Ecology and evolution of climatic niches in birds

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SUMMARY

The term *climatic niche* refers to the climatic conditions within which a species can maintain a stable population. The quantification of the climatic niche from distribution data provides insight into how individual species relate to the environment. However, owing to the speed of current environmental changes, the development of models that apply to whole ecosystems is necessary to effectively assess the impact of climate change and inform conservation. Furthermore, as species adapt to new climatic conditions, their climatic niches can change. It is thus important to study climatic niches at evolutionary timescales. To this end, a macroecological and evolutionary approach in which ecological systems are studied at large taxonomic, spatial or temporal scales is required. However, for studies adopting this approach to make meaningful comparisons, climatic niches must be quantified in a consistent manner.

One important factor influencing the study of niche occupancy and quantification is that the distributions of species and climatic conditions are dynamic. As ~20% of species are migratory, birds provide an interesting group in which to study climatic niches. Until this thesis, a database of migratory behaviour across birds did not exist, so the impact of migration on both the occupation of niche space by birds, and the accurate, comparable quantification of niche space was unclear. Understanding the seasonal dynamics of climatic niches in migratory birds is important for understanding the evolution of migration and the factors affecting species' geographic distributions.

Secondly, a major assumption of the majority of studies projecting species distributions in response to climate change is that the climatic niche remains unchanged. In the context of climate change, it is important to know whether species are able to cope with new climatic conditions by adapting their climatic niche. A lack of spatially resolved climatic data for the deep past has, until now, precluded explicitly testing for a relationship between rates of climatic niche change and climatic conditions.

The overall objective of this thesis is to investigate the ecological and evolutionary dynamics of climatic niches. Using birds as a study system, I combine macroecological and evolutionary approaches to work at large taxonomic and temporal scales. The first chapter is a review paper addressing the question of how best to quantify climatic niches in birds, taking into account movement dynamics. To assess the relative impact of migration on climatic niche quantification from distribution data, a database of migratory behaviour for all 10,443 extant bird species was compiled. Past studies quantifying climatic niches in birds were surveyed in a literature review. This showed the majority of studies ignoring seasonal dynamics and quantifying climatic niches using distribution data of breeding ranges and annual climatic data only. Finally, using the Australian aviafauna as a case study, I asked how to take migration into account for accurate comparison of niches across bird species. The chapter provides a framework recommending appropriate occurrence data and methods for quantifying climatic niches depending on migratory behaviour and the spatial and temporal focus.

Secondly, I examine the seasonal dynamics of climatic niches of migratory birds. To test the hypothesis that birds migrate to track climatic conditions, I used breeding and wintering range maps to characterise the climatic niches of 437 closely related species of migratory and resident birds. Ordination methods were used to quantify seasonal niche overlap. Although I found some evidence of niche tracking, migrants were never found to track climatic niches perfectly (and – contrary to expectations - were found to track niches less closely than closely related non-migratory species). Evidence for niche tracking was found to vary according to breeding location and the direction of migration, indicating that the drivers of migration may vary according to geography as well as the direction of migration.

Finally, I used Wheatears (Genus *Oenanthe*) as a case study to test the hypothesis that there is a relationship between rates of climatic niche evolution and climatic conditions. I calculated the rates of niche evolution across the phylogeny using a variable rates model. Terrestrial climatic conditions were inferred from the mammal fossil record using methods from the field of paleo-biology. No relationship was found. This suggests that birds -which are highly mobile organisms- cope with changing climatic conditions through moving rather than adapting their climatic niche. However, as climatic niches did vary through time, I propose that factors such as biotic interactions drive niche evolution at this taxonomic scale.

This thesis highlights the importance of temporal dynamics in the niche space occupied by species across both ecological and evolutionary timescales. In doing so, this work has methodological implications for future studies. As migratory birds do not occupy the same climatic conditions in each season, it follows that accurate quantification of climatic niches should consider the climatic conditions experienced by a species over its entire geographic range. This study also has important theoretical and practical conclusions. First, I show that migratory birds do not occupy identical climatic conditions in each part of their range. Second, I show that climatic niche evolution is not driven by climatic conditions. The results at both temporal scales suggest that climate is not the sole determinant of bird distribution. Although these findings suggest a perhaps unexpected degree of resilience to changing conditions, other factors such as biotic interactions are important drivers of bird distribution. Climatic change may have negative impacts on species distributions indirectly through these factors. Further research on these, and their interaction with climate would be of great value.

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CONTENTS

ZUSAMMENFASSUNG

Hintergrund

Die klimatische Nische beschreibt die klimatischen Bedingungen, unter denen eine Art eine stabile Population aufrechterhalten kann. Da die klimatische Nische einen starken Einfluss darauf ausübt, wo eine Art existieren kann, ist sie ein nützliches Konzept, um wichtige ökologische Prozesse, wie zum Beispiel die Interaktionen zwischen Arten und ihrer Umgebung oder Diversifikation, zu verstehen. Des Weiteren ist die Nische, die eine Art füllt, auch ein Ergebnis evolutionärer Prozesse, wie zum Beispiel die Vererbung physiologischer Merkmale. Da klimatische Nischen als solche das Ergebnis sowohl evolutionärer als auch ökologischer Prozesse ist, ist es von Vorteil Methoden aus diesen beiden Disziplinen zu berücksichtigen.

