis 1 (H1) different seasonal climatic niches. (b) Four alternative hypotheses when comparing breeding and non-breeding climatic niches of two sister species. H0: all similar climatic niches; H1: only breeding climatic niches similar; H2: only non-breeding climatic niches similar; H3: all different climatic niches.

As the conservation of the niche over short evolutionary times has been shown in multiple organisms (Peterson, 1999; Wiens *et al.*, 2010), it can also be hypothesized that sister or phylogenetically closely related species will show more similar climatic conditions in their breeding or non-breeding ranges than more distant taxa. However, there are examples in birds where migratory behaviour can evolve fast (Berthold *et al.*, 1992), which may be related to a plastic response in relation to climatic conditions. In this context, we propose four possible scenarios and assess which are more frequent in comparisons between pairs of phylogenetically closely related species (Fig. 3.1). If niches are fully conserved (Fig. 3.1b; H0) two sister species will show similar climatic conditions both in breeding and non-breeding seasons. Alternatively, those two sister species could share similar climatic conditions during their breeding season but not in the non-breeding season (Fig. 3.1b; H1), or the other way around (Fig. 3.1b; H2). Finally, the climatic conditions could differ in both seasons within and between species (Fig. 3.1b; H3).

MATERIALS AND METHODS

Bird distribution ranges

We revised all European, Asian and African species, and selected 355 migratory bird species from Europe-Asia to Africa for all analyses, that encompass almost all directional migratory species (*sensu* Eyres *et al.*, 2017) from Africa and European continent and some that also occur in Asia during at least one of the two seasons. We only discarded the likely extinct species *Numenius tenuirostris* given the uncertainty on its breeding and non-breeding distribution. The taxonomy of birds was based on the Handbook of the Birds of the World Alive (del Hoyo *et al.*, 2018). BirdLife International and NatureServe (2011) distribution maps were compiled from all species. We discarded incorporating data from ebird due to the lack and the bias of the occurrence data in some geographical areas, especially in the African continent and in Eastern Europe, where the density of occurrence points is limited by the reduced number of observers. The lack of data from most of Africa impeded the use of such otherwise useful dataset. However, Birdlife maps overestimate real distributions of species because they include areas with non-suitable habitat for each species. We refined all species distribution maps by overlapping Birdlife occurrence maps with landcover layers of suitable habitats for each species [according with the habitat information category (level 1) from BirdLife International and NatureServe (2011)], for breeding and non-breeding ranges independently (Ocampo-Peñuela *et al.*, 2016, See **General Methods,** Section “Correction of bird distribution maps and data extraction”). We used the landcover layer from GLOBCOVER (Bontemps *et al.*, 2011), the water layer from the Global Land Cover Facility (GLCF) (Carroll *et al.*, 2009) and altitude from WordClim

1.4 (Hijmans *et al.*, 2005). Landcover and water layers were re-scaled as the same grid size of the altitude layer and reclassified to create habitat maps according to Birdlife habitat categories for each species. All species maps resulted in more accurate breeding and non-breeding distribution ranges with a resolution of 30 arc-seconds (~1km). ArcGis 10 (ESRI, 2011) was used for all map calculations. For the analyses, we randomly sampled each species distribution selecting 10000 points both from the breeding and non-breeding ranges.

Environmental data

We used current climatic conditions (~1950-2000) from WorldClim (Hijmans *et al.*, 2005), with the same resolution of the distribution ranges (30 arc-seconds). The minimum, maximum and mean temperature and accumulated precipitation layers were used to define the climatic niche. As we wanted to test if the climatic conditions of the breeding and non-breeding ranges are similar or not, for each species we considered the climate of the months during the breeding period and within the breeding area separately, and the climate of the months during the non-breeding period and within the non-breeding area. For this, we created new macroclimatic layers by calculating the mean of temperatures of the months that each species spend in breeding or non-breeding areas and the accumulated precipitation for those months (**Appendix Chapter 3**, Table A3.1), based on the information compiled from the literature (Brown *et al.*, 1982-2004; Cramp *et al.*, 1977-1994; del Hoyo *et al.*, 2018).

Niche overlap and niche breadth analyses

The climatic niche exploration was performed using the multivariate ordination approach described in Broennimann *et al.* (2012), (See **General Methods**, Section “Spatial distribution models and ecological niche comparisons”). We calculated the climatic niche overlap between breeding and non-breeding ranges for all 355 species. Although each species can only have a climatic niche, here and thereafter we will mention niche comparisons between seasons to report similarities and differences between them. First, for each species, we performed a principal component analysis (PCA) including the climatic variables of both the breeding and non-breeding periods for all the studied biogeographic regions where these species occur (Palearctic, Afrotropical, Indo-Malay and Australia). Given the high resolution of the climatic layers, we used a subset of 200,000 random points for each climatic variable belonged to each season for all the study extent. The climatic space defined by the two main principal components was divided in a grid of 100 x 100 cells, with each cell containing a unique vector of climatic conditions. For each species, 10,000 random points per season were used as occurrence data. The occurrences of species were converted into smoothed densities, using the kernel function (Worton, 1989) that takes into account the availability of climatic conditions in the background, and mapped into the whole climatic space (Broennimann *et al.*, 2012). To estimate the niche overlap between the two seasons, we used the D metric (Schoener, 1970; Warren *et al.*, 2008) that varies from 0 (no overlap) to 1 (totally overlap). This metric was calculated a hundred times for each species to perform the test of equivalency, that determines if the observed niche overlap is similar to the expected niche overlap when randomly reallocated occurrence points to the two ranges compared. If the observed value of the niche overlap falls outside the 95% of the simulated values of niche overlap, it means that the two niches are not equivalent. The similarity test was also performed with a hundred repetitions. In this test, the total observed occurrence density of a range is shifted randomly and calculated the niche overlap with the other observed range. If the observed value of niche overlap is greater than 95% of the simulated values, it means that the two niches are more similar to each other that expected by chance. We used the categories proposed by Rödder and Engler (2011) to interpret the degree of overlap given de D metric: (0–0.2 = no or very limited overlap, 0.2–0.4 = low overlap, 0.4–0.6 = moderate overlap, 0.6–0.8 = high overlap, 0.8–1.0 = very high overlap).

To evaluate if the differences between climatic niches are higher within species in different seasons (breeding and non-breeding) or between sister species in the same season (breeding ranges or non-breeding ranges), we selected 51 pairs of sister species or very phylogenetically closely-related species from the total (using 76 species), as we expected a conservation of the climatic niche in those pairs. We did not performed phylogenetic analyses given the lack of genetic information for many migratory species from Africa and Europe. We selected all sister species present in our dataset and also some trios when the relationship between species is not clear but are very close phylogenetically. We calculated the niche overlap between breeding ranges or non-breeding ranges of those species pairs, using the same methodology described above.

To calculate niche breadths, we took the PCA coordinate points of the climatic available space for each species and calculate the minimum convex polygon (MCP) using 95% of the points. Seasonal niche breadths were calculated separately and total niche breadth was calculated performing MCP using both seasonal points together. Pracma and adehabitatHR (Calenge, 2006) packages for R were used for the analyses.

Statistical analyses

We compared the means of the niche overlaps (D) obtained from intraspecific analyses (between breeding and non-breeding climatic niche of each species) and from interspecific analyses (niche overlap between breeding ranges or non-breeding ranges of pairs of sister or closely-related species). We conducted a non-parametric ANOVA (Kruskal-Wallis test) as data do not meet conditions of normality for all comparisons (Shapiro-Wilk test <0.05), and a Dunn post-hoc test. Reported results are shown as mean ± standard deviation (SD).

Linear regression models were performed to analyse the relationship between migratory distance and niche characteristics: overlap between breeding and non-breeding ranges within species, total niche breadth, niche breadth of the breeding range and niche breadth of the non-breeding range. We also explored the relationships between breeding and non-breeding areas with the niche breadth of the same ranges. Before performing all those analyses we applied square root transformations to all variables, and double square root transformation for areas, in order to improve normality. All analyses were performed in R with ade4 and ggplot2 packages (Dray & Dufour, 2007; Wickham, 2010).

RESULTS

By filtering Birdlife distribution maps with the habitat information for each species, we excluded from 0 to up to 98% of the distribution of breeding and non-breeding ranges.

Climatic niche overlap

In all PCA analyses, the two principal components explained almost 99% of the variation, with ~74% for PC1 (temperature variables) and ~25% for PC2 (precipitation variables) (See **Appendix Chapter 3**, Table A3.2).Migratory species from Africa and Europe present climatic niche overlaps (D) between breeding and non-breeding ranges from 0 (e.g. *Phylloscopus sibilatrix*) to 0.7 (*Ardea purpurea*), with a mean for all 355 species of D = 0.21 ± 0.18 (SD) (See **Appendix Chapter 3**, Table A3.2). The 57% of migratory species present climatic niche overlap lower than 0.2 (almost null overlap) and the 82% do not surpass a D value of 0.4 (low overlap) (*sensu* Rödder & Engler, 2011) (Fig. 3.2a). In general, all bird Orders present low values of climatic niche overlap between breeding and non-breeding ranges. However, the order Charadriiformes stands out with the 63% of the species presenting D < 0.1, in particular the family Scolopacidae, with all species with D < 0.1, with the exception of *Scolopax rusticola* (D = 0.635). On the opposite side, the 30% of Pelecaniformes species present a D > 0.5 (moderate overlap) (**Appendix Chapter 3**, Figures A3.1 and A3.2).

Krustal-Wallis sum test (KW) show that there are statistically significant differences between the three climatic niche overlap (D) statistics calculated (KW = 26.252, df = 2, P < 0.0001). For the 76 species selected for pairwise comparisons, the climatic niche overlap between breeding and non-breeding ranges within species is lower (mean=0.19±0.18) than the climatic niche overlap between the breeding areas (mean=0.36±0.19) and between the non-breeding areas (mean=0.32±0.23) of the pairs of closely related species. Differences lied in the intraspecific climatic niche overlap metrics and the other two interspecific ones (Breeding (Bre)-Non-Breeding (NonB) and Bre-Bre comparison, P<0.0001; Bre-NonB and NonB-NonB comparison, P= 0.0015). Those species present D metrics similar when comparing niche overlap metrics from breeding areas or non-breeding areas of pairs of closely-related species, with no statistically significant differences (Bre-Bre and NonB-NonB comparison, P=0.652) given possibly the low effect size metric (Cohen´s d= 0.18, Cohen, 1988) (Fig. 3.3). 81% of the species present higher D values when comparing the breeding climatic niche of one species with the breeding climatic niche of its sister species, than when comparing intraspecific niches (breeding and non-breeding), suggesting a conservation of the breeding climatic niche between sister species in the majority of them. When comparing niche overlap metrics between non-breeding ranges of sister species versus intraspecific niche overlap values, 62% of the species recovered higher D values in interspecific than in intraspecific comparisons, suggesting that less sister species share similar climatic conditions in winter than considering the breeding period.

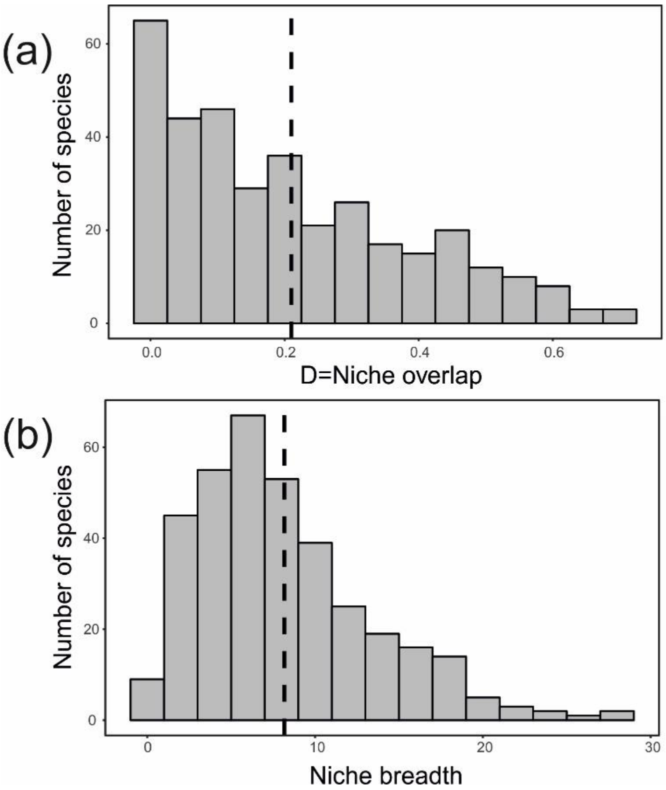

Figure 3.2. (a) Histogram of the climatic niche overlap metrics and (b) Histogram of the climatic niche breadth for all 355 migratory species of Africa and Europe. Dashes lines correspond to the mean of the values of climatic niche overlap and the climatic niche breadth respectively.

For all intraspecific or interspecific niche comparisons, the hypothesis of niche equivalency is rejected, as all tests showed $P < 0.05$ (See **Appendix Chapter 3**, Tables A3.2 and A3.3). For 21 species, the niche similarities between breeding and non-breeding ranges were higher than expected by chance ($P < 0.05$), and for 55 species the niche similarity hypothesis was rejected but only in one direction (See **Appendix Chapter 3**, Table A3.2).

Regarding the comparison between breeding ranges, only for three pairs of sister species the niches share more similitudes than expected by chance (*Oenanthe chrysopygia* and *Oenanthe xanthoprymna*; *Luscinia luscinia* and *Luscinia megarhynchos*; *Hippolais languida* and *Hippolais olivetorum*) and for other three pairwise species comparisons, $P<0.05$ are present only in one direction (**Appendix Chapter 3**, Table A3.3). When comparing non-breeding ranges, nine pairwise comparisons of sister species present closer niches than expected by chance, including *Oenanthe chrysopygia* and *Oenanthe xanthoprymna* with high similarities also in breeding ranges and high value of niche overlap between breeding ($D = 0.82$) and between non-breeding areas ($D = 0.48$). Other five pairwise comparisons of sister species present more niche similarities that expected by chance in only one direction (**Appendix Chapter 3**, Table A3.3).

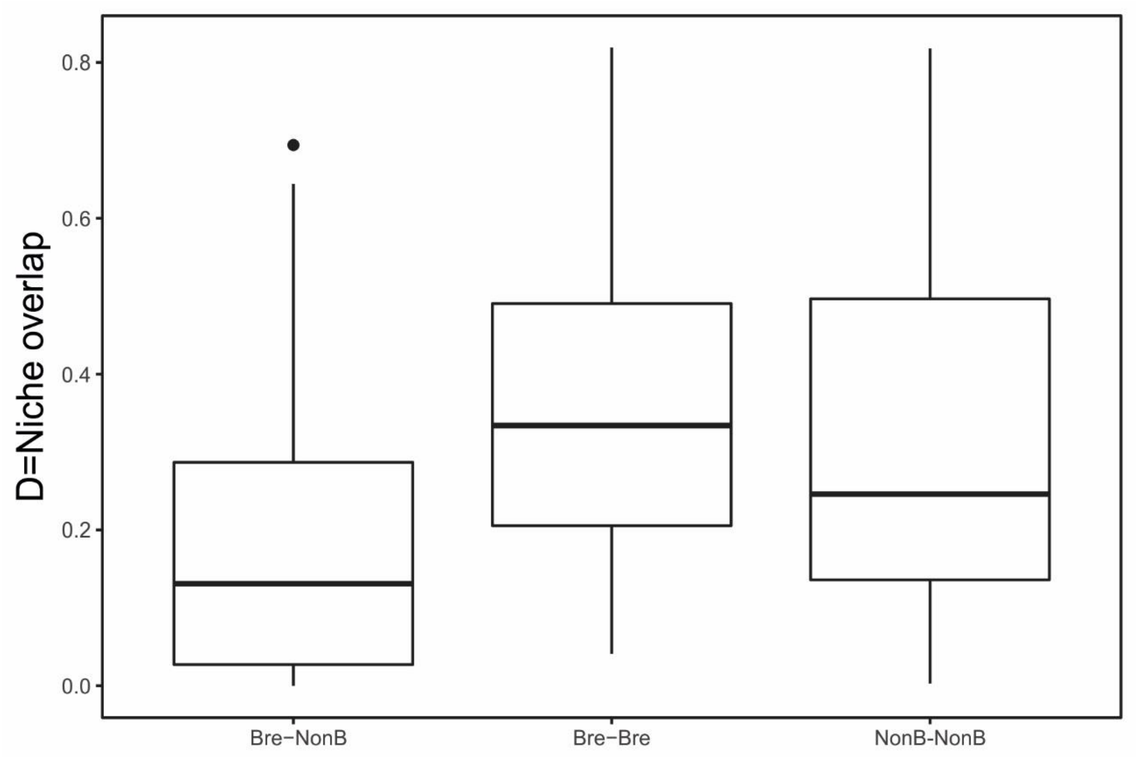

Figure 3.3. Boxplot with climatic niche overlap metrics for the subset of 76 migratory species. Bre-NonB refers to the niche overlap between breeding and non-breeding ranges for each species, Bre-Bre refers to the niche overlap between breeding ranges of pairs of sister or close species and NonB-NonB refers to the niche overlap between non-breeding ranges of pairs of sister or close species.

Climatic niche breadth

Most species tend to have a rather reduced climatic niche in the available environmental space, as species concentrate in the middle left of the histogram (Fig. 3.2b). Species with wider niche breadths correspond to the Order Charadriiformes, Passeriformes and Pelecaniformes, namely the families Scolopacidae, Fringillidae and Ardeidae (**Appendix Chapter 3**, Figures A3.3, A3.4 and A3.5). However, the more noteworthy species are *Falco peregrinus* and *Charadrius mongolus* showing the widest climatic niches.

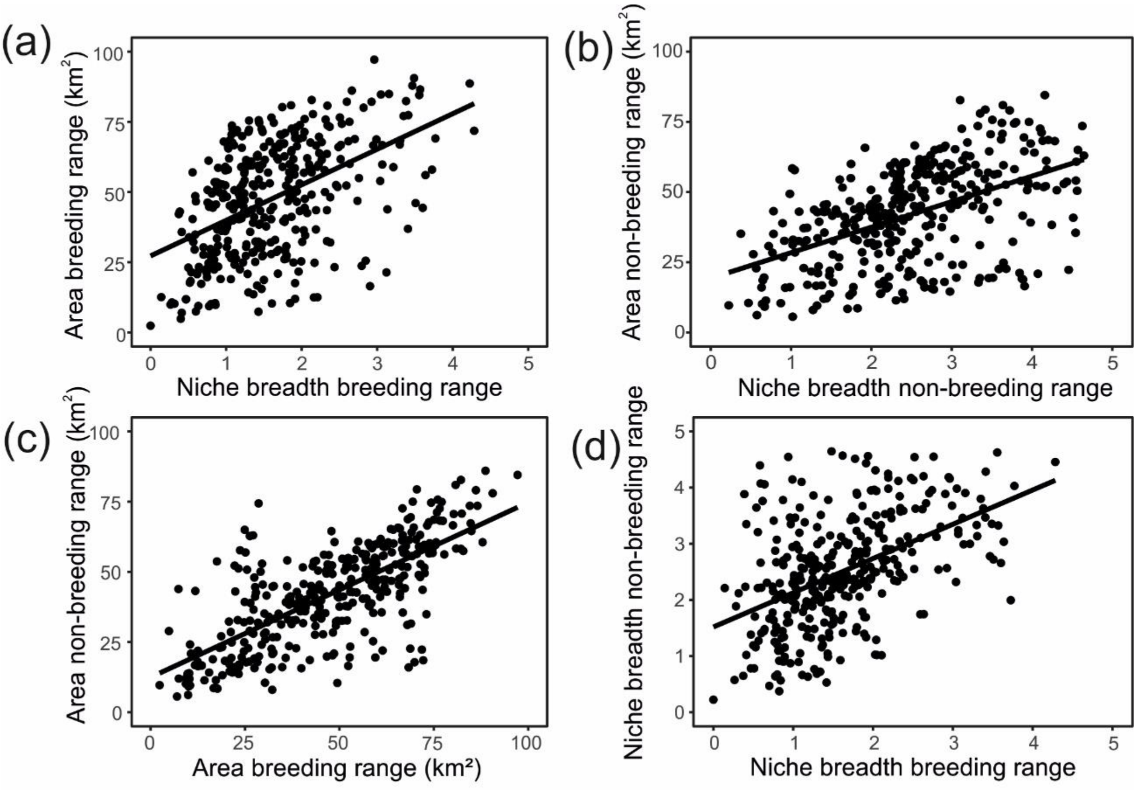

Figure 3.4. Regressions relating breeding niche breadth with the area of the breeding range (a) ($F_{1,353}$ = 110.5, P < 0.0001, R^2 = 0.24), non-breeding niche breadth with the area of the non-breeding range (b) ($F_{1,353}$ = 125.8, P < 0.0001, R^2 =0.26), area of the breeding range with the area of the non-breeding range (c) ($F_{1,353}$ = 371, P < 0.0001, R^2 =0.51), and breeding niche breadth with the non-breeding niche breadth (d) ($F_{1,353}$ = 118.3, P < 0.000, R^2 = 0.25).

As the dimension of the climatic niche might be due to the extent of the geographical range, we calculated the relationship between each breeding or non-breeding range with the area of each seasonal territory. We find that the climatic niche breadth of the breeding range is related to the extent of the breeding range ($F_{1,353}$ = 110.5, P < 0.0001, R^2 = 0.24) (Fig. 3.4a), as well as the climatic niche breadth of the non-breeding range is related to the extent of the non-breeding range ($F_{1,353}$ = 125.8, P < 0.0001, R^2 =0.26) (Fig. 3.4b). Furthermore, species with a large breeding range present also a wide non-breeding range ($F_{1,353}$ = 371, P < 0.0001, R^2 =0.51) (Fig. 3.4c). Nevertheless, the relationship between niche breadth of breeding and non-breeding ranges is not so strong ($F_{1,353}$ = 118.3, P < 0.0001, R^2 = 0.25), but also statistically significant (Fig. 3.4d).

Climatic niche and migratory distance

We found a statistically significant negative relationship between migratory distance and climatic niche overlap between breeding and non-breeding ranges ($F_{1,353}$ = 133.9, P < 0.0001, R^2 = 0.27) (Fig. 3.5a). No relationships were found between total niche breadth and migratory distance (Fig. 3.5b) or non-breeding niche breadth and migratory distance (Fig. 3.5d); however, a low but significant and negative relationship appears between breeding climatic niche breadth and migratory distance ($F_{1,353}$ = 52.46, P < 0.000 R^2 = 0.13) (Fig. 3.5c).

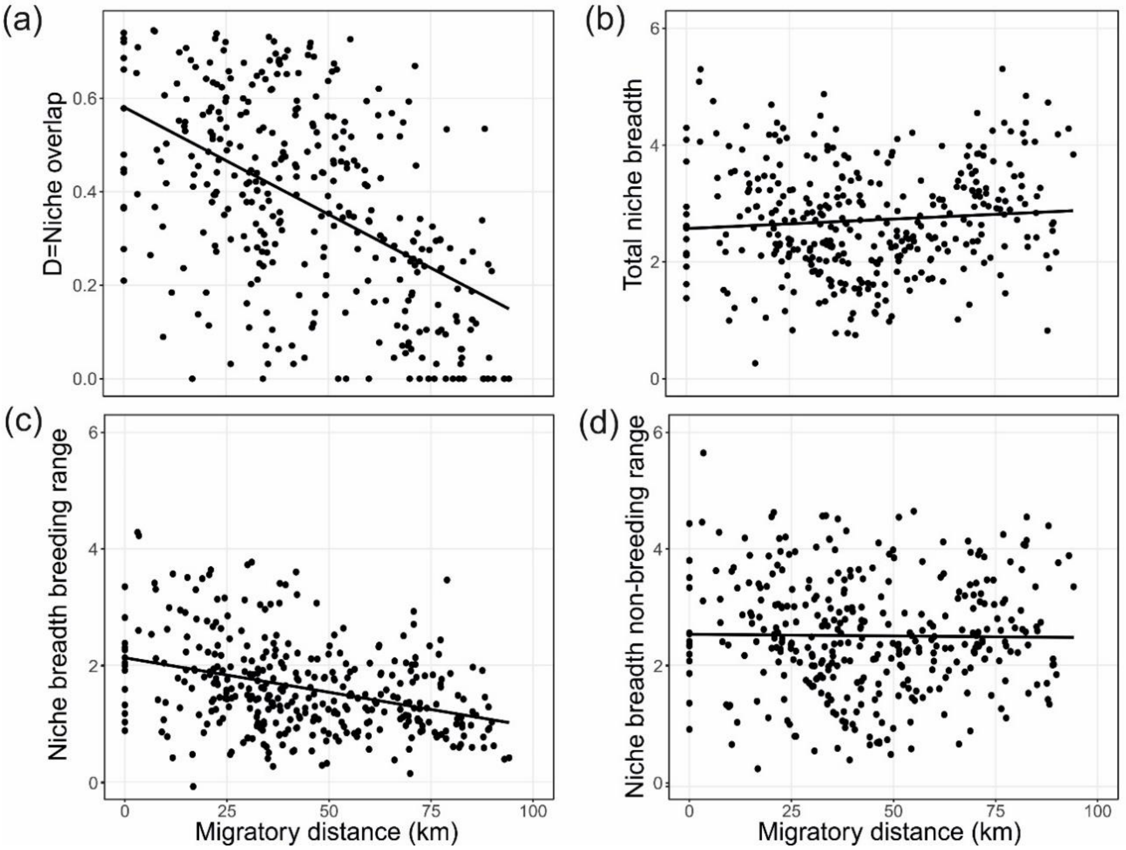

Figure 3.5. Regressions relating median migratory distance with climatic niche overlap (a) ($F_{1,353}$ = 133.9, P < 0.0001, R^2 = 0.27), total climatic niche breadth (b) ($F_{1,353}$ = 1.541, P = 0.2153, R^2 = 0.0015), breeding climatic niche breadth (c) ($F_{1,353}$ = 52.46, P < 0.0001, R^2 = 0.13) and non-breeding climatic niche breadth (d) ($F_{1,353}$ = 0.1708, P = 0.6796, R^2 = 0.0004).

DISCUSSION

Our results support a scenario where most species experience different climatic conditions during breeding and non-breeding seasons, rejecting the hypothesis that species select areas throughout the annual cycle with similar or overlapping climates (climatic niche tracking). This suggests that niche breadths of most migratory bird species are wider than expected, hence severely underestimated when only considering the annual climate, as many studies modelling their distributions do (e.g. Doswald *et al.*, 2009; Hu *et al.*, 2010; Zink & Gardner, 2017). Our study comprises all migratory species from Africa to Europe and some that also migrate from Asia to Africa, showing that this pattern is global, being shared by different taxonomic groups and from small-bodied to larger species.

We find a significant negative relationship between migratory distance and the overlap between seasonal climatic niches, unlike the study of Laube *et al.* (2015), which considered only *Sylvia* warblers, where this relationship was not significant. The increase in migratory distance goes along with the increase in the divergence of seasonal climatic niches. Species showing among the longest migratory distances in birds, mainly shorebirds, breed in northern latitudes, experiencing summer arctic conditions, but do not winter in similar environments in the southern hemisphere given the reduced or the lack of area extent in those latitudes (Piersma, 2007). On the contrary, one of the orders with more overlap between seasonal climatic niches is Pelecaniformes, which also has a significant part of their occurrence area shared between both seasons, as some individuals remain sedentary in temperate latitudes (del Hoyo *et al.*, 2018). The high level of seasonal niche differentiation suggests that migratory birds have wider niche breadths than expected by their distributions, being able to better deal with a wide range of climatic conditions.

An unexpected result is the negative relationship between the breeding climatic niche breadth and the migratory distance, and the non-relationship between total niche breadth and migratory distance. Given the decrease in niche overlap between seasons coupled with the increase in migratory distance, we expected that species with longer movements would show wider niches (Gómez *et al.*, 2016), as seasonal environmental conditions would differ substantially. Indeed, Laube *et al.* (2015) found an increase of land cover niche breadth with migratory distance, while a decrease of land cover niche overlap with migratory distance, although they did not find any relationships when using climate to define the niche. This pattern can be explained as our study includes dissimilar species with breeding ranges in distinct latitudes, and typically birds that breed in temperate latitudes show larger extent of occurrence rather than arctic species that remain confined at high latitudes (Brommer *et al.*, 2012).

It has been shown in several taxonomic groups that sister species share similar environmental niches (Alexandre *et al.*, 2017; Losos, 2008; Peterson *et al.*, 1999; Schluter, 2000). In our study, we reported both phylogenetically closely-related species with similar breeding or non-breeding niches, but also others that did not show climatic niches conservation (**Appendix Chapter 3**, Table A3.3). This agrees with the fact that endotherm species tend to switch their climatic niche very fast in evolutionary time (Rolland *et al.*, 2018). However, globally, sister species showed higher niche overlaps between breeding or non-breeding ranges than intraspecific seasonal climatic niche. Martínez-Meyer *et al.* (2004) stated that the non-breeding niches were more conserved than breeding ones in populations of *Passerina* in a phylogenetic context, supporting the directionality of evolution of migration with the origin in tropical areas (Rappole, 1995). Generally, we observe higher conservation of breeding niches than the non-breeding ones (in 35 out of 51 pairwise comparisons of sister species present higher values of niche overlap between breeding areas than non-breeding ones). This could be explained because birds could have particular environmental requirements depending on the stage of their life cycle, specifically in the breeding season.

The switch of climatic conditions during seasonal movements suggests that climate may not be the main driver of bird migration. Several drivers have been proposed to explain the origin of bird migrations, including competition avoidance (Cox, 1968), reduced parasitism (Piersma, 1997) or lower predation risk (McKinnon *et al.*, 2010). However, the main driver of such long journeys may be related to the availability of food, particularly in breeding ranges, as it has been shown in other studies (Thorup *et al.*, 2017). It is likely that long-range migratory species move from breeding to non-breeding areas to profit from the peaks of Net Primary Productivity in each season, showing enough plasticity and physiological breadth to abide different climatic conditions between breeding and non-breeding periods.

There is a growing interest in understanding both how bird species migrate and select their breeding and non-breeding areas, as well as how they will be affected by and react to climate change. Migratory connectivity, the link between breeding and non-breeding areas at the population level (Webster *et al.*, 2002), has been shown in several species (Hahn *et al.*, 2013; Kramer *et al.*, 2018), while in others is weak (e.g. Finch *et al.*, 2017), and it has been related to population declines in populations with strong connectivity (Kramer *et al.*, 2018). Population declines in European migratory birds seem to also be partially related to the degree of dispersal during non-breeding periods, where species with restricted distributions showed larger declines than broad dispersers (Fuller, 2016; Gilroy *et al.*, 2016). As we found that most long-distance European-African species show wide climatic niche breadths, other factors than climate like habitat destruction may be more likely to be the cause of these declines.

Modelling species distributions is currently approached by using either correlative models, that build on point locality data and a statistical model to predict species distributions in space (Guisan & Zimmermann, 2000), or mechanistic models that include physiological data (Kearney & Porter, 2009). As the general lack of physiological data for most species hampers the use of mechanistic models, correlative models are the common practice. The fact that climatic characteristics for migratory birds differ in both seasons makes breeding and non-breeding seasons and climate not equivalent to infer present, future or past distributions in SDMs. In fact, even in short-distance migratory birds with breeding and non-breeding ranges very closed geographically, is not always possible to predict one seasonal range using the other one (Nakazawa *et al.*, 2004). Indeed, some studies have used annual conditions to predict the other seasons´ distribution range (Doswald *et al.*, 2009; Hu *et al.*, 2010; Zink & Gardner, 2017). This could underestimate the potential distribution ranges using climate as predictor, since part of the niche breadth would be not considered in the models, as highlighted by Eyres *et al.* (2017). According to our results and in agreement with Laube *et al.* (2015) and Eyres *et al.* (2017), this would not be the correct approach, as species may search different conditions for breeding and non-breeding periods. For this reason, SDMs should be performed with seasonal environmental conditions for each seasonal area (Heikkinen *et al.*, 2006). Our results suggest that most long-range migratory species have better cards to deal with climatic change than what it would be expected by considering only the climate from their breeding ranges, although there are also other constraints related to migration that may prevent colonising novel suitable areas under climate change (Toews, 2017), which needs to be further explored.

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Chapter 4:

Lack of evidence of a Pleistocene migratory switch in actual bird long-distance migrants between Eurasia and Africa

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Lack of evidence of a Pleistocene migratory switch in actual bird long-distance migrants between Eurasia and Africa

Abstract:

During the Plio-Pleistocene, glacial cycles have shaped Northern Hemisphere species' distributions causing range contractions followed by posterior re-expansions during interglacial periods. In bird migratory species, climatic changes could result in a rapid re-shape of their distribution ranges and/or migratory behaviour, given their capacity of movement. In this context, it has been suggested that long-distance north American migratory species could have lost their migratory condition during cold periods regaining it later in warmer periods. Here, we wanted to test this hypothesis in Eurasian-African extant migratory bird species. If these species switched from long distance migratory behaviour to sedentary behaviour during the Last Glacial Maximum (LGM), hindcasted species distribution models should show a significant overlap in their breeding and wintering ranges around the Mediterranean Basin year around. We modelled present and last glacial maximum distribution of 80 trans-Saharan bird migratory species and we revised the available fossil record for the Plio-Pleistocene covering Europe and Africa. Our results show a southwards reduction of the breeding distributions during the LGM compared to the present. However, the current wintering areas were somehow similar in the Pleistocene, with the Saharan belt gap always present through time, not overlapping with breeding ranges. Pleistocene fossils from Africa support that these species were present in Subsaharan Africa as migrants based on the lack of medullary bone, not supporting the hypothesis of a loss of migratory condition in these species. Interestingly, in almost all species there was a reduction of migratory distances, and fossils support that several species like geese and swans were long-distance Sub-Saharan Pleistocene migrants that do not migrate across the Sahara anymore.

Keywords: bird migration, Pleistocene, LGM, Species Distribution Models, trans-Saharan migratory birds.

INTRODUCTION

The recent biogeographic history of species distributed in the Northern Hemisphere has been largely influenced by Quaternary glacial cycles. Plio-Pleistocene glaciations shaped species' distributions causing range contractions, followed by posterior expansions of some species during interglacial periods until today (Hewitt, 1999; Webb & Bartlein, 1992). The shifts in species ranges depended on the extent of suitable areas available for their survival, as a large part of the Northern Hemisphere was covered by ice sheets intermittently (Ehlers & Gibbard, 2004). During glaciations, Palearctic and Nearctic species experienced a northern contraction of their distribution ranges to southward latitudes were climatic conditions were suitable, which in some cases supposed an important constriction of their distributions and confinement to the so-called glacial refugia (Hewitt, 1999; Stewart *et al.*, 2010). Those range expansions and contractions may have led to population splits and had demographic impacts, likely acting as a driver in species diversification and population divergence processes (Hewitt, 2000; Kvist *et al.*, 2004; Lovette, 2005; Weir & Schluter, 2004).

Migratory species, like birds, can show more plastic responses to such climatic cycles than sedentary ones, as they can move fast from one area to another in search for resources (see **Chapter 2** and **Chapter 3**, Ponti *et al.*, 2018) and suitable conditions. This could result in a rapid re-shape of their distribution ranges and/or migratory behaviour [e.g. *Serinus serinus* (Newton, 2010), *Sylvia atricapilla* (Plummer *et al.*, 2015), or introduced *Carpodacus mexicanus* (Able & Belthoff, 1998)]. Birds can be sedentary, nomadic, dispersive or migratory (Eyres *et al.*, 2017), the latter performing short-distance (SD) or long-distance (LD) migrations at a continental scale. The ongoing discussion about the origins of migratory behaviour is sometimes mixed with the re-shaping of distribution ranges and migratory distances caused by recent Quaternary glaciations.

Two competing hypotheses were usually advocated to explain the origins of migration linked to geography: the “southern home hypothesis”, where migratory behaviour evolved from a tropical ancestor that spread northwards (Berthold, 2001; Rappole, 1995; Rappole & Jones, 2002; Safriel, 1995); and a “northern home hypothesis” where Northern Hemisphere birds colonised tropical areas driven by climate change (Gauthreaux, 1982; Rappole, 1995; Salewski & Bruderer, 2007). The major flaw of both hypotheses is that they are based on current climate and biogeographical setting, but they do not account for the latitudinal shifts of tropical climates during the Cenozoic, as many areas in the Northern Hemisphere experienced wet tropical climate since the Paleocene to the Oligocene-Miocene (Mosbrugger *et al.*, 2005). Considering this, a novel "shifting home model" hypothesis was proposed (Louchart, 2008), where latitudinal shifts of ancestral tropical zones are considered. The model is exemplified by Palearctic-Paleotropical (Ethiopian) species but can be applied to other biogeographical regions. Under this model, the ancestors of western Palearctic LD migrants had a tropical ecology, and the fossil record proves that many non-migratory tropical bird species where present in the western Palearctic until the Miocene and missing in the Plio-Pleistocene (Louchart, 2008; Mayr, 2005; Mlíkovsky, 2002; Mourer-Chauviré, 1993; Sánchez Marco, 2004; lower vertebrate database: fosFARbase (Böhme & Ilg, 2003) (http://www.wahre-staerke.com/); Paleobiology Database: https://paleobiodb.org/#/). The transition from non-migratory to SD first and LD migration later was driven by the increasing climatic seasonality at several time periods during the Cenozoic, which shifted bird winter ranges to the equator searching for more distant favourable wintering areas (Louchart, 2008). LD migration could have repeatedly arisen at the boundary of the Eocene-Oligocene, the late Miocene or the Pliocene, when the latitudinal gap between winter and summer northern limits of humid tropical conditions increased (Louchart, 2008). The general cooling since the Pliocene, that became the ice ages during the Pleistocene (Zachos *et al.*, 2001), as well as the aridification of Africa in the Plio-Pleistocene (DeMenocal, 1995; Trauth *et al.*, 2009), reshaped ranges and probably migratory distances, but those likely happened after migratory behaviour originated in Palearctic species.

Migratory behaviour has been considered a labile character that appeared and disappeared independently multiple times in the evolutionary history of birds (Rappole *et al.*, 2003; Zink, 2011). However, there are no data on how fast this switch from sedentary to migratory could have happened in evolutionary times, and there are few examples of island populations that became sedentary from migratory ancestors (Dietzen *et al.*, 2008; Salomonsen, 1950). Some authors proposed the hypothesis that the last glaciation could have shifted the migratory behaviour and migratory routes of some North American species (Winger *et al.*, 2014; Zink & Gardner, 2017), that may have lost their migratory condition to recover it later. This has also been suggested for some species of the genus *Junco* (Milá *et al.*, 2006), *Charadrius* complex (Joseph *et al.*, 1999) or the genus *Catharus* (Ruegg *et al.*, 2006), which could became LD migratory from a sedentary state after the retreat of the

Last Glacial Maximum (LGM) ice sheets. Although none of these studies could completely discard short distance migration in these species during glaciations, it is unclear if a pattern of losing the migratory condition during ice cycles is a general rule or circumscribed to specific regions and species. In other words: did LD Eurasian to Africa migratory species lose their migratory condition as well as it has been suggested for North American species during glaciations?

The extent and latitudinal range of ice sheets during the LGM in the Northern Hemisphere was not equal in the Nearctic and in the Palearctic (Ehlers & Gibbard, 2004). Ice sheets covered most of North America south to *ca.* 40º latitude north, with some refugia in western North America, Appalachia or Beringia. In the Palearctic, the ice sheets extended to *ca*. 50º latitude north, being some parts of central Europe and the European Peninsulas ice-free, as well as the Mediterranean basin. This scenario suggests that Eurasian migratory bird species were able to persist during cold cycles around the Mediterranean basin and central Europe, corroborated by the fossil record (Blondel, 1987; Finlayson *et al.*, 2012; Moreau, 1972; Mourer-Chauviré, 1993; Sánchez Marco, 2004). Otherwise, in Africa the cooling was much less intense, but since the Plio-Pleistocene the aridification increased extending the Saharan belt (DeMenocal, 1995; Trauth *et al.*, 2009), generating a potential barrier between northern breeding and sub-Saharan wintering quarters. This desert may have prevented sub-Saharan migration in some species.

Here, we aimed to explore the hypothesis proposed for North American species (e.g. Zink & Gardner, 2017) in Eurasian-African extant migratory bird species: did their breeding and wintering potential distribution ranges overlapped during the LGM around the Mediterranean basin and they switched from LD migratory to sedentary? And in this particular case, did the Sahara contribute as well acting as a full barrier preventing also this trans-Saharan migration? For doing this, we used eighty one LD migratory trans-Saharan bird species from different orders and families. We integrated two approaches: current and hindcasting paleoclimatic modelling of their potential breeding and wintering distributions and a literature review of the fossil record in breeding and wintering ranges through the Plio-Pleistocene to detect potential evidences of migratory behaviour during the Pleistocene.

Species distribution models (SDMs) have been broadly used to infer the current species geographical distributions based on environmental variables (Peterson *et al.*, 2011), as well as to hindcast by modelling into the past using paleoclimatic layers (Nogués-Bravo, 2009) and forecast (Botkin *et al.*, 2007) their potential distributions into the future. Although the niche of a species is composed by both biotic and abiotic components, the climatic component is commonly used to perform SDMs, which identify specie's potential distributions (Hutchinson, 1957; Peterson *et al.*, 2011), by correlating species' occurrence and the climate from where they occur. To better quantify the climatic niche of migratory species, their dynamic distribution and climatic conditions have to be taken into consideration (Eyres *et al.*, 2017; Laube *et al.*, 2015). Given that, in migratory bird species, to define their climatic niche and to model the present and past potential distributions, both season, time and distribution range have to be accounted for independently. The Plio-Pleistocene fossil record is rich in Europe, but scarce in sub-Saharan Africa. By the scrutiny of the fossil bird literature, we looked for examples of European LD migratory species that appeared in sub-Saharan Africa during the Plio-Pleistocene that would support the hypothesis of persistence of LD migration in these periods.

MATERIALS AND METHODS

Species distribution models (SDMs)

Eighty-one species of trans-Saharan migratory birds were selected to explore our hypotheses. We performed present and LGM SDMs for the breeding and the wintering ranges separately for each species. All the species studied breed in Eurasia and spend the winter in Africa, crossing the Sahara desert to reach their wintering areas each season. The pool of species is heterogeneous both phenotypically and phylogenetically, including species from 13 different orders and 27 families (full list in **Appendix Chapter 4**, Table A4.1). This taxonomic coverage is essential to explore a possible global pattern in the trans-Saharan migratory birds. All species distribution maps came from Birdlife (BirdLife International and NatureServe, 2011). Those maps provide raw distributions and are not pruned, so they include some unsuitable areas for each species. Thus, we redefined the distribution maps by overlapping habitat maps with the habitat categories that are suitable for each species and should occur, following the same approach as in **Chapter 2 and 3**, see **General Methods**, Section "Correction of bird distribution maps and data extraction". From the corrected maps, we randomly generated 10,000 points used as points of occurrence using GME V. 7.1 package for ArcGIS (Beyer, 2012). We used as maximum geographical extent for our models Africa, Eurasia and Australasia. Depending on the original extent of each species, we maintained the maximum extent or reduced the area in which we performed and projected the SDMs. In this extent, we randomly generated 20,000 points considered as background.

As climatic variables, we used monthly precipitation and temperature (mean, maximum and minimum) for the months that spent each species in the breeding and wintering ranges separately. We retrieved 2.5 min resolution (~5x5km) global maps for each variable from WorldClim 2.0 (Fick & Hijmans, 2017) for the present. For the LGM, we retrieved the available data from WorldClim 1.4 (Hijmans *et al.*, 2005) and calculated the mean temperature by averaging maximum and minimum temperature maps.

From the suite of available models for predicting species distributions, we ended with a selection of four that best suited our variables and type of absences: general linear model (GLM), polynomial GLM, general additive model (GAM) and BIOCLIM. After testing, we discarded MaxEnt and DOMAIN algorithms due to its overall poor performance when applied to our data. For each species, we trained each model using the climate of the present months corresponding to its breeding or wintering season. To avoid possible bias linked to each model, we created an ensemble forecast by averaging the results from the four models, since evidence exist that averaging several model outputs reduces the uncertainty induced from individual model projections (Araújo & New, 2006; Araújo *et al.*, 2005). We evaluated all those models using the Area Under the Curve ROC (AUC) and COR (correlation) approach. The AUC value ranges from 0.5 to 1, where 1 indicates a perfect discrimination between presences and absences and 0.5 indicates a random discrimination. If AUC < 0.5, the discrimination is less than random (Elith *et al.*, 2006).

Each model was projected under present and past (LGM) climates. As it is not known whether phenological changes happened during the LGM, given the observed climatic variation along the year during the LGM from paleoclimatic layers, we assumed that the LGM breeding and wintering seasons did not greatly differ from the present ones. All studied species have a breeding season within the interval from March to September and a wintering season between September to March. To exclude overlapping and passage months, we selected the interval from May to August as main breeding season and from October to March as main wintering season. We then projected the model into these seasons to have a common framework to compare between species and periods. We converted the ensemble forecasts into a presence-absence (0/1) map. To do so, we considered as presence all the values above a certain presence probability threshold. This threshold was calculated for each species as the point where the sensibility and the specificity diverge in the model (Liu *et al.*, 2005).

All present distribution models were compared with the current real distribution of each species, to ensure that the models performed well. We summed all SDMs of the breeding and the wintering season during the present and the LGM independently to identify the areas with higher diversity of migratory bird species in both periods and in both seasons. All the steps were computed using raster (Hijmans & van Etten, 2014), dismo (Hijmans *et al.*, 2017), rgeos (Bivand & Rundel, 2014), rgdal (Keitt, 2010), plotmo (Milborrow, 2015) and mgcv (Wood & Wood, 2015) packages for R.

Statistical analyses

For each present and hindcasted SDMs, we exported the mean latitude of each species' breeding and wintering ranges. Considering all 81 species together, we compared the mean of the latitudes in the present and in the LGM in both seasons, by using a non-parametric statistical test (Mann-Whitney-Wilcoxon test), as the data do not meet conditions of normality for all comparisons.

To quantify the changes in migratory distances in both seasons, as a proxy of migratory distance we calculated the distance between the mean latitude of the breeding range and the mean latitude of the wintering range, both in the present and in the LGM. We plotted the migratory distance in the present and in the LGM for each species. We also performed a Mann-Whitney-Wilcoxon test to explore if there are statistically significant differences between the migratory distances in the present and in the LGM.

Fossil record

We revised the available literature for the Plio-Pleistocene covering Europe and Africa, as well as global databases like the Pelaobiology database (https://paleobiodb.org) and the fosFARbase (Böhme & Ilg, 2003) (http://www.wahre-staerke.com/). The data from Paleobiology database were downloaded on 15 July 2018, using the group name 'aves' and the following parameters: time intervals = Pleistocene, region = Europe + Africa, output = coordinates.

RESULTS

The species distribution models suggest an overall pattern of contraction of northern breeding range margins during the LGM and posterior recolonization of northern latitudes in the Holocene, and a general stability in wintering sub-Saharan distribution ranges from the LGM to the present. All ensemble forecast SDMs showed an AUC > 0.7, a threshold broadly used to consider it a good model (Hijmans, 2012), for both breeding and wintering ranges. Only two species, *Coracias garrulus* and *Gallinago media*, showed a lower AUC (0.65) in their wintering SDMs (**Appendix Chapter 4**, Table A4.1). However, the wintering distributions of both models are in agreement with the actual wintering distribution of both species. Moreover, 119 out of 161 (74%) SDMs showed an AUC > 0.8. We did not perform the SDM of the wintering range of *Caprimulgus ruficollis* as its current distribution is too reduced that made it impossible to model with such few records.

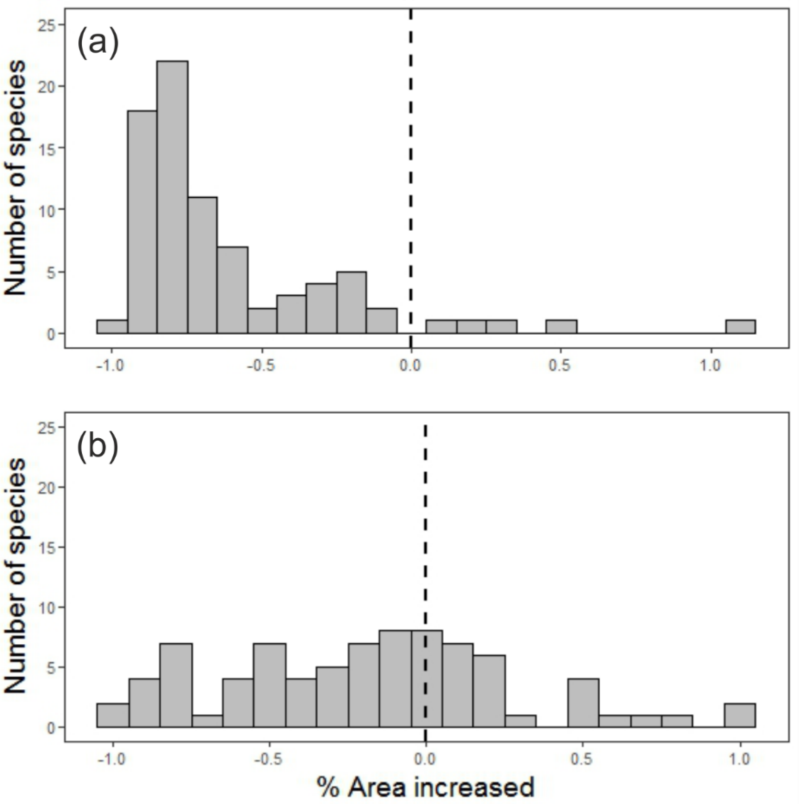

Figure 4.1. Area extent (in percentage %) increased from the present to the LGM, in the (a) breeding season and in the (b) wintering season, for the 80 migratory bird species (excluding *Caprimulgus ruficollis*). Negative values indicate a reduction in the extent during LGM compared with the present.

All migratory species show a displacement southwards of their breeding range during the LGM, compared to their present breeding range (**Appendix Chapter 4**, Figures A4.1). Moreover, all species (save five) exhibit an important decrease in the extent of their breeding range during the LGM (Fig. 4.1a). The only species that shows an extreme decrease in its breeding range during the LGM is *Clanga pomarina* (**Appendix Chapter 4**, Figures A4.1). Mann-Whitney-Wilcoxon test (V) shows that there are statistically significant differences between the mean latitudes of the breeding ranges in the present and in the LGM (V=3321, p-value<0.0001) (Fig. 4.2).

Models suggest slight distribution shifts towards the equator (Fig. 4.2) but not significant range reductions of wintering ranges during the LGM that remained somehow similar. (Fig. 4.1b, **Appendix Chapter 4**, Figures A4.1). Mann-Whitney-Wilcoxon test shows statistically significant differences between the mean latitudes of the wintering ranges during the present and during the LGM (V=2356, p=0.0004). 49 of the 80 modelled species showed a decrease in their wintering distribution extent during the LGM compared to the present, but other 23 out of 80 species increased their area extent (29%). However, the variation in extent remained negligible compared with the breeding range variation.

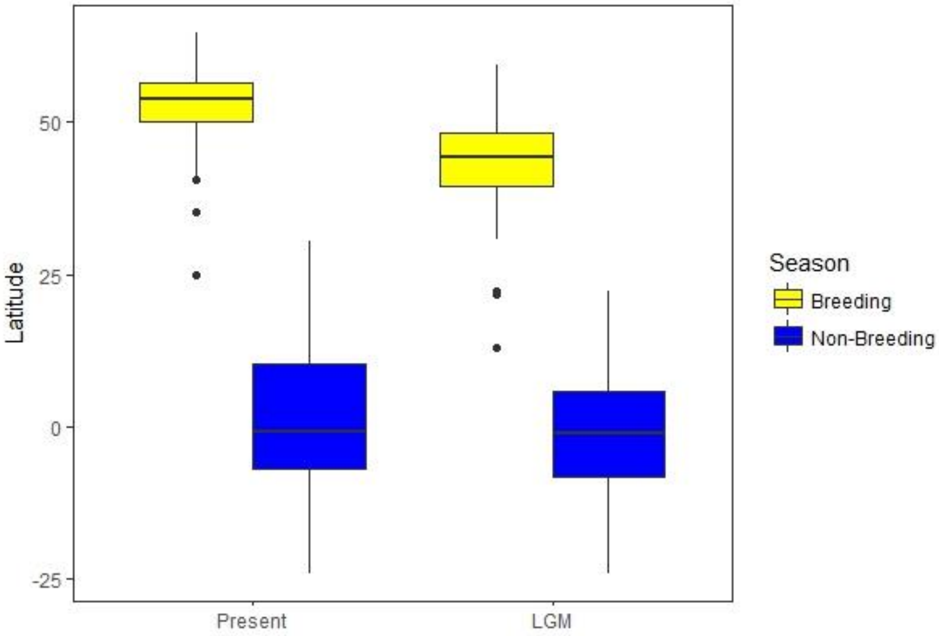

Figure 4.2. Boxplot indicating the mean latitudes during the present and the LGM in the breeding and non-breeding season for 80 bird migratory species and 1 more in breeding season (*Caprimulgus ruficollis*).

The richness maps of the breeding and wintering seasons during the present and the LGM suggest a shift of the breeding bird diversity towards the Mediterranean basin in the LGM (Fig. 4.3a and b), while in the present LD migratory species occupy most of the Eurosiberian region. Conversely, the areas with higher diversity in the wintering ranges barely differ from the LGM to the present, richness peaking in tropical areas (Fig. 4.3c and d). The Sahara desert remained as a potential barrier in the LGM, with almost no species predicted to occur in this area.

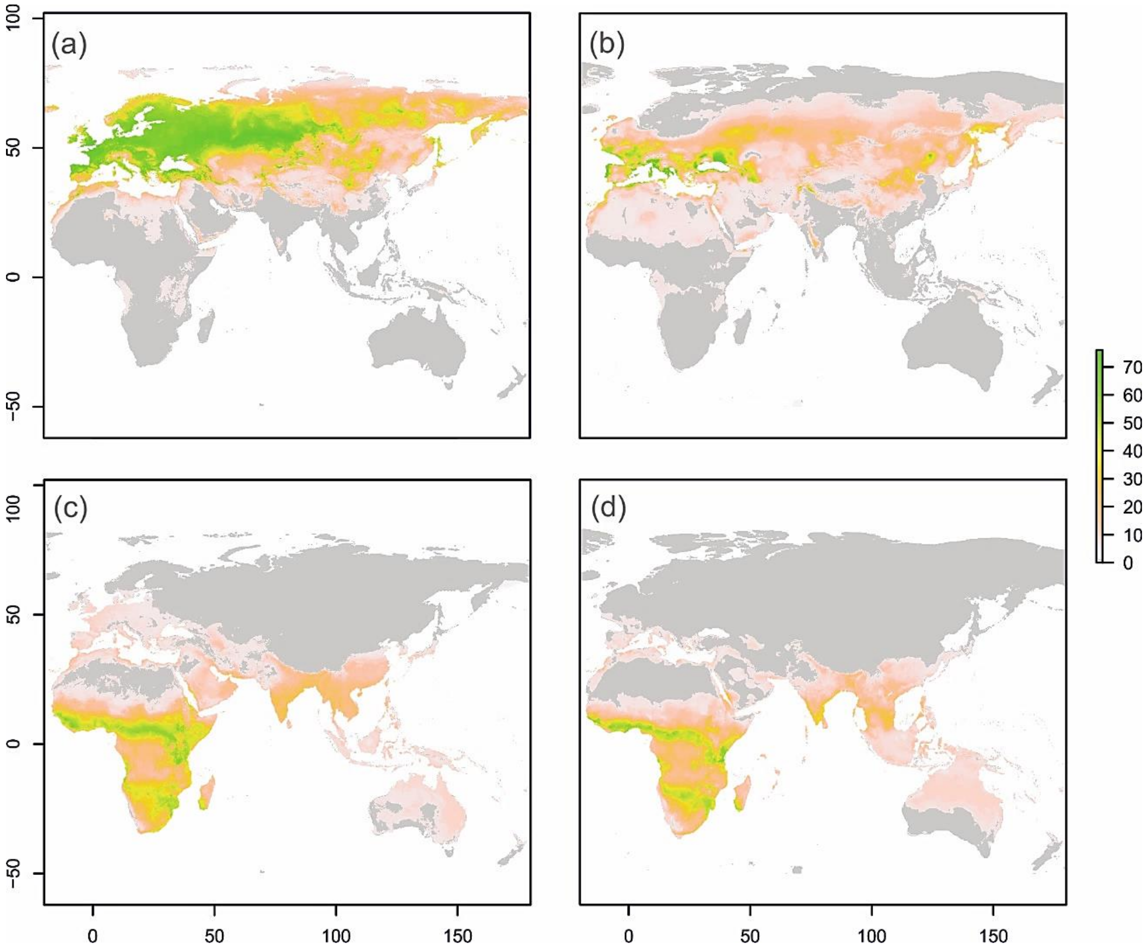

Figure 4.3. Maps of richness of the 81 bird migratory species during breeding season in (a) Present and (b) LGM; and wintering season (80 species) in (c) Present and (d) LGM.

As consequence of the shifts in the distribution of bird migratory species from the LGM to the present, the migratory distances from the breeding to the wintering ranges presented also variations. 64 out of 80 (80%) bird migratory species reduced their migratory distance in the LGM, while 16 out of 80 (20%) increased it (Fig. 4.4). However, all species that increased their migratory distance have increased it less than 700 km in average, excepting *Hieraaetus pennatus* that increased its migratory distance in 952 km because probably extended the wintering suitable area in South Africa. Three species decreased their migratory distances from the present to the LGM in more than 3700 km (*Locustella fluviatilis*, *Acrocephalus scirpaceus* and *Glareola nordmanni*), as their wintering range (that in the present occur around South Africa) shifted northward to the tropics, as well as their breeding grounds shifted southwards to the Mediterranean basin. The increase in migratory distances is linked to the increase of suitable areas in sub-Saharan Africa in the LGM for some species. There were also statistically significant differences between the mean migratory distance in the present and in the LGM, according to the Wilcoxon test (V=2987, $p<0.0001$).

The fossil record is uneven in part because the taphonomic conditions of particular habitats, like wetlands, are usually better to fossilise than other environments such as tropical forests or Savannah. Hence, the fossil record from the Plio-Pleistocene of Africa is biased to large birds in many places (mainly *Struthio camelus*) and wetland birds. Several studies of the fossil Pleistocene avifaunal communities from the Lowermost Bed II (Olduvai Gorge, Tanzania), provided a glimpse of the bird community of the existing paleo-lake around 1.72 MYA (Prassack, 2014; Prassack *et al.*, 2018). Apart from African species, fossil remains of many LD migratory Eurasian aquatic species were identified, including *Aythya cf. a. fuligula , Anas cf. A. crecca, cf. Cygnus aff. C. olor, Anser aff. A. erythropus, Pelecanus onocrotalus. Ciconia cf. C. ciconia, Recurvirostra cf. R. avosetta, cf. Calidris sp.,* and *Crex crex*. Matthiesen (1990b) reported more than 5000 sandpipers from this site, fossils that it seem to belong mainly to the genus *Calidris,* but also *Numenius, Limosa, Tringa, Lymnocryptes, Arenaria, Phalaropus* or *Limicola* (see Louchart, 2008). In Olduvai Gorge bed I (*ca.* 1.88 MYA), (Harrison, 1980) reports fossil remains of *Crex crex, Numenius phaeopus* and a possible *Charadrius hiaticula*, all LD migratory Palearctic species. In Olduvai Gorge but at the Zinjanthropus Land Surface (1.84 MYA) remains of sandpipers and plovers, as well as *Anas crecca* and *Aythya sp.* were found (Prassack, 2010). Some LD migratory Eurasian shorebirds were distributed down to South Africa in the Pleistocene, with a record of *Limosa sp.* from the Sibudu Cave (60,000 ->75,000 YA, Val, 2016). The fossil bird remains of Kom Ombo in the Upper Nile of Egypt, provide a good representation of the waterbird community present in the late Pleistocene (between 12,000 and 10,500 YA, Churcher & Smith, 1972), including 19 LD Palearctic migratory species: *Platalea leucorodia, Anas acuta, Anser albifrons, Anser fabalis, Branta bernicla/ruficollis, Tadorna ferruginea, Anas platyrhynchos, Anas penelope, Anas acuta, Aythya ferina, Mergus merganser, Mergus serrator, Mergellus albellus, Anas crecca, Ardea cinerea, Grus grus, Numenius arquata* and *Pandion haliaetus*. There are many fossil remains from the European Pleistocene for LD migrants (Sánchez-Marco, 2004; Paleobiology database (https://paleobiodb.org), the fosFARbase (Böhme & Ilg, 2003) (http://www.wahre-staerke.com/), but in most cases they cannot be assigned to precise glacial or interglacial periods.

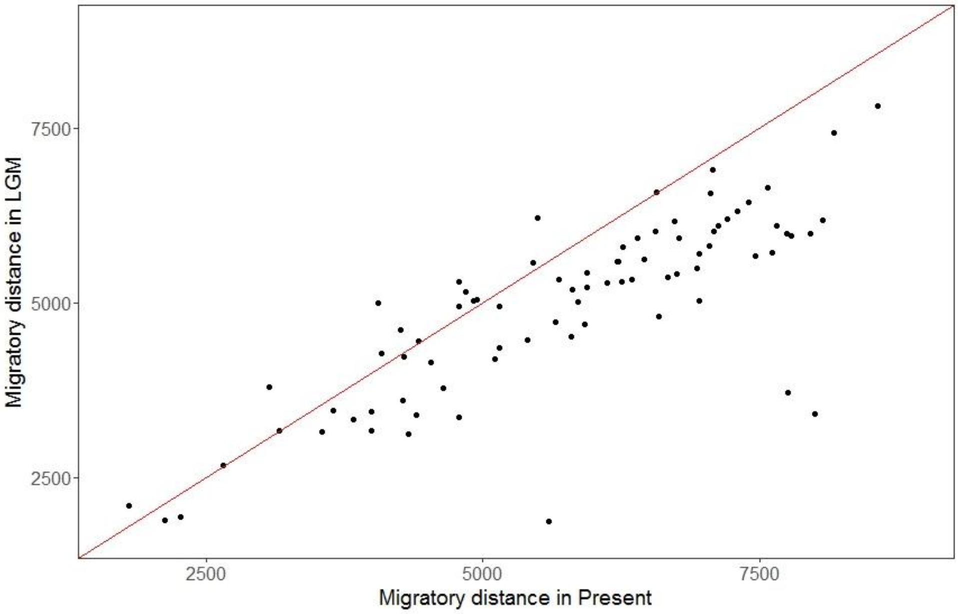

Figure 4.4. Plot of the migratory distance of each species (excluding *Caprimulgus ruficollis*) during the present and during the LGM. The red line reflects the equality of distances in both periods. Points above the red line correspond to species with larger migratory distances during the LGM compared with the present, and points below the red line correspond to species with shorter migratory distances during the LGM compared with the present.

DISCUSSION

Reconstructing the past biogeographic history of a group is always challenging, as the available lines of evidence are usually scarce and limited. Most works investigating the effects of glaciations on species distributions rely on modelling their current ranges and projecting them into the past using available paleo-climatic layers (e. g. Fløjgaard *et al.*, 2009; Nogués-Bravo, 2009; Smith *et al.*, 2013). Genetic data provide also clues like evidence of recent expansions to northern latitudes from refugia (e. g. Hansson *et al.*, 2008; Milá *et al.*, 2006; Seddon *et al.*, 2001), for which distribution inferences can be made. Few studies incorporate fossils, but in most cases, the lack of those data is the consequence of the general scarcity of fossils from particular species, periods and areas. Here, we wanted to test if the proposed hypothesis for North American birds (Zink & Gardner, 2017) of losing migratory behaviour during glacial periods, based on the overlap of breeding and wintering ranges using SDMs, fits also Eurasian-African LD migratory bird species. We combined the use of SDMs with a review of the fossil record, which also allowed us to assess the potential impact of the Saharan dry belt as an historical barrier for LD migratory species.

Our models show, as expected, a general reduction of breeding distribution ranges during the LGM. Although this was proposed since decades ago (e.g. Blondel, 1987; Moreau, 1954, 1972; Mourer-Chauviré, 1993; Sánchez Marco, 2004), we here provide the first explicit paleo-distribution models for LD migratory Palearctic-Paleotropical species and the overall species richness pattern that supports a main Mediterranean and Black sea basins distribution, matching proposed Pleistocene refugia. However, there are species nowadays distributed close to Arctic latitudes that are recovered near the 50º latitude ice boundary in hindcasted models, suggesting that they were widespread in central Europe and less affected by the general cooling. In fact, fossils show that cold adapted species like *Nyctea scandica* or *Lagopus muta* were present from central Europe south to the Pyrenees, the latter still present in few high mountain refugia (Arribas, 2004; Sánchez Marco, 2004), and most genera and species of extant European bird species survived through the Pleistocene to the present day (Finlayson *et al.*, 2012).

Migratory behaviour likely arose before the Pleistocene glaciations (Louchart, 2008). There are some African Miocene fossils that could be assigned to migratory Eurasian clades, like a *Pandion sp.* from the Abu Asa formation (Ethiopia, 5.6-5.8 MYA, Louchart *et al.*, 2008) or *Ciconia ciconia/nigra* from the Lake Victoria (14.5-16.5 MYA, Dyke & Walker, 2008). However, the bulk of evidence of the existence of ancient migratory behaviour from Eurasia to Africa comes from African Pleistocene fossils of Eurasian LD migrants than span across all Pleistocene period (Churcher & Smith, 1972; Harrison, 1980; Louchart *et al.*, 2008; Matthiesen, 1990b; Prassack, 2010, 2014; Prassack *et al.*, 2018; Val, 2016). Most of these fossils came from the Olduvai Gorge, a key hominid site that has been extensively studied, that had a lacustrine environment harbouring waterbird populations. From some of these fossils (more than 5,000 sandpipers analysed) came the conclusive and definitive evidence that those species were wintering in the LGM and not staying all year round, because they lacked medullary bone that would indicate reproduction which was present in other coetaneous fossils belonging to other waterbird species (Matthiesen, 1990a). Fossils support migratory behaviour between Europe and Africa in the Pleistocene, and our SDMs are in agreement with this showing that the actual wintering areas were somehow similar in the Pleistocene, with the Saharan belt gap always present through time.

The most parsimonious scenario is that migratory behaviour was stable, persisted through time and was not lost during glaciations.

The idea that migratory behaviour is a very labile character that can switch in a few generations is widespread. In fact, some cases have been reported of rapid switch from migratory to sedentary behaviour (Aguirre, 2013; Salomonsen, 1950) and the other way around (Helm & Gwinner, 2006; Milá *et al.*, 2006; Newton, 2010). Most of the reported cases of probable re-expression of migratory behaviour refer to American species. The glaciation setting in North America was different from Eurasia, with a much southern distribution of ice sheets, which may supposed a drastic reduction of geographic ranges and overlap between wintering and breeding areas (Zink & Gardner, 2017). This was the base to propose that migratory species lost their migratory conditions, largely based on SDMs (e.g. Zink & Gardner, 2017), but SD migration cannot be fully discarded with available data. The extension of ice sheets in Europe was smaller and SMDs and fossils do not support neither range overlap between wintering and breeding areas in LD migrants as well as lack of migratory behaviour.

The historical effect of the Saharan belt as a barrier for birds has not been fully assessed. The Plio-Pleistocene aridification of this region (DeMenocal, 1995; Trauth *et al.*, 2009) affected both current bird populations as well as Pleistocene ones. Our SDMs and available fossils support that both in the LGM and the present, LD migratory species were able to deal with this potential barrier and crossed it back and forth. For the studied species, the LGM retreat of breeding ranges to the Mediterranean basin just supposed a decrease in their migratory distances (Moreau, 1954). However, we found that fossils clearly indicate that the Sahara acted as a barrier to some LD migratory species that do not migrate to Africa anymore. Harrison (1980) reports the first *Cygnus olor* fossil record from Africa (Olduvai Pleistocene), which is later reported too by Prassack (2014). In this last work, it was also reported *Anser aff. A. erythropus*, a genus that was also present in the high Nile during the Pleistocene, where *A. albifrons* and *A. fabalis* were reported together with *Branta bernicla/ruficollis*. Those geeese and swans were clearly migratory in the Pleistocene from Eurasia to Africa but they do not occur any more para in the African continent, likely because they prefer colder environments and probably the Sahara aridification prevented them to keep their sub-Saharan occurrence. Those species likely lasted through the Holocene in Africa as evidenced by very detailed ancient wall paintings of *Anser anser*, *Anser albifrons* and *Branta ruficollis* from Egyptian empire temples, the most well known from Maidûm, tomb of Nefermaet and Itet from the 4th Dynasty that can be seen in the Cairo Egyptian Museum.

Most Palearctic-Paleotropical LD migratory bird species migrate now through routes and between regions that likely were established during the Pleistocene or before (Finlayson *et al.*, 2012). Others like swans and geese lost their LD migratory condition to Africa, probably as a consequence of the increasing Saharan belt and continuous climate warming. This is the first time where fossil evidence is interpreted in this way to support the loss of sub-Saharan LD migratory condition for some groups like geese and swans. It is not known if other bird groups for which there is no fossil record may have lost this condition too and considering the global warming scenarios expected for the next decades, how many species and how much will reduce their migratory ranges in the future.

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INTEGRATIVE DISCUSSION

The principal aim of this thesis was to explore the patterns and processes of the evolution of migratory behaviour in birds. The present thesis reached this objective from two perspectives. We first used one bird group, *Sylvia* warblers, to study the evolution of migration and the factors involved in a phylogenetic context; second, we investigated the general patterns of migration from a biogeographic and macro-ecological perspectives in several orders of migratory birds. The results exposed here shed light on the topic and contribute to a better understanding of the mechanisms involved in the evolution of migration.

One of the most intriguing aspects of bird biology is how they evolved their migratory behaviour. During the twentieth century, multiple hypotheses have been formulated to explain the historical processes involved in bird migration. In the last decades, the development of phylogenetic comparative methods and the increase of available genetic data have allowed a deeper investigation of this subject. As a classic idea, it was proposed that the transition from a sedentary population or species to a migratory one went through an obligate intermediate step were populations become partial migratory (Berthold, 1999; Berthold *et al.*, 1990). Recent studies, however, have shown that the change from a state to another can happen in a very short evolutionary time (Kondo & Omland, 2007; Kondo *et al.*, 2008; Outlaw & Voelker, 2006; Zink, 2011), although in some cases the partial migratory step is the most parsimonious one (do Amaral *et al.*, 2009). In this thesis, we claim that the evolution from the migratory to sedentary states happened very fast in *Sylvia* warblers (**Chapter 1, Chapter 2**), although conflicting and opposite results arise depending on which model is used to reconstruct the ancestral state (**Chapter 1**). In fact, if only one method is used, the interpretation could be misleading. In some analyses, the reconstruction of some ancestral nodes showed an equal probability of being sedentary or migratory, suggesting either an unresolved analysis or that the ancestral species had both migratory and sedentary populations (**Chapter 1**).

Our results are in contradiction with other groups studied like the Motacillidae family (Outlaw & Voelker, 2006) and *Icterus* species (Kondo & Omland, 2007), but in agreement with Winger *et al.* (2012) that studied the Parulidae family which showed a more probable transition from migratory to sedentary status. In some bird groups, like *Icterus*, migratory behaviour appeared more recently in some species within a group mainly sedentary being the ancestry probably also sedentary (Kondo & Omland, 2007). In other groups, like *Sylvia* (**Chapter 1**) or Parulids (Winger *et al.*, 2012), the ancestral state of the clade is migratory and sedentariness appeared later in their evolutionary history. This means that, at least in some bird groups, including *Sylvia* warblers, the cost of changing from migratory to sedentary may be less than the other way around (**Chapter 1**). Likewise, considering the morphological or physiological changes that a species may undergo when shifting migratory behaviour, the cost of reducing structures already developed is possibly less than develop them again. In this thesis (**Chapter 2**), we explored the changes in biometric characters, like the tail length, the wing length or the mass in *Sylvia* warblers, and we observed that sedentary species reduced their wing length, as it has been observed in other studies (Lo Valvo *et al.*, 1988; Pérez-Tris & Tellería, 2003; Voelker, 2001). Possibly, sedentary *Sylvia* warblers regulated the expression of certain genes related with the development of wing feathers.

These examples support the idea that migratory behaviour has evolved multiple times in the evolutionary history of birds (Zink, 2011), starting from a sedentary common ancestor of all birds, as found by Rolland *et al.* (2014) using the complete tree of birds. Rolland *et al.* (2014) also found that migratory species often have a higher diversification rate than sedentary ones, and that the migratory species generally diversify generating a sedentary daughter in addition to the migratory one. This could explain why inside an ancestral migratory clade as *Sylvia*, it can be found more recently sedentary species (**Chapter 1**).

The variability in ecological and biogeographical characteristics of each bird group makes challenging to find a general pattern concerning the appearance and disappearance of migratory behaviour. In *Sylvia* warblers, all transitions are from migratory to sedentary status, with no exception. Furthermore, most of sedentary taxa occur in islands and tropical areas, except for *Sylvia undata* that occurs in the Mediterranean Basin. In fact, it is common that bird species that colonize islands become resident and stop migrating (Dietzen *et al.*, 2008; Ferrer *et al.*, 2011), possibly due to the stable climatic conditions and the absence or reduced competition in comparison with the mainland (Crowell, 1962; Diamond, 1970; Keast, 1970). Islands in temperate latitudes, however, show yearly fluctuations in the climatic conditions as in mainland. However birds become sedentary as well possibly because islands act as a trap from where it is difficult to leave and return, promoting the evolution of sedentariness.

The advantage of living in tropical areas could be related with the high and constant availability of resources and climate (**Chapter 2**). Nevertheless, despite the more stable climatic conditions in the tropical-equatorial zones (Hastenrath, 1995), the productivity drops during some months of the year, coinciding with the dry season and the breeding season of migratory birds. This minor decrease in productivity in the tropical areas also matches with a very high increase in productivity in temperate latitudes (**Chapter 2**). Thus, migratory birds bet on the strategy of performing long journeys, by profit the peaks of productivity and reproduce in a limited number of months. On the other hand, sedentary birds remain in more constant conditions, with the possibility of producing more than one clutch per year (Catchpole & Phillips, 1992).

Migratory birds do not only profit from the peaks of productivity in temperate latitudes, but also profit from the increase in productivity while migrating and in their wintering ranges, as it has been shown in several works that used radio tracking and geo-locator technologies (Aharon-Rotman *et al.*, 2016; La Sorte *et al.*, 2014; Thorup *et al.*, 2017). In fact, Zurell *et al.* (2018) show that migratory bird species track similar conditions of productivity or NDVI from their breeding to their wintering ranges or vice versa. These findings suggest that the availability of resources is a crucial element in bird migration and possibly the reason why some species migrate. In this thesis, we found that productivity, besides its importance in current migratory yearly dynamic, it likely has been the key factor in the evolution and the appearance of migratory behaviour (**Chapter 2**). The advantage of higher availability of resources during some months in the temperate latitudes summed with the less density of species and individuals in higher latitudes (Cox, 1968) could have driven the movements of some populations or bird species and leading to the establishment of migratory behaviour.

The net primary productivity and hence the availability of resources are correlated with the climatic conditions. In fact, birds' departure from the temperate breeding regions has been related with the onset of adverse climatic conditions linked to the reduction of resources during winter (Berthold, 2001; Salewski & Bruderer, 2007). Aiming to understand how birds migrate and how they select their breeding and wintering ranges, several studies (Laube *et al.*, 2015; Martínez-Meyer *et al.*, 2004; Nakazawa *et al.*, 2004), including the **Chapter 3** of this thesis, studied the climatic characteristics of each seasonal range. The null hypothesis was that species track the same climatic conditions, and when the conditions turn inadequate in their breeding ranges, they return to tropical areas with similar conditions of those in the temperate latitudes during the spring-summer season. We did not find support for such a pattern, neither using a single group in a phylogenetic context nor in a global sense exploring all migratory birds from Africa and Europe belonging to different families. According to Laube *et al.*, (2015) that also used *Sylvia* warblers in their study and did not found a climatic niche tracking pattern in the migratory species, in **Chapter 2** we found that migratory species present a higher temperature tolerance than sedentary species. Considering that the breadth in temperature tolerance was calculated using the extremes of temperature from the breeding and wintering ranges, it means that the conditions from one season to another are different in migratory *Sylvia* warblers. Furthermore, the climate in our analyses was an essential variable in the evolution of migration, but not as important as the NPP (**Chapter 2**). Evidence of niche tracking or switching in studies from Nakazawa *et al.* (2004) and Martínez-Meyer *et al.* (2004) is ambiguous. These two studies, that reported both results of birds from Neotropical-Nearctic zones, showed that some species share similar climatic conditions in their breeding and non-breeding seasons, but also others that differ entirely. Nevertheless, those works used migratory species that move between North America and Central America but not further south. In **Chapter 3** we explored the climatic niche of species that can cover up to 8000 km of migratory distance, reaching remote places with very different characteristics from the breeding to wintering areas. Besides, we found that the longer distance birds migrate, the lesser is the climatic niche overlap between breeding and wintering areas. In other words, long migratory bird species do not move to reach similar climatic conditions, but they have higher climatic tolerance instead (niche breadth).

The wider climatic niche breath of migratory bird species suggests that the climate is not the factor that drives the evolution of migration, but the productivity (**Chapter 2**), or at least the combination of productivity and climate (Zurell *et al.*, 2018). Nonetheless, the changes in climate during the evolutionary history of birds have affected their distributions and possibly their migratory behaviour and the routes used (Winger *et al.*, 2014; Zink & Gardner, 2017). During the Pleistocene glacial periods, the ice sheet coverage of part of the Northern Hemisphere forced the breeding ranges of migratory birds to shift southwards, as well as the ranges of other animals and plants (Fløjgaard *et al.*, 2009; Hewitt, 2000; Stireman, 2005; Tarasov *et al.*, 2000; Weir & Schluter, 2004), since northern latitudes were less suitable for survival. Under this scenario, one of the questions explored in the present thesis is how migratory birds changed their distributions and especially: did they switch their migratory behaviour to sedentary during the Last Glacial Maximum (LGM), when the ice coverage was at its maximum? The studies using ancestral state reconstruction of migratory behaviour (**Chapter 1**, Kondo & Omland, 2007; Outlaw & Voelker, 2006) have shown that the shifts between sedentary and migratory states could happen in very short evolutionary time. However, how fast did these changes happen? Zink and Gardner (2017) suggested that current migratory birds, which breed in North America and winter in Central-South America, stopped migrating during the LGM remaining in their current wintering grounds. This point would support that migration change very fast within a species, being a very labile character, difficult to track in the phylogeny. Our results, from **Chapter 4**, that explore the evolution of the distributions of migratory birds from Africa and Europe, do not support this hypothesis. We found that birds during the LGM, shift southwards their breeding range, concentrating most of the breeding distributions in the Mediterranean Basin. The wintering ranges during the LGM would remain similar to the current ones. Thus, even the migratory distances would be reduced during the LGM given the lack of available ranges in northern latitudes; trans-Saharan migratory birds did not stop migrating, save that some species of geese and swans for which the fossil record suggests so.

In conclusion, according to our results, migratory behaviour would be a more conserved character than previously thought, at least during the Pleistocene. The changes in the character probably happened before in the evolutionary history of birds, and only recent island colonisation have shifted the behaviour to sedentary (**Chapter 1**).

Methodological remarks

One of the aims of this thesis, in addition to the fundamental biological questions, was to explore and to evaluate some methodologies that are commonly used in evolutionary biology, macroecology and modelling, primarily focused in migratory birds.

Chapter 1 investigates if some parameters involved in the ancestral state reconstruction methods can affect the results and the posterior biological interpretation. We found that the number of taxa included in the phylogeny (taxa sampling), the branch length of the tree, the method and the software used, affects the results and support alternative hypotheses depending on the combination used. Such result leads to relevant problems when performing those analyses and to minimise the bias, we strongly recommend exploring different methods for the same question and trying to validate with external sources like the fossil record. The fact that most of the studies published performed one single method when answering an evolutionary question makes the problem more worrisome, being probably some of the interpretations misleading. Therefore, it is of great importance to take into account the limitations of these methods for future work.

The second point that it is worth remarking here is the importance of the spatio-temporal component of the distribution of the species, especially when referring to migratory species. This issue is mainly commented in **Chapter 3** and **Chapter 4**, but all the thesis takes it into account. It is commonly assumed that Species Distribution Models (SDM), niche model evolution analyses or even macroecological studies, consider the overall yearly environmental characteristics of a particular area, without considering the temporal view. However, when the study species is migratory, only the environmental characteristics corresponding to each season for each area should be used to explore its niche. If the year-round climate is used, part of the ecological information associated to the species would be erroneous, including environmental information of months when the species is not present in the considered area.

Here, we only comment on some of them but it is undeniable that methodologies must be used with caution and the biology of each species must be considered to explore and structure the investigation of a biological question.

Future directions

This thesis contributes to the debate about how the migratory behaviour evolves in birds. Here we show that the migratory behaviour is a challenging aspect of birds' biology. We reported that in *Sylvia* warblers the best explanation of its evolution is the loss of migration of some taxa instead of gaining it and that the productivity is the main factor involved in its evolution. However, other groups must be explored to unravel if the same factors are equally important in the evolution of migration of different families and genera. On the other hand, this thesis focused one part on the incongruences in some phylogenetic comparative methods. However, to determine precisely which the problems are involved in those differences extensive simulations should be performed. Finally, one of the most exciting aspects that we want to explore as the following up of those studies is the effect of future climatic changes in the shifts of migratory behaviour of birds.

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CONCLUSIONS

1. Ancestral State Reconstruction analyses, both using continuous and discrete characters, recover different results using several combinations of branch length, taxon sampling, methods and software. Thus, such analyses must be used with caution and several methods must be performed to answer an evolutionary question.

2. In the evolution of *Sylvia* warblers, migratory behaviour switched only from migratory to sedentary status and the ancestral state of the genus was fully migratory. This may indicate a lower cost of becoming sedentary from migratory than the other way around. The evolution from migratory to sedentary state in *Sylvia* warbles probably happened in a very short evolutionary time. Some of the sedentary species occur in islands, where probably their ancestral arrived and stopped migrating immediately.

3. The phylogeny of *Sylvia* warblers performed in this thesis showed that, the species before considered *Lioptelus nigricapillus*, *Parophasma gallineri* and *Pseudoalcippe atriceps,* are nested within *Sylvia*. This suggests that all belong to *Sylvia* we propose their taxonomic change to this genus.

4. The evolution of migratory behaviour in *Sylvia* warblers was correlated in our analyses with the productivity in the breeding areas, suggesting that migration could have evolved in order to reach resources during the breeding season.

5. Morphologically, there are differences in the length of the wings between sedentary and migratory species or even subspecies of *Sylvia*. This shows a high degree of plasticity or a difference in gene expression in a very short evolutionary time.

6. The climatic conditions from the breeding and wintering ranges differ completely in migratory birds (both in *Sylvia* warblers and in Euro-African migratory species). Thus, the climatic niche breadth of migratory birds is larger than only considering the climatic conditions from one season, and possibly migratory birds have a larger range of tolerance of temperature and precipitation. This important aspect should be considered when performing species distributions models (SDMs).

7. Migratory birds do not track climatic conditions, suggesting that the climate itself is not likely the driver of the evolution of migratory behaviour.

8. SDM analyses suggest that trans-Saharan bird migratory species did also migrate during the Pleistocene, and there is no evidence to presume that they stopped migrating during the Last Glacial Maximum. Given that, the origin of migratory behaviour probably were before the Pleistocene, and the glaciation modified routes and migratory distances of migratory birds.

9. Our results also sustain that the Sahara acted as a barrier also in the Pleistocene, and that its aridification probably increased the separation between the breeding and wintering area in the present, linked with the shift northwards of the breeding ranges with the retreat of the ice sheets.

APPENDIX CHAPTER 1

Appendix A1.1. Genbank accession numbers

Sylvia abyssinica abyssinica AJ534548, EU652717; *Sylvia atricapilla heineken* EF446845; *Sylvia atricapilla gularis* EF446851; *Sylvia atricapilla atricapilla* JF502273, JF502313; *Sylvia atricapilla3* JF502275, JF502315; *Sylvia atricapilla2* JF502274, JF502314; *Sylvia atricapilla1* JF502276, JF502316; *Sylvia balearica* JF502277, JF502317; *Sylvia boehmi boehmi* JF502278, JF502318; *Sylvia boehmi* JF502279, JF502319; *Sylvia boehmi somalicum* AJ534530; *Sylvia borin* AJ534549; *Sylvia borin woodwardi* JF502281, JF502321; *Sylvia borin* JF502280, JF502320; *Sylvia buryi* JF502282, JF502322; *Sylvia cantillans1* JF502283, JF502323; *Sylvia cantillans*2 JF502284, JF502324; *Sylvia cantillans cantillans* EU760645; *Sylvia cantillans3* EU760670; *Sylvia subalpina2* EU760693; *Sylvia subalpina* EU760650; *Sylvia communis communis1* JF502285, JF502325; *Sylvia communis volgensis* JF502286, JF502326; *Sylvia communis communis2* JF502287, JF502327; *Sylvia communis* JF502288, JF502328; *Sylvia conspicillata orbitalis* EF446885; *Sylvia conspicillata conspicillata* JF502289, JF502329; *Sylvia crassirostris* JF502290, JF502330; *Sylvia hortensis* AJ534534; *Sylvia curruca althaea* KC512557; *Sylvia curruca2* JF502292, JF502332; *Sylvia curruca3* JF502293, JF502333; *Sylvia curruca blythi* JF502291, JF502331; *Sylvia curruca blythi1* KC512466; *Sylvia curruca blythi2* KC512508; *Sylvia curruca halimodendri1* KC512524; *Sylvia curruca halimodendri2* KC512544; *Sylvia margelanica1* KC512573; *Sylvia margelanica2* KC512603, KC512593; *Sylvia curruca curruca* KC512656; *Sylvia curruca minula* KC512631; *Sylvia deserticola maroccana* JF502294, JF502334; *Sylvia dohrni* FJ976085, FJ976085; *Sylvia layardi* JF502296, JF502336; *Sylvia layardi2* JF502297, JF502337; *Sylvia leucomelaena* AJ534533; *Sylvia lugens clara* JF502298, JF502338; *Sylvia lugens lugens* AJ534532; *Sylvia melanocephala melanocephala2* EF446859; *Sylvia melanocephala1* JF502299, JF502339; *Sylvia melanocephala2* JF502300, JF502340; *Sylvia melanocephala melanocephala1* EF446858; *Sylvia melanocephala momus* EF446883; *Sylvia melanothorax* JF502301, JF502341; *Sylvia mystacea mystacea* JF502302, JF502342; *Sylvia mystacea rubescens* AJ534545; *Sylvia nana nana* JF502304, JF502344; *Sylvia nana* JF502303, JF502343; *Sylvia nisoria nisoria* JF502305, JF502345; *Sylvia nisoria* JF502306, JF502346; *Sylvia rueppelli1* JF502307, JF502347; *Sylvia rueppelli2* JF502308, JF502348; *Sylvia sarda* JF502309, JF502349; *Sylvia subcaerulea* JF502311, JF502351; *Sylvia subcaerulea subcaerulea*

JF502310, JF502350; *Sylvia undata undata* JF502312, JF502352, *Sylvia nigricapilla* JN827093, JN826570; *Sylvia galinieri* FJ357999; *Sylvia atriceps1* JN827159, JN826633; *Sylvia atriceps2* JN827158, JN826632, *Paradoxornis guttaticollis* JX565695, JX565688; *Phylloscopus collybita* EU851075, DQ125988.

Figures A1.1-A1.62. Supplementary figures showing results for every Ancestral State reconstruction analysis performed for discrete and continuous characters.