Die Quantifizierung der klimatischen Nische basierend auf Verbreitungsdaten ist ein wichtiges Werkzeug, um tiefergehende Einsichten in individuelle Art-Umwelt Beziehungen zu erlangen, zum Beispiel um Vorhersagen treffen zu können wie Arten auf den Klimawandel reagieren werden. Im Hinblick auf den Umfang und die Geschwindigkeit, mit der sich die Umwelt im Moment verändert ist es notwendig Modelle zu entwickeln, die sich auf ganze Ökosysteme und globale Prozesse anwenden lassen, um den Effekt des Klimawandels effektiv zu bewerten, und um Arten- und Naturschutz zu unterstützen. Des Weiteren ist es wichtig klimatische Nischen über evolutionäre Zeiträume zu untersuchen, um die Prozesse zu verstehen, die Evolution, Diversifikation und Extinktion unterliegen, da sich klimatische Nischen mit der Anpassung einzelner Arten an neue klimatische Gegebenheiten ebenfalls wandeln. Zu diesem Zweck ist es von Vorteil einen makroökologischen Ansatz zu wählen, und Ökosysteme über ein breites taxonomisches, geographisches und zeitliches Spektrum zu untersuchen. Durch den Fokus auf übergreifende Muster versucht der makroökologische Ansatz die grundlegenden Mechanismen, jenseits der Eigenheiten einzelner Arten, Örtlichkeiten und Zeiträume zu identifizieren, die Ökosysteme formen.

Die Verfügbarkeit detaillierter Datensätze mit breitem taxonomischem Fokus, zum Beispiel Verbreitungsdaten oder DNA Sequenzdaten, hat in den vergangenen Jahren rapide zugenommen. Zusammen mit Fortschritten in statistischen und phylogenetischen Methoden hat dies dazu geführt, dass viele Forschungsprojekte einen makroevolutionären und -ökologischen Ansatz gewählt haben, um klimatische Nischen zu untersuchen. Allerdings ist es notwendig, dass klimatische Nischen über viele Arten hinweg auf eine konsistente Art und Weise quantifiziert werden, damit ein sinnvoller Vergleich möglich ist. Ein besonders wichtiger Punkt in dieser Hinsicht ist die zeitliche Dynamik denen klimatische Nischen unterliegen, sowohl über kurze (ökologische) als auch evolutionäre Zeiträume. Sowohl die Verbreitung einer Art als auch klimatische Gegebenheiten sind dynamisch, und dies ist ein wichtiger, aber oft missachteter Faktor für die Quantifizierung von Nischen. Ein gutes Beispiel hierfür sind Zugvögel, die etwa 20% aller Vogelarten ausmachen. Zugvögel stellen eine interessante, aber auch herausfordernde Artengruppe für die Untersuchung klimatischer Nischen dar. Obwohl Vögel generell überproportional gut erforscht sind, gibt es zurzeit keine umfassende Datenbank, die das Zugverhalten aller Vögel einheitlich erfasst. In Folge dessen ist der Einfluss des Vogelzuges auf die Position einzelner Arten im Nischenraum, und auf die präzise Quantifizierung desselben nicht gut verstanden. Ein besseres Verständnis der saisonalen Dynamik klimatischer Nischen hat wichtige Konsequenzen für das Verständnis der Evolution von Zugverhalten, der Faktoren die die Verbreitung von Arten beeinflussen, sowie der Reaktionen von Arten auf vergangenen und zukünftigen Klimawandel. Eine gängige Hypothese zur Erklärung des Vogelzuges ist, dass die Bewegung einzelner Arten dazu dient bestimmte klimatische Bedingungen über den Jahreszyklus zu verfolgen. Sollte diese Hypothese zutreffend sein, wäre zu erwarten, dass jene Arten dieselbe klimatische Nische über das ganze Jahr einnehmen.

Des Weiteren liegt vielen bisherigen Studien die Vorhersagen über klimawandelbedingte Veränderungen von Artverbreitungen machen eine wichtige Annahme zugrunde, nämlich dass die klimatische Nische einer Art an sich konstant ist. Allerdings ist bekannt, dass Arten ihre klimatischen Präferenzen auf unterschiedlichen Zeitskalen verändern. Im Kontext des aktuellen Klimawandels ist es allerdings wichtig zu verstehen, ob Arten in der Lage sind ihre klimatische Nische anzupassen, um auf neue klimatische Gegebenheiten reagieren zu können. Während viele Studien die Annahme machen dass die Veränderung von klimatischen Nischen durch Veränderung in Temperatur und Niederschlag angetrieben wird, hat bislang ein Mangel an geographisch expliziten Daten über terrestrische Umweltbedingungen durch evolutionäre Zeiträume eine explizite Überprüfung dieser Zusammenhänge verhindert.

Durchgeführte Studien

Das übergeordnete Ziel dieser Dissertation war es, die ökologische (d.h. saisonale) und evolutionäre Dynamik klimatischer Nischen von Vögeln zu untersuchen. Um dieses Ziel zu erreichen, wurde ein Ansatz gewählt der makroökologische, und evolutionsbiologische Methoden vereint, um ein breites taxonomisches und zeitliches Spektrum abzudecken.