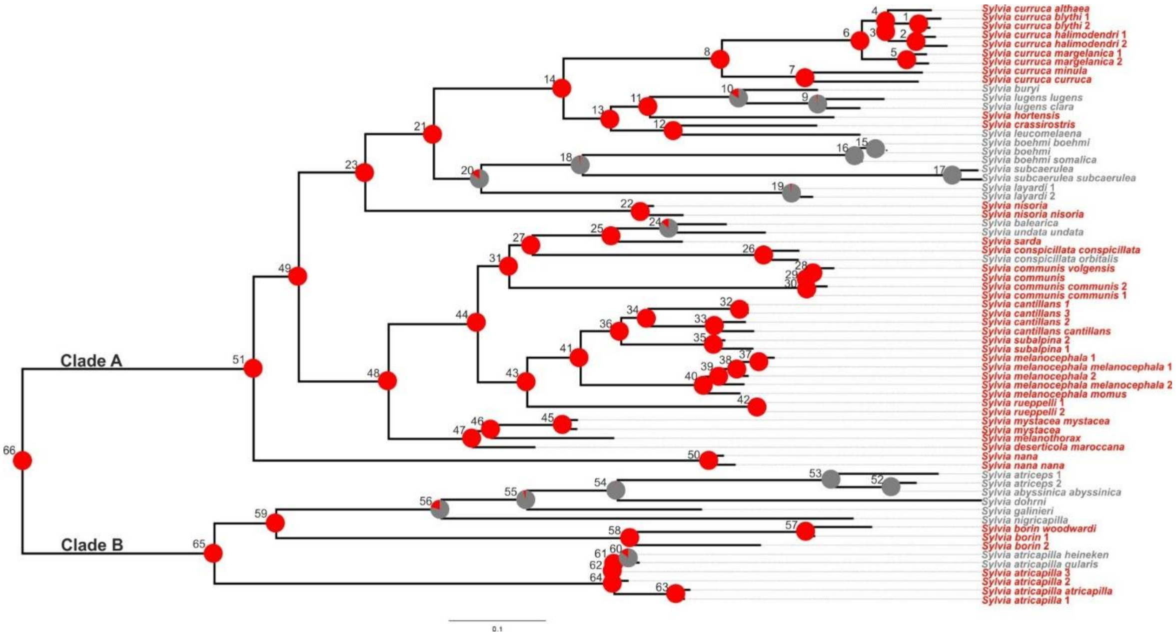

Figure A1.1. BISSE ASR analysis in Diversitree package using a phylogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

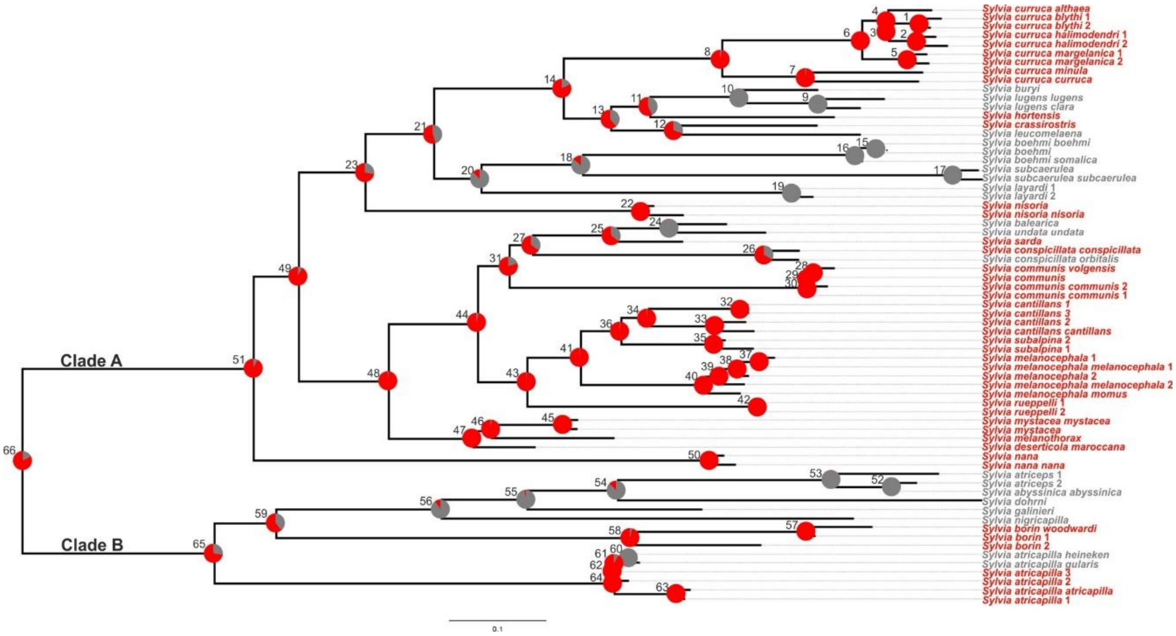

Figure A1.2. MCMC ASR analysis in Bayestraits using a phylogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

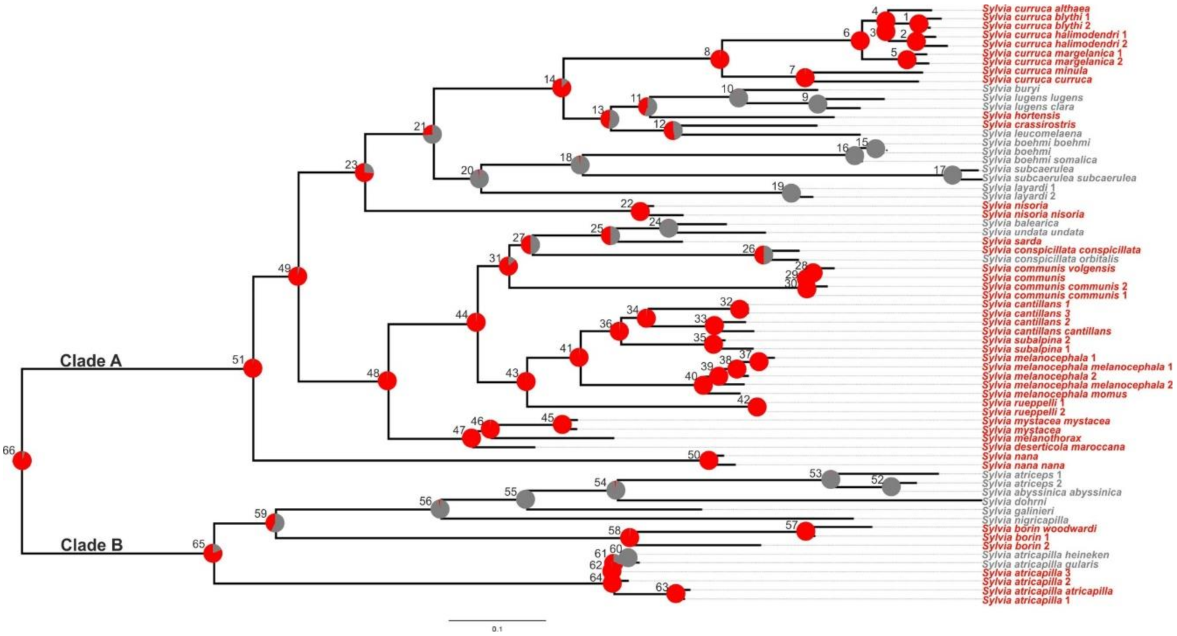

Figure A1.3. Mk1 ASR analysis in Bayestraits using a phylogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

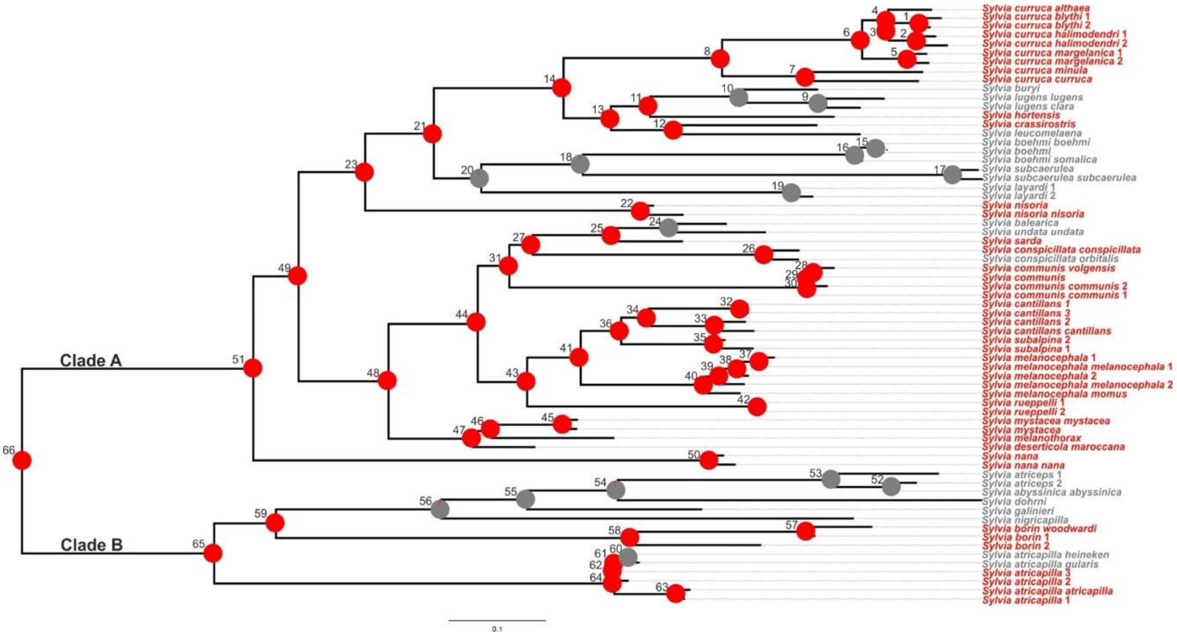

Figure A1.4. Mk2 ASR analysis in Bayestraits using a phylogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

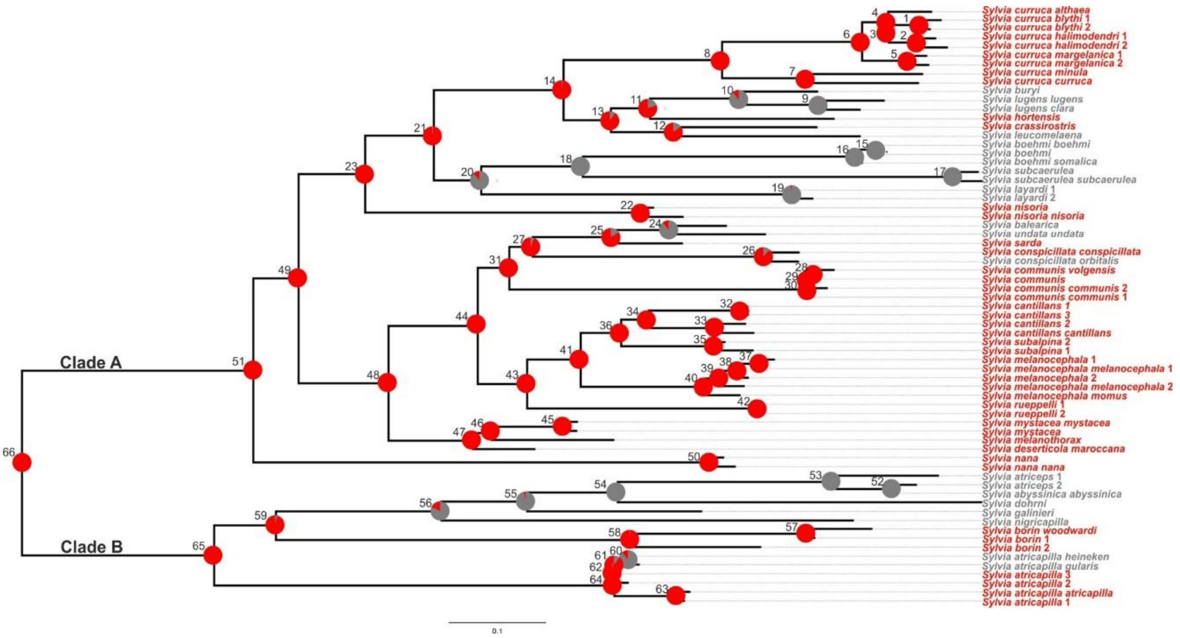

Figure A1.5. Mk1 ASR analysis in Diversitree package using a phylogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

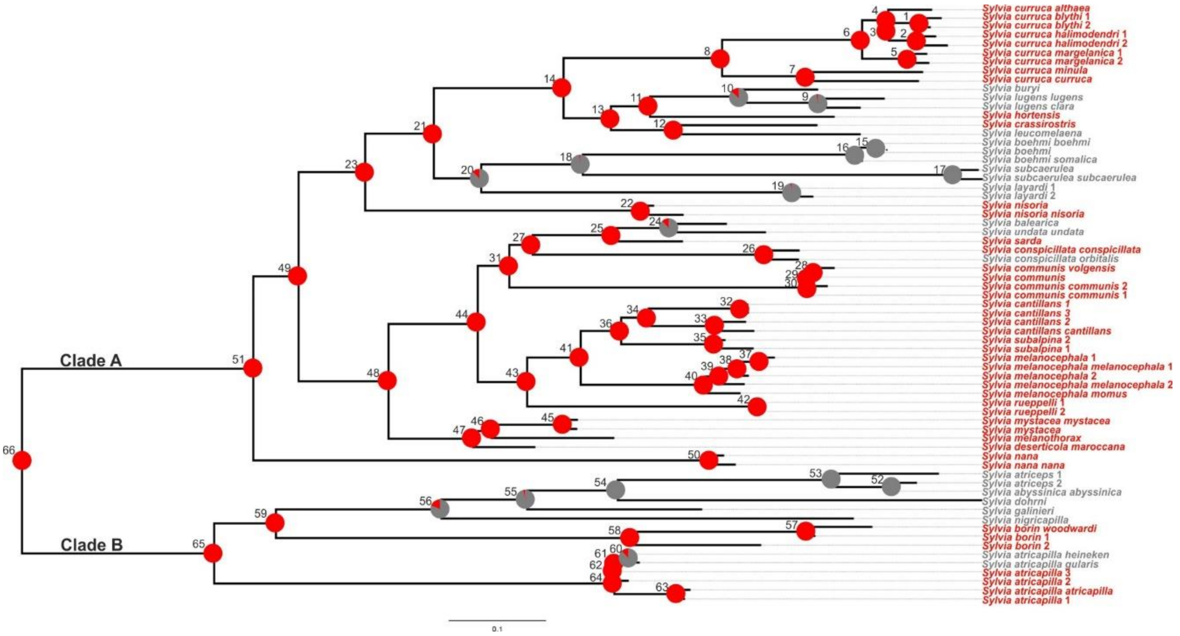

Figure A1.6. Mk2 ASR analysis in Diversitree package using a phylogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

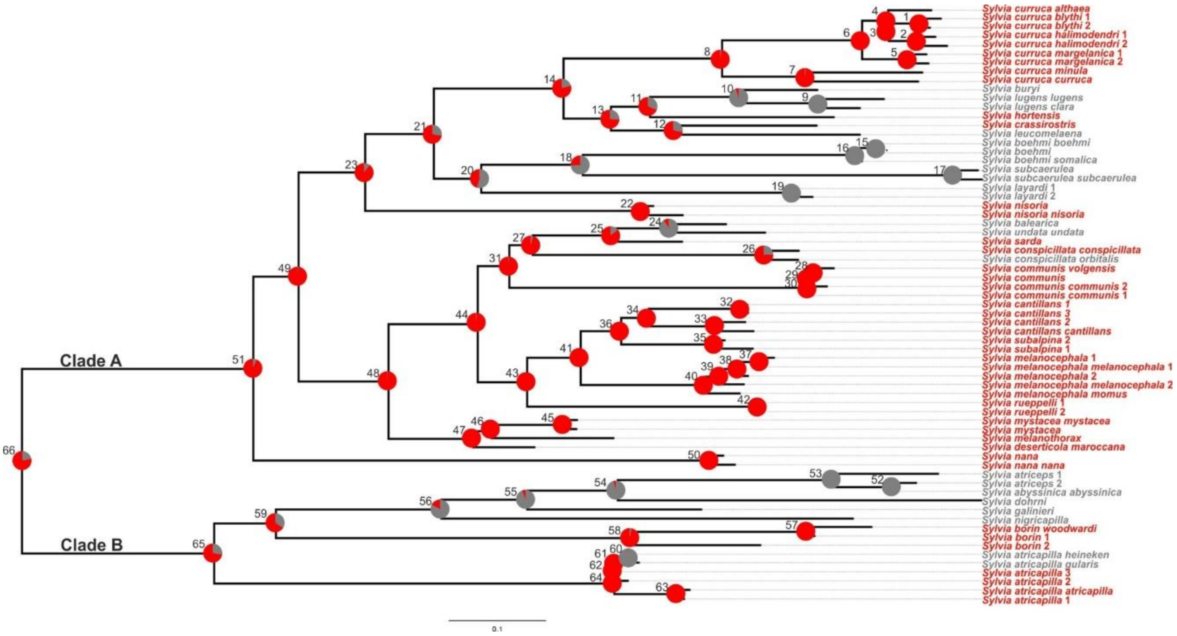

Figure A1.7. Mk1 ASR analysis in Ape package/Mesquite using a phylogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

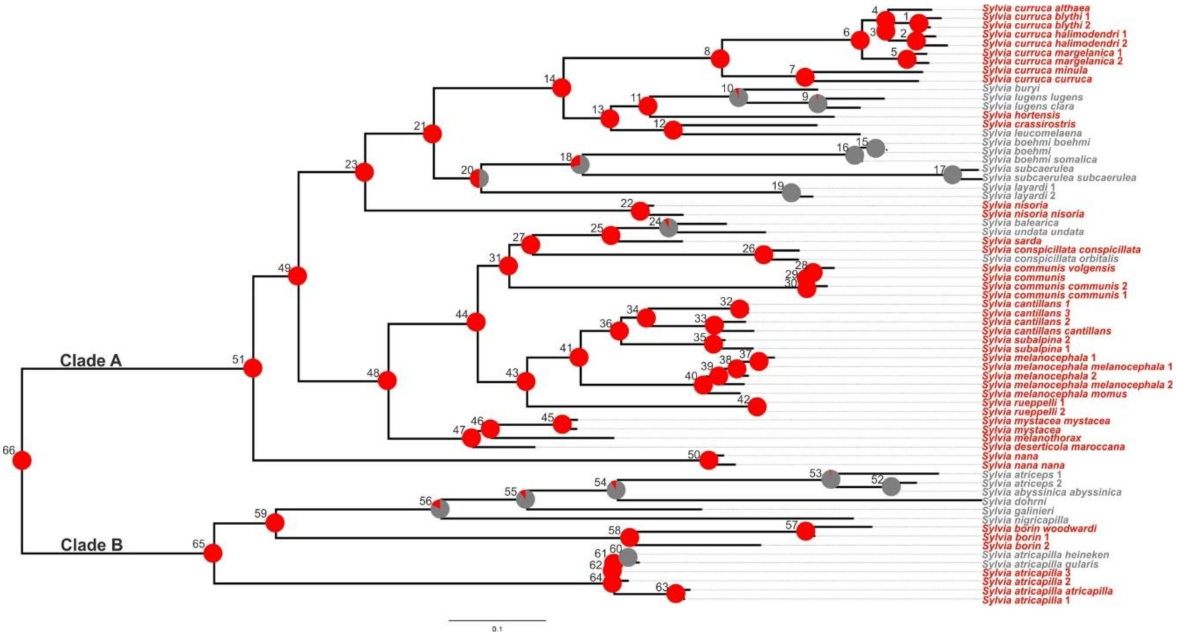

Figure A1.8. Mk2 ASR analysis in Ape package using a phylogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

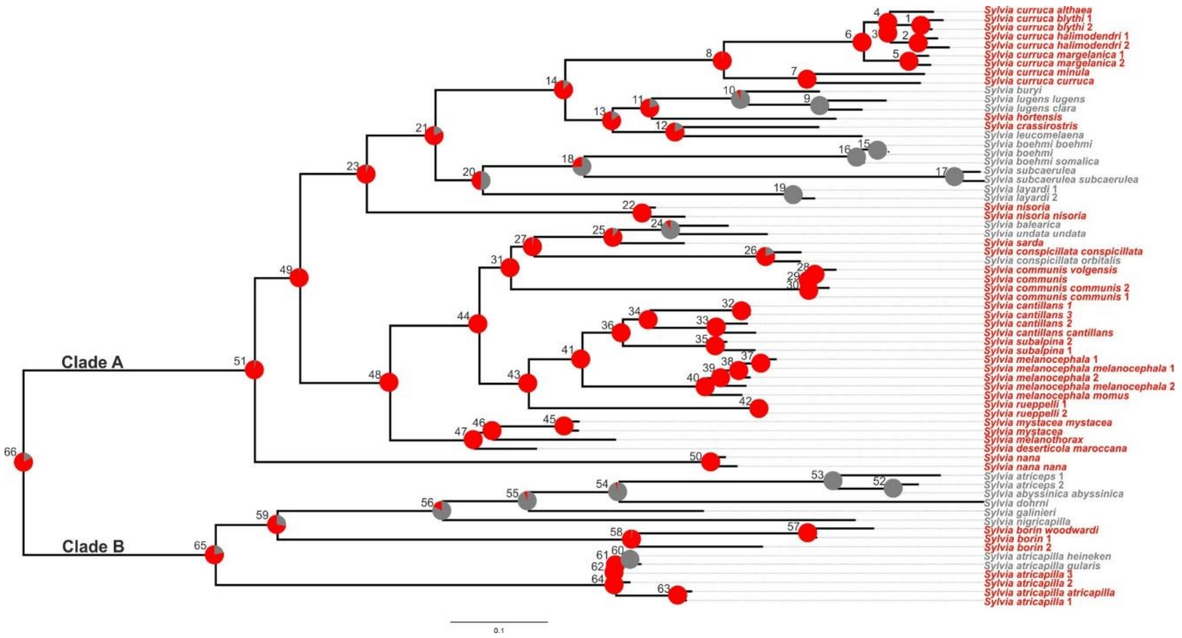

Figure A1.9. Mk2 ASR analysis in Mesquite using a phylogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

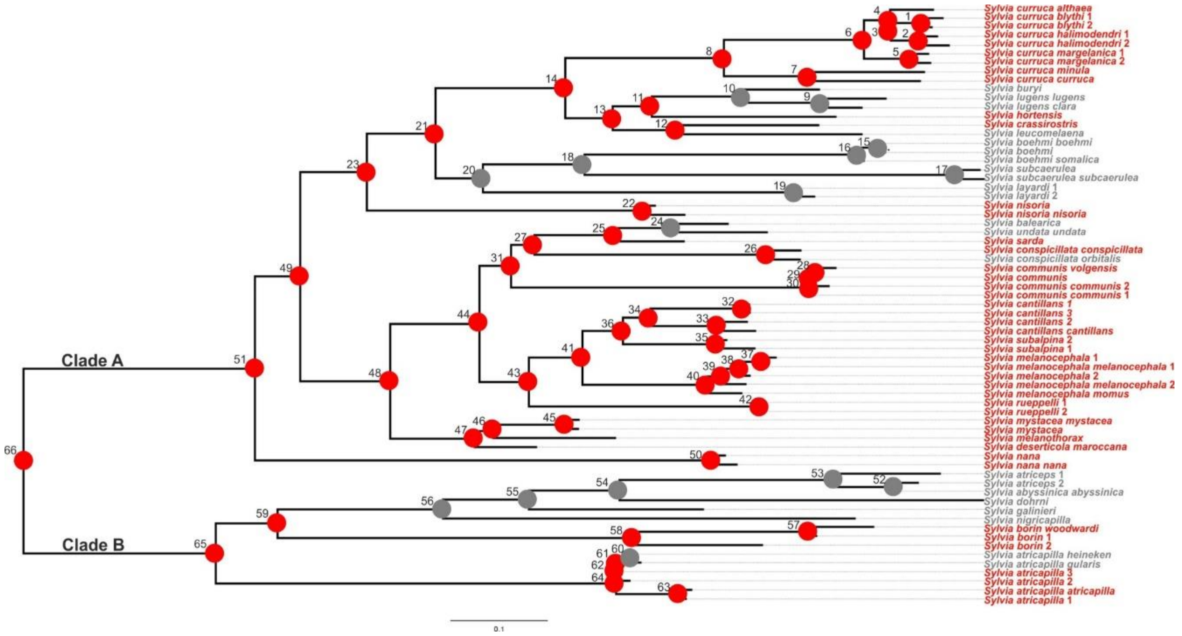

Figure A1.10. Parsimony ASR analysis in Mesquite using a phylogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

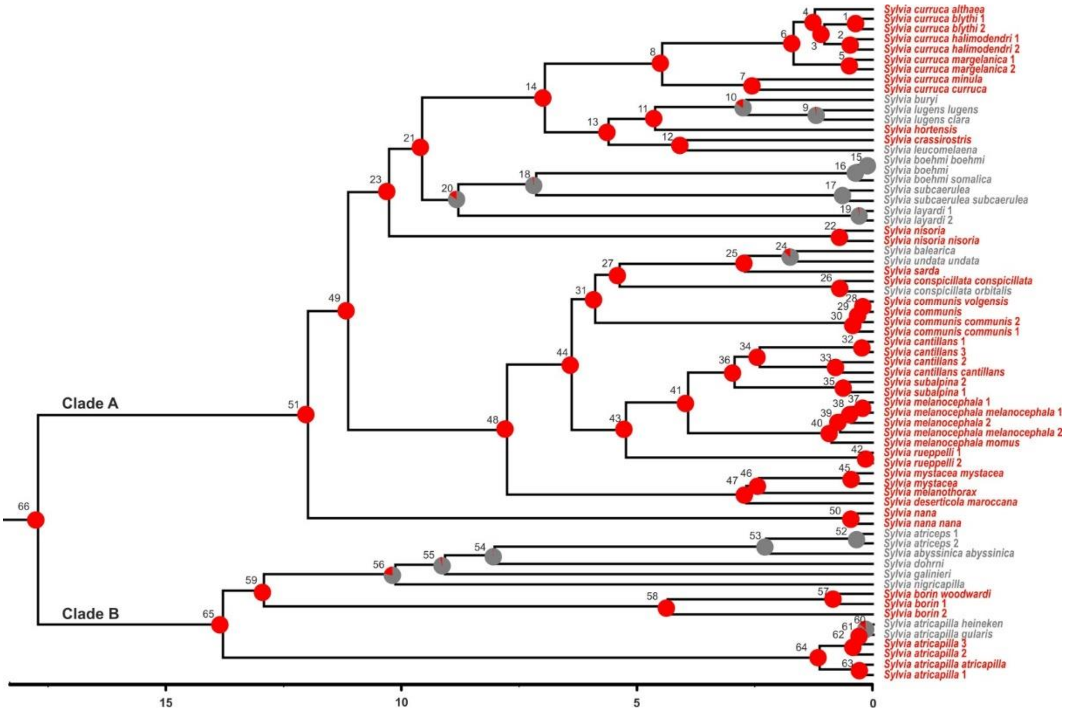

Figure A1.11. BISSE ASR analysis in Diversitree package using a chronogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years.

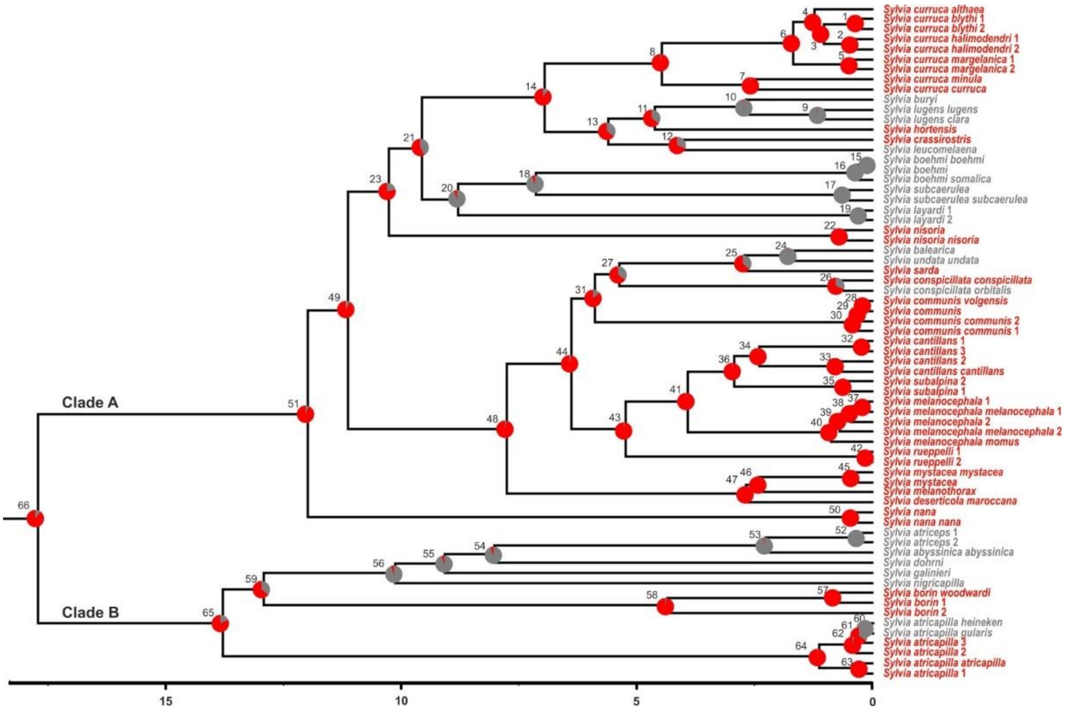

Figure A1.12. MCMC ASR analysis in Bayestraits using a chronogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years.

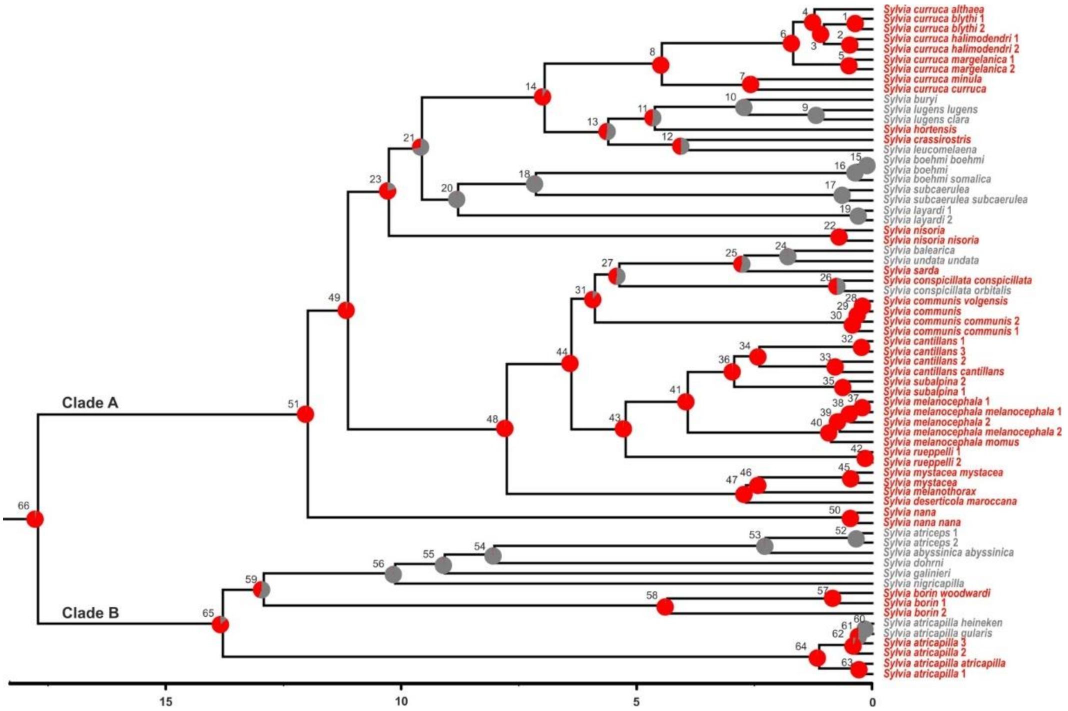

Figure A1.13. Mk1 ASR analysis in Bayestraits using a chronogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years

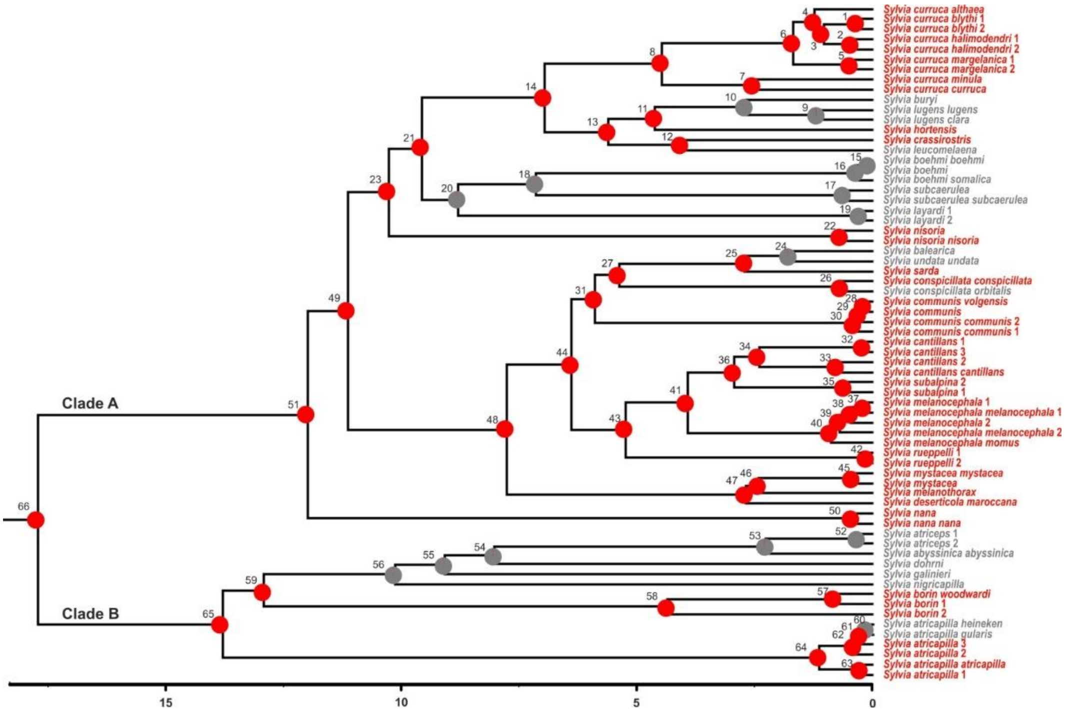

Figure A1.14. Mk2 ASR analysis in Bayestraits using a chronogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years

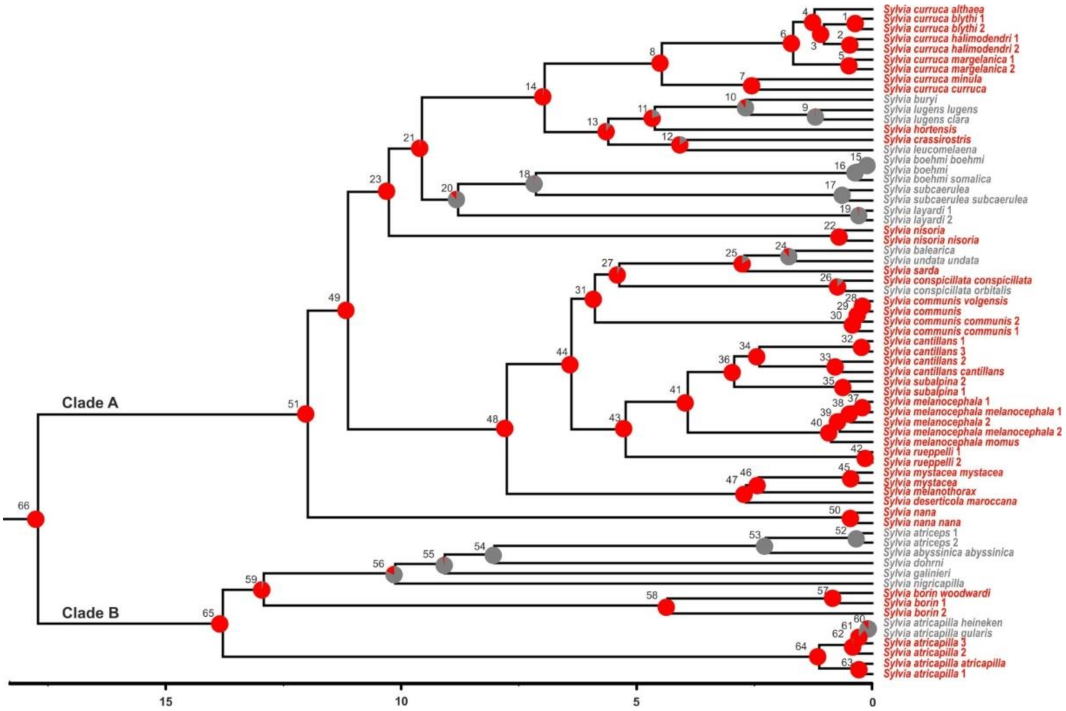

Figure A1.15. Mk1 ASR analysis in Diversitree package using a chronogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years

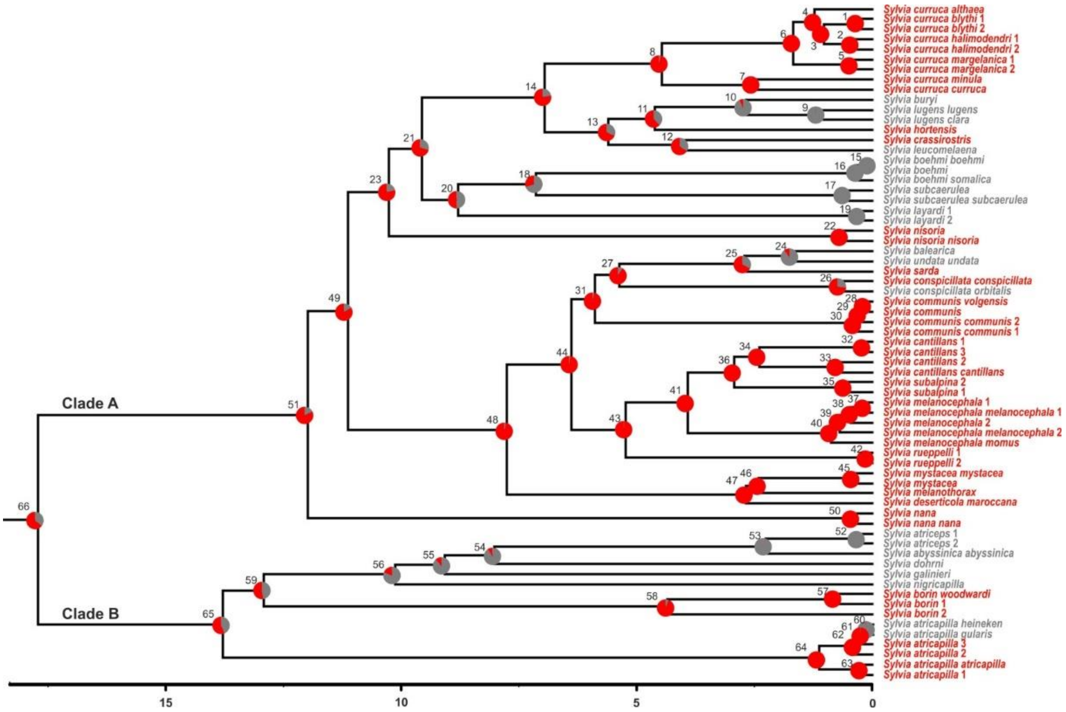

Figure A1.16. Mk1 ASR analysis in Ape package/Mesquite using a chronogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years

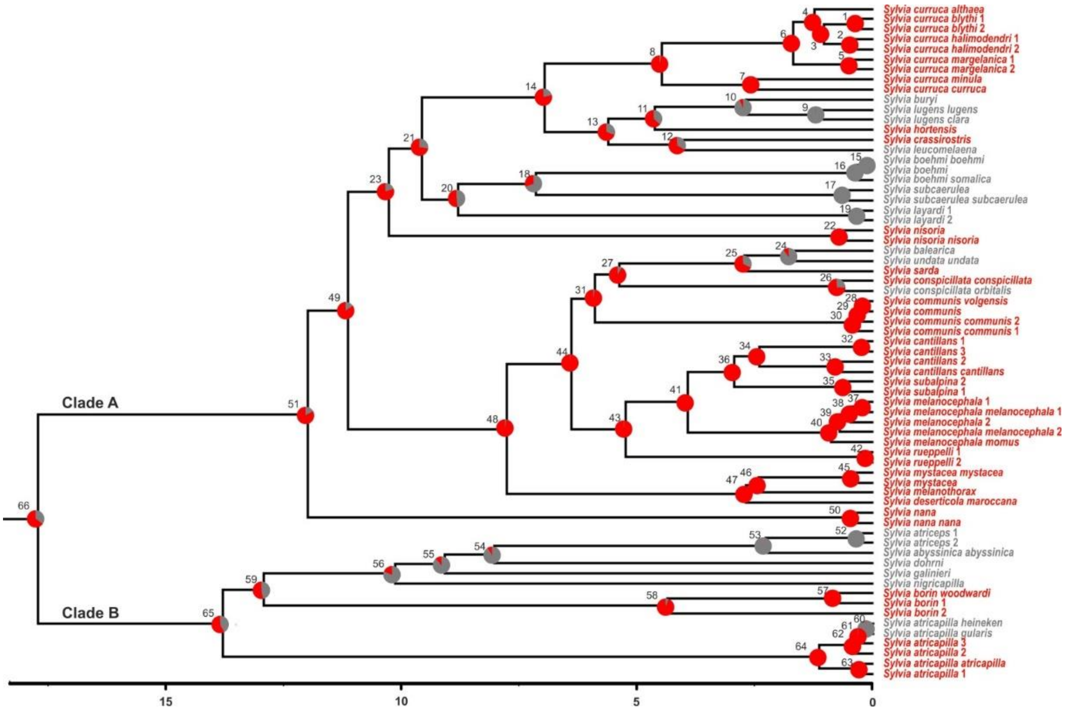

Figure A1.17. Mk2 ASR analysis in Ape package using a chronogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years

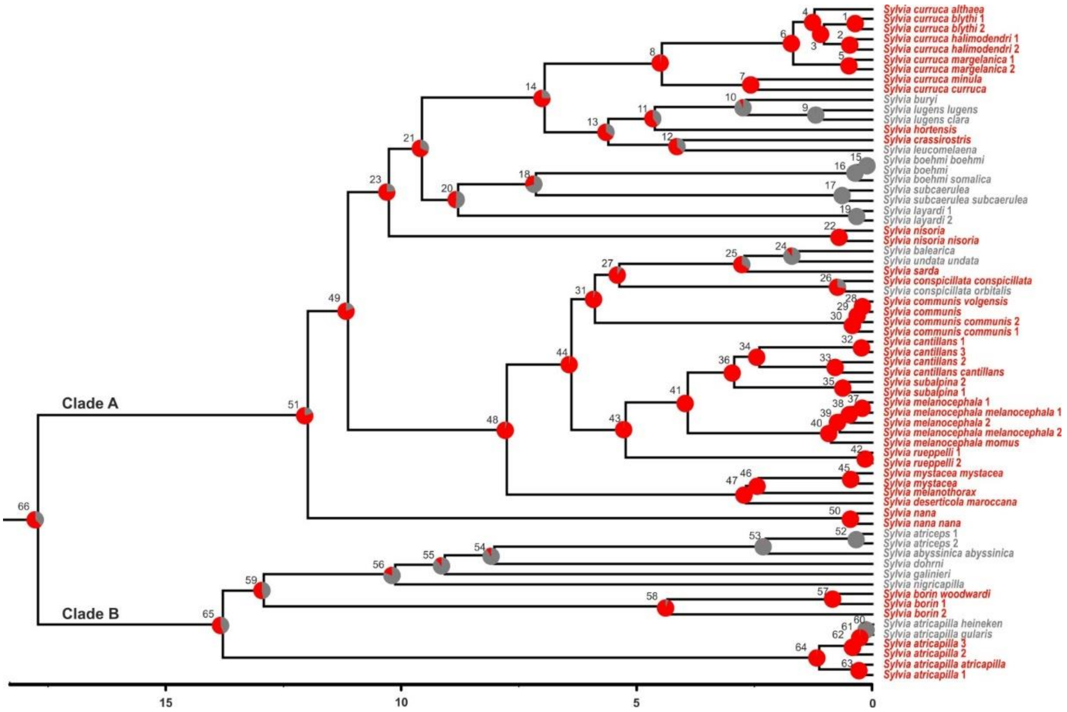

Figure A1.18. Mk2 ASR analysis in Mesquite using a chronogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years

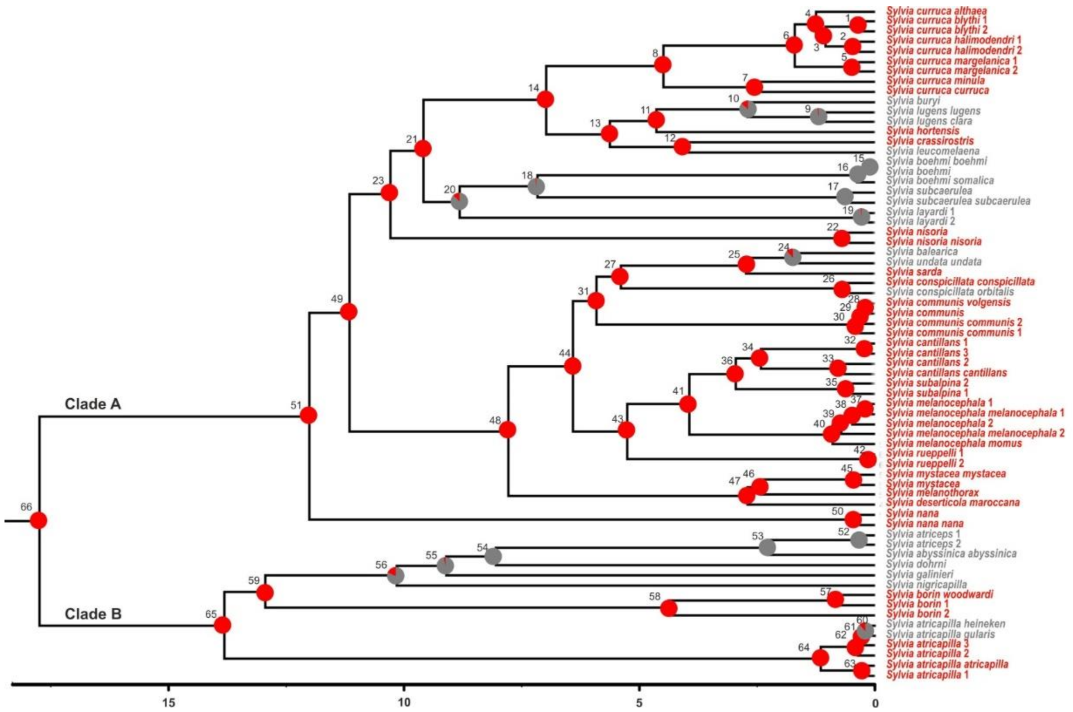

Figure A1.19. Mk2 ASR analysis in Diversitree package using a chronogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years

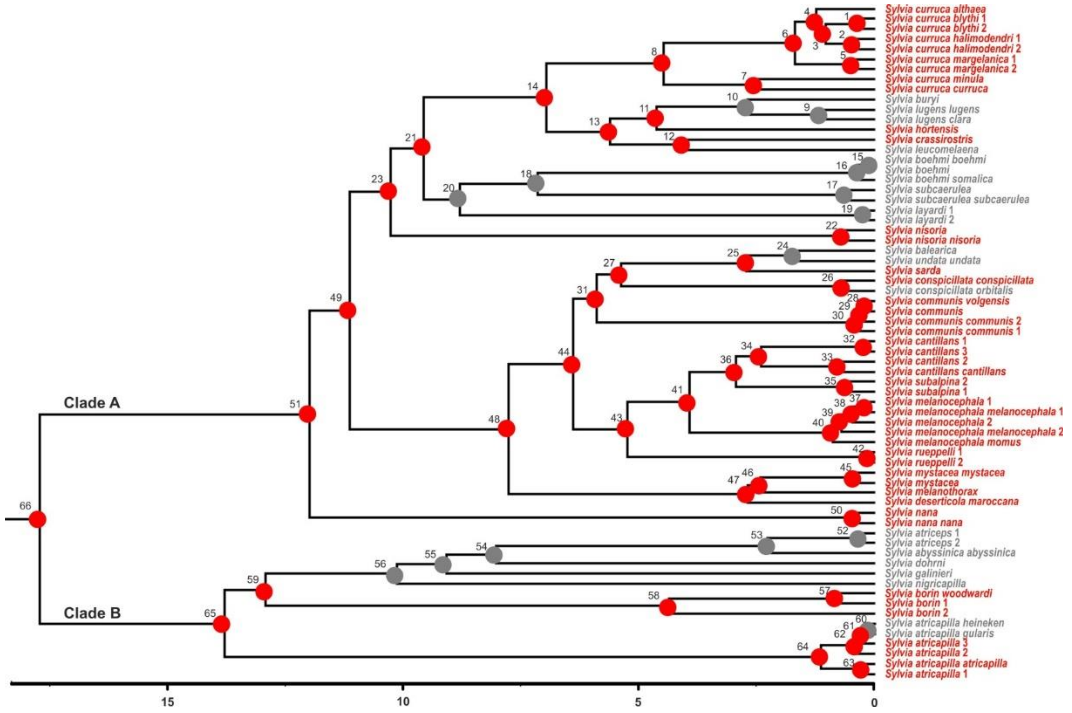

Figure A1.20. Parsimony analysis in Mesquite using a chronogram and a full dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years.

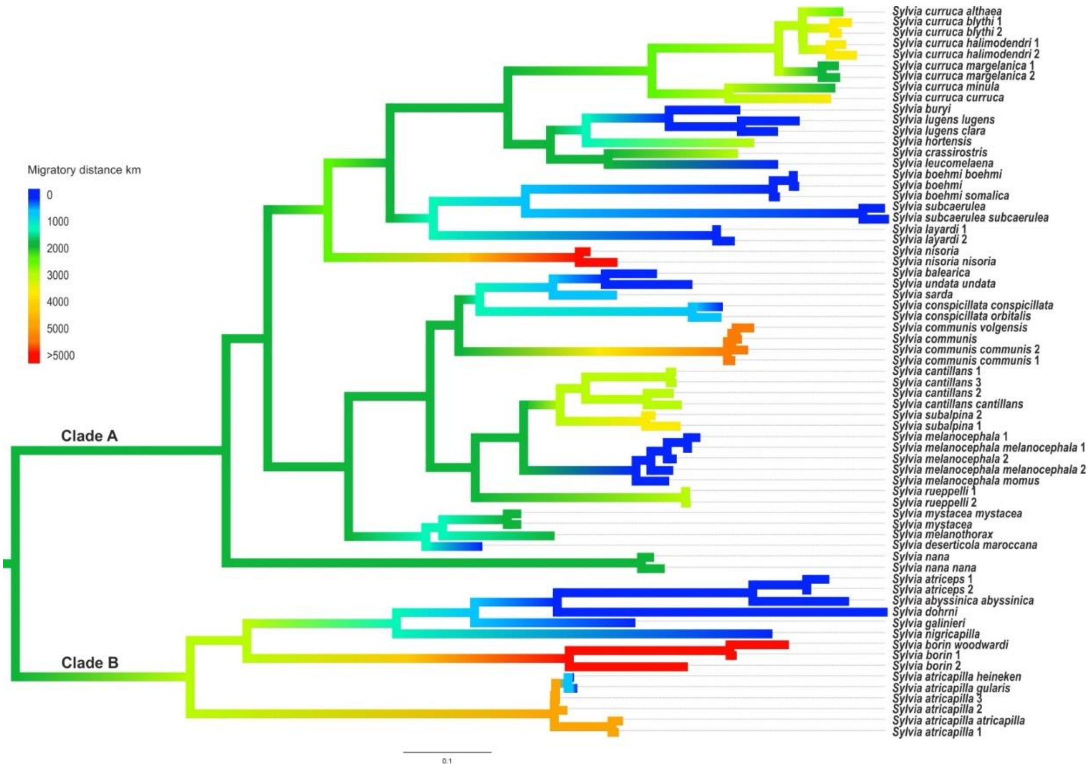

Figure A1.21. GLS analysis in Ape package using a phylogram and a full dataset. Color corresponds to reconstructed migratory distance.

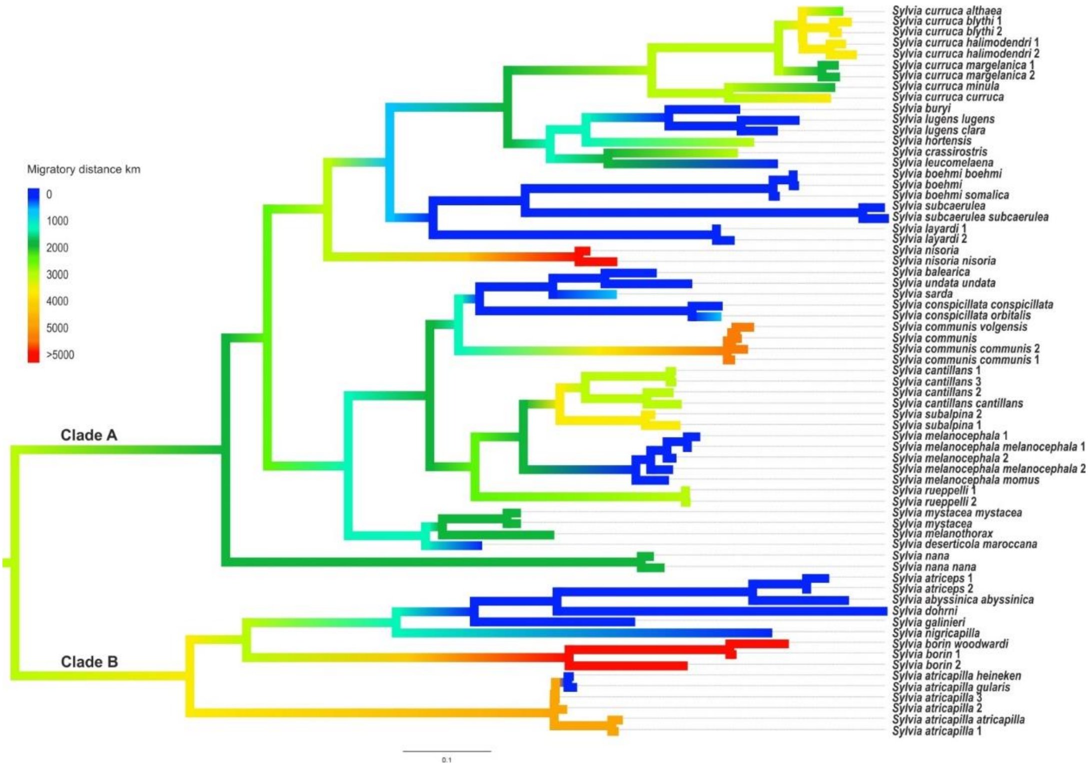

Figure A1.22. PIC analysis in Ape package using a phylogram and a full dataset. Color corresponds to reconstructed migratory distance.

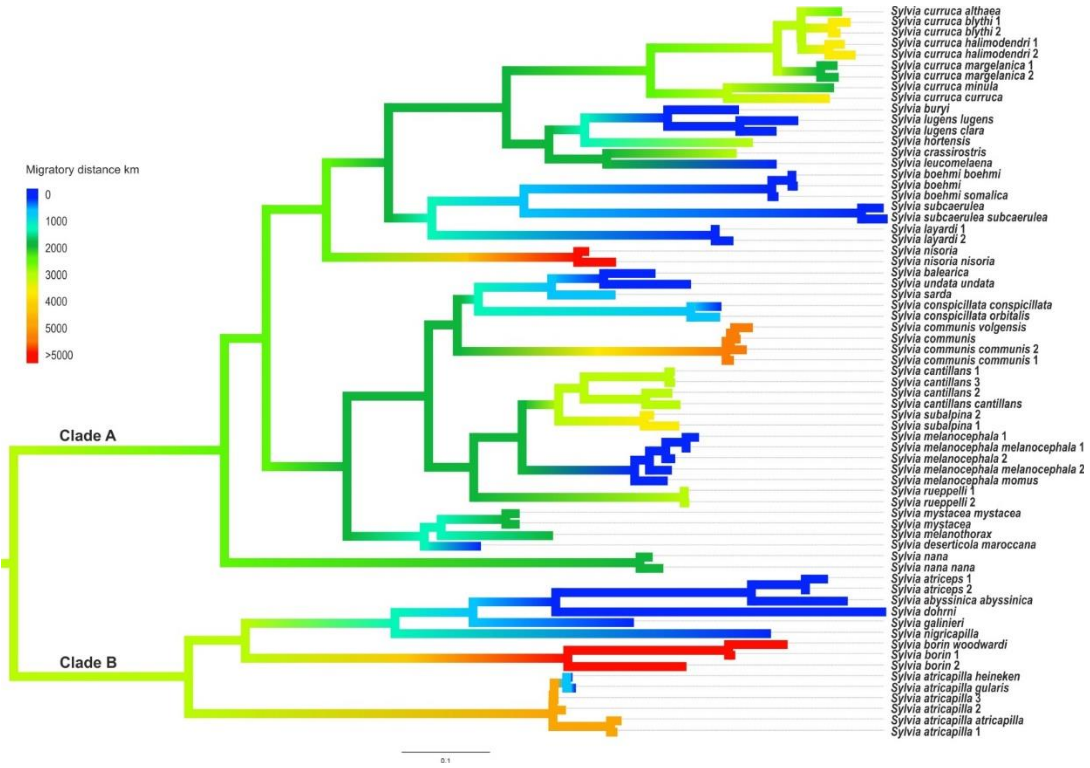

Figure A1.23. REML analysis in Ape package/ Parsimony analysis in Mesquite using a phylogram and a full dataset. Color corresponds to reconstructed migratory distance.

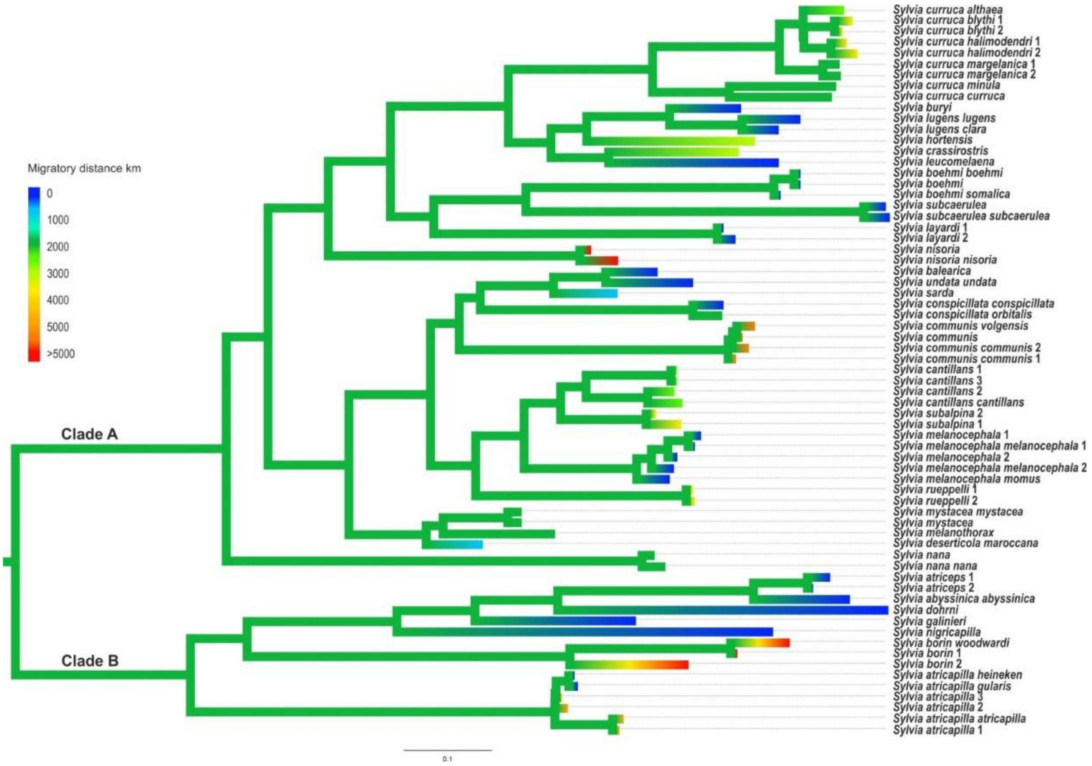

Figure A1.24. ML /Parsimony analysis in Ape package using a phylogram and a full dataset. Color corresponds to reconstructed migratory distance.

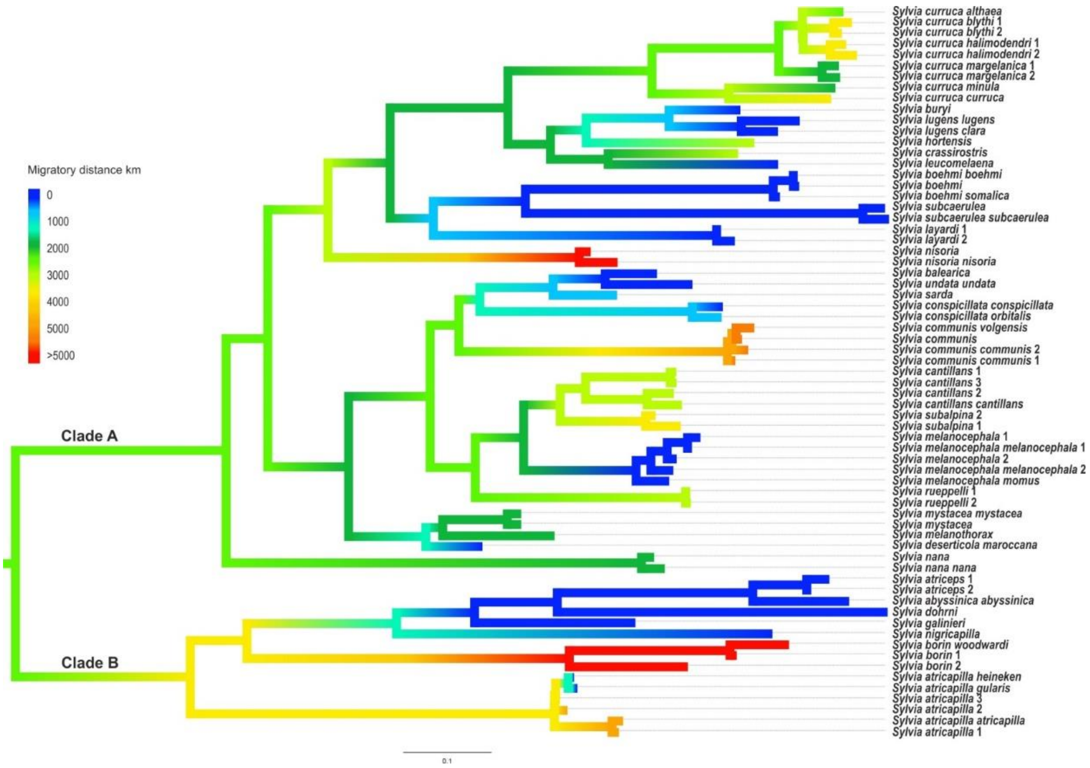

Figure A1.25. MCMC A analysis in Bayestraits using a phylogram and a full dataset. Color corresponds to reconstructed migratory distance.

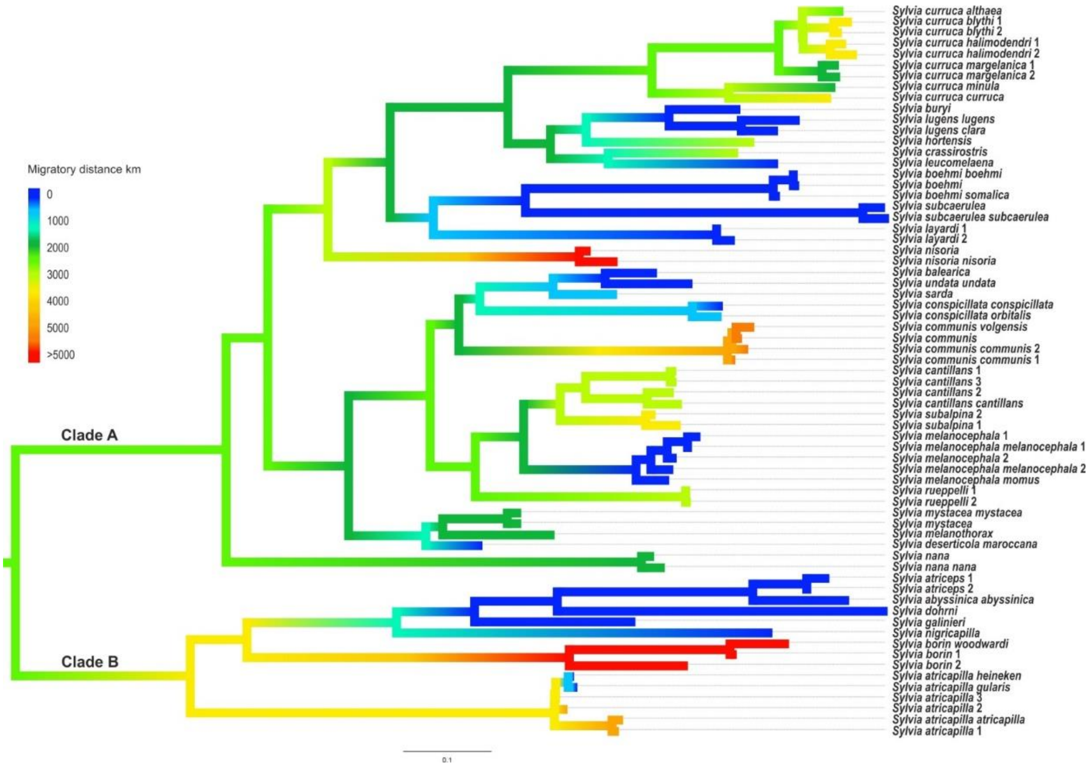

Figure A1.26. MCMC B analysis in Bayestraits using a phylogram and a full dataset. Color corresponds to reconstructed migratory distance.

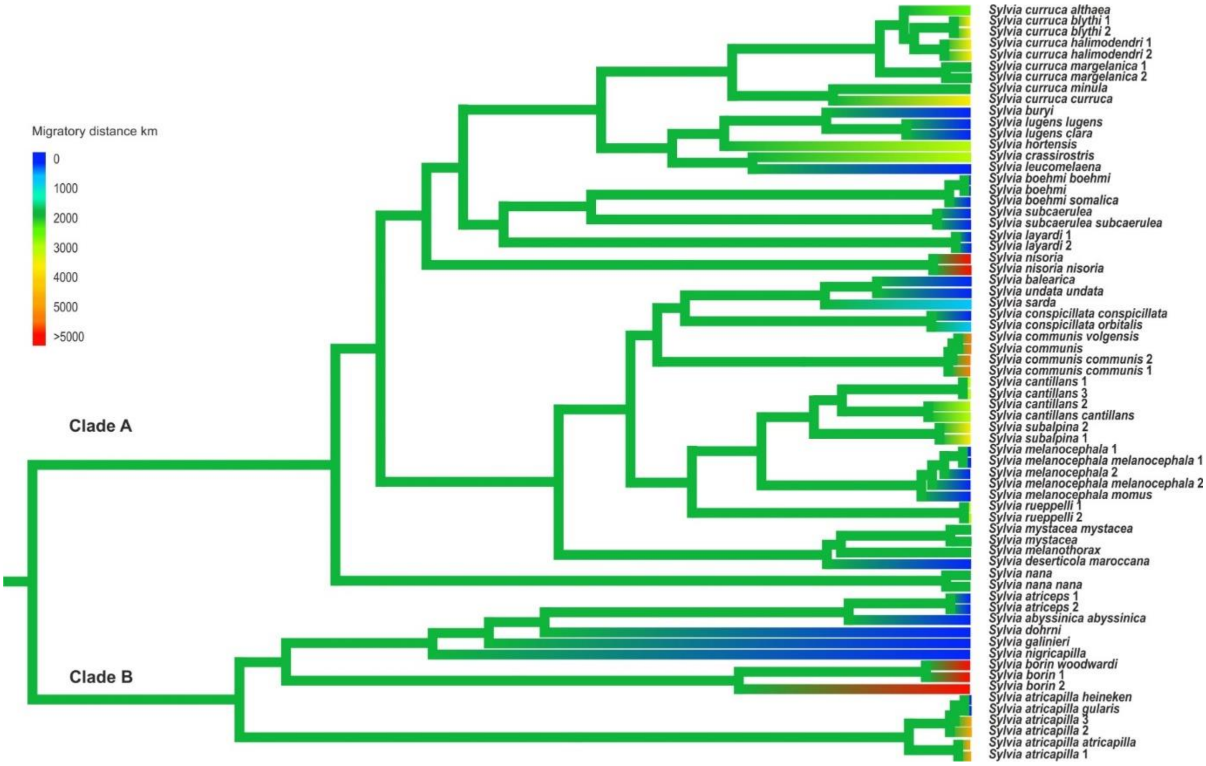

Figure A1.27. ML/Parsimony analyses in Ape package using a chronogram and a full dataset. Color corresponds to reconstructed migratory distance.

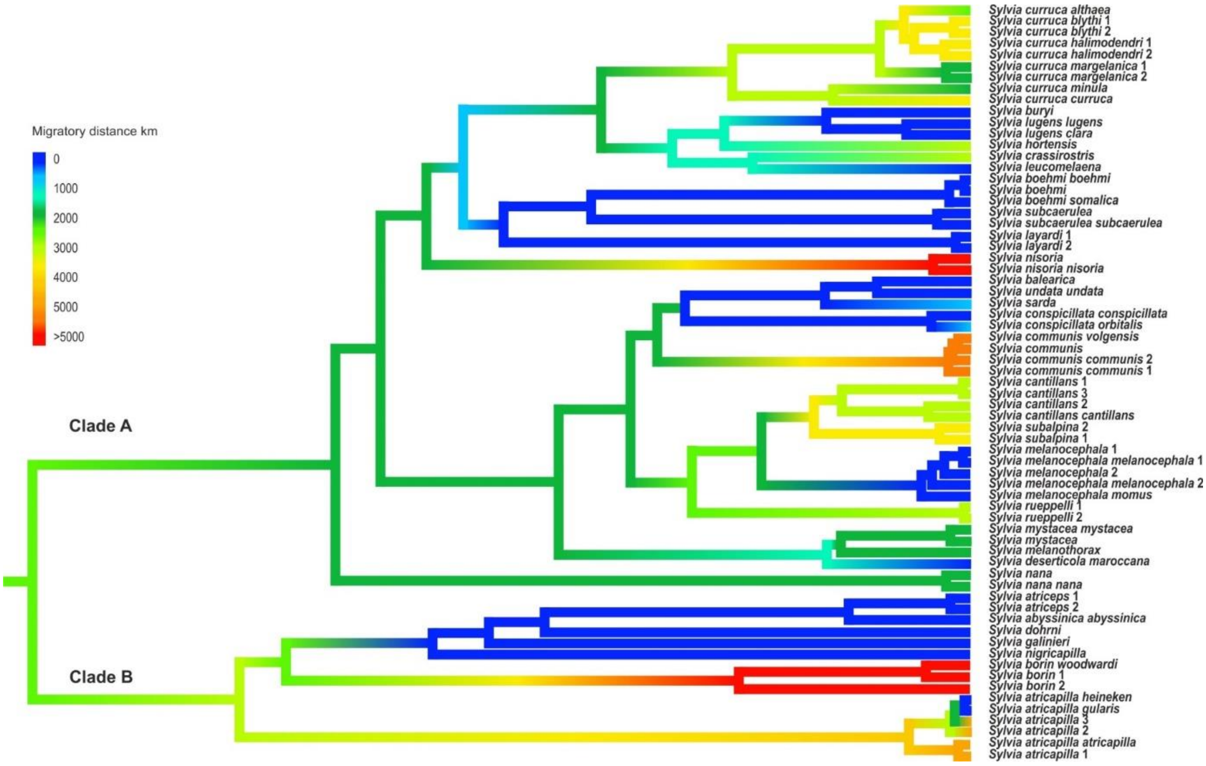

Figure A1.28. PIC analyses in Ape package using a chronogram and a full dataset. Color corresponds to reconstructed migratory distance.

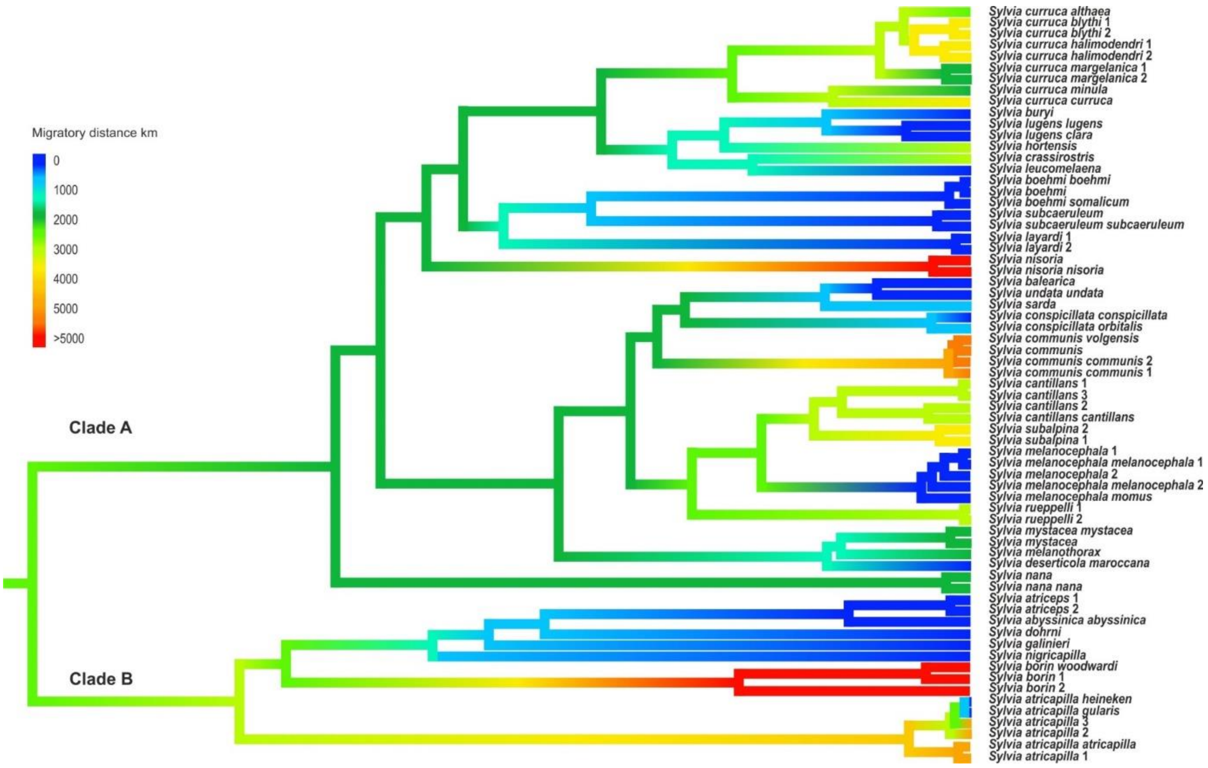

Figure A1.29. REML/GLS analyses in Ape package/ Parsimony in Mesquite using a chronogram and a full dataset. Color corresponds to reconstructed migratory distance.

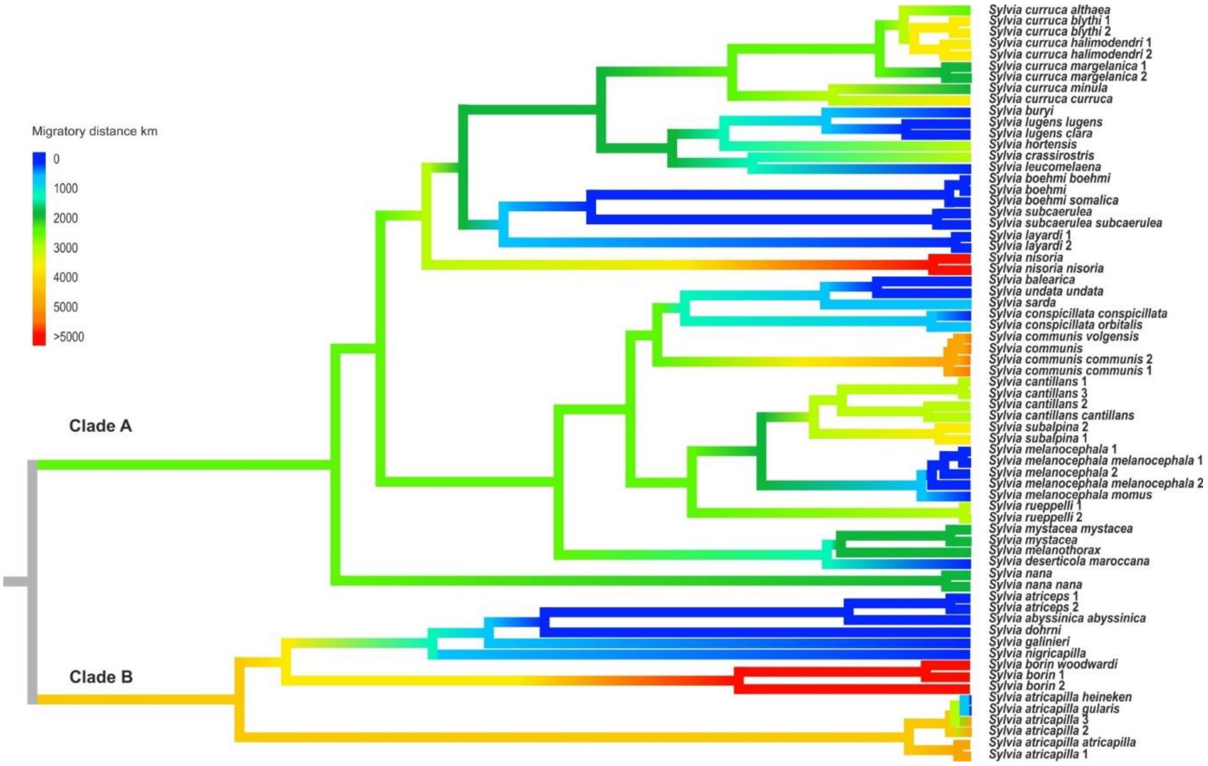

Figure A1.30. MCMC A analysis in Bayestraits using a chronogram and a full dataset. Color corresponds to reconstructed migratory distance. Color gray correspond to a no-data.

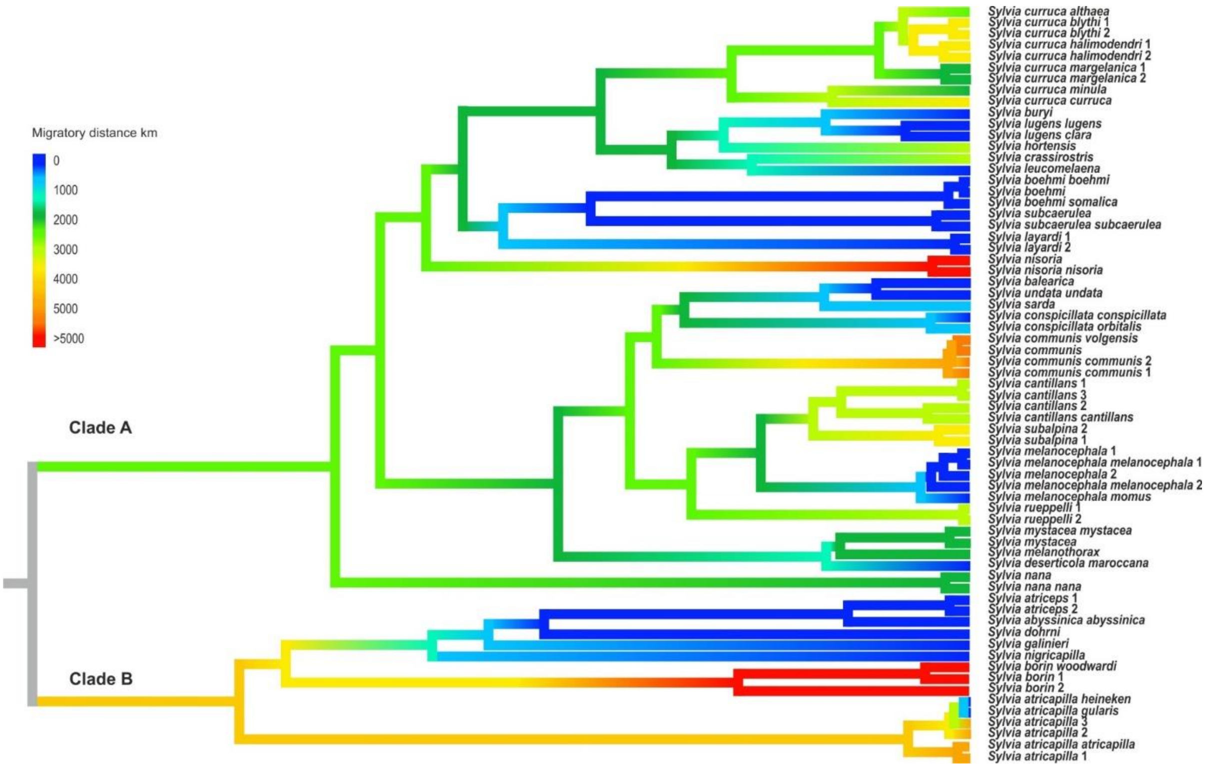

Figure A1.31. MCMC B analysis in Bayestraits using a chronogram and a full dataset. Color corresponds to reconstructed migratory distance. Color gray correspond to a no-data.

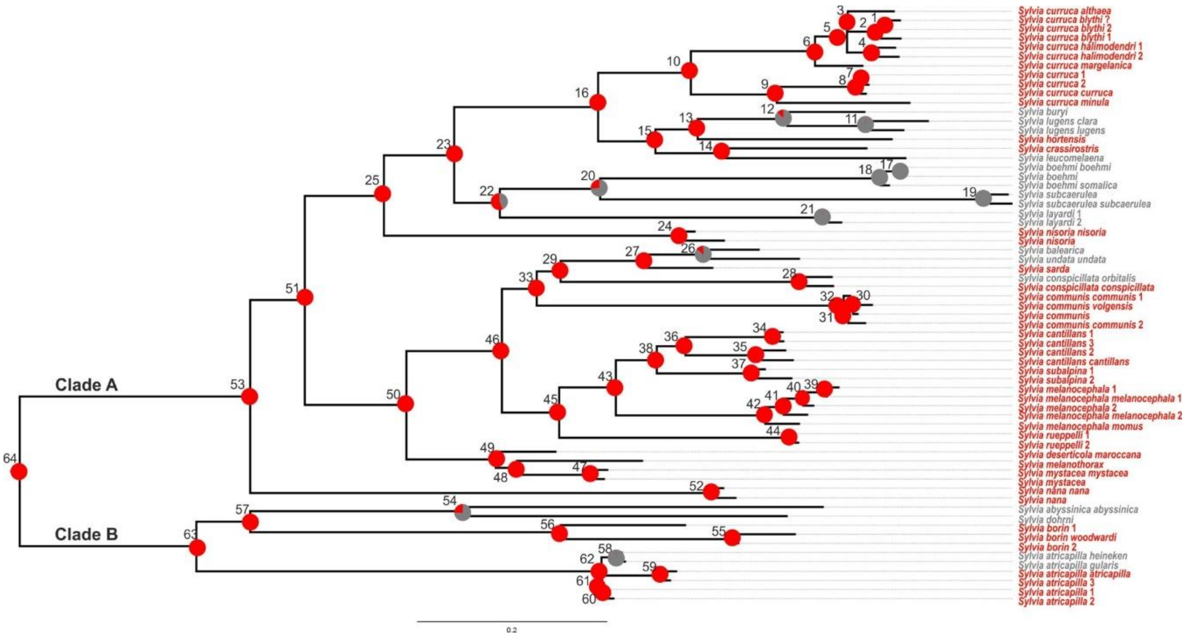

Figure A1.32. BISSE ASR analysis in Diversitree package using a phylogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

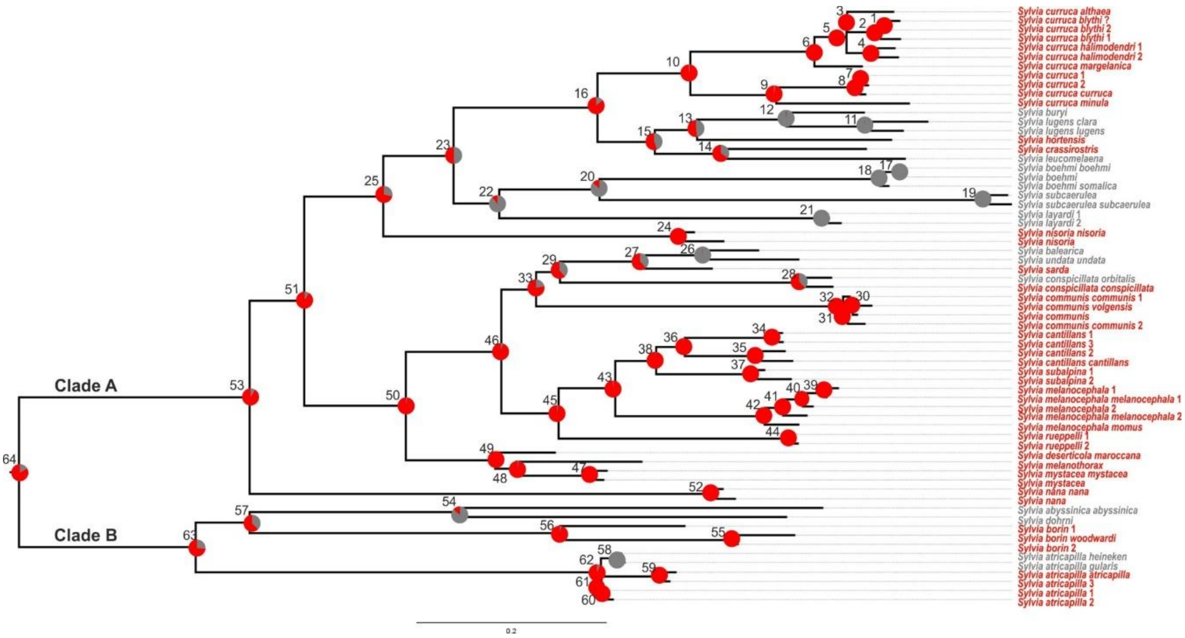

Figure A1.33. MCMC ASR analysis in Bayestraits using a phylogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

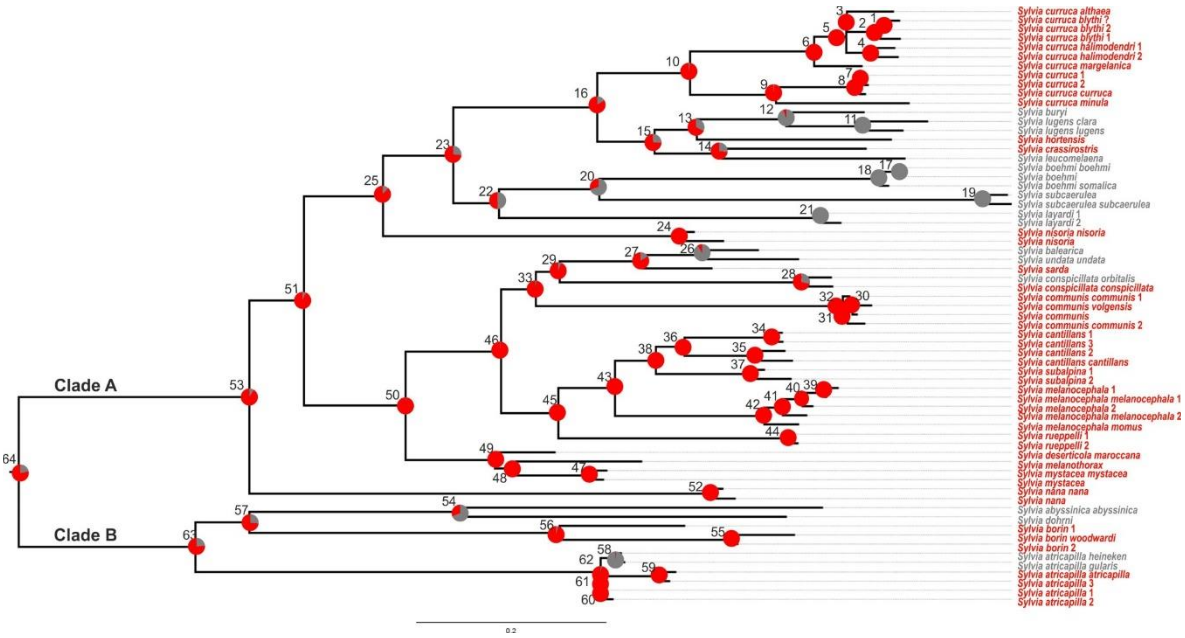

Figure A1.34. Mk1 ASR analysis in Ape package/Mesquite using a phylogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

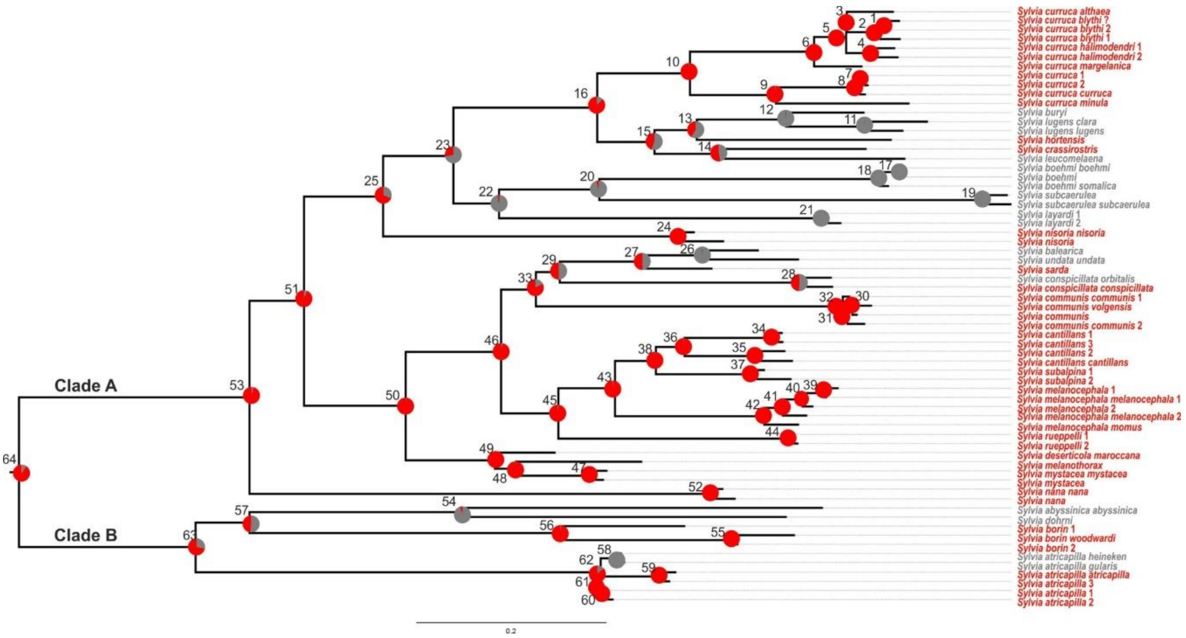

Figure A1.35. Mk1 ASR analysis in Bayestraits using a phylogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

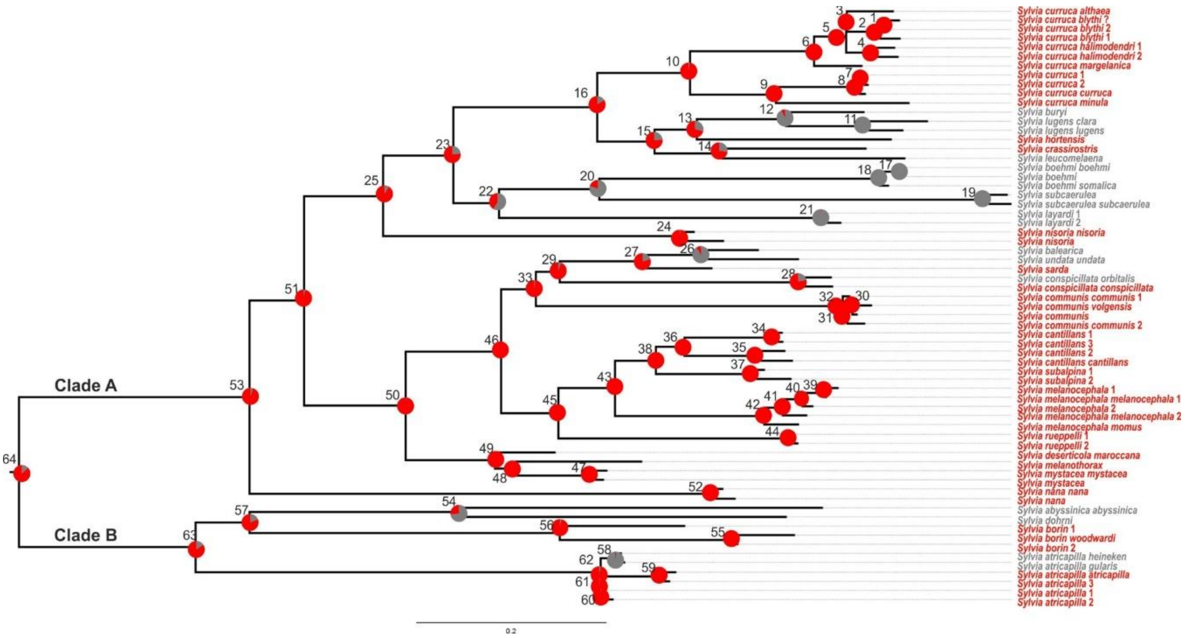

Figure A1.36. Mk1 ASR analysis in Diversitree package using a phylogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

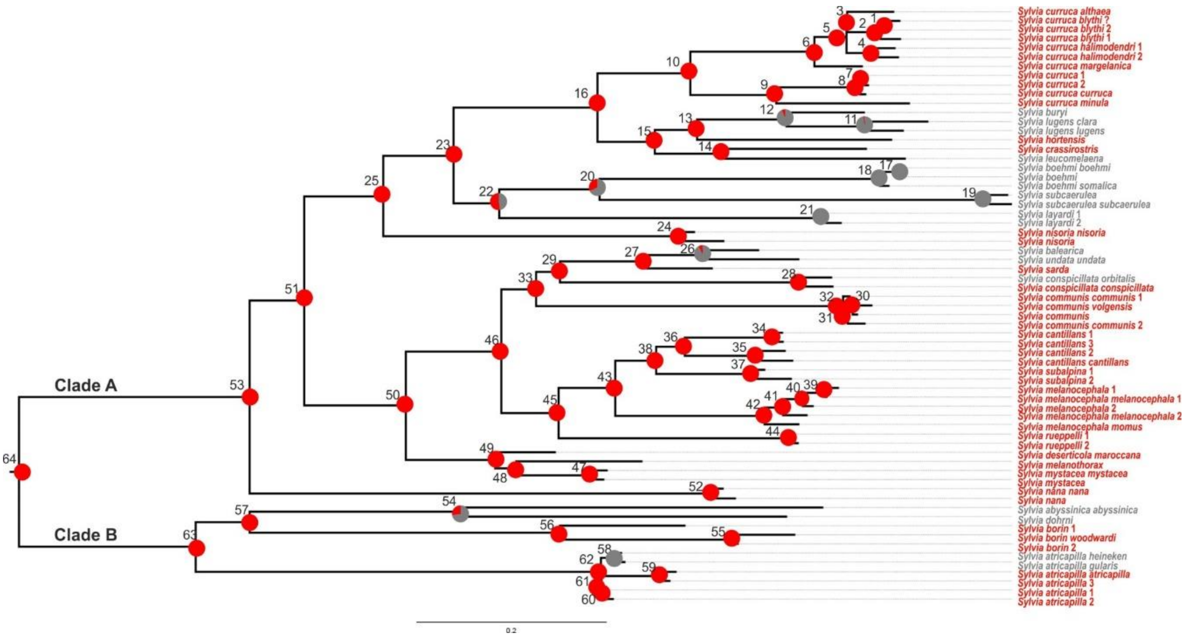

Figure A1.37. Mk2 ASR analysis in Ape package using a phylogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

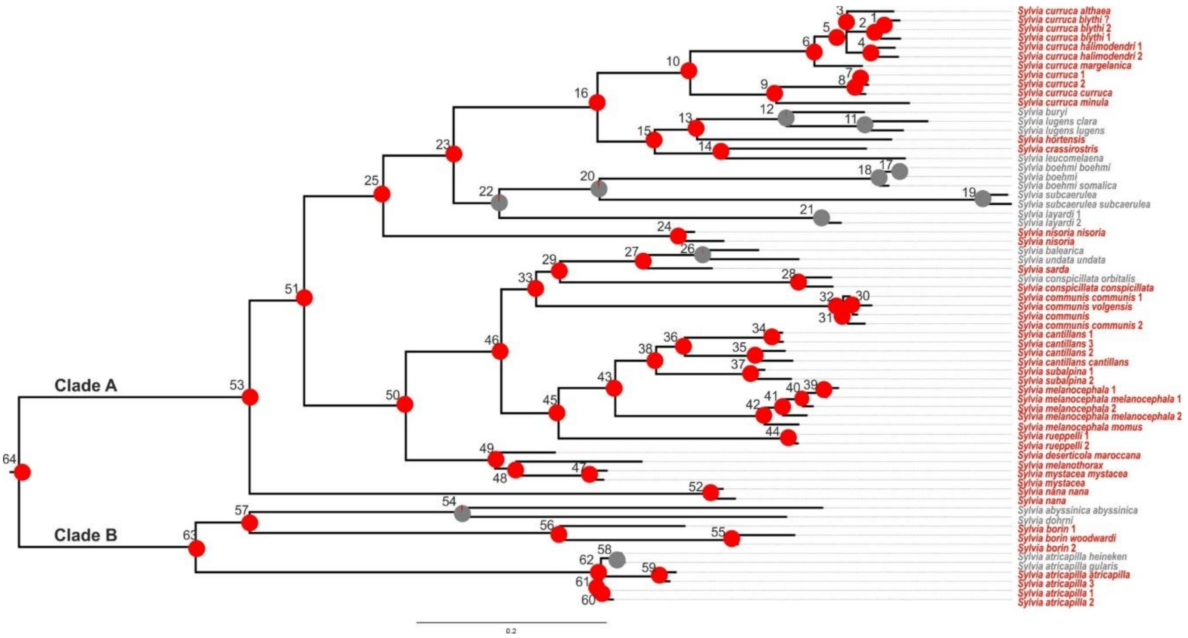

Figure A1.38. Mk2 ASR analysis in Bayestraits using a phylogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

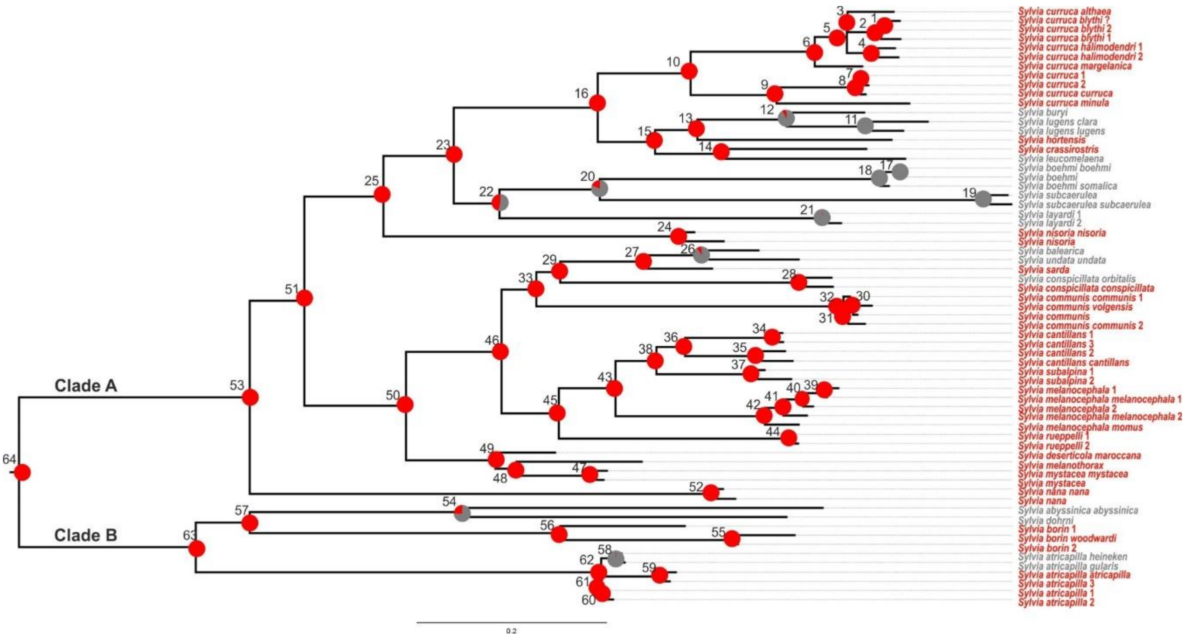

Figure A1.39. Mk2 ASR analysis in Diversitree package using a phylogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

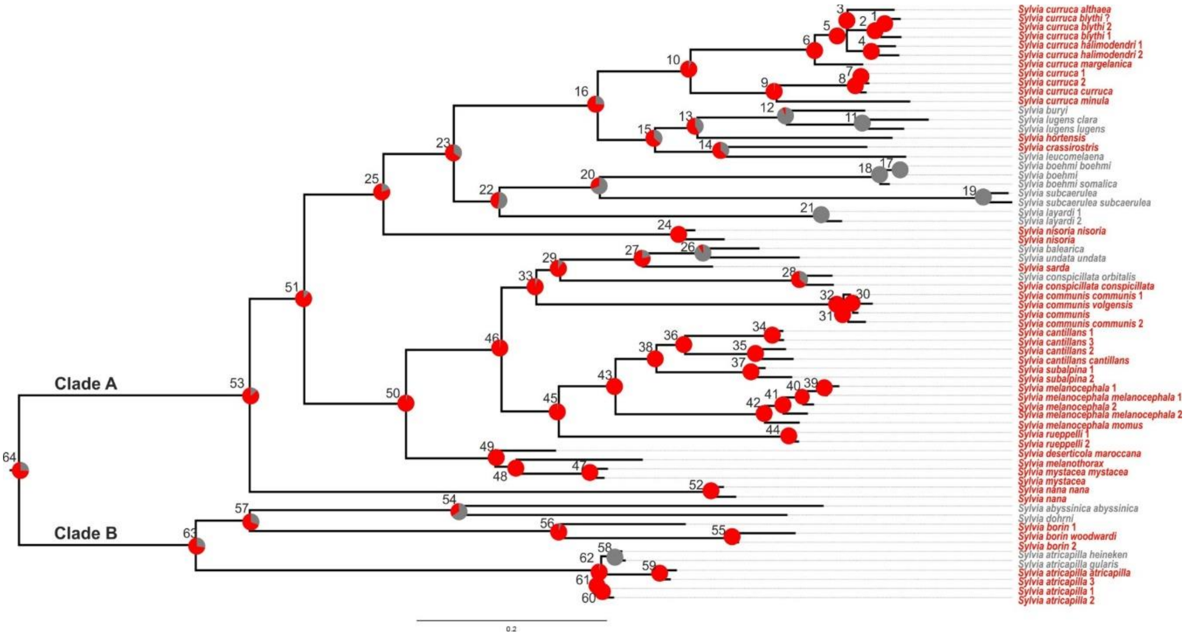

Figure A1.40. Mk2 ASR analysis in Mesquite using a phylogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state.