Das erste Kapitel dieser Dissertation ist ein Übersichtsartikel, in dem ich die Frage beantworte wie klimatische Nischen am besten zu quantifizieren sind, wenn man die Dynamik des Vogelzuges in Betracht zieht. Um den Einfluss des Vogelzuges auf die

Nischenquantifizierung mittels artspezifischer Verbreitungsdaten abzuschätzen haben wir zunächst eine Datenbank erstellt, die das Zugverhalten aller 10.443 lebenden Vogelarten katalogisiert. Insgesamt haben wir 78,9% aller Arten als Standvögel eingeordnet, sowie 19,9% aller Arten als Zugvögel. Darüber hinaus wurden 1% der Arten als nomadisch eingestuft, d.h. Arten die unregelmäßige, und von Jahr zu Jahr unterschiedliche Zugbewegungen durchführen. Eine konsistente Klassifizierung des Zugverhaltens für alle bekannten Vogelarten hat bislang nicht existiert. In einem zweiten Schritt habe ich eine Übersicht über die Methoden zur Quantifizierung klimatischer Nischen in der makroökologischen Literatur erstellt. Das Ergebnis derselben ist, dass die überwiegende Mehrzahl der Veröffentlichungen auf Verbreitungsdaten aus der Brutzeit sowie jährlichen Klimadaten basieren, obwohl die saisonalen Zugbewegungen vieler Arten wohlbekannt sind. Im dritten und letzten Teil dieses Kapitels habe ich die Frage bearbeitet wie man Zugbewegungen am besten für eine präzise und zwischenartlich vergleichbare Nischenquantifizierung in Betracht ziehen kann. Zu diesem Zweck habe ich die Avifauna Australiens als Fallstudie gewählt, um zu untersuchen welche Vor- und Nachteile die Verwendung von Verbreitungskarten gegenüber Punktverbreitungsdaten zur Erfassung saisonaler geographischer Muster der Artenvielfalt hat. Da die Quantifizierung klimatischer Nischen auf Verbreitungsdaten basiert, wurde die Annahme gemacht, dass die Fähigkeit saisonale Artenvielfaltsmuster abzubilden eine adäquate Näherungsvariable für die Fähigkeit ist, Muster in den saisonalen Klimanischen einer gesamten kontinentalen Avifauna abzubilden. Es wurde festgestellt, dass saisonale Verbreitungskarten insbesondere für die Untersuchung nomadischer Arten von geringem Wert sind. Als Ganzes bietet dieses Kapitel Rahmenempfehlungen für die Datenanforderungen und Methoden, die je nach Zugverhalten einer Art, und dem geographischen, beziehungsweise zeitlichen Fokus einer Studie für eine optimale Nischenquantifizierung notwendig sind. Diese Rahmenempfehlungen liefern eine Basis für verbesserte und robustere Ansätze zur Quantifizierung dynamischer Klimanischen.

Im zweiten Kapitel meiner Dissertation untersuchte ich die saisonale Dynamik klimatischer Nischen von Zugvögeln. Dabei überprüfte ich die Hypothese, dass Zugvögel in ihrem Jahreszyklus durch die Zugbewegung eine gewisse klimatische Nische verfolgen. Zu diesem Zweck habe ich auf der Basis von Brut- und Überwinterungsarealkarten saisonale klimatische Nischen für 437 Zug- und Standvogelarten aus acht Kladen der Sperlingsvögel (Passeriformes) charakterisiert. Mit Hilfe von Ordinationsmethoden wurde dann der innerartliche saisonale Nischenüberlapp quantifiziert. Obwohl ich ein gewisses Maß an klimatischer Nischenverfolgung bei Zugvögeln belegen konnte, war diese nie perfekt, sondern entgegen der Arbeitshypothese war der Nischenüberlapp zwischen Brut- und Überwinterungsnische bei Standvögeln grösser als bei Zugvögeln. Der Beweis für die

Verfolgung einer klimatischen Nische in einer Art war von mehreren Faktoren, wie zum Beispiel der geographischen Verortung des Brutgebietes und der Zugrichtung, abhängig. Dies lässt darauf schließen, dass sich die Ursachen für den Vogelzug sowohl geographisch als auch saisonal (d.h. abhängig von der Zugrichtung) unterscheiden. Neben klimatischen Faktoren scheint es, dass auch die Suche nach Ressourcen sowie wechselseitige Artbeziehungen, z.B. die Vermeidung von Wettbewerb, das Zugverhalten beeinflussen.

Im dritten Kapitel untersuchte ich die evolutionäre Dynamik klimatischer Nischen. Im Kontext des heutigen Klimawandels ist es wichtig zu verstehen, wie Arten auf neue Umweltbedingungen reagieren. Bisherige Studien haben die Vermutung angestellt, dass Zeiträume, in denen sich das Klima wandelt mit Veränderungen klimatischer Nischen assoziiert sind. Diese Vermutung wurde bislang allerdings noch nicht formal überprüft, weshalb ich die Steinschmätzer (Gattung *Oenanthe*) als Fallstudie wählte, um explizit zu untersuchen ob es einen Zusammenhang zwischen den Raten klimatischer Nischenevolution und den Veränderungen paläoklimatischer Bedingungen gibt. Zu diesem Zweck habe ich Methoden der Klimanischenquantifizierung mit datierten molekularen Phylogenien verknüpft, um die Raten klimatischer Nischenevolution mit einem variablen Ratenmodell abzuschätzen. Paläoklimatische Umweltbedingungen wurden mit Hilfe paläobiologischer Methoden aus dem Fossilbericht altweltlicher Säugetiere der vergangenen 20 Millionen Jahre erschlossen. Die Fallstudie konnte keinen Zusammenhang zwischen Nischenevolution und Umweltbedingungen feststellen. Dieses Ergebnis legt nahe, dass Vögel als überaus mobile Organismen, auf klimatische Veränderungen eher durch Arealverschiebungen reagieren, als durch eine Anpassung ihrer klimatischen Nische. Die klimatischen Nischen der Steinschmätzer waren allerdings an sich nicht statisch, so dass andere Faktoren wie zum Beispiel biologische Wechselbeziehungen für die Nischenevolution dieser Gattung verantwortlich sein müssen.

Fazit

Meine Dissertation beleuchtet die zentrale Bedeutung zeitlicher Dynamiken für den Nischenraum, den Arten über ökologische (d.h. saisonale) und evolutionäre Zeiträume einnehmen. Aus ihr ergeben sich methodische Konsequenzen für Zukünftige Studien klimatischer Nischen. Der Befund, dass die klimatischen Nischen von Zugvögeln nicht saisonal konstant sind, zeigt dass es für mobile Kladen wie Vögel notwendig ist die klimatischen Bedingungen über den gesamten Jahreszyklus und das gesamte Verbreitungsgebiet in Betracht zu nehmen, um die jeweiligen klimatischen Nischen voll charakterisieren zu können. Meine Dissertation stellt Rahmenempfehlungen für Datenqualität und Methoden auf, die einen optimalen Ansatz zur Berücksichtigung von Zugbewegungen in die Nischenquantifizierung erlauben, und damit weitere Fortschritte in diesem Forschungsfeld ermöglichen. Des Weiteren ist diese Arbeit eine der ersten Studien, die die Mechanismen der Nischenevolution formal überprüft. Der Arbeitsablauf, der in den jeweiligen Fallstudien gewählt wurde, kann somit als Blaupause dienen, um weitere Faktoren, wie zum Beispiel wechselseitige Artbeziehungen, Zugfähigkeit oder evolutionäre Schlüsselanpassungen, zu untersuchen die diesen evolutionären Prozessen unterliegen könnten.

Über diese methodischen Innovationen hinaus, hat meine Arbeit auch wichtige theoretische und praktische Schlussfolgerungen produziert. Zum einen zeigt die Betrachtung saisonaler Klimanischen, dass Zugvögel entgegen gängiger Annahmen nicht denselben Umweltbedingungen in ihren Brut- und Überwinterungsarealen ausgesetzt sind. Zum anderen zeigt meine Betrachtung von Klimanischen über evolutionäre Zeiträume, dass die Nischenevolution nicht von klimatischen Bedingungen angetrieben wird. Zusammengenommen zeigen diese Ergebnisse auf unterschiedlichen Zeitskalen, dass das Klima nicht der alleinige Faktor ist, der die Artverbreitung von Vögeln bestimmt. Während dieser Befund Raum für Optimismus schafft, was die Auswirkungen des aktuellen Klimawandels auf Vögel angeht, zeigt er auch auf, dass Faktoren wie wechselseitige Artbeziehungen und das Mobilitätspotential von Arten einen wichtigen Einfluss auf Artverbreitungen ausüben. Diese Faktoren könnten jedoch an sich vom Klimawandel beeinflusst sein, und Untersuchungen dieses Zusammenspiels zwischen Klima und anderen Faktoren und die daraus resultierenden Einflüsse auf Artareale bieten ein vielversprechendes Arbeitsfeld für zukünftige Studien.

1 INTRODUCTION

Understanding what determines species' distribution is a fundamental question in ecology, crucial not only to our understanding of the geographic range limits of individual species, but also overall patterns of biodiversity (Butlin et al. 2002). There are many factors that influence where a species is able to persist. These factors can be broadly categorised as being either abiotic or biotic. Abiotic factors describe all of the non-living components that determine the range limit of a species such as climate (e.g. temperature, precipitation) (Ricklefs and Miller 1999). In contrast, biotic factors describe the living components that shape the distribution of a species, for example the presence or absence of competitors, predators, parasites, prey or mutualistic species (Soberon and Peterson 2005). In the light of current changes, for example climate change (Bellard et al. 2012), habitat loss (Newbold 2018) and the introduction of non-native species (Early et al. 2016), it is increasingly pressing that we understand those factors that limit the distribution of species. This understanding is key for predicting where species will be able to maintain populations in the future.

One subset of abiotic factors that researchers have long associated with species distribution is climate. Climate refers to the generally prevailing weather conditions in a given region and is a composite of many factors such as precipitation, temperature and humidity (Reside et al. 2010). Climate can directly limit species distributions through physiological constraints, for example small-leaved lime (*Tillia cordata*) is unable to extend its distribution northwards in UK as cold conditions inhibit the growth of its pollen tubes (Rosbakh and Poschlod 2016). Alternatively, climate can indirectly influence species distribution by altering interspecific interactions such as predation and competition (Tylianakis et al. 2008).