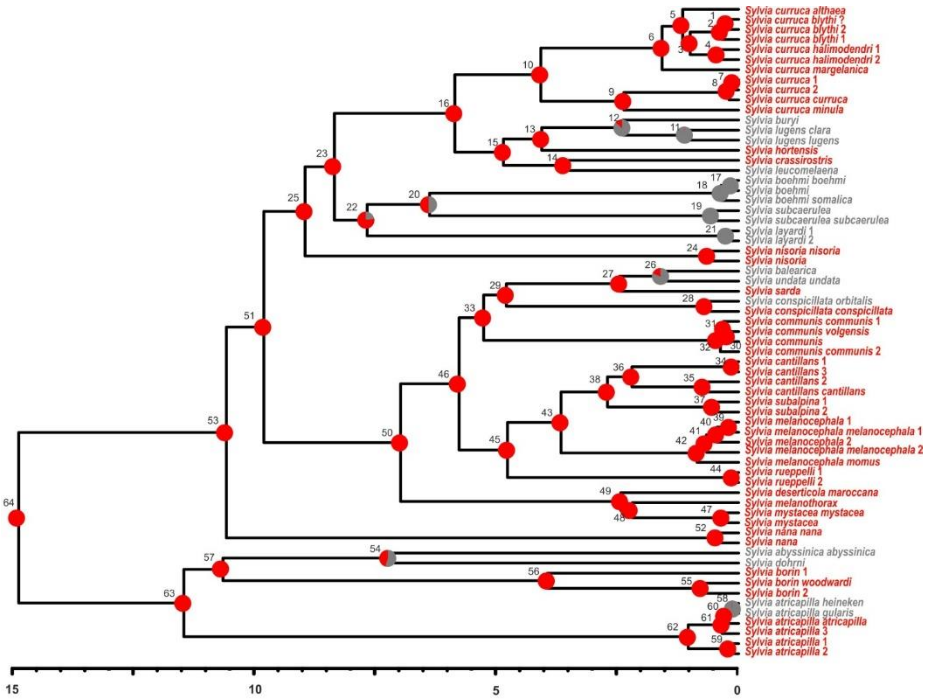

Figure A1.41. BISSE analysis in Diversitree package using a chronogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years.

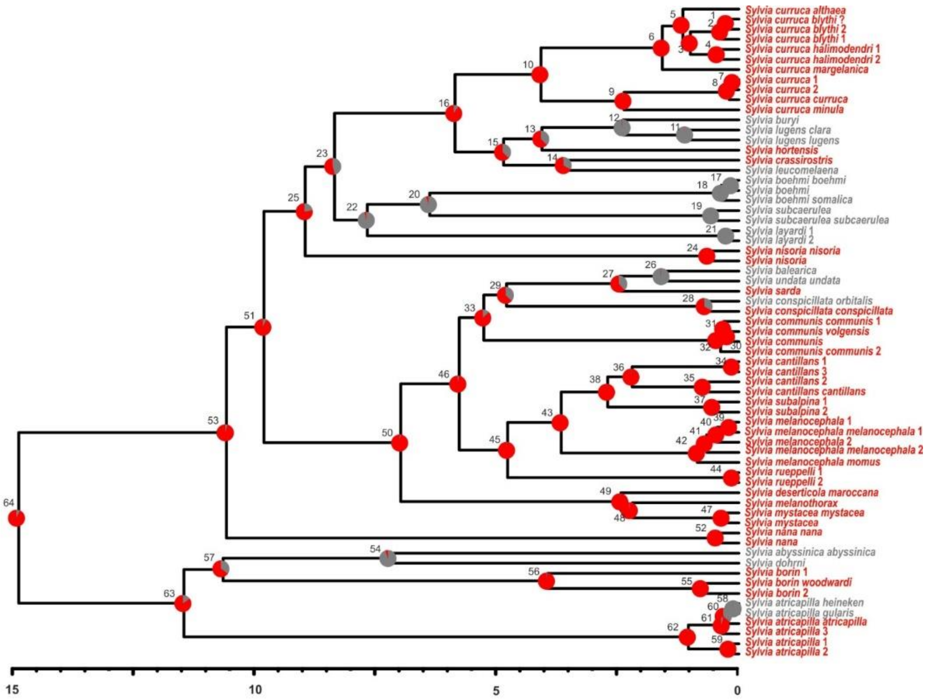

Figure A1.42. MCMC analysis in Bayestraits using a chronogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years.

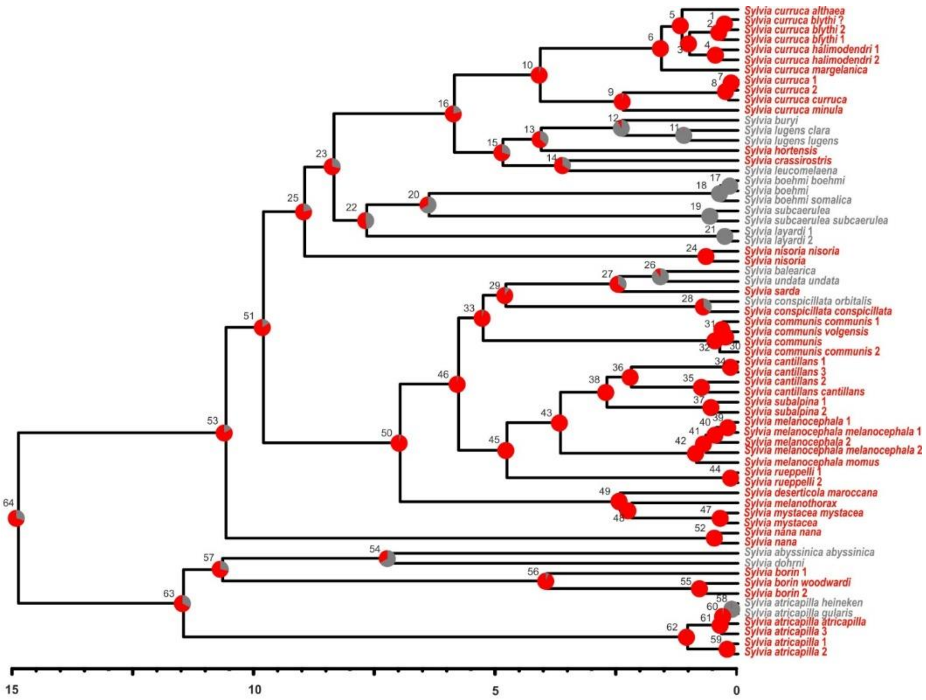

Figure A1.43. Mk1 analyses in Ape package/Mesquite using a chronogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years.

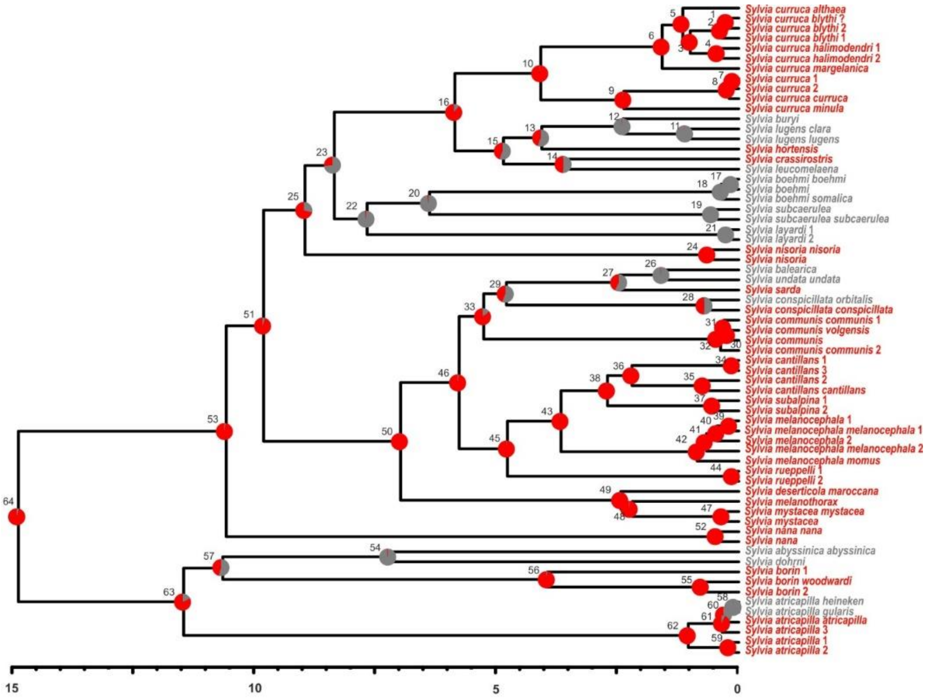

Figure A1.44. Mk1 analyses in Bayestraits using a chronogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years.

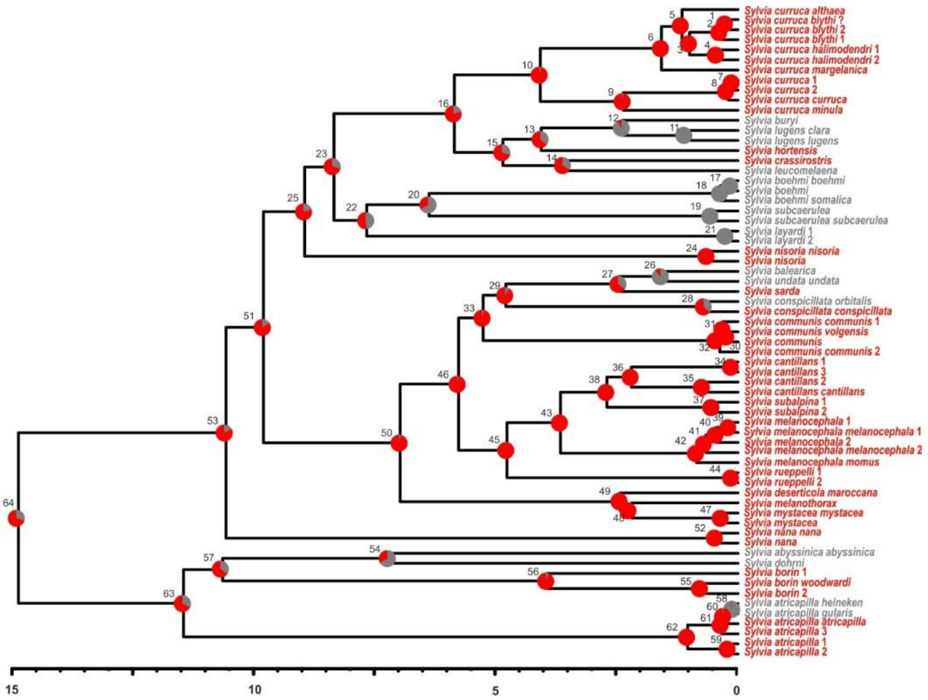

Figure A1.45. Mk1 analyses in Diversitree package using a chronogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years.

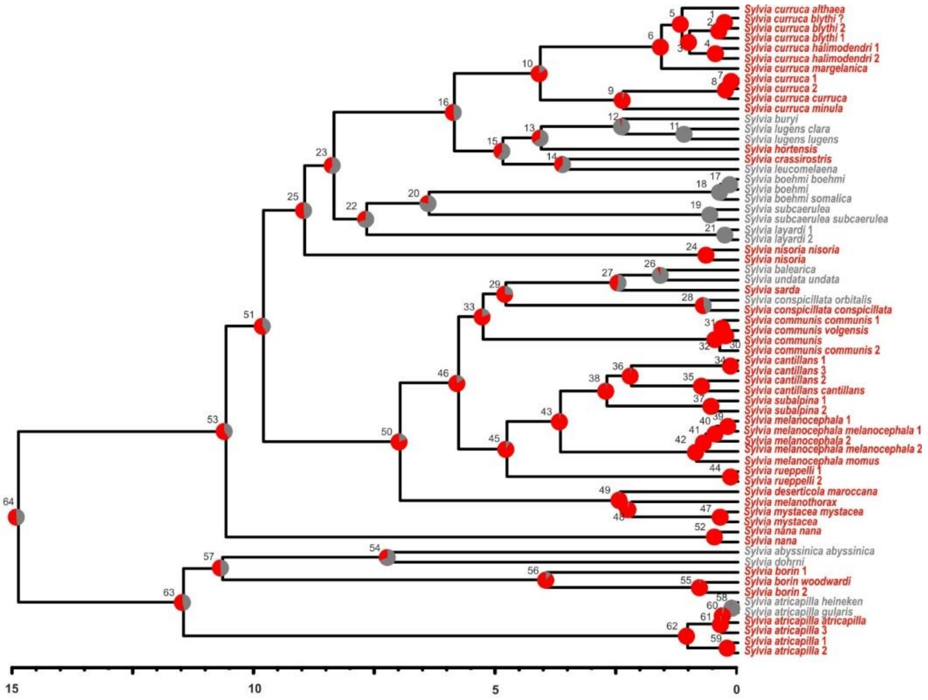

Figure A1.46. Mk2 analyses in Ape package using a chronogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years.

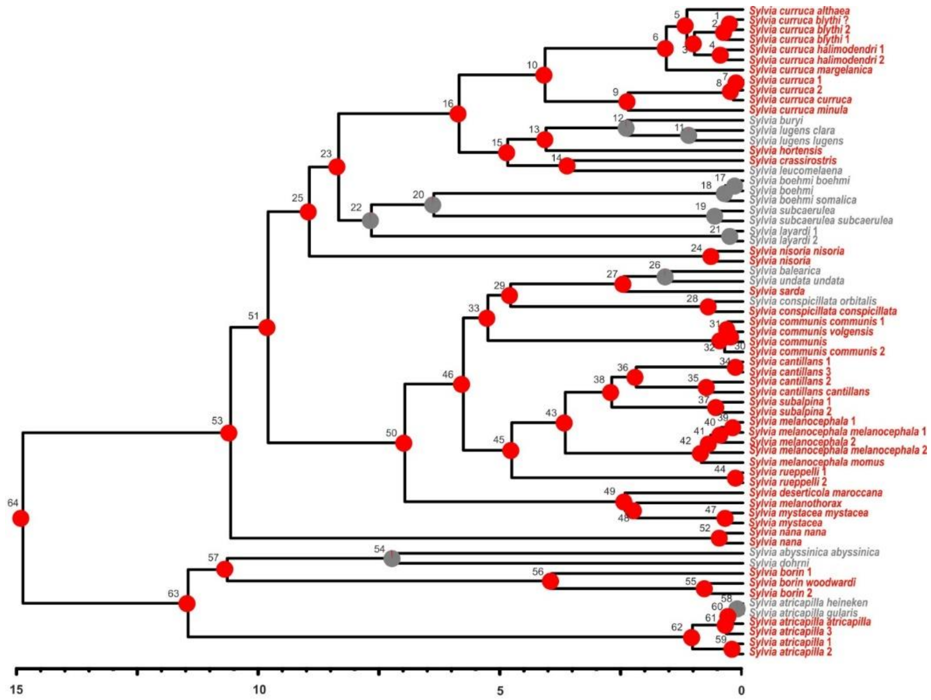

Figure A1.47. Mk2 analyses in Bayestraits using a chronogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years.

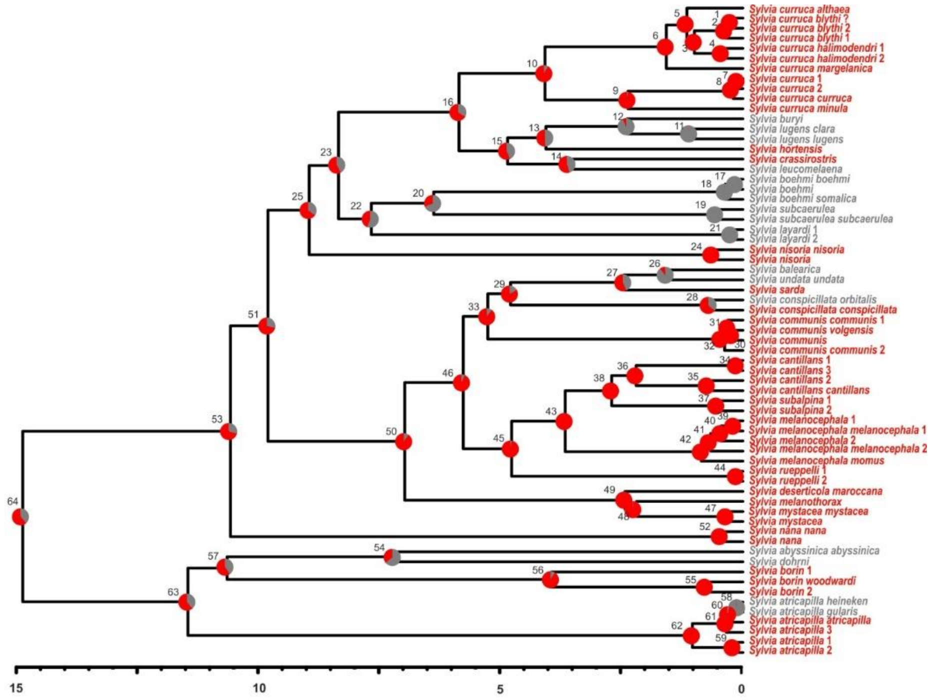

Figure A1.48. Mk2 analyses in Diversitree package using a chronogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years.

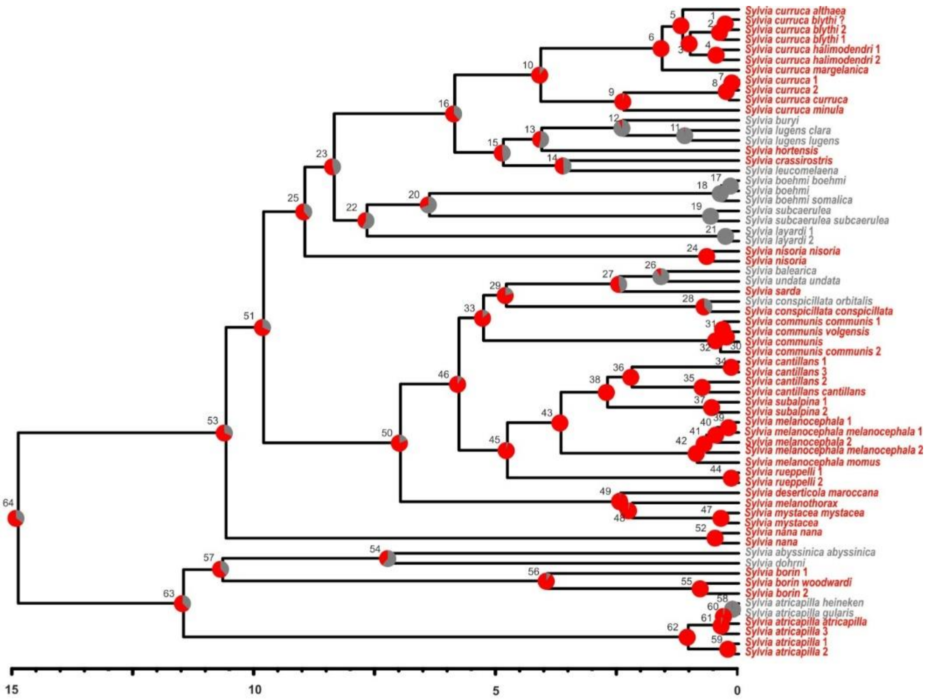

Figure A1.49. Mk2 analyses in Mesquite using a chronogram and a partial dataset. In species names, red color corresponds to migratory and gray to sedentary lineages. Nodes show the same color coding being proportional to the reconstructed probability of each character state. Scale in millions of years.

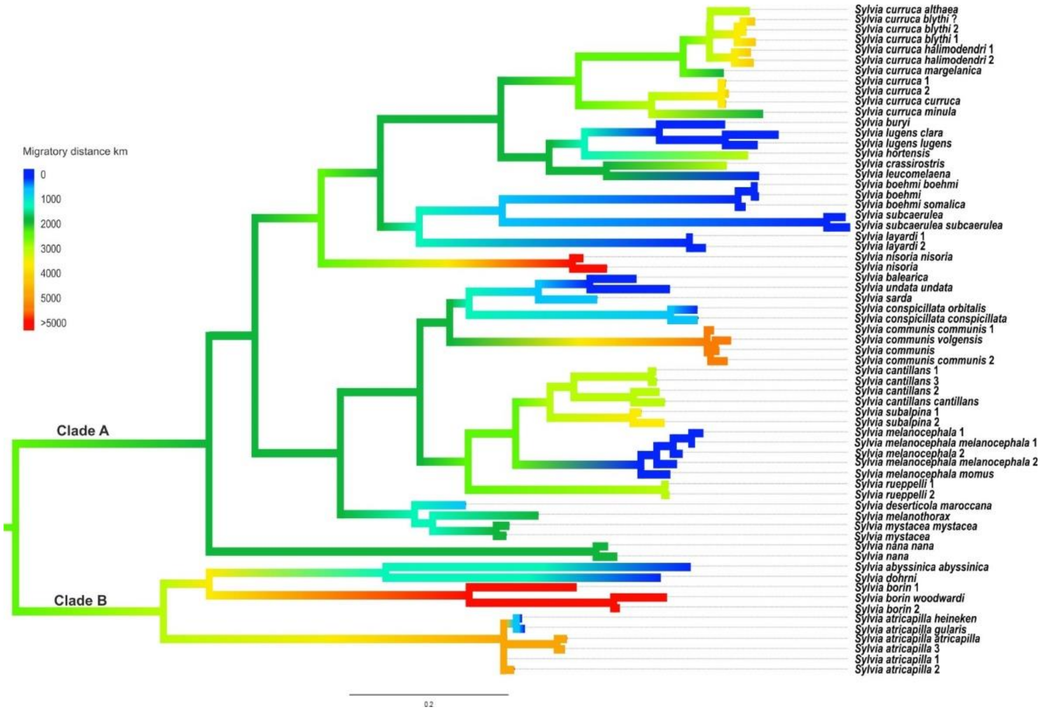

Figure A1.50. GLS analysis in Ape package using a phylogram and a partial dataset. Color corresponds to reconstructed migratory distance.

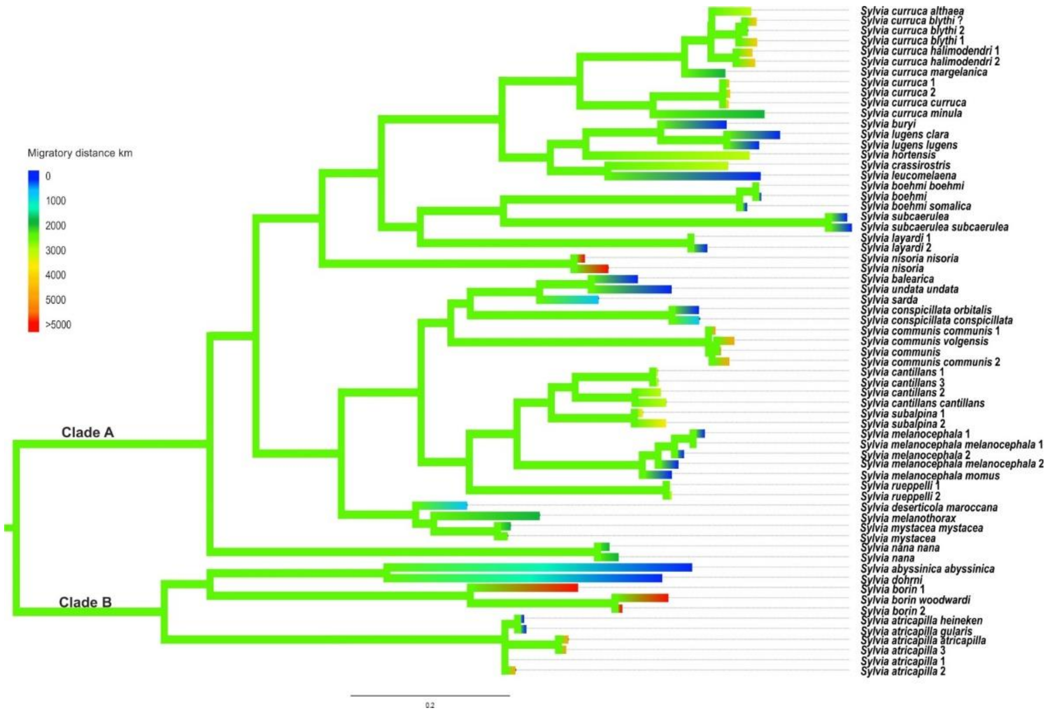

Figure A1.51. ML/Parsimony analyses in Ape package using a phylogram and a partial dataset. Color corresponds to reconstructed migratory distance.

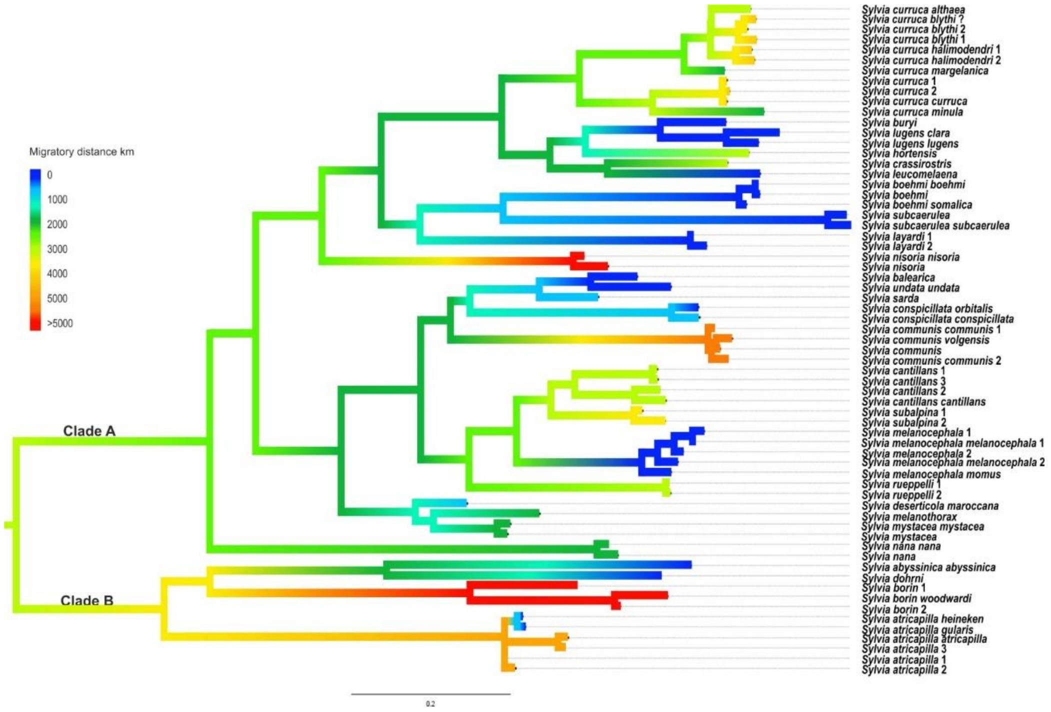

Figure A1.52. REML analysis in Ape package using a phylogram and a partial dataset. Color corresponds to reconstructed migratory distance.

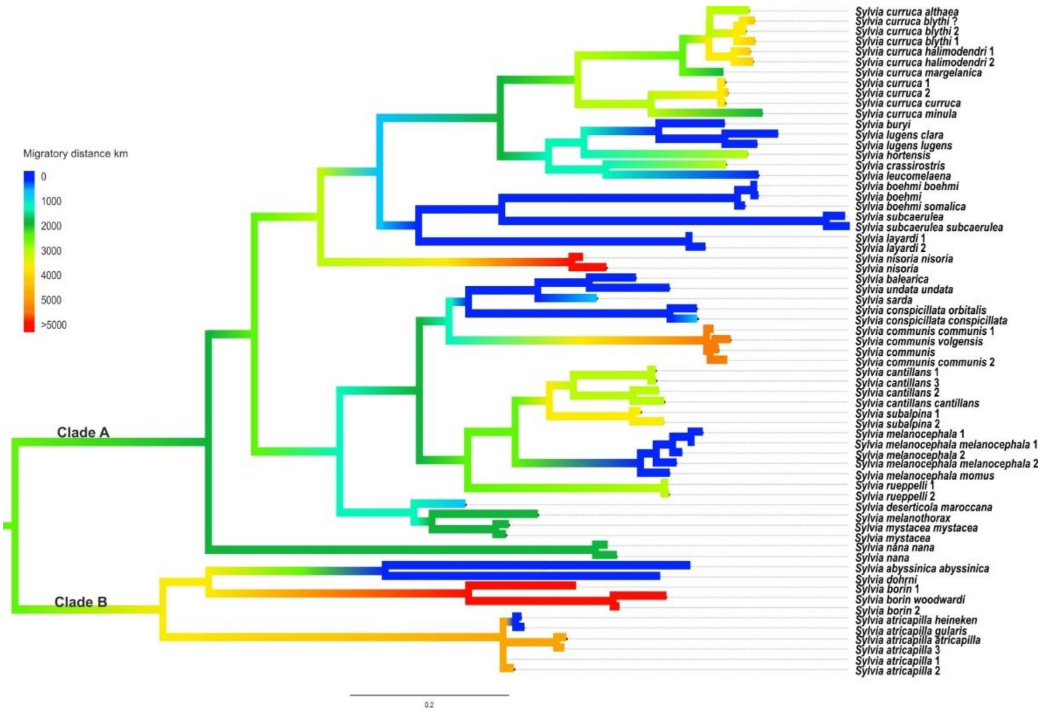

Figure A1.53. PIC analysis in Ape package using a phylogram and a partial dataset. Color corresponds to reconstructed migratory distance.

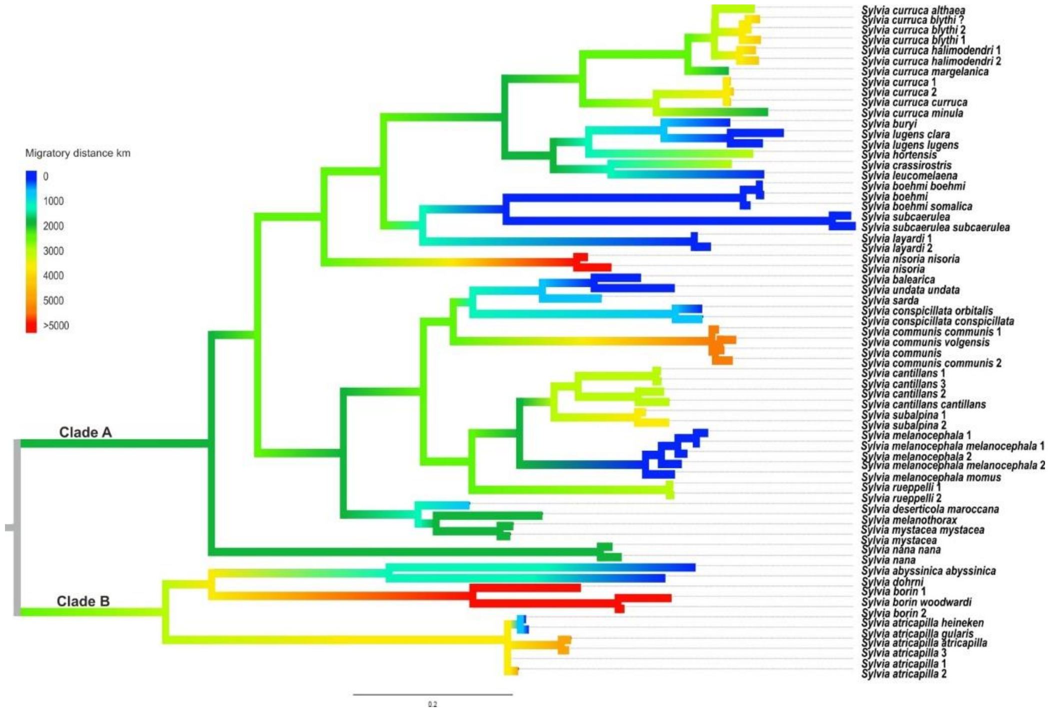

Figure A1.54. MCMC A analysis in Bayestraits using a phylogram and a partial dataset. Color corresponds to reconstructed migratory distance. Gray correspond to no data.

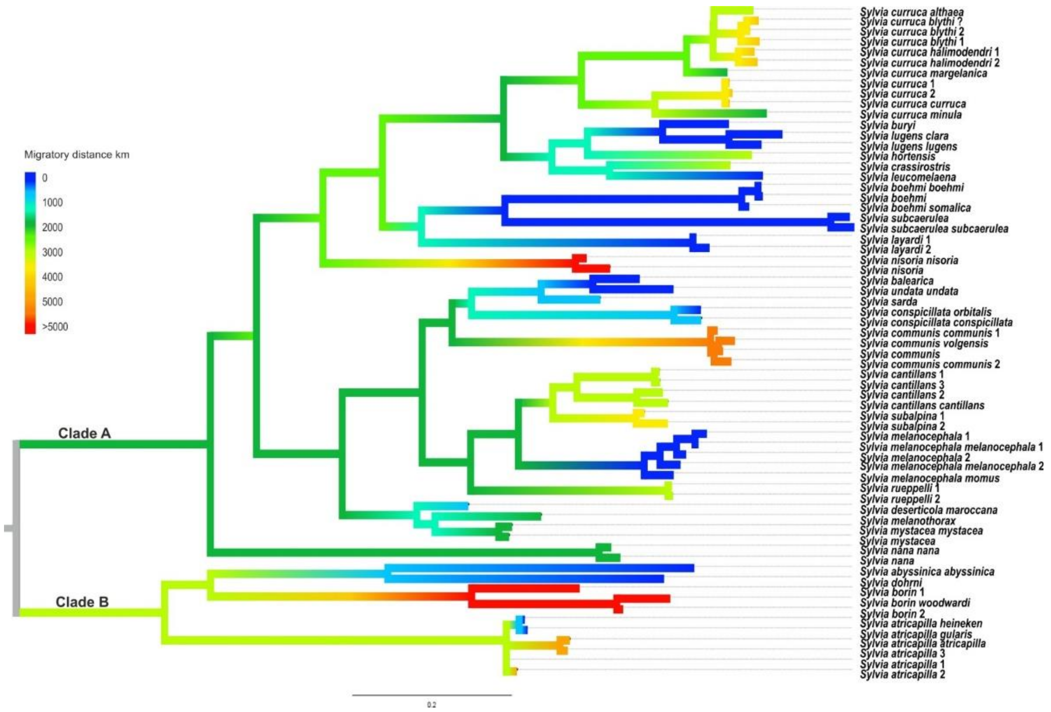

Figure A1.55. MCMC B analysis in Bayestraits using a phylogram and a partial dataset. Color corresponds to reconstructed migratory distance. Gray correspond to no data.

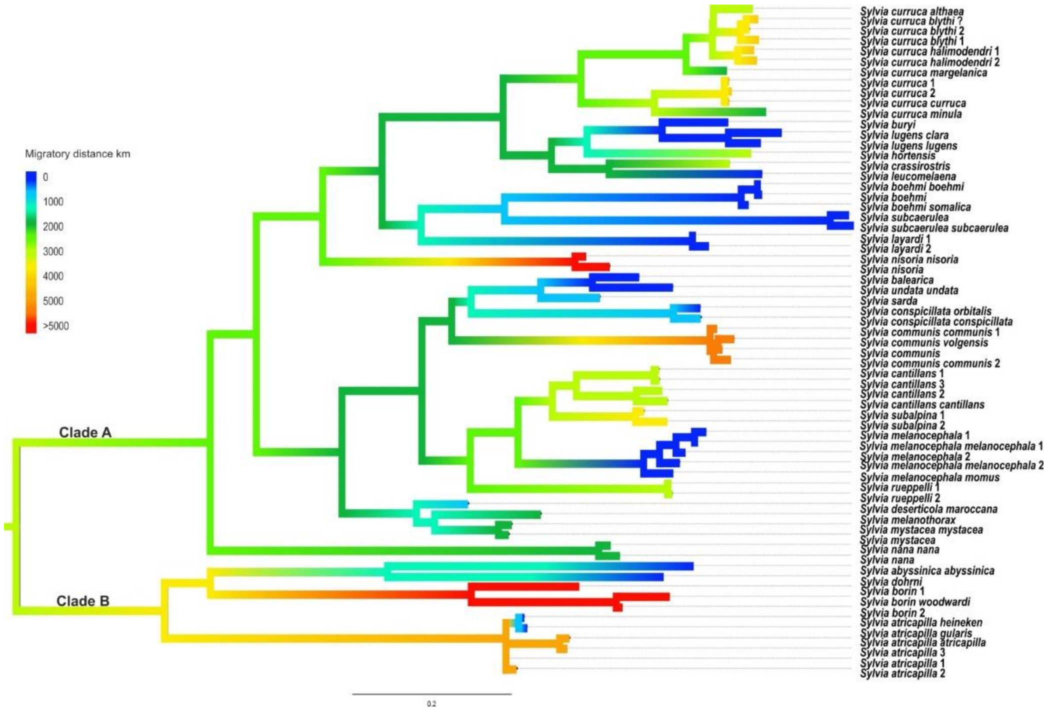

Figure A1.56. Parsimony analysis in Mesquite using a phylogram and a partial dataset. Color corresponds to reconstructed migratory distance.

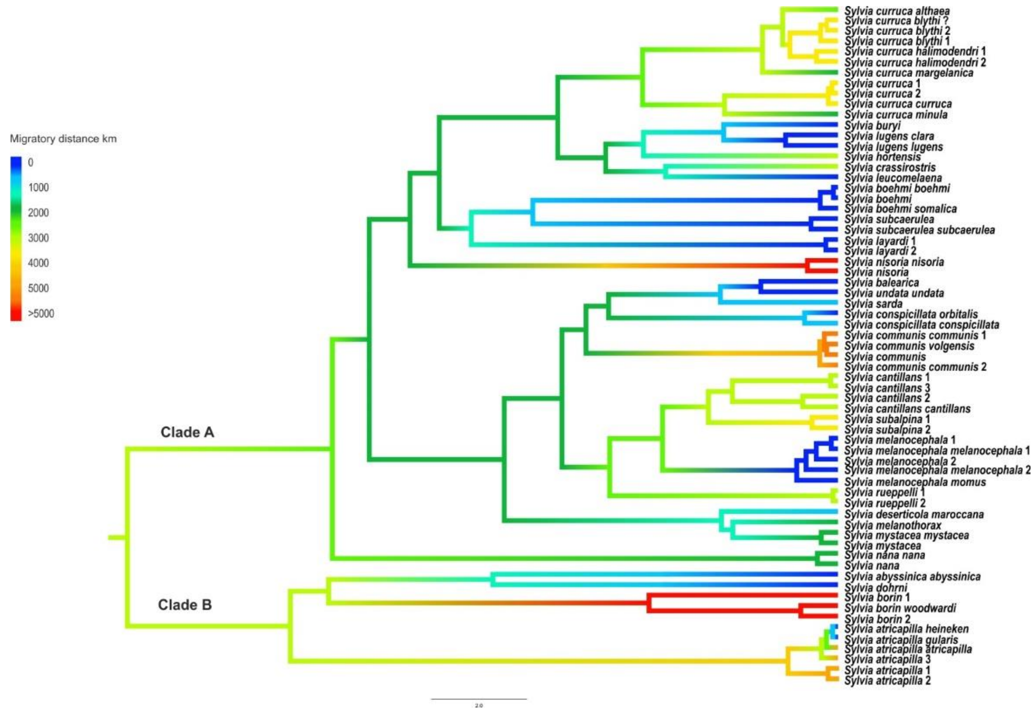

Figure A1.57. GLS analysis in Ape package using a chronogram and a partial dataset. Color corresponds to reconstructed migratory distance.

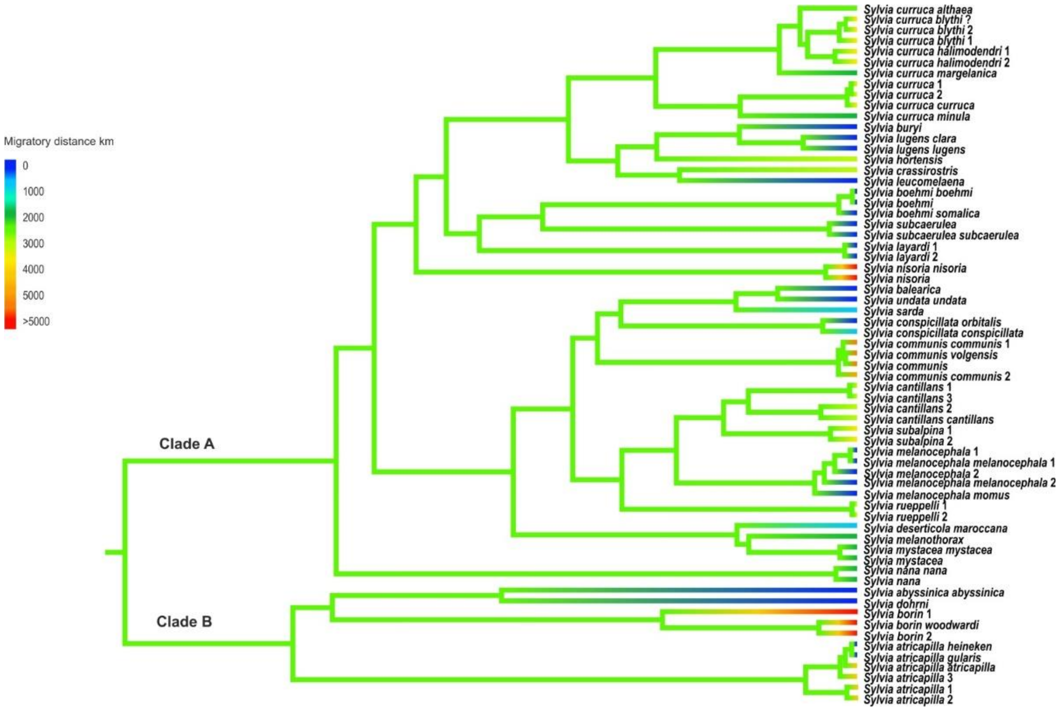

Figure A1.58. ML/Parsimony analyses in Ape package using a chronogram and a partial dataset. Color corresponds to reconstructed migratory distance.

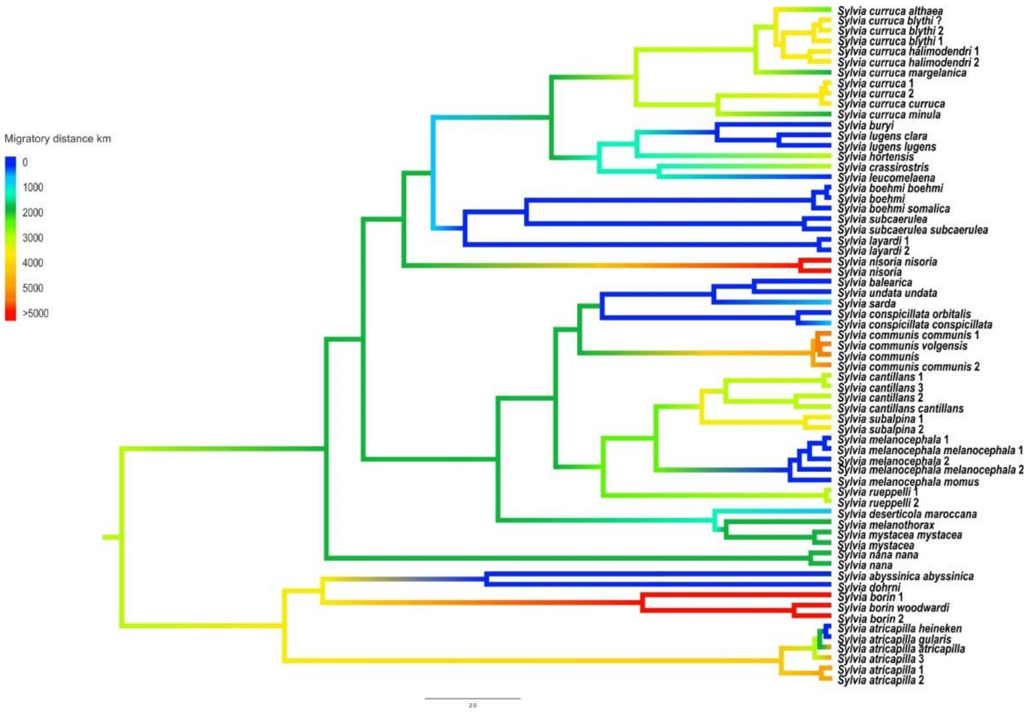

Figure A1.59. PIC analyses in Ape package using a chronogram and a partial dataset. Color corresponds to reconstructed migratory distance.

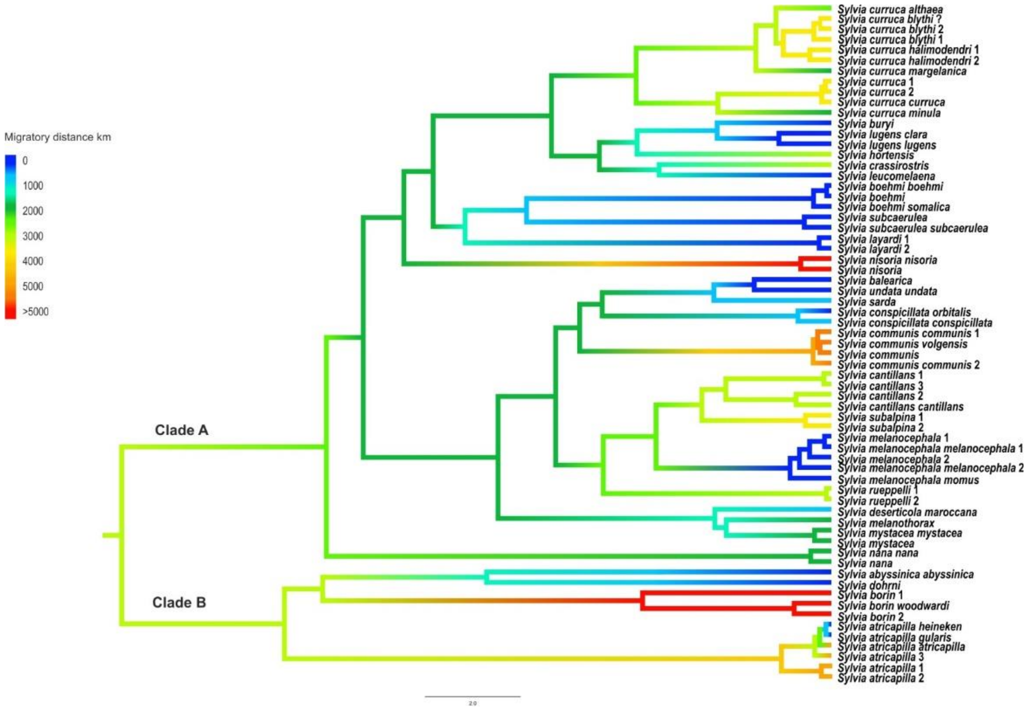

Figure A1.60. REML analyses in Ape package using a chronogram and a partial dataset. Color corresponds to reconstructed migratory distance.

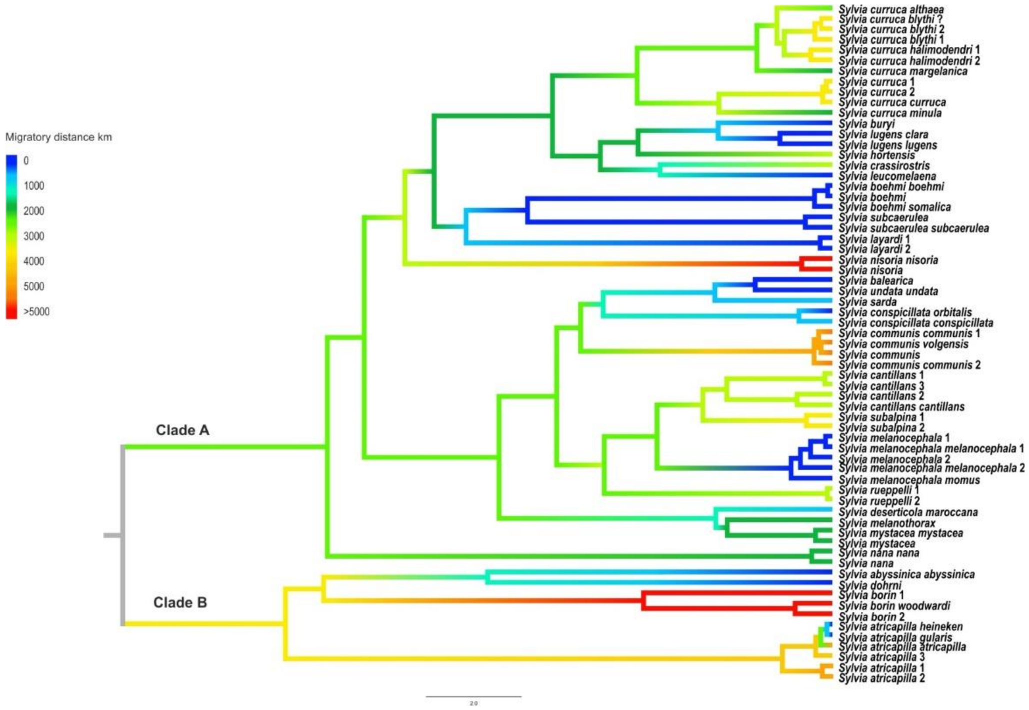

Figure A1.61. MCMC A analysis in Bayestraits using a chronogram and a partial dataset. Color corresponds to reconstructed migratory distance. Gray correspond to no data.

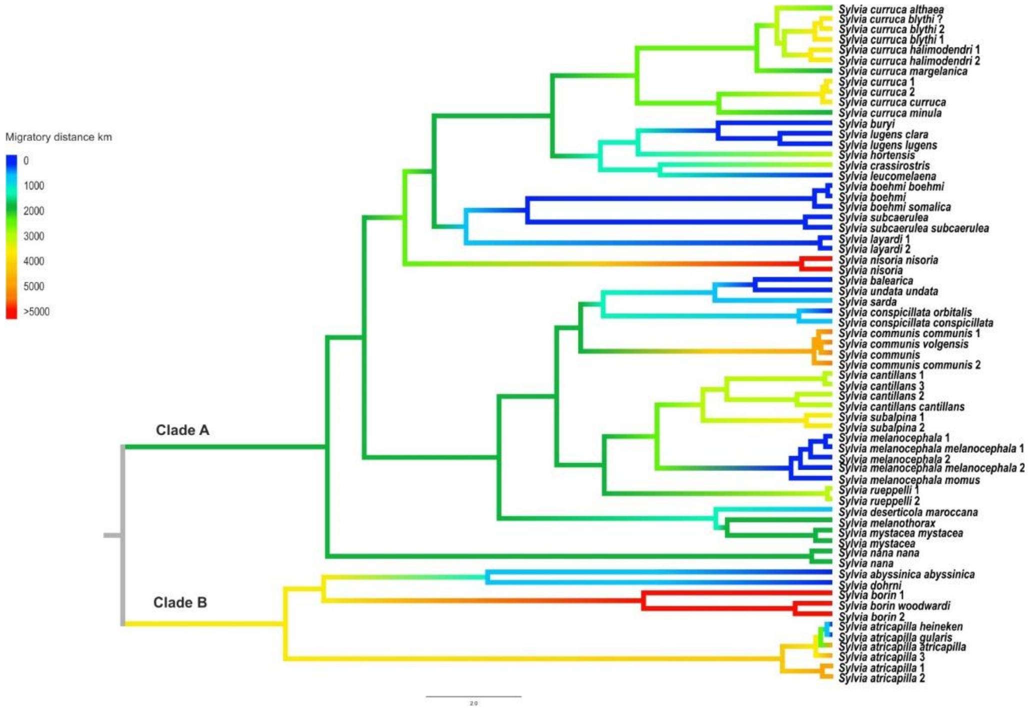

Figure A1.62. MCMC B analysis in Bayestraits using a chronogram and a partial dataset. Color corresponds to reconstructed migratory distance. Gray correspond to no data.

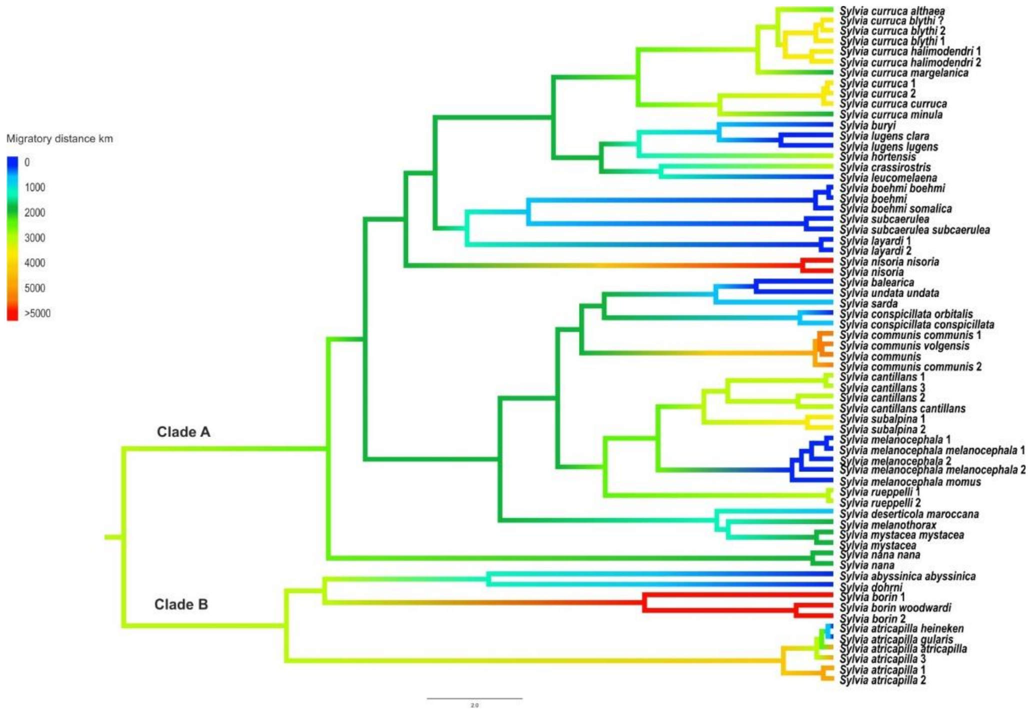

Figure A1.63. Parsimony analysis in Mesquite using a chronogram and a partial dataset. Color corresponds to reconstructed migratory distance

APPENDIX CHAPTER 2

Table A2.1. Biometric data from *Sylvia* species and subspecies Mass in (g) and lengths in (cm).

Taxa	Min Mass	Max Mass	Min Wing length	Max Wing length	Min Tail length	Max Tail length	Min Wing load	Max Wing load	Min Total length	Max Total length
Sylvia abyssinica abyssinica	15	21	6.4	7.3	5.6	6.6	0.30	0.22	13	15
Sylvia atricapilla	8.5	29	6.4	8.4	5	6	0.13	0.29	14	14
Sylvia atricapilla atricapilla	8.5	29	6.4	8.4	5	6	0.13	0.29	14	14
Sylvia atricapilla gularis	8.5	29	6.7	7.8	5	6	0.13	0.31	14	14
Sylvia atricapilla heineken	8.5	29	6.7	7.6	5	6	0.13	0.32	14	14
Sylvia atriceps	15	21	6.4	7.3	5.6	6.6	0.21	0.22	13	15
Sylvia balearica	5.9	9.1	4.8	5.4	5.1	5.8	0.12	0.15	12	12
Sylvia boehmi	14	14	5.8	6.3	5.4	6.1	0.22	0.18	12	12
Sylvia boehmi boehmi	14	14	5.8	6.3	5.4	6.1	0.22	0.18	12	12
Sylvia boehmi somalica	14	14	5.8	6.3	5.4	6.1	0.22	0.18	12	12
Sylvia borin	13.5	24.7	7.3	8.5	4.9	5.8	0.19	0.25	14	14
Sylvia borin woodwardi	13.5	24.7	7.4	8.5	4.9	5.8	0.19	0.25	14	14
Sylvia buryi	22	22	6.8	7	6.9	7.1	0.20	0.22	15	15
Sylvia cantillans	7	13.2	5.1	6.8	4.8	6	0.30	0.16	12	12
Sylvia cantillans cantillans	7	13.2	5.1	6.8	4.8	6	0.30	0.16	12	12
Sylvia communis	10.9	24.6	6.5	7.9	5.4	6.2	0.16	0.25	14	14
Sylvia communis communis	10.9	24.6	6.5	7.8	5.4	6.8	0.40	0.23	14	14
Sylvia conspicillata conspicillata	7.8	13.1	5.1	6.1	4.5	5.3	0.17	0.20	12	12
Sylvia conspicillata orbitalis	7.8	13.1	5.2	5.9	4.6	5.1	0.16	0.22	12	12
Sylvia crassirostris	16.2	30.5	7.3	8.4	6	6.7	0.18	0.27	15	15
Sylvia curruca althaea	11.2	16.3	6.3	7.6	5.2	6.3	0.17	0.18	13	13
Sylvia curruca blythi	6.8	18	5.9	6.9	5	6.3	0.12	0.21	12.5	14
Sylvia curruca curruca	6.8	18	6	7	5	6.1	0.11	0.21	12.5	14
Sylvia curruca halimodendri	6.8	18	6.2	7.2	5.4	6.2	0.10	0.20	12.5	14
Sylvia curruca margelanica	12	16.7	6.2	7.2	5.5	6.6	0.18	0.18	13	14
Sylvia curruca minula	12	16.7	5.8	6.5	4.7	6	0.22	0.21	13	14
Sylvia deserticola maroccana	7.7	10	5.2	5.8	5	5.7	0.15	0.15	12	12
Sylvia dohrni	17	22	6.7	6.9	5	5.9	0.30	0.27	14	15
Sylvia galinieri	27	31	7.6	8.8	6.8	8.3	0.26	0.21	17	19

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Sylvia hortensis	16.2	30.5	7.3	8.4	6	6.7	0.18	0.27	15	15
Sylvia layardi	13	16	6.3	6.7	6.1	6.4	0.17	0.19	13	13
Sylvia leucomelaena	12.5	16	6.5	7	5.9	6.7	0.16	0.17	15	15
Sylvia lugens clara	12	18	6	6.4	5.6	6.1	0.18	0.23	14	14
Sylvia lugens lugens	12	18	6	6.4	5.6	6.1	0.18	0.23	14	14
Sylvia melanocephala	9.6	20	5.2	6.7	5	6.7	0.18	0.22	13.5	13.5
Sylvia melanocephala melanocephala	9.6	20	5.2	6.7	5	6.7	0.18	0.22	13.5	13.5
Sylvia melanocephala momus	9.6	20	5.5	6	5	5.7	0.17	0.29	13.5	13.5
Sylvia melanothorax	9.4	15	5.9	6.3	5	5.7	0.16	0.21	13.5	13.5
Sylvia mystacea	8	11.5	5.1	6.3	5	5.8	0.16	0.16	13	13
Sylvia mystacea mystacea	8	11.5	5.5	6.3	5.1	5.7	0.14	0.16	13	13
Sylvia nana	7	10.5	5.4	6	4.3	5.1	0.15	0.17	11.5	11.5
Sylvia nana nana	7	10.5	5.4	6	4.3	5.1	0.15	0.17	11.5	11.5
Sylvia nigricapilla	21	21.5	8.2	8.6	7	8.4	0.18	0.15	17	19
Sylvia nisoria	18	28.8	8.6	9.2	6.6	7.3	0.16	0.21	15.5	15.5
Sylvia nisoria nisoria	18	28.8	8.6	9.2	6.6	7.3	0.16	0.21	15.5	15.5
Sylvia rueppelli	12.6	13.1	6.5	7.4	5.4	6.4	0.18	0.14	14	14
Sylvia sarda	7.5	13.5	5.1	5.9	5.3	6.2	0.14	0.18	12.5	12.5
Sylvia subalpina	7	13.2	5.7	6.4	5	5.4	0.20	0.19	12	12
Sylvia subcaerulea	11.6	18.6	6.2	7.1	6.2	7.4	0.15	0.18	14	14
Sylvia subcaerulea subcaerulea	11.6	18.6	6.2	7.1	6.2	7.4	0.15	0.18	14	14
Sylvia undata undata	9.7	11.8	5.1	5.6	5.6	6.5	0.17	0.16	13	13

APPENDIX CHAPTER 3

Table A3.1. Species breeding periods from the starting month to the last month. The non-breeding period correspond to the rest of the months.

Order	Family	Genus	Species	Breeding period
Accipitriformes	Accipitridae	*Accipiter*	*brevipes*	Apr - Aug
Accipitriformes	Accipitridae	*Accipiter*	*gentilis*	Apr - Aug
Accipitriformes	Accipitridae	*Accipiter*	*nisus*	May - Aug
Accipitriformes	Accipitridae	*Aquila*	*chrysaetos*	Apr - Sep
Accipitriformes	Accipitridae	*Aquila*	*heliaca*	Mar - Sep
Accipitriformes	Accipitridae	*Aquila*	*nipalensis*	Apr - Aug
Accipitriformes	Accipitridae	*Buteo*	*buteo*	Apr - Aug
Accipitriformes	Accipitridae	*Buteo*	*lagopus*	May - Aug
Accipitriformes	Accipitridae	*Buteo*	*rufinus*	Mar - Aug
Accipitriformes	Accipitridae	*Chelictinia*	*riocourii*	Mar - Aug
Accipitriformes	Accipitridae	*Circaetus*	*gallicus*	Apr - Aug
Accipitriformes	Accipitridae	*Circus*	*aeruginosus*	May - Jul
Accipitriformes	Accipitridae	*Circus*	*cyaneus*	Apr - Aug
Accipitriformes	Accipitridae	*Circus*	*macrourus*	Apr - Aug
Accipitriformes	Accipitridae	*Circus*	*maurus*	Jul - Sep
Accipitriformes	Accipitridae	*Circus*	*pygargus*	May - Aug
Accipitriformes	Accipitridae	*Clanga*	*clanga*	Apr - Sep
Accipitriformes	Accipitridae	*Clanga*	*pomarina*	May - Aug
Accipitriformes	Accipitridae	*Gyps*	*coprotheres*	Aprl - Jul
Accipitriformes	Accipitridae	*Gyps*	*fulvus*	May - Sep
Accipitriformes	Accipitridae	*Haliaeetus*	*albicilla*	Apr - Aug
Accipitriformes	Accipitridae	*Hieraaetus*	*pennatus*	Apr - Aug
Accipitriformes	Accipitridae	*Milvus*	*migrans*	Aprl - Jul
Accipitriformes	Accipitridae	*Milvus*	*milvus*	Aprl - Jul
Accipitriformes	Accipitridae	*Neophron*	*percnopterus*	May - Aug
Accipitriformes	Accipitridae	*Pernis*	*apivorus*	May - Aug
Accipitriformes	Pandionidae	*Pandion*	*haliaetus*	Aprl - Jul
Anseriformes	Anatidae	*Anas*	*crecca*	Apr - Aug
Anseriformes	Anatidae	*Anas*	*platyrhynchos*	May - Aug
Anseriformes	Anatidae	*Anser*	*anser*	Mar - Aug
Anseriformes	Anatidae	*Anser*	*brachyrhynchus*	May - Aug
Anseriformes	Anatidae	*Anser*	*erythropus*	Jun - Aug
Anseriformes	Anatidae	*Anser*	*fabalis*	May - Sep
Anseriformes	Anatidae	*Aythya*	*ferina*	Apr - Aug
Anseriformes	Anatidae	*Aythya*	*fuligula*	May - Sep
Anseriformes	Anatidae	*Aythya*	*marila*	May - Sep
Anseriformes	Anatidae	*Aythya*	*nyroca*	Apr - Aug
Anseriformes	Anatidae	*Branta*	*leucopsis*	May - Aug
Anseriformes	Anatidae	*Branta*	*ruficollis*	Jun - Sep

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Anseriformes	Anatidae	*Bucephala*	*clangula*	May - Sep
Anseriformes	Anatidae	*Cygnus*	*columbianus*	May - Sep
Anseriformes	Anatidae	*Cygnus*	*cygnus*	May - Sep
Anseriformes	Anatidae	*Cygnus*	*olor*	Apr - Oct
Anseriformes	Anatidae	*Mareca*	*penelope*	May - Aug
Anseriformes	Anatidae	*Mareca*	*strepera*	Apr - Aug
Anseriformes	Anatidae	*Marmaronetta*	*angustirostris*	Apr - Sep
Anseriformes	Anatidae	*Mergellus*	*albellus*	May - Sep
Anseriformes	Anatidae	*Mergus*	*merganser*	May - Sep
Anseriformes	Anatidae	*Mergus*	*serrator*	May - Sep
Anseriformes	Anatidae	*Netta*	*rufina*	Apr - Aug
Anseriformes	Anatidae	*Oxyura*	*leucocephala*	May - Aug
Anseriformes	Anatidae	*Polysticta*	*stelleri*	Jun - Aug
Anseriformes	Anatidae	*Spatula*	*querquedula*	Apr - Aug
Anseriformes	Anatidae	*Tadorna*	*ferruginea*	Apr - Aug
Anseriformes	Anatidae	*Tadorna*	*tadorna*	Apr - Aug
Bucerotiformes	Upupidae	*Upupa*	*epops*	May - Aug
Caprimulgiformes	Apodidae	*Apus*	*affinis*	Aprl - Jul
Caprimulgiformes	Apodidae	*Apus*	*apus*	May - Aug
Caprimulgiformes	Apodidae	*Apus*	*pallidus*	Aprl - Jul
Caprimulgiformes	Apodidae	*Tachymarptis*	*melba*	Mar - Sep
Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*aegyptius*	Mar - Sep
Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*europaeus*	May - Sep
Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*inornatus*	Mar - Aug
Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*longipennis*	Mar - Aug
Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*ruficollis*	May - Aug
Caprimulgiformes	Caprimulgidae	*Caprimulgus*	*vexillarius*	Jul - Dec
Charadriiformes	Alcidae	*Alca*	*torda*	Apr - Aug
Charadriiformes	Burhinidae	*Burhinus*	*oedicnemus*	Apr - Sep
Charadriiformes	Charadriidae	*Charadrius*	*alexandrinus*	May - Aug
Charadriiformes	Charadriidae	*Charadrius*	*asiaticus*	Apr - Aug
Charadriiformes	Charadriidae	*Charadrius*	*dubius*	Aprl - Jul
Charadriiformes	Charadriidae	*Charadrius*	*hiaticula*	Apr - Aug
Charadriiformes	Charadriidae	*Charadrius*	*leschenaultii*	Aprl - Jul
Charadriiformes	Charadriidae	*Charadrius*	*mongolus*	Apr - Aug
Charadriiformes	Charadriidae	*Eudromias*	*morinellus*	May - Aug
Charadriiformes	Charadriidae	*Pluvialis*	*apricaria*	May - Sep
Charadriiformes	Charadriidae	*Pluvialis*	*squatarola*	Jun - Aug
Charadriiformes	Charadriidae	*Vanellus*	*gregarius*	Apr - Aug
Charadriiformes	Charadriidae	*Vanellus*	*vanellus*	Mar - Sep
Charadriiformes	Dromadidae	*Dromas*	*ardeola*	Aprl - Jul
Charadriiformes	Glareolidae	*Cursorius*	*cursor*	Apr - Aug
Charadriiformes	Glareolidae	*Glareola*	*nordmanni*	May - Aug
Charadriiformes	Glareolidae	*Glareola*	*pratincola*	Apr - Aug
Charadriiformes	Haematopodidae	*Haematopus*	*ostralegus*	Apr - Aug
Charadriiformes	Laridae	*Chlidonias*	*hybrida*	May - Aug

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Charadriiformes	Laridae	*Chlidonias*	*leucopterus*	May - Aug
Charadriiformes	Laridae	*Chlidonias*	*niger*	May - Aug
Charadriiformes	Laridae	*Gelochelidon*	*nilotica*	May - Jun
Charadriiformes	Laridae	*Hydrocoloeus*	*minutus*	May - Aug
Charadriiformes	Laridae	*Hydroprogne*	*caspia*	Apr - Aug
Charadriiformes	Laridae	*Larus*	*argentatus*	Apr - Aug
Charadriiformes	Laridae	*Larus*	*audouinii*	Apr - Aug
Charadriiformes	Laridae	*Larus*	*cachinnans*	Mar - Aug
Charadriiformes	Laridae	*Larus*	*canus*	May - Sep
Charadriiformes	Laridae	*Larus*	*cirrocephalus*	Apr - Aug
Charadriiformes	Laridae	*Larus*	*fuscus*	Apr - Sep
Charadriiformes	Laridae	*Larus*	*genei*	Apr - Aug
Charadriiformes	Laridae	*Larus*	*glaucoides*	Apr - Aug
Charadriiformes	Laridae	*Larus*	*hyperboreus*	May - Aug
Charadriiformes	Laridae	*Larus*	*ichthyaetus*	May - Aug
Charadriiformes	Laridae	*Larus*	*melanocephalus*	May - Aug
Charadriiformes	Laridae	*Larus*	*ridibundus*	Apr - Aug
Charadriiformes	Laridae	*Onychoprion*	*anaethetus*	May - Aug
Charadriiformes	Laridae	*Onychoprion*	*fuscatus*	May - Aug
Charadriiformes	Laridae	*Sterna*	*dougallii*	May - Aug
Charadriiformes	Laridae	*Sterna*	*hirundo*	May - Sep
Charadriiformes	Laridae	*Sterna*	*repressa*	May - Sep
Charadriiformes	Laridae	*Sternula*	*balaenarum*	Oct - Jan
Charadriiformes	Laridae	*Sternula*	*saundersi*	May - Aug
Charadriiformes	Laridae	*Thalasseus*	*maximus*	Aprl - Jul
Charadriiformes	Laridae	*Thalasseus*	*sandvicensis*	Apr - Sep
Charadriiformes	Laridae	*Xema*	*sabini*	May - Aug
Charadriiformes	Recurvirostridae	*Recurvirostra*	*avosetta*	Apr - Aug
Charadriiformes	Scolopacidae	*Actitis*	*hypoleucos*	May - Jul
Charadriiformes	Scolopacidae	*Arenaria*	*interpres*	May - Jul
Charadriiformes	Scolopacidae	*Calidris*	*alba*	May - Jul
Charadriiformes	Scolopacidae	*Calidris*	*alpina*	Jun - Jul
Charadriiformes	Scolopacidae	*Calidris*	*canutus*	Jun - Jul
Charadriiformes	Scolopacidae	*Calidris*	*falcinellus*	Jun - Jul
Charadriiformes	Scolopacidae	*Calidris*	*ferruginea*	Jun - Jul
Charadriiformes	Scolopacidae	*Calidris*	*maritima*	May - Aug
Charadriiformes	Scolopacidae	*Calidris*	*minuta*	May - Jul
Charadriiformes	Scolopacidae	*Calidris*	*ruficollis*	Jun - Jul
Charadriiformes	Scolopacidae	*Calidris*	*temminckii*	May - Jul
Charadriiformes	Scolopacidae	*Gallinago*	*gallinago*	Aprl - Jul
Charadriiformes	Scolopacidae	*Gallinago*	*media*	May - Aug
Charadriiformes	Scolopacidae	*Gallinago*	*stenura*	May - Jul
Charadriiformes	Scolopacidae	*Limosa*	*lapponica*	May - Aug
Charadriiformes	Scolopacidae	*Limosa*	*limosa*	Aprl - Jul
Charadriiformes	Scolopacidae	*Lymnocryptes*	*minimus*	May - Aug
Charadriiformes	Scolopacidae	*Numenius*	*phaeopus*	May - Jul

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Charadriiformes	Scolopacidae	*Scolopax*	*rusticola*	Apr - Oct
Charadriiformes	Scolopacidae	*Tringa*	*erythropus*	May - Jun
Charadriiformes	Scolopacidae	*Tringa*	*glareola*	May - Jul
Charadriiformes	Scolopacidae	*Tringa*	*nebularia*	May - Jul
Charadriiformes	Scolopacidae	*Tringa*	*ochropus*	May - Jul
Charadriiformes	Scolopacidae	*Tringa*	*stagnatilis*	May - Jul
Charadriiformes	Scolopacidae	*Tringa*	*totanus*	Apr - Jun
Charadriiformes	Scolopacidae	*Xenus*	*cinereus*	May - Jul
Ciconiiformes	Ciconiidae	*Ciconia*	*abdimii*	May - Aug
Ciconiiformes	Ciconiidae	*Ciconia*	*ciconia*	Apr - Aug
Ciconiiformes	Ciconiidae	*Ciconia*	*nigra*	Apr - Aug
Columbiformes	Columbidae	*Columba*	*oenas*	Apr - Sep
Columbiformes	Columbidae	*Columba*	*palumbus*	Apr - Sep
Columbiformes	Columbidae	*Streptopelia*	*roseogrisea*	Aprl - Jul
Columbiformes	Columbidae	*Streptopelia*	*turtur*	May - Aug
Coraciiformes	Alcedinidae	*Alcedo*	*atthis*	May - Sep
Coraciiformes	Coraciidae	*Coracias*	*garrulus*	May - Aug
Coraciiformes	Meropidae	*Merops*	*albicollis*	Mar - Aug
Coraciiformes	Meropidae	*Merops*	*apiaster*	May - Aug
Coraciiformes	Meropidae	*Merops*	*persicus*	Mar - Aug
Cuculiformes	Cuculidae	*Clamator*	*glandarius*	Aprl - Jul
Cuculiformes	Cuculidae	*Clamator*	*jacobinus*	Oct - Apr
Cuculiformes	Cuculidae	*Clamator*	*levaillantii*	Oct - Apr
Cuculiformes	Cuculidae	*Cuculus*	*canorus*	Apr - Aug
Cuculiformes	Cuculidae	*Cuculus*	*rochii*	Oct - Mar
Falconiformes	Falconidae	*Falco*	*amurensis*	Apr - Sep
Falconiformes	Falconidae	*Falco*	*cherrug*	Apr - Aug
Falconiformes	Falconidae	*Falco*	*columbarius*	May - Aug
Falconiformes	Falconidae	*Falco*	*concolor*	Apr - Aug
Falconiformes	Falconidae	*Falco*	*eleonorae*	Jul - Oct
Falconiformes	Falconidae	*Falco*	*naumanni*	Aprl - Jul
Falconiformes	Falconidae	*Falco*	*peregrinus*	Apr - Aug
Falconiformes	Falconidae	*Falco*	*rusticolus*	Aprl - Jul
Falconiformes	Falconidae	*Falco*	*subbuteo*	May - Aug
Falconiformes	Falconidae	*Falco*	*tinnunculus*	Mar - Aug
Falconiformes	Falconidae	*Falco*	*vespertinus*	May - Jul
Galliformes	Phasianidae	*Coturnix*	*coturnix*	Mar - Jun
Gruiformes	Gruidae	*Anthropoides*	*virgo*	Apr - Aug
Gruiformes	Gruidae	*Grus*	*grus*	Apr - Sep
Gruiformes	Rallidae	*Crex*	*crex*	May - Aug
Gruiformes	Rallidae	*Fulica*	*atra*	May - Sep
Gruiformes	Rallidae	*Gallinula*	*chloropus*	May - Aug
Gruiformes	Rallidae	*Porzana*	*porzana*	Apr - Aug
Gruiformes	Rallidae	*Rallus*	*aquaticus*	May - Aug
Gruiformes	Rallidae	*Sarothrura*	*ayresi*	Apr - Aug
Gruiformes	Rallidae	*Zapornia*	*parva*	May - Aug

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Gruiformes	Rallidae	*Zapornia*	*pusilla*	May - Aug
Otidiformes	Otididae	*Chlamydotis*	*undulata*	Apr - Aug
Otidiformes	Otididae	*Otis*	*tarda*	Apr - Aug
Otidiformes	Otididae	*Tetrax*	*tetrax*	Apr - Aug
Passeriformes	Acrocephalidae	*Acrocephalus*	*arundinaceus*	May - Aug
Passeriformes	Acrocephalidae	*Acrocephalus*	*dumetorum*	May - Jul
Passeriformes	Acrocephalidae	*Acrocephalus*	*griseldis*	Apr - Aug
Passeriformes	Acrocephalidae	*Acrocephalus*	*melanopogon*	Aprl - Jul
Passeriformes	Acrocephalidae	*Acrocephalus*	*paludicola*	May - Jul
Passeriformes	Acrocephalidae	*Acrocephalus*	*palustris*	May - Jul
Passeriformes	Acrocephalidae	*Acrocephalus*	*schoenobaenus*	May - Aug
Passeriformes	Acrocephalidae	*Acrocephalus*	*scirpaceus*	May - Aug
Passeriformes	Acrocephalidae	*Hippolais*	*icterina*	May - Aug
Passeriformes	Acrocephalidae	*Hippolais*	*languida*	Aprl - Jul
Passeriformes	Acrocephalidae	*Hippolais*	*olivetorum*	May - Jul
Passeriformes	Acrocephalidae	*Hippolais*	*polyglotta*	May - Jul
Passeriformes	Acrocephalidae	*Iduna*	*opaca*	Apr - Jun
Passeriformes	Acrocephalidae	*Iduna*	*pallida*	May - Jun
Passeriformes	Aegithalidae	*Aegithalos*	*caudatus*	Apr - Aug
Passeriformes	Alaudidae	*Alauda*	*leucoptera*	May - Aug
Passeriformes	Alaudidae	*Alaudala*	*rufescens*	Mar - Jul
Passeriformes	Alaudidae	*Calandrella*	*brachydactyla*	Mar - Aug
Passeriformes	Alaudidae	*Eremophila*	*alpestris*	May - Jul
Passeriformes	Alaudidae	*Lullula*	*arborea*	Apr - Aug
Passeriformes	Alaudidae	*Melanocorypha*	*bimaculata*	Apr - Oct
Passeriformes	Alaudidae	*Melanocorypha*	*yeltoniensis*	Apr - Sep
Passeriformes	Alaudidae	*Pinarocorys*	*erythropygia*	Oct - Apr
Passeriformes	Alaudidae	*Pinarocorys*	*nigricans*	Jul - Sep
Passeriformes	Bombycillidae	*Bombycilla*	*garrulus*	Apr - Sep
Passeriformes	Calcariidae	*Calcarius*	*lapponicus*	May - Sep
Passeriformes	Calcariidae	*Plectrophenax*	*nivalis*	Mar - Sep
Passeriformes	Corvidae	*Corvus*	*corone*	Apr - Aug
Passeriformes	Corvidae	*Corvus*	*frugilegus*	Mar - Aug
Passeriformes	Corvidae	*Corvus*	*monedula*	Apr - Aug
Passeriformes	Emberizidae	*Emberiza*	*caesia*	Apr - Aug
Passeriformes	Emberizidae	*Emberiza*	*cineracea*	May - Sep
Passeriformes	Emberizidae	*Emberiza*	*hortulana*	May - Aug
Passeriformes	Emberizidae	*Emberiza*	*schoeniclus*	Apr - Aug
Passeriformes	Fringillidae	*Acanthis*	*flammea*	Apr - Aug
Passeriformes	Fringillidae	*Carduelis*	*carduelis*	May - Aug
Passeriformes	Fringillidae	*Chloris*	*chloris*	Aprl - Jul
Passeriformes	Fringillidae	*Coccothraustes*	*coccothraustes*	Apr - Aug
Passeriformes	Fringillidae	*Fringilla*	*coelebs*	Apr - Aug
Passeriformes	Fringillidae	*Fringilla*	*montifringilla*	May - Aug
Passeriformes	Fringillidae	*Linaria*	*cannabina*	Apr - Aug
Passeriformes	Fringillidae	*Linaria*	*flavirostris*	Apr - Aug

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Passeriformes	Fringillidae	*Pyrrhula*	*pyrrhula*	Apr - Aug
Passeriformes	Fringillidae	*Serinus*	*serinus*	Apr - Aug
Passeriformes	Fringillidae	*Serinus*	*syriacus*	Apr - Sep
Passeriformes	Fringillidae	*Spinus*	*spinus*	Apr - Aug
Passeriformes	Hirundinidae	*Cecropis*	*cucullata*	Jan - Mar
Passeriformes	Hirundinidae	*Cecropis*	*daurica*	Apr - Sep
Passeriformes	Hirundinidae	*Delichon*	*urbicum*	Apr - Aug
Passeriformes	Hirundinidae	*Hirundo*	*albigularis*	Sep - Mar
Passeriformes	Hirundinidae	*Hirundo*	*atrocaerulea*	Jan - Mar
Passeriformes	Hirundinidae	*Hirundo*	*rustica*	May - Aug
Passeriformes	Hirundinidae	*Neophedina*	*cincta*	Oct - Apr
Passeriformes	Hirundinidae	*Petrochelidon*	*spilodera*	Aug - Apr
Passeriformes	Hirundinidae	*Ptyonoprogne*	*rupestris*	May - Aug
Passeriformes	Hirundinidae	*Riparia*	*riparia*	May - Aug
Passeriformes	Laniidae	*Lanius*	*collurio*	Apr - Aug
Passeriformes	Laniidae	*Lanius*	*excubitor*	Apr - Aug
Passeriformes	Laniidae	*Lanius*	*isabellinus*	Apr - Sep
Passeriformes	Laniidae	*Lanius*	*minor*	Apr - Aug
Passeriformes	Laniidae	*Lanius*	*nubicus*	May - Aug
Passeriformes	Laniidae	*Lanius*	*senator*	May - Aug
Passeriformes	Locustellidae	*Locustella*	*fluviatilis*	May - Aug
Passeriformes	Locustellidae	*Locustella*	*luscinioides*	Apr - Aug
Passeriformes	Locustellidae	*Locustella*	*naevia*	May - Aug
Passeriformes	Motacillidae	*Anthus*	*campestris*	May - Aug
Passeriformes	Motacillidae	*Anthus*	*cervinus*	May - Aug
Passeriformes	Motacillidae	*Anthus*	*hoeschi*	Oct - Jan
Passeriformes	Motacillidae	*Anthus*	*petrosus*	Apr - Sep
Passeriformes	Motacillidae	*Anthus*	*pratensis*	Mar - Sep
Passeriformes	Motacillidae	*Anthus*	*richardi*	Aprl - Jul
Passeriformes	Motacillidae	*Anthus*	*trivialis*	May - Sep
Passeriformes	Motacillidae	*Motacilla*	*alba*	Apr - Aug
Passeriformes	Motacillidae	*Motacilla*	*cinerea*	May - Aug
Passeriformes	Motacillidae	*Motacilla*	*flava*	Apr - Aug
Passeriformes	Muscicapidae	*Cercotrichas*	*galactotes*	May - Sep
Passeriformes	Muscicapidae	*Cyanecula*	*svecica*	May - Aug
Passeriformes	Muscicapidae	*Erithacus*	*rubecula*	Apr - Aug
Passeriformes	Muscicapidae	*Ficedula*	*albicollis*	Aprl - Jul
Passeriformes	Muscicapidae	*Ficedula*	*hypoleuca*	May - Aug
Passeriformes	Muscicapidae	*Ficedula*	*parva*	May - Jul
Passeriformes	Muscicapidae	*Ficedula*	*semitorquata*	May - Aug
Passeriformes	Muscicapidae	*Irania*	*gutturalis*	May - Aug
Passeriformes	Muscicapidae	*Luscinia*	*luscinia*	May - Aug
Passeriformes	Muscicapidae	*Luscinia*	*megarhynchos*	Aprl - Jul
Passeriformes	Muscicapidae	*Monticola*	*saxatilis*	Apr - Sep
Passeriformes	Muscicapidae	*Monticola*	*solitarius*	May - Aug
Passeriformes	Muscicapidae	*Muscicapa*	*striata*	May - Aug

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Passeriformes	Muscicapidae	*Oenanthe*	*chrysopygia*	May - Sep
Passeriformes	Muscicapidae	*Oenanthe*	*cypriaca*	Apr - Aug
Passeriformes	Muscicapidae	*Oenanthe*	*deserti*	Apr - Sep
Passeriformes	Muscicapidae	*Oenanthe*	*finschii*	May - Aug
Passeriformes	Muscicapidae	*Oenanthe*	*hispanica*	May - Aug
Passeriformes	Muscicapidae	*Oenanthe*	*isabellina*	Apr - Aug
Passeriformes	Muscicapidae	*Oenanthe*	*oenanthe*	Apr - Aug
Passeriformes	Muscicapidae	*Oenanthe*	*pleschanka*	May - Aug
Passeriformes	Muscicapidae	*Oenanthe*	*xanthoprymna*	May - Sep
Passeriformes	Muscicapidae	*Phoenicurus*	*ochruros*	Apr - Aug
Passeriformes	Muscicapidae	*Phoenicurus*	*phoenicurus*	Apr - Aug
Passeriformes	Muscicapidae	*Saxicola*	*rubetra*	Apr - Aug
Passeriformes	Muscicapidae	*Saxicola*	*torquatus*	Apr - Aug
Passeriformes	Oriolidae	*Oriolus*	*oriolus*	May - Jul
Passeriformes	Passeridae	*Carpospiza*	*brachydactyla*	Aprl - Jul
Passeriformes	Passeridae	*Passer*	*moabiticus*	Aprl - Jul
Passeriformes	Phylloscopidae	*Phylloscopus*	*bonelli*	Apr - Aug
Passeriformes	Phylloscopidae	*Phylloscopus*	*borealis*	Jun - Aug
Passeriformes	Phylloscopidae	*Phylloscopus*	*collybita*	May - Aug
Passeriformes	Phylloscopidae	*Phylloscopus*	*ibericus*	Aprl - Jul
Passeriformes	Phylloscopidae	*Phylloscopus*	*inonartus*	Jun - Aug
Passeriformes	Phylloscopidae	*Phylloscopus*	*sibilatrix*	May - Jul
Passeriformes	Phylloscopidae	*Phylloscopus*	*sindianus*	May - Aug
Passeriformes	Phylloscopidae	*Phylloscopus*	*trochiloides*	May - Aug
Passeriformes	Phylloscopidae	*Phylloscopus*	*trochilus*	May - Jul
Passeriformes	Pittidae	*Pitta*	*angolensis*	Jan - Mar
Passeriformes	Prunellidae	*Prunella*	*modularis*	Apr - Aug
Passeriformes	Reguliidae	*Regulus*	*ignicapilla*	Aprl - Jul
Passeriformes	Reguliidae	*Regulus*	*regulus*	Apr - Aug
Passeriformes	Remizidae	*Remiz*	*pendulinus*	Apr - Sep
Passeriformes	Scotocercidae	*Cettia*	*cetti*	Apr - Aug
Passeriformes	Sturnidae	*Lamprotornis*	*shelleyi*	Mar - Jun
Passeriformes	Sturnidae	*Sturnus*	*vulgaris*	Apr - Aug
Passeriformes	Sylviidae	*Sylvia*	*atricapilla*	Apr - Aug
Passeriformes	Sylviidae	*Sylvia*	*borin*	Apr - Aug
Passeriformes	Sylviidae	*Sylvia*	*cantillans*	Mar - Aug
Passeriformes	Sylviidae	*Sylvia*	*communis*	Aprl - Jul
Passeriformes	Sylviidae	*Sylvia*	*conspicillata*	May - Aug
Passeriformes	Sylviidae	*Sylvia*	*curruca*	Apr - Aug
Passeriformes	Sylviidae	*Sylvia*	*deserticola*	May - Jul
Passeriformes	Sylviidae	*Sylvia*	*hortensis*	May - Aug
Passeriformes	Sylviidae	*Sylvia*	*melanocephala*	Apr - Aug
Passeriformes	Sylviidae	*Sylvia*	*melanothorax*	Mar - Aug
Passeriformes	Sylviidae	*Sylvia*	*mystacea*	Apr - Aug
Passeriformes	Sylviidae	*Sylvia*	*nana*	Mar - Aug
Passeriformes	Sylviidae	*Sylvia*	*nisoria*	May - Jul

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Passeriformes	Sylviidae	*Sylvia*	*rueppeli*	Apr - Aug
Passeriformes	Sylviidae	*Sylvia*	*sarda*	Aprl - Jul
Passeriformes	Troglodytidae	*Troglodytes*	*troglodytes*	May - Aug
Passeriformes	Turdidae	*Neophedina*	*guttata*	Oct - Feb
Passeriformes	Turdidae	*Turdus*	*iliacus*	Apr - Aug
Passeriformes	Turdidae	*Turdus*	*merula*	Mar - Aug
Passeriformes	Turdidae	*Turdus*	*philomelos*	Apr - Aug
Passeriformes	Turdidae	*Turdus*	*pilaris*	Apr - Aug
Passeriformes	Turdidae	*Turdus*	*ruficollis*	Apr - Sep
Passeriformes	Turdidae	*Turdus*	*torquatus*	May - Jul
Passeriformes	Turdidae	*Turdus*	*viscivorus*	Aprl - Jul
Pelecaniformes	Ardeidae	*Ardea*	*alba*	Apr - Aug
Pelecaniformes	Ardeidae	*Ardea*	*cinerea*	Mar - Aug
Pelecaniformes	Ardeidae	*Ardea*	*purpurea*	Apr - Aug
Pelecaniformes	Ardeidae	*Ardeola*	*idae*	Oct - Mar
Pelecaniformes	Ardeidae	*Ardeola*	*ralloides*	Apr - Aug
Pelecaniformes	Ardeidae	*Botaurus*	*stellaris*	Apr - Aug
Pelecaniformes	Ardeidae	*Bubulcus*	*ibis*	May - Aug
Pelecaniformes	Ardeidae	*Egretta*	*garzetta*	May - Aug
Pelecaniformes	Ardeidae	*Ixobrychus*	*minutus*	May - Aug
Pelecaniformes	Pelecanidae	*Pelecanus*	*onocrotalus*	Apr - Sep
Pelecaniformes	Threskiornithidae	*Geronticus*	*eremita*	Feb - Apr
Pelecaniformes	Threskiornithidae	*Platalea*	*leucorodia*	Apr - Aug
Pelecaniformes	Threskiornithidae	*Plegadis*	*falcinellus*	May - Aug
Phoenicpoteriformes	Phoenicopteridae	*Phoenicopterus*	*roseus*	Apr - Aug
Piciformes	Picidae	*Jynx*	*torquilla*	May - Aug
Podicipediformes	Podicipedidae	*Podiceps*	*auritus*	Apr - Oct
Podicipediformes	Podicipedidae	*Podiceps*	*cristatus*	Apr - Oct
Podicipediformes	Podicipedidae	*Podiceps*	*grisegena*	Apr - Sep
Podicipediformes	Podicipedidae	*Podiceps*	*nigricollis*	Apr - Sep
Pterocliformes	Pteroclidae	*Pterocles*	*alchata*	Apr - Aug
Pterocliformes	Pteroclidae	*Pterocles*	*orientalis*	Mar - Aug
Strigiformes	Strigidae	*Asio*	*flammeus*	Apr - Aug
Strigiformes	Strigidae	*Asio*	*otus*	Aprl - Jul
Strigiformes	Strigidae	*Bubo*	*scandiaca*	Apr - Sep
Strigiformes	Strigidae	*Otus*	*brucei*	Apr - Sep
Strigiformes	Strigidae	*Otus*	*scopus*	Apr - Aug
Suliformes	Phalacrocoracidae	*Microcarbo*	*pygmeus*	Aprl - Jul
Suliformes	Phalacrocoracidae	*Phalacrocorax*	*carbo*	Mar - Aug
Suliformes	Phalacrocoracidae	*Phalacrocorax*	*nigrogularis*	Jan - Mar

Table A3.2. Niche overlap values between breeding and non-breeding climatic niches within species, using D metric. P-values obtained from tests of niche similarity and equivalence via randomization. Significant P-values are shown in bold. Variances explained from PC1 and PC2, which correspond mainly to temperature (PC1) and precipitation (PC2).

Family	Genus	species	D=Niche overlap	Niche equivalency	Niche similarity 2->1	Niche similarity 1->2	PC1 % (T)	PC2 % (P)
Accipitridae	*Accipiter*	*brevipes*	0.006	**0.020**	0.713	0.455	75.02%	24.42%
Accipitridae	*Accipiter*	*gentilis*	0.195	**0.020**	1.010	**0.020**	75.16%	24.30%
Accipitridae	*Accipiter*	*nisus*	0.335	**0.020**	0.158	0.416	75.97%	23.71%
Accipitridae	*Aquila*	*chrysaetos*	0.156	**0.020**	0.277	**0.020**	77.58%	22.17%
Accipitridae	*Aquila*	*heliaca*	0.528	**0.020**	**0.040**	0.139	77.93%	21.81%
Accipitridae	*Aquila*	*nipalensis*	0.086	**0.020**	0.970	0.653	75.07%	24.36%
Accipitridae	*Buteo*	*buteo*	0.318	**0.020**	0.594	**0.020**	77.85%	20.94%
Accipitridae	*Buteo*	*lagopus*	0.127	**0.020**	0.396	0.099	76.11%	23.55%
Accipitridae	*Buteo*	*rufinus*	0.535	**0.020**	0.059	0.079	77.33%	22.40%
Accipitridae	*Chelictinia*	*riocourii*	0.123	**0.020**	0.079	0.257	76.96%	22.78%
Accipitridae	*Circaetus*	*gallicus*	0.205	**0.020**	0.554	0.257	74.67%	24.33%
Accipitridae	*Circus*	*aeruginosus*	0.067	**0.020**	0.772	0.832	75.33%	24.30%
Accipitridae	*Circus*	*cyaneus*	0.226	**0.020**	0.752	0.376	75.08%	24.37%
Accipitridae	*Circus*	*macrourus*	0.058	**0.020**	0.752	0.792	75.07%	24.37%
Accipitridae	*Circus*	*maurus*	0.044	**0.020**	0.198	0.951	75.11%	24.43%
Accipitridae	*Circus*	*pygargus*	0.086	**0.020**	0.594	0.951	75.99%	23.69%
Accipitridae	*Clanga*	*clanga*	0.455	**0.020**	**0.040**	0.059	77.44%	22.30%
Accipitridae	*Clanga*	*pomarina*	0.016	**0.020**	0.574	0.713	76.26%	23.42%
Accipitridae	*Gyps*	*coprotheres*	0.133	**0.020**	0.356	0.871	75.96%	23.70%
Accipitridae	*Gyps*	*fulvus*	0.281	**0.020**	0.713	0.535	76.50%	23.21%
Accipitridae	*Haliaeetus*	*albicilla*	0.155	**0.020**	0.951	0.693	75.07%	24.37%
Accipitridae	*Hieraaetus*	*pennatus*	0.325	**0.020**	0.812	0.317	75.17%	24.26%
Accipitridae	*Milvus*	*migrans*	0.579	**0.020**	**0.020**	**0.020**	76.09%	23.59%
Accipitridae	*Milvus*	*milvus*	0.305	**0.020**	0.178	0.079	75.92%	23.75%
Accipitridae	*Neophron*	*percnopterus*	0.319	**0.020**	0.059	0.396	75.89%	23.80%
Accipitridae	*Pernis*	*apivorus*	0.018	**0.020**	0.772	0.911	76.27%	23.41%
Pandionidae	*Pandion*	*haliaetus*	0.263	**0.020**	0.218	**0.020**	76.35%	23.33%
Anatidae	*Anas*	*crecca*	0.125	**0.020**	0.891	0.139	75.16%	24.29%
Anatidae	*Anas*	*platyrhynchos*	0.223	**0.020**	0.733	0.832	75.94%	23.74%
Anatidae	*Anser*	*anser*	0.413	**0.020**	0.238	0.277	77.49%	22.23%
Anatidae	*Anser*	*brachyrhynchus*	0.060	**0.020**	0.376	0.139	75.94%	23.69%
Anatidae	*Anser*	*erythropus*	0.035	**0.020**	0.455	0.554	75.18%	24.41%
Anatidae	*Anser*	*fabalis*	0.316	**0.020**	0.218	**0.020**	76.83%	22.88%
Anatidae	*Aythya*	*ferina*	0.068	**0.020**	0.733	0.713	75.06%	24.37%
Anatidae	*Aythya*	*fuligula*	0.212	**0.020**	0.297	0.475	76.67%	23.04%
Anatidae	*Aythya*	*marila*	0.332	**0.020**	0.099	0.238	76.84%	22.86%
Anatidae	*Aythya*	*nyroca*	0.162	**0.020**	0.812	0.198	75.10%	24.35%

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Anatidae	*Branta*	*leucopsis*	0.004	**0.020**	0.574	0.594	75.86%	23.77%
Anatidae	*Branta*	*ruficollis*	0.115	**0.020**	0.257	0.198	75.96%	23.68%
Anatidae	*Bucephala*	*clangula*	0.277	**0.020**	0.139	0.139	76.76%	22.95%
Anatidae	*Cygnus*	*columbianus*	0.120	**0.020**	0.416	0.257	76.82%	22.88%
Anatidae	*Cygnus*	*cygnus*	0.189	**0.020**	0.317	**0.020**	76.71%	23%
Anatidae	*Cygnus*	*olor*	0.132	**0.020**	0.238	0.337	77.97%	21.77%
Anatidae	*Mareca*	*penelope*	0.173	**0.020**	0.277	0.851	75.87%	23.80%
Anatidae	*Mareca*	*strepera*	0.098	**0.020**	0.772	**0.040**	75.07%	24.36%
Anatidae	*Marmaronetta*	*angustirostris*	0.195	**0.020**	0.297	0.733	77.22%	22.53%
Anatidae	*Mergellus*	*albellus*	0.298	**0.020**	0.158	**0.040**	76.74%	22.97%
Anatidae	*Mergus*	*merganser*	0.279	**0.020**	0.059	0.119	76.81%	22.89%
Anatidae	*Mergus*	*serrator*	0.145	**0.020**	0.713	**0.020**	76.78%	22.93%
Anatidae	*Netta*	*rufina*	0.084	**0.020**	0.832	0.792	75.10%	24.34%
Anatidae	*Oxyura*	*leucocephala*	0.163	**0.020**	0.277	0.713	75.92%	23.76%
Anatidae	*Polysticta*	*stelleri*	0.000	**0.020**	0.733	0.475	75.14%	24.46%
Anatidae	*Spatula*	*querquedula*	0.071	**0.020**	0.376	0.851	75.18%	24.26%
Anatidae	*Tadorna*	*ferruginea*	0.239	**0.020**	0.851	0.594	75.11%	24.33%
Anatidae	*Tadorna*	*tadorna*	0.201	**0.020**	0.951	0.455	74.94%	24.47%
Upupidae	*Upupa*	*epops*	0.230	**0.020**	0.356	0.535	76.04%	23.63%
Apodidae	*Apus*	*affinis*	0.501	**0.020**	0.198	**0.020**	76.21%	23.47%
Apodidae	*Apus*	*apus*	0.078	**0.020**	1.010	0.634	76.24%	23.44%
Apodidae	*Apus*	*pallidus*	0.020	**0.020**	0.614	0.931	75.98%	23.69%
Apodidae	*Tachymarptis*	*melba*	0.282	**0.020**	0.554	0.277	77.84%	21.91%
Caprimulgidae	*Caprimulgus*	*aegyptius*	0.253	**0.020**	0.178	0.119	77.24%	22.52%
Caprimulgidae	*Caprimulgus*	*europaeus*	0.089	**0.020**	0.832	0.832	76.97%	22.75%
Caprimulgidae	*Caprimulgus*	*inornatus*	0.326	**0.020**	0.079	0.238	77.55%	22.19%
Caprimulgidae	*Caprimulgus*	*longipennis*	0.008	**0.020**	0.634	0.752	77.79%	21.94%
Caprimulgidae	*Caprimulgus*	*ruficollis*	0.032	**0.020**	0.396	0.475	75.78%	23.89%
Caprimulgidae	*Caprimulgus*	*vexillarius*	0.292	**0.020**	0.376	0.238	77.49%	22.21%
Alcidae	*Alca*	*torda*	0.235	**0.020**	0.574	**0.020**	75%	24.43%
Burhinidae	*Burhinus*	*oedicnemus*	0.174	**0.020**	0.574	0.752	77.37%	22.37%
Charadriidae	*Charadrius*	*alexandrinus*	0.411	**0.020**	**0.020**	0.059	75.85%	23.83%
Charadriidae	*Charadrius*	*asiaticus*	0.097	**0.020**	0.990	0.475	75.06%	24.38%
Charadriidae	*Charadrius*	*dubius*	0.464	**0.020**	**0.020**	**0.020**	76.28%	23.40%
Charadriidae	*Charadrius*	*hiaticula*	0.088	**0.020**	0.733	0.277	75.18%	24.24%
Charadriidae	*Charadrius*	*leschenaultii*	0.010	**0.020**	0.653	0.713	76.39%	23.29%
Charadriidae	*Charadrius*	*mongolus*	0.010	**0.020**	0.614	0.693	75.62%	23.82%
Charadriidae	*Eudromias*	*morinellus*	0.179	**0.020**	0.218	0.792	76.04%	23.62%
Charadriidae	*Pluvialis*	*apricaria*	0.428	**0.020**	0.158	0.416	76.76%	22.92%
Charadriidae	*Pluvialis*	*squatarola*	0.000	**0.020**	0.792	0.079	75.50%	24.10%
Charadriidae	*Vanellus*	*gregarius*	0.077	**0.020**	0.752	0.634	74.98%	24.45%
Charadriidae	*Vanellus*	*vanellus*	0.644	**0.020**	**0.040**	0.059	77.96%	21.78%
Dromadidae	*Dromas*	*ardeola*	0.049	**0.020**	0.515	**0.020**	75.86%	23.81%
Glareolidae	*Cursorius*	*cursor*	0.351	**0.020**	0.238	0.356	74.82%	24.64%
Glareolidae	*Glareola*	*nordmanni*	0.011	**0.020**	0.693	0.891	75.95%	23.73%
Glareolidae	*Glareola*	*pratincola*	0.318	**0.020**	0.257	0.158	75.13%	24.30%

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Haematopodidae	*Haematopus*	*ostralegus*	0.079	**0.020**	0.911	0.653	74.98%	24.45%
Laridae	*Chlidonias*	*hybrida*	0.253	**0.020**	0.653	0.119	76.15%	23.53%
Laridae	*Chlidonias*	*leucopterus*	0.077	**0.020**	0.871	0.792	76.13%	23.55%
Laridae	*Chlidonias*	*niger*	0.012	**0.020**	0.673	0.891	75.88%	23.80%
Laridae	*Gelochelidon*	*nilotica*	0.062	**0.020**	0.951	0.535	74.96%	24.60%
Laridae	*Hydrocoloeus*	*minutus*	0.111	**0.020**	0.337	0.535	76.01%	23.66%
Laridae	*Hydroprogne*	*caspia*	0.466	**0.020**	0.416	**0.020**	75.12%	24.31%
Laridae	*Larus*	*argentatus*	0.095	**0.020**	0.554	0.812	75.26%	24.21%
Laridae	*Larus*	*audouinii*	0.005	**0.020**	0.416	0.574	75.10%	24.32%
Laridae	*Larus*	*cachinnans*	0.061	**0.020**	0.356	0.693	77.45%	22.25%
Laridae	*Larus*	*canus*	0.362	**0.020**	**0.040**	0.178	76.73%	22.98%
Laridae	*Larus*	*cirrocephalus*	0.445	**0.020**	0.317	0.198	75.29%	24.15%
Laridae	*Larus*	*fuscus*	0.352	**0.020**	**0.020**	**0.040**	77.36%	22.38%
Laridae	*Larus*	*genei*	0.074	**0.020**	0.792	0.970	75.01%	24.42%
Laridae	*Larus*	*glaucoides*	0.041	**0.020**	0.752	0.119	75.14%	24.30%
Laridae	*Larus*	*hyperboreus*	0.001	**0.020**	0.871	0.198	75.97%	23.71%
Laridae	*Larus*	*ichthyaetus*	0.268	**0.020**	0.119	0.079	75.90%	23.78%
Laridae	*Larus*	*melanocephalus*	0.143	**0.020**	0.337	0.257	75.95%	23.72%
Laridae	*Larus*	*ridibundus*	0.195	**0.020**	0.594	**0.020**	74.97%	24.44%
Laridae	*Onychoprion*	*anaethetus*	0.521	**0.020**	0.119	**0.020**	76.35%	23.33%
Laridae	*Onychoprion*	*fuscatus*	0.177	**0.020**	0.436	0.099	76.45%	23.21%
Laridae	*Sterna*	*dougallii*	0.354	**0.020**	0.158	**0.020**	76.49%	23.17%
Laridae	*Sterna*	*hirundo*	0.032	**0.020**	0.812	0.515	76.97%	22.75%
Laridae	*Sterna*	*repressa*	0.253	**0.020**	0.059	0.139	76.39%	23.31%
Laridae	*Sternula*	*balaenarum*	0.005	**0.020**	0.812	0.574	77.68%	22.02%
Laridae	*Sternula*	*saundersi*	0.101	**0.020**	0.158	0.238	75.89%	23.77%
Laridae	*Thalasseus*	*maximus*	0.465	**0.020**	**0.020**	**0.020**	76.38%	23.30%
Laridae	*Thalasseus*	*sandvicensis*	0.117	**0.020**	0.218	0.376	77.50%	22.23%
Laridae	*Xema*	*sabini*	0.000	**0.020**	0.990	0.337	76.15%	23.53%
Recurvirostridae	*Recurvirostra*	*avosetta*	0.207	**0.020**	0.891	0.891	75.05%	24.36%
Scolopacidae	*Actitis*	*hypoleucos*	0.059	**0.020**	0.436	0.416	75.41%	24.21%
Scolopacidae	*Arenaria*	*interpres*	0.002	**0.020**	0.554	**0.040**	75.60%	24%
Scolopacidae	*Calidris*	*alba*	0.000	**0.020**	0.614	0.139	75.62%	23.99%
Scolopacidae	*Calidris*	*alpina*	0.028	**0.020**	0.693	0.238	74.67%	24.85%
Scolopacidae	*Calidris*	*canutus*	0.035	**0.020**	0.475	0.059	74.68%	24.82%
Scolopacidae	*Calidris*	*falcinellus*	0.000	**0.020**	0.673	0.257	75.09%	24.45%
Scolopacidae	*Calidris*	*ferruginea*	0.000	**0.020**	0.832	0.119	74.84%	24.69%
Scolopacidae	*Calidris*	*maritima*	0.032	**0.020**	0.752	0.119	75.71%	23.94%
Scolopacidae	*Calidris*	*minuta*	0.000	**0.020**	0.911	0.297	75.41%	24.21%
Scolopacidae	*Calidris*	*ruficollis*	0.000	**0.020**	0.951	0.218	75.06%	24.48%
Scolopacidae	*Calidris*	*temminckii*	0.002	**0.020**	0.733	0.139	75.38%	24.24%
Scolopacidae	*Gallinago*	*gallinago*	0.098	**0.020**	0.693	0.693	76.09%	23.59%
Scolopacidae	*Gallinago*	*media*	0.004	**0.020**	0.871	0.297	76.13%	23.55%
Scolopacidae	*Gallinago*	*stenura*	0.000	**0.020**	0.475	0.436	75.58%	24.05%
Scolopacidae	*Limosa*	*lapponica*	0.001	**0.020**	0.752	0.099	76.37%	23.31%
Scolopacidae	*Limosa*	*limosa*	0.063	**0.020**	0.911	0.515	76.15%	23.52%

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Scolopacidae	*Lymnocryptes*	*minimus*	0.044	**0.020**	0.238	0.832	75.92%	23.75%
Scolopacidae	*Numenius*	*phaeopus*	0.004	**0.020**	0.752	0.554	75.56%	24.06%
Scolopacidae	*Scolopax*	*rusticola*	0.635	**0.020**	**0.040**	0.139	77.89%	21.86%
Scolopacidae	*Tringa*	*erythropus*	0.006	**0.020**	0.951	0.257	74.96%	24.62%
Scolopacidae	*Tringa*	*glareola*	0.015	**0.020**	0.891	0.475	75.35%	24.27%
Scolopacidae	*Tringa*	*nebularia*	0.009	**0.020**	0.871	0.871	75.41%	24.20%
Scolopacidae	*Tringa*	*ochropus*	0.045	**0.020**	0.772	0.713	75.33%	24.29%
Scolopacidae	*Tringa*	*stagnatilis*	0.025	**0.020**	0.515	0.990	75.34%	24.28%
Scolopacidae	*Tringa*	*totanus*	0.065	**0.020**	1.010	0.673	75.61%	24.03%
Scolopacidae	*Xenus*	*cinereus*	0.011	**0.020**	0.931	0.931	75.63%	24%
Ciconiidae	*Ciconia*	*abdimii*	0.432	**0.020**	0.139	0.178	76.23%	23.46%
Ciconiidae	*Ciconia*	*ciconia*	0.134	**0.020**	0.871	0.851	75.10%	24.33%
Ciconiidae	*Ciconia*	*nigra*	0.187	**0.020**	0.990	0.990	75.16%	24.28%
Columbidae	*Columba*	*oenas*	0.263	**0.020**	0.396	0.594	77.49%	22.25%
Columbidae	*Columba*	*palumbus*	0.402	**0.020**	**0.020**	0.515	77.44%	22.29%
Columbidae	*Streptopelia*	*roseogrisea*	0.331	**0.020**	**0.020**	0.218	75.59%	24.10%
Columbidae	*Streptopelia*	*turtur*	0.199	**0.020**	0.376	0.673	75.86%	23.81%
Alcedinidae	*Alcedo*	*atthis*	0.556	**0.020**	**0.020**	**0.020**	76.88%	22.84%
Coraciidae	*Coracias*	*garrulus*	0.087	**0.020**	0.812	0.693	76.06%	23.61%
Meropidae	*Merops*	*albicollis*	0.058	**0.020**	0.574	0.416	77.54%	22.20%
Meropidae	*Merops*	*apiaster*	0.107	**0.020**	0.713	0.495	76.13%	23.54%
Meropidae	*Merops*	*persicus*	0.269	**0.020**	0.614	0.772	77.40%	22.34%
Cuculidae	*Clamator*	*glandarius*	0.548	**0.020**	0.158	0.119	76.13%	23.55%
Cuculidae	*Clamator*	*jacobinus*	0.438	**0.020**	0.376	0.099	76.92%	22.80%
Cuculidae	*Clamator*	*levaillantii*	0.519	**0.020**	**0.040**	**0.020**	77.22%	22.49%
Cuculidae	*Cuculus*	*canorus*	0.285	**0.020**	0.713	0.257	75.40%	24.03%
Cuculidae	*Cuculus*	*rochii*	0.093	**0.020**	0.455	0.634	77.90%	21.85%
Falconidae	*Falco*	*amurensis*	0.286	**0.020**	0.277	0.218	77.62%	22.13%
Falconidae	*Falco*	*cherrug*	0.153	**0.020**	0.851	0.713	75.10%	24.35%
Falconidae	*Falco*	*columbarius*	0.425	**0.020**	0.158	0.178	75.99%	23.68%
Falconidae	*Falco*	*concolor*	0.005	**0.020**	0.178	0.554	75.20%	24.22%
Falconidae	*Falco*	*eleonorae*	0.000	**0.020**	0.733	0.812	76.30%	23.32%
Falconidae	*Falco*	*naumanni*	0.118	**0.020**	0.851	1.010	76.02%	23.66%
Falconidae	*Falco*	*peregrinus*	0.503	**0.020**	**0.020**	0.257	75.26%	24.18%
Falconidae	*Falco*	*rusticolus*	0.034	**0.020**	0.653	0.178	76.10%	23.60%
Falconidae	*Falco*	*subbuteo*	0.448	**0.020**	0.356	0.317	76.15%	23.53%
Falconidae	*Falco*	*tinnunculus*	0.600	**0.020**	**0.020**	**0.020**	77.63%	22.09%
Falconidae	*Falco*	*vespertinus*	0.053	**0.020**	0.396	0.772	75.27%	24.35%
Phasianidae	*Coturnix*	*coturnix*	0.211	**0.020**	0.871	0.990	76.38%	23.29%
Gruidae	*Anthropoides*	*virgo*	0.122	**0.020**	0.911	0.713	75.05%	24.39%
Gruidae	*Grus*	*grus*	0.438	**0.020**	0.059	0.079	77.39%	22.35%
Rallidae	*Crex*	*crex*	0.060	**0.020**	0.693	0.653	76.19%	23.49%
Rallidae	*Fulica*	*atra*	0.365	**0.020**	**0.040**	**0.020**	76.74%	22.98%
Rallidae	*Gallinula*	*chloropus*	0.488	**0.020**	0.119	**0.020**	76.16%	23.51%
Rallidae	*Porzana*	*porzana*	0.063	**0.020**	0.673	0.851	75.16%	24.28%
Rallidae	*Rallus*	*aquaticus*	0.360	**0.020**	0.376	0.416	75.97%	23.70%

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Rallidae	*Sarothrura*	*ayresi*	0.074	**0.020**	0.673	0.733	75.10%	24.31%
Rallidae	*Zapornia*	*parva*	0.353	**0.020**	**0.040**	0.079	75.88%	23.80%
Rallidae	*Zapornia*	*pusilla*	0.220	**0.020**	0.792	**0.020**	76.13%	23.55%
Otididae	*Chlamydotis*	*undulata*	0.530	**0.020**	0.257	0.158	74.87%	24.57%
Otididae	*Otis*	*tarda*	0.081	**0.020**	0.931	0.614	75.12%	24.32%
Otididae	*Tetrax*	*tetrax*	0.079	**0.020**	0.851	0.772	75.08%	24.36%
Acrocephalidae	*Acrocephalus*	*arundinaceus*	0.208	**0.020**	0.594	0.297	76.22%	23.46%
Acrocephalidae	*Acrocephalus*	*dumetorum*	0.184	**0.020**	0.653	0.911	75.19%	24.44%
Acrocephalidae	*Acrocephalus*	*griseldis*	0.000	**0.020**	0.178	0.535	74.87%	24.58%
Acrocephalidae	*Acrocephalus*	*melanopogon*	0.155	**0.020**	0.337	0.119	75.70%	23.98%
Acrocephalidae	*Acrocephalus*	*paludicola*	0.002	**0.020**	0.257	0.337	75.19%	24.44%
Acrocephalidae	*Acrocephalus*	*palustris*	0.002	**0.020**	0.931	0.733	75.41%	24.21%
Acrocephalidae	*Acrocephalus*	*schoenobaenus*	0.063	**0.020**	0.693	0.812	76.01%	23.66%
Acrocephalidae	*Acrocephalus*	*scirpaceus*	0.218	**0.020**	0.218	0.337	75.99%	23.69%
Acrocephalidae	*Hippolais*	*icterina*	0.000	**0.020**	0.713	1.010	76.31%	23.37%
Acrocephalidae	*Hippolais*	*languida*	0.170	**0.020**	0.455	0.634	75.76%	23.93%
Acrocephalidae	*Hippolais*	*olivetorum*	0.001	**0.020**	0.851	0.653	75.20%	24.42%
Acrocephalidae	*Hippolais*	*polyglotta*	0.000	**0.020**	0.951	1.248	75.48%	24.14%
Acrocephalidae	*Iduna*	*opaca*	0.000	**0.020**	0.871	1.446	75.62%	24.02%
Acrocephalidae	*Iduna*	*pallida*	0.020	**0.020**	0.733	0.772	74.88%	24.69%
Aegithalidae	*Aegithalos*	*caudatus*	0.070	**0.020**	0.277	**0.020**	75.19%	24.29%
Alaudidae	*Alauda*	*leucoptera*	0.026	**0.020**	0.554	0.990	75.99%	23.70%
Alaudidae	*Alaudala*	*rufescens*	0.519	**0.020**	0.059	0.277	76.68%	23.02%
Alaudidae	*Calandrella*	*brachydactyla*	0.517	**0.020**	**0.040**	0.198	77.36%	22.37%
Alaudidae	*Eremophila*	*alpestris*	0.420	**0.020**	0.178	0.079	75.25%	24.38%
Alaudidae	*Lullula*	*arborea*	0.013	**0.020**	0.277	0.871	75%	24.43%
Alaudidae	*Melanocorypha*	*bimaculata*	0.083	**0.020**	0.772	0.772	0.7777	21.99%
Alaudidae	*Melanocorypha*	*yeltoniensis*	0.001	**0.020**	0.733	0.752	77.57%	22.19%
Alaudidae	*Pinarocorys*	*erythropygia*	0.135	**0.020**	0.416	0.178	76.94%	22.78%
Alaudidae	*Pinarocorys*	*nigricans*	0.001	**0.020**	0.337	0.812	75.10%	24.44%
Bombycillidae	*Bombycilla*	*garrulus*	0.176	**0.020**	0.178	0.337	77.61%	22.13%
Calcariidae	*Calcarius*	*lapponicus*	0.280	**0.020**	0.277	0.119	76.96%	22.75%
Calcariidae	*Plectrophenax*	*nivalis*	0.384	**0.020**	**0.020**	0.178	78.23%	21.52%
Corvidae	*Corvus*	*corone*	0.143	**0.020**	0.812	0.713	75.19%	24.28%
Corvidae	*Corvus*	*frugilegus*	0.546	**0.020**	0.238	0.238	77.55%	22.17%
Corvidae	*Corvus*	*monedula*	0.135	**0.020**	0.733	0.931	75.02%	24.42%
Emberizidae	*Emberiza*	*caesia*	0.099	**0.020**	0.436	0.218	74.83%	24.60%
Emberizidae	*Emberiza*	*cineracea*	0.630	**0.020**	0.059	0.059	76.33%	23.38%
Emberizidae	*Emberiza*	*hortulana*	0.269	**0.020**	0.238	0.416	75.97%	23.70%
Emberizidae	*Emberiza*	*schoeniclus*	0.121	**0.020**	0.891	0.079	75.24%	24.21%
Fringillidae	*Acanthis*	*flammea*	0.056	**0.020**	0.257	**0.020**	75.30%	24.21%
Fringillidae	*Carduelis*	*carduelis*	0.399	**0.020**	0.059	**0.020**	75.92%	23.76%
Fringillidae	*Chloris*	*chloris*	0.240	**0.020**	0.119	**0.020**	75.89%	23.78%
Fringillidae	*Coccothraustes*	*coccothraustes*	0.155	**0.020**	1.010	0.871	75.08%	24.37%
Fringillidae	*Fringilla*	*coelebs*	0.191	**0.020**	0.990	0.634	75.01%	24.43%
Fringillidae	*Fringilla*	*montifringilla*	0.249	**0.020**	0.317	0.099	75.98%	23.70%

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Fringillidae	*Linaria*	*cannabina*	0.199	**0.020**	0.951	0.693	75.12%	24.33%
Fringillidae	*Linaria*	*flavirostris*	0.160	**0.020**	0.891	0.079	75.40%	24.08%
Fringillidae	*Pyrrhula*	*pyrrhula*	0.077	**0.020**	0.515	**0.020**	75.20%	24.28%
Fringillidae	*Serinus*	*serinus*	0.327	**0.020**	0.257	0.119	74.97%	24.46%
Fringillidae	*Serinus*	*syriacus*	0.034	**0.020**	0.614	0.752	77.49%	22.26%
Fringillidae	*Spinus*	*spinus*	0.100	**0.020**	0.733	0.554	75.12%	24.34%
Hirundinidae	*Cecropis*	*cucullata*	0.382	**0.020**	0.218	0.198	77.81%	21.95%
Hirundinidae	*Cecropis*	*daurica*	0.605	**0.020**	**0.020**	**0.040**	77.64%	22.11%
Hirundinidae	*Delichon*	*urbicum*	0.076	**0.020**	0.416	0.416	75.29%	24.14%
Hirundinidae	*Hirundo*	*albigularis*	0.114	**0.020**	0.554	0.832	75.02%	24.37%
Hirundinidae	*Hirundo*	*atrocaerulea*	0.186	**0.020**	0.079	0.158	78.95%	20.82%
Hirundinidae	*Hirundo*	*rustica*	0.301	**0.020**	0.356	0.416	76.20%	23.48%
Hirundinidae	*Neophedina*	*cincta*	0.530	**0.020**	0.158	0.059	77.17%	22.54%
Hirundinidae	*Petrochelidon*	*spilodera*	0.012	**0.020**	0.693	0.851	75.21%	24.37%
Hirundinidae	*Ptyonoprogne*	*rupestris*	0.433	**0.020**	0.119	**0.020**	75.91%	23.77%
Hirundinidae	*Riparia*	*riparia*	0.106	**0.020**	0.653	0.455	76.08%	23.60%
Laniidae	*Lanius*	*collurio*	0.074	**0.020**	0.931	0.832	75.25%	24.17%
Laniidae	*Lanius*	*excubitor*	0.236	**0.020**	0.891	0.713	75.01%	24.45%
Laniidae	*Lanius*	*isabellinus*	0.203	**0.020**	0.495	0.851	77.22%	22.53%
Laniidae	*Lanius*	*minor*	0.115	**0.020**	0.970	0.455	75.14%	24.29%
Laniidae	*Lanius*	*nubicus*	0.406	**0.020**	0.178	0.119	75.66%	24.01%
Laniidae	*Lanius*	*senator*	0.130	**0.020**	0.535	0.772	75.94%	23.74%
Locustellidae	*Locustella*	*fluviatilis*	0.005	**0.020**	0.851	0.772	76.24%	23.44%
Locustellidae	*Locustella*	*luscinioides*	0.094	**0.020**	0.931	0.733	75.25%	24.17%
Locustellidae	*Locustella*	*naevia*	0.089	**0.020**	0.594	0.653	75.96%	23.72%
Motacillidae	*Anthus*	*campestris*	0.268	**0.020**	0.396	0.376	75.82%	23.86%
Motacillidae	*Anthus*	*cervinus*	0.004	**0.020**	0.436	0.139	76.15%	23.52%
Motacillidae	*Anthus*	*hoeschi*	0.012	**0.020**	0.277	0.218	78.06%	21.64%
Motacillidae	*Anthus*	*petrosus*	0.224	**0.020**	**0.040**	**0.040**	77.41%	22.31%
Motacillidae	*Anthus*	*pratensis*	0.586	**0.020**	**0.020**	0.079	77.95%	21.79%
Motacillidae	*Anthus*	*richardi*	0.484	**0.020**	0.376	0.594	76.09%	23.59%
Motacillidae	*Anthus*	*trivialis*	0.052	**0.020**	0.792	0.733	76.84%	22.88%
Motacillidae	*Motacilla*	*alba*	0.474	**0.020**	0.099	0.356	75.07%	24.37%
Motacillidae	*Motacilla*	*cinerea*	0.126	**0.020**	0.673	**0.020**	76.07%	23.60%
Motacillidae	*Motacilla*	*flava*	0.066	**0.020**	0.238	0.119	75.29%	24.15%
Muscicapidae	*Cercotrichas*	*galactotes*	0.504	**0.020**	**0.020**	**0.020**	76.39%	23.32%
Muscicapidae	*Cyanecula*	*svecica*	0.243	**0.020**	0.475	0.653	76%	23.68%
Muscicapidae	*Erithacus*	*rubecula*	0.272	**0.020**	0.554	0.455	74.98%	24.46%
Muscicapidae	*Ficedula*	*albicollis*	0.000	**0.020**	1.109	1.109	76.26%	23.42%
Muscicapidae	*Ficedula*	*hypoleuca*	0.000	**0.020**	0.772	0.951	76.33%	23.35%
Muscicapidae	*Ficedula*	*parva*	0.216	**0.020**	0.455	0.257	75.25%	24.37%
Muscicapidae	*Ficedula*	*semitorquata*	0.003	**0.020**	0.832	0.772	76.23%	23.45%
Muscicapidae	*Irania*	*gutturalis*	0.027	**0.020**	0.931	0.634	75.94%	23.73%
Muscicapidae	*Luscinia*	*luscinia*	0.000	**0.020**	0.653	0.990	76.06%	23.62%
Muscicapidae	*Luscinia*	*megarhynchos*	0.028	**0.020**	0.871	0.792	76.23%	23.45%
Muscicapidae	*Monticola*	*saxatilis*	0.184	**0.020**	0.574	0.970	77.33%	22.41%

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Muscicapidae	*Monticola*	*solitarius*	0.412	**0.020**	0.535	**0.020**	76.13%	23.54%
Muscicapidae	*Muscicapa*	*striata*	0.037	**0.020**	0.951	0.713	76.31%	23.36%
Muscicapidae	*Oenanthe*	*chrysopygia*	0.694	**0.020**	**0.040**	**0.040**	76.42%	23.29%
Muscicapidae	*Oenanthe*	*cypriaca*	0.121	**0.020**	0.158	0.139	74.89%	24.55%
Muscicapidae	*Oenanthe*	*deserti*	0.278	**0.020**	0.139	0.099	77.10%	22.65%
Muscicapidae	*Oenanthe*	*finschii*	0.219	**0.020**	0.376	0.970	75.75%	23.94%
Muscicapidae	*Oenanthe*	*hispanica*	0.195	**0.020**	0.198	0.297	75.73%	23.95%
Muscicapidae	*Oenanthe*	*isabellina*	0.119	**0.020**	0.951	0.891	75.04%	24.39%
Muscicapidae	*Oenanthe*	*oenanthe*	0.087	**0.020**	0.436	0.475	75.08%	24.37%
Muscicapidae	*Oenanthe*	*pleschanka*	0.323	**0.020**	0.574	0.535	75.98%	23.70%
Muscicapidae	*Oenanthe*	*xanthoprymna*	0.579	**0.020**	0.099	**0.020**	76.33%	23.38%
Muscicapidae	*Phoenicurus*	*ochruros*	0.460	**0.020**	0.099	**0.020**	75.06%	24.38%
Muscicapidae	*Phoenicurus*	*phoenicurus*	0.113	**0.020**	0.713	0.891	75.10%	24.33%
Muscicapidae	*Saxicola*	*rubetra*	0.056	**0.020**	0.891	0.396	75.17%	24.27%
Muscicapidae	*Saxicola*	*torquatus*	0.494	**0.020**	0.356	**0.020**	75.20%	24.23%
Oriolidae	*Oriolus*	*oriolus*	0.034	**0.020**	0.891	0.970	75.46%	24.17%
Passeridae	*Carpospiza*	*brachydactyla*	0.431	**0.020**	0.158	0.198	75.59%	24.09%
Passeridae	*Passer*	*moabiticus*	0.216	**0.020**	0.218	0.119	75.71%	23.98%
Phylloscopidae	*Phylloscopus*	*bonelli*	0.020	**0.020**	0.911	0.851	74.97%	24.46%
Phylloscopidae	*Phylloscopus*	*borealis*	0.021	**0.020**	0.871	0.594	75.67%	23.94%
Phylloscopidae	*Phylloscopus*	*collybita*	0.302	**0.020**	0.238	0.257	75.94%	23.74%
Phylloscopidae	*Phylloscopus*	*ibericus*	0.000	**0.020**	1.465	1.703	76.11%	23.58%
Phylloscopidae	*Phylloscopus*	*inonartus*	0.014	**0.020**	0.970	0.832	75.33%	24.30%
Phylloscopidae	*Phylloscopus*	*sibilatrix*	0.000	**0.020**	0.574	0.931	75.54%	24.08%
Phylloscopidae	*Phylloscopus*	*sindianus*	0.453	**0.020**	0.139	0.574	75.82%	23.86%
Phylloscopidae	*Phylloscopus*	*trochiloides*	0.314	**0.020**	0.396	0.733	76.14%	23.54%
Phylloscopidae	*Phylloscopus*	*trochilus*	0.014	**0.020**	0.673	0.733	75.47%	24.15%
Pittidae	*Pitta*	*angolensis*	0.247	**0.020**	0.574	0.178	78.61%	21.15%
Prunellidae	*Prunella*	*modularis*	0.396	**0.020**	**0.040**	**0.020**	74.98%	24.46%
Reguliidae	*Regulus*	*ignicapilla*	0.335	**0.020**	0.119	**0.020**	75.88%	23.79%
Reguliidae	*Regulus*	*regulus*	0.175	**0.020**	0.911	0.772	75.10%	24.36%
Remizidae	*Remiz*	*pendulinus*	0.110	**0.020**	0.396	0.832	77.49%	22.25%
Scotocercidae	*Cettia*	*cetti*	0.169	**0.020**	0.574	0.891	75%	24.43%
Sturnidae	*Lamprotornis*	*shelleyi*	0.694	**0.020**	**0.040**	**0.040**	75.98%	23.70%
Sturnidae	*Sturnus*	*vulgaris*	0.385	**0.020**	0.673	**0.020**	75.01%	24.42%
Sylviidae	*Sylvia*	*atricapilla*	0.236	**0.020**	0.851	**0.020**	75.08%	24.35%
Sylviidae	*Sylvia*	*borin*	0.013	**0.020**	0.238	1.010	75.39%	24.05%
Sylviidae	*Sylvia*	*cantillans*	0.002	**0.020**	0.970	0.594	77.24%	22.49%
Sylviidae	*Sylvia*	*communis*	0.055	**0.020**	0.891	0.891	75.98%	23.70%
Sylviidae	*Sylvia*	*conspicillata*	0.319	**0.020**	0.257	0.356	75.77%	23.90%
Sylviidae	*Sylvia*	*curruca*	0.218	**0.020**	0.970	0.871	75%	24.43%
Sylviidae	*Sylvia*	*deserticola*	0.581	**0.020**	0.059	0.079	75.01%	24.59%
Sylviidae	*Sylvia*	*hortensis*	0.580	**0.020**	0.218	0.218	75.71%	23.97%
Sylviidae	*Sylvia*	*melanocephala*	0.089	**0.020**	0.990	0.970	74.96%	24.46%
Sylviidae	*Sylvia*	*melanothorax*	0.011	**0.020**	0.416	0.495	77.77%	21.98%
Sylviidae	*Sylvia*	*mystacea*	0.475	**0.020**	0.277	0.238	74.93%	24.50%

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Sylviidae	*Sylvia*	*nana*	0.425	**0.020**	0.139	0.059	77%	22.74%
Sylviidae	*Sylvia*	*nisoria*	0.011	**0.020**	0.673	1.010	75.27%	24.34%
Sylviidae	*Sylvia*	*rueppeli*	0.155	**0.020**	0.495	0.495	74.99%	24.44%
Sylviidae	*Sylvia*	*sarda*	0.227	**0.020**	0.059	0.139	75.86%	23.78%
Troglodytidae	*Troglodytes*	*troglodytes*	0.302	**0.020**	0.059	**0.020**	75.98%	23.69%
Turdidae	*Neophedina*	*guttata*	0.368	**0.020**	0.040	0.079	78.15%	21.60%
Turdidae	*Turdus*	*iliacus*	0.210	**0.020**	0.673	0.317	75.04%	24.41%
Turdidae	*Turdus*	*merula*	0.553	**0.020**	**0.020**	**0.020**	77.53%	22.19%
Turdidae	*Turdus*	*philomelos*	0.389	**0.020**	0.099	**0.020**	74.98%	24.45%
Turdidae	*Turdus*	*pilaris*	0.194	**0.020**	0.713	0.396	75.16%	24.29%
Turdidae	*Turdus*	*ruficollis*	0.194	**0.020**	0.139	0.455	77.56%	22.19%
Turdidae	*Turdus*	*torquatus*	0.480	**0.020**	0.079	**0.020**	75.19%	24.42%
Turdidae	*Turdus*	*viscivorus*	0.352	**0.020**	0.257	0.178	75.92%	23.76%
Ardeidae	*Ardea*	*alba*	0.428	**0.020**	**0.020**	**0.040**	75.44%	23.99%
Ardeidae	*Ardea*	*cinerea*	0.578	**0.020**	**0.020**	0.178	77.77%	21.96%
Ardeidae	*Ardea*	*purpurea*	0.701	**0.020**	**0.020**	**0.020**	75.52%	23.91%
Ardeidae	*Ardeola*	*idae*	0.045	**0.020**	0.535	0.792	77.67%	22.08%
Ardeidae	*Ardeola*	*ralloides*	0.457	**0.020**	**0.020**	**0.020**	75.35%	24.07%
Ardeidae	*Botaurus*	*stellaris*	0.173	**0.020**	0.990	0.574	75.07%	24.36%
Ardeidae	*Bubulcus*	*ibis*	0.574	**0.020**	**0.020**	**0.040**	76.22%	23.46%
Ardeidae	*Egretta*	*garzetta*	0.569	**0.020**	**0.040**	**0.020**	76.20%	23.48%
Ardeidae	*Ixobrychus*	*minutus*	0.494	**0.020**	0.535	0.733	0.7618	23.49%
Pelecanidae	*Pelecanus*	*onocrotalus*	0.077	**0.020**	0.693	0.554	77.39%	22.35%
Threskiornithidae	*Geronticus*	*eremita*	0.073	**0.020**	0.139	0.059	77.32%	22.37%
Threskiornithidae	*Platalea*	*leucorodia*	0.358	**0.020**	0.119	0.178	75.15%	24.29%
Threskiornithidae	*Plegadis*	*falcinellus*	0.309	**0.020**	0.634	0.297	76.18%	23.50%
Phoenicopteridae	*Phoenicopterus*	*roseus*	0.292	**0.020**	**0.020**	**0.020**	74.90%	24.43%
Picidae	*Jynx*	*torquilla*	0.208	**0.020**	0.594	0.713	76.10%	23.58%
Podicipedidae	*Podiceps*	*auritus*	0.178	**0.020**	0.515	**0.040**	78.02%	21.74%
Podicipedidae	*Podiceps*	*cristatus*	0.397	**0.020**	0.436	0.277	77.89%	21.85%
Podicipedidae	*Podiceps*	*grisegena*	0.143	**0.020**	0.851	**0.020**	77.53%	22.22%
Podicipedidae	*Podiceps*	*nigricollis*	0.337	**0.020**	**0.040**	0.436	77.45%	22.29%
Pteroclidae	*Pterocles*	*alchata*	0.019	**0.020**	0.337	0.396	74.94%	24.49%
Pteroclidae	*Pterocles*	*orientalis*	0.471	**0.020**	0.139	0.416	77.41%	22.31%
Strigidae	*Asio*	*flammeus*	0.212	**0.020**	0.911	0.178	75.24%	24.22%
Strigidae	*Asio*	*otus*	0.289	**0.020**	0.455	**0.020**	75.97%	23.71%
Strigidae	*Bubo*	*scandiaca*	0.157	**0.020**	0.891	0.059	77.72%	22.03%
Strigidae	*Otus*	*brucei*	0.289	**0.020**	0.515	0.594	77.08%	22.67%
Strigidae	*Otus*	*scops*	0.136	**0.020**	0.752	0.713	75.15%	24.28%
Phalacrocoracidae	*Microcarbo*	*pygmeus*	0.106	**0.020**	0.257	0.970	75.88%	23.80%
Phalacrocoracidae	*Phalacrocorax*	*carbo*	0.458	**0.020**	0.218	0.158	77.73%	22%
Phalacrocoracidae	*Phalacrocorax*	*nigrogularis*	0.000	**0.020**	1.861	1.941	78.10%	21.64%

Table A3.3. Pairwise niche overlap values for breeding climatic niches and non-breeding climatic niches of sister species, using D metric. P-values obtained from tests of niche similarity and equivalence via randomization. Significant P-values are shown in bold. Variances explained from PC1 and PC2, which correspond mainly to temperature (PC1) and precipitation (PC2).

Species 1 vs Species 2	**D=Niche overlap Breeding**	**Niche Equivalency**	**Niche similarity 2->1**	**Niche similarity 1->2**	**PC1% (T)**	**PC2% (P)**	**D=Niche overlap Non-breeding**	**Niche Equivalency**	**Niche similarity 2->1**	**Niche similarity 1->2**	**PC1% (T)**	**PC2% (P)**
Buteo buteo vs B. lagopus	0.255	**0.020**	0.614	**0.020**	74.74	24.54	0.209	**0.020**	0.653	0.436	78.54	21.23
Circus macrourus vs C. maurus	0.146	**0.020**	0.970	0.752	74.31	24.81	0.142	**0.020**	0.317	0.574	76.03	23.65
Circus cyaneus vs C. pygargus	0.242	**0.020**	0.634	0.832	74.66	24.65	0.081	**0.020**	0.772	0.198	76.66	23.05
Milvus migrans vs M. milvus	0.152	**0.020**	0.079	0.970	75.29	24.20	0.185	**0.020**	0.832	0.832	78.69	21.06
Cygnus columbianus vs C. cygnus	0.209	**0.020**	0.158	0.515	74.55	24.69	0.681	**0.020**	**0.020**	**0.020**	78.84	20.94
Mergus merganser vs M. serrator	0.531	**0.020**	**0.020**	0.079	74.44	24.78	0.509	**0.020**	**0.020**	**0.040**	78.9	20.88
Apus apus vs A. pallidus	0.477	**0.020**	0.277	0.455	74.76	24.60	0.333	**0.020**	0.574	0.218	79.14	20.63
Apus affinis vs A. pallidus	0.135	**0.020**	0.693	0.851	75.29	24.19	0.449	**0.020**	0.059	0.238	78.83	20.93
Apus affinis vs A. apus	0.261	**0.020**	0.871	0.772	74.89	24.47	0.750	**0.020**	**0.020**	**0.020**	79.31	20.46
Charadrius leschenaultii vs C. mongolus	0.345	**0.020**	0.792	0.713	75.18	24.28	0.527	**0.020**	0.356	0.059	77.24	22.45
Charadrius dubius vs C. hiaticula	0.163	**0.020**	0.574	0.059	75.32	24.13	0.319	**0.020**	0.297	0.436	76.47	23.22
Pluvialis apricaria vs P. squatarola	0.202	**0.020**	0.178	0.356	74.09	25	0.074	**0.020**	0.851	0.574	79.05	20.72
Vanellus gregarius vs V. vanellus	0.146	**0.020**	0.515	0.475	75.26	24.20	0.043	**0.020**	0.832	0.614	77.24	22.51
Gallinago media vs G. stenura	0.490	**0.020**	0.337	0.139	74.48	24.76	0.224	**0.020**	0.356	0.535	79.12	20.66
Tringa glareola vs T. stagnatilis	0.334	**0.020**	0.475	0.396	74.52	24.76	0.751	**0.020**	**0.040**	**0.020**	78.69	21.07
Tringa stagnatilis vs T. totanus	0.619	**0.020**	0.257	0.257	75.20	24.27	0.688	**0.020**	0.079	**0.020**	78.52	21.23
Tringa glaréola vs T. totanus	0.331	**0.020**	0.158	0.198	75.21	24.26	0.623	**0.020**	**0.020**	**0.040**	78.47	21.28
Clamator jacobinus vs C. levaillantii	0.569	**0.020**	0.218	0.119	78.82	20.98	0.527	**0.020**	0.119	0.079	74.79	24.41
Falco amurensis vs F. vespertinus	0.079	**0.020**	0.475	0.990	74.46	24.81	0.532	**0.020**	0.099	**0.040**	78.99	20.79
Falco cherrug vs F. rusticolus	0.064	**0.020**	0.693	0.495	75.37	24.10	0.194	**0.020**	0.099	0.099	76.32	23.38
Falco concolor vs F. eleonorae	0.246	**0.020**	0.178	0.337	74.47	24.83	0.757	**0.020**	**0.040**	**0.020**	77.31	22.39
Falco eleonorae vs F. subbuteo	0.087	**0.020**	0.772	0.594	74.34	24.87	0.360	**0.020**	0.158	0.297	79.32	20.46
Falco concolor vs F. subbuteo	0.165	**0.020**	0.752	0.673	74.47	24.85	0.414	**0.020**	0.119	0.059	77.26	22.46
Acrocephalus melanopogon vs A. schoenobaenus	0.289	**0.020**	0.317	0.277	74.78	24.58	0.194	**0.020**	0.515	0.436	78.36	21.41
Acrocephalus melanopogon vs A. paludicola	0.215	**0.020**	0.178	0.198	74.76	24.62	0.003	**0.020**	0.832	0.535	78.05	21.71
Acrocephalus melanopogon vs A. scirpaceus	0.396	**0.020**	0.257	0.079	74.74	24.62	0.246	**0.020**	0.079	0.337	78.45	21.31
Acrocephalus paludícola vs A. schoenobaenus	0.159	**0.020**	0.059	0.178	74.40	24.82	0.129	**0.020**	0.059	0.139	78.39	21.39
Acrocephalus paludicola vs A. scirpaceus	0.109	**0.020**	0.574	0.455	74.37	24.84	0.107	**0.020**	0.139	0.158	78.48	21.3
Acrocephalus schoenobaenus vs A. scirpaceus	0.491	**0.020**	0.238	0.436	74.30	24.89	0.818	**0.020**	**0.020**	**0.020**	78.75	21.04
Hippolais icterina vs H. polyglotta	0.452	**0.020**	0.218	0.277	74.37	24.84	0.271	**0.020**	0.594	0.139	79.54	20.23
Hippolais lánguida vas H. olivetorum	0.665	**0.020**	**0.020**	**0.040**	74.67	24.70	0.317	**0.020**	0.495	0.139	78.42	21.34
Pinarocorys erythropygia vs P. nigricans	0.041	**0.020**	0.574	0.178	75.64	23.99	0.026	**0.020**	0.337	0.673	76.26	23.4
Emberiza caesia vs E. cineracea	0.504	**0.020**	0.218	0.139	74.52	24.77	0.334	**0.020**	0.059	0.059	76.48	23.26
Emberiza cineracea vs E. hortulana	0.249	**0.020**	0.673	0.455	74.20	24.98	0.215	**0.020**	0.713	0.376	78.39	21.39
Emberiza caesia vs E. hortulana	0.454	**0.020**	0.277	0.139	74.61	24.68	0.086	**0.020**	0.733	0.376	76.3	23.42
Fringilla coelebs vs F. montifringilla	0.493	**0.020**	0.277	0.297	74.68	24.63	0.569	**0.020**	0.139	**0.040**	76. 6	23.1

(Continued on next page)

Lanius collurio vs L.isabellinus	0.411	**0.020**	0.475	0.416	75.03	24.37	0.317	**0.020**	0.297	0.594	77.33	22.42
Locustella fluviatilis vs L. luscinioides	0.590	**0.020**	**0.020**	0.059	74.63	24.67	0.563	**0.020**	**0.020**	**0.020**	77.11	22.61
Luscinia luscinia vs L. megarhynchos	0.472	**0.020**	**0.040**	**0.020**	74.84	24.53	0.465	**0.020**	0.119	**0.020**	79.05	20.72
Monticola saxatilis vs M. solitarius	0.262	**0.020**	0.495	0.951	74.59	24.69	0.161	**0.020**	0.594	0.693	78.79	21
Oenanthe chrysopygia vs O. xanthoprymna	0.819	**0.020**	**0.020**	**0.040**	74.15	25.02	0.484	**0.020**	**0.020**	**0.020**	78.12	21.67
Oenanthe deserti vs O. hispanica	0.342	**0.020**	0.139	0.436	74.47	24.81	0.141	**0.020**	0.317	0.455	78.13	21.66
Oenanthe hispánica vs O. pleschanka	0.540	**0.020**	0.257	0.178	74.27	24.91	0.178	**0.020**	0.158	0.158	78.3	21.49
Oenanthe deserti vs O. pleschanka	0.403	**0.020**	0.772	0.634	74.53	24.77	0.094	**0.020**	0.475	0.673	78.47	21.32
Oenanthe isabellina vs O. oenanthe	0.441	**0.020**	0.851	0.455	75.03	24.39	0.412	**0.020**	0.139	**0.020**	75.09	24.36
Phylloscopus collybita vs P. sindianus	0.481	**0.020**	0.495	0.317	74.34	24.86	0.131	**0.020**	0.653	0.594	78.28	21.5
Phylloscopus sindianus vs P. trochilus	0.330	**0.020**	0.693	0.376	74.42	24.80	0.025	**0.020**	0.871	0.713	78.68	21.09
Phylloscopus collybita vs P. trochilus	0.669	**0.020**	0.218	0.139	74.46	24.77	0.224	**0.020**	1.010	0.792	78.85	20.92
Sylvia melanocephala vs S. mystacea	0.590	**0.020**	0.119	0.158	74.94	24.46	0.015	**0.020**	0.713	0.416	74.95	24.5
Sylvia atricapilla vs S. borin	0.687	**0.020**	0.079	0.059	75.05	24.36	0.230	**0.020**	0.158	0.257	75.4	24.05
Otus brucei vs O.scops	0.318	**0.020**	0.634	0.733	74.86	24.55	0.063	**0.020**	0.515	0.752	77.26	22.49

Figure A3.1. Histograms of the climatic niche overlap metrics (D) for each bird order.

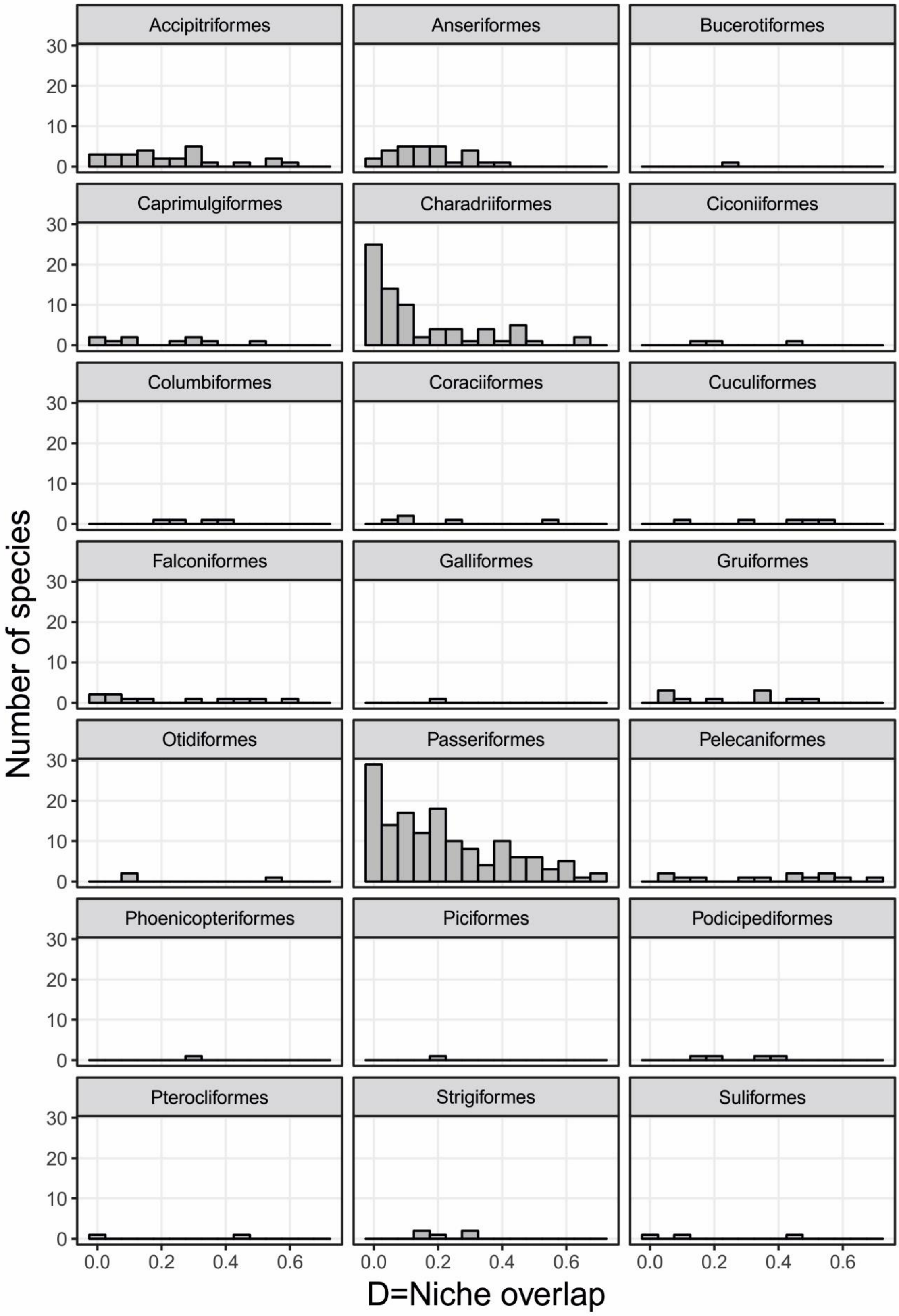


Figure A3.2. Histograms of the climatic niche overlap metrics (D) for each bird family.

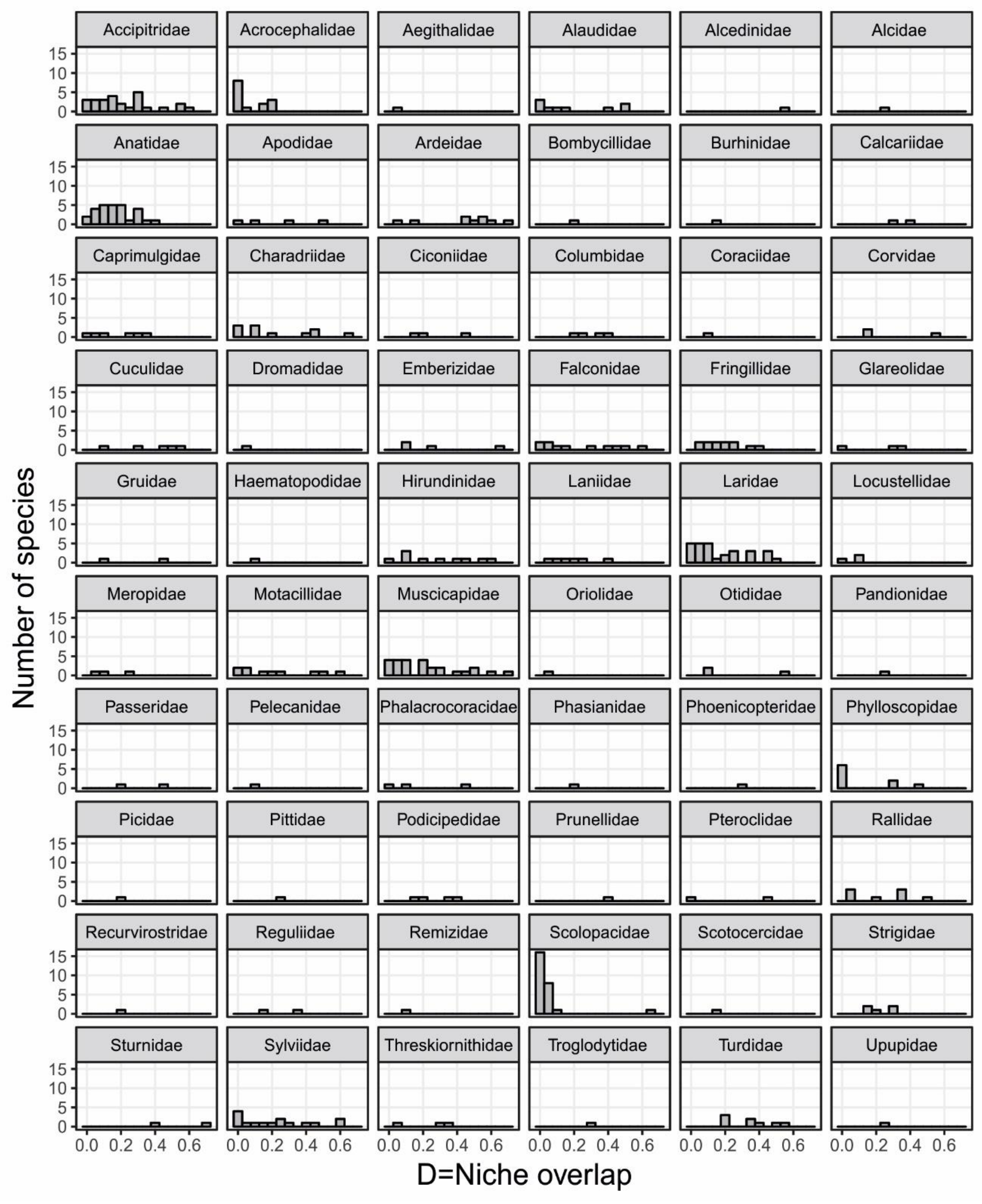


Figure A3.3. Histograms of the climatic niche breadth for each bird order.

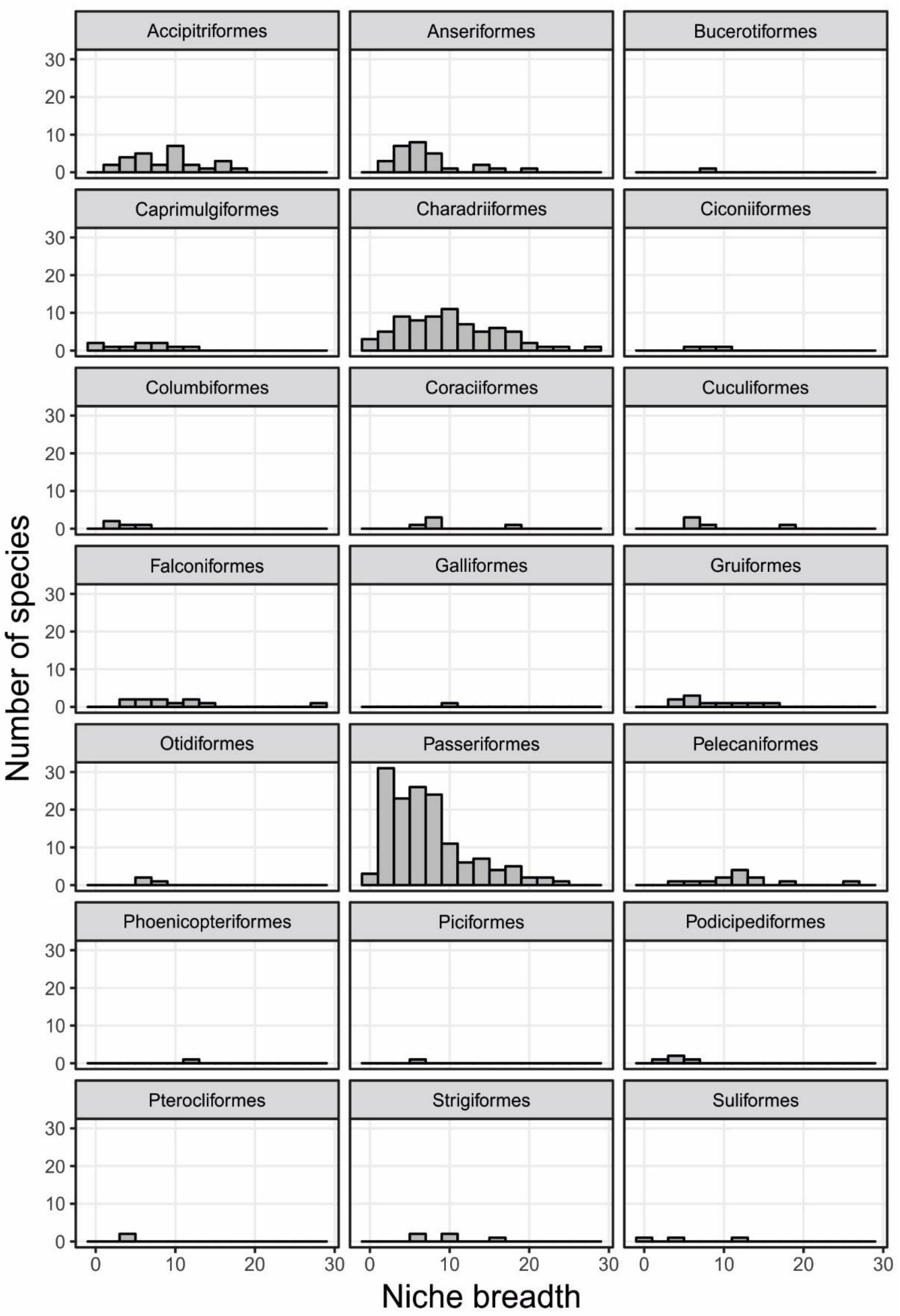
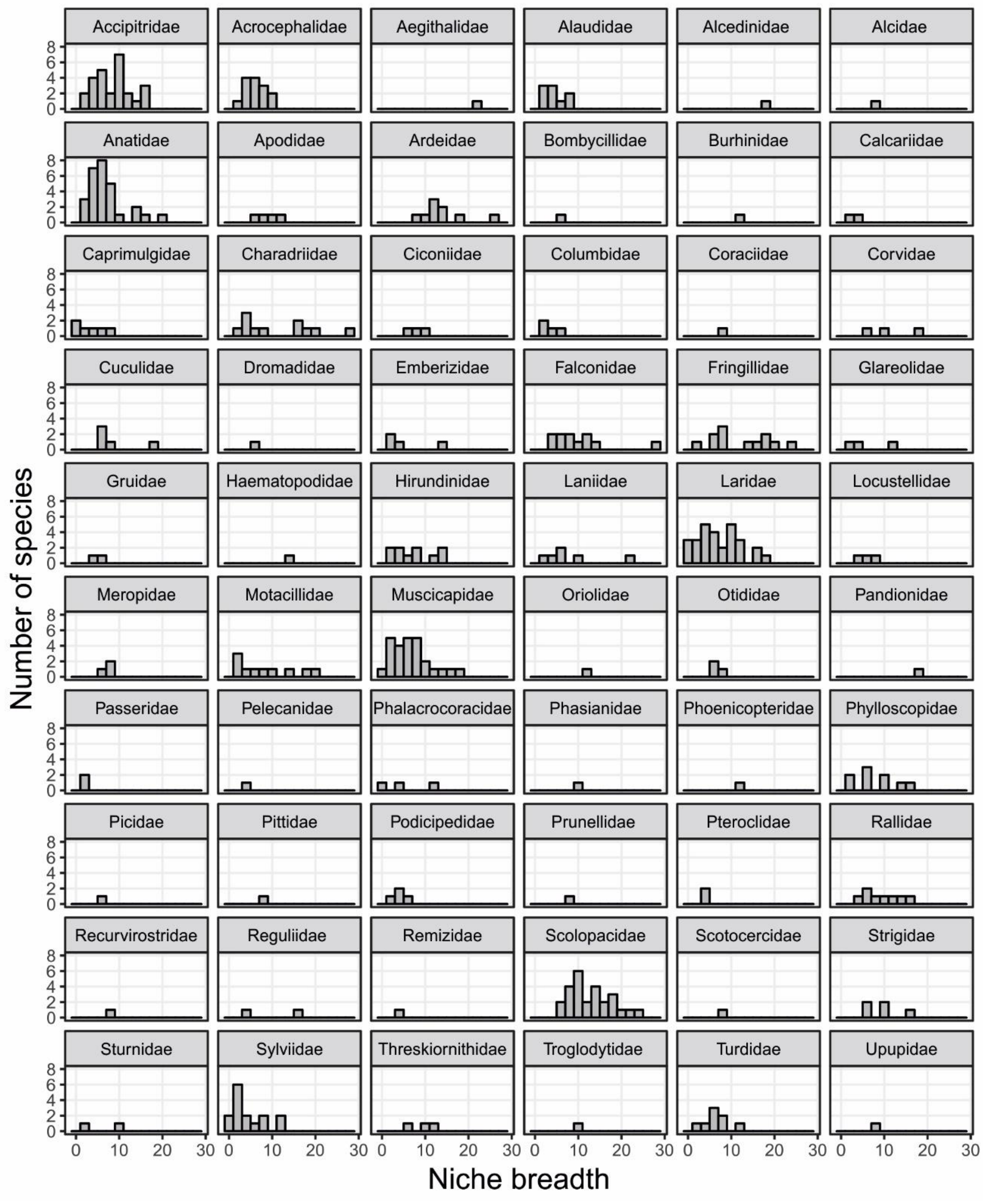
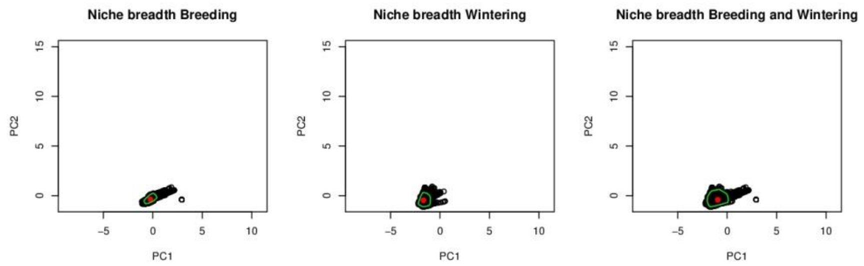


Figure A3.4. Histograms of the climatic niche breadth for each bird family.

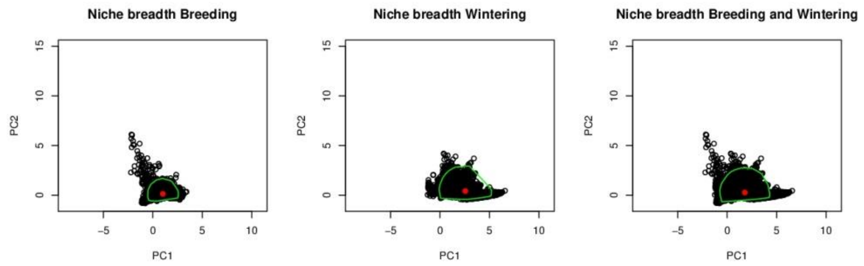


Figures A3.5. Climatic niche breadths of breeding ranges, wintering ranges and the sum of both ranges of Africa-Europe migratory species. Niche breadth is considered as the area of the minimum convex polygon of the 95% of the points from the climatic space for each species taken from PCA analyses.

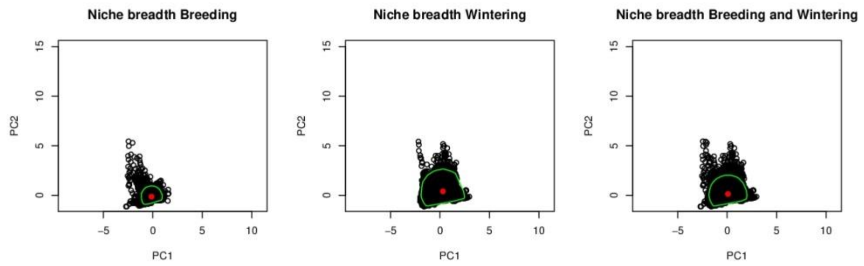
1) **Accipitriformes**
    a. Accipitridae
        i. *Accipiter brevipes*