Support for the influence of climate on species distribution comes from a wide diversity of sources. For example, as early as 1807, Alexander Von Humboldt proposed that the general increase in species diversity observed towards the equator was associated with climatic conditions. More recently, studies have shown that shifts in range limits of species occur over a wide variety of time scales in relation to changing climatic conditions. For example the daily movements of zooplankton in the water column have been linked to climate fluctuations (Williamson et al. 2011), abundance records for British birds showed that the range margins of 80 species have shifted during a 10 year period of period of warming (Massimino et al. 2015) and finally examination of the fossil pollen record has showed that plant species (e.g. Hemlock) shifted their distribution over 1000s of years in response to climatic changes occurring since the last glacial maximum (Graham and Grimm 1990). In particular, changes in species distribution consistent with climate change that have occurred over the last century have provided directly observable evidence of the role of climate (Parmesan et al. 1999, Tingley et al. 2009, Massimino et al. 2015). These changes also highlight that it is increasingly urgent to understand the influence of climate on species distributions. In the light of the strong evidence that climate is an important influence on the distribution of species, and that climate is predicted to change in the coming years (IPCC 2014) it is increasingly important to study this relationship (La Sorte et al. 2018, 2019).

1.1 The climatic niche

The ecological niche is a central concept to ecology. Despite definitions of the term varying in detail, at their root, each interpretation describes the relationship between a species and its environment. Grinnell (1917) defined the niche as being the habitat requirements and the behavioural adaptations that allow a species to persist, whereas Elton (Soberón 2007) defined the niche of a species as its place in the biotic environment (i.e. its relation to resources and competitors). An important subset of the ecological niche is the climatic niche which can be defined as the climatic conditions under which a species is able to maintain a stable population. This is a useful concept to help understand the relationship between species and climate (Pearson and Dawson 2003, Soberón 2007). A further important distinction to make is between the fundamental and the realised niche. The fundamental climatic niche of a species describes all of the climatic conditions in which a species could potentially survive. However, a species rarely occupies its entire fundamental niche because of factors such as interactions with other species and dispersal limitations (Soberón 2007). Therefore, the climatic niche space that a species actually occupies is usually a subset of the fundamental niche, termed its realised niche (Malanson et al. 1992).

The climatic niche of a species can be quantified in a variety of ways. For example, the climatic niche can be determined by direct measurement of individual physiological tolerances, such as the upper and lower thermal limits of a species (Bennett et al. 2018, Buckley et al. 2018). This is the approach taken by mechanistic studies, which seek to provide mechanistic explanations for the observed correlations between species distributions and climate (i.e. causation). A strength of this method is that it allows quantification of something approximating the fundamental niche (i.e. all of the climatic conditions in which a species is able to exist independent of limiting factors such as biotic interactions, and dispersal). However as quantifying climatic niches through manipulative experiments is expensive and time-consuming, data of this quality are only available for a limited, non-random sample of species. For example the GlobTherm database (Bennett et al. 2018) comprises data on the upper thermal limits for less than 5% of mammal species. Further, a comprehensive survey of the literature by Khaliq et al. (2014) found that data on the physiological niche was only available for 349 of the more than 10,000 extant species of birds (<4%), the majority of which were range resident. Additionally, intraspecific variation and local adaptation mean that physiological quantifications based on measurements of a few individuals are unlikely to represent the full range of conditions that the species as a whole can tolerate (Herrando-Pérez et al. 2019).

Alternatively, climatic niches can be quantified using a correlative approach in which the species' observed distribution is regressed with climatic data. Dimension reducing techniques such as ecological niche modelling and ordination can then be used to infer a species' climatic niche from its geographic distribution (Dolédec et al. 2000, Thuiller et al. 2009).The underlying assumption of this method is that the climatic conditions in which a species is currently found living are representative of its climatic niche. However in reality, niches quantified using correlative methods rarely identify the full combination of climatic conditions in which the species could exist, i.e. its fundamental climatic niche (Hutchinson 1957, Soberón 2007) both because of incomplete data and because a species' distribution is in practice limited by other factors (Warren et al. 2014). Despite these limitations, given the paucity and often biased availability of physiological data, the majority of studies adopt a correlative approach to quantify climatic niches. In fact, climatic niches quantified from broad-scale distribution data are considered to be a reasonable approximation of species' fundamental climatic niche (Wisz et al. 2013) and have been confirmed to produce similar results to mechanistic studies (Kearney et al. 2010).

Climatic niches have been quantified using these methods in order to answer a wide range of research questions: for example, to explain current distribution patterns of species (Moreno-Letelier et al. 2014), to predict distribution in new climatic conditions (Peterson et al. 2002, Hof et al. 2011) or geographical areas (Peterson 2003), to study niche evolution (Cooney et al. 2016) and to support conservation (Zhang et al. 2012). Recent studies have confirmed that the climatic niche concept is an effective tool for predicting how species will respond to climate change. For example, Bowler et al. (2015) showed that the climatic niche successfully explains the variation in recent population trends of many species, whilst Rinnan and Lawler (2019) were able to confirm a relationship between the climatic niche and a species' vulnerability to climate change.

Although, as illustrated above, climatic niche quantification has proved an extremely effective and useful tool for gaining an in-depth understanding of how individual species relate to the climate, adopting this individual species approach is limited in its explanatory power. Owing to the nature and speed of current natural and anthropogenic environmental changes, the development of models that apply to whole ecosystems and global processes is urgently needed. To this end, given the relative lack of, and taxonomic biases in physiological measures of the climatic niche, climatic niches quantified using correlative approaches are particularly useful.

1.2 Macroecological and macroevolutionary approaches

In order to examine climatic niches across multiple species and across time, macroecological and macroevolutionary approaches can be used. Macroecological studies investigate ecological systems at large taxonomic, spatial or temporal scales (Brown and Maurer 1989). By focusing on broad patterns at large spatial scales, across many species, macroecology seeks to generalise beyond the particularities of individual species, regions and points in time and instead identify general mechanisms that shape ecological systems (Blackburn and Gaston 2003).

An important, but often overlooked aspect of the macroecological approach is that it encompasses studies with large temporal scales. The study of population trends observed over decades (Bowler et al. 2017) or tens of thousands of years (Bálint et al. 2018), and studies that examine the ecology of species over millions of years (e.g. diversity dynamics of mammals over the last 20 million years (Fritz et al. 2016)) can all be considered macroecological studies based on the temporal scale. This long term perspective is particularly important as the relationship between species and climate is not necessarily constant through time and any species' present climatic niche is the result of both ecological and evolutionary processes (Holt 2009). It follows, then, that the study of climatic niches benefits from an approach that combines the methods of macroecology and evolutionary biology. It is particularly important to study climatic niches at very large, evolutionary timescales in order to understand the processes that drive trait evolution, diversification and extinction. The study of macroevolutionary processes makes use of phylogenetic reconstruction to investigate these large scale evolutionary trends at, or above the species level (Stanley 1982).

The combination of increasing availability of distribution data and molecular data with broad taxonomic coverage, alongside advances in analytical methods has led to great numbers of studies examining climatic niches across many species (e.g. Title and Burns 2015, Cooney et al. 2016). Such macroecological and macroevolutionary studies have enhanced our understanding of the general taxonomic, geographic, and temporal trends of climatic niches and fundamental processes that have shaped them (Böhning-Gaese 2005, Gaston and Blackburn 2007). For example, the understanding of global patterns in niche breadth (Quintero and Wiens 2013a, Khaliq et al. 2014), species-energy relationships (Anderson and Jetz 2005) and niche evolution (Araújo et al. 2013) has benefited from taking a broad-scale approach. However, in order for such studies to make meaningful comparisons and inferences, it is essential that climatic niches be quantified consistently across species. In particular, one aspect that has received little attention from researchers is the dynamics of climatic niches, both current (ecological) and over evolutionary timescales. For example, the impact that migration has on both the occupation of niche space, and the accurate, comparable quantification of niche space remains unclear.

1.3 Seasonal dynamics

An important factor influencing niche occupancy and quantification that has often been overlooked in macroecological studies is that both the distribution of species and the environmental conditions available to them are highly dynamic in space and time at a variety of scales (e.g. days, seasons, decades). For example, animals from across a variety of taxa, including arthropods, birds, fish, and mammals, are known to be seasonal migrants, shifting distribution in a predictable way each year. Over a longer time period, range shifts have been observed in a variety of taxa in response to changes in the climate that have occurred in the preceeding decades (e.g. in plants; Gehrig-Fasel et al. 2007, and birds; Massimino et al. 2015). Although seasonal variations in climate, which are most pronounced in temperate regions, perhaps offer the most striking patterns of climatic variation, short term weather variations (Reside et al. 2010), and long term climate trends are also important aspects of climate variation (IPCC 2014). Accurate quantification of climatic niches from distribution data crucially depends on knowing the precise spatial and temporal occurrence of species, and the corresponding climatic conditions at those locations and times. Therefore, these dynamics pose a challenge to accurate quantification of climatic niches.

Because birds are highly mobile, they represent a particularly interesting, yet challenging, group in which to study climatic niches. Migration is a widespread and diverse phenomenon in birds, with almost one fifth of all bird species displaying some degree of migratory behaviour (Kirby et al. 2008). It follows from this that in order to accurately quantify climatic niches in birds it is necessary to take into account the dynamic nature of their distributions and the climatic conditions, within and between years (Laube et al. 2015). The true challenge that needs to be addressed for accurate niche quantification is identifying which climatic conditions migratory species experience when they occupy each part of their dynamic distribution (Laube et al. 2015, La Sorte et al. 2019).

The wide variety of migratory behaviours found both across and within bird species has important implications for the kind of data and methods required in order to achieve consistent quantification of climatic niches across many species. For example, for the northern wheatear *Oenanthe oenanthe* which travels almost 15,000km each year between

Alaska and eastern Africa, accurate climatic niche quantification from distribution data requires consideration of the climatic conditions experienced at their breeding sites, along their migratory flyways, at stopover sites, and at their non-breeding sites. Although the conditions they experience at the breeding and non-breeding sites can be reasonably ascertained from seasonal range maps, in reality we know relatively little about where they are found in-between. This problem is even worse for nomadic species such as the budgerigar *Melopsittacus undulatus* that move and breed opportunistically throughout their range and have unpredictable year-to-year movements (Allen and Saunders 2002, Newton 2008). For such species, detailed, temporally explicit distribution data are needed across several years to quantify their climatic niches appropriately (Reside et al. 2010, Schidelko et al. 2013). Data that have sufficiently high resolution, both spatially and temporally, are currently limited to only a few species (Teitelbaum et al. 2016, Thorup et al. 2017, Tucker et al. 2019). Although data derived from new tracking techniques are rapidly accumulating across many species (Bridge et al. 2011, Kays et al. 2015) it is unlikely that tracking can solve problems of taxonomic coverage.