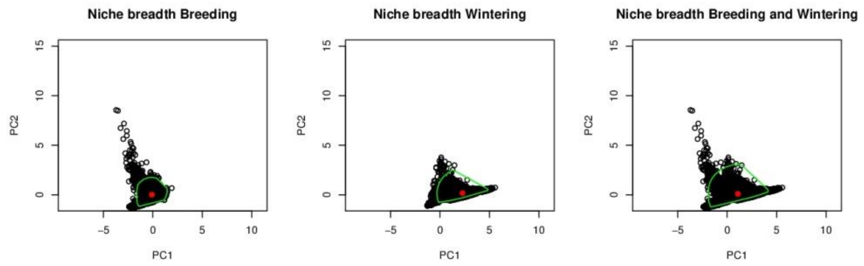
        ii. *Accipiter gentilis*



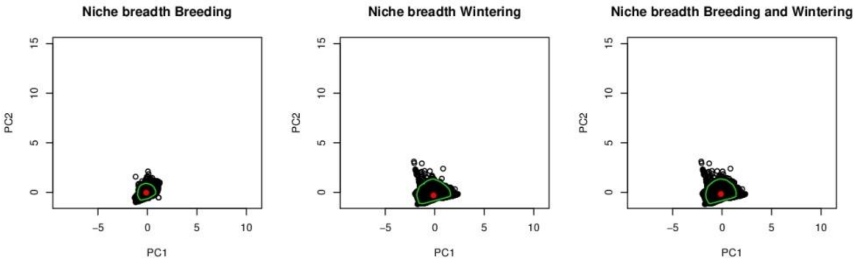
        iii. *Accipiter nisus*



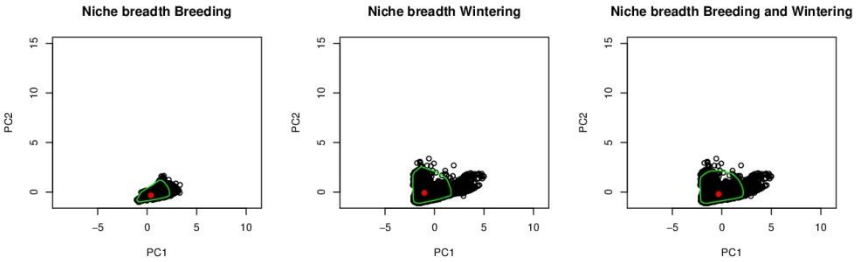
        iv. *Aquila chrysaetos*



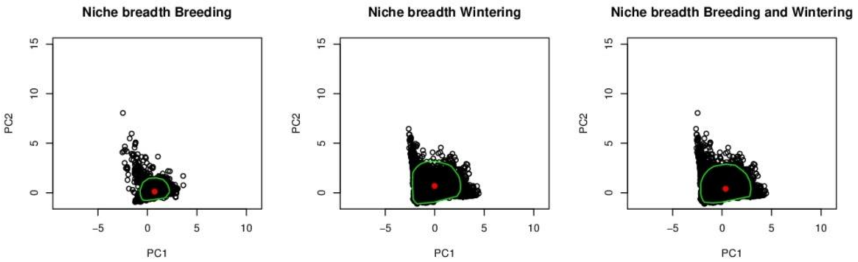
v. *Aquila heliaca*



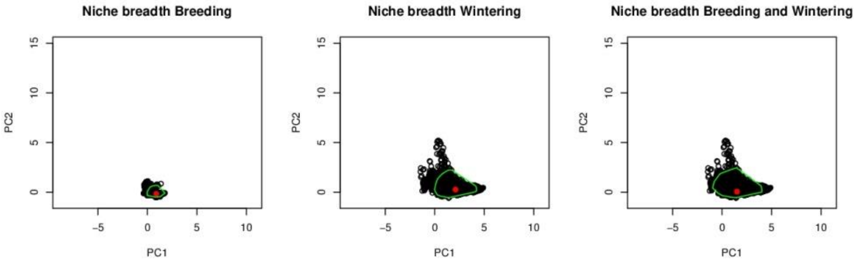
vi. *Aquila nipalensis*



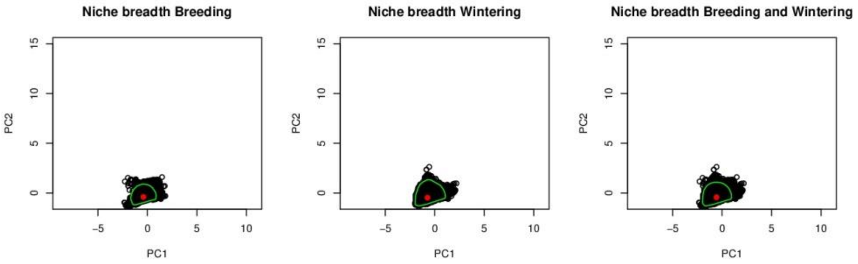
vii. *Buteo buteo*



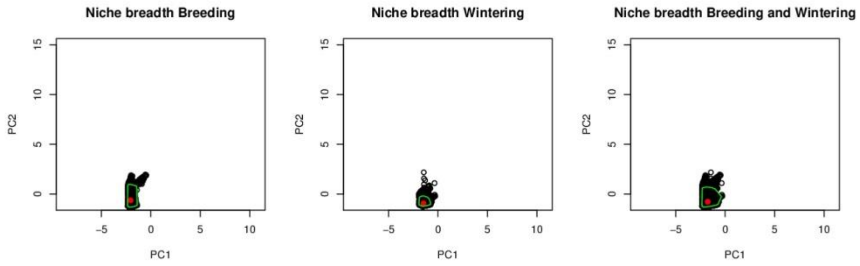
viii. *Buteo lagopus*



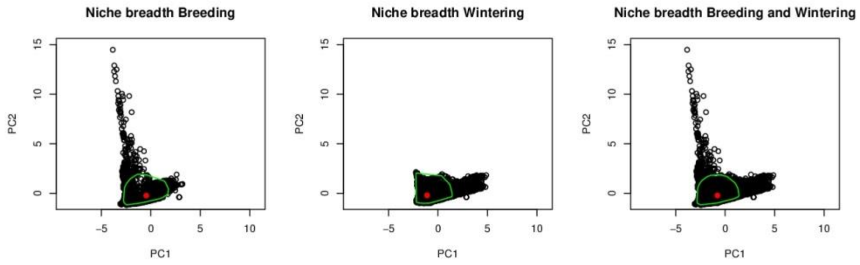
ix. *Buteo rufinus*



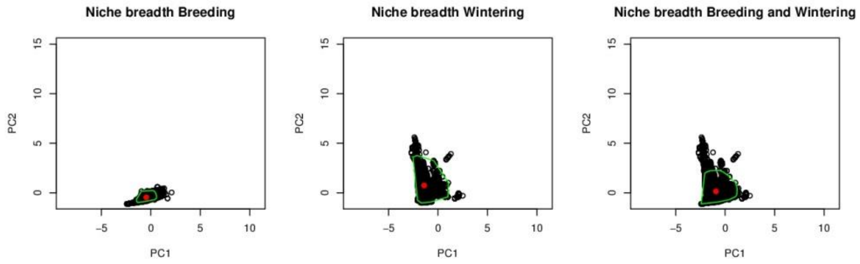
x. *Chelictinia riocourii*



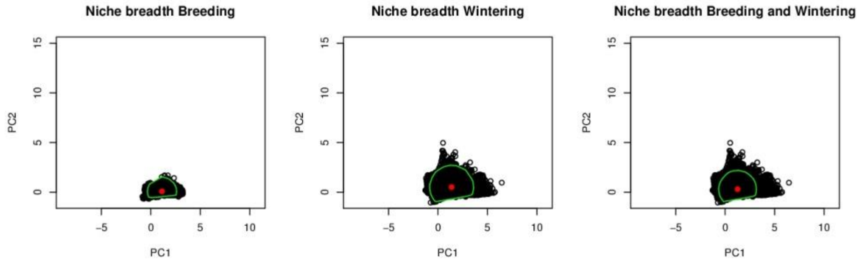
xi. *Circaetus gallicus*



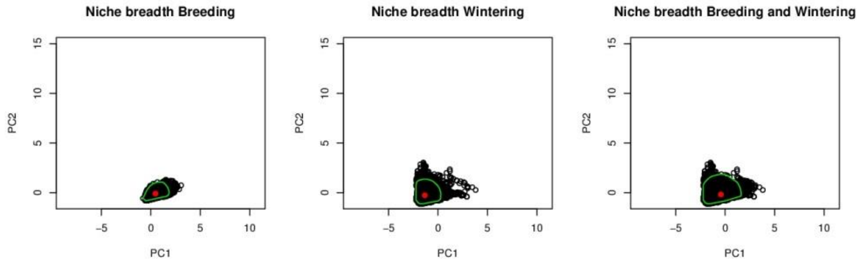
xii. *Circus aeruginosus*



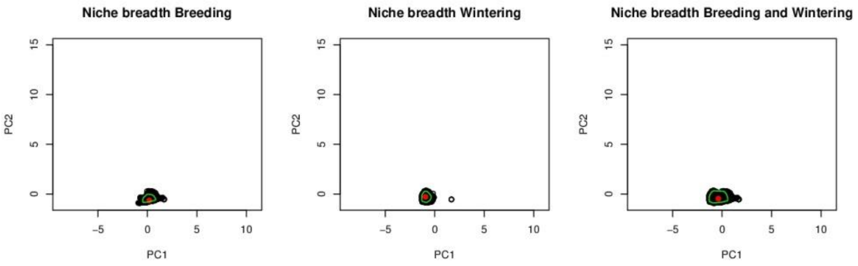
xiii. *Circus cyaneus*



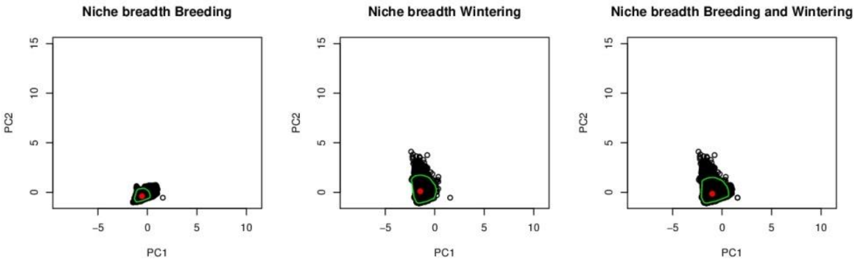
xiv. *Circus macrourus*



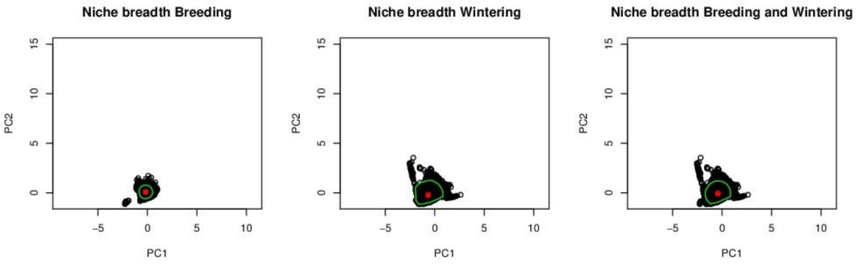
xv. *Circus maurus*



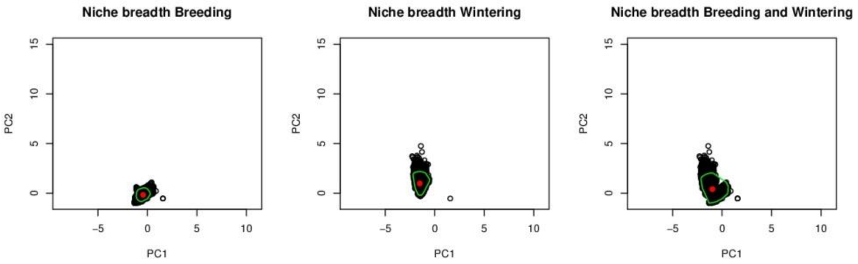
xvi. *Circus pygargus*



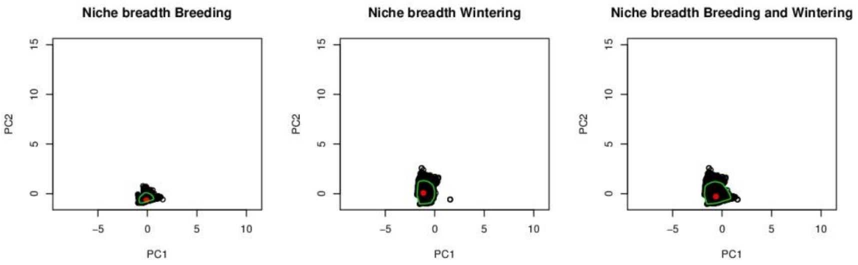
xvii. *Clanga clanga*



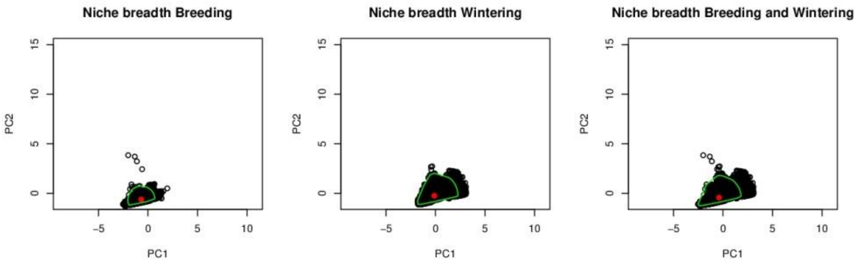
xviii. *Clanga pomarina*



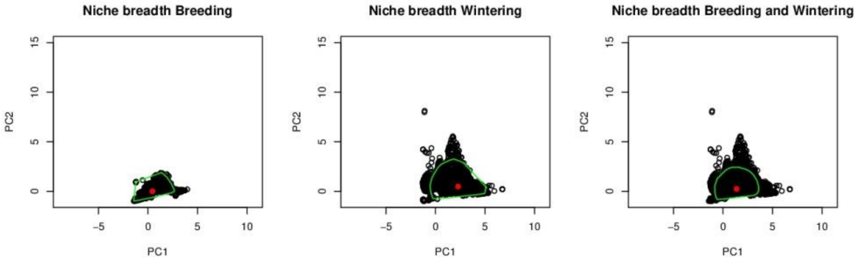
xix. *Gyps coprotheres*



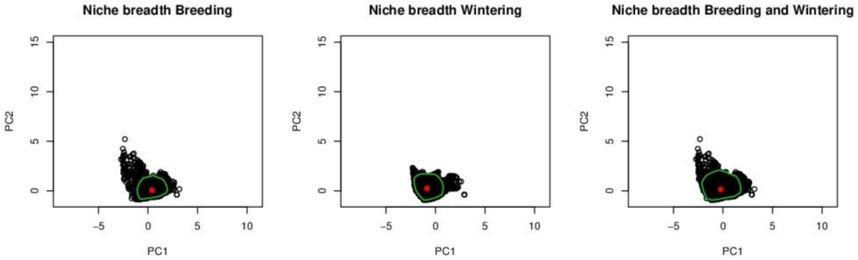
xx. *Gyps fulvus*



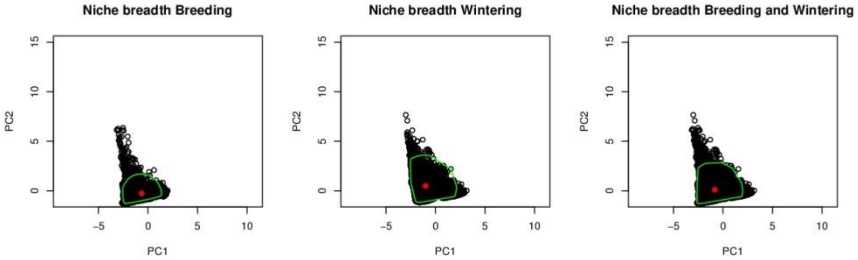
xxi. *Haliaeetus albicilla*



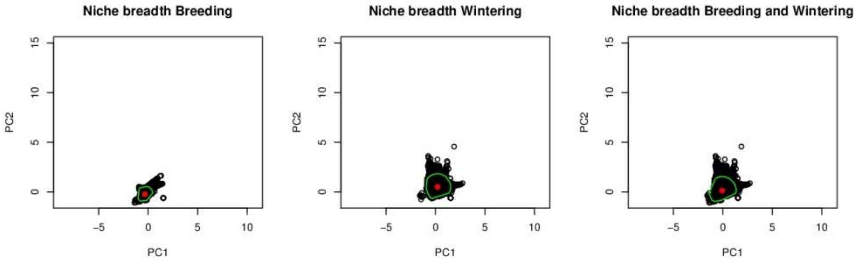
xxii. *Hieraaetus pennatus*



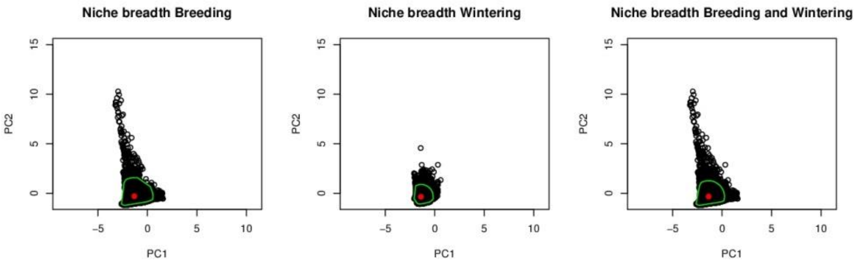
xxiii. *Milvus migrans*



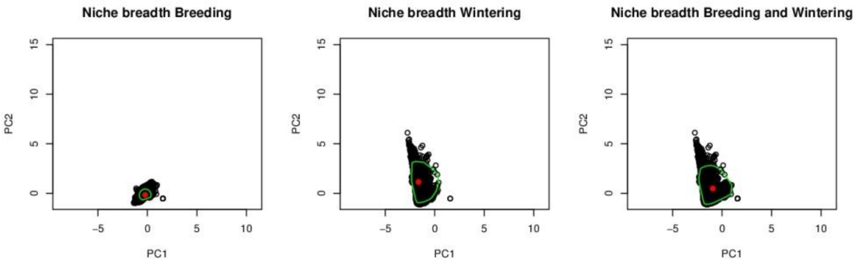
xxiv. *Milvus milvus*



xxv. *Neophron percnopterus*

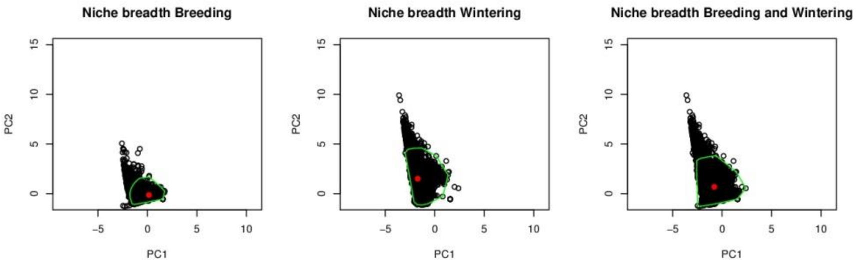


xxvi. *Pernis apivorus*



b. Pandionidae

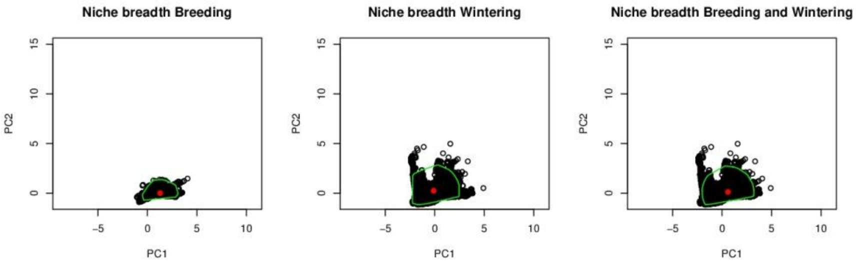
i. *Pandion haliaetus*



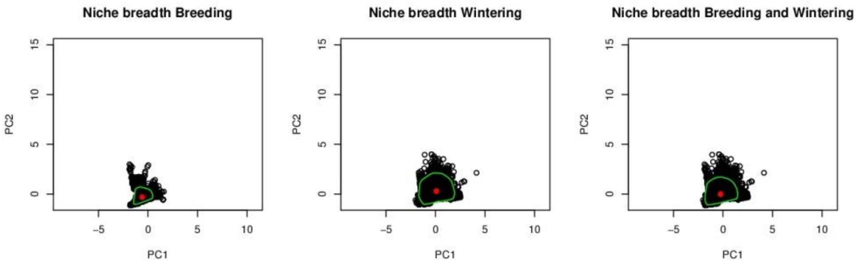
2) Anseriformes

a. Anatidae

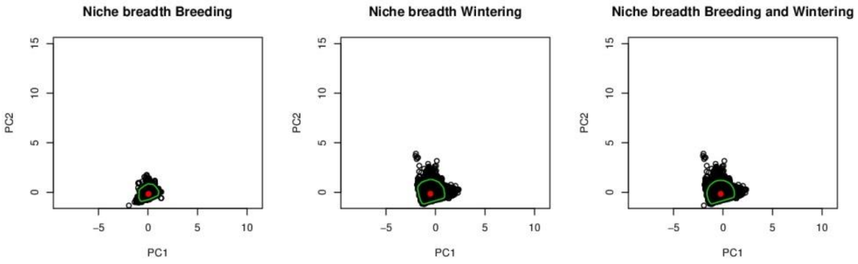
i. *Anas crecca*



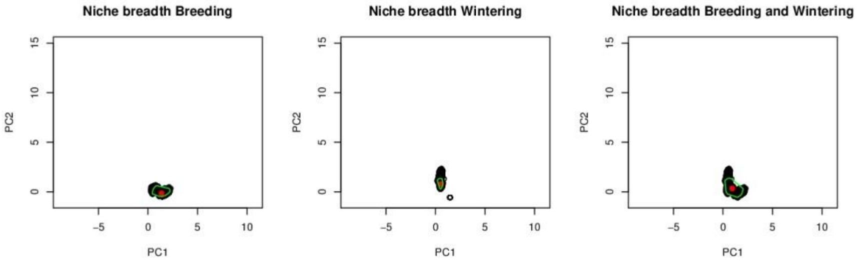
ii. *Anas platyrhynchos*



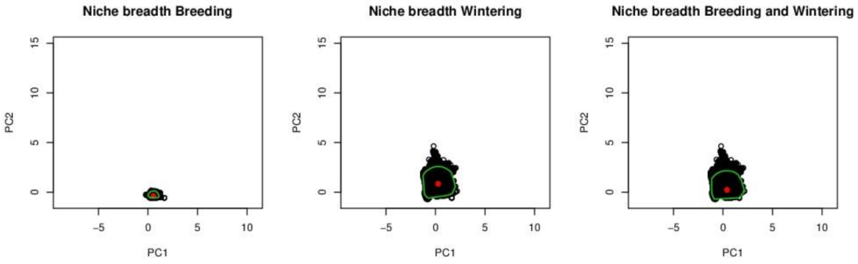
iii. *Anser anser*



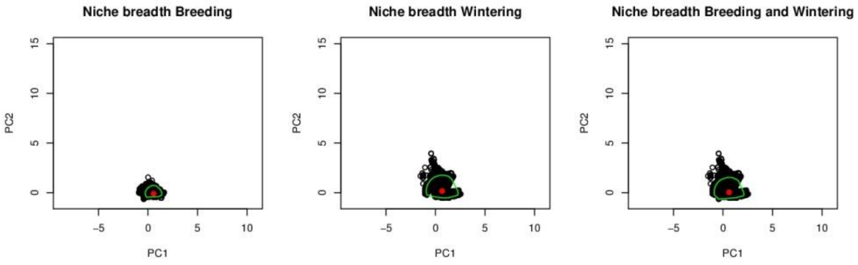
iv. *Anser brachyrhynchus*



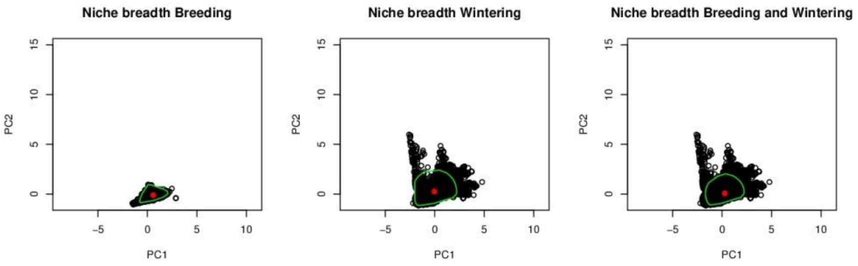
v. *Anser erythropus*



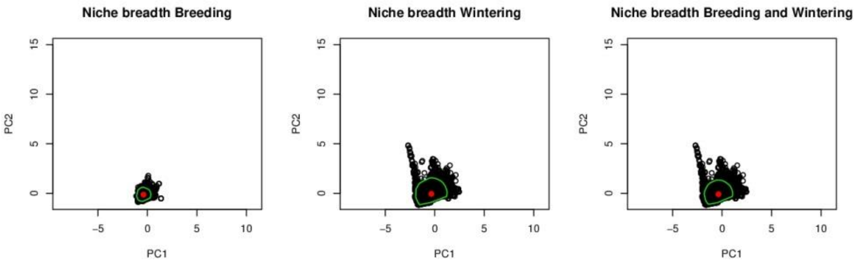
vi. *Anser fabalis*



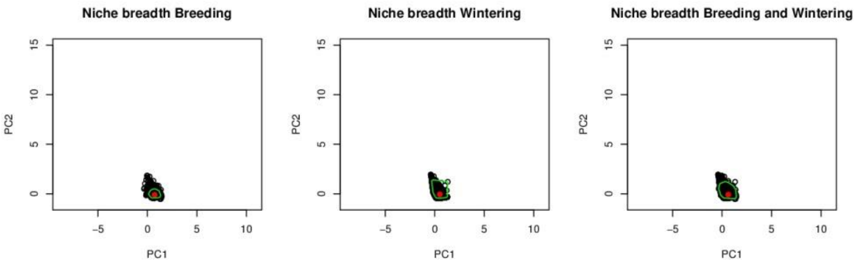
vii. *Aythya ferina*



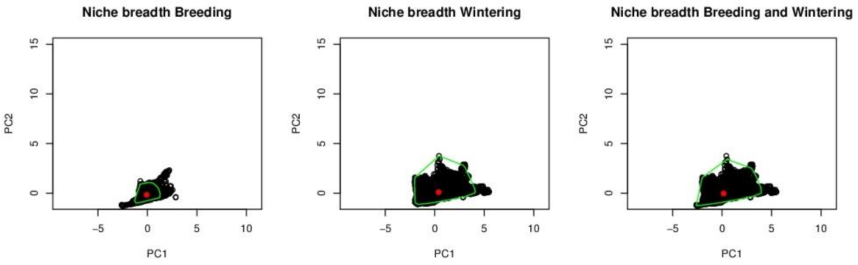
viii. *Aythya fuligula*



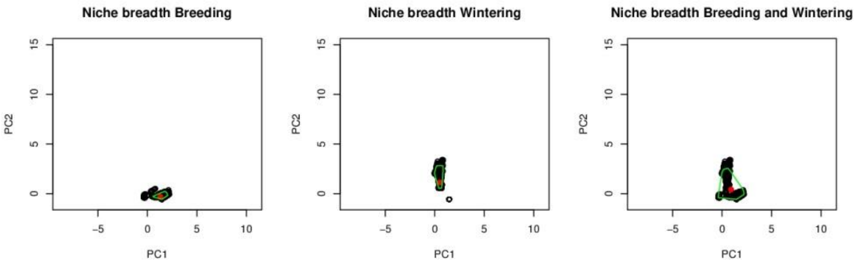
ix. *Aythya marila*



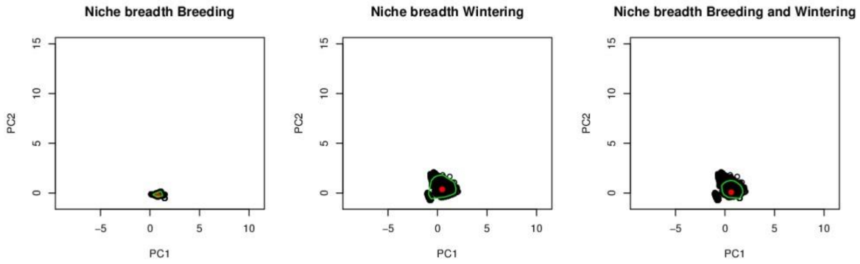
x. *Aythya nyroca*



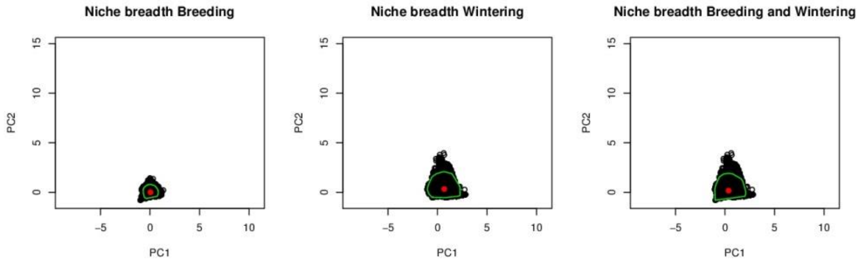
xi. *Branta leucopsis*



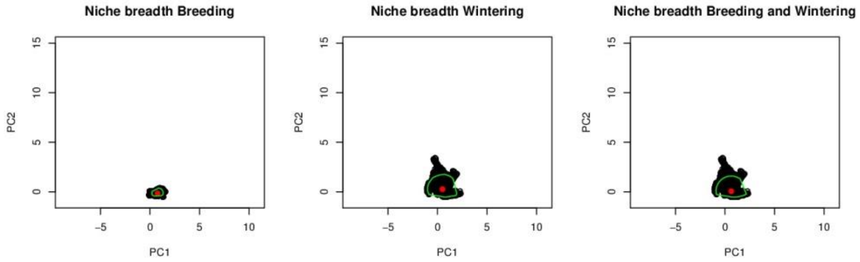
xii. *Branta ruficollis*



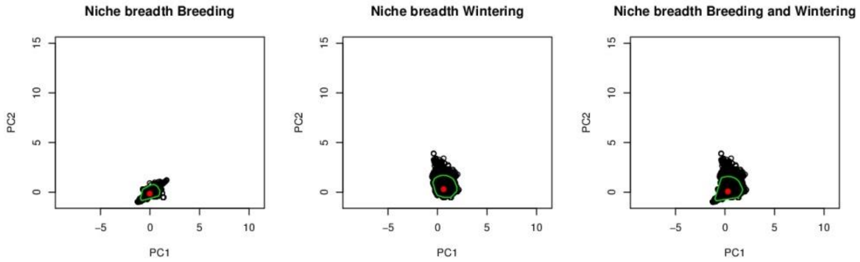
xiii. *Bucephala clangula*



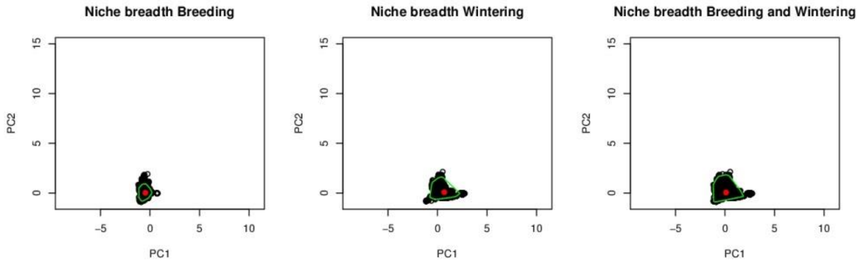
xiv. *Cygnus columbianus*



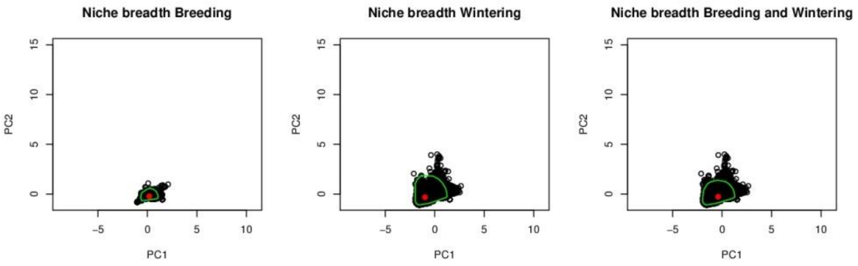
xv. *Cygnus cygnus*



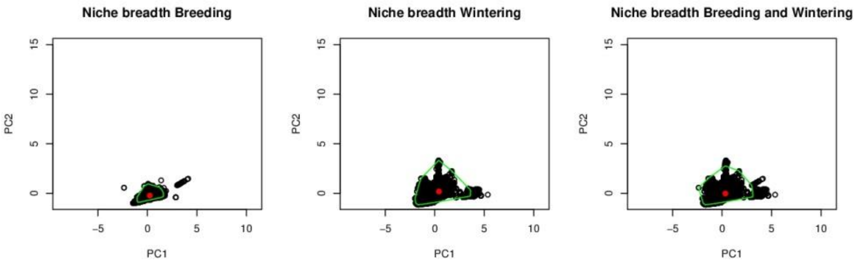
xvi. *Cygnus olor*



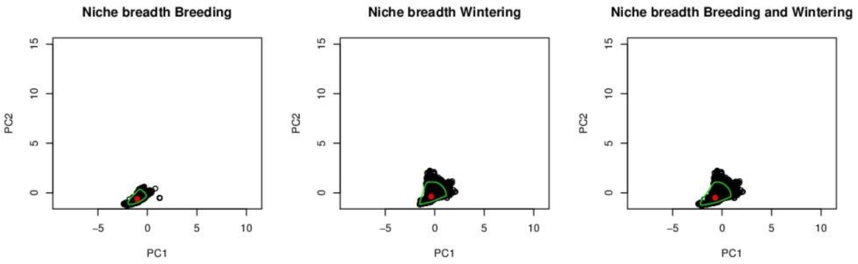
xvii. *Mareca penelope*



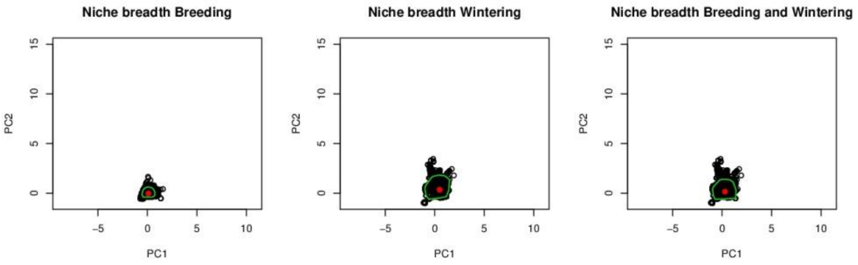
xviii. *Mareca strepera*



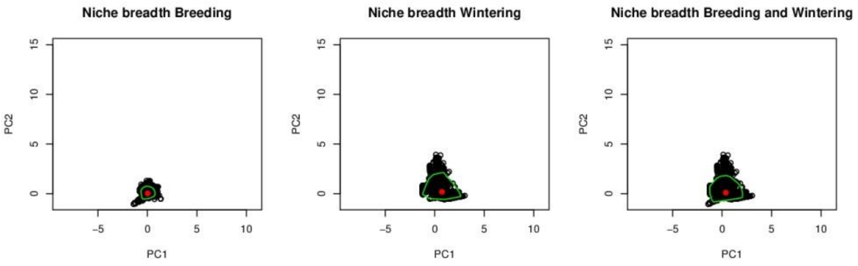
xix. *Marmaronetta angustirostris*



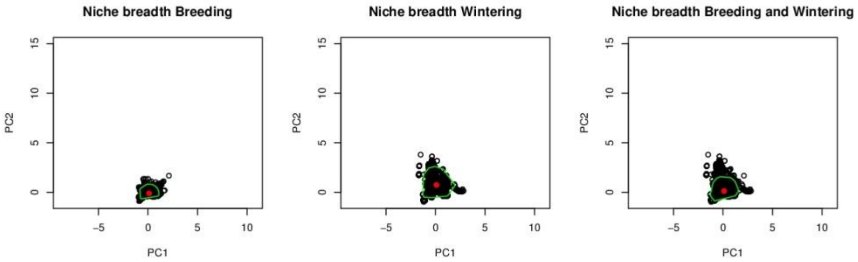
xx. *Mergellus albellus*



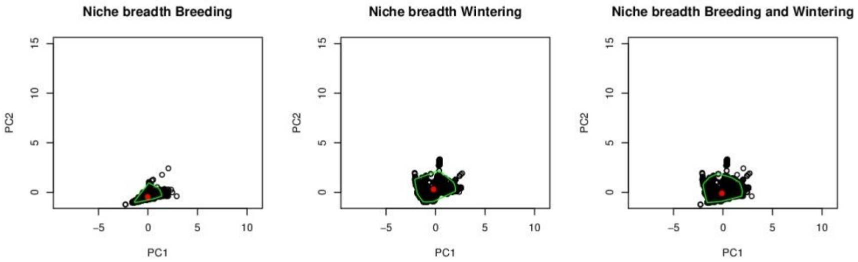
xxi. *Mergus merganser*



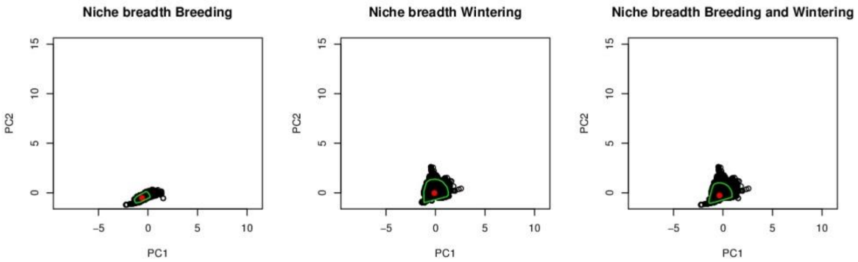
xxii. *Mergus serrator*



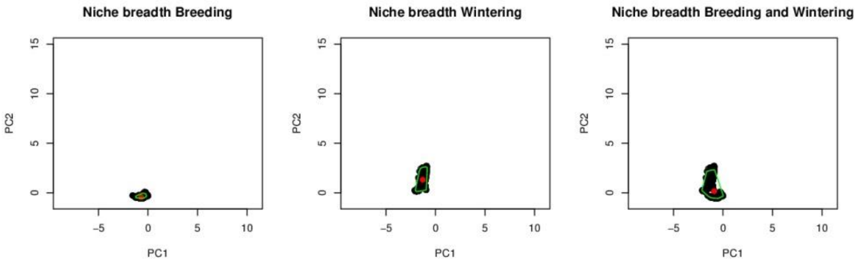
xxiii. *Netta rufina*



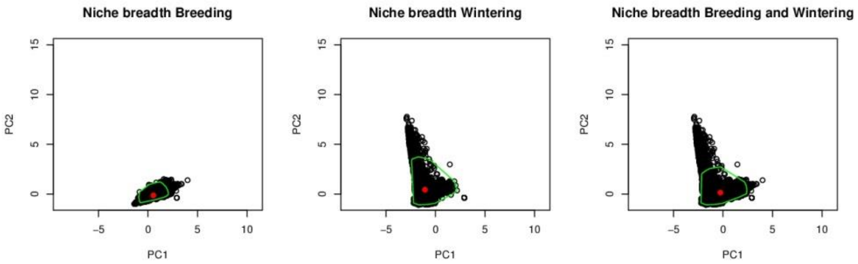
xxiv. *Oxyura leucocephala*



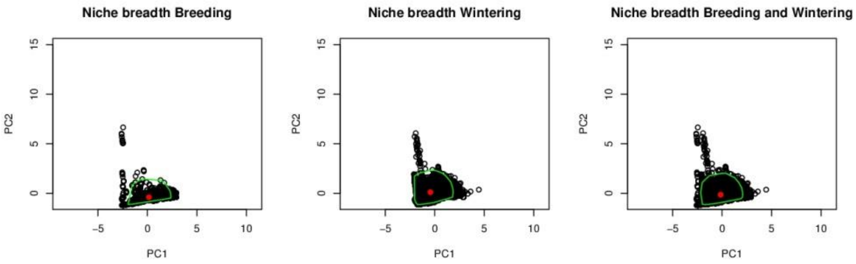
xxv. *Polysticta stelleri*



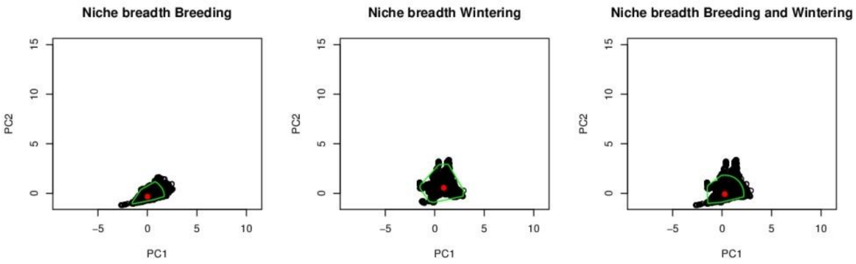
xxvi. *Spatula querquedula*



xxvii. *Tadorna ferruginea*



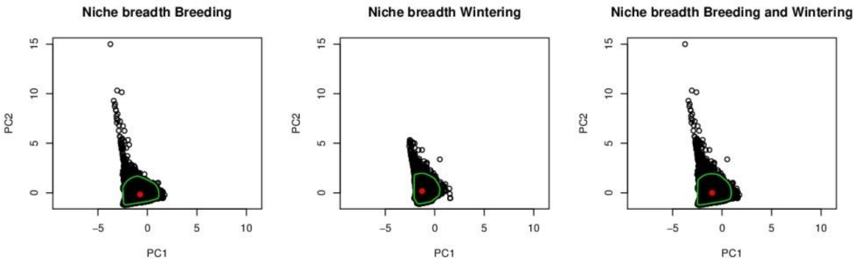
xxviii. *Tadorna tadorna*



3) Bucerotiformes

a. Upupidae

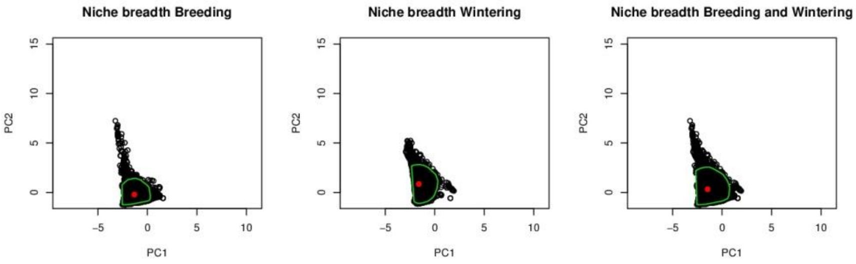
i. *Upupa epops*



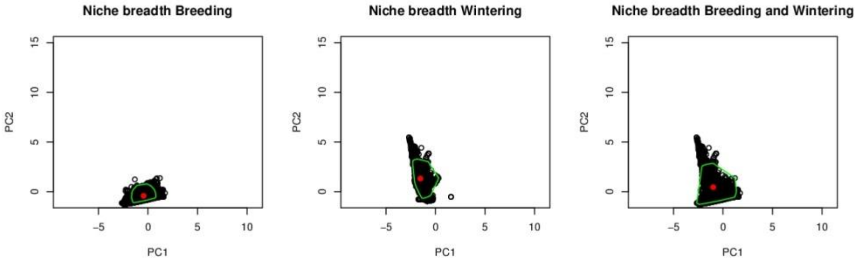
4) Caprimulgiformes

a. Apodidae

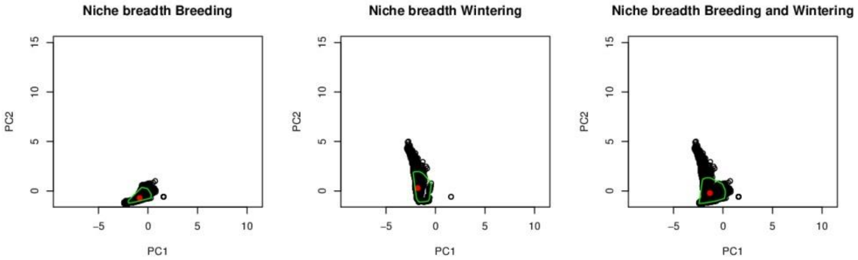
i. *Apus affinis*



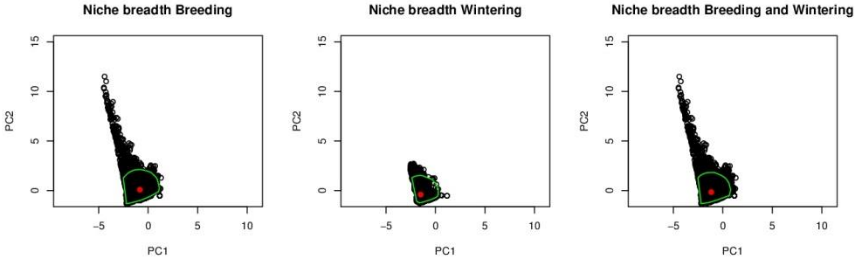
ii. *Apus apus*



iii. *Apus pallidus*

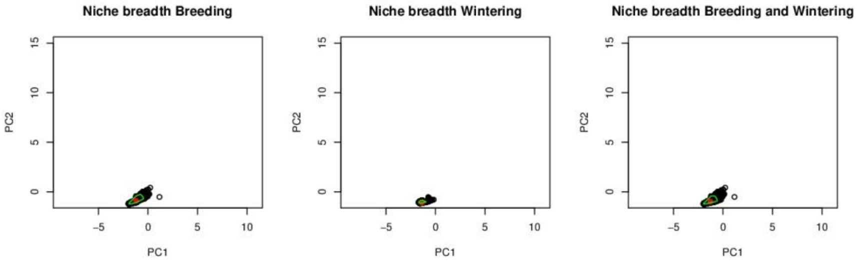


iv. *Tachymarptis melba*

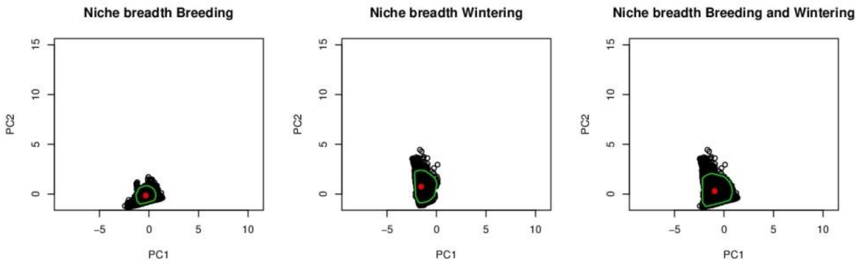


b. Caprimulgidae

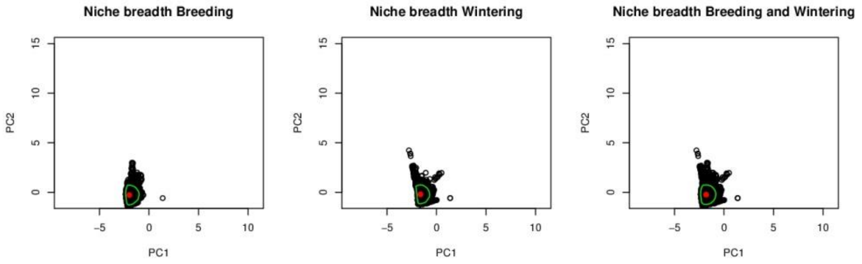
i. *Caprimulgus aegyptius*



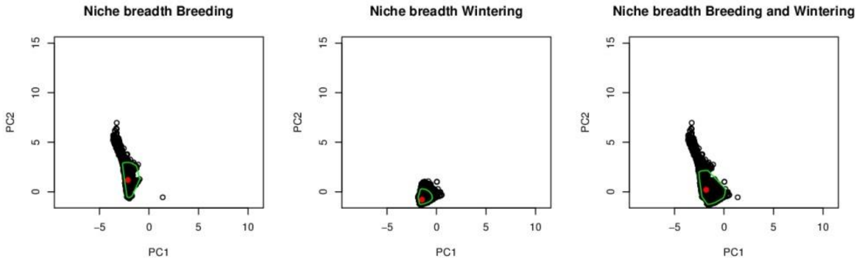
ii. *Caprimulgus europaeus*



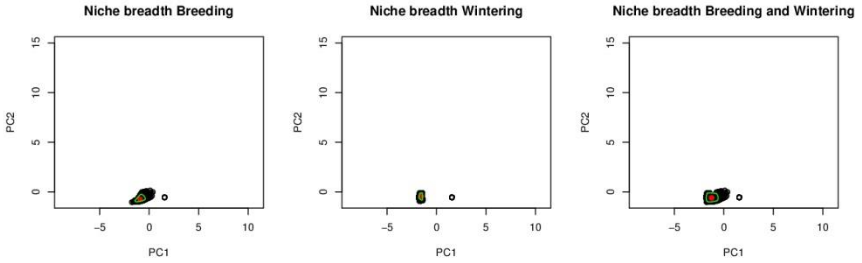
iii. *Caprimulgus inornatus*



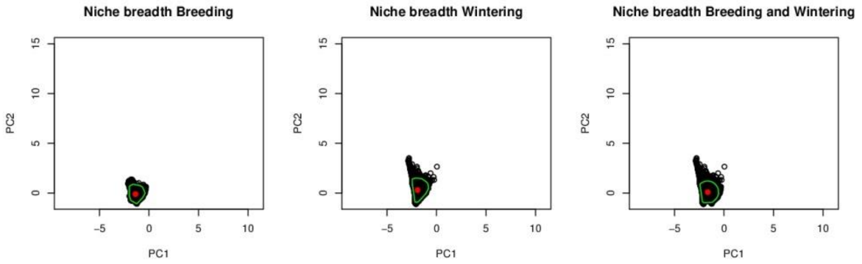
iv. *Caprimulgus longipennis*



v. *Caprimulgus ruficollis*



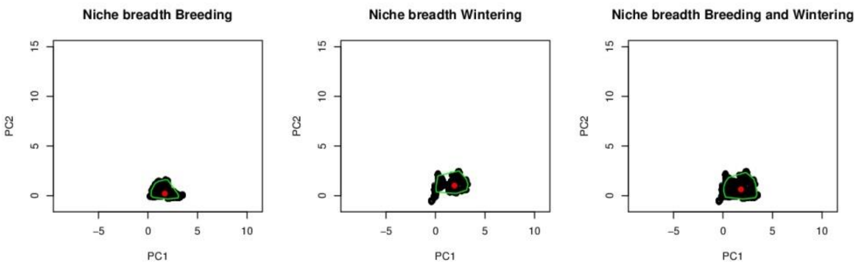
vi. *Caprimulgus vexillarius*



5) Charadriiformes

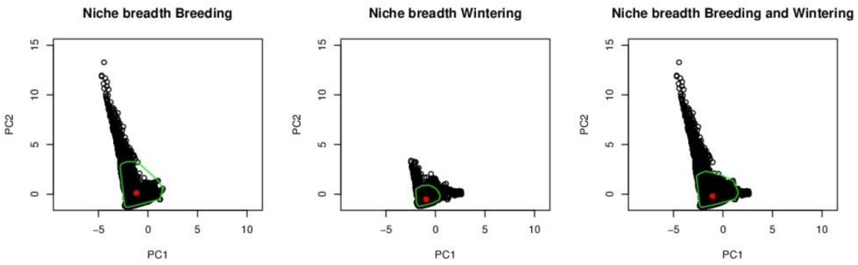
a. Alcidae

i. *Alca torda*



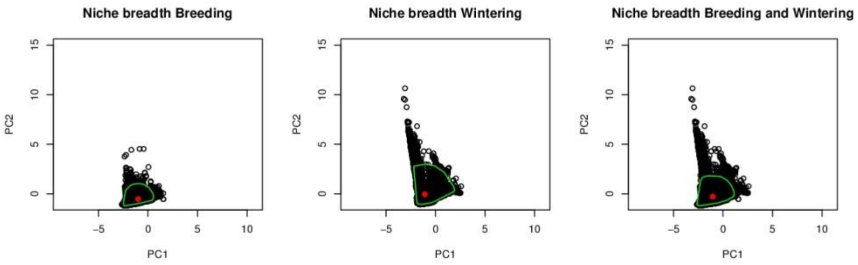
b. Burhinidae

i. *Burhinus oedicnemus*

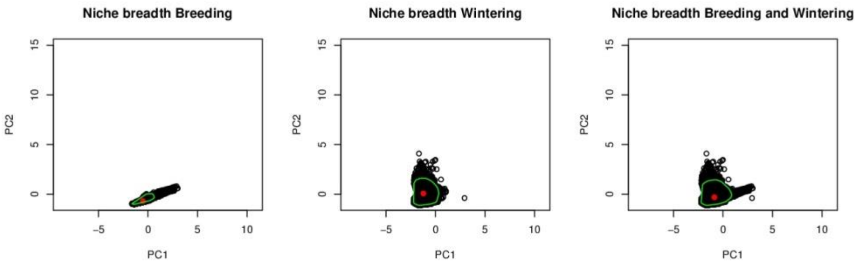


c. Charadriidae

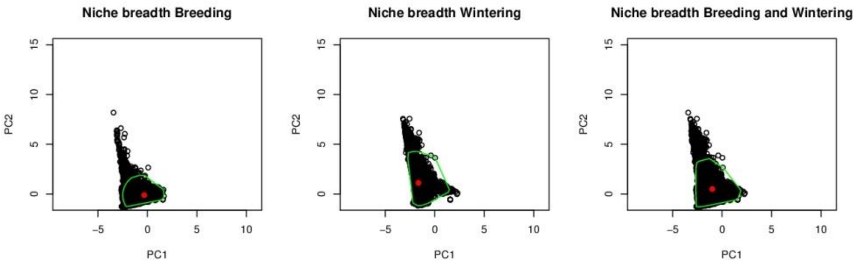
i. *Charadrius alexandrinus*



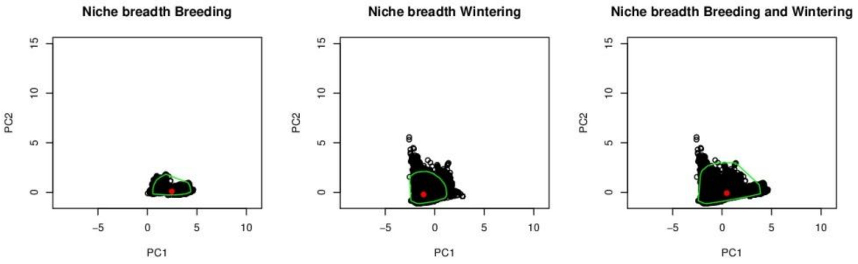
ii. *Charadrius asiaticus*



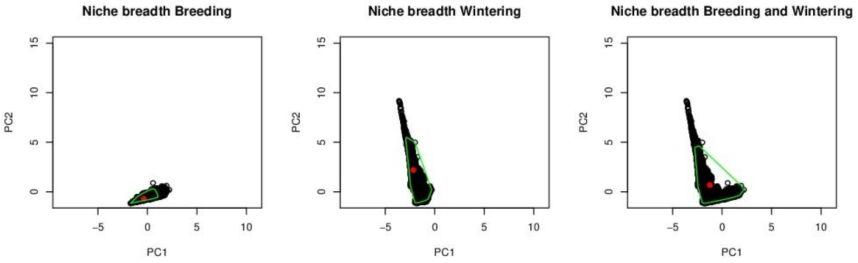
iii. *Charadrius dubius*



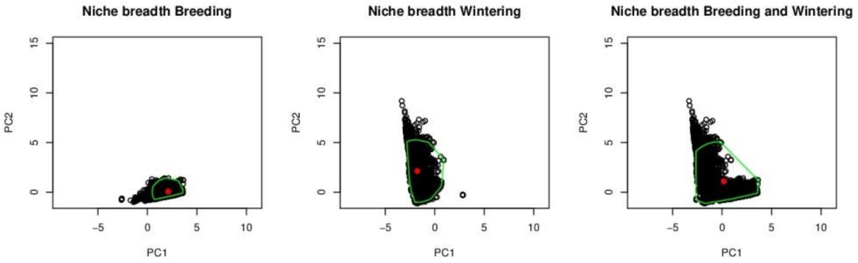
iv. *Charadrius hiaticula*



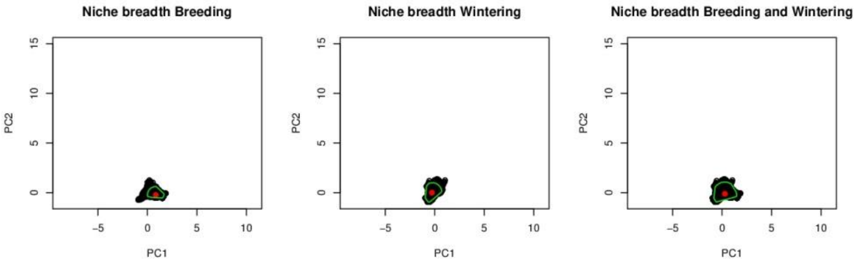
v. *Charadrius leschenaultia*



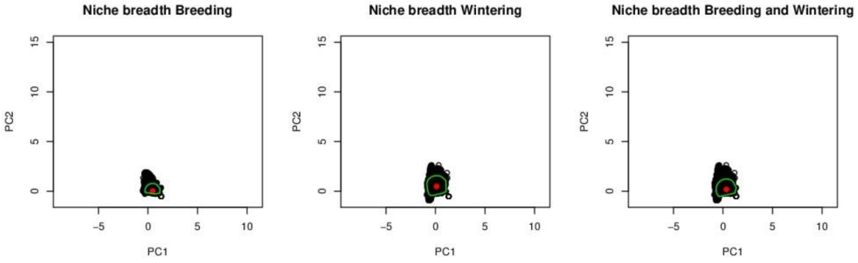
vi. *Charadrius mongolus*



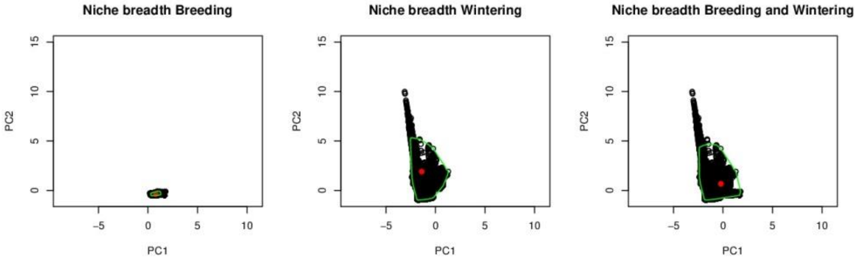
vii. *Eudromias morinellus*



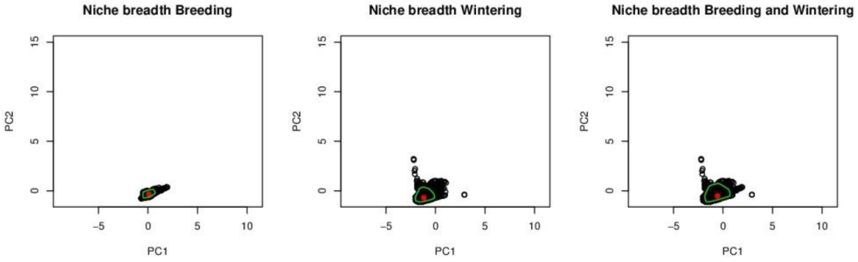
viii. *Pluvialis apricaria*



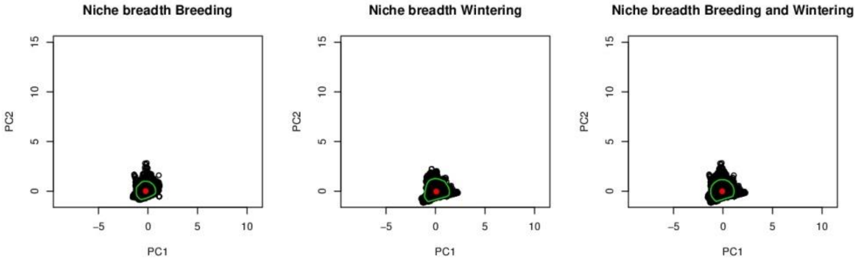
ix. *Pluvialis squatarola*



x. *Vanellus gregarius*

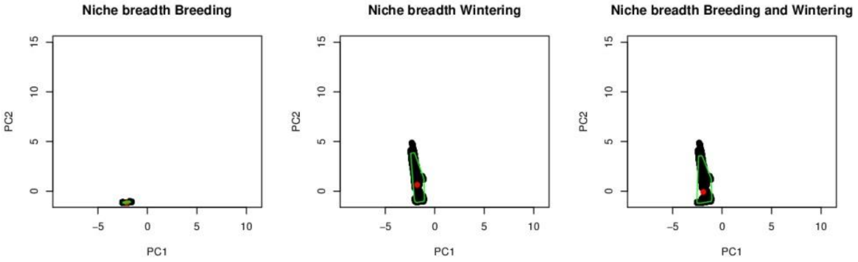


xi. *Vanellus vanellus*



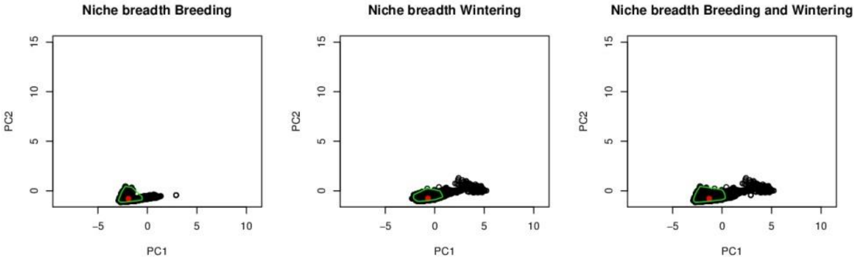
d. Dromadidae

i. *Dromas ardeola*

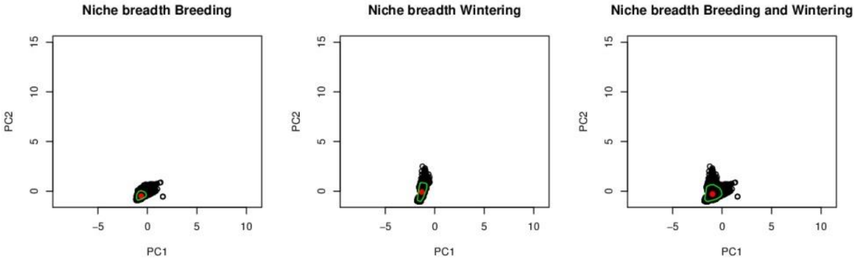


e. Glareolidae

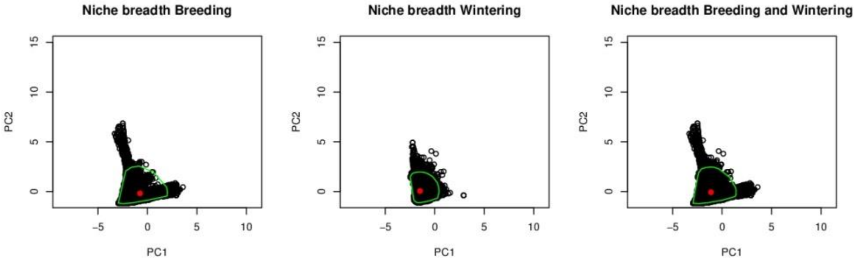
i. *Cursorius cursor*



ii. *Glareola nordmanni*

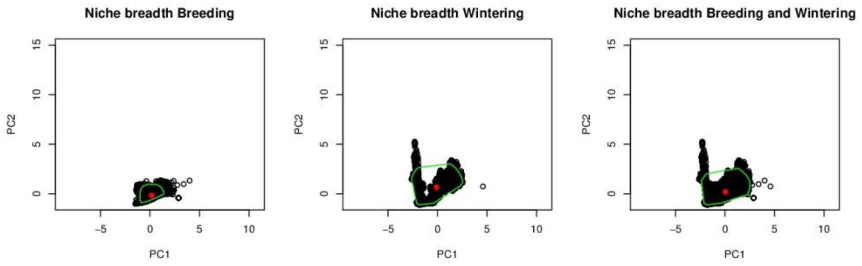


iii. *Glareola pratincola*



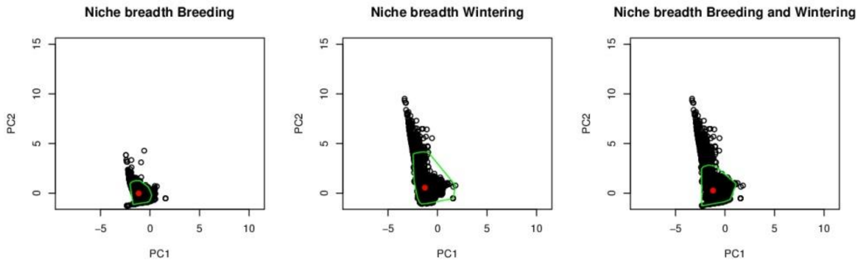
f. Haematopodidae

i. *Haematopus ostralegus*

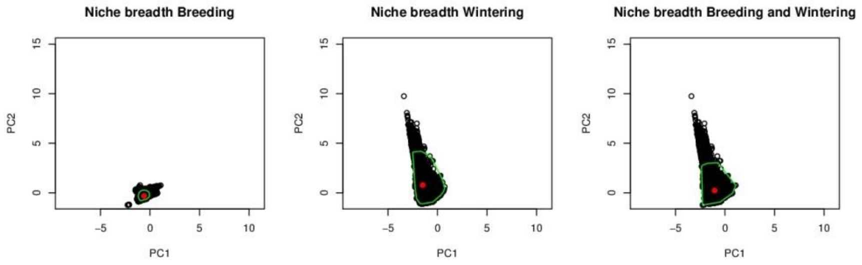


g. Laridae

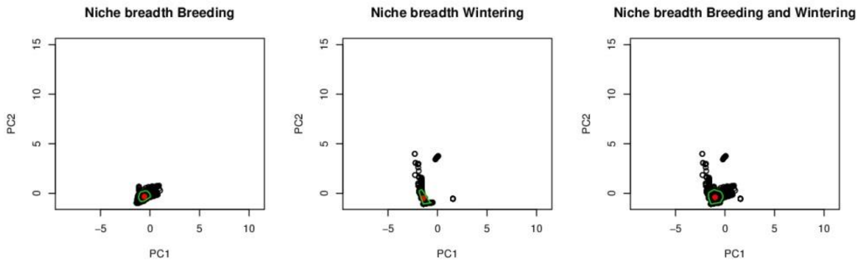
i. *Chlidonias hybrida*



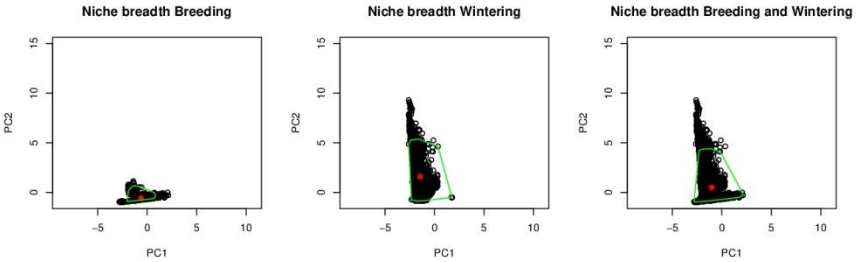
ii. *Chlidonias leucopterus*



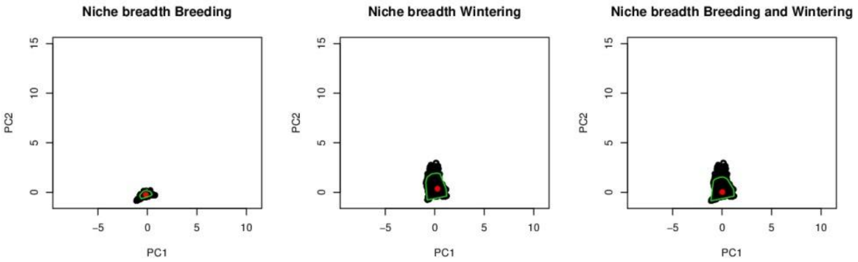
iii. *Chlidonias niger*



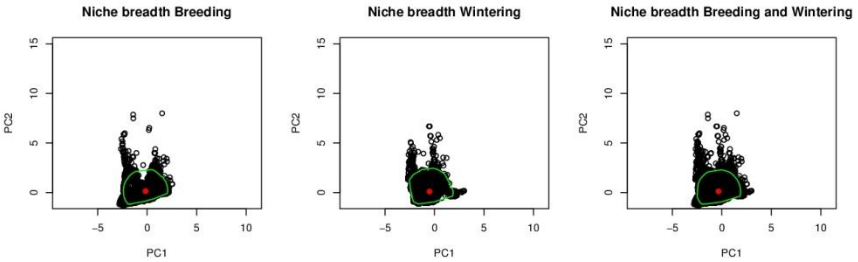
iv. *Gelochelidon nilotica*



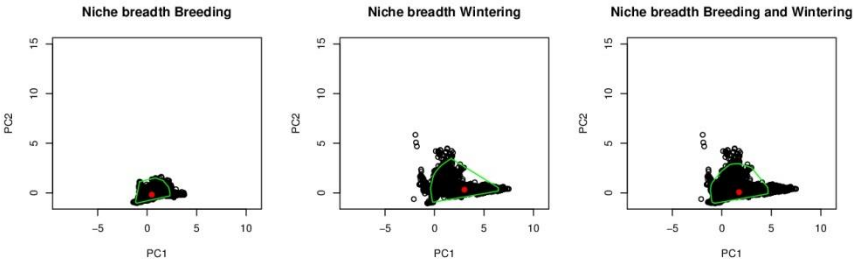
v. *Hydrocoloeus minutus*



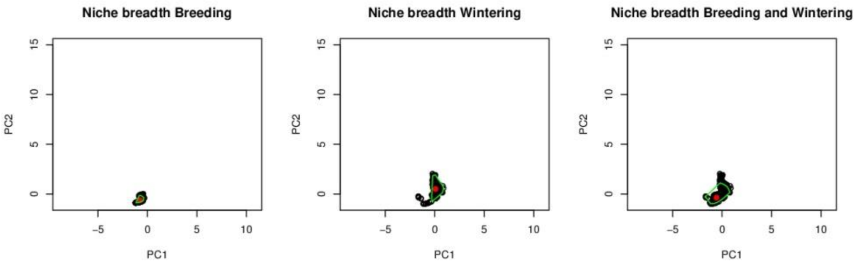
vi. *Hydroprogne caspia*



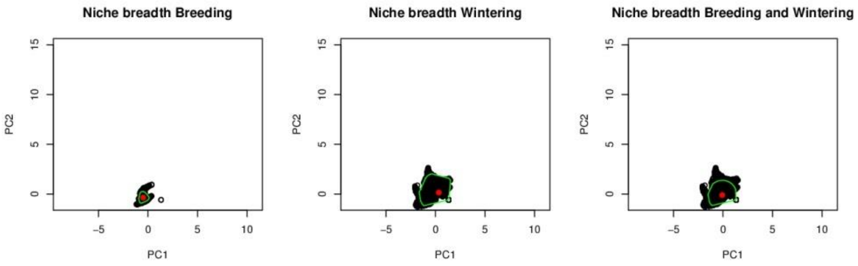
vii. *Larus argentatus*



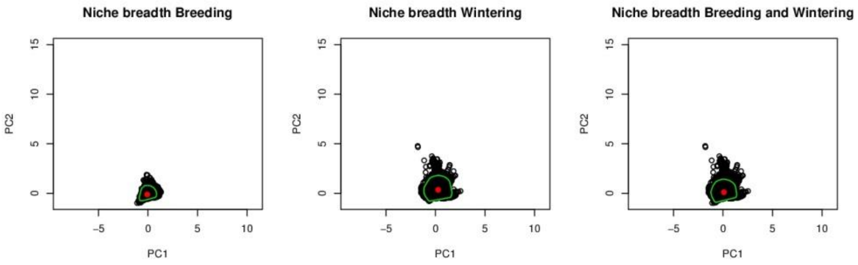
viii. *Larus audouinii*



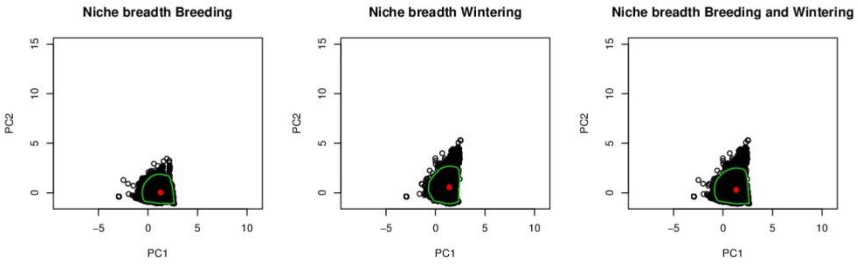
ix. *Larus cachinnans*



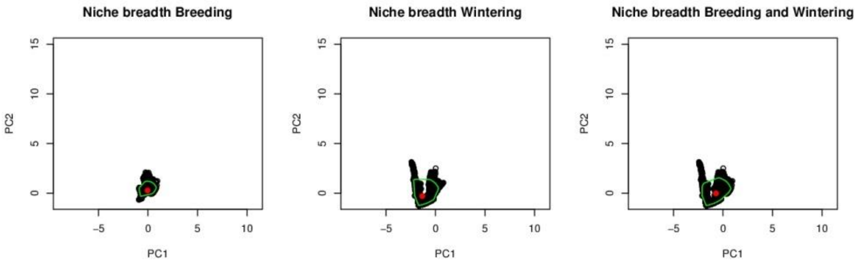
x. *Larus canus*



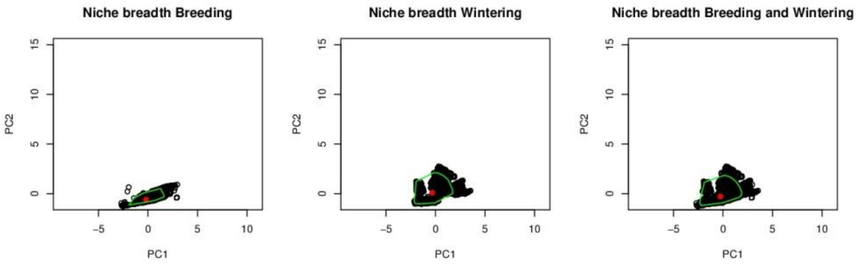
xi. *Larus cirrocephalus*



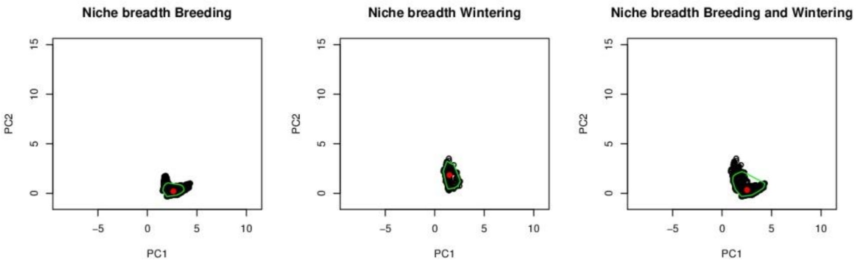
xii. *Larus fuscus*



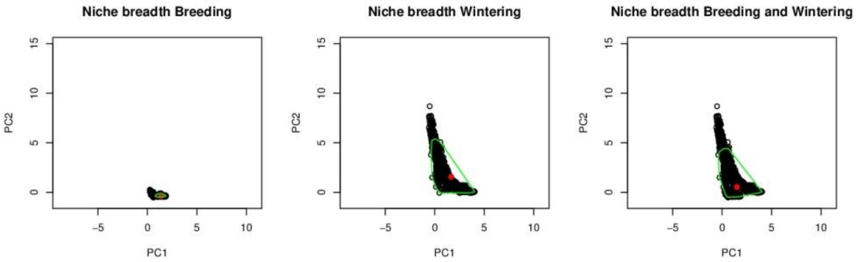
xiii. *Larus genei*



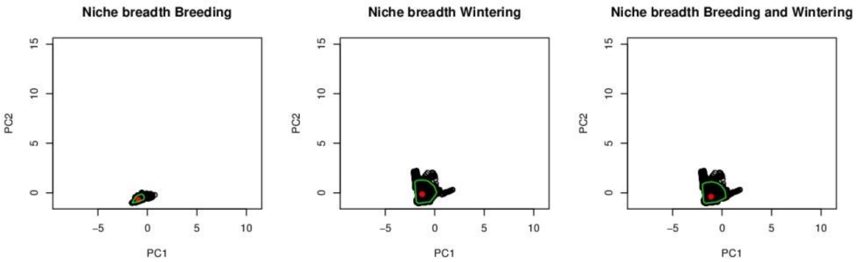
xiv. *Larus glaucoides*



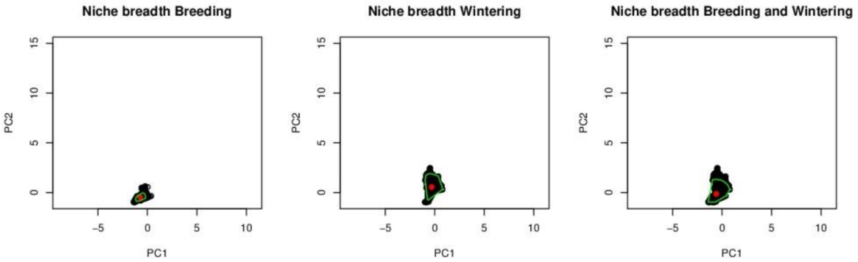
xv. *Larus hyperboreus*



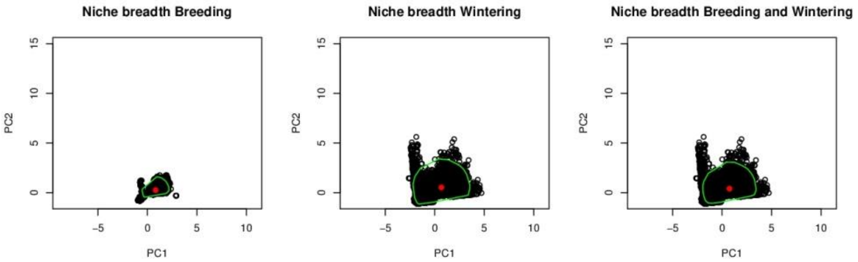
xvi. *Larus ichthyaetus*



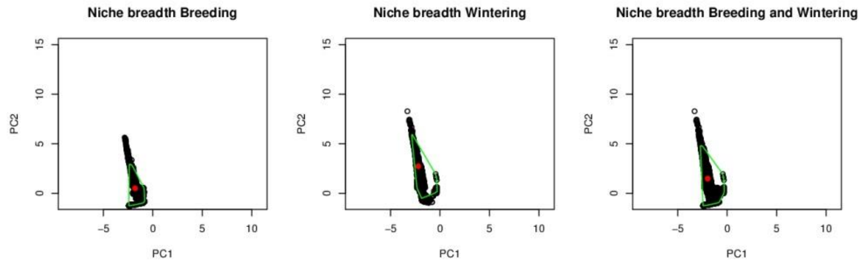
xvii. *Larus melanocephalus*



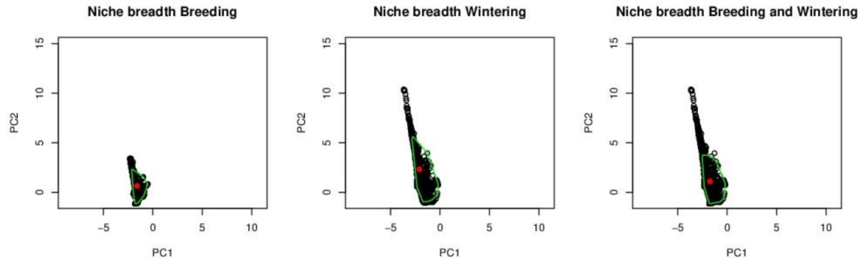
xviii. *Larus ridibundus*



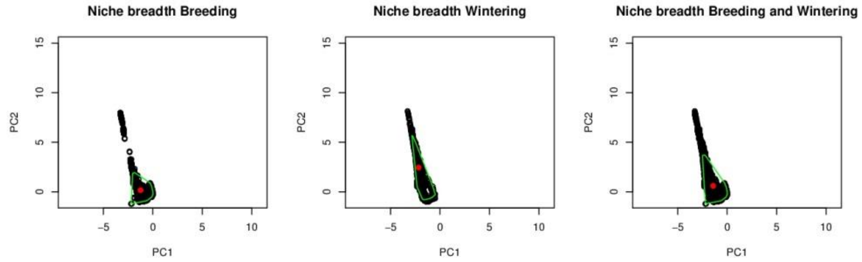
xix. *Onychoprion anaethetus*



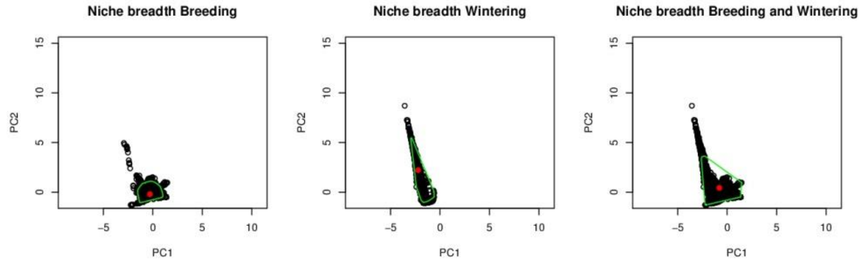
xx. *Onychoprion fuscatus*



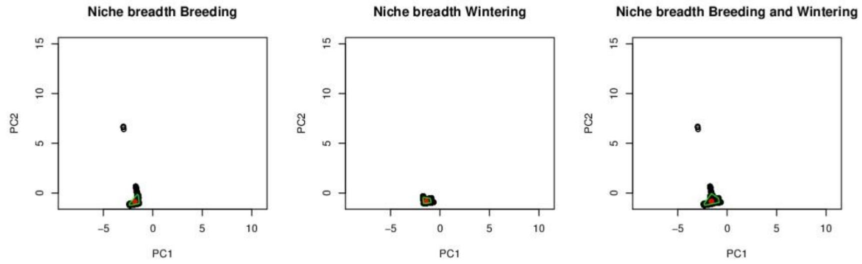
xxi. *Sterna dougallii*



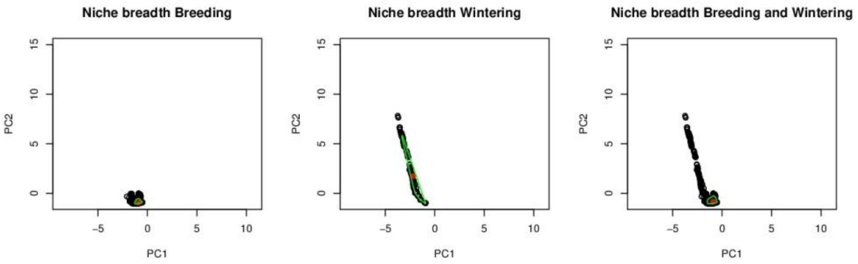
xxii. *Sterna hirundo*



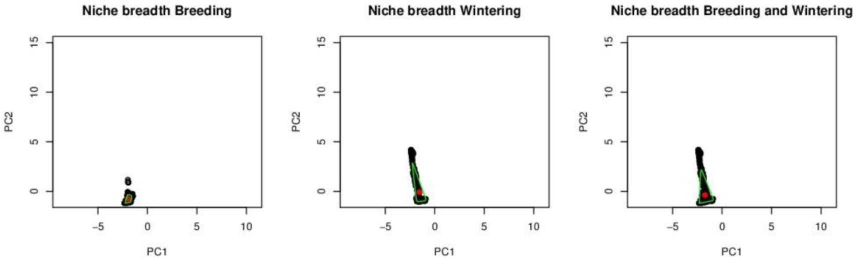
xxiii. *Sterna repressa*



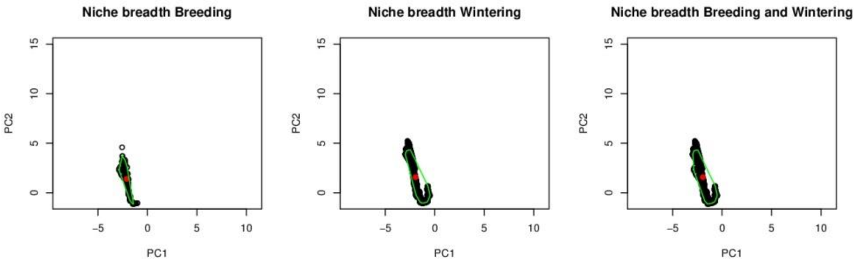
xxiv. *Sternula balaenarum*



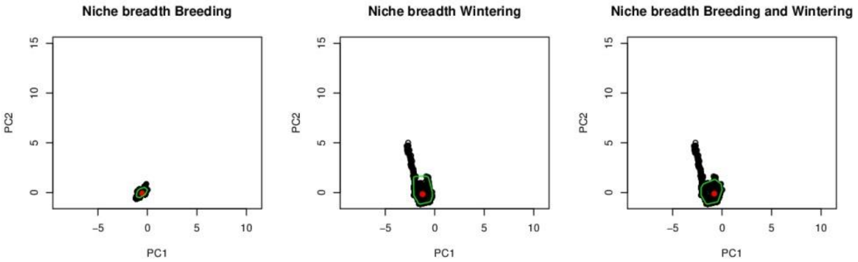
xxv. *Sternula saundersi*



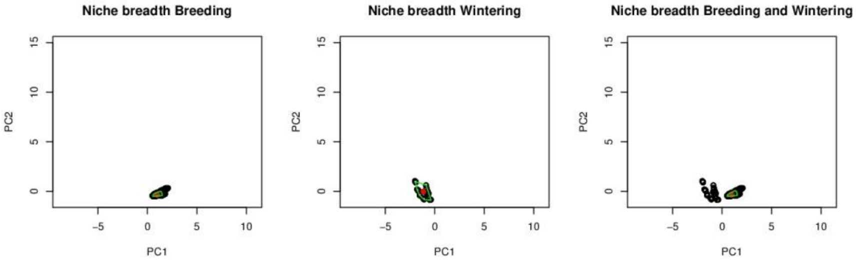
xxvi. *Thalasseus maxima*



xxvii. *Thalasseus sandvicensis*

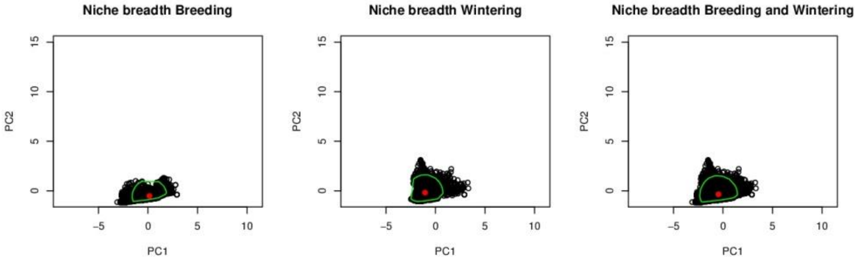


xxviii. *Xema sabini*



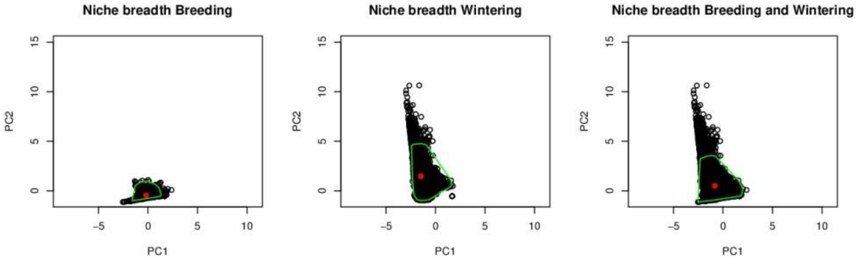
h. Recurvirostridae

i. *Recurvirostra avosetta*

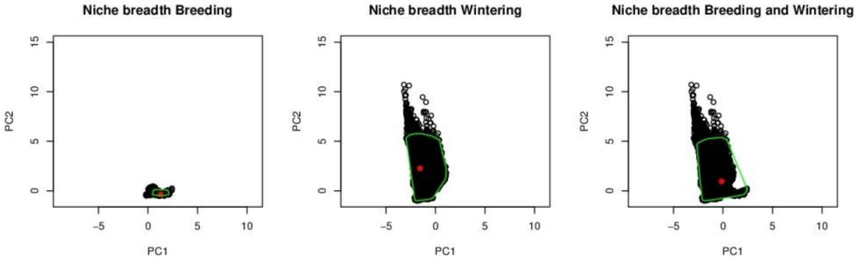


i. Scolopacidae

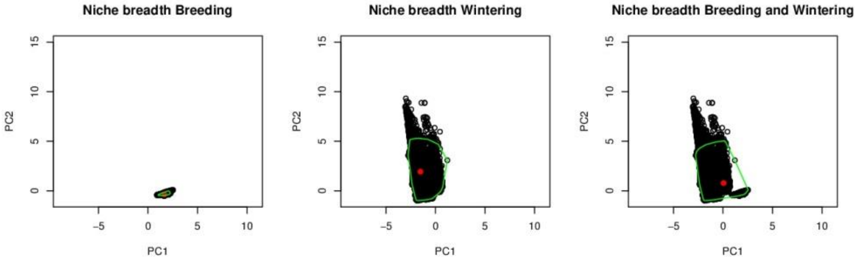
i. *Actitis hypoleucos*



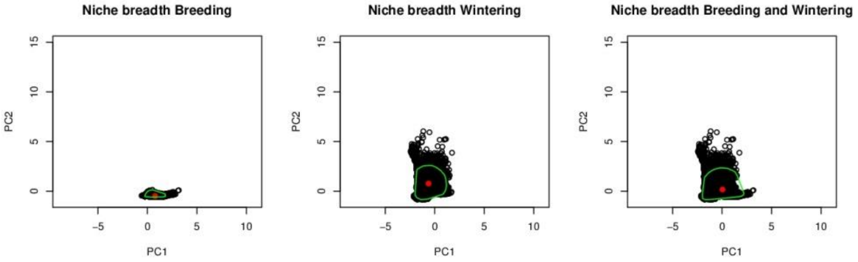
ii. *Arenaria interpres*



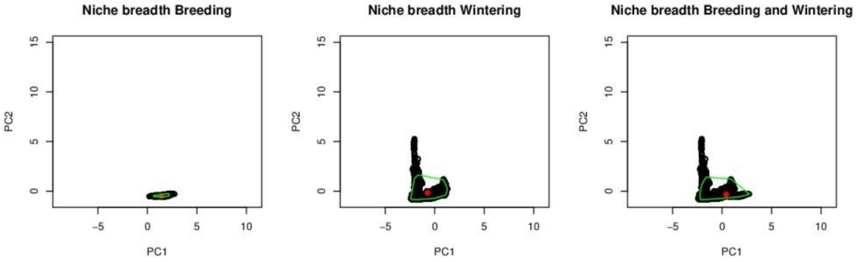
iii. *Calidris alba*



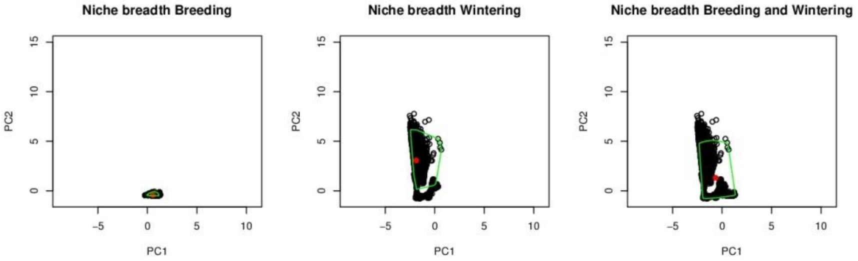
iv. *Calidris alpina*



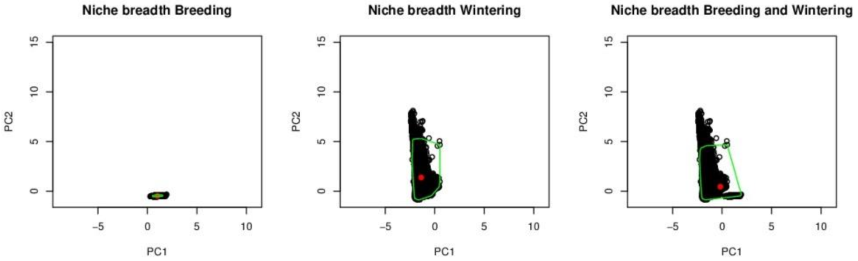
v. *Calidris canutus*



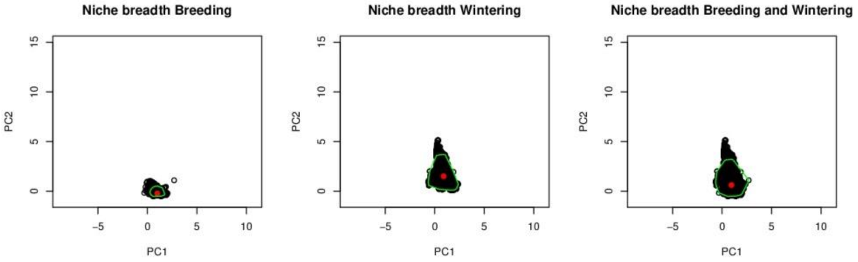
vi. *Calidris falcinellus*



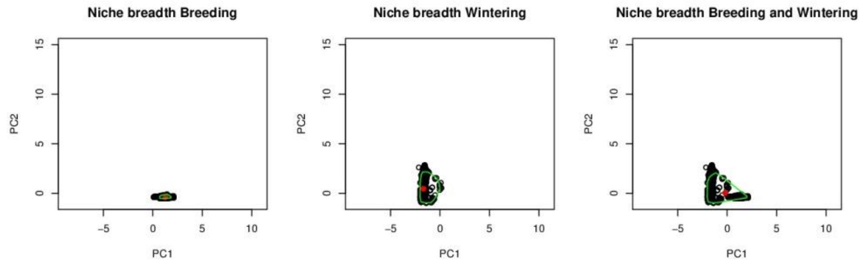
vii. *Calidris ferruginea*



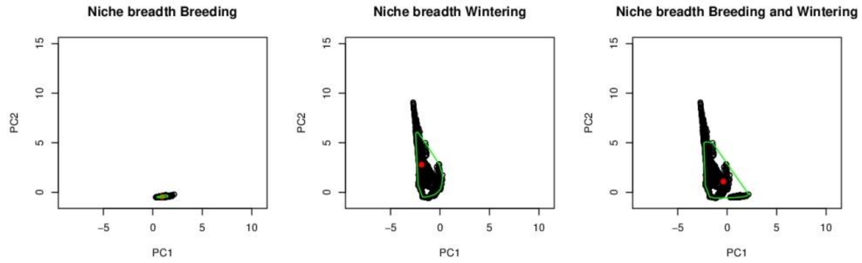
viii. *Calidris maritima*



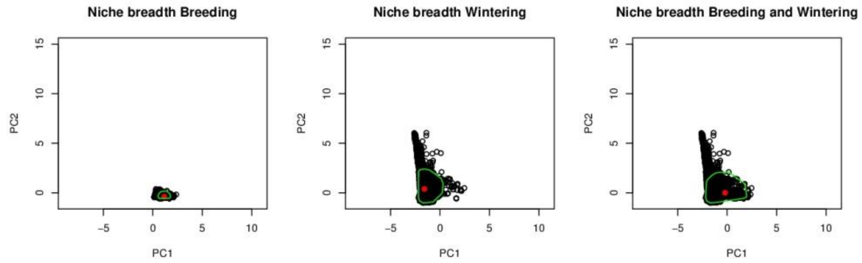
ix. *Calidris minuta*



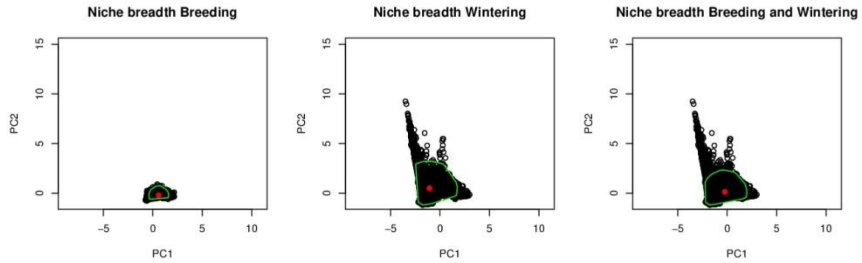
x. *Calidris ruficollis*



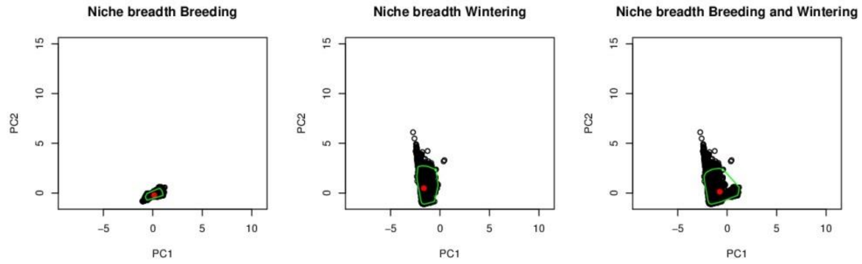
xi. *Calidris temminckii*



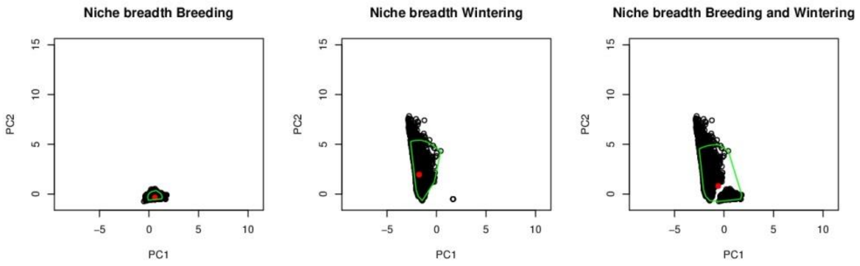
xii. *Gallinago gallinago*



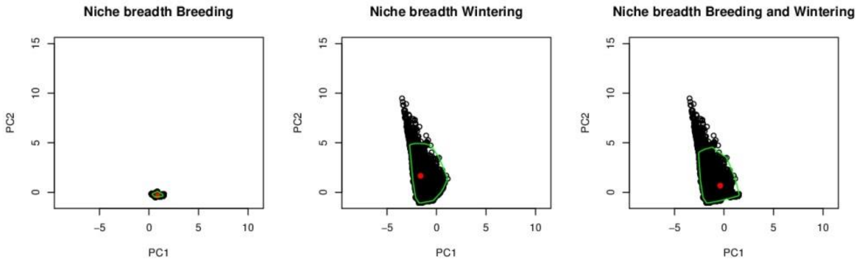
xiii. *Gallinago media*



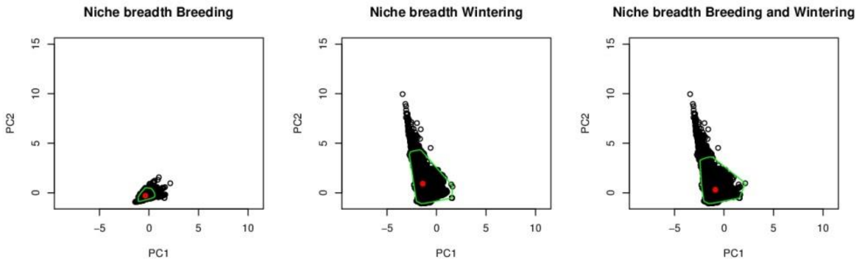
xiv. *Gallinago stenura*



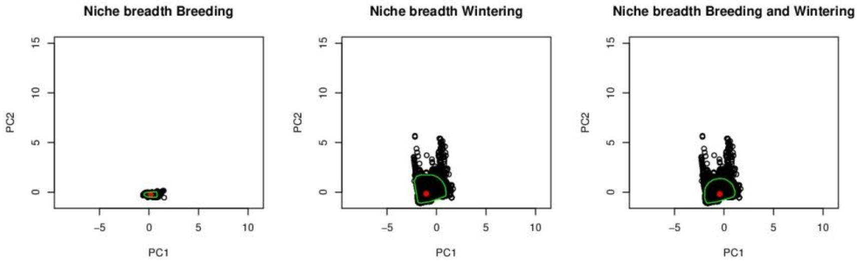
xv. *Limosa lapponica*



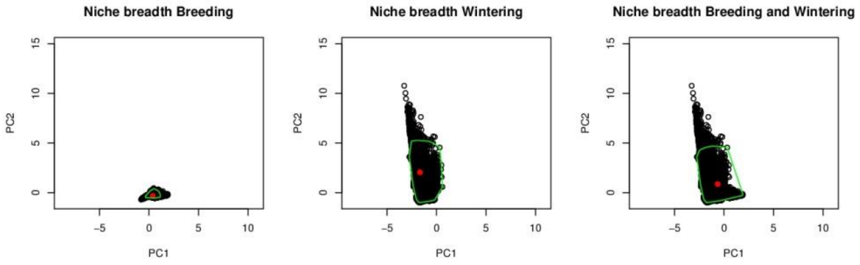
xvi. *Limosa limosa*



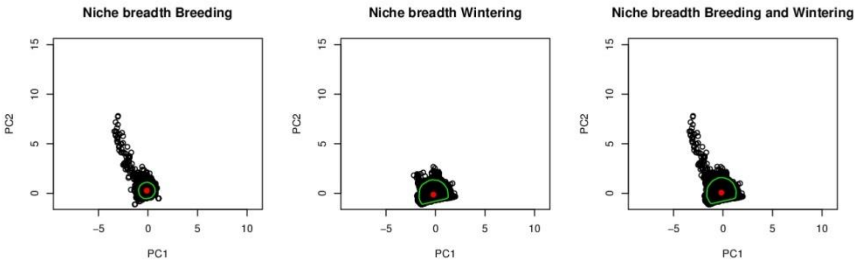
xvii. *Lymnocryptes minimus*



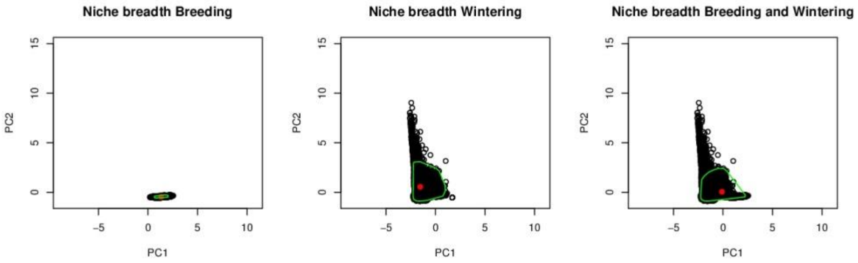
xviii. *Numenius phaeopus*



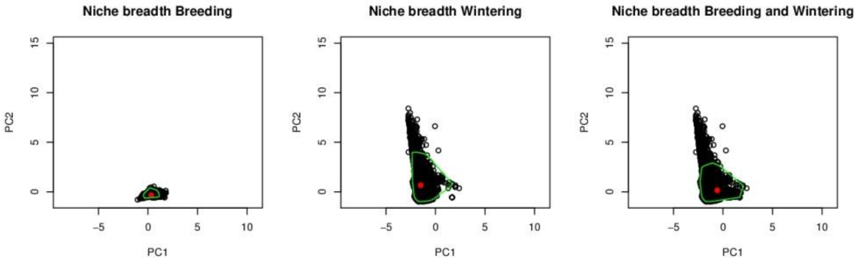
xix. *Scolopax rusticola*



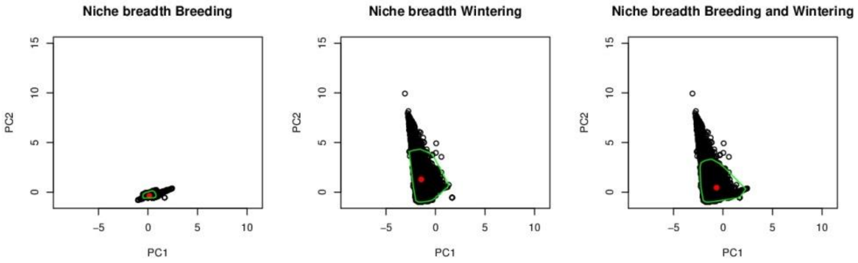
xx. *Tringa erythropus*



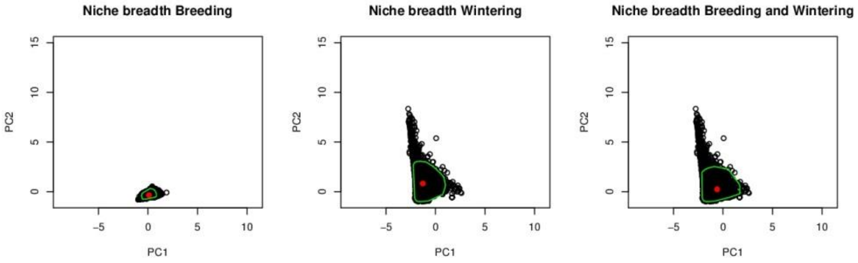
xxi. *Tringa glareola*



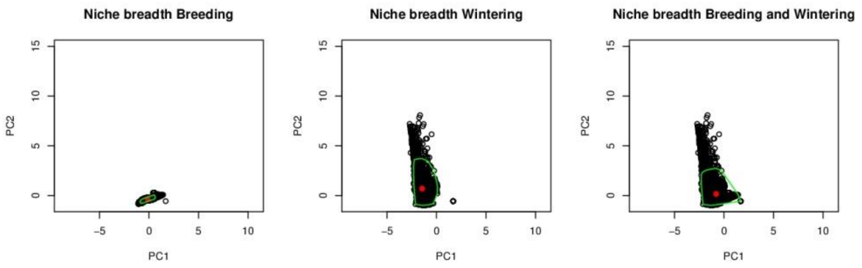
xxii. *Tringa nebularia*



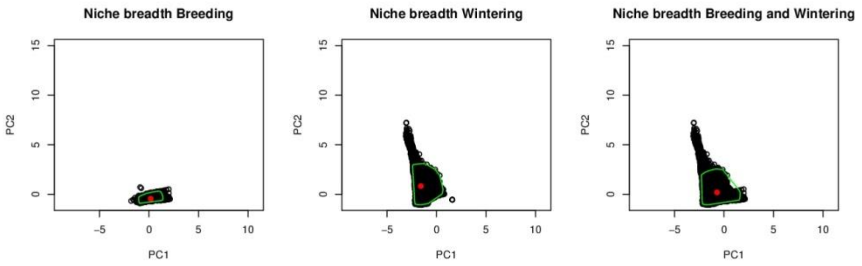
xxiii. *Tringa ochropus*



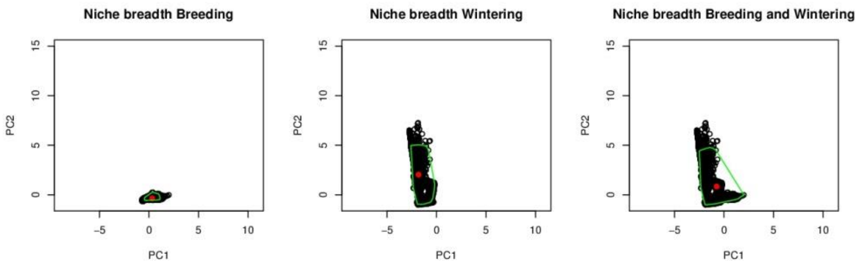
xxiv. *Tringa stagnatilis*



xxv. *Tringa totanus*



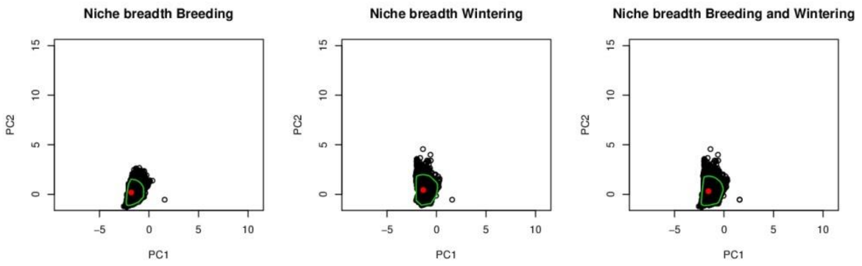
xxvi. *Xenus cinereus*



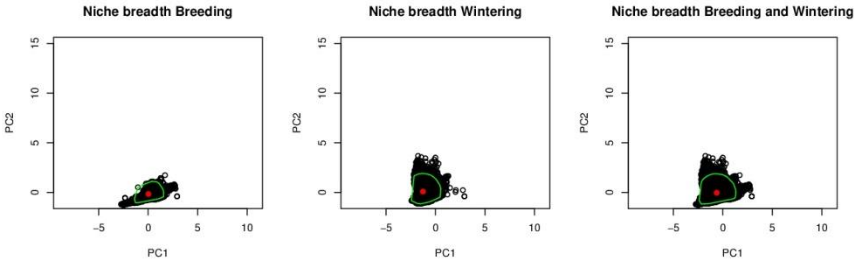
6) Ciconiiformes

a. Ciconiidae

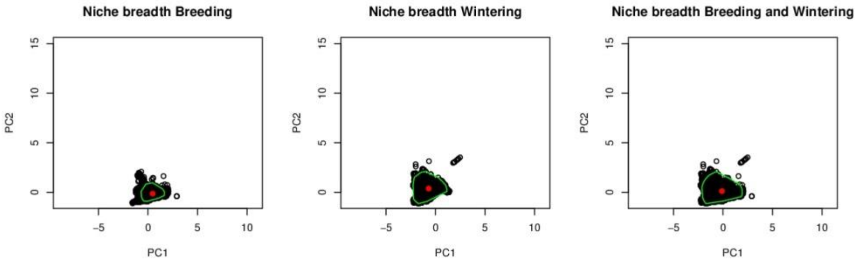
i. *Ciconia abdimii*



ii. *Ciconia ciconia*



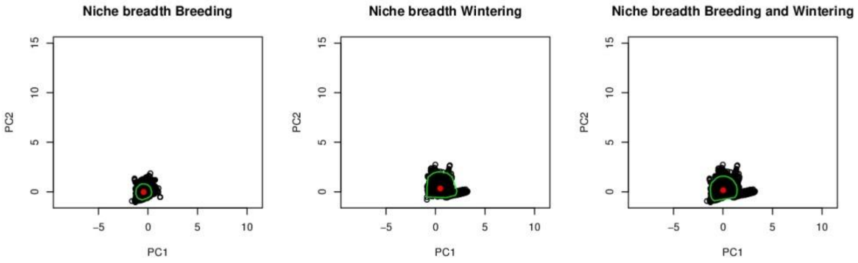
iii. *Ciconia nigra*



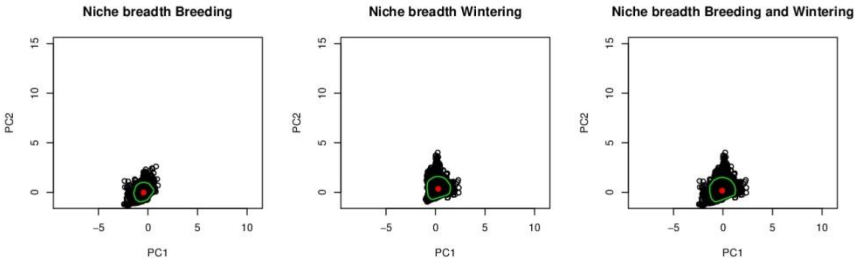
7) Columbiformes

a. Columbidae

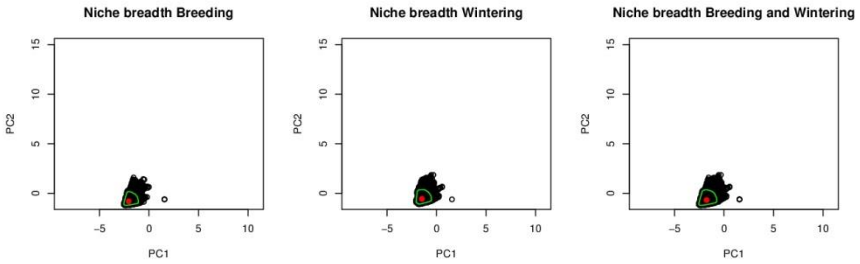
i. *Columba oenas*



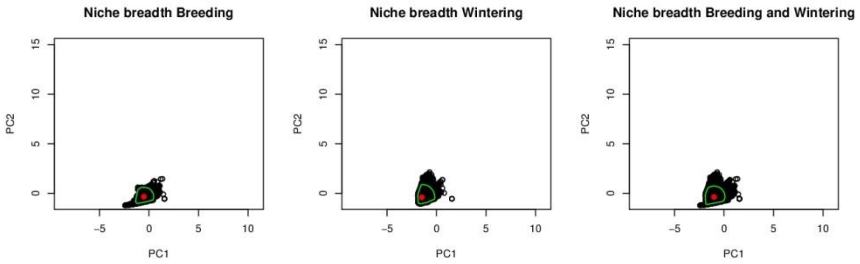
ii. *Columba palumbus*



iii. *Streptopelia roseogrisea*


Niche breadth Breeding
Niche breadth Wintering
Niche breadth Breeding and Wintering

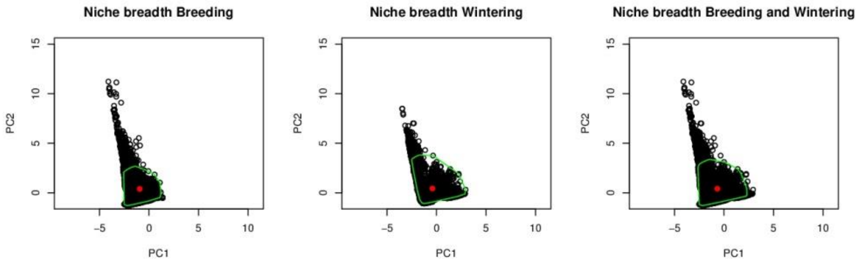
iv. *Streptopelia turtur*


Niche breadth Breeding
Niche breadth Wintering
Niche breadth Breeding and Wintering

8) Coraciiformes

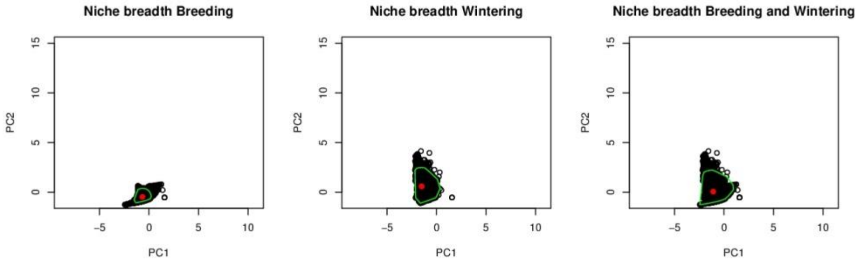
a. Alcedinidae

i. *Alcedo atthis*


Niche breadth Breeding
Niche breadth Wintering
Niche breadth Breeding and Wintering