Owing to a lack of information on the distribution of bird species outside of their breeding range and a lack of knowledge about the timing of such migrations (i.e. when species are present in each part of their range), in practice the distribution data used to quantify climatic niches of birds usually ignore temporal dynamics and focus exclusively on the annual climatic conditions for the breeding range only (e.g. Pigot et al. 2010, Cooney et al. 2016). Although such an approach is able to accurately quantify the climatic niche of resident species that remain on the breeding range year-round, it is incapable of accounting for migratory species. In taking such an approach the quantified niche for migratory species includes conditions that migratory species definitely do not experience whilst potentially excluding conditions that are experienced in the non-breeding range. This means that climatic niche quantifications are at risk of over- or under-estimating the climatic niches of migratory birds. Since climatic niches quantified using this method are not comparable between migratory and resident species this is a particular problem for macroecological and evolutionary studies which examine climatic niches across many species with different migratory behaviour.

Further, although birds are disproportionately well-studied and are arguably one of classes of organisms of which we have the greatest knowledge (Clark 2002, Orme et al. 2006, Jetz et al. 2012), there was no comprehensive database of migratory behaviour compiled in a consistent way prior to the work undertaken for this thesis. The lack of a comparable classification of migratory behaviour across all birds compounds the problem as it prevents an assessment of the relative impact migration has on accurate, comparable niche quantification in birds.

1.4 Seasonal dynamics of climatic niches: Niche tracking vs niche switching

Migratory species offer a unique opportunity to study the seasonal (ecological) dynamics of climatic niches. This has important implications for understanding the evolution of migration (Nakazawa et al. 2004); the factors affecting species' geographic distribution (Boucher-Lalonde et al. 2013); and the responses of species to past or future climate change (Thomas et al. 2004).

One hypothesis proposed to explain the seasonal movements of migratory species is that they move to track preferred climatic conditions throughout the year; this is known as "niche-tracking" (Joseph and Stockwell 2000). However, despite the considerable attention that has been given to migration (Greenberg and Marra 2005), it remains unclear to what degree species track specific climatic conditions by seasonal movements. Migratory species might be expected to move to track climatic conditions directly if they cannot survive the seasonal variation in climate, as a result of physiological limitations (Joseph and Stockwell 2000, Somveille et al. 2015). Although birds are able to regulate their internal body temperature independently of the ambient conditions, this is expensive in terms of energy, meaning that there are limits to the climatic conditions under which a species is able to survive (Khaliq et al. 2014). As well as responding to direct physiological limitations, migrants might track climatic conditions indirectly by moving to track seasonally available resources (Greenberg and Marra 2005, Luis Tellería et al. 2008, Thorup et al. 2017). If migratory species are moving to track specific climatic conditions, one would expect them to occupy the same climatic niche throughout the year.

Alternatively, migratory species might occupy different sections of their climatic niche space at different point in the year; this is commonly referred to in the literature as "niche-switching" (Nakazawa et al. 2004). This would be expected if migratory species move to avoid extreme climatic conditions, rather than to track specific conditions (Newton 2008), if they have different requirements in each season (Spencer 1982), or because their movement is driven by factors other than climate, such as nest predation (McKinnon et al. 2010).

Several studies have used the concept of the climatic niche to assess whether seasonal migrants track the climatic conditions in their breeding grounds when moving to non-breeding grounds, and vice versa (Boucher-Lalonde et al. 2013, Laube et al. 2015). Mixed support has been found for climatic niche-tracking, with some species occupying the same climatic conditions across seasons (niche-tracking) and others not (Nakazawa et al. 2004, Martinez-Meyer et al. 2004, Zurell et al. 2018). For example, although Joseph and Stockwell (2000) found that the Swainson’s flycatcher tracks its niche throughout the year, subsequent studies on different taxa have shown that this is not the case for all migratory species (Nakazawa et al. 2004, Martinez-Meyer et al. 2004, Zurell et al. 2018). Migratory species in the family Parulidae (American wood-warblers) were found to track their niche to a greater extent than resident species (Gómez et al. 2016). As these studies were carried out on different groups of birds, in different geographic regions, and using a variety of different methods, generalisation across studies is difficult and the reasons behind the observed variation in niche tracking across species remain unclear.

1.5 Evolutionary dynamics

A major assumption of predictive studies is that lineages retain their ancestral niche, or change very slowly, over millions of years (i.e. niche conservatism; Cooper et al. 2010). However over the past 25 years, increased availability of distribution data, advances in modelling methods for quantifying climatic niches together with an increasing availability of molecular data allowing inference of the phylogenetic relationships among species have provided the components necessary to allow the study of rates of niche change through time. These studies have showed that climatic niches can and do change over a wide range of timescales. For example, studies of invasive species have shown that changes in climatic niches can occur over a period of just a few years (Broennimann et al. 2007), studies of birds found that climatic niches are not conserved and instead change gradually (Pearman et al. 2014), and the rate of change was found to vary across different clades (Title and Burns 2015).

Although these advances have enabled a greater understanding of niche dynamics (in terms of describing patterns) relatively little is still known about which ecological conditions result in changes in niches, and the time scales over which these changes occur. Consequently relatively little is known about the mechanisms underlying changes in niches. As the climatic niche of a species strongly influences where a species can survive, in both space and time, examining the drivers of climatic niche change is an important aspect of biology which can help us to understand patterns of speciation, extinction, and how climate shapes both past and future species diversity patterns.