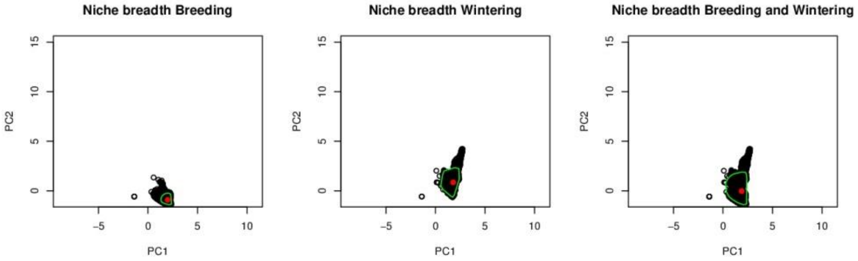
b. Coraciidae

i. *Coracias garrulus*

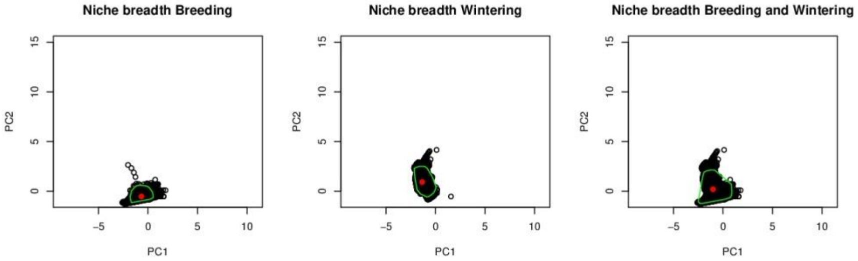

Niche breadth Breeding
Niche breadth Wintering
Niche breadth Breeding and Wintering

c. Meropidae

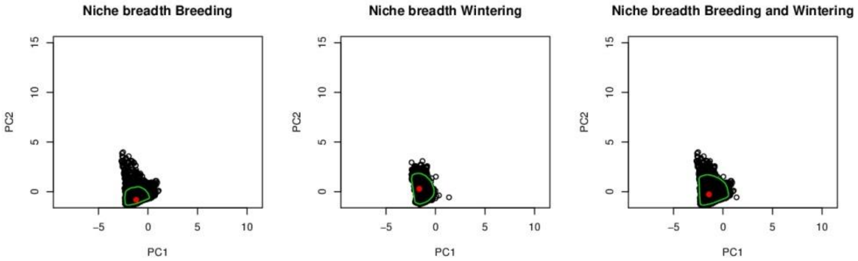
i. *Merops albicollis*



ii. *Merops apiaster*



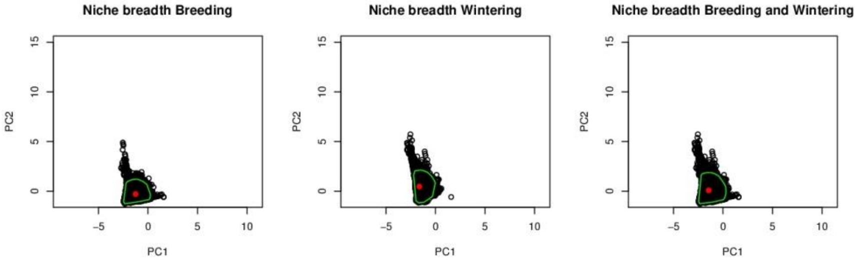
iii. *Merops persicus*



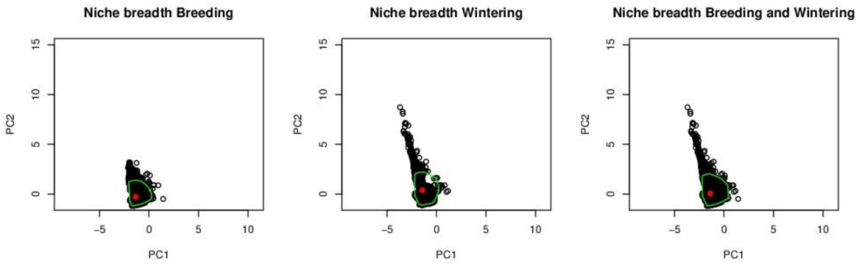
9) Cuculiformes

a. Cuculidae

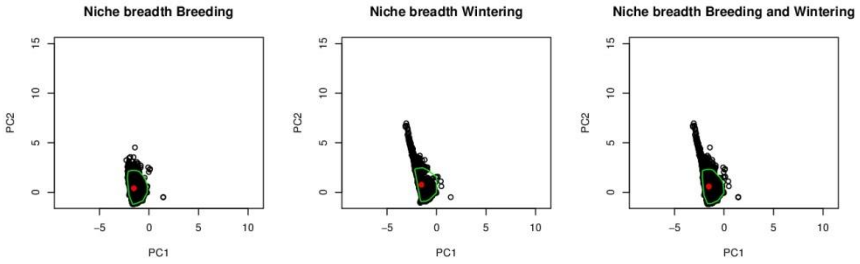
i. *Clamator glandarius*



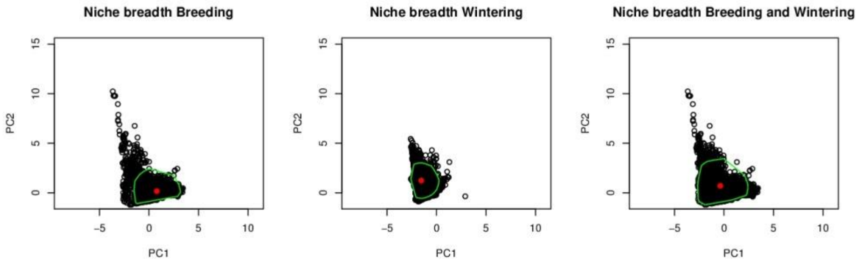
ii. *Clamator jacobinus*



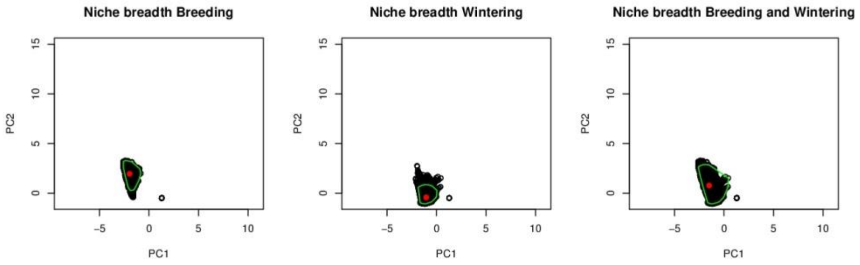
iii. *Clamator levaillantii*



iv. *Cuculus canorus*



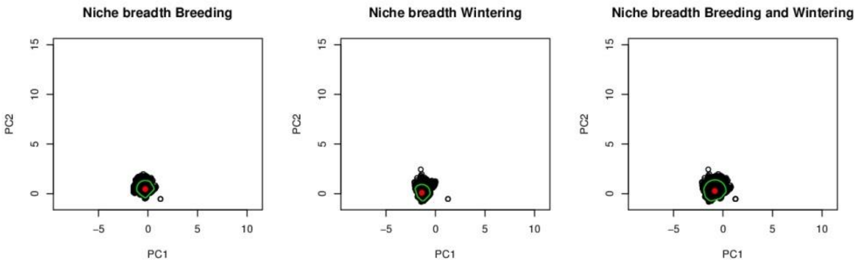
v. *Cuculus rochii*



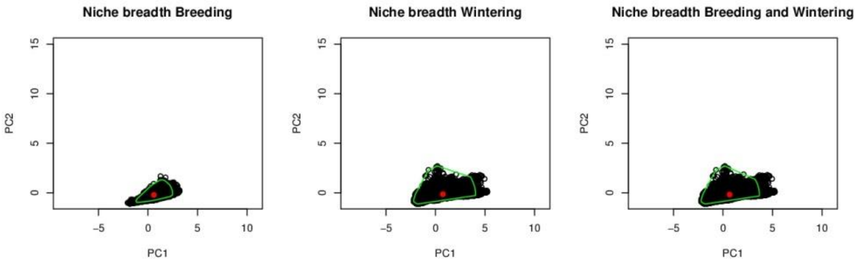
10) Falconiformes

a. Falconidae

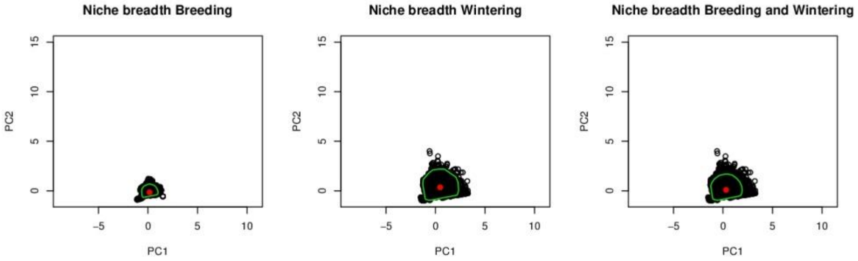
i. *Falco amurensis*



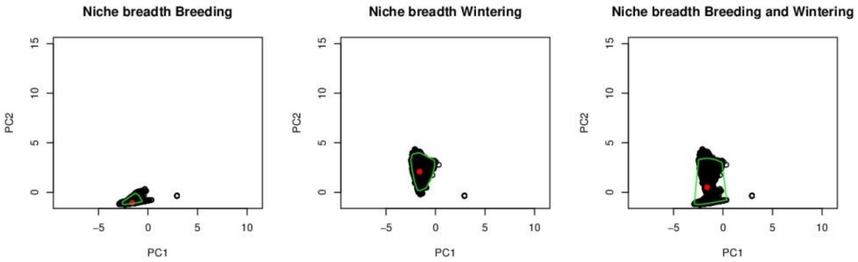
ii. *Falco cherrug*



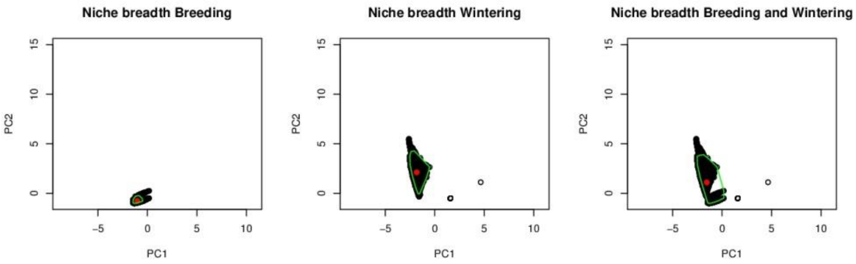
iii. *Falco columbarius*



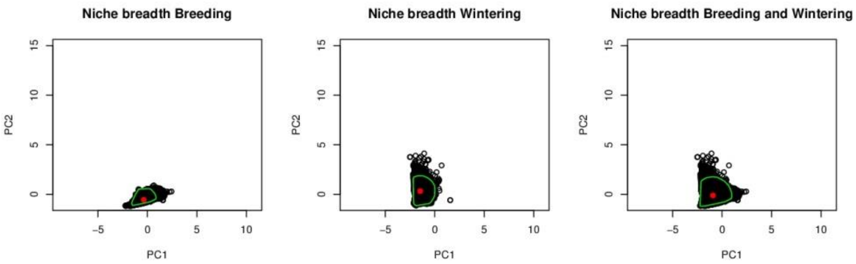
iv. *Falco concolor*



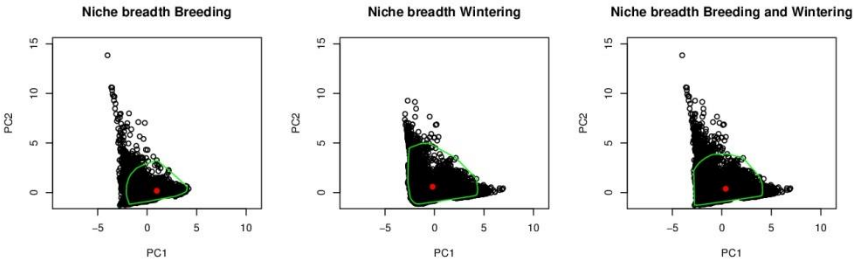
v. *Falco eleonorae*



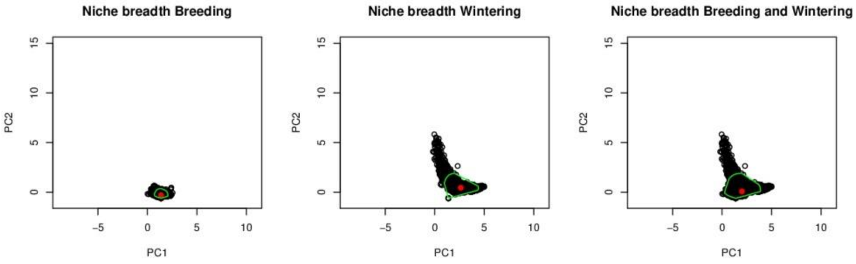
vi. *Falco naumanni*



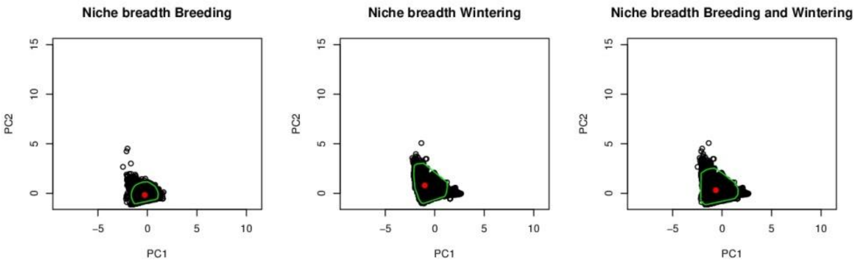
vii. *Falco peregrinus*



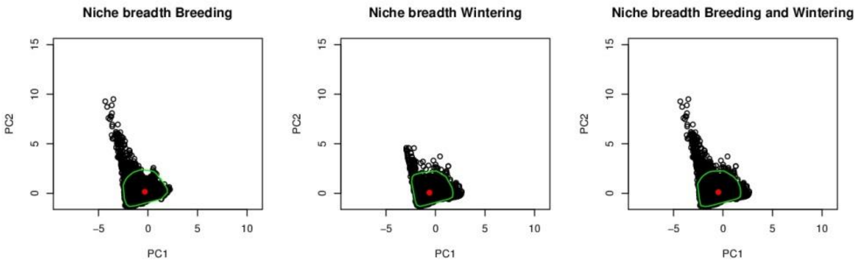
viii. *Falco rusticolus*



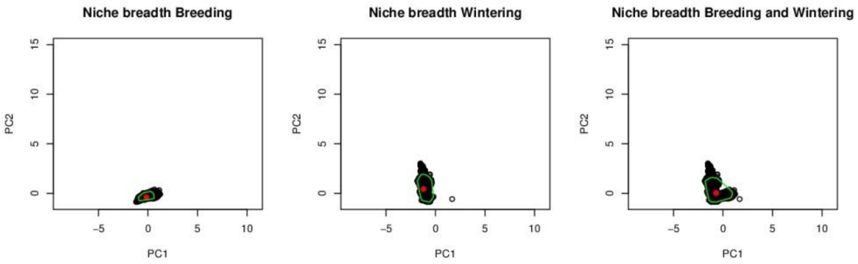
ix. *Falco subbuteo*



x. *Falco tinnunculus*



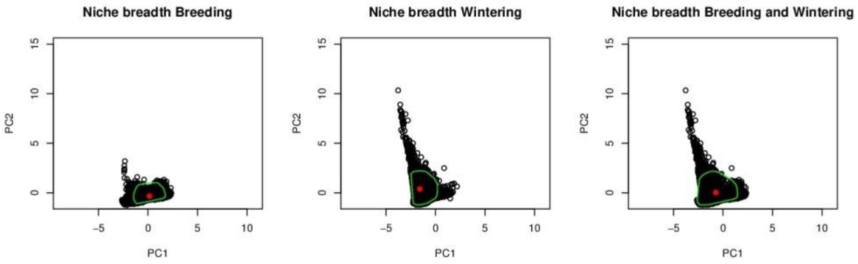
xi. *Falco vespertinus*



11) Galliformes

a. Phasianidae

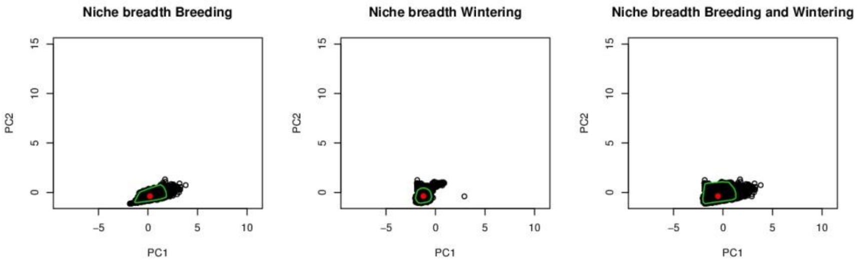
i. *Coturnix coturnix*



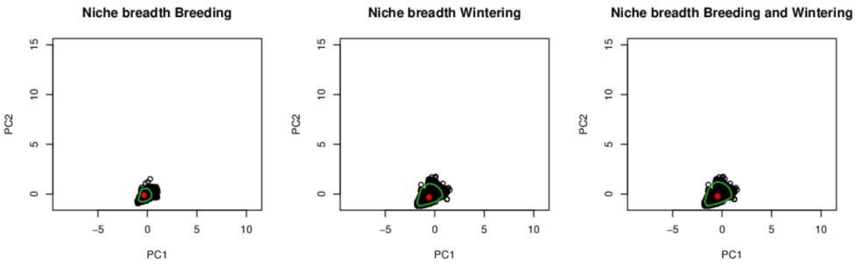
12) Gruiformes

a. Gruidae

i. *Anthropoides virgo*

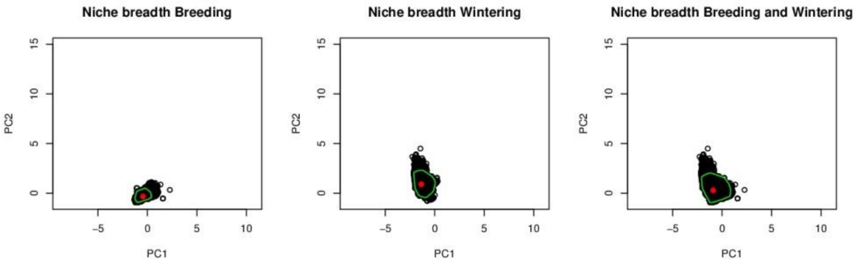


ii. *Grus grus*

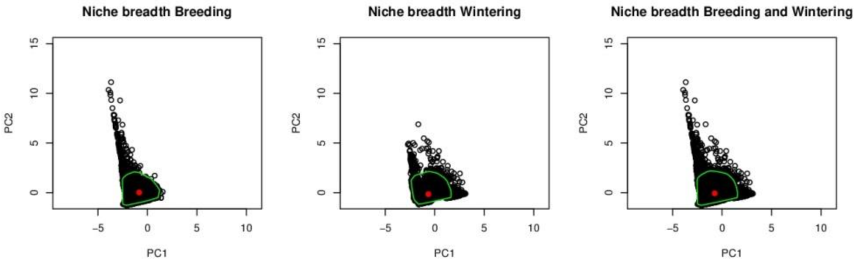


b. Rallidae

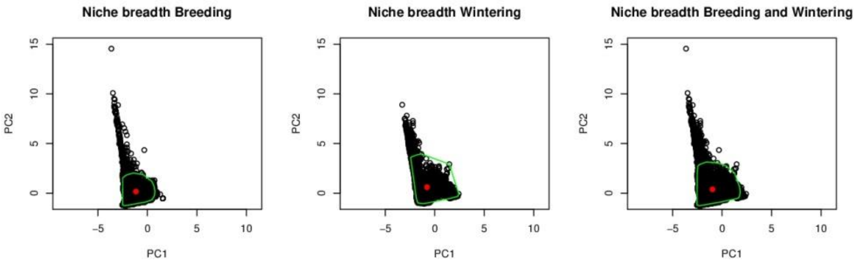
i. *Crex crex*



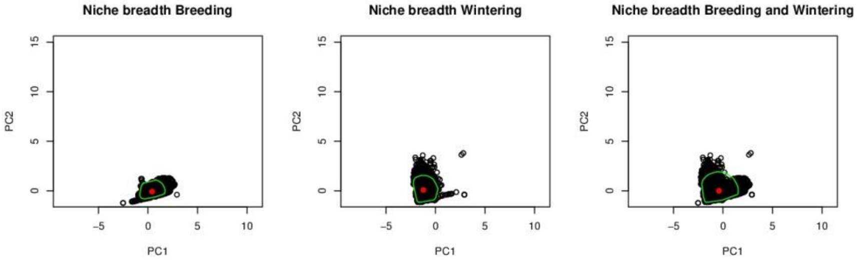
ii. *Fulica atra*



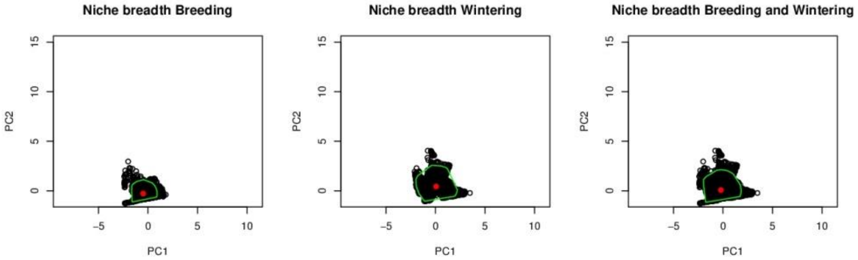
iii. *Gallinula chloropus*



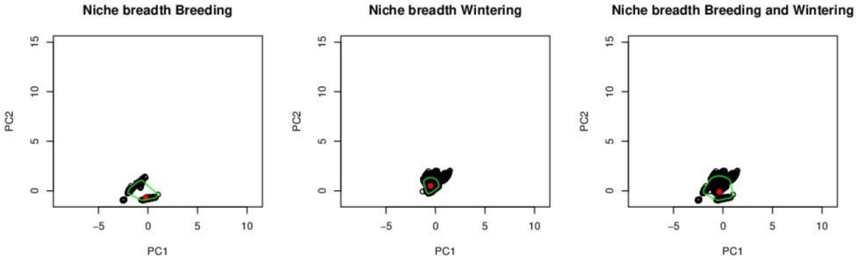
iv. *Porzana porzana*


Niche breadth Breeding
Niche breadth Wintering
Niche breadth Breeding and Wintering

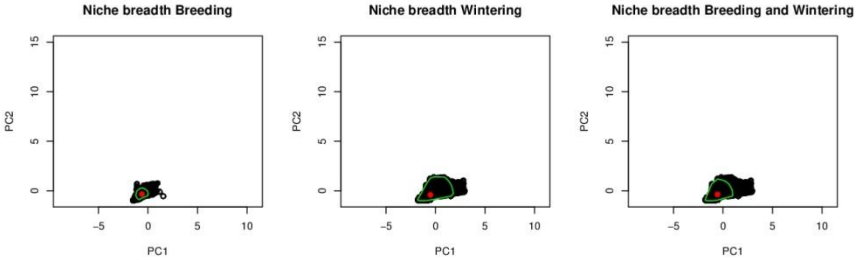
v. *Rallus aquaticus*


Niche breadth Breeding
Niche breadth Wintering
Niche breadth Breeding and Wintering

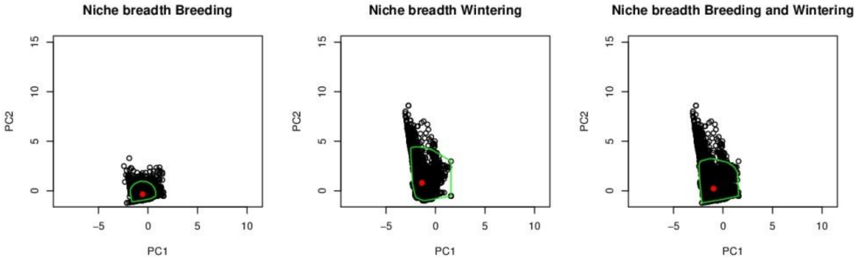
vi. *Sarothrura ayresi*


Niche breadth Breeding
Niche breadth Wintering
Niche breadth Breeding and Wintering

vii. *Zapornia parva*


Niche breadth Breeding
Niche breadth Wintering
Niche breadth Breeding and Wintering

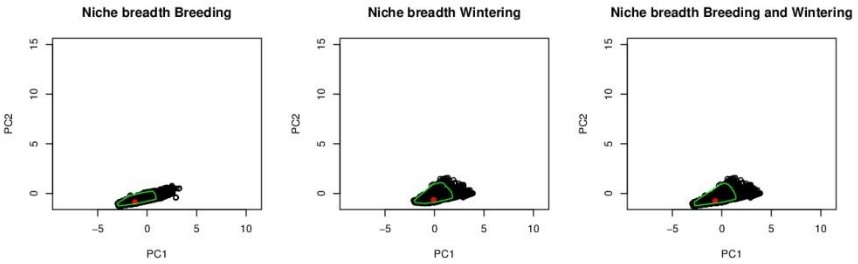
viii. *Zapornia pusilla*


Niche breadth Breeding
Niche breadth Wintering
Niche breadth Breeding and Wintering

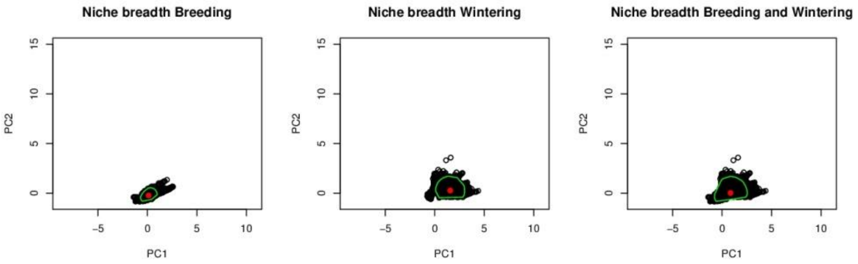
13) Otidiformes

a. Otididae

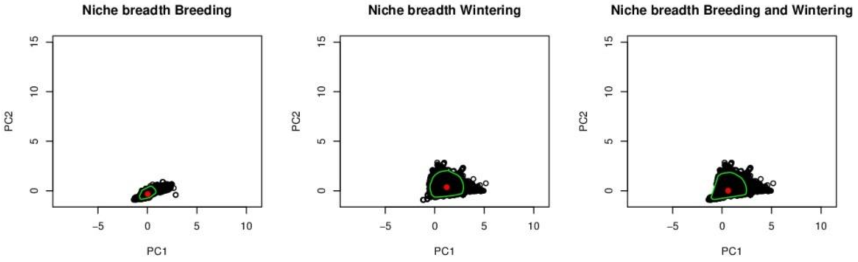
i. *Chlamydotis undulata*



ii. *Otis tarda*



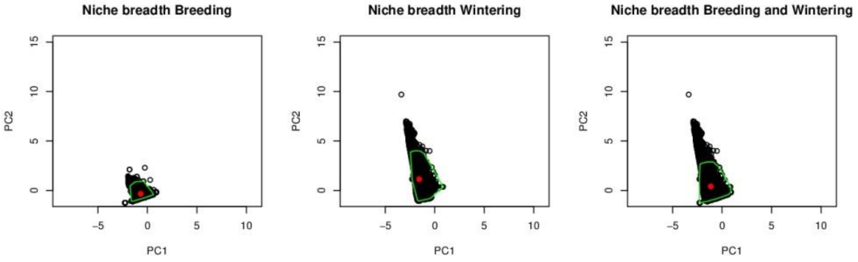
iii. *Tetrax tetrax*



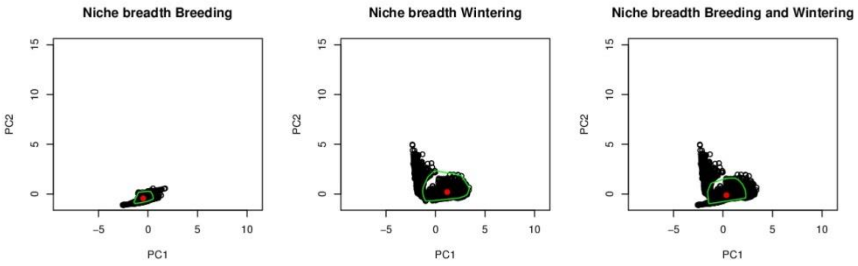
14) Passeriformes

a. Acrocephalidae

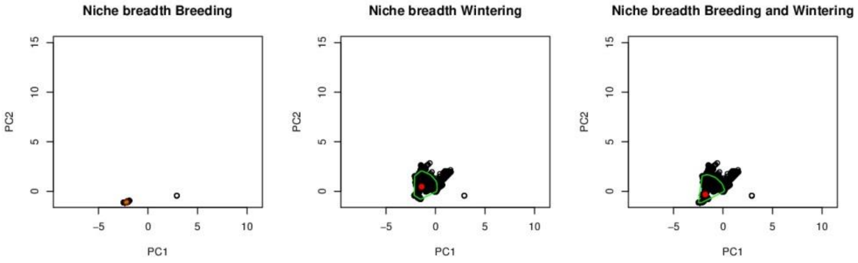
i. *Acrocephalus arundinaceus*



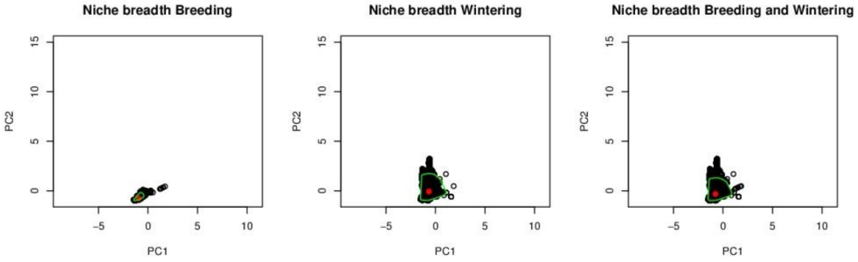
ii. <u>*Acrocephalus dumetorum*</u>



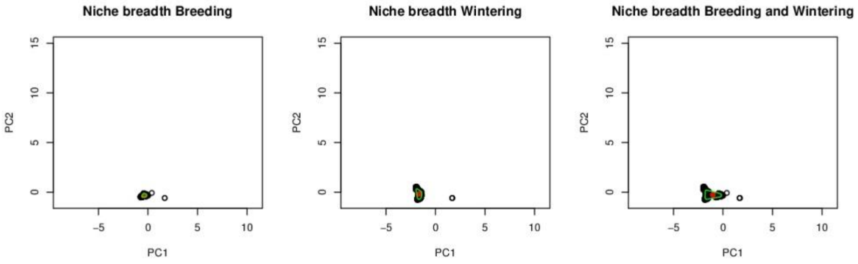
iii. <u>*Acrocephalus griseldis*</u>



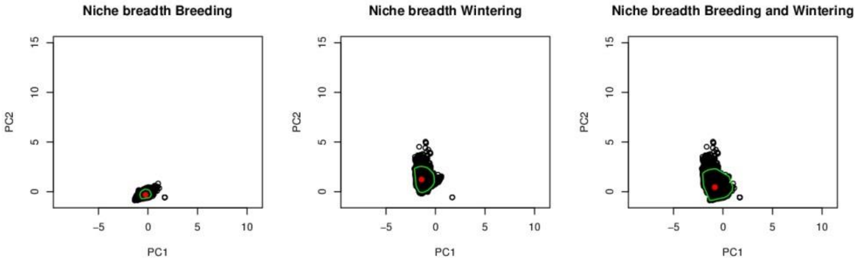
iv. <u>*Acrocephalus melanopogon*</u>



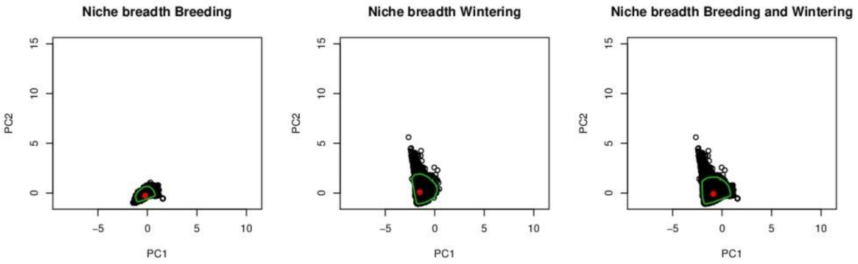
v. <u>*Acrocephalus paludicola*</u>



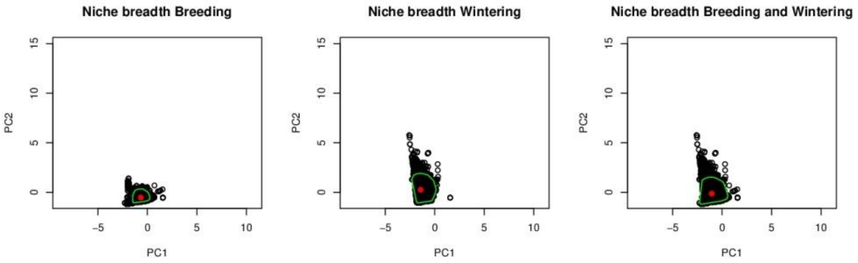
vi. <u>*Acrocephalus palustris*</u>



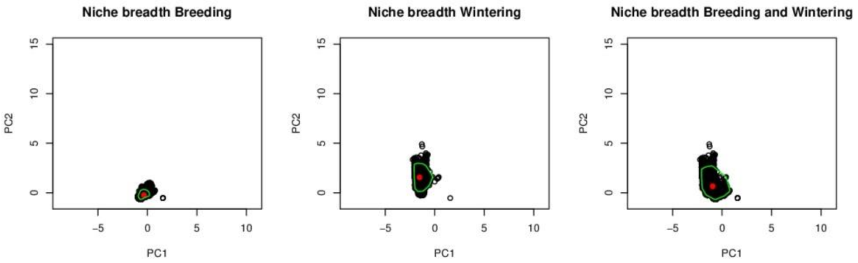
vii. *Acrocephalus schoenobaenus*



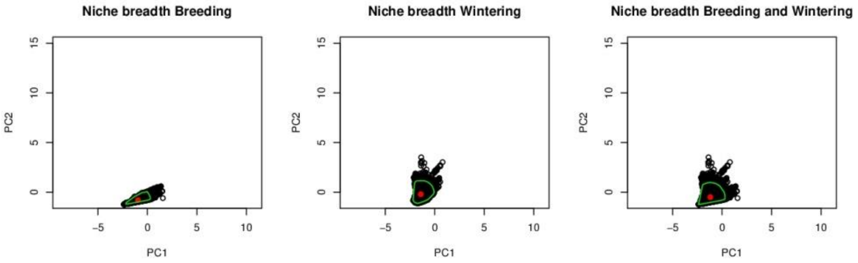
viii. *Acrocephalus scirpaceus*



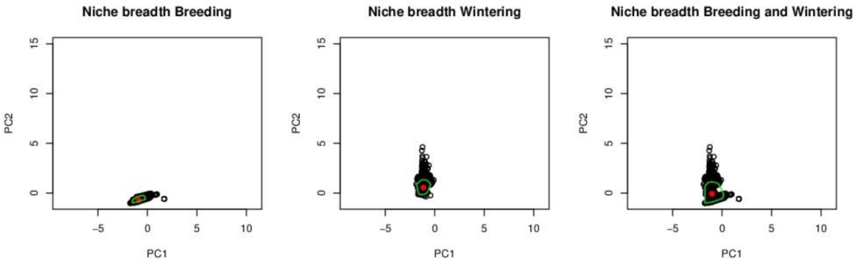
ix. *Hippolais icterina*



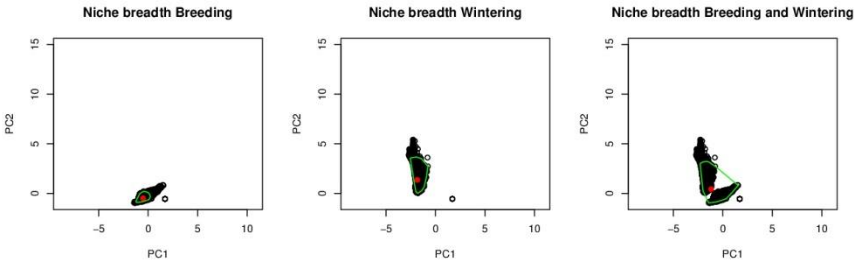
x. *Hippolais languida*



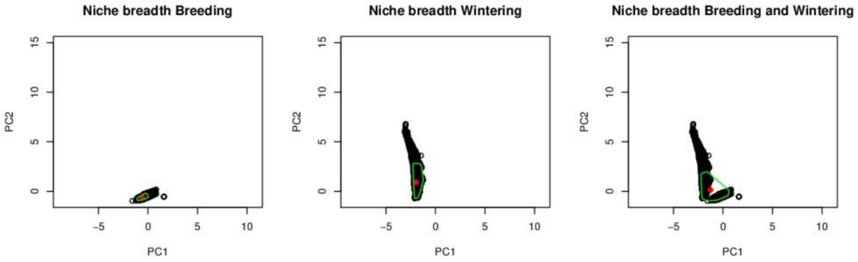
xi. *Hippolais olivetorum*



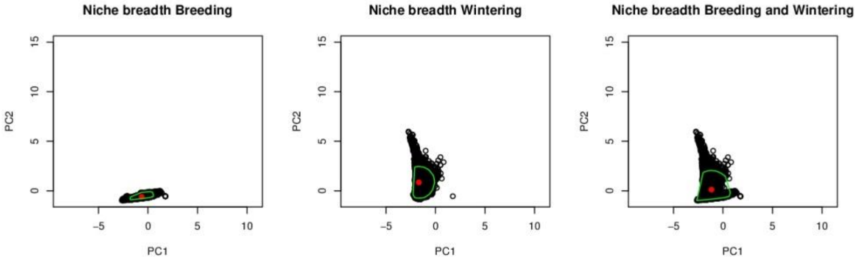
xii. *Hippolais polyglotta*



xiii. *Iduna opaca*

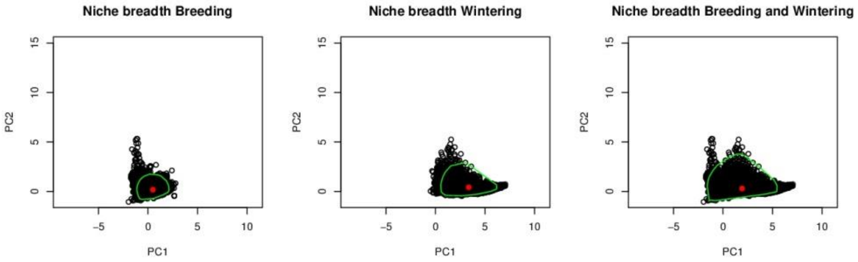


xiv. *Iduna pallida*



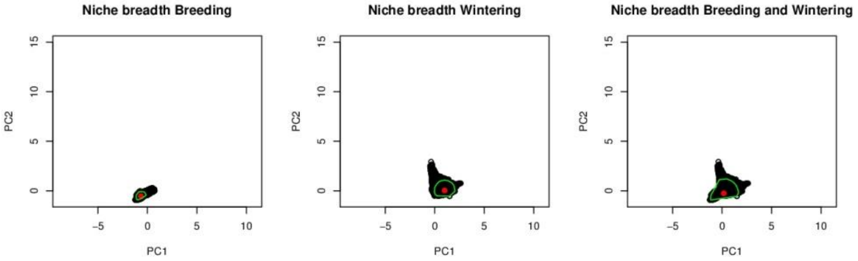
b. Aegithalidae

i. *Aegithalos caudatus*

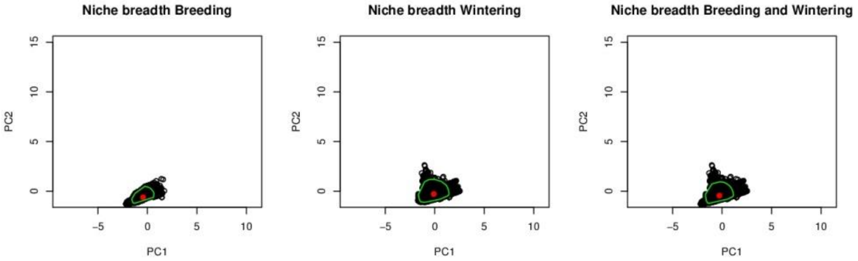


c. Alaudidae

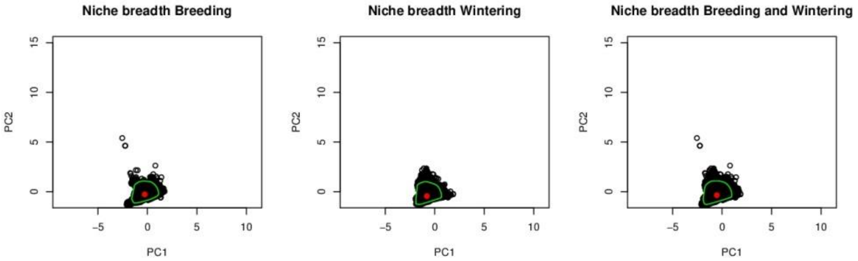
i. *Alauda leucoptera*



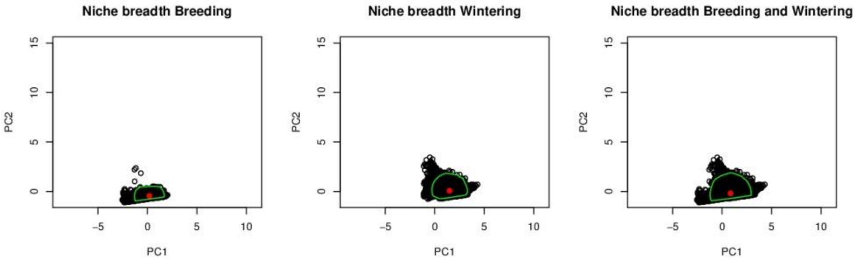
ii. *Alaudala rufescens*



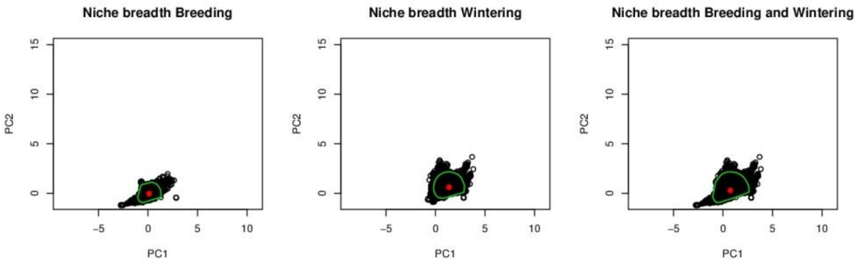
iii. *Calandrella brachydactyla*



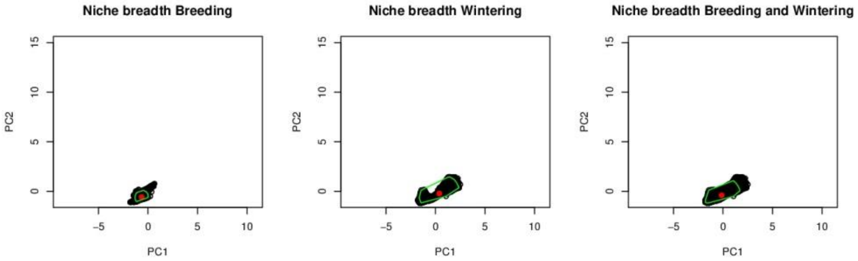
iv. *Eremophila alpestris*



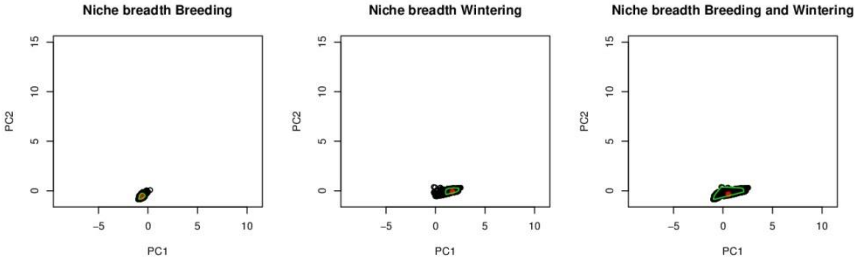
v. *Lullula arborea*



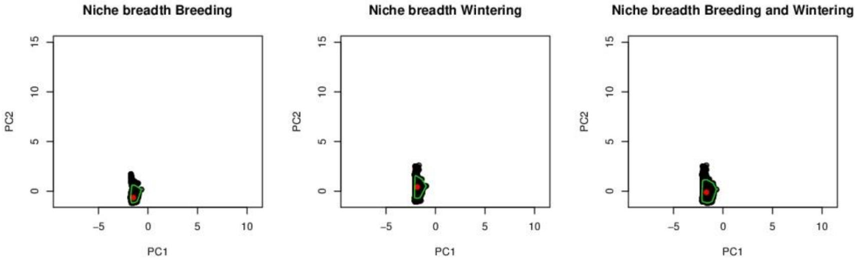
vi. *Melanocorypha bimaculata*



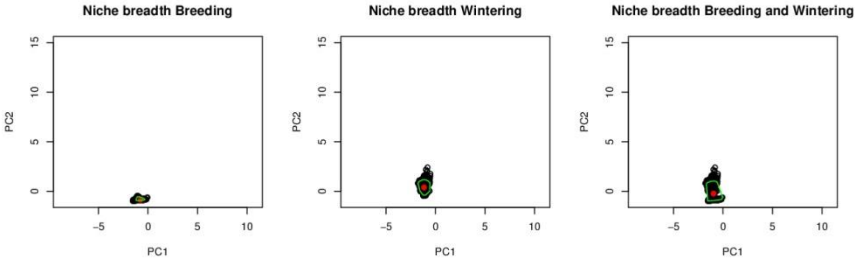
vii. *Melanocorypha yeltoniensis*



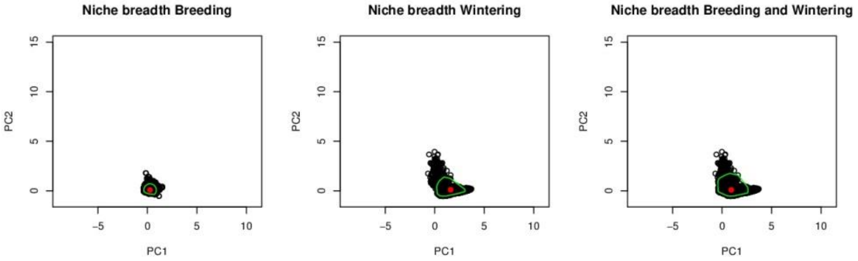
viii. *Pinarocorys erythropygia*



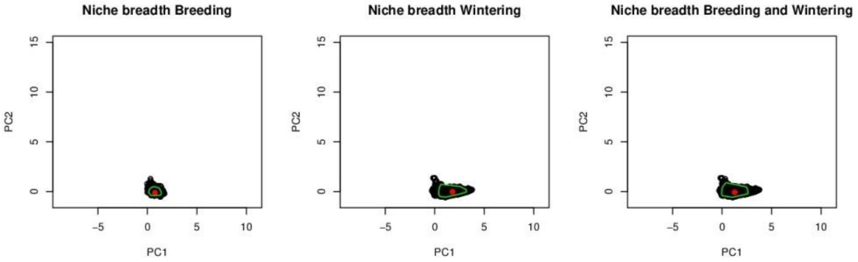
ix. *Pinarocorys nigricans*



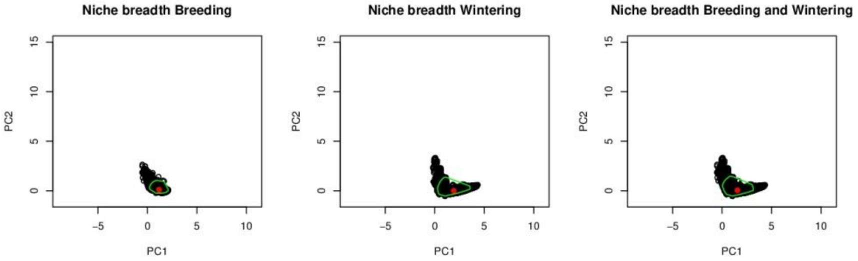
d. Bombycillidae
   i. *Bombycilla garrulus*



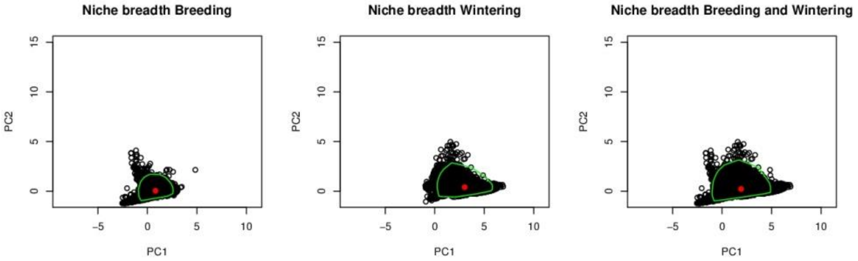
e. Calcariidae
   i. *Calcarius lapponicus*



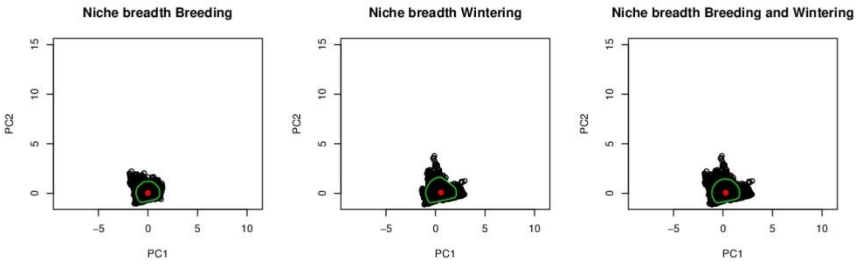
   ii. *Plectrophenax nivalis*



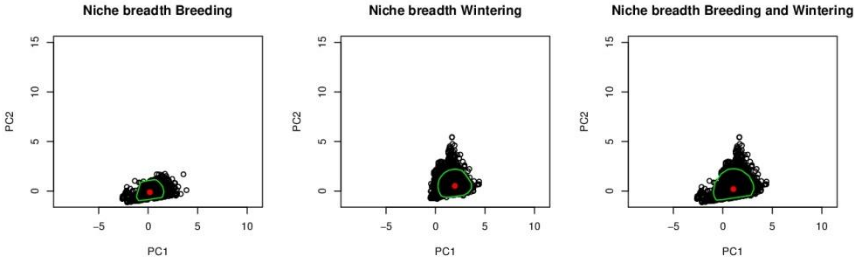
f. Corvidae
   i. *Corvus corone*



ii. *Corvus frugilegus*

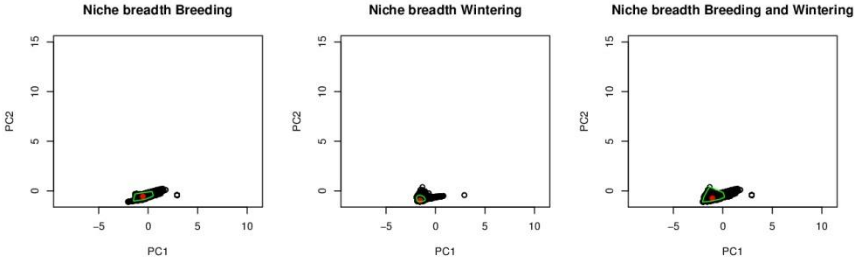


iii. *Corvus monedula*

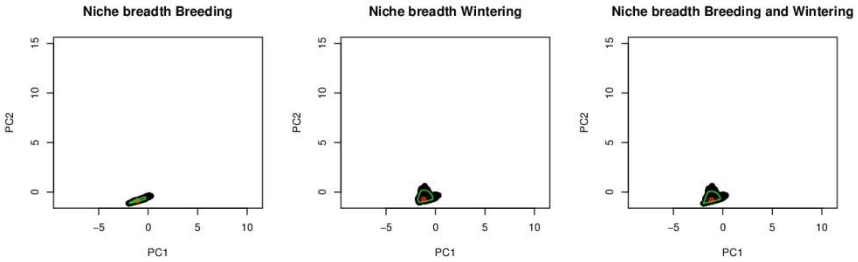


g. Emberizidae

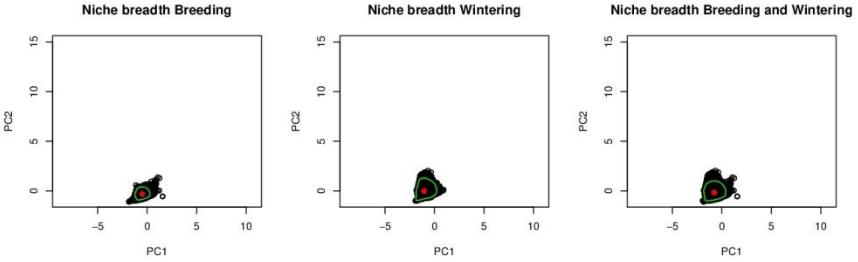
i. *Emberiza caesia*



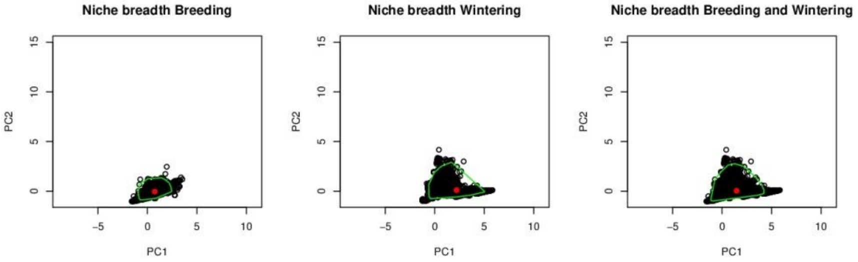
ii. *Emberiza cineracea*



iii. *Emberiza hortulana*

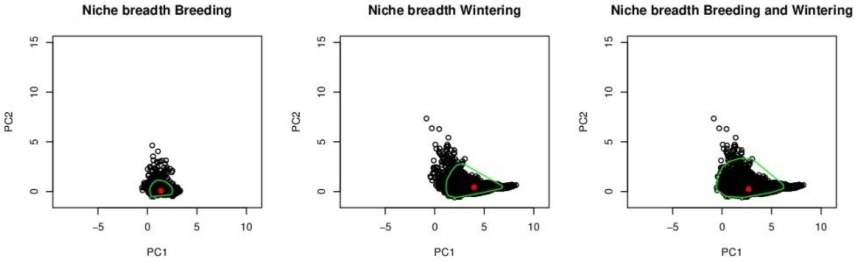


iv. *Emberiza schoeniclus*

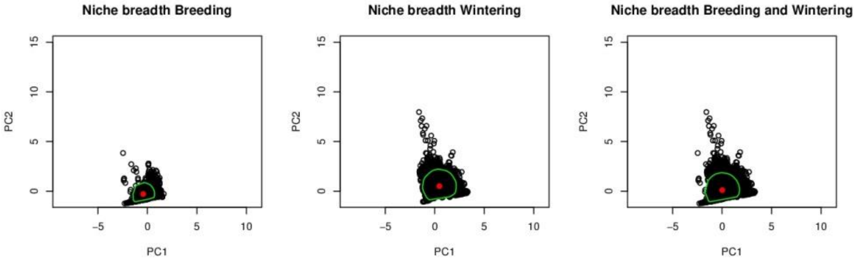


h. Fringillidae

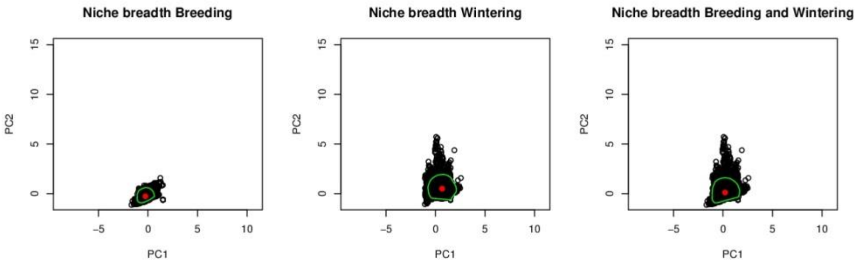
i. *Acanthis flammea*



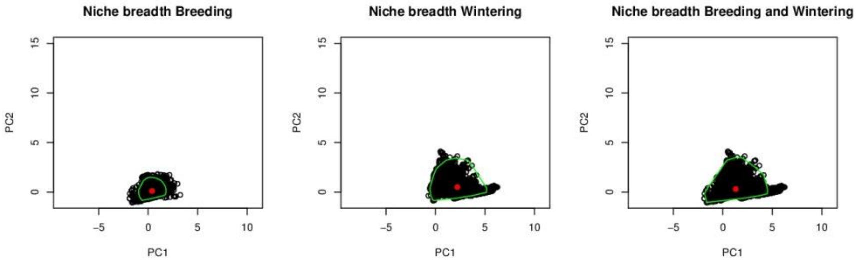
ii. *Carduelis carduelis*



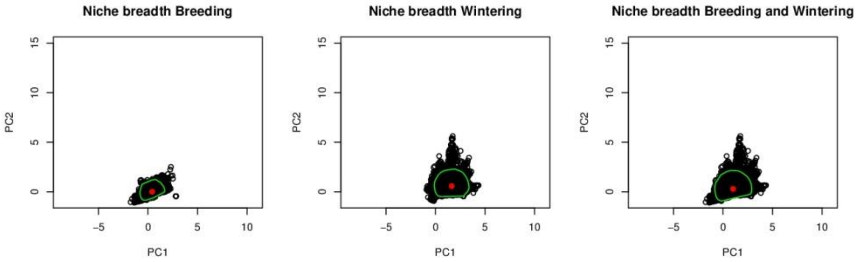
iii. *Chloris chloris*



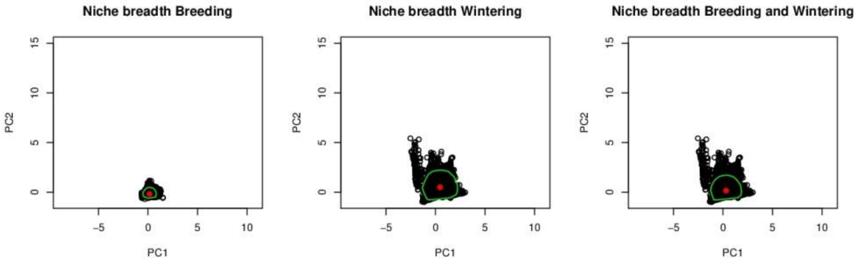
iv. *Coccothraustes coccothraustes*



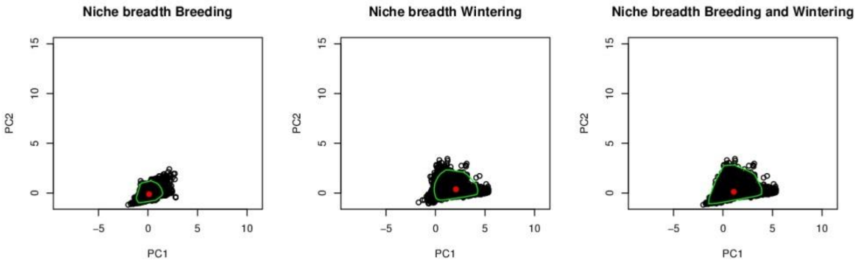
v. *Fringilla coelebs*



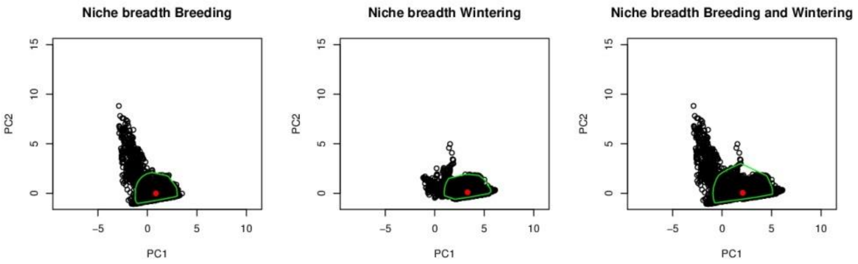
vi. *Fringilla montifringilla*



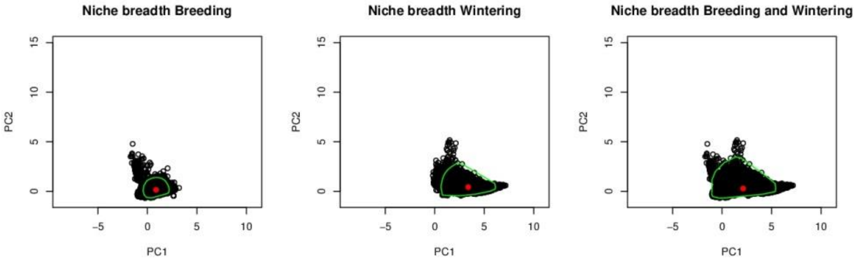
vii. *Linaria cannabina*



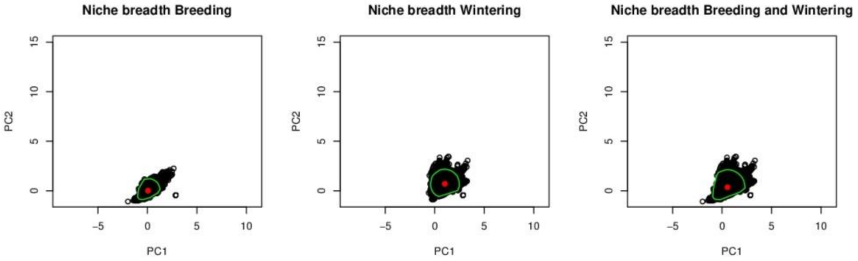
viii. *Linaria flavirostris*



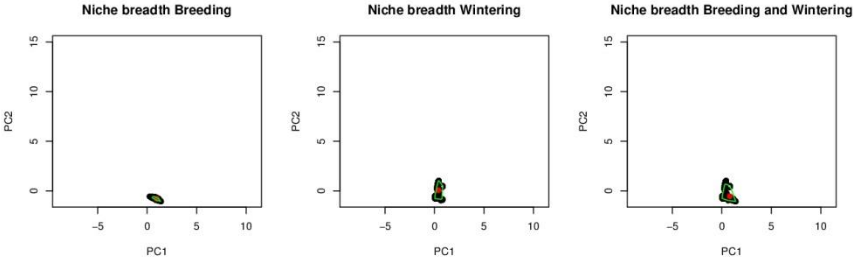
ix. *Pyrrhula pyrrhula*



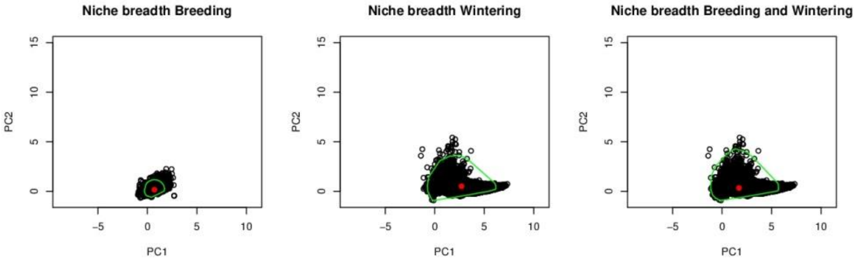
x. *Serinus serinus*



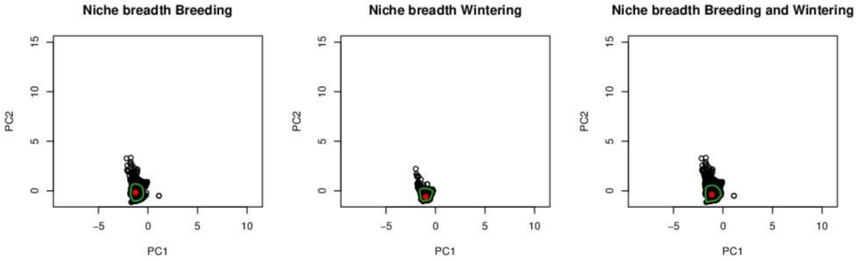
xi. *Serinus syriacus*



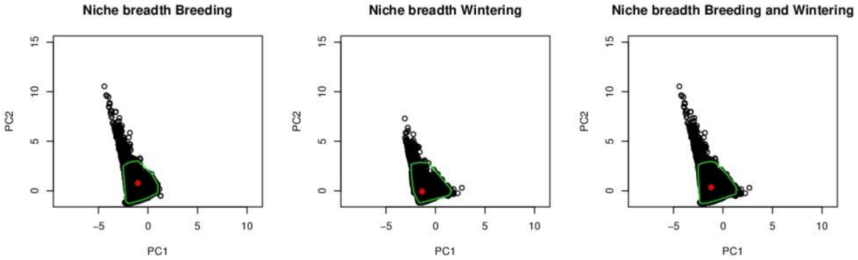
xii. *Spinus spinus*



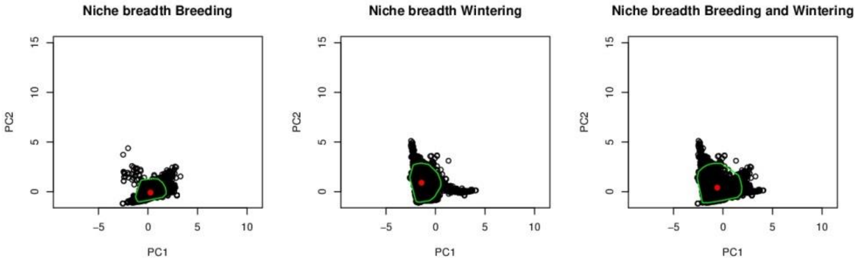
1. Hirundinidae
    1. *Cecropis cucullata*



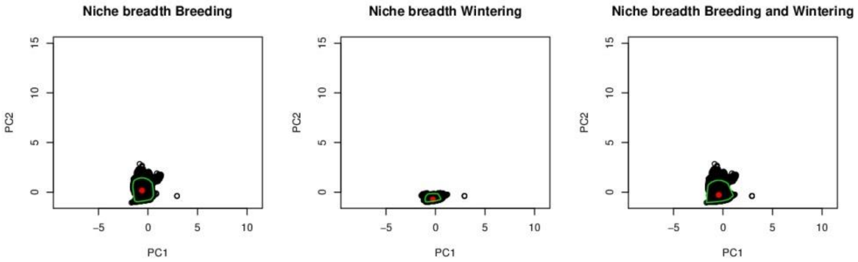
    2. *Cecropis daurica*



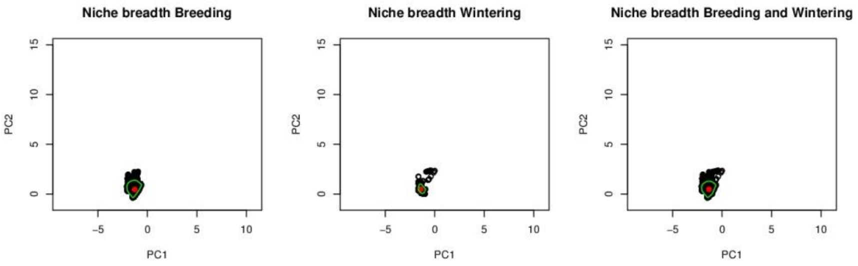
    3. *Delichon urbicum*



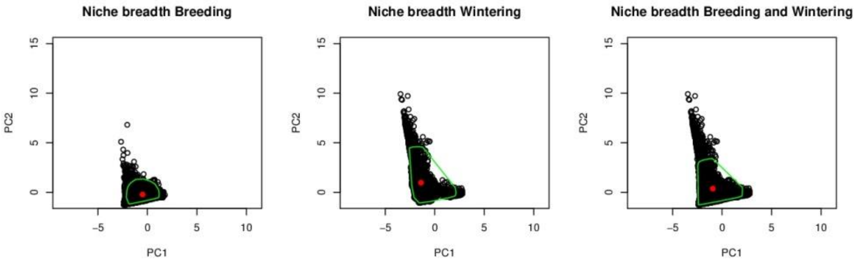
    4. *Hirundo albigularis*



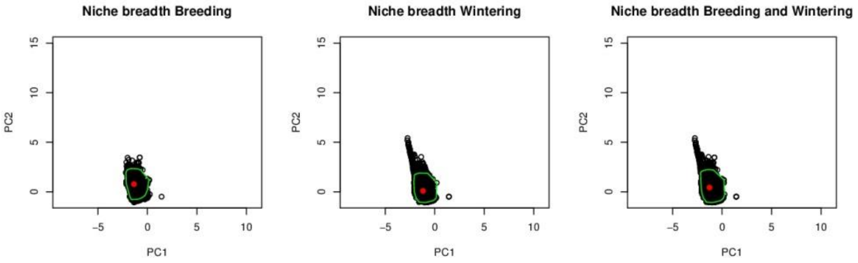
v. *Hirundo atrocaerulea*



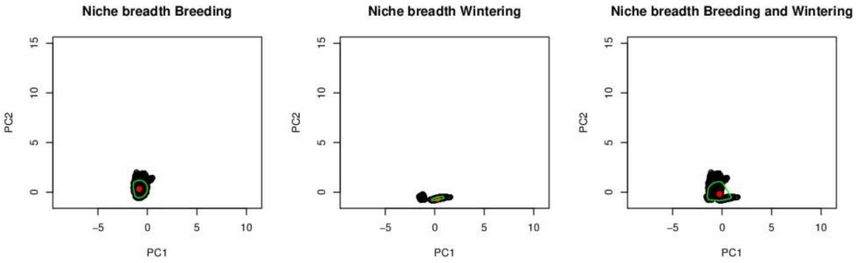
vi. *Hirundo rustica*



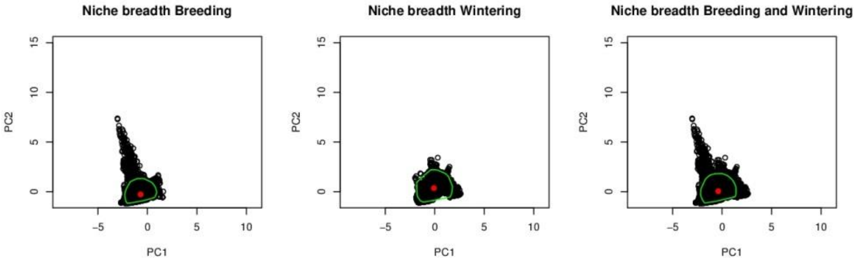
vii. *Neophedina cincta*



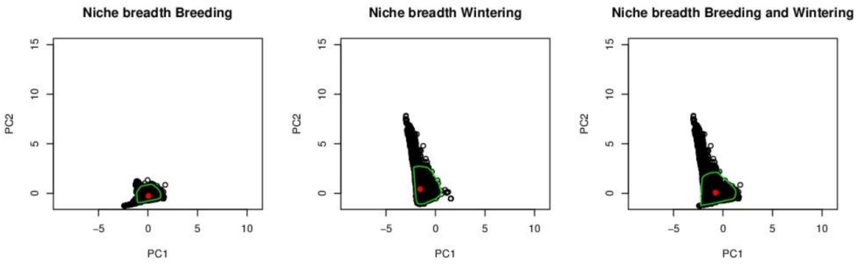
viii. *Petrochelidon spilodera*



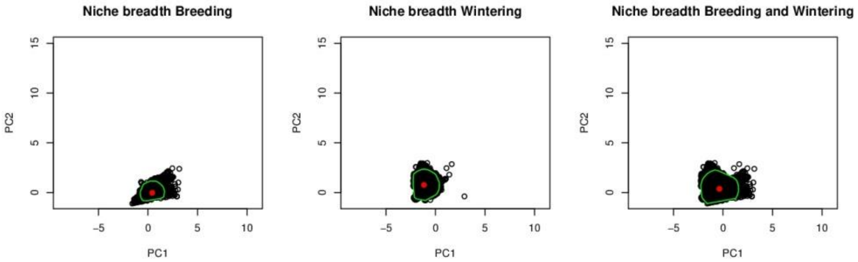
ix. *Ptyonoprogne rupestris*



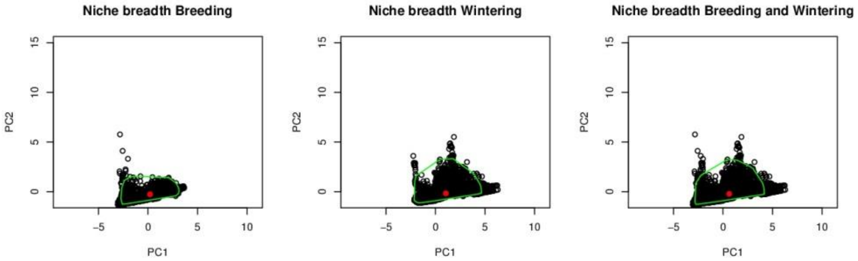
x. *Riparia riparia*



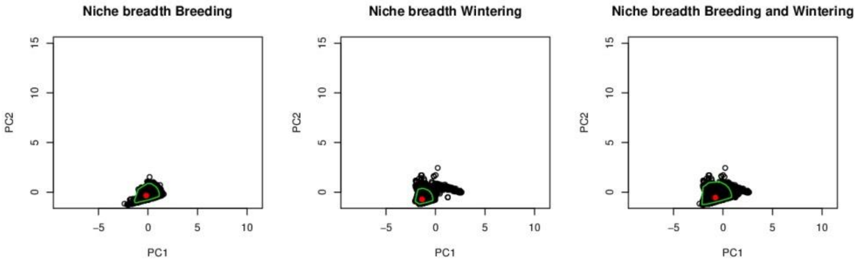
j. Laniidae
   i. *Lanius collurio*



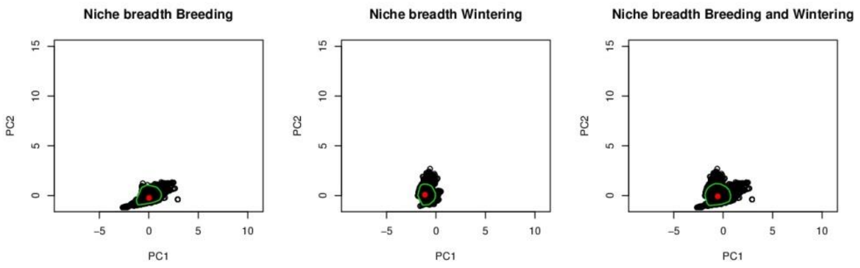
ii. *Lanius excubitor*



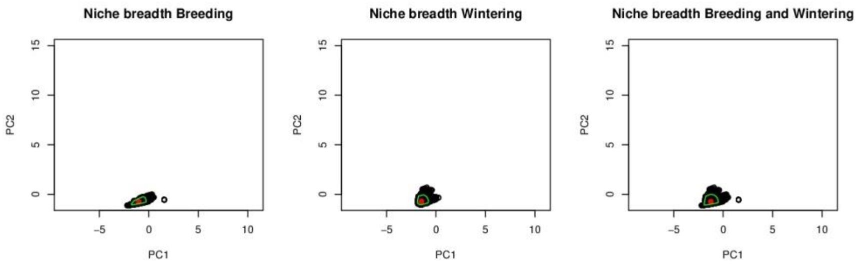
iii. *Lanius isabellinus*



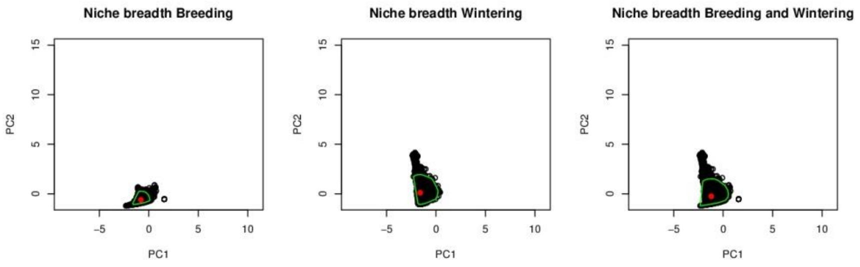
iv. *Lanius minor*



v. *Lanius nubicus*

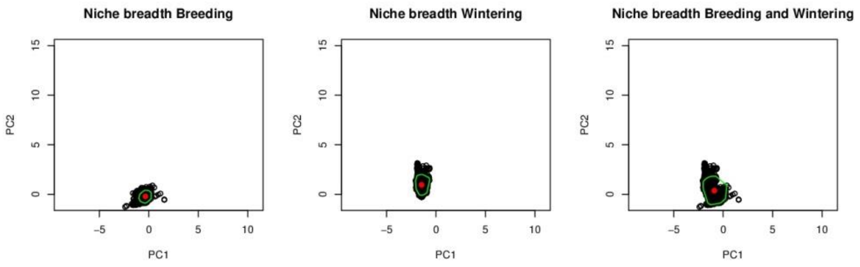


vi. *Lanius senator*

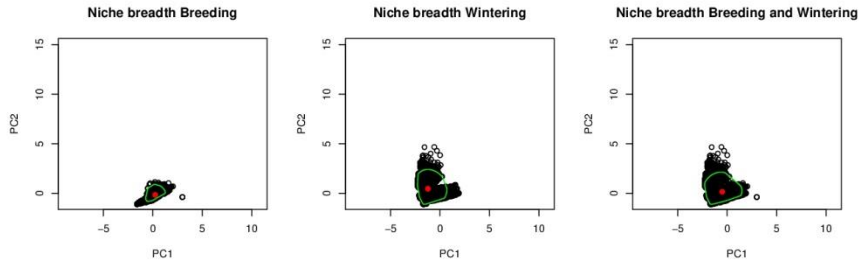


k. Locustellidae

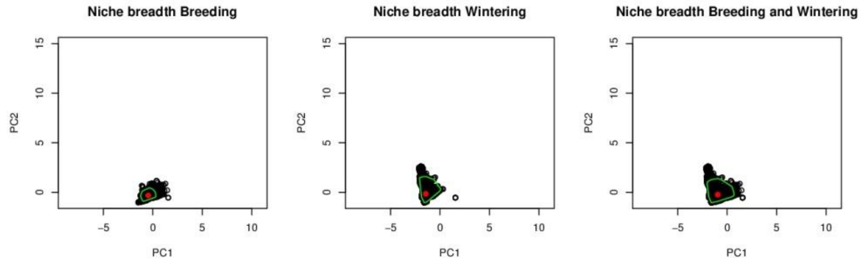
i. *Locustella fluviatilis*



ii. *Locustella luscinioides*

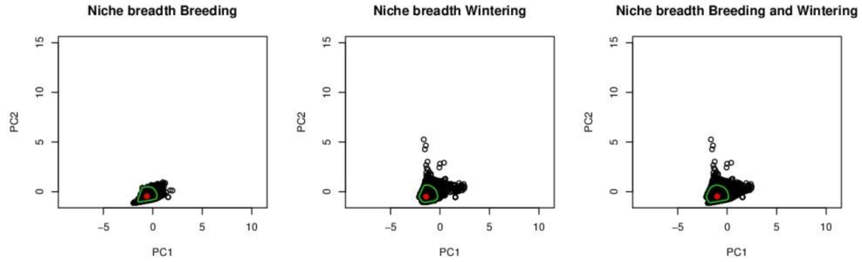


iii. *Locustella naevia*

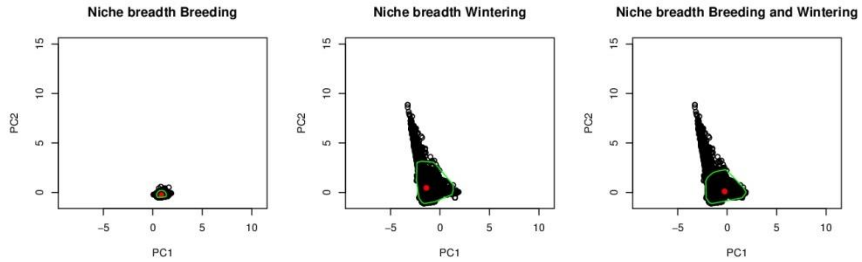


l. Motacillidae

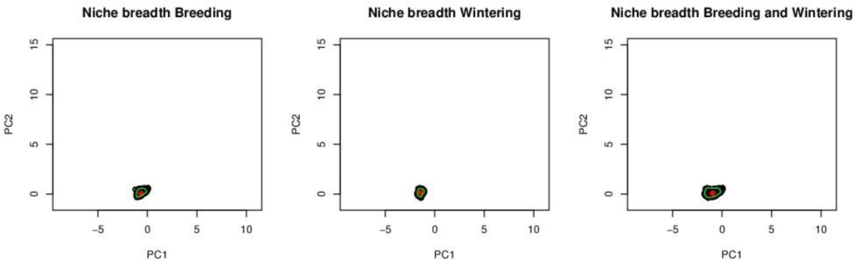
i. *Anthus campestris*



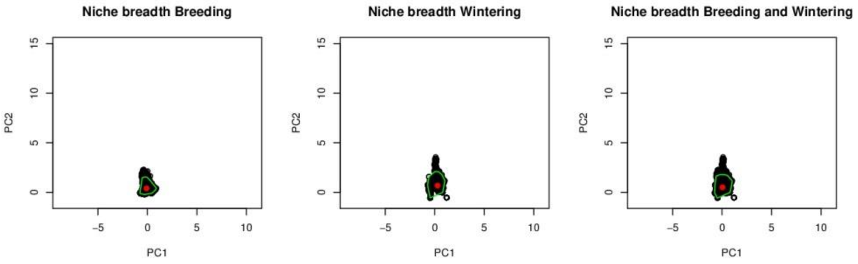
ii. *Anthus cervinus*



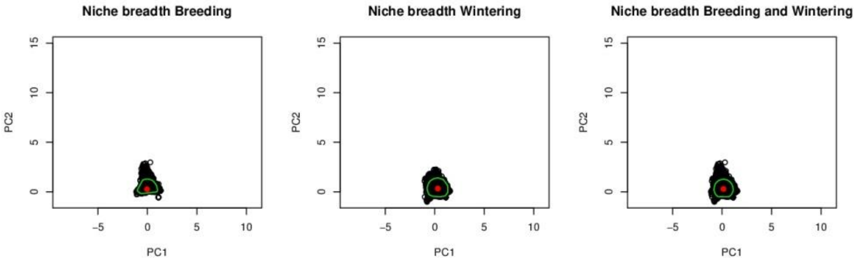
iii. *Anthus hoeschi*



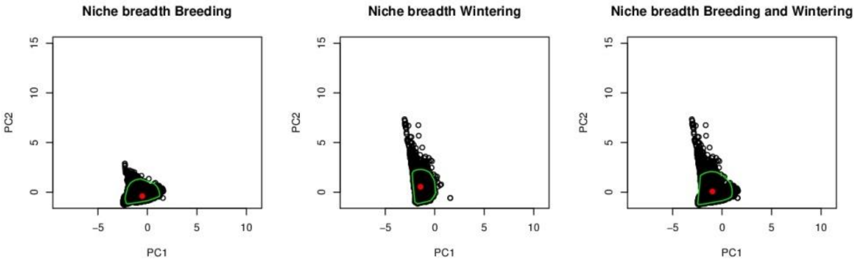
iv. *Anthus petrosus*



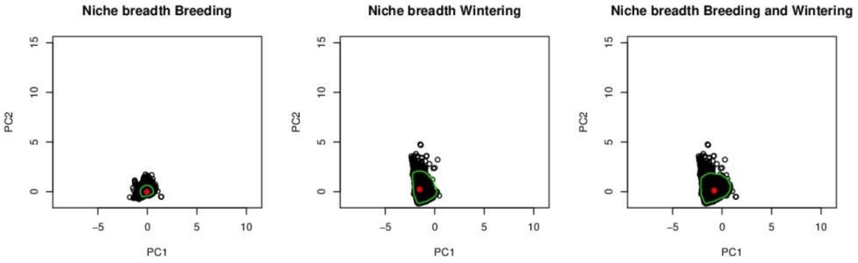
v. *Anthus pratensis*



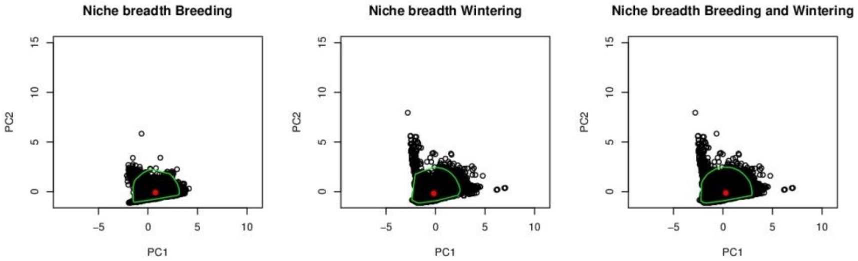
vi. *Anthus richardi*



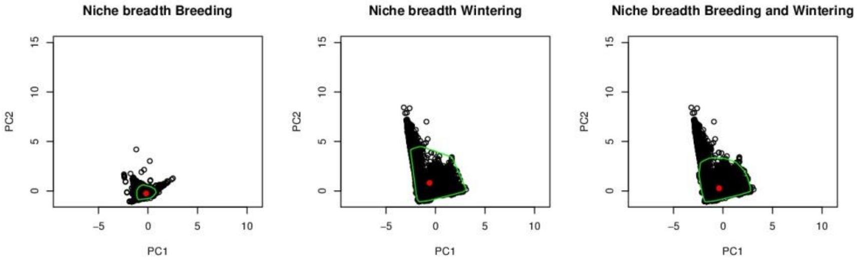
vii. *Anthus trivialis*



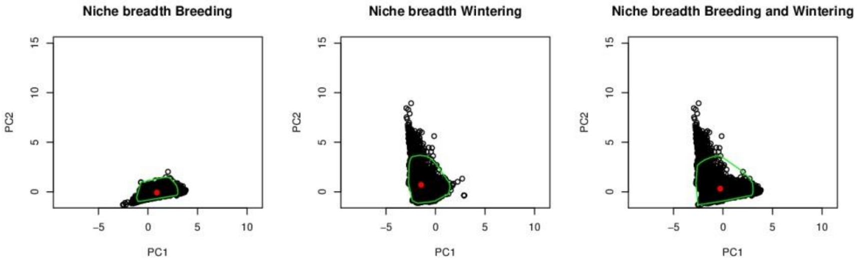
viii. *Motacilla alba*



ix. *Motacilla cinerea*

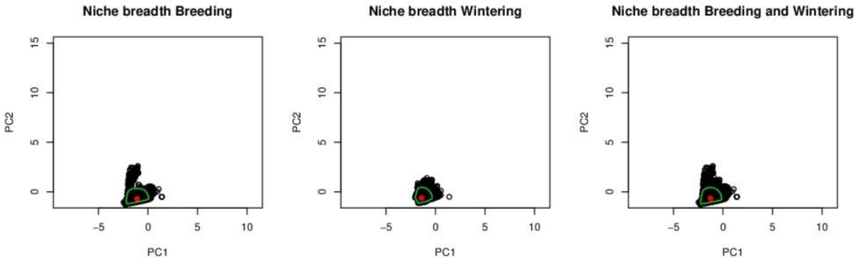


x. *Motacilla flava*

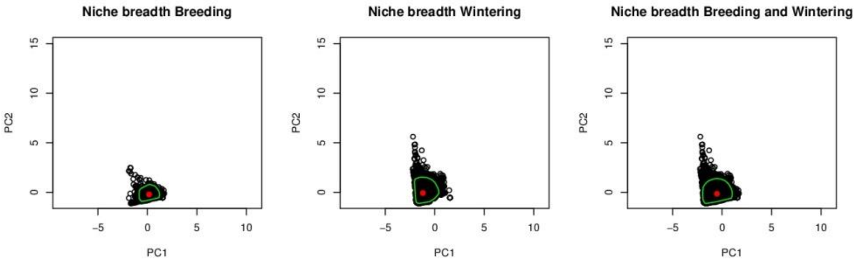


m. Muscicapidae

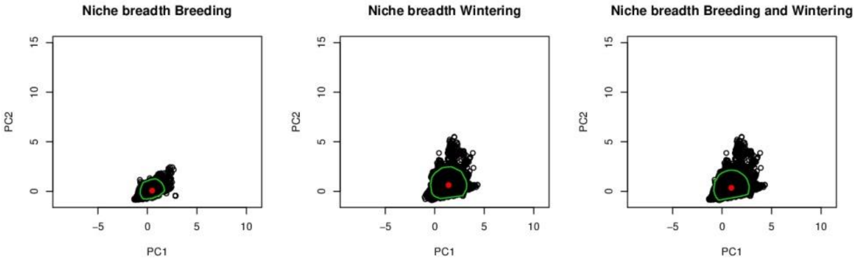
i. *Cercotrichas galactotes*



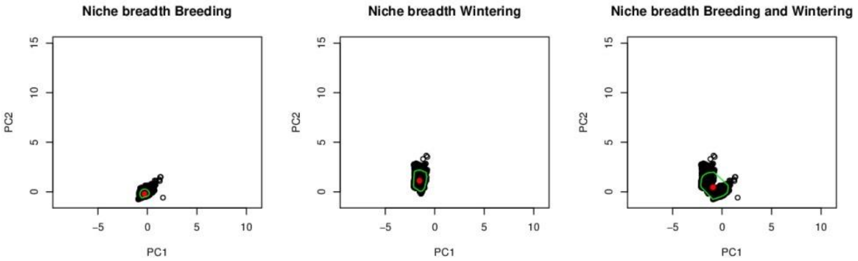
ii. *Cyanecula svecica*



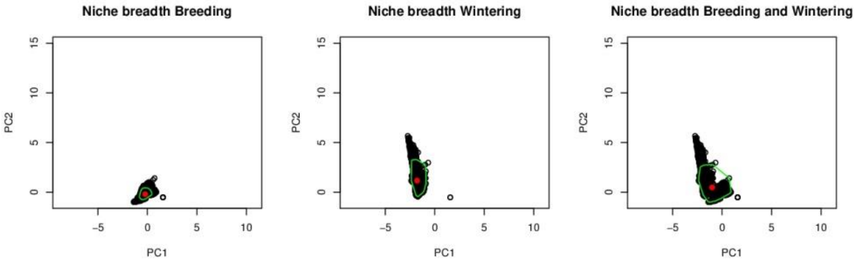
iii. *Erithacus rubecula*



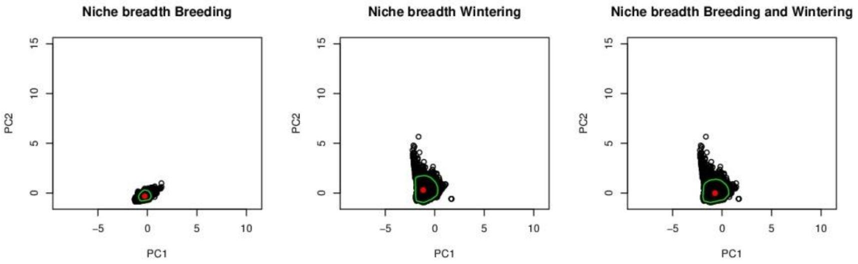
iv. *Ficedula albicollis*



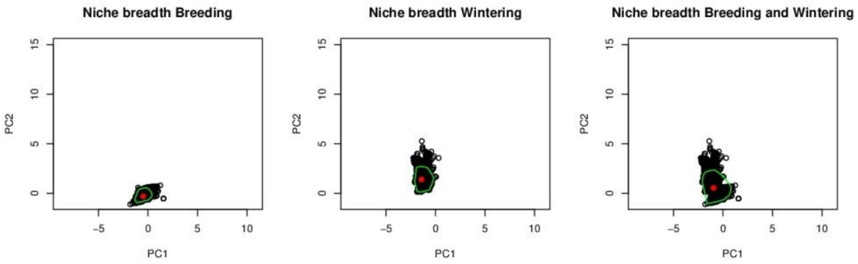
v. *Ficedula hypoleuca*



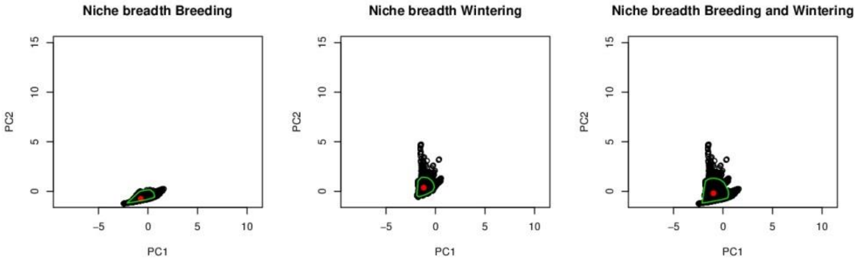
vi. *Ficedula parva*



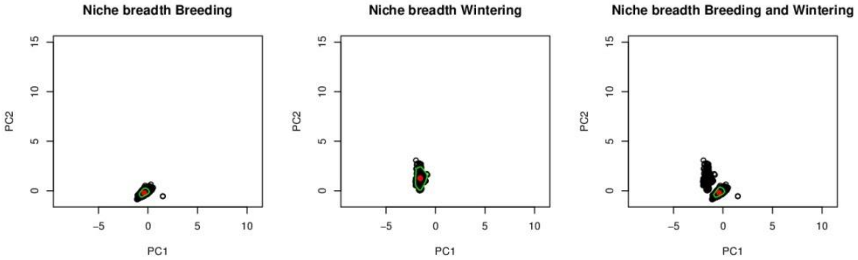
vii. *Ficedula semitorquata*



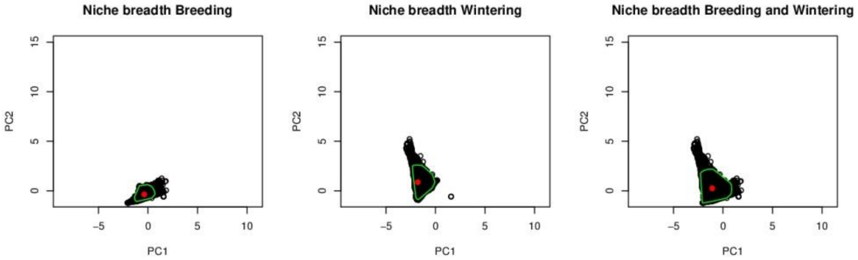
viii. *Irania gutturalis*



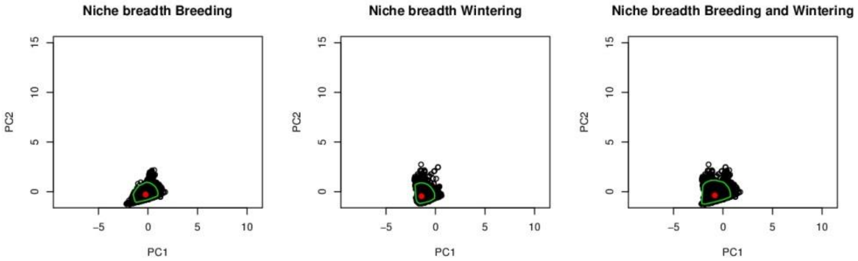
ix. *Luscinia luscinia*



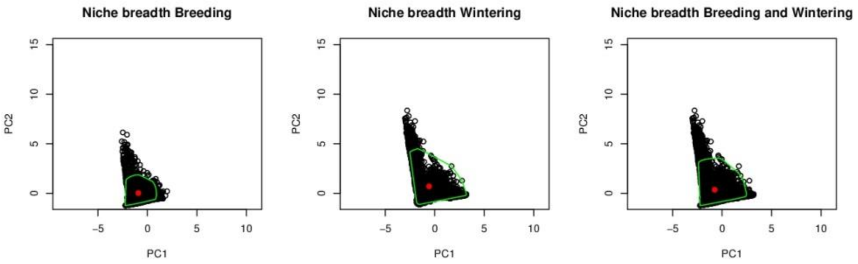
x. *Luscinia megarhynchos*



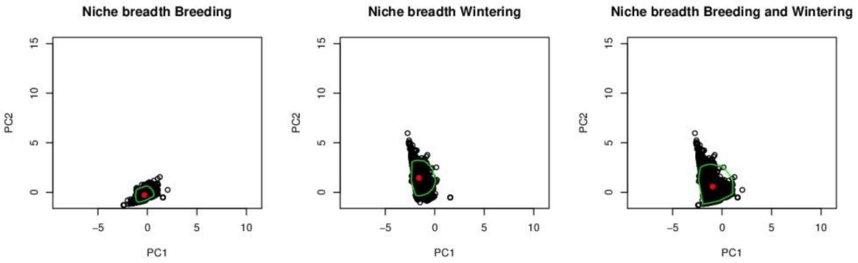
xi. *Monticola saxatilis*



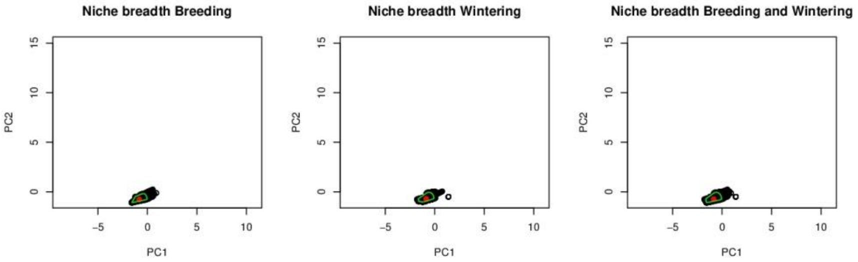
xii. *Monticola solitarius*



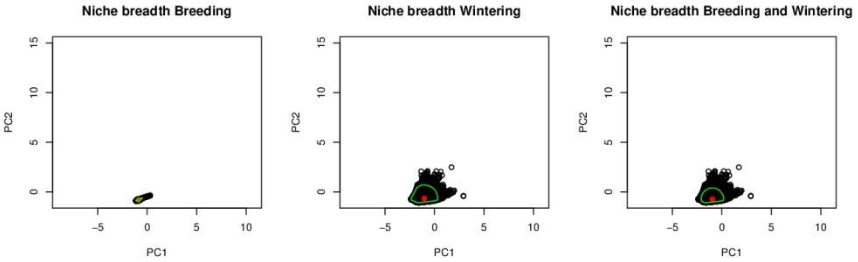
xiii. *Muscicapa striata*



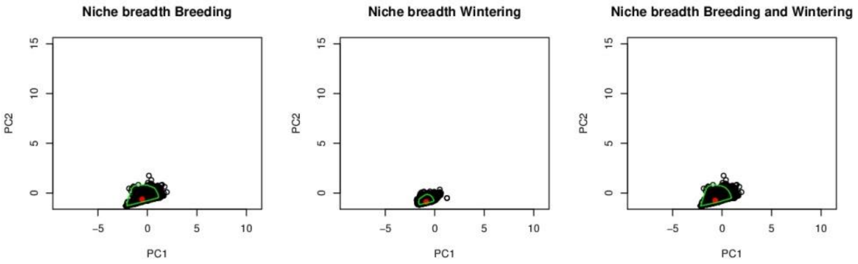
xiv. *Oenanthe chrysopygia*



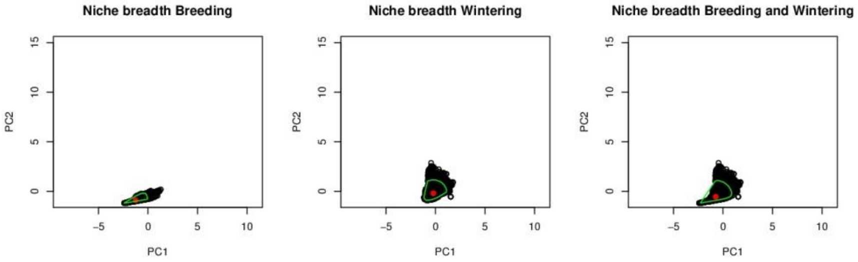
xv. *Oenanthe cypriaca*



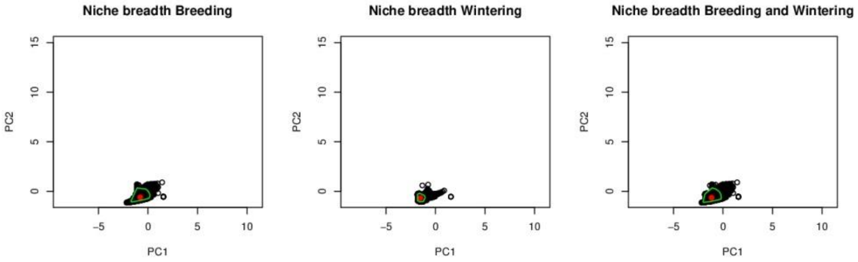
xvi. *Oenanthe deserti*



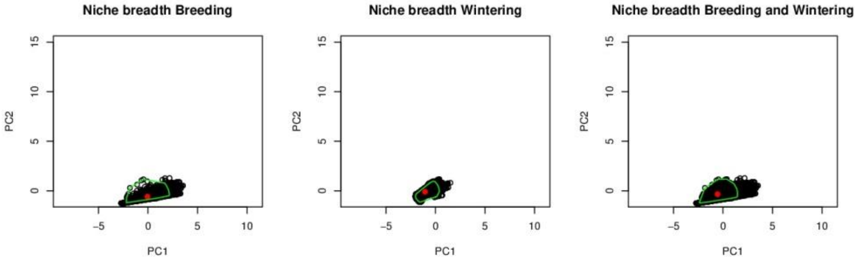
xvii. *Oenanthe finschii*



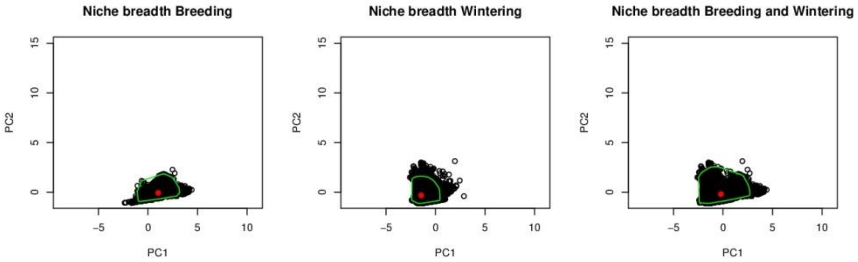
xviii. *Oenanthe hispanica*



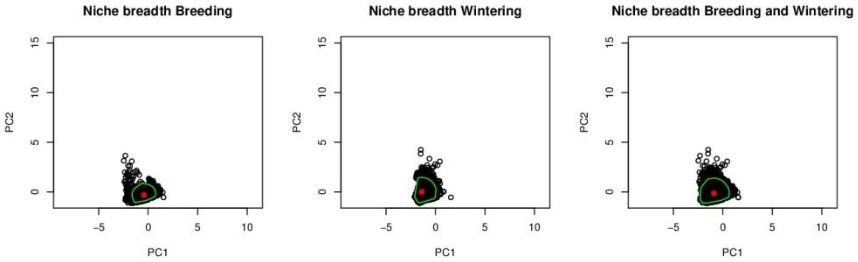
xix. *Oenanthe isabellina*



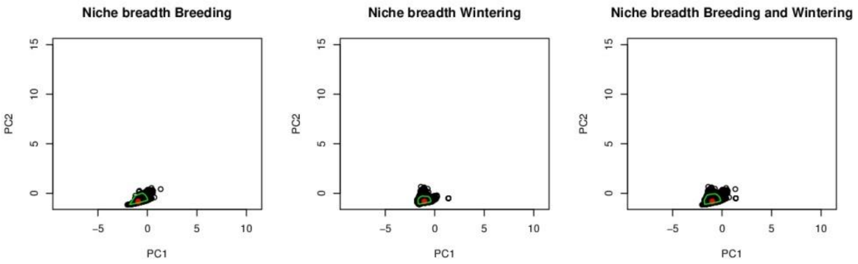
xx. *Oenanthe oenanthe*



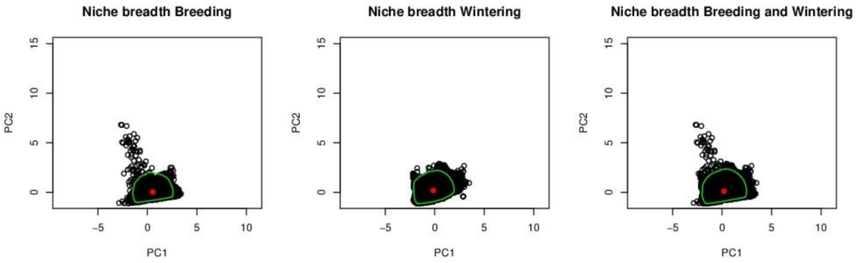
xxi. *Oenanthe pleschanka*



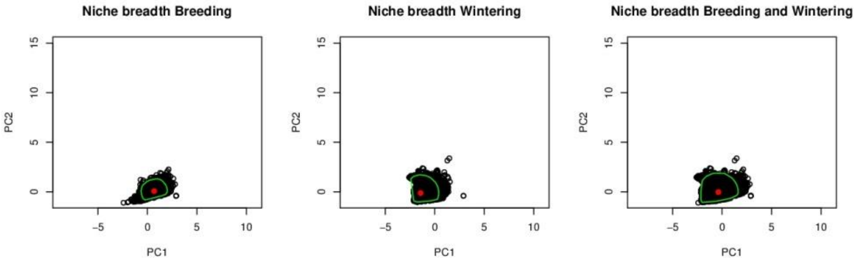
xxii. *Oenanthe xanthoprymna*



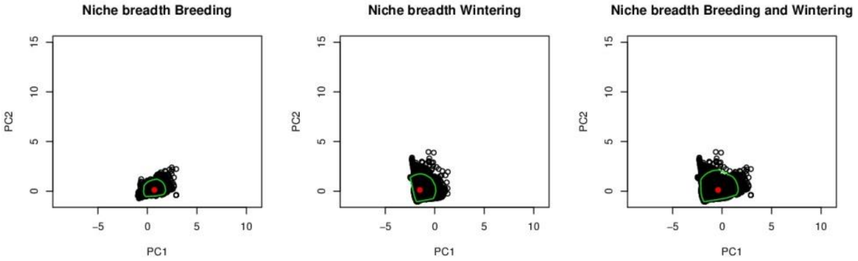
xxiii. *Phoenicurus ochruros*



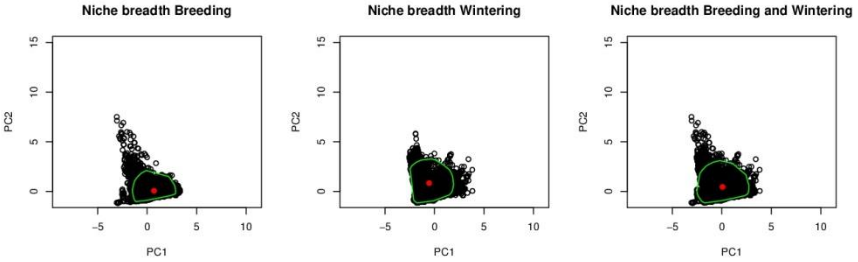
xxiv. *Phoenicurus phoenicurus*



xxv. *Saxicola rubetra*

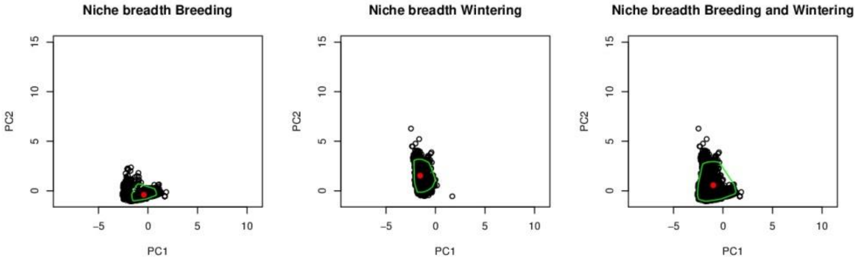


xxvi. *Saxicola torquatus*



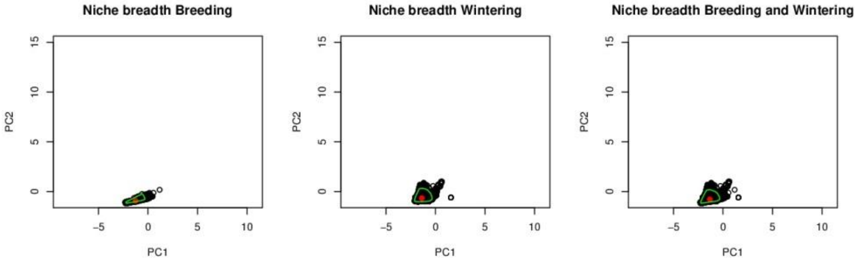
n. Oriolidae

i. *Oriolus oriolus*

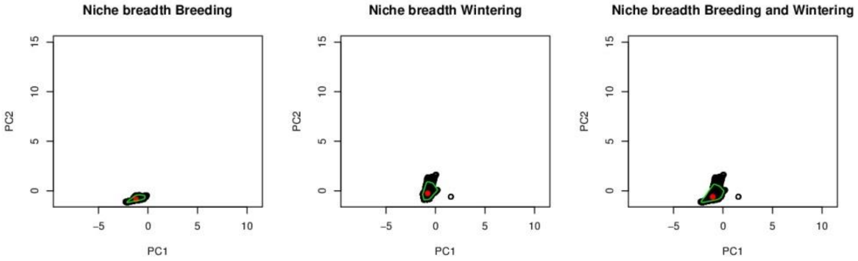


o. Passeridae

i. *Carpospiza brachydactyla*

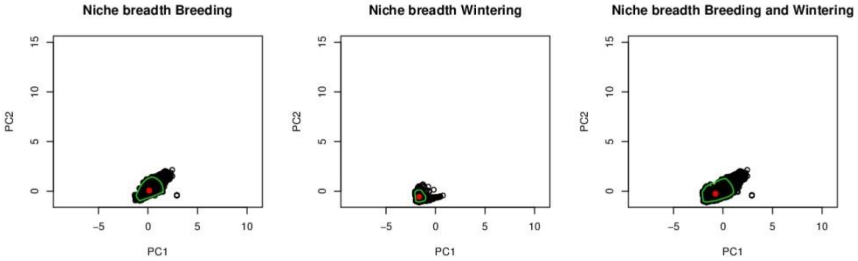


ii. *Passer moabiticus*

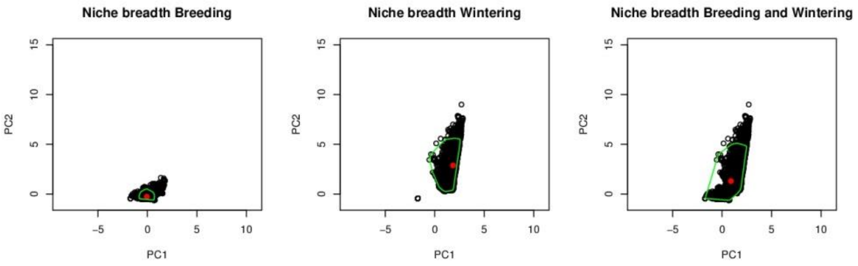


p. Phylloscopidae

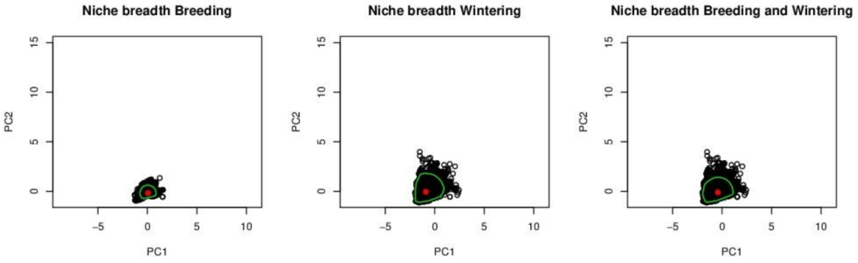
i. *Phylloscopus bonelli*



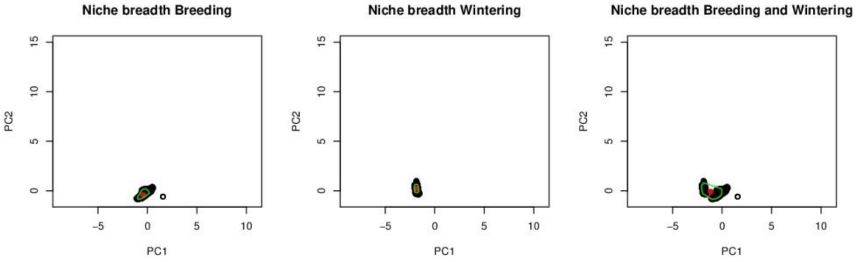
ii. *Phylloscopus borealis*



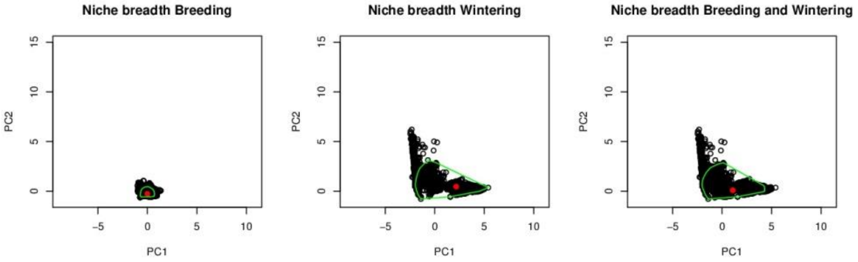
iii. *Phylloscopus collybita*



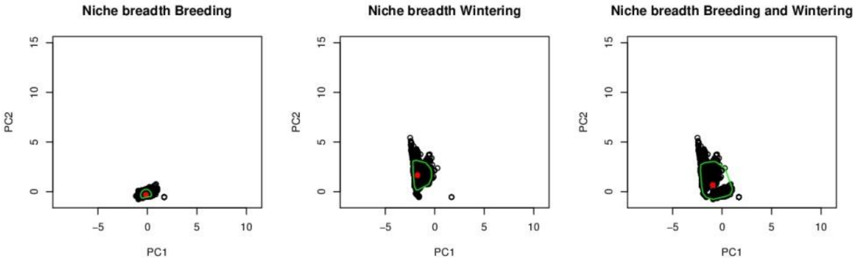
iv. *Phylloscopus ibericus*



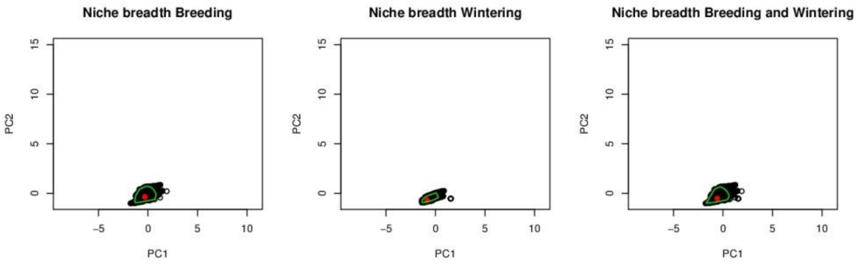
v. *Phylloscopus inonartus*



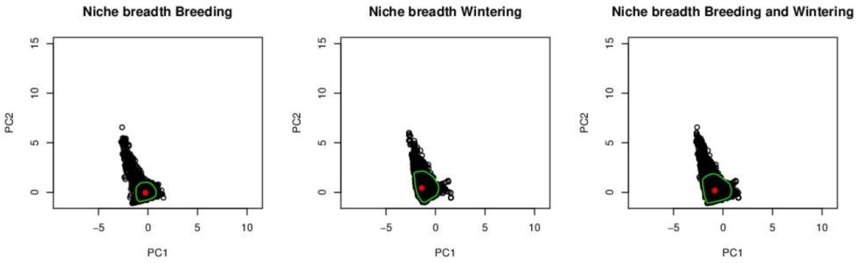
vi. *Phylloscopus sibilatrix*



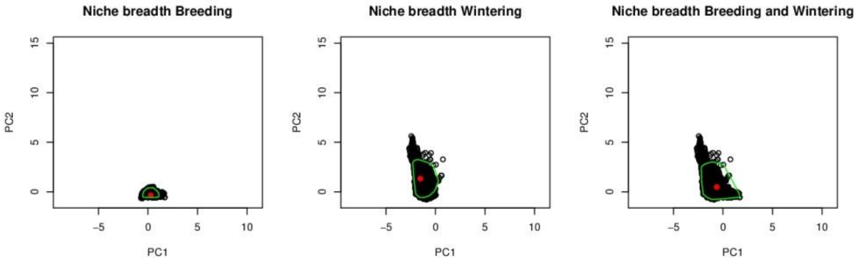
vii. *Phylloscopus sindianus*



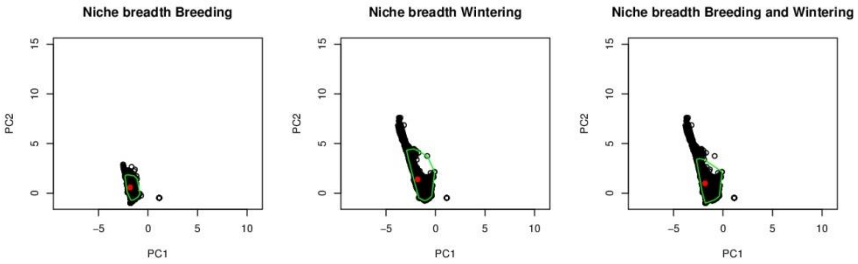
viii. *Phylloscopus trochiloides*



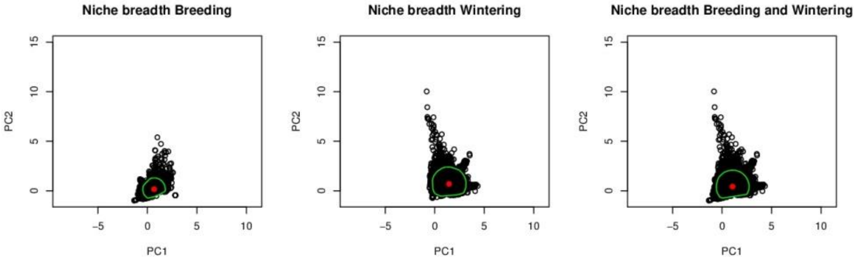
ix. *Phylloscopus trochilus*



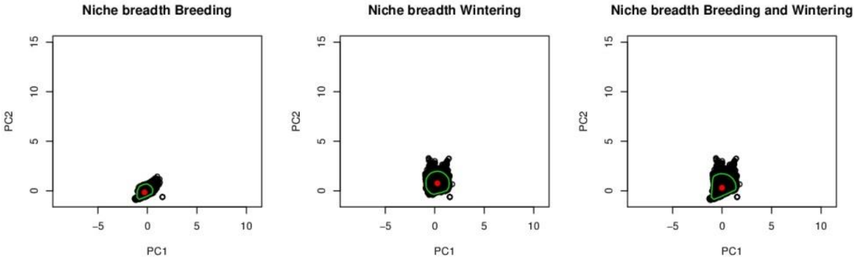
q. Pittidae
   i. *Pitta angolensis*



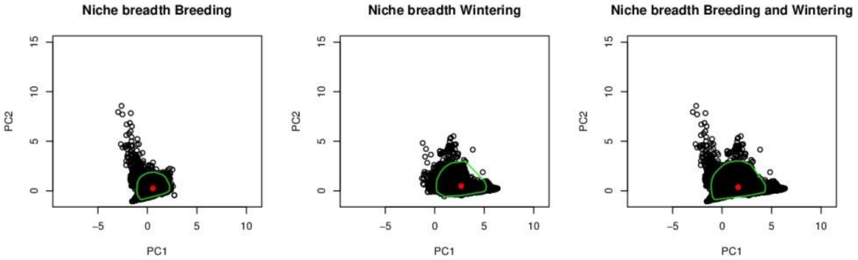
r. Prunellidae
   i. *Prunella modularis*



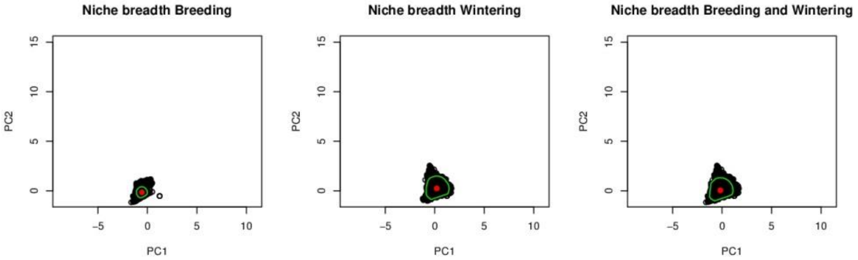
s. Regulidae
   i. *Regulus ignicapilla*



   ii. *Regulus regulus*

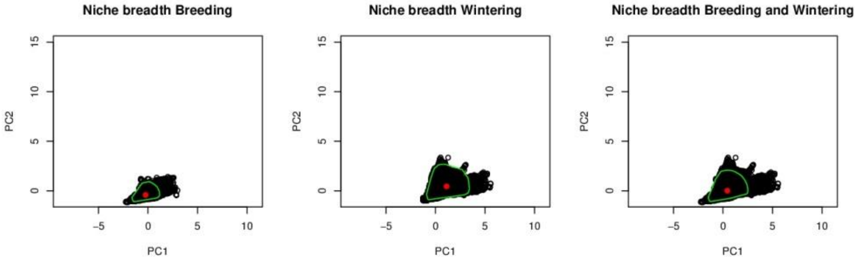


t. Remizidae
   i. *Remiz pendulinus*



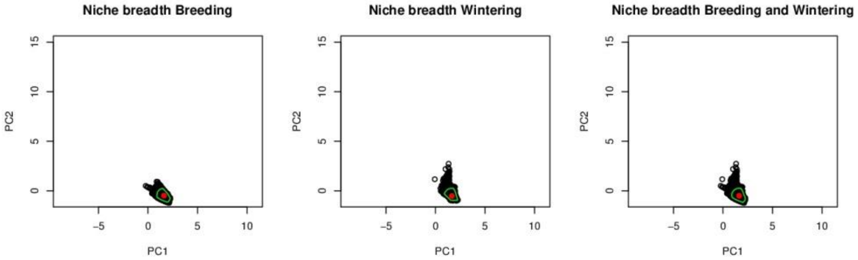
u. Scotocercidae

i. *Cettia cetti*

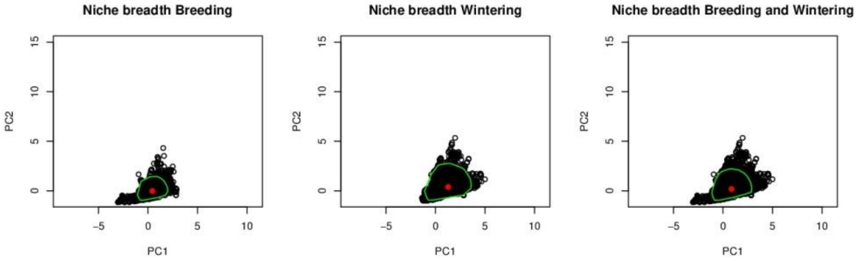


v. Sturnidae

i. *Lamprotornis shelleyi*

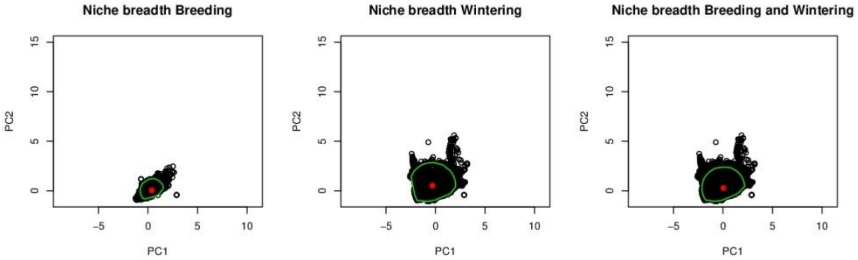


ii. *Sturnus vulgaris*

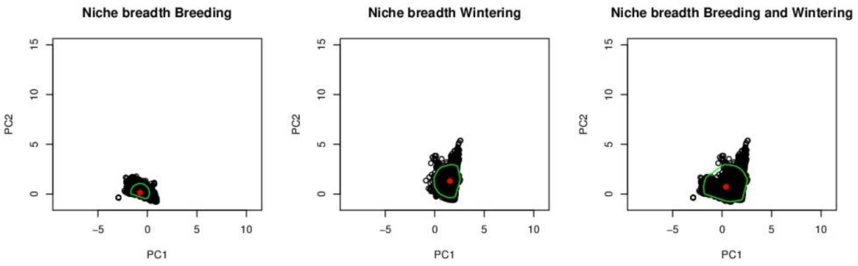


w. Sylviidae

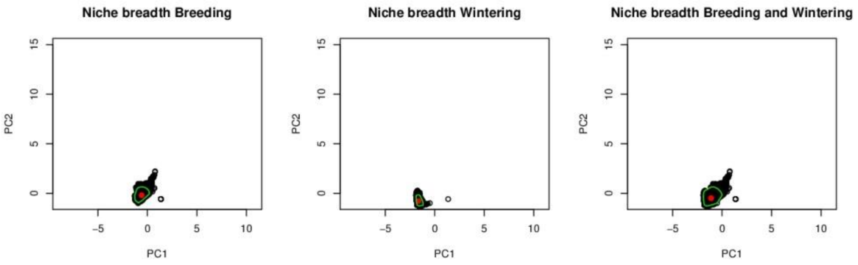
i. *Sylvia atricapilla*



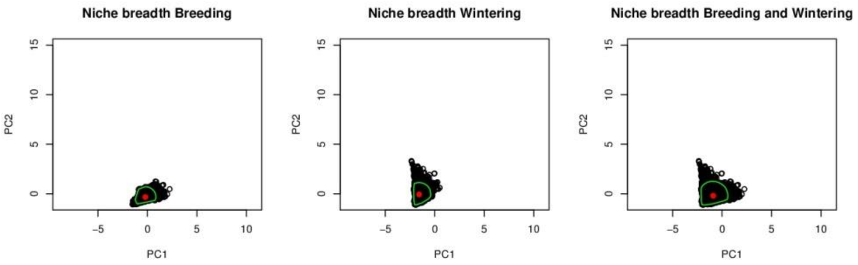
ii. *Sylvia borin*



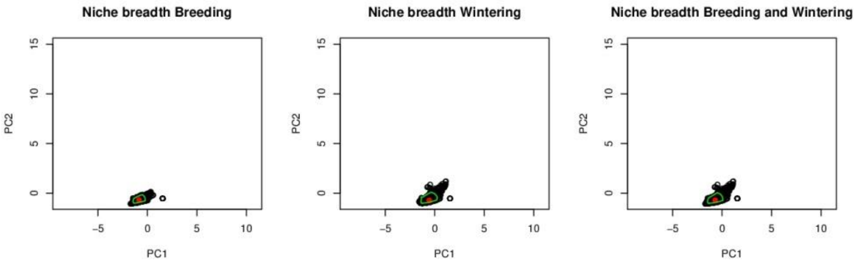
iii. *Sylvia cantillans*



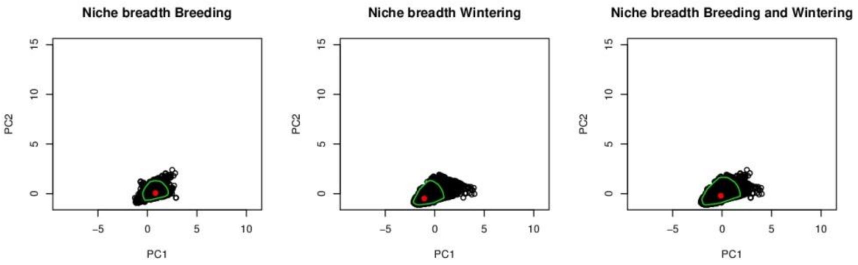
iv. *Sylvia communis*



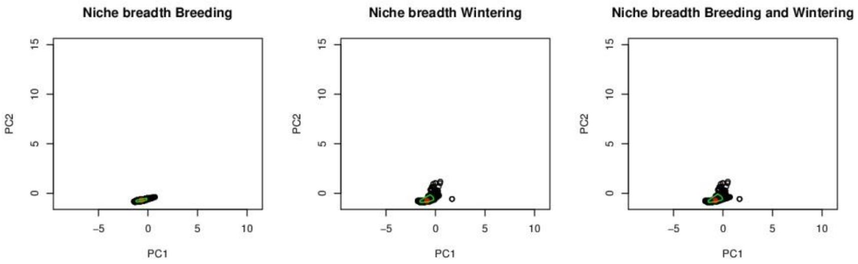
v. *Sylvia conspicillata*



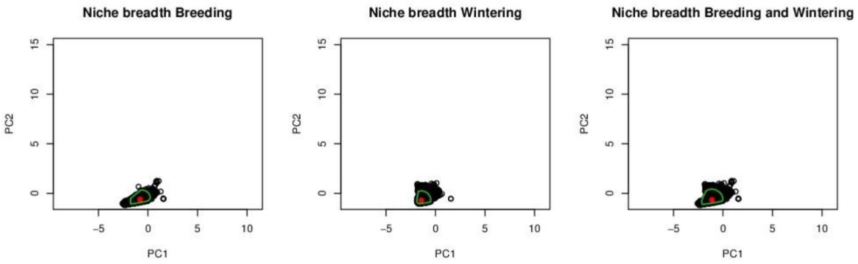
vi. *Sylvia curruca*



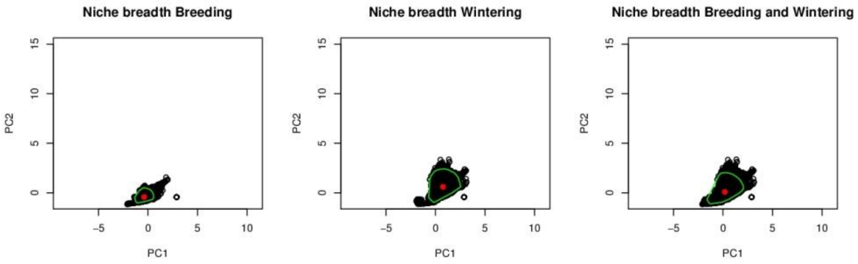
vii. *Sylvia deserticola*



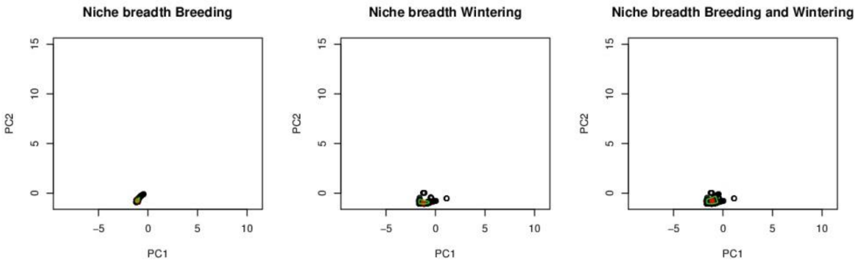
viii. *Sylvia hortensis*



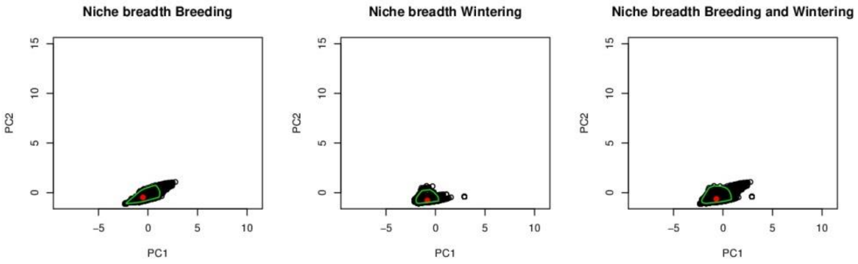
ix. *Sylvia melanocephala*



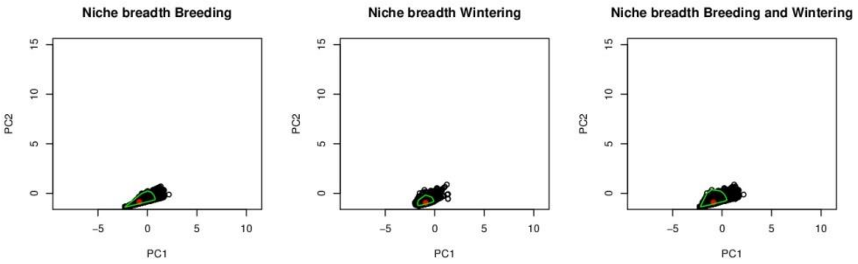
x. *Sylvia melanothorax*



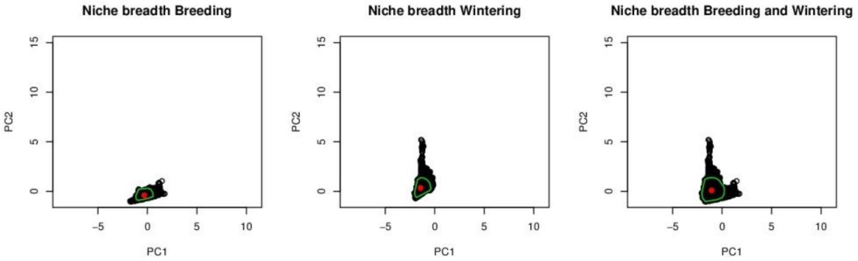
xi. *Sylvia mystacea*



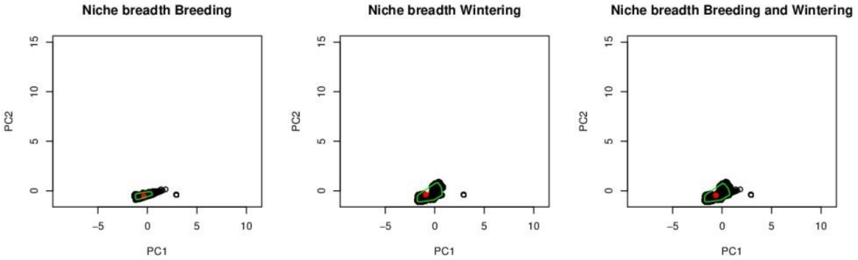
xii. *Sylvia nana*



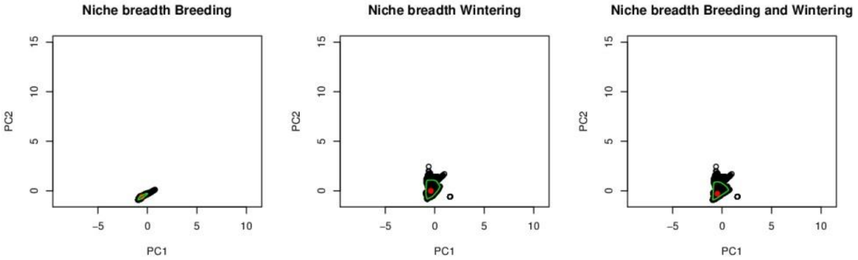
xiii. *Sylvia nisoria*



xiv. *Sylvia rueppeli*

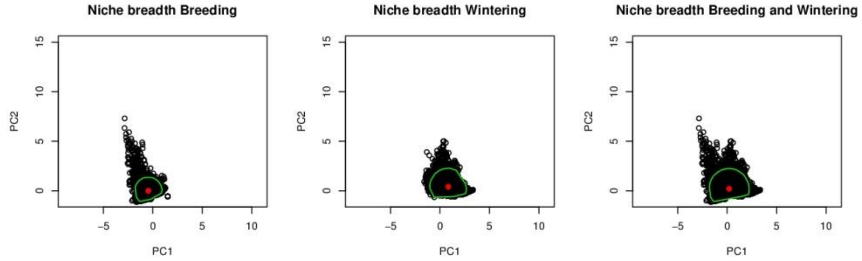


xv. *Sylvia sarda*



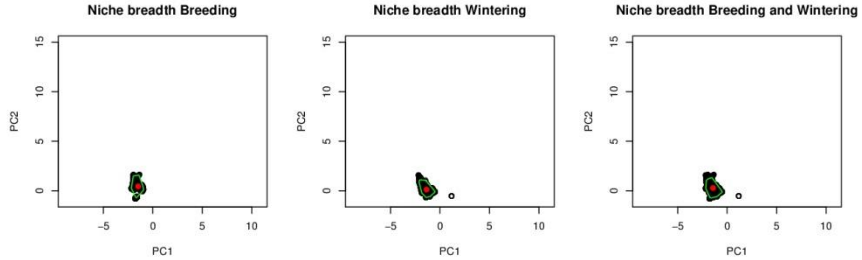
x. Troglodytidae

i. *Troglodytes troglodytes*

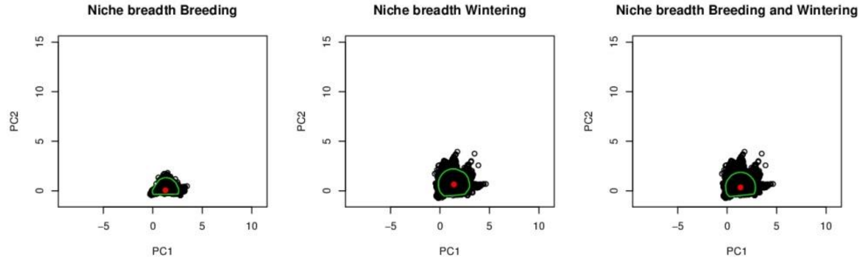


y. Turdidae

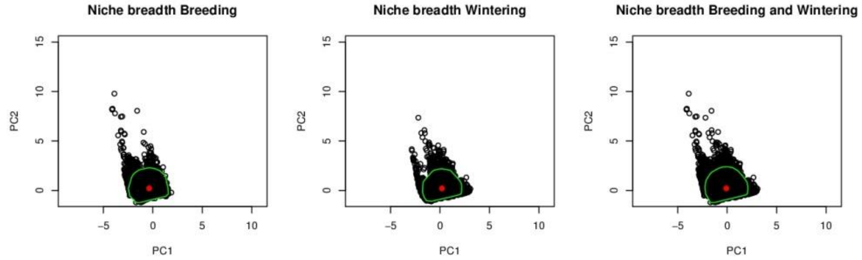
i. *Neophedina guttata*



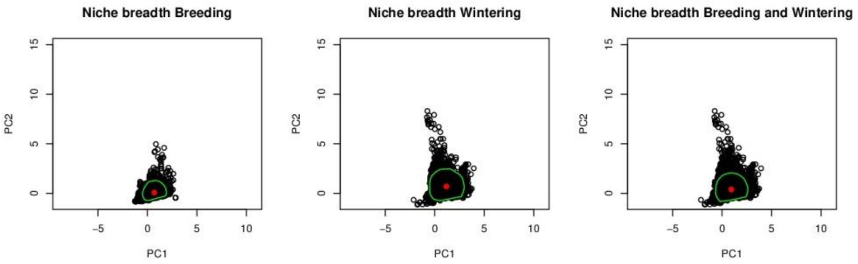
ii. *Turdus iliacus*



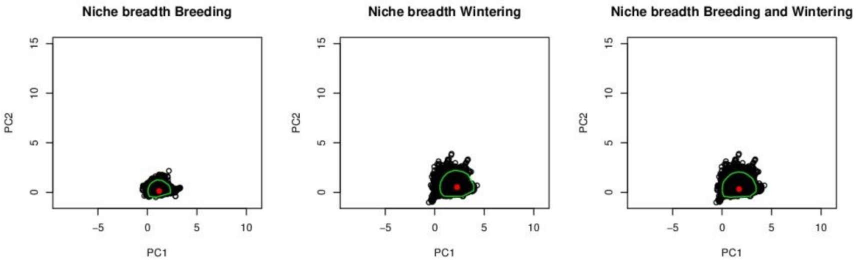
iii. *Turdus merula*



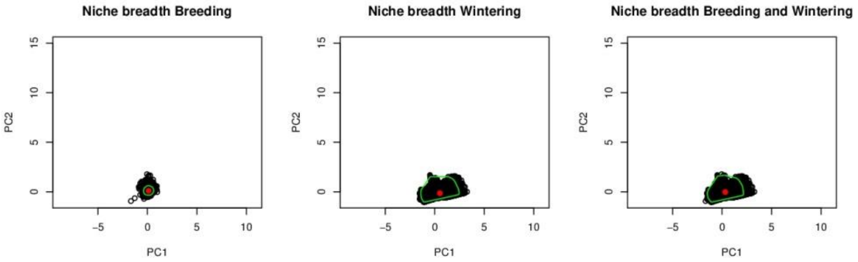
v. *Turdus philomelos*



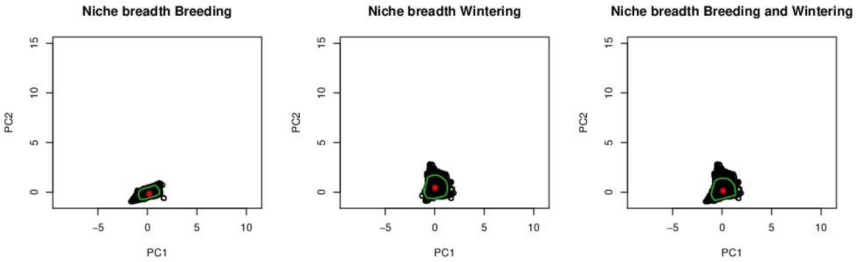
vi. *Turdus pilaris*



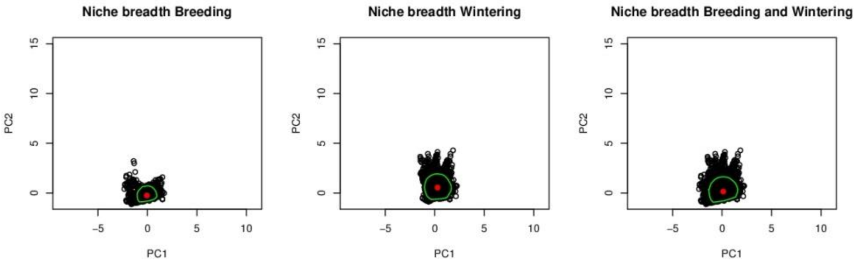
vii. *Turdus ruficollis*



viii. *Turdus torquatus*



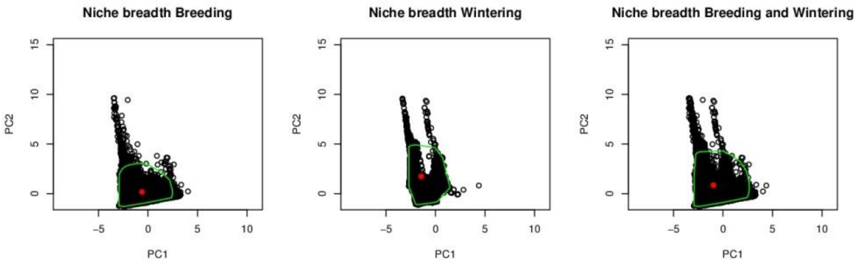
ix. *Turdus viscivorus*



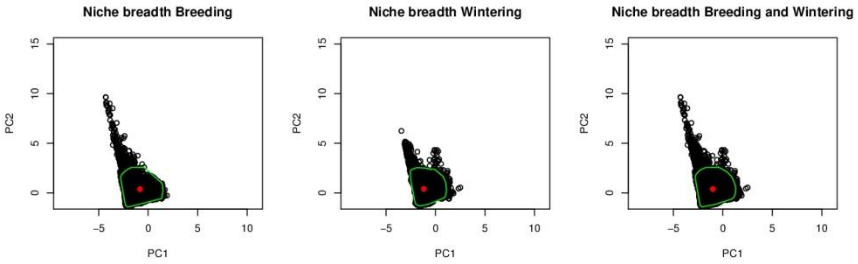
15) Pelecaniformes

a. Ardeidae

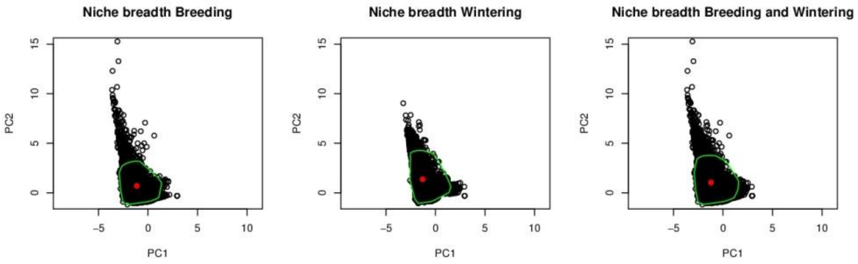
i. *Ardea alba*



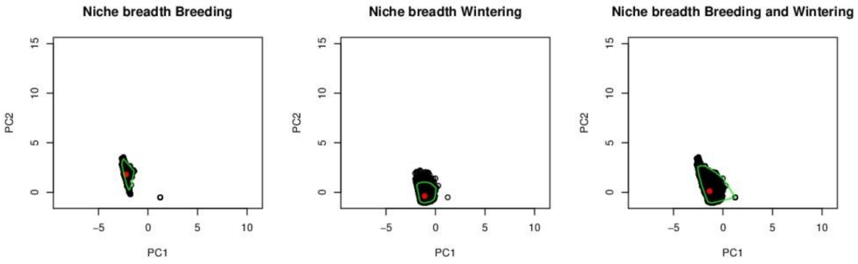
ii. *Ardea cinerea*



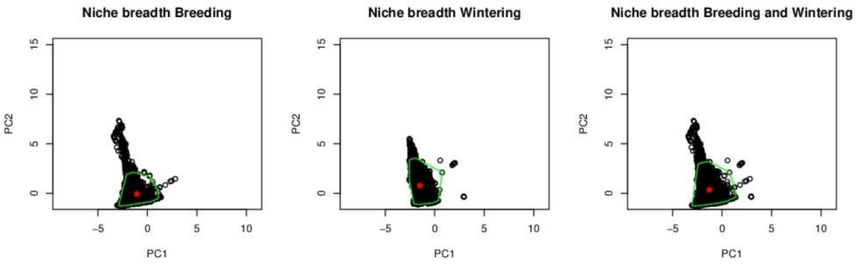
iii. *Ardea purpurea*



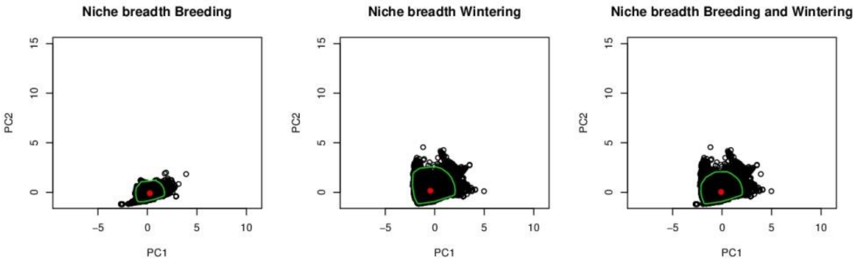
iv. *Ardeola idae*



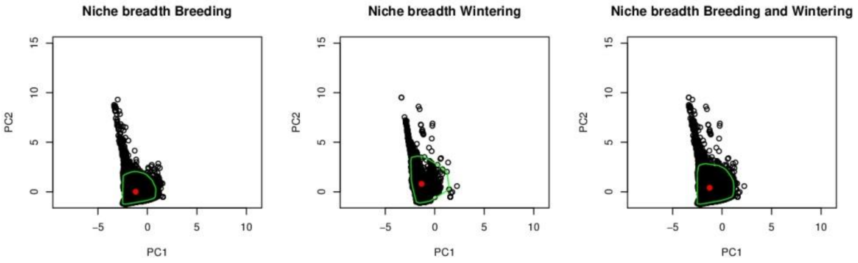
v. *Ardeola ralloides*



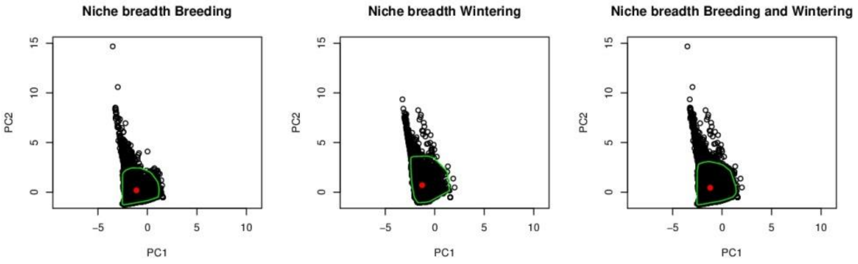
vi. *Botaurus stellaris*



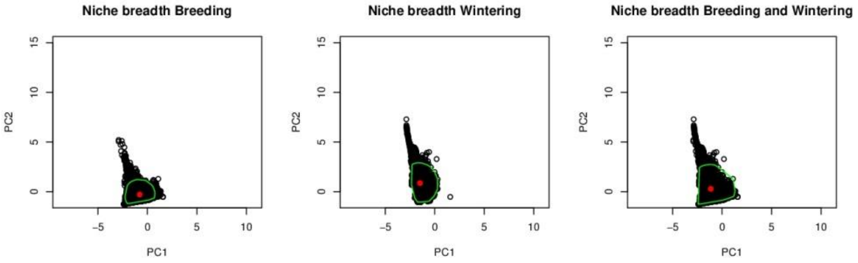
vii. *Bubulcus ibis*



viii. *Egretta garzetta*

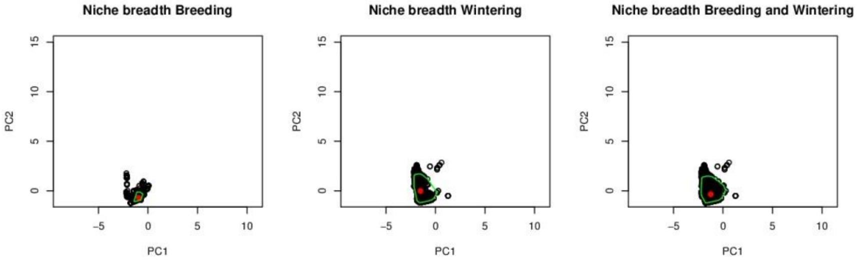


ix. *Ixobrychus minutus*



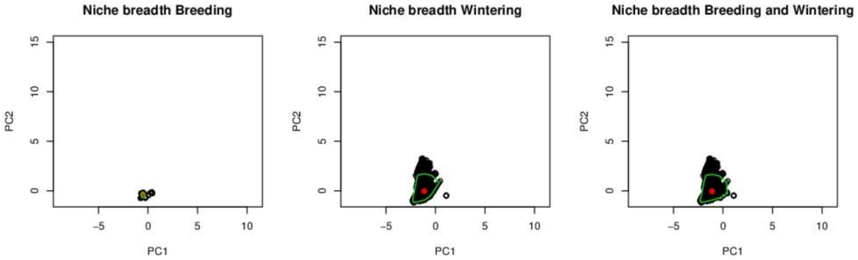
b. Pelecanidae

i. *Pelecanus onocrotalus*

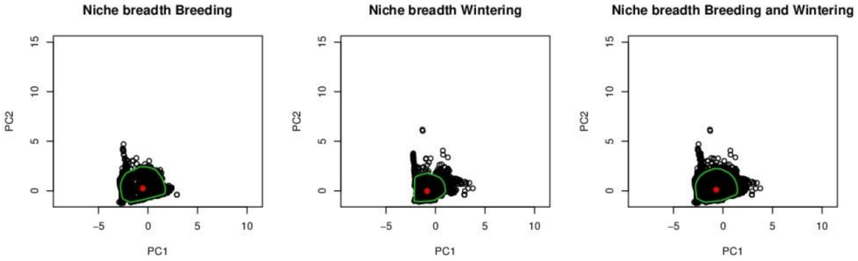


c. Threskiornithidae

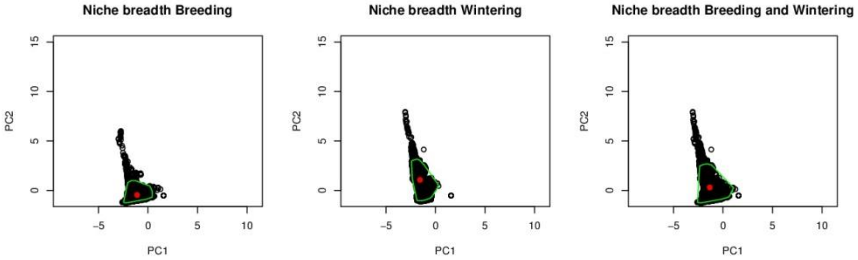
i. *Geronticus eremita*



ii. *Platalea leucorodia*



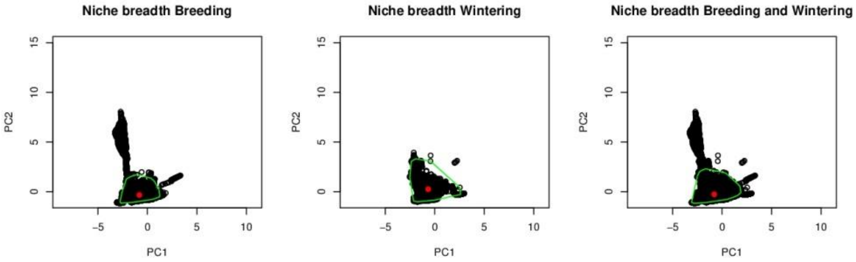
iii. *Plegadis falcinellus*



16) Phoenicopteriformes

a. Phoenicopteridae

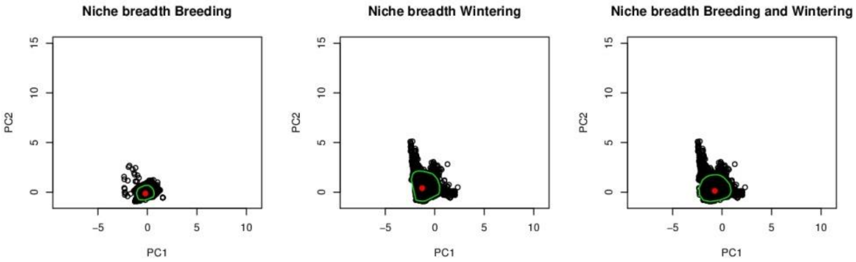
i. *Phoenicopterus roseus*



17) Piciformes

a. Picidae

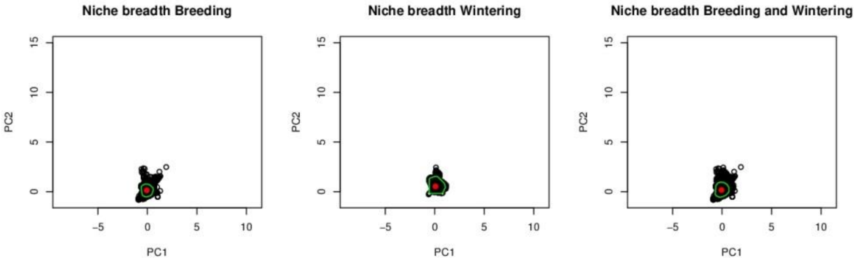
i. *Jynx torquilla*



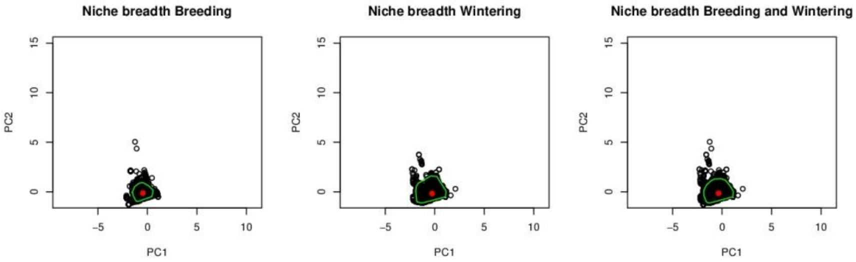
18) Podicipediformes

a. Podicipedidae

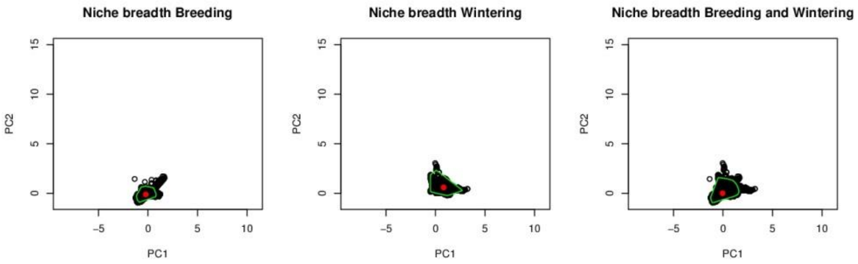
i. *Podiceps auritus*



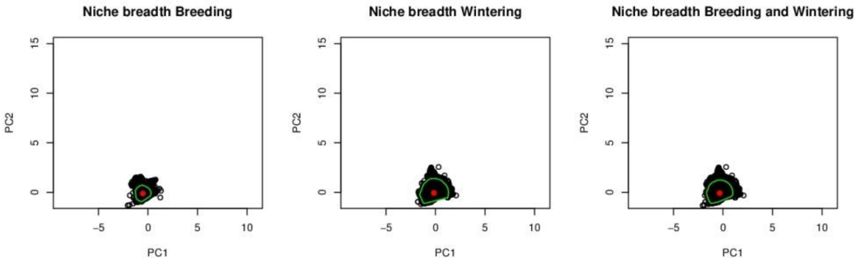
ii. *Podiceps cristatus*



iii. *Podiceps grisegena*



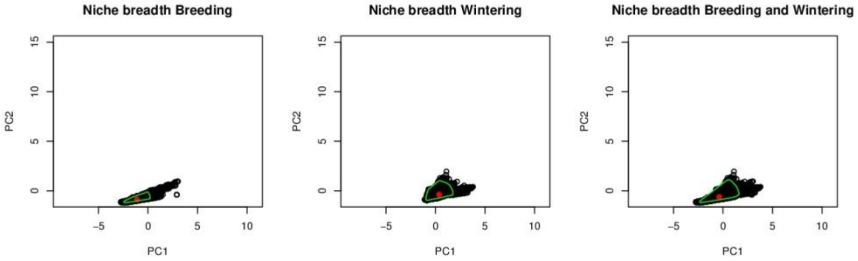
iv. *Podiceps nigricollis*



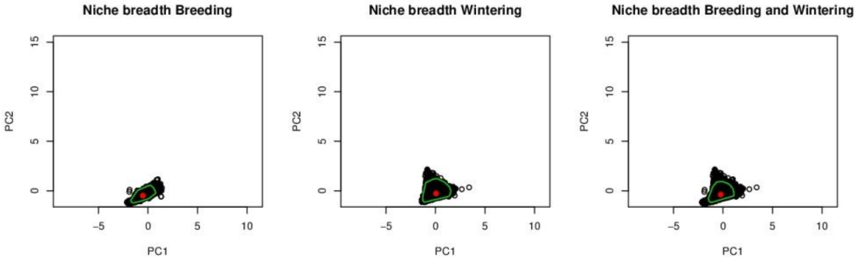
19) Pterocliformes

a. Pteroclidae

i. *Pterocles alchata*



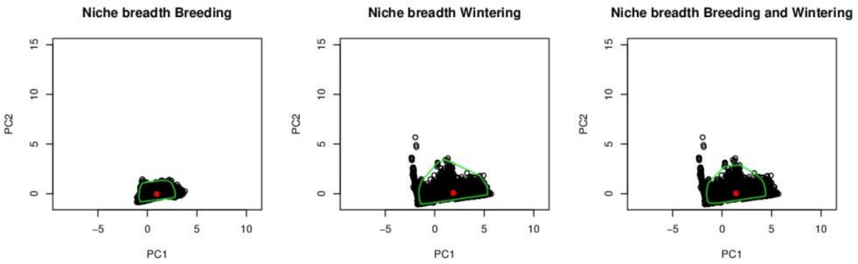
ii. *Pterocles orientalis*



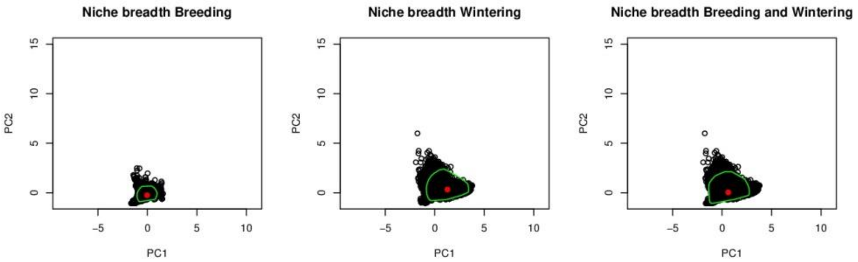
20) Strigiformes

a. Strigidae

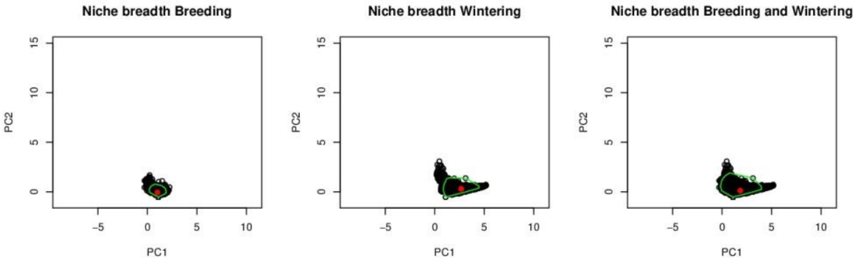
i. *Asio flammeus*



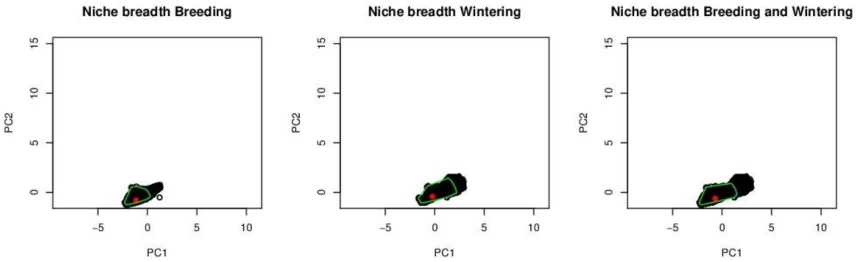
ii. *Asio otus*



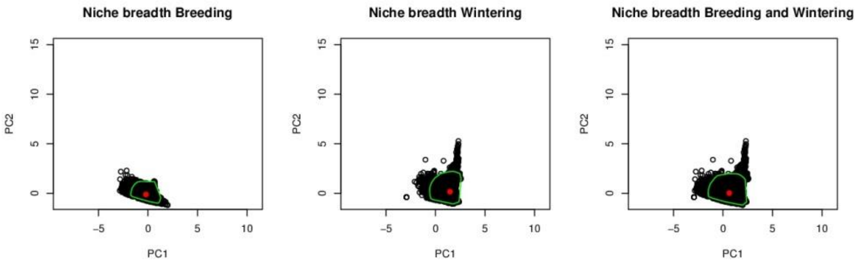
iii. *Bubo scandiaca*



iv. *Otus brucei*



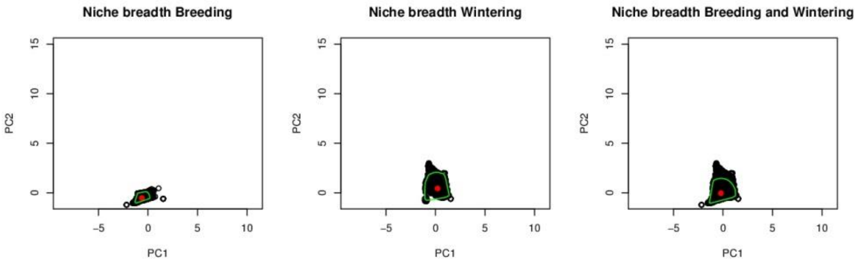
v. *Otus scops*



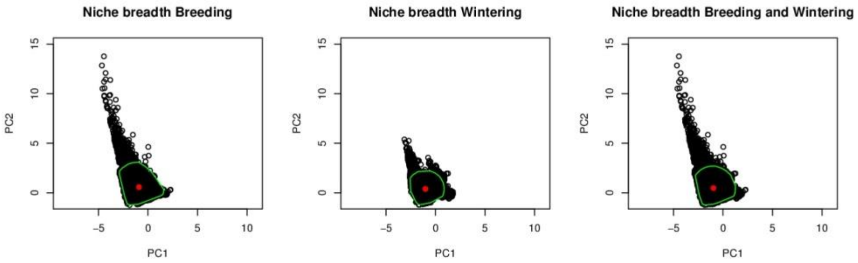
21) Suliformes

a. Phalacrocoracidae

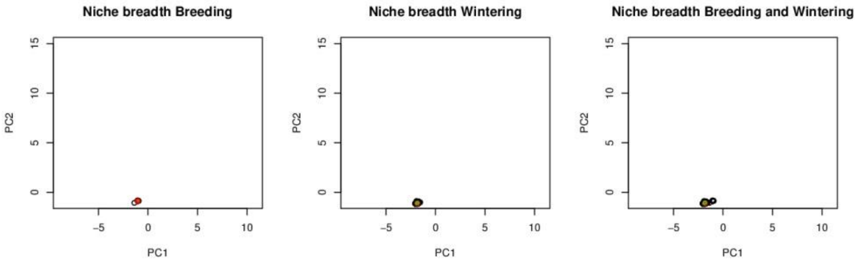
i. *Microcarbo pygmeus*



ii. *Phalacrocorax carbo*



iii. *Phalacrocorax nigrogularis*



APPENDIX CHAPTER 4

Table A4.1. AUC scores of the SMD performed for breeding and non-breeding ranges for each species.

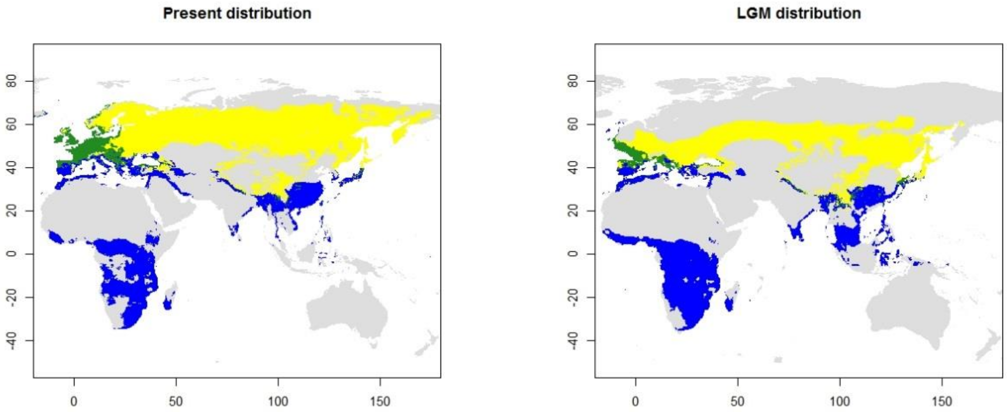
			AUC Breeding models					AUC Non-Breeding models				
Family	Genus	species	GLM	GAM	GLM poly	Bioclim	Ensemble	GLM	GAM	GLM poly	Bioclim	Ensemble
Accipitridae	*Buteo*	*buteo*	0.648	0.813	0.798	0.808	0.808	0.651	0.795	0.765	0.747	0.774
Accipitridae	*Circaetus*	*gallicus*	0.65	0.825	0.795	0.807	0.81	0.754	0.858	0.84	0.795	0.847
Accipitridae	*Circus*	*aeruginosus*	0.686	0.872	0.849	0.847	0.858	0.836	0.869	0.856	0.761	0.861
Accipitridae	*Circus*	*macrourus*	0.638	0.86	0.821	0.817	0.845	0.805	0.858	0.852	0.808	0.848
Accipitridae	*Circus*	*pygargus*	0.73	0.882	0.87	0.858	0.872	0.742	0.841	0.826	0.78	0.824
Accipitridae	*Clanga*	*pomarina*	0.877	0.914	0.888	0.89	0.907	0.637	0.795	0.78	0.735	0.782
Accipitridae	*Hieraaetus*	*pennatus*	0.589	0.834	0.787	0.795	0.813	0.825	0.568	0.909	0.867	0.909
Accipitridae	*Pernis*	*apivorus*	0.801	0.931	0.924	0.914	0.925	0.772	0.782	0.78	0.746	0.784
Anatidae	*Anas*	*crecca*	0.859	0.917	0.903	0.828	0.907	0.836	0.882	0.873	0.778	0.876
Anatidae	*Aythya*	*ferina*	0.841	0.932	0.916	0.867	0.925	0.674	0.865	0.83	0.843	0.854
Anatidae	*Aythya*	*fuligula*	0.752	0.899	0.88	0.873	0.888	0.753	0.854	0.834	0.808	0.841
Anatidae	*Aythya*	*nyroca*	0.772	0.923	0.911	0.905	0.911	0.614	0.832	0.746	0.757	0.799
Anatidae	*Mareca*	*penelope*	0.859	0.92	0.91	0.862	0.911	0.78	0.877	0.826	0.752	0.853
Anatidae	*Spatula*	*querquedula*	0.636	0.836	0.78	0.794	0.812	0.751	0.833	0.761	0.744	0.814
Apodidae	*Apus*	*apus*	0.608	0.74	0.725	0.728	0.731	0.746	0.766	0.757	0.714	0.758
Apodidae	*Apus*	*pallidus*	0.717	0.864	0.908	0.908	0.913	0.902	0.915	0.905	0.904	0.916
Caprimulgidae	*Caprimulgus*	*aegyptius*	0.753	0.722	0.899	0.899	0.899	0.904	0.499	0.908	0.9	0.918
Caprimulgidae	*Caprimulgus*	*europaeus*	0.761	0.865	0.846	0.843	0.855	0.681	0.806	0.779	0.719	0.777
Caprimulgidae	*Caprimulgus*	*ruficollis*	0.759	0.943	0.931	0.926	0.933	-	-	-	-	-
Charadriidae	*Charadrius*	*alexandrinus*	0.604	0.795	0.779	0.751	0.782	0.734	0.776	0.744	0.707	0.766
Charadriidae	*Charadrius*	*dubius*	0.633	0.768	0.727	0.721	0.745	0.728	0.764	0.736	0.709	0.754
Glareolidae	*Glareola*	*nordmanni*	0.685	0.933	0.923	0.911	0.926	0.9	0.929	0.922	0.886	0.924
Scolopacidae	*Gallinago*	*media*	0.812	0.918	0.9	0.859	0.91	0.604	0.674	0.649	0.597	0.645
Scolopacidae	*Limosa*	*limosa*	0.654	0.876	0.842	0.839	0.862	0.75	0.828	0.76	0.755	0.788
Scolopacidae	*Tringa*	*stagnatilis*	0.715	0.95	0.92	0.922	0.943	0.689	0.844	0.725	0.735	0.799
Ciconiidae	*Ciconia*	*ciconia*	0.727	0.889	0.88	0.874	0.88	0.703	0.812	0.789	0.748	0.792
Ciconiidae	*Ciconia*	*nigra*	0.784	0.907	0.894	0.854	0.892	0.784	0.888	0.858	0.778	0.866
Columbidae	*Streptopelia turtur*		0.775	0.868	0.865	0.851	0.864	0.774	0.909	0.887	0.858	0.898
Coraciidae	*Coracias*	*garrulus*	0.746	0.867	0.863	0.859	0.862	0.538	0.667	0.653	0.615	0.646
Meropidae	*Merops*	*apiaster*	0.718	0.857	0.841	0.84	0.847	0.766	0.876	0.837	0.793	0.855
Cuculidae	*Cuculus*	*canorus*	0.688	0.749	0.734	0.737	0.742	0.722	0.731	0.729	0.711	0.731
Falconidae	*Falco*	*naumanni*	0.613	0.585	0.837	0.831	0.784	0.682	0.825	0.797	0.784	0.804
Falconidae	*Falco*	*subbuteo*	0.695	0.794	0.778	0.785	0.789	0.591	0.812	0.776	0.757	0.796
Falconidae	*Falco*	*vespertinus*	0.642	0.87	0.861	0.855	0.864	0.812	0.84	0.835	0.797	0.835
Rallidae	*Crex*	*crex*	0.739	0.867	0.854	0.838	0.858	0.707	0.821	0.787	0.704	0.799
Rallidae	*Porzana*	*porzana*	0.736	0.883	0.878	0.864	0.875	0.767	0.862	0.852	0.796	0.85
Acrocephalidae	*Acrocephalus*	*arundinaceus*	0.819	0.891	0.866	0.789	0.871	0.735	0.803	0.771	0.766	0.786

(Continued on next page)

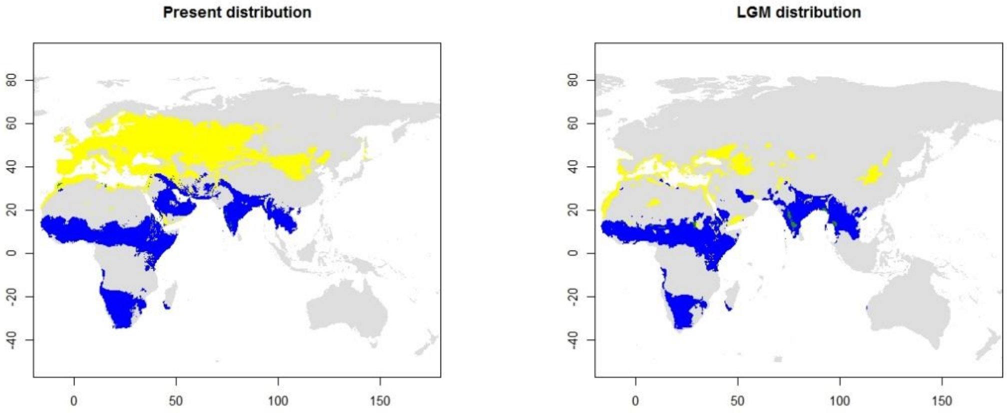
Acrocephalidae	*Acrocephalus*	*palustris*	0.824	0.94	0.937	0.926	0.938	0.605	0.819	0.797	0.691	0.784
Acrocephalidae	*Acrocephalus*	*schoenobaenus*	0.799	0.867	0.858	0.816	0.862	0.614	0.712	0.69	0.633	0.697
Acrocephalidae	*Acrocephalus*	*scirpaceus*	0.912	0.947	0.937	0.857	0.937	0.582	0.72	0.709	0.665	0.712
Acrocephalidae	*Hippolais*	*icterina*	0.844	0.925	0.922	0.911	0.924	0.747	0.823	0.82	0.767	0.819
Acrocephalidae	*Hippolais*	*polyglotta*	0.761	0.919	0.899	0.881	0.909	0.871	0.942	0.91	0.896	0.927
Acrocephalidae	*Iduna*	*opaca*	0.831	0.963	0.953	0.949	0.955	0.758	0.866	0.832	0.841	0.851
Acrocephalidae	*Iduna*	*pallida*	0.678	0.858	0.839	0.839	0.846	0.613	0.794	0.76	0.736	0.78
Alaudidae	*Calandrella*	*brachydactyla*	0.623	0.855	0.808	0.804	0.839	0.646	0.869	0.76	0.777	0.829
Emberizidae	*Emberiza*	*hortulana*	0.789	0.918	0.909	0.905	0.913	0.664	0.924	0.893	0.847	0.911
Hirundinidae	*Delichon*	*urbicum*	0.695	0.869	0.851	0.859	0.862	0.746	0.832	0.809	0.795	0.823
Hirundinidae	*Hirundo*	*rustica*	0.588	0.744	0.696	0.702	0.722	0.692	0.75	0.712	0.705	0.731
Hirundinidae	*Riparia*	*riparia*	0.787	0.834	0.808	0.767	0.813	0.673	0.774	0.707	0.683	0.736
Lanidae	*Lanius*	*collurio*	0.761	0.887	0.885	0.869	0.883	0.79	0.9	0.88	0.829	0.881
Lanidae	*Lanius*	*minor*	0.677	0.901	0.886	0.896	0.893	0.772	0.828	0.824	0.805	0.823
Lanidae	*Lanius*	*senator*	0.747	0.902	0.89	0.874	0.89	0.719	0.803	0.761	0.748	0.789
Locustellidae	*Locustella*	*fluviatilis*	0.886	0.948	0.938	0.936	0.944	0.778	0.941	0.929	0.888	0.926
Motacillidae	*Anthus*	*campestris*	0.721	0.879	0.869	0.86	0.868	0.791	0.836	0.816	0.777	0.824
Motacillidae	*Anthus*	*trivialis*	0.797	0.901	0.893	0.887	0.897	0.736	0.791	0.788	0.744	0.788
Motacillidae	*Motacilla*	*flava*	0.738	0.82	0.779	0.764	0.791	0.684	0.748	0.716	0.723	0.734
Muscicapidae	*Cercotrichas*	*galactotes*	0.718	0.832	0.812	0.814	0.828	0.789	0.845	0.83	0.755	0.826
Muscicapidae	*Cyanecula*	*svecica*	0.804	0.857	0.849	0.838	0.853	0.758	0.84	0.809	0.795	0.829
Muscicapidae	*Ficedula*	*albicollis*	0.764	0.962	0.959	0.952	0.961	0.674	0.889	0.879	0.8	0.874
Muscicapidae	*Ficedula*	*hypoleuca*	0.853	0.93	0.926	0.908	0.926	0.811	0.874	0.837	0.832	0.857
Muscicapidae	*Luscinia*	*luscinia*	0.822	0.938	0.933	0.931	0.935	0.744	0.842	0.829	0.741	0.826
Muscicapidae	*Luscinia*	*megarhynchos*	0.645	0.861	0.835	0.834	0.851	0.683	0.827	0.79	0.751	0.81
Muscicapidae	*Monticola*	*saxatilis*	0.745	0.875	0.858	0.827	0.866	0.699	0.858	0.831	0.776	0.839
Muscicapidae	*Musicapa*	*striata*	0.764	0.855	0.844	0.835	0.847	0.742	0.748	0.748	0.725	0.748
Muscicapidae	*Oenanthe*	*hispanica*	0.7	0.902	0.881	0.878	0.888	0.869	0.951	0.945	0.926	0.947
Muscicapidae	*Oenanthe*	*oenanthe*	0.745	0.784	0.768	0.746	0.769	0.736	0.771	0.763	0.678	0.758
Muscicapidae	*Phoenicurus*	*phoenicurus*	0.764	0.871	0.861	0.852	0.866	0.71	0.874	0.856	0.844	0.862
Muscicapidae	*Saxicola*	*rubetra*	0.816	0.913	0.909	0.89	0.91	0.618	0.814	0.782	0.727	0.796
Oriolidae	*Oriolus*	*oriolus*	0.693	0.856	0.831	0.841	0.842	0.828	0.855	0.845	0.842	0.852
Phylloscopidae	*Phylloscopus*	*bonelli*	0.743	0.879	0.859	0.839	0.87	0.85	0.901	0.884	0.89	0.894
Phylloscopidae	*Phylloscopus*	*collybita*	0.807	0.879	0.875	0.865	0.876	0.638	0.819	0.765	0.742	0.792
Phylloscopidae	*Phylloscopus*	*sibilatrix*	0.825	0.945	0.944	0.931	0.942	0.829	0.876	0.857	0.812	0.863
Phylloscopidae	*Phylloscopus*	*trochilus*	0.798	0.88	0.873	0.871	0.877	0.675	0.694	0.691	0.667	0.687
Sylviidae	*Sylvia*	*atricapilla*	0.806	0.911	0.907	0.891	0.907	0.688	0.86	0.8	0.783	0.834
Sylviidae	*Sylvia*	*borin*	0.832	0.939	0.935	0.924	0.937	0.738	0.746	0.74	0.739	0.749
Sylviidae	*Sylvia*	*cantillans*	0.783	0.932	0.915	0.902	0.923	0.886	0.76	0.923	0.923	0.906
Sylviidae	*Sylvia*	*communis*	0.682	0.866	0.851	0.852	0.859	0.659	0.807	0.787	0.769	0.796
Sylviidae	*Sylvia*	*curruca*	0.726	0.862	0.852	0.846	0.855	0.774	0.868	0.853	0.775	0.856
Sylviidae	*Sylvia*	*hortensis*	0.782	0.938	0.931	0.908	0.932	0.946	0.957	0.955	0.946	0.956
Picidae	*Jynx*	*torquilla*	0.713	0.845	0.84	0.843	0.845	0.738	0.834	0.812	0.782	0.819
Strigidae	*Otus*	*scops*	0.688	0.868	0.856	0.855	0.858	0.742	0.83	0.802	0.78	0.817

Figures A4.1.Present and past (Last Glacial Maximum (LGM)) species distribution models (SDM) of 80 trans-Saharan migratory birds. Yellow correspond to the breeding distribution, blue correspond to the wintering distribution, and green correspond to areas where species are resident.

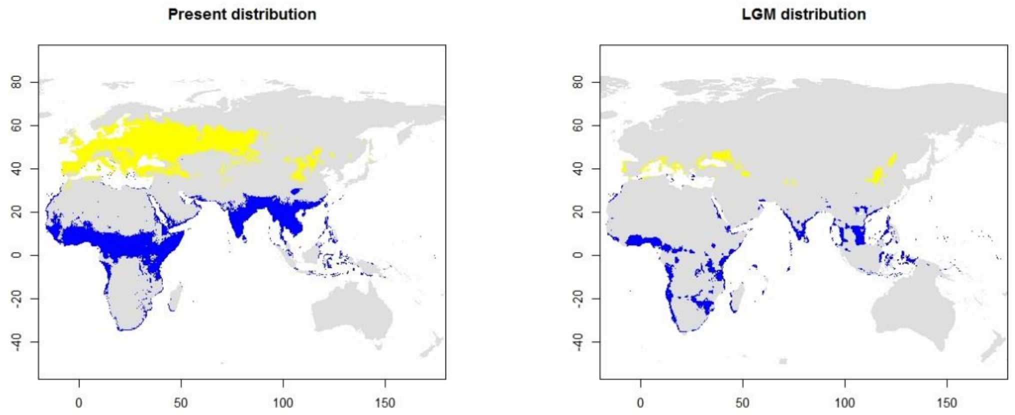
1) **Accipitriformes**
   a. Accipitridae
      i. *Buteo buteo*



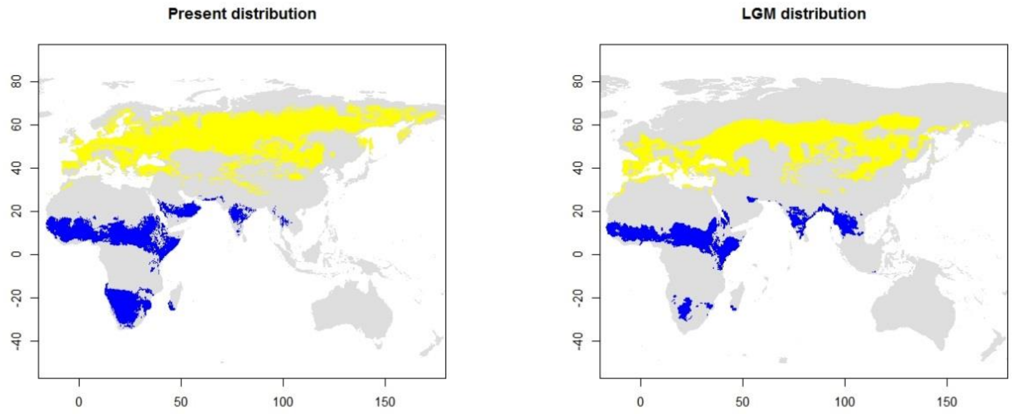
      ii. *Circaetus gallicus*



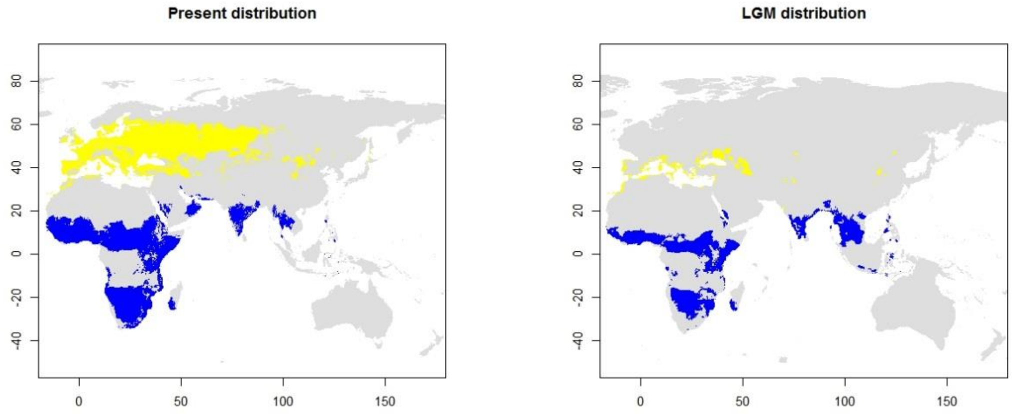
iii. *Circus aeruginosus*



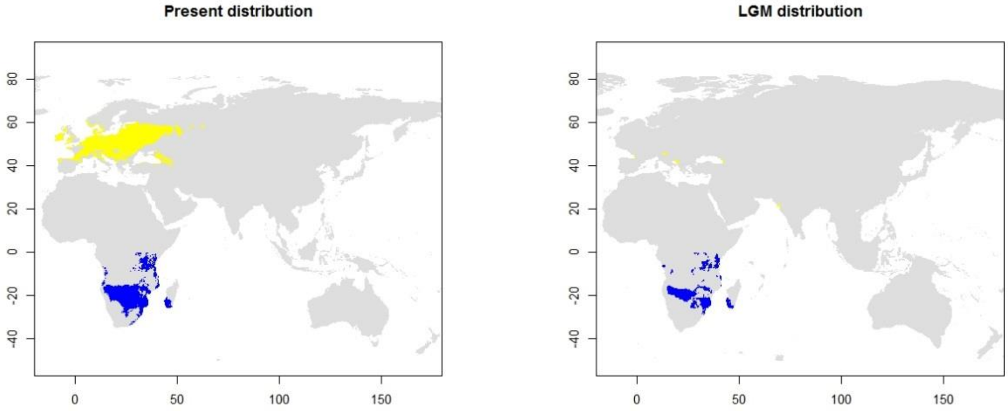
iv. *Circus macrourus*



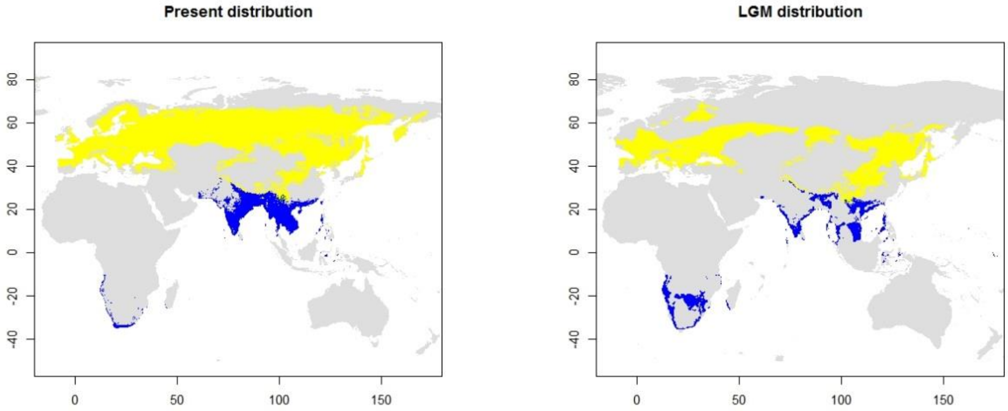
v. *Circus pygargus*



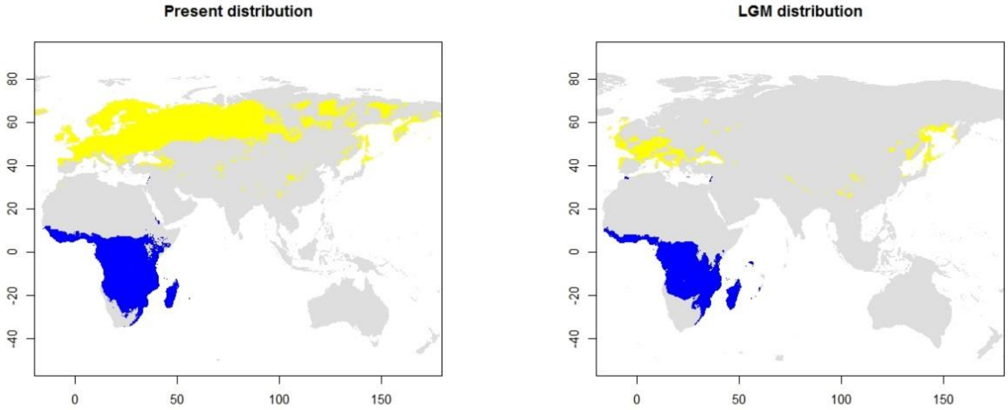
vi. *Clanga pomarina*



vii. *Hieraaetus pennatus*



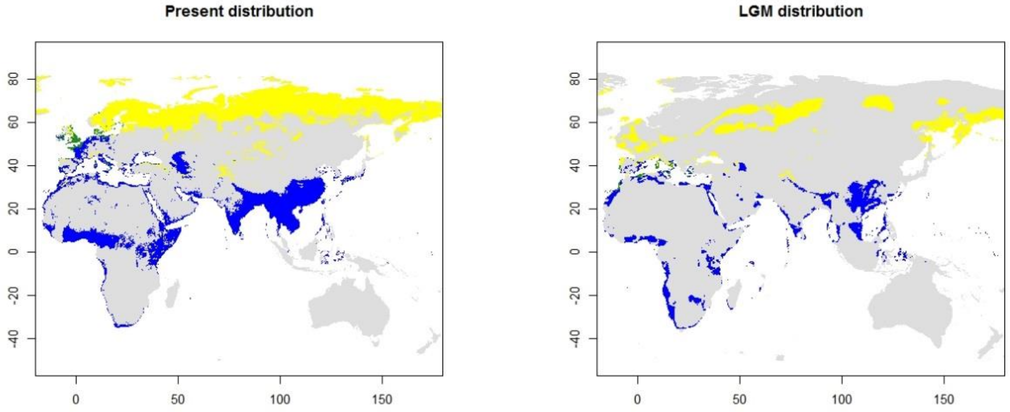
viii. *Pernis apivorus*



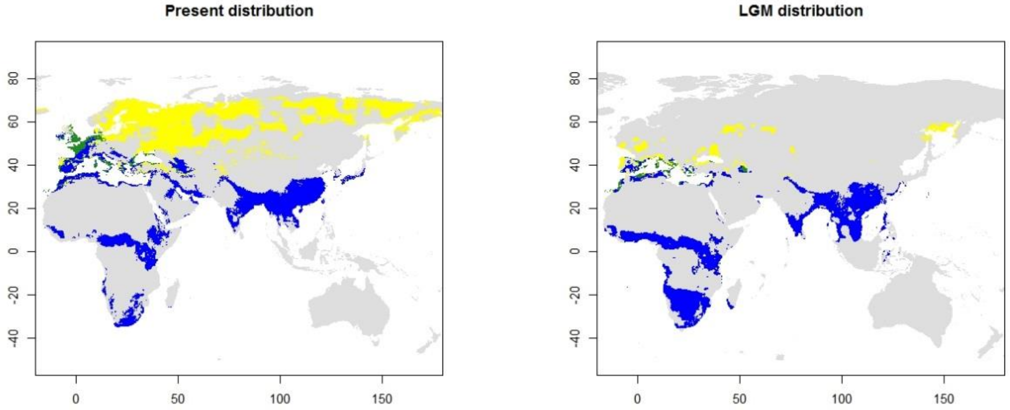
2) Anseriformes

a. Anatidae

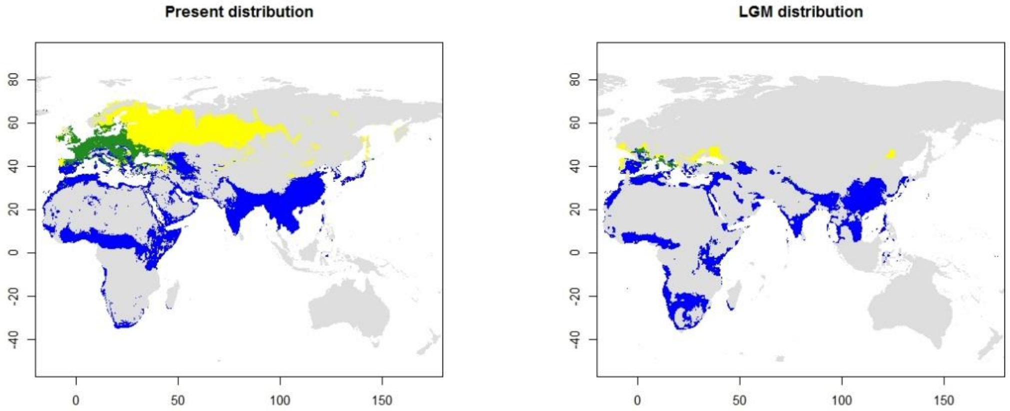
i. *Anas crecca*



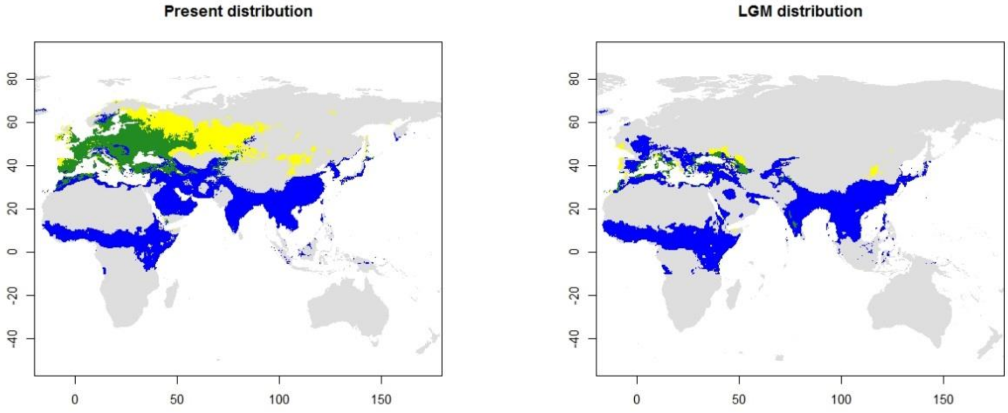
ii. *Aythya ferina*



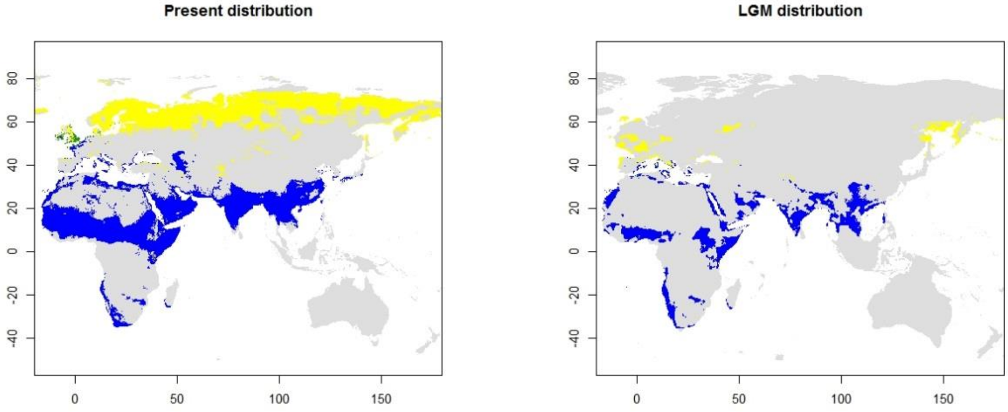
iii. *Aythya fuligula*



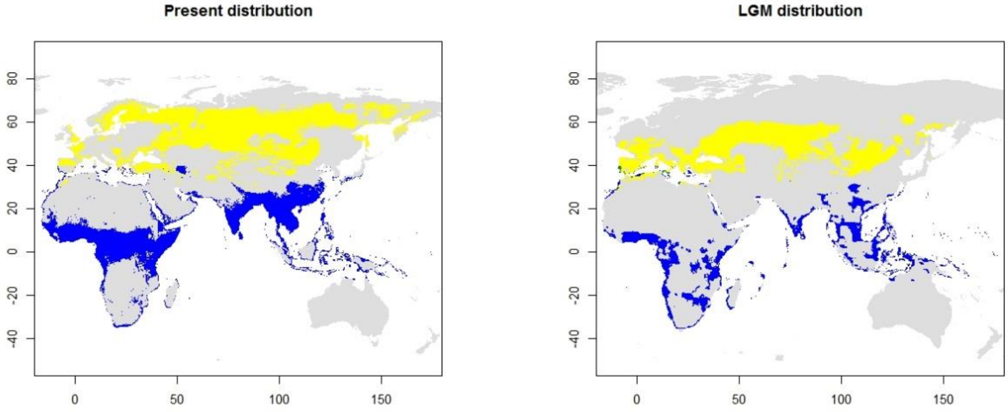
iv. *Aythya nyroca*



v. *Mareca penelope*



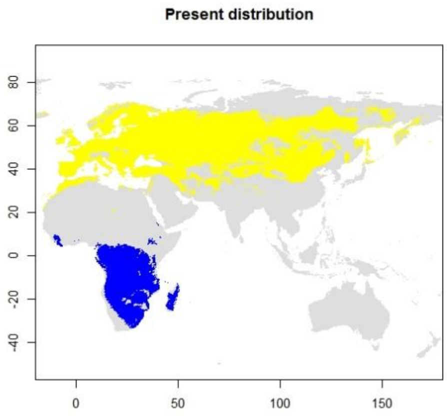
vi. *Spatula querquedula*

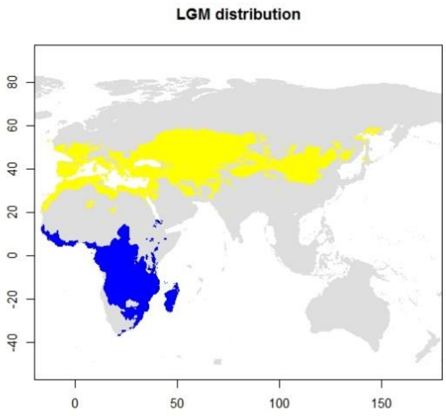


3) Caprimulgiformes

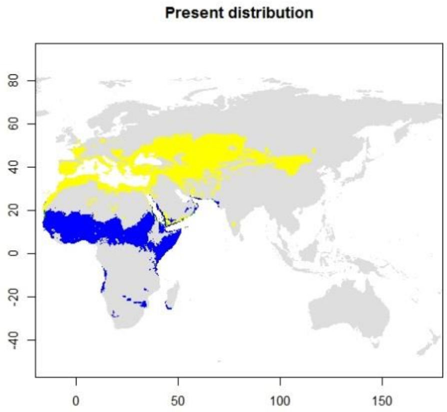
a. Apodidae

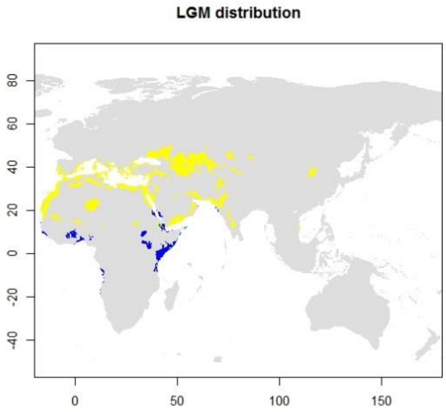
i. *Apus apus*


Present distribution


LGM distribution

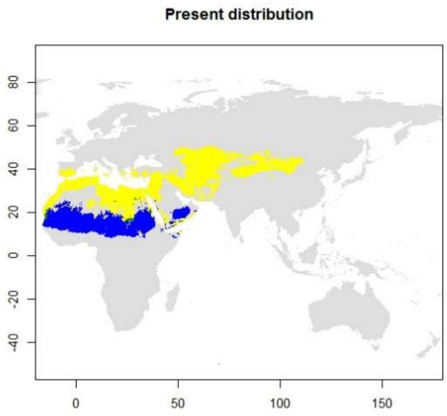
ii. *Apus pallidus*

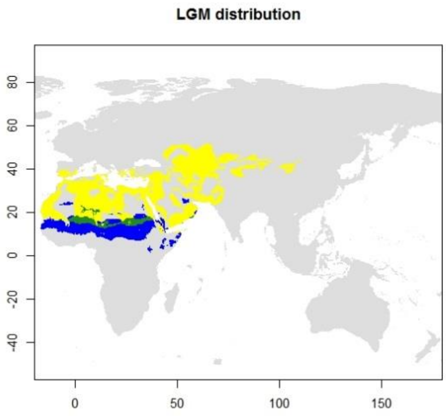

Present distribution


LGM distribution

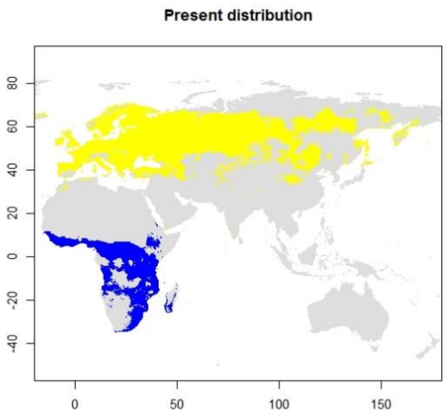
b. Caprimulgidae

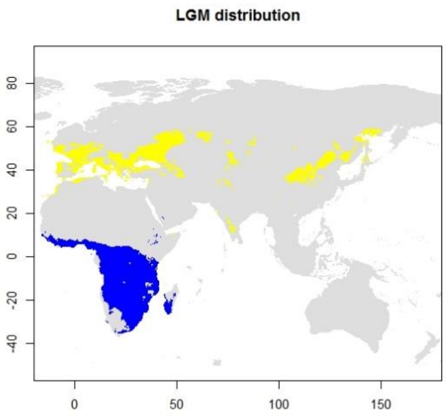
i. *Caprimulgus aegyptius*


Present distribution


LGM distribution

ii. *Caprimulgus europaeus*

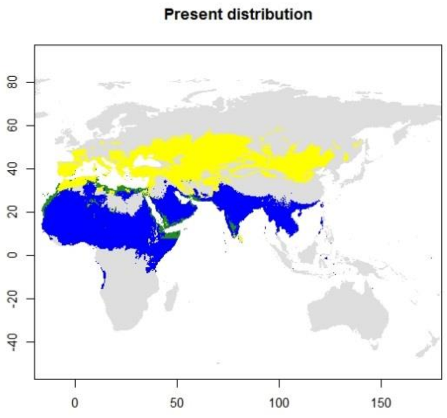

Present distribution

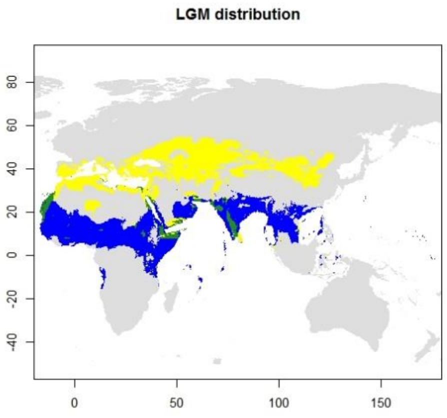

LGM distribution

4) Charadriiformes

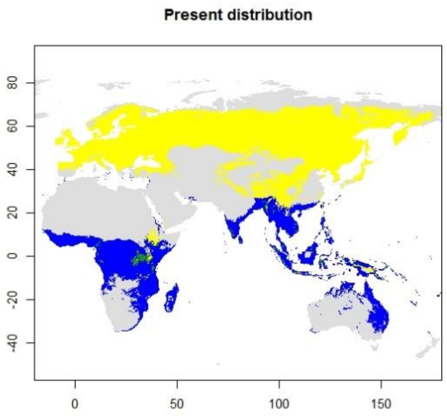
a. Charadriidae

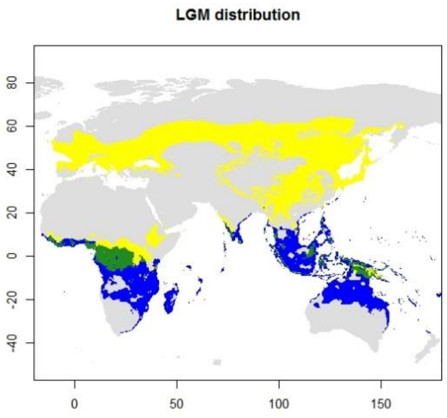
i. *Charadrius alexandrinus*


Present distribution


LGM distribution

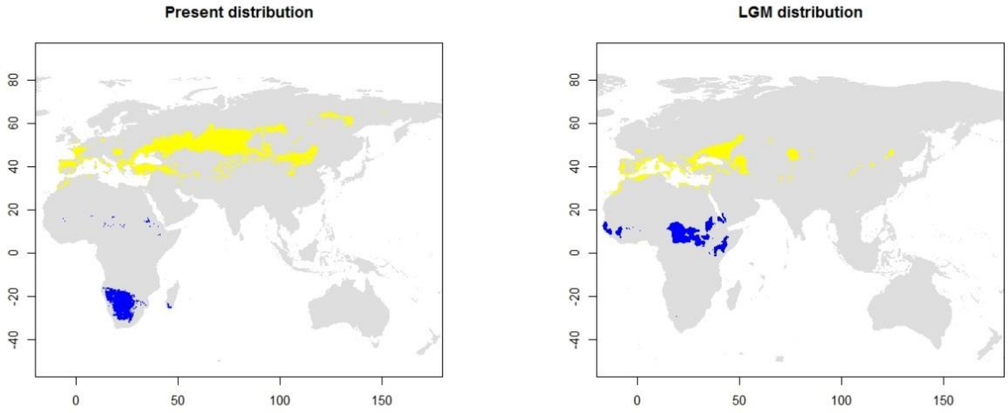
ii. *Charadrius dubius*


Present distribution


LGM distribution

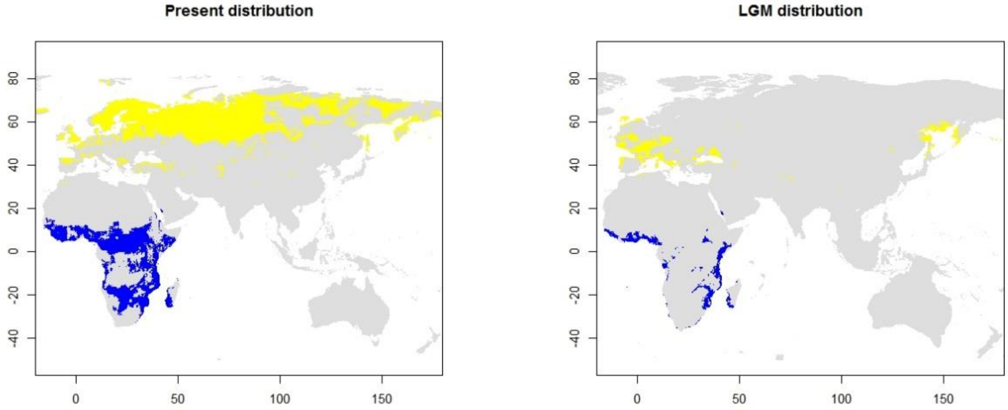
b. Glareolidae

i. *Glareola nordmanni*

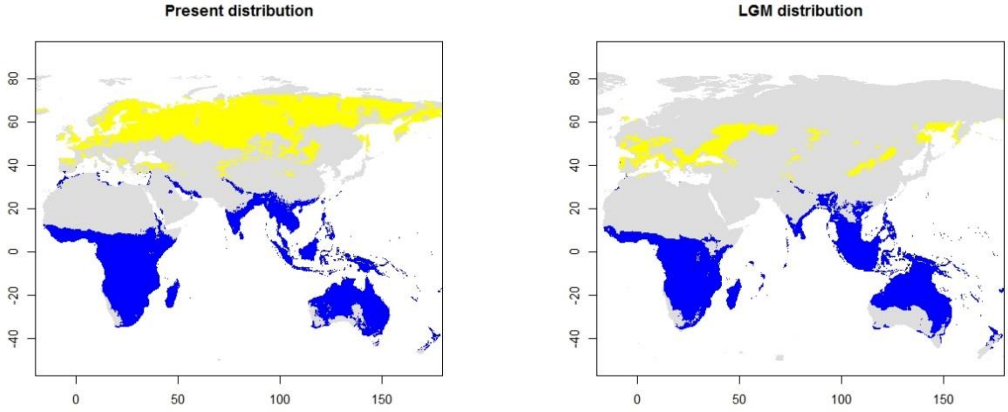


c. Scolopacidae

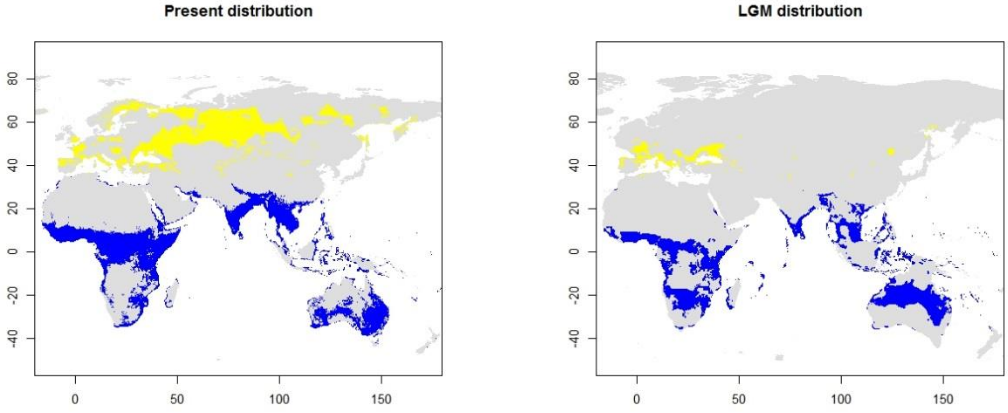
i. *Gallinago media*



ii. *Limosa limosa*



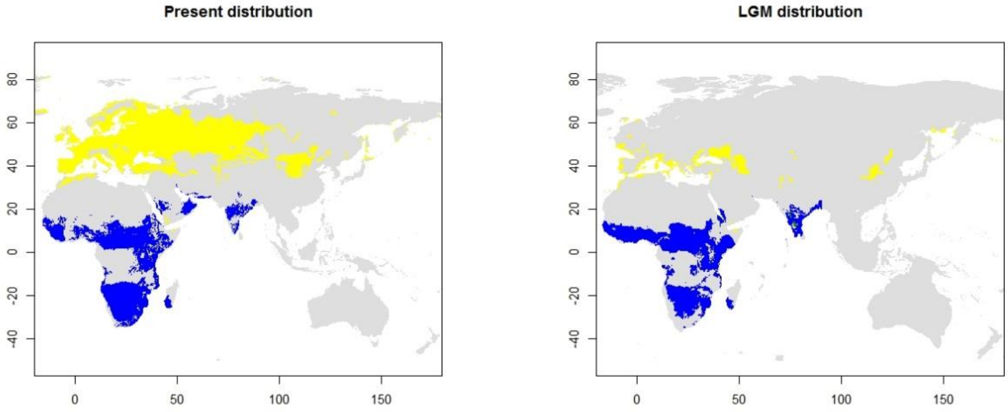
iii. *Tringa stagnatilis*



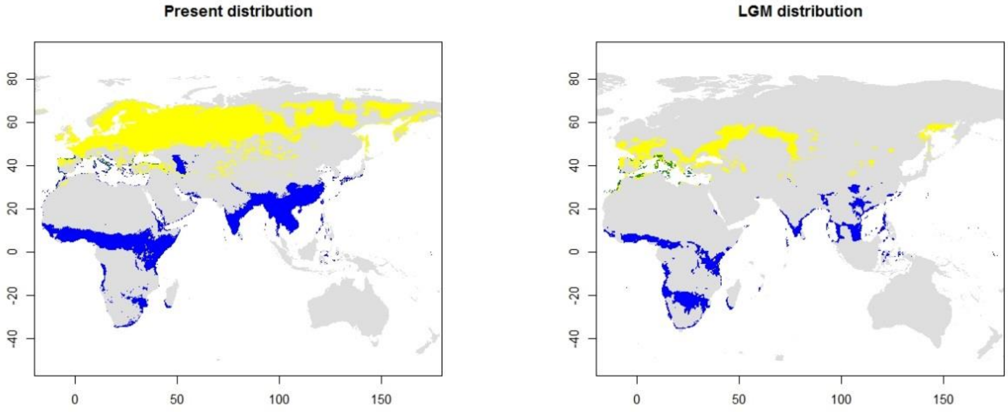
5) Ciconiiformes

a. Ciconiidae

i. *Ciconia ciconia*



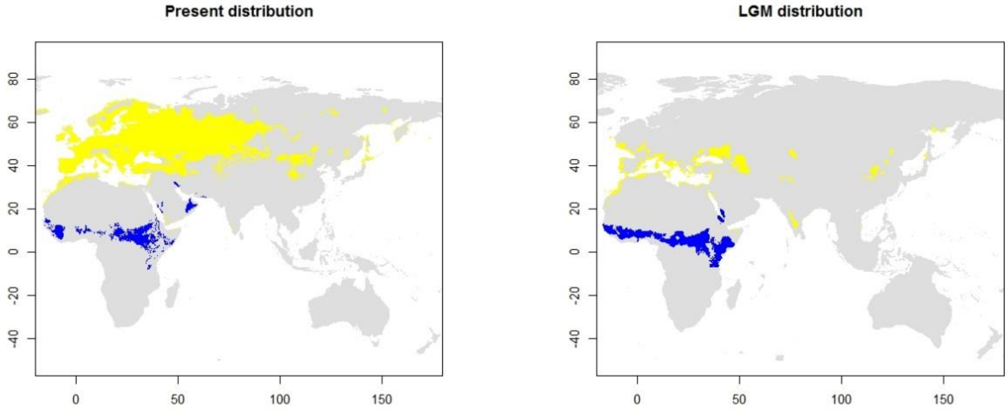
ii. *Ciconia nigra*



6) Columbiformes

a. Columbidae

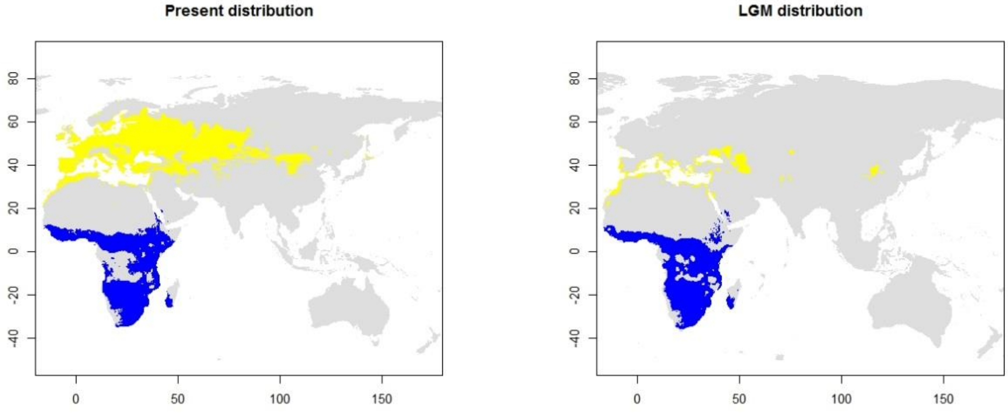
i. *Streptopelia turtur*



7) Coraciiformes

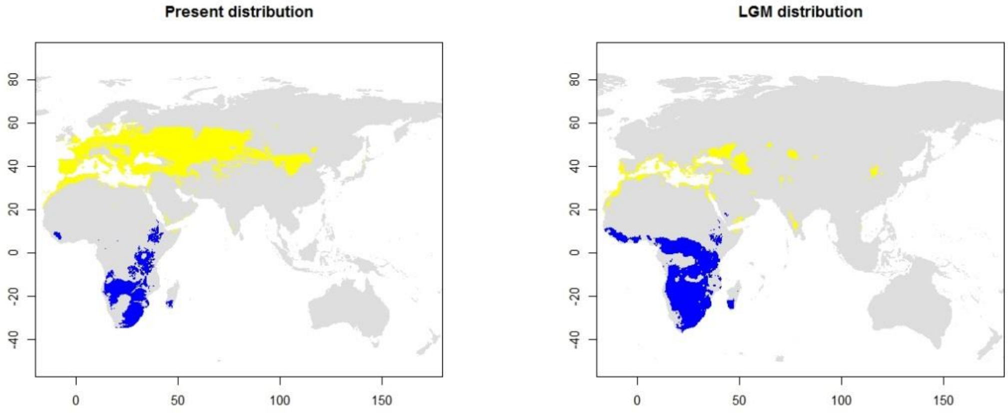
a. Coraciidae

i. *Coracias garrulus*



b. Meropidae

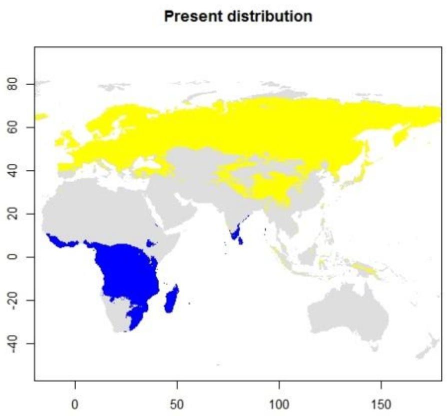
i. *Merops apiaster*

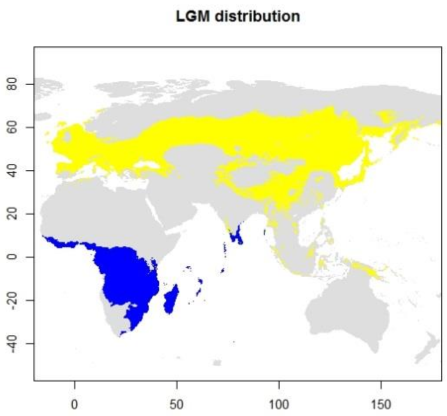


8) Cuculiformes

a. Cuculidae

i. *Cuculus canorus*

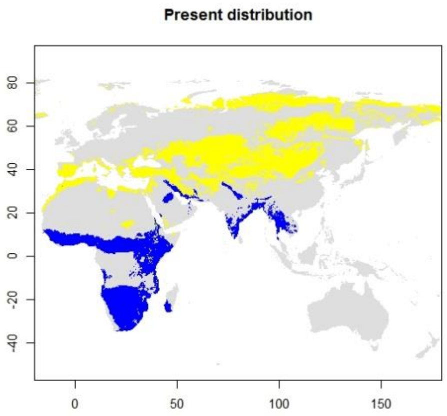


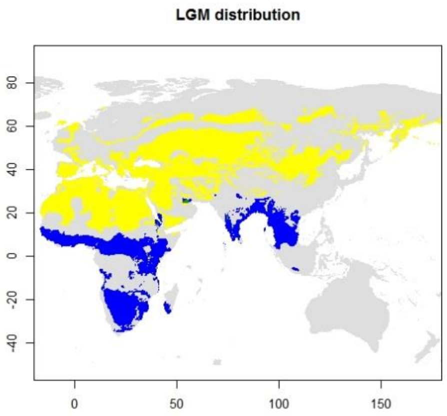


9) Falconiformes

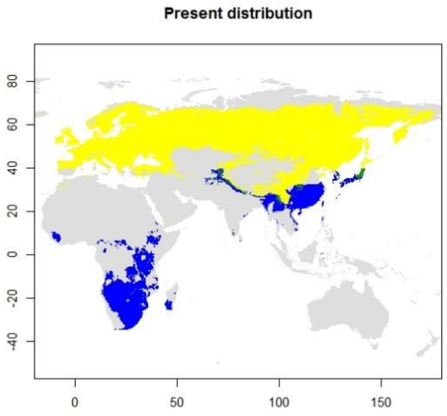
a. Falconidae

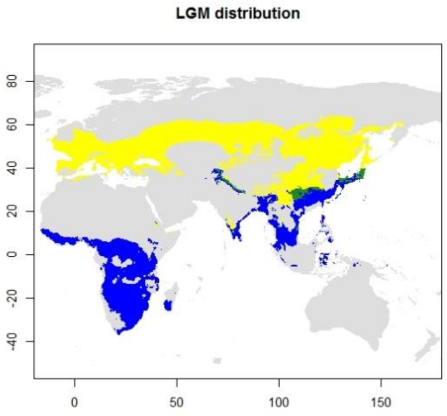
i. *Falco naumanni*



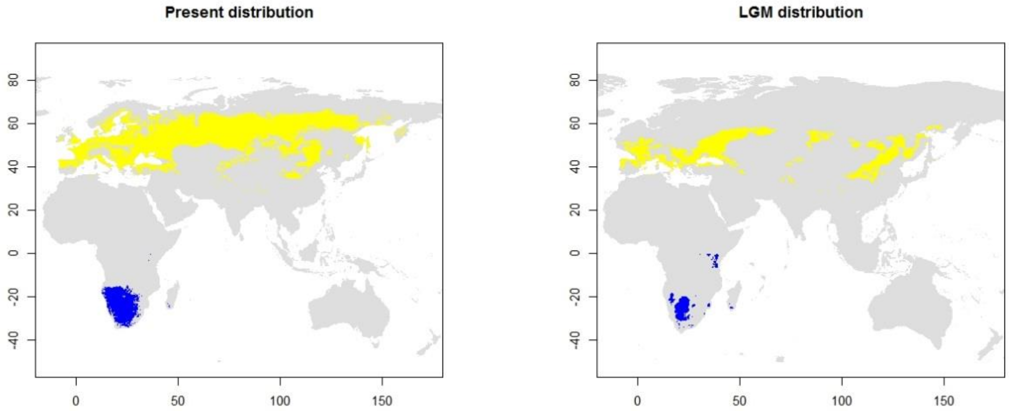


ii. *Falco subbuteo*





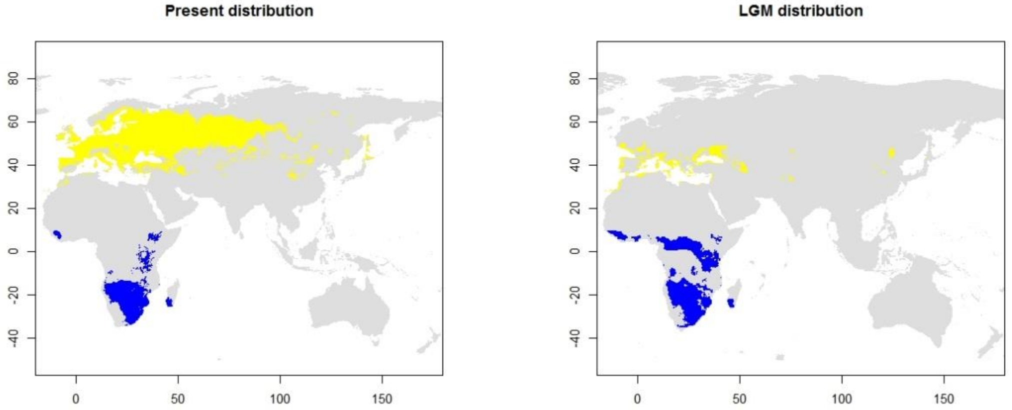
i. *Falco vespertinus*



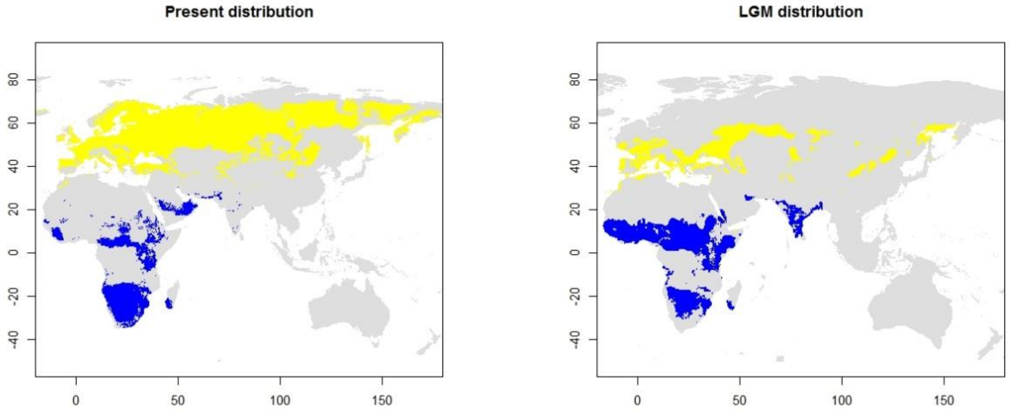
10) Gruiformes

a. Rallidae

i. *Crex crex*



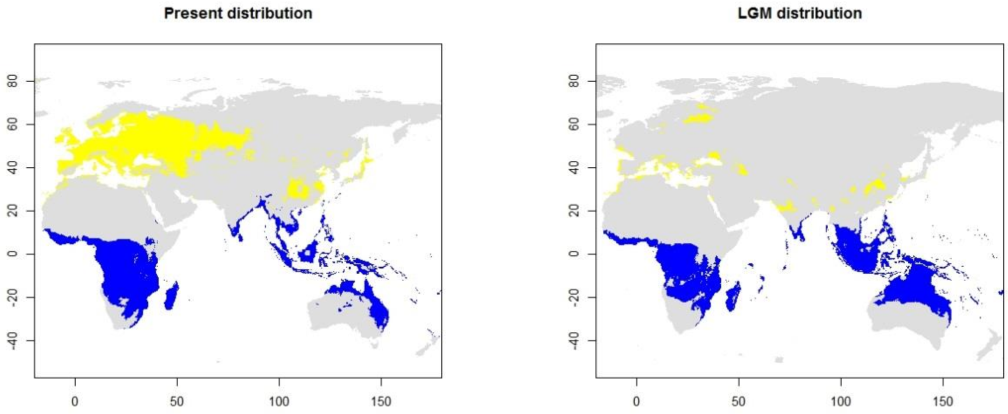
ii. *Porzana porzana*



11) Passeriformes

a. Acrocephalidae

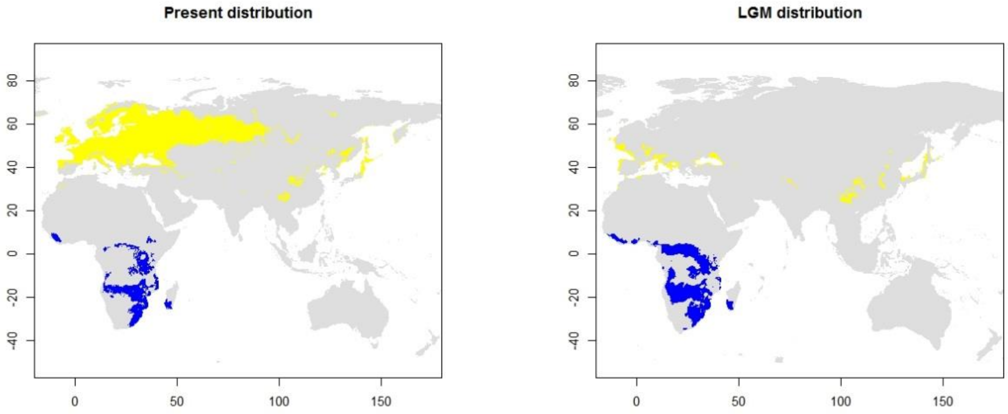
i. *Acrocephalus arundinaceus*



Present distribution

LGM distribution

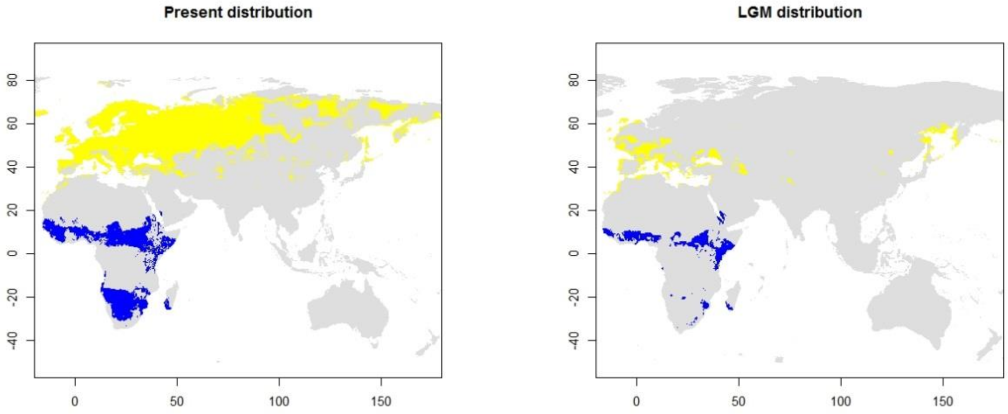
ii. *Acrocephalus palustris*



Present distribution

LGM distribution

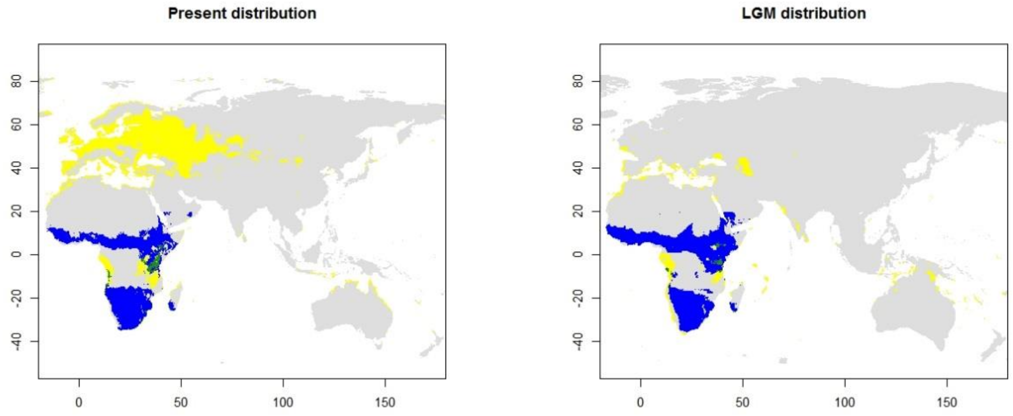
iii. *Acrocephalus schoenobaenus*



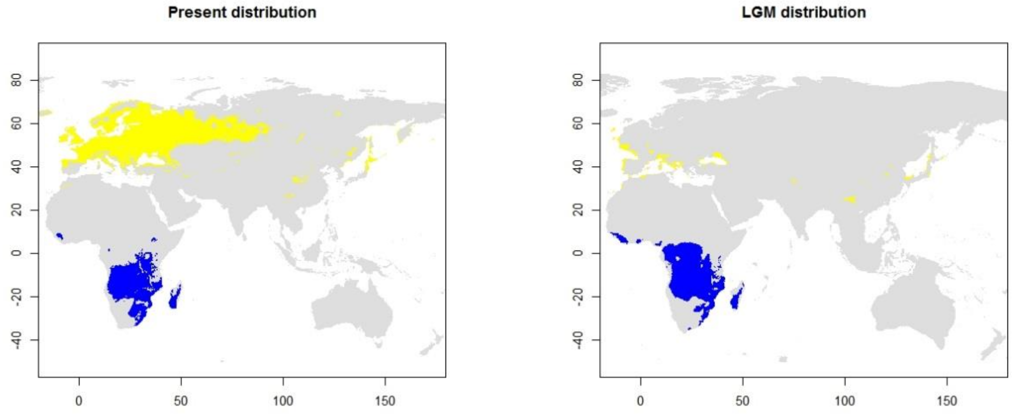
Present distribution

LGM distribution

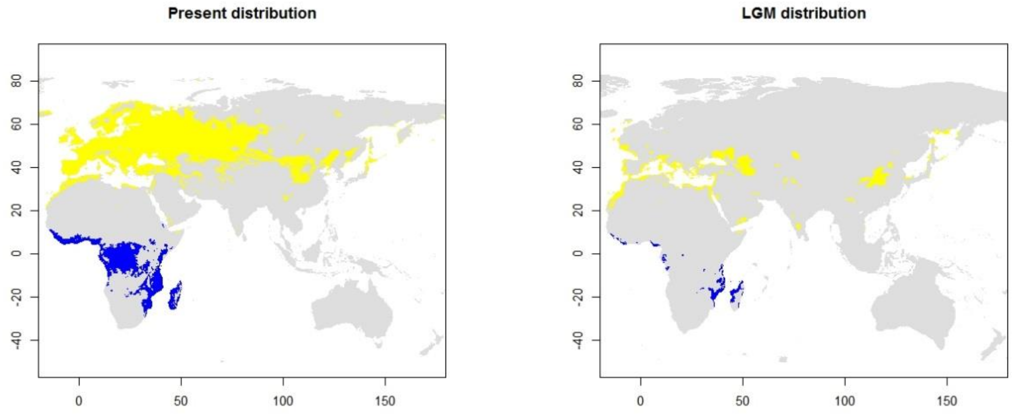
iv. *Acrocephalus scirpaceus*



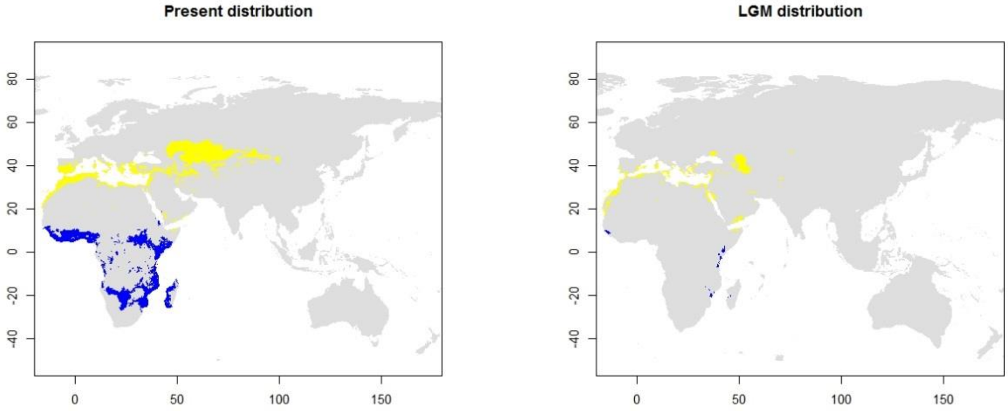
v. *Hippolais icterina*



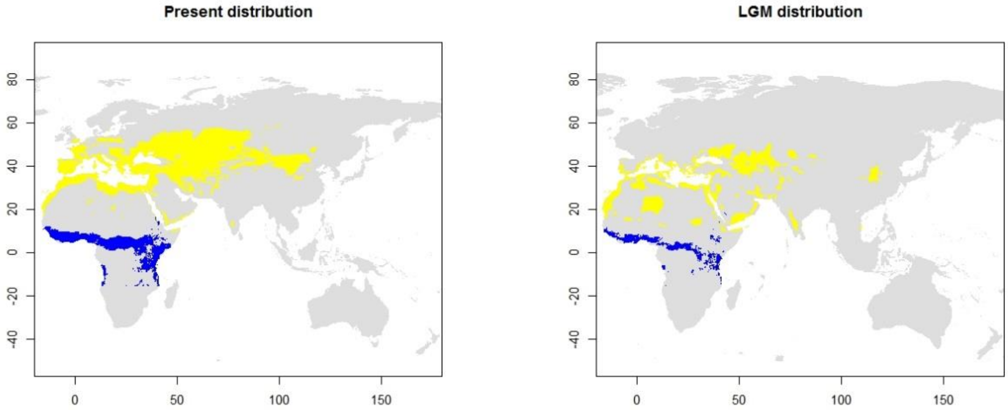
vi. *Hippolais polyglotta*



vii. *Iduna opaca*

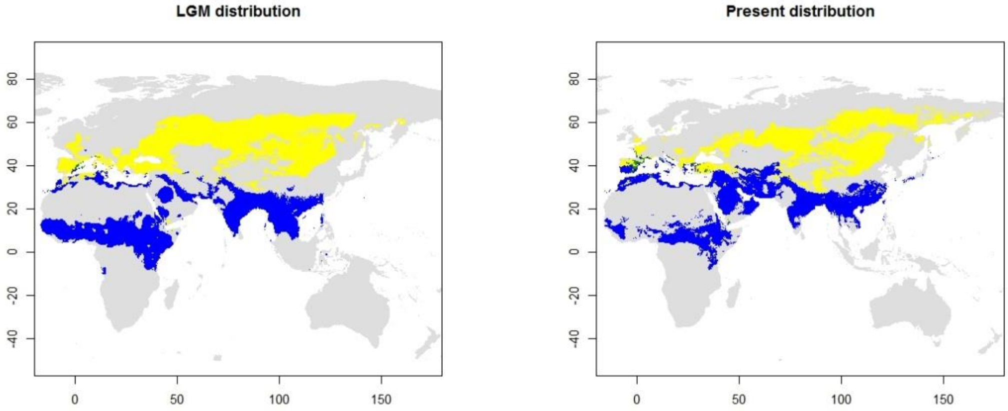


viii. *Iduna pallida*



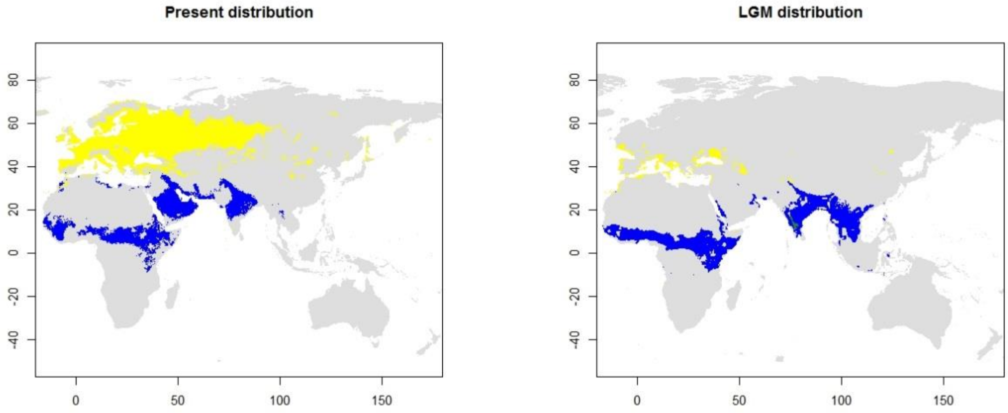
b. Alaudidae

i. *Calandrella brachydactyla*



c. Emberizidae

i. *Emberiza hortulana*

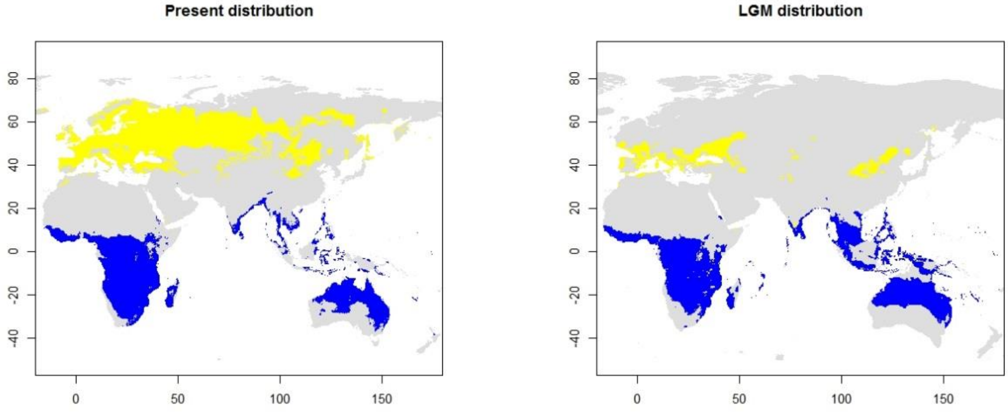


Present distribution

LGM distribution

d. Hirundinidae

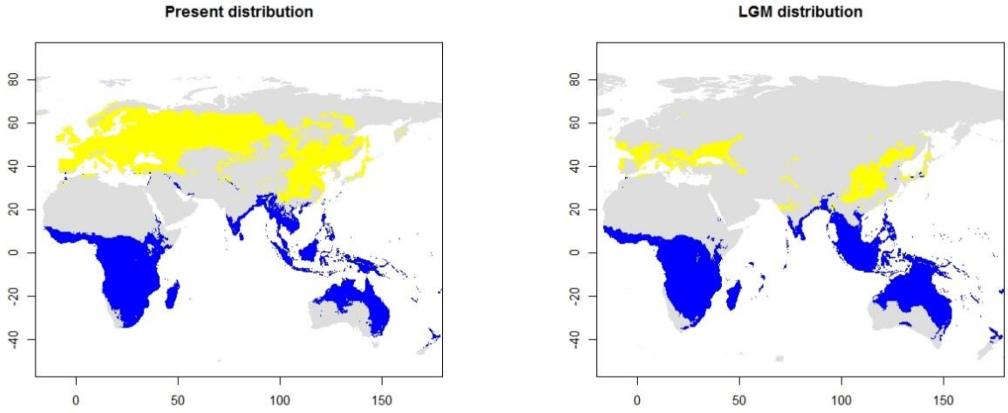
i. *Delichon urbicum*



Present distribution

LGM distribution

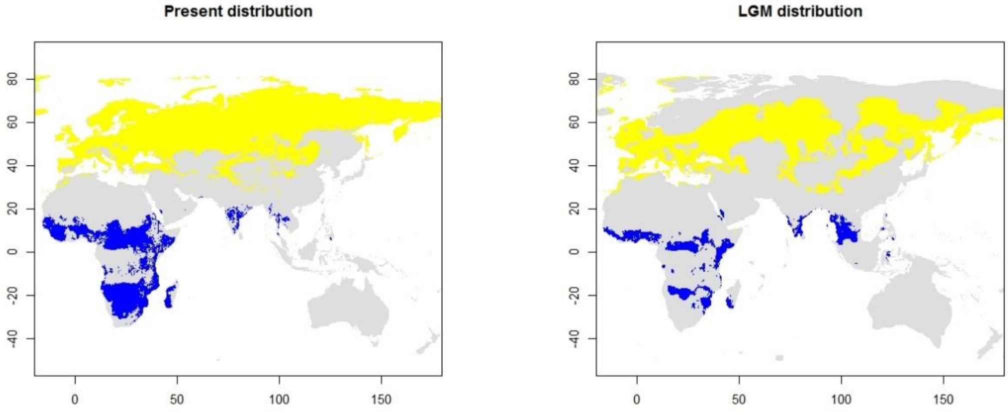
ii. *Hirundo rustica*



Present distribution

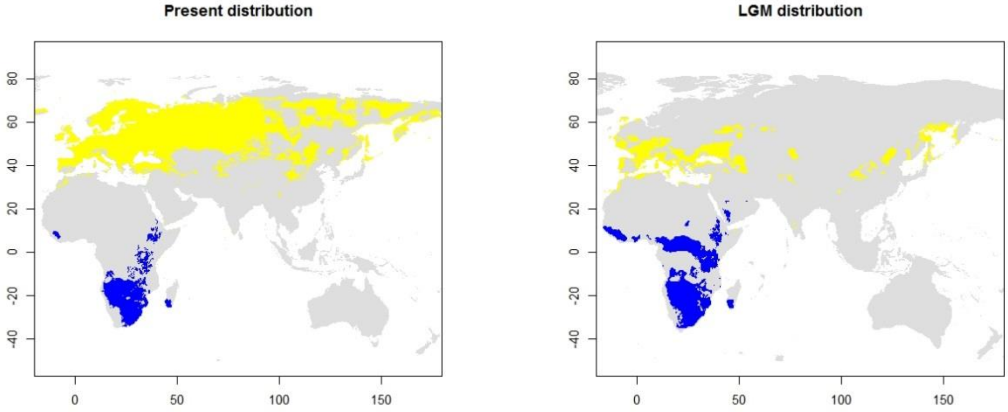
LGM distribution

iii. *Riparia riparia*

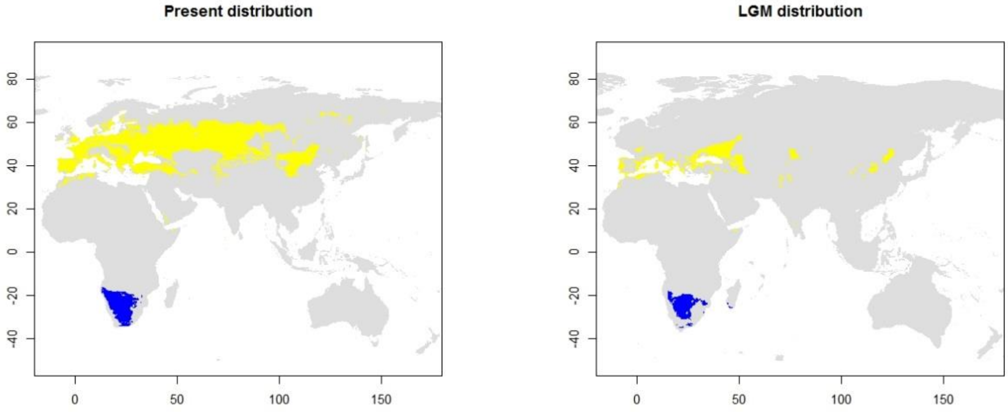


e. Lanidae

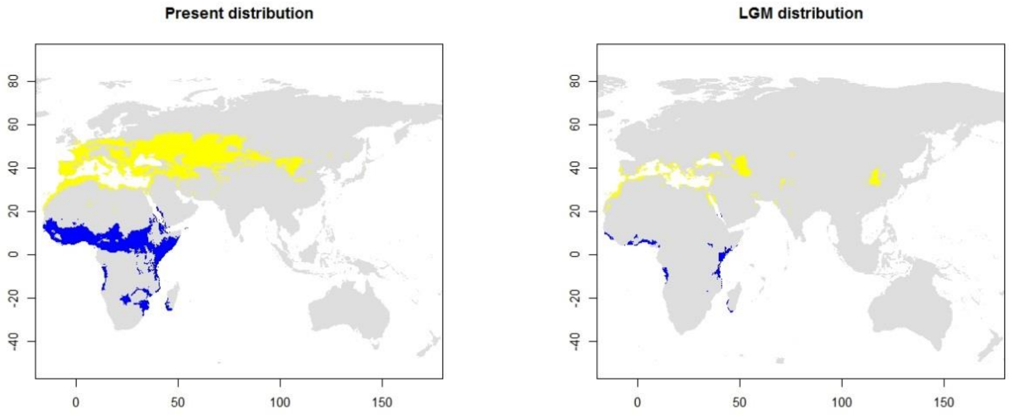
i. *Lanius collurio*



ii. *Lanius minor*

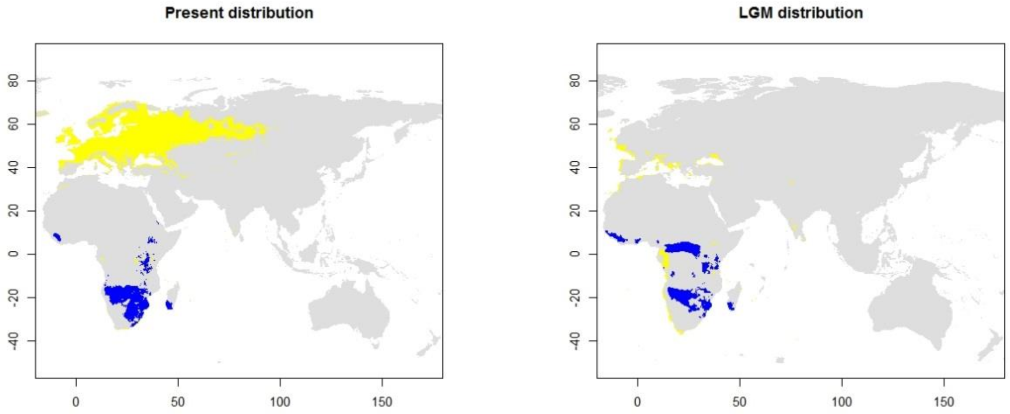


iii. *Lanius senator*



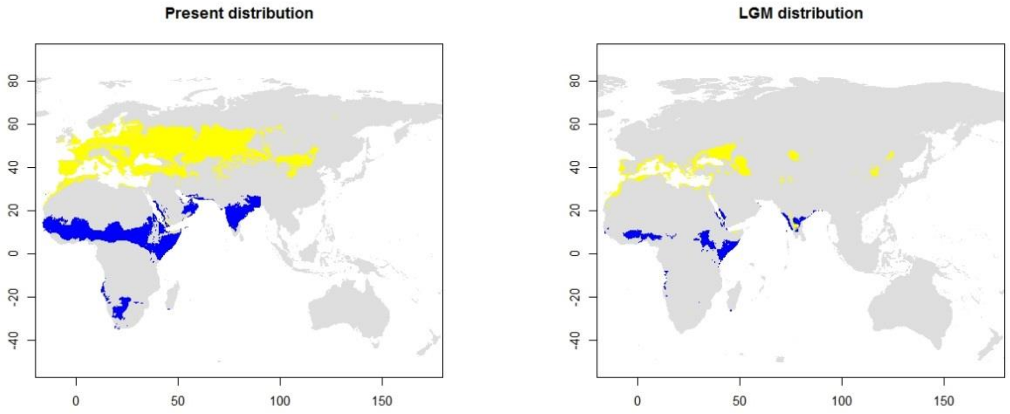
f. Locustellidae

i. *Locustella fluviatilis*

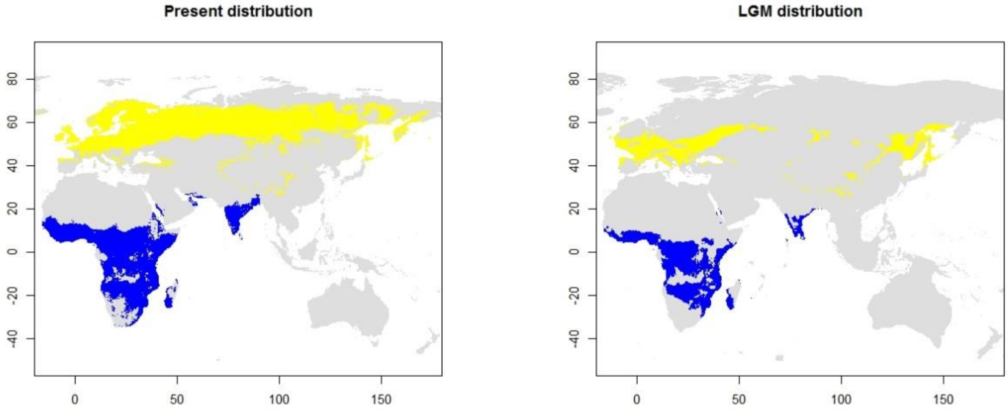


g. Motacillidae

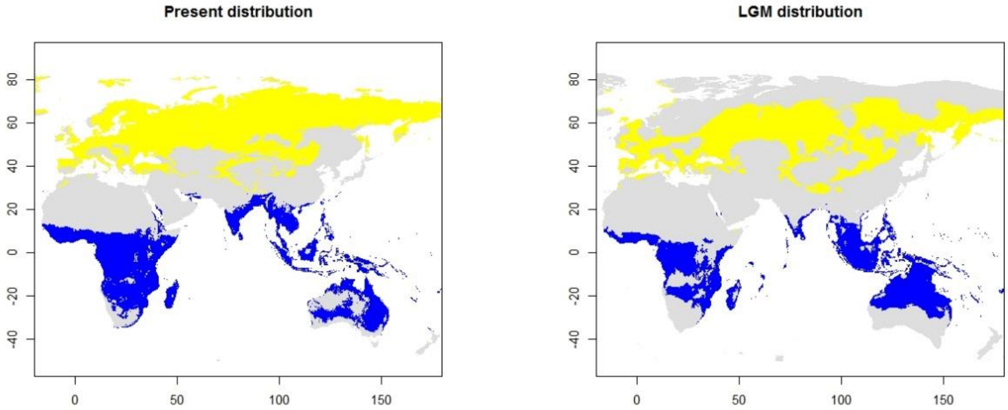
i. *Anthus campestris*



ii. *Anthus trivialis*

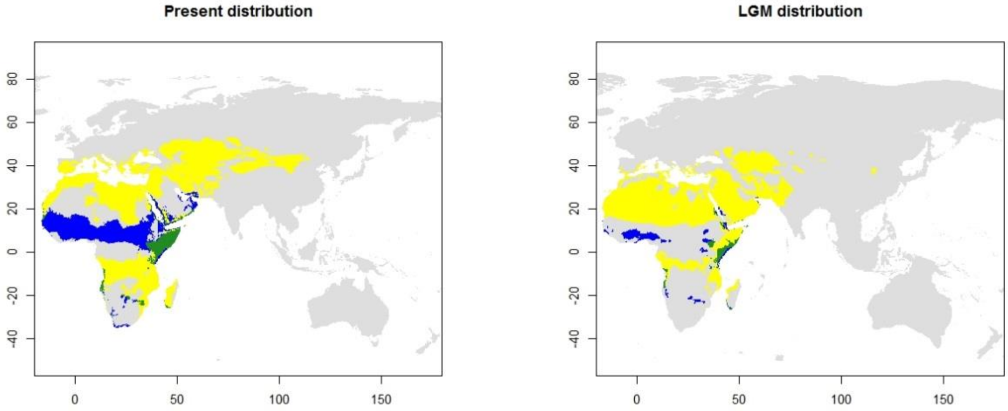


iii. *Motacilla flava*

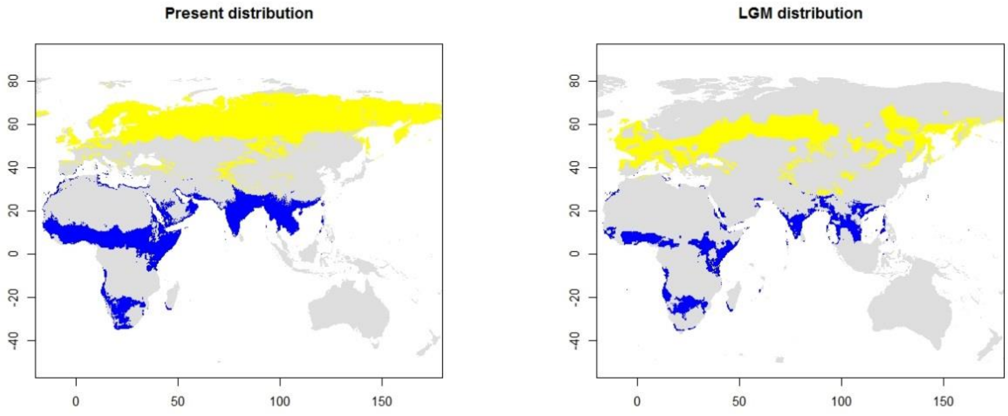


h. Muscicapidae

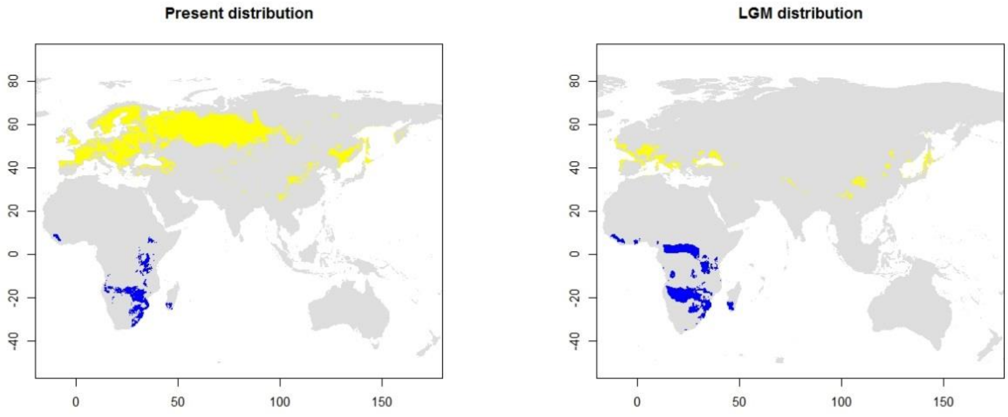
i. *Cercotrichas galactotes*



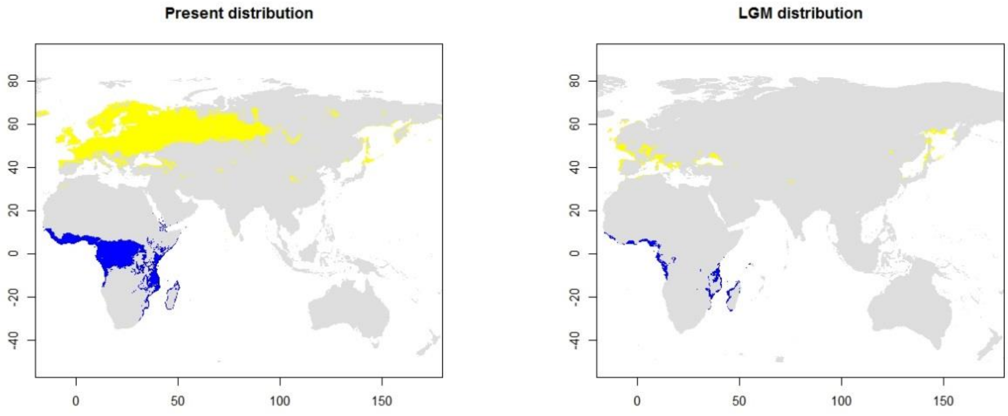
ii. *Cyanecula svecica*


Present distribution
LGM distribution

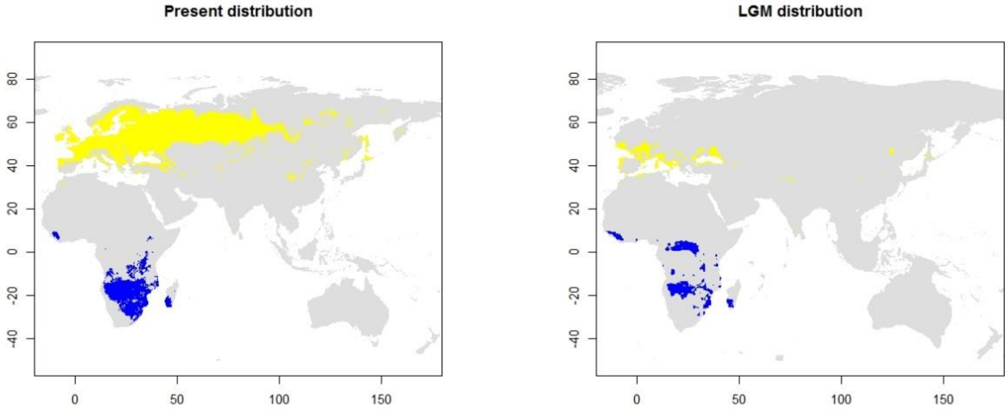
iii. *Ficedula albicollis*


Present distribution
LGM distribution

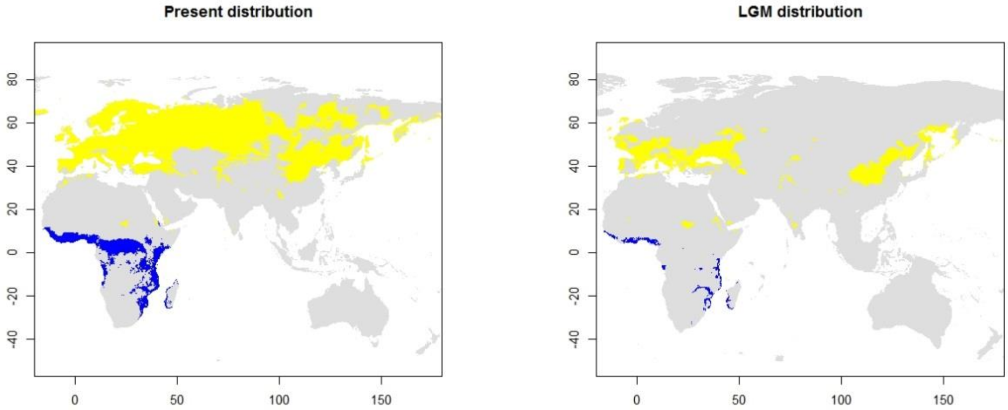
iv. *Ficedula hypoleuca*


Present distribution
LGM distribution

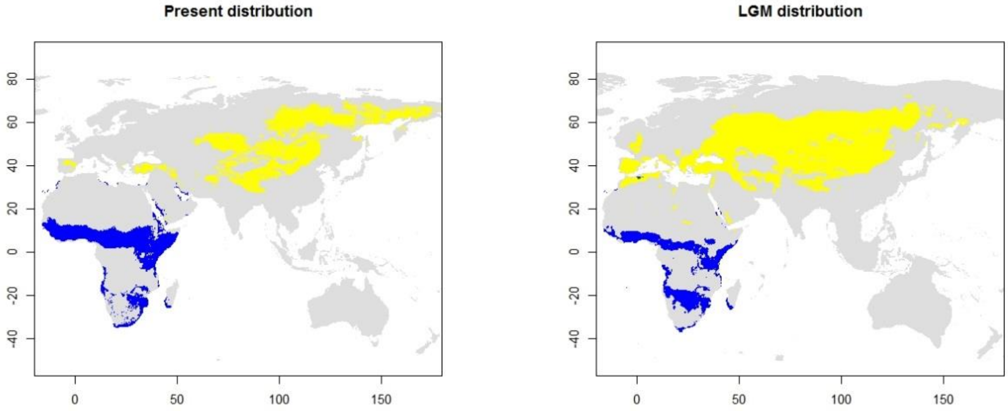
v. *Luscinia luscinia*



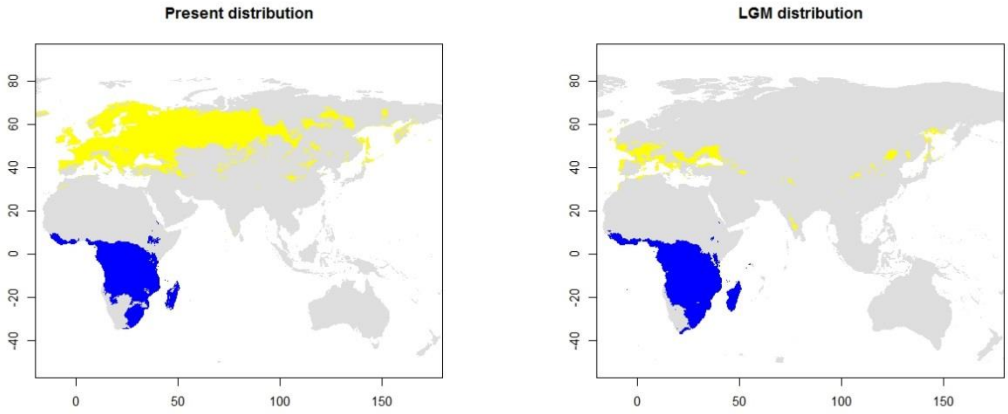
vi. *Luscinia megarhynchos*



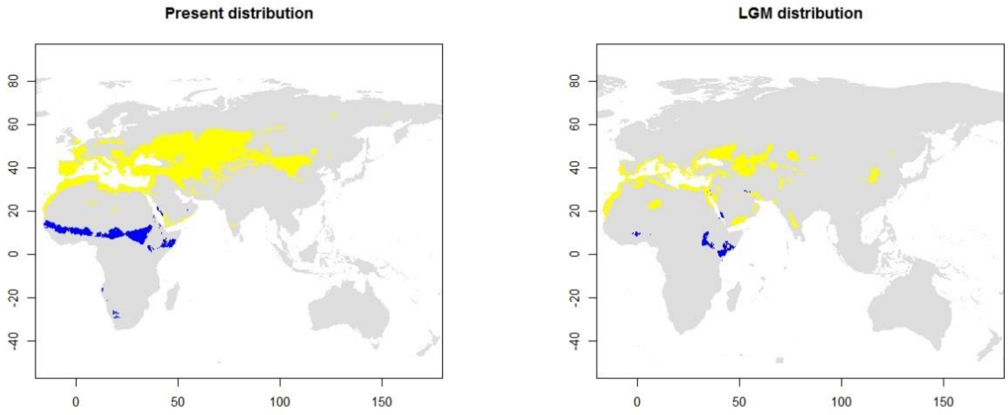
vii. *Monticola saxatilis*



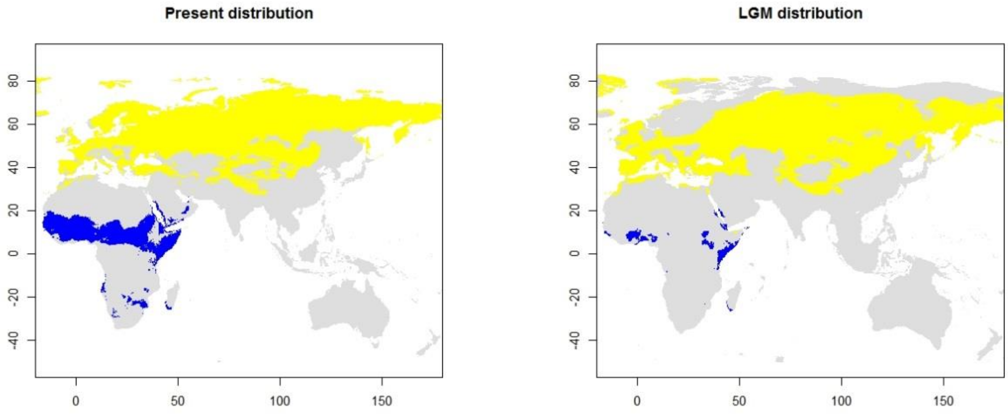
viii. *Muscicapa striata*



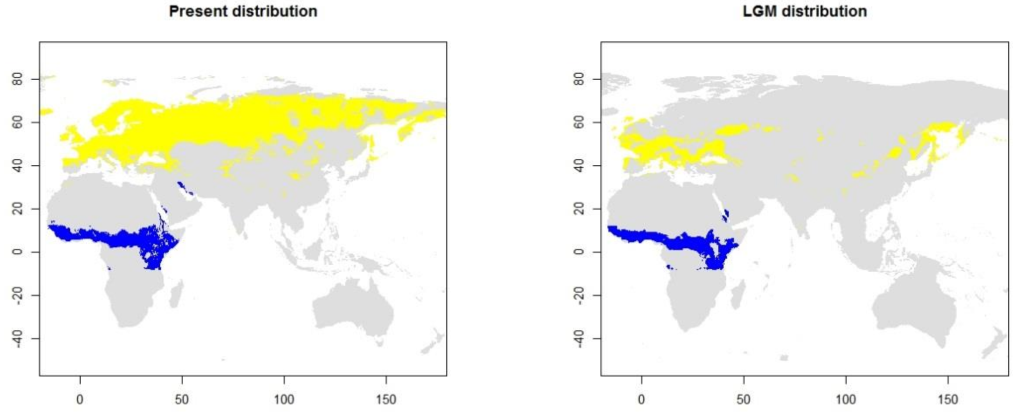
ix. *Oenanthe hispanica*



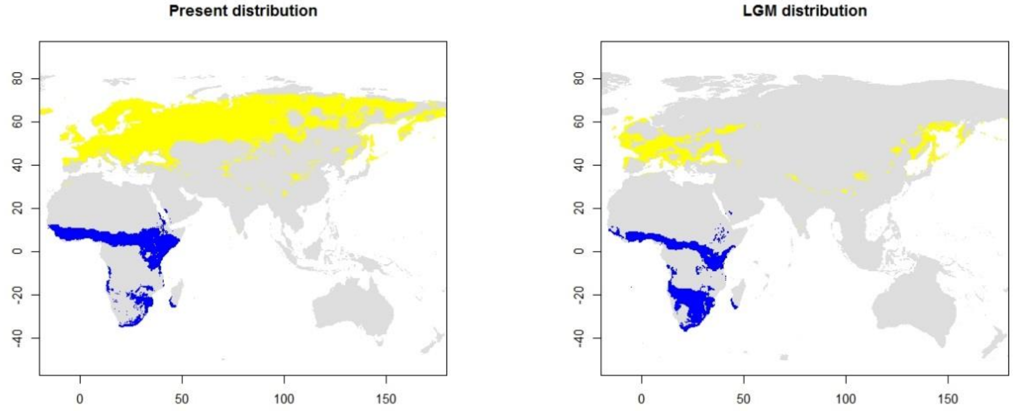
x. *Oenanthe oenanthe*



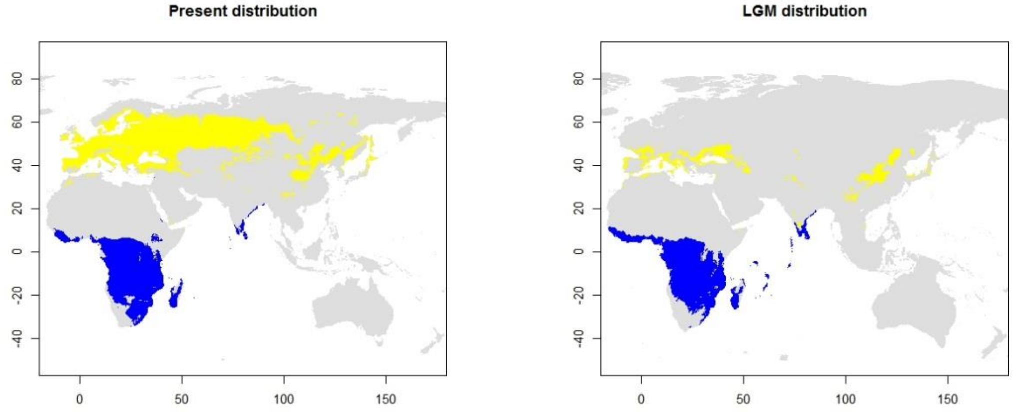
xi. *Phoenicurus phoenicurus*



xii. *Saxicola rubetra*

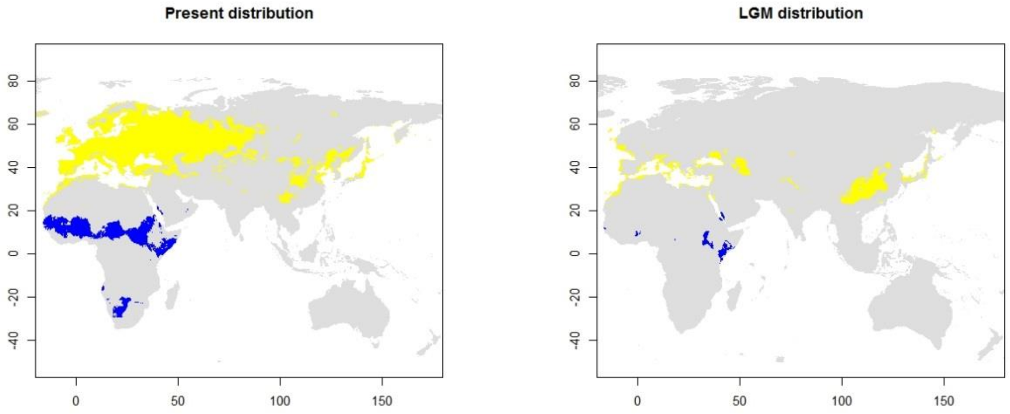


i. Oriolidae
    i. *Oriolus oriolus*

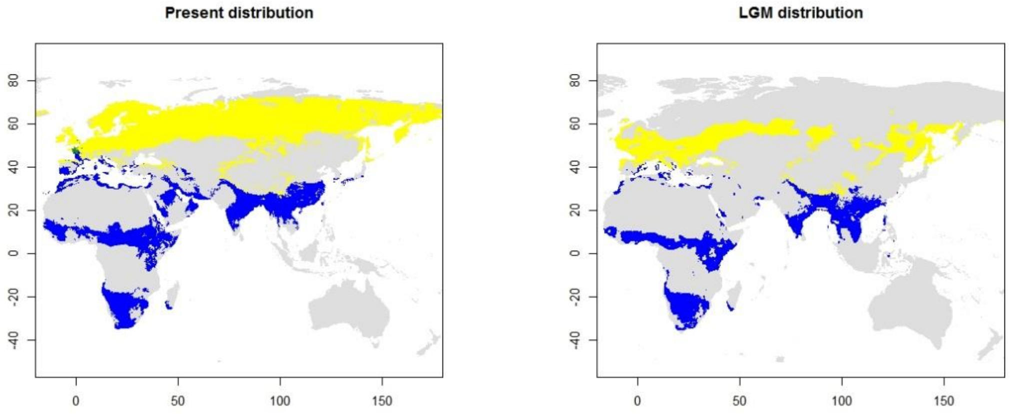


j. Phylloscopidae

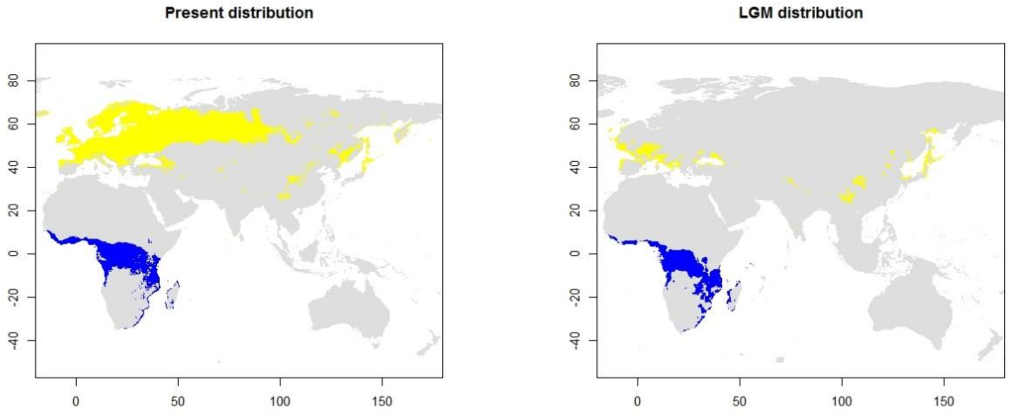
i. *Phylloscopus bonelli*



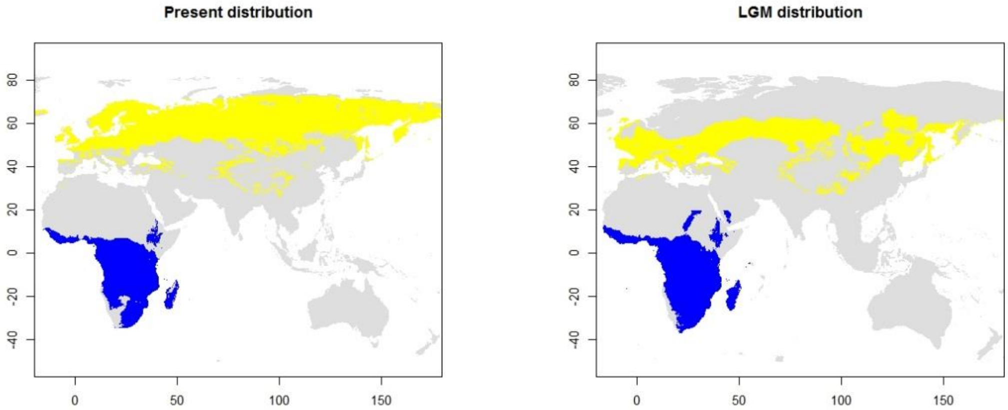
ii. *Phylloscopus collybita*



iii. *Phylloscopus sibilatrix*

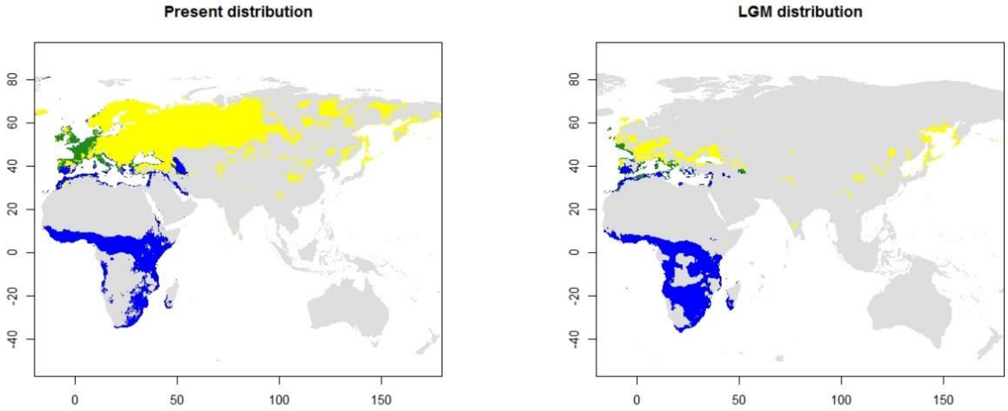


iv. *Phylloscopus trochilus*

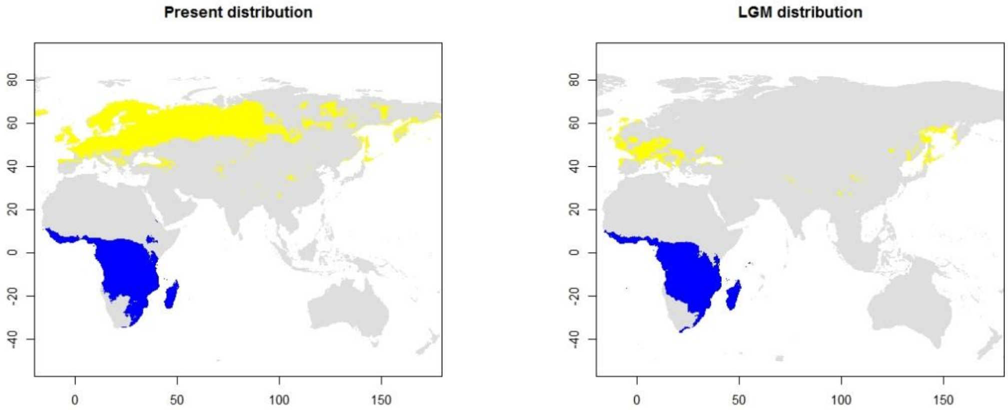


k. Sylviidae

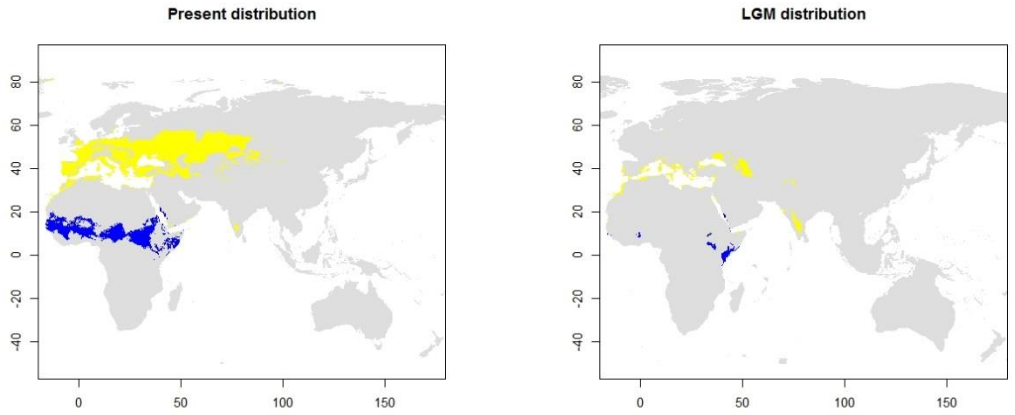
i. *Sylvia atricapilla*



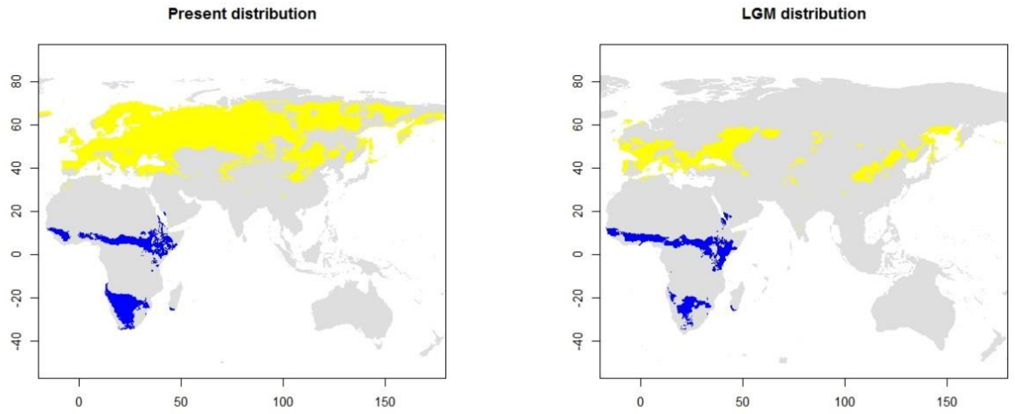
ii. *Sylvia borin*



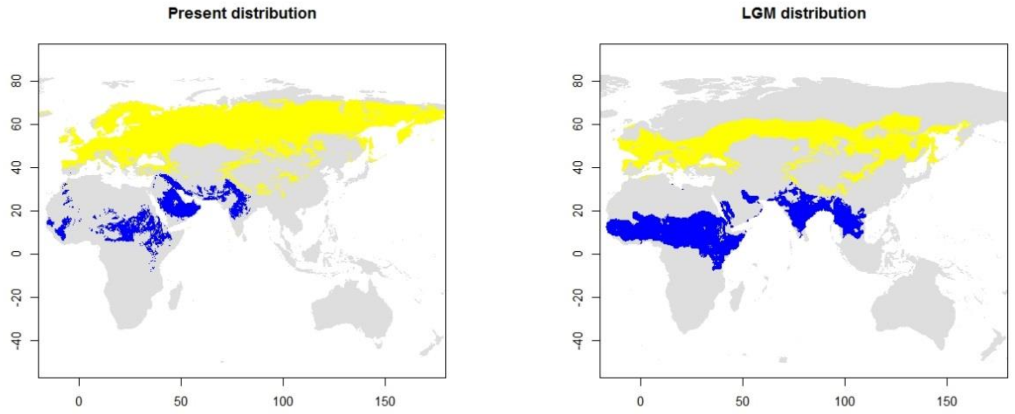
iii. *Sylvia cantillans*



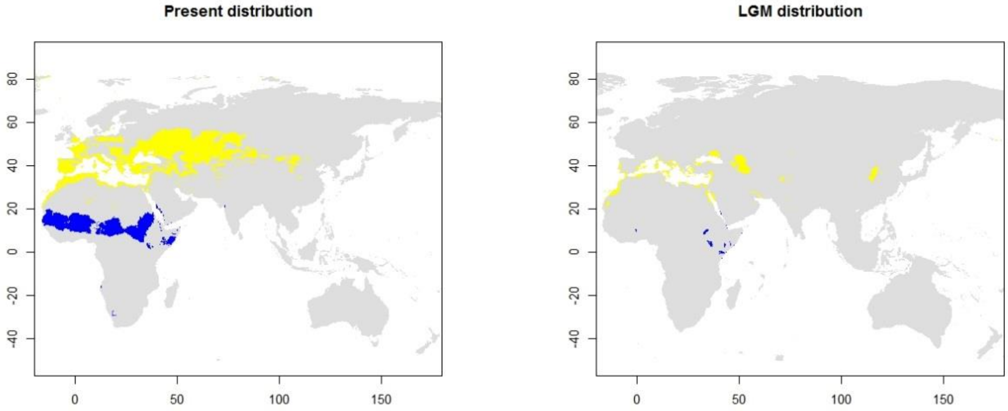
iv. *Sylvia communis*



v. *Sylvia curruca*



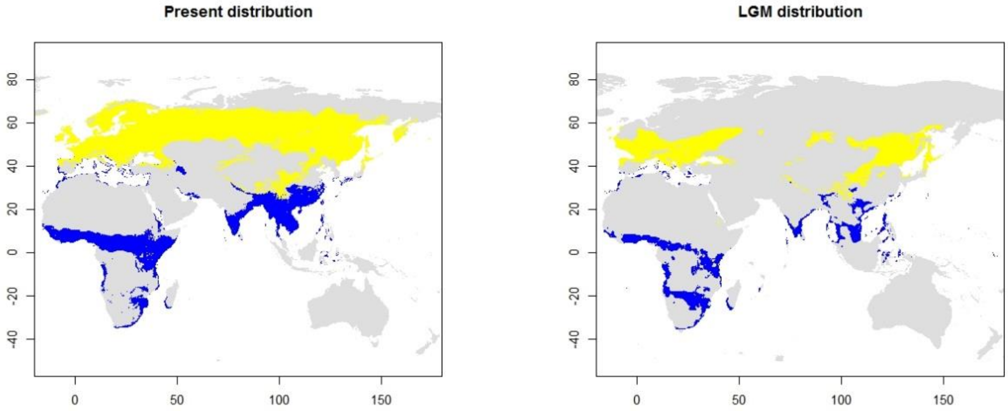
vi. *Sylvia hortensis*



12) Piciformes

a. Picidae

i. *Jynx torquilla*



13) Strigiformes

a. Strigidae

i. *Otus scops*