In the light of climate change it is especially important to know whether species’ modify their climatic niches in order to adapt to new climatic conditions (Quintero and Wiens 2013b, La Sorte et al. 2019). Studies across a diversity of taxa have hypothesised that rates of climatic niche change are driven by variations in temperature and precipitation, for example in plants

(Nürk et al. 2015) and primates, (Duran and Pie 2015). However, a lack of appropriate information on conditions from the deep past has precluded explicitly testing for a relationship. Further, studies which have related particular traits to past climatic conditions have had to rely on global temperature curves derived from the marine record, such as the Zachos curve, a deep sea benthic foraminiferal oxygen-isotope curve (Zachos et al. 2008), and these are unlikely to represent local or even regional terrestrial climatic conditions adequately (Clavel and Morlon 2017).

Changes in niche could be driven by absolute climatic conditions (i.e. the actual climate values at a particular point in time). As higher mutation rates are associated with increasing temperature, a positive relationship would be expected between temperature and rates of climatic niche evolution if genetic change is correlated with phenotypic change (Oppold et al. 2016, Foucault et al. 2018). However, contrary to theoretical expectations based on mutation rates, Clavel and Morlon (2017) found that the evolution of body mass across virtually all birds and mammals was faster during periods of cold temperature. This suggests that the rate of niche evolution that emerges at such large phylogenetic scales (many million years) might instead be driven by underlying selection pressure. Higher recent rates of phenotypic evolution in temperate regions than in the tropics (Lawson and Weir 2014) suggest that cold and dry conditions pose a stronger selection pressure than warm moist conditions. Consequently, a negative relationship between rates of niche evolution and both temperature and precipitation could be expected. Secondly, as faster rates of climatic changes are expected to impose a stronger selection pressure on species, higher rates of change in climatic niches are anticipated under periods of rapid climate change (Benton 2009, Duran and Pie 2015).

1.6 Thesis structure

The overall objective of this PhD thesis is to investigate the ecological (in this case seasonal) and evolutionary dynamics of climatic niches in birds. These dynamics remain a relatively overlooked area, despite many previous studies that have successfully applied the climatic niche concept in order to understand the relationship between bird species and their current climate. In pursuit of this aim I combine a macroecological and evolutionary approach working at large taxonomic or temporal scales (see Figure 1A for research approach and Figure 1B for scales of study). In taking this approach I aim to gain generality and predictive power across taxa, time and space.

The thesis is divided into three chapters (Appendices 1-3). Although each chapter is self-contained and answers its own research question, each directly builds on the data and conclusions of the previous one. Conceptually, the dissertation can be split into two parts, each based on the temporal scale of climatic niche dynamics examined. In the first two chapters (Q1 & Q2) I consider seasonal dynamics (i.e. ecological dynamics) of climatic niches in migratory and resident bird species in the present day. In the final chapter (Q3) I examine the dynamics of climatic niches over evolutionary time scales (>15 million years).

Previously, relatively little consideration has been given to the impact of migration on climatic niche quantification using distribution data in birds, so it was first crucial to assess what proportion of bird species are migratory, the impact this has on climatic niche quantification, and how best to quantify the climatic niches of migratory species. For these reasons my first chapter is a review paper in which I address these issues, fundamental to any study of the seasonal dynamics of climatic niches in birds (Q1). In the second chapter, I make use of these migratory definitions and recommendations to quantify climatic niches of migratory and resident bird species in an accurate and comparable manner in order to investigate the seasonal dynamics of climatic niches in birds. Specifically, I ask whether migratory birds are moving to track climatic conditions (Q2). Finally, in the third chapter, I combine the present-day climatic niches quantified in chapter two with phylogenetic inference and apply macro-evolutionary methods to study how climatic niches change over evolutionary timescales. Specifically, I ask whether climatic conditions drive niche change (Q3).

Each chapter is a research paper of which I am the principal author. Each was submitted to an international and peer-reviewed scientific journal. The first (Appendix 1) was published in the Journal of Avian Biology (Eyres et al. 2017). The second and third manuscripts (Appendix 2 and 3) are currently under review at Ecography and Evolution respectively.

1.7 Research questions and hypotheses

1.7.1 How does migration impact climatic niche quantification and how can we address this?

In the first chapter of my thesis (Appendix 1) I address three questions relating to niche quantification in birds: i) What is the impact of migration on climatic niche quantification, ii) How have previous studies quantified climatic niches in birds, and iii) How can we best take migration into account for accurate, comparable quantification of climatic niches across many species?

In order to assess the relative impact of migration on climatic niche quantification from distribution data (Q1 i) I compiled a database of migratory behaviour for all 10,443 known extant species of birds. Previous studies have classified movement behaviour on the basis of distribution data. Here, I make use of descriptions from the literature (Handbook of the birds of the world, del Hoyo et al. 2019) in order to classify migratory behaviour in a consistent way, taking into account intra-specific variation.

Focusing on macroecological studies, I then assess the literature to examine how current studies of climatic niche ecology and evolution have quantified the climatic niche (Q1 ii). This is to understand how well climatic niches of species are currently quantified, given the diversity of migratory behaviours that exists.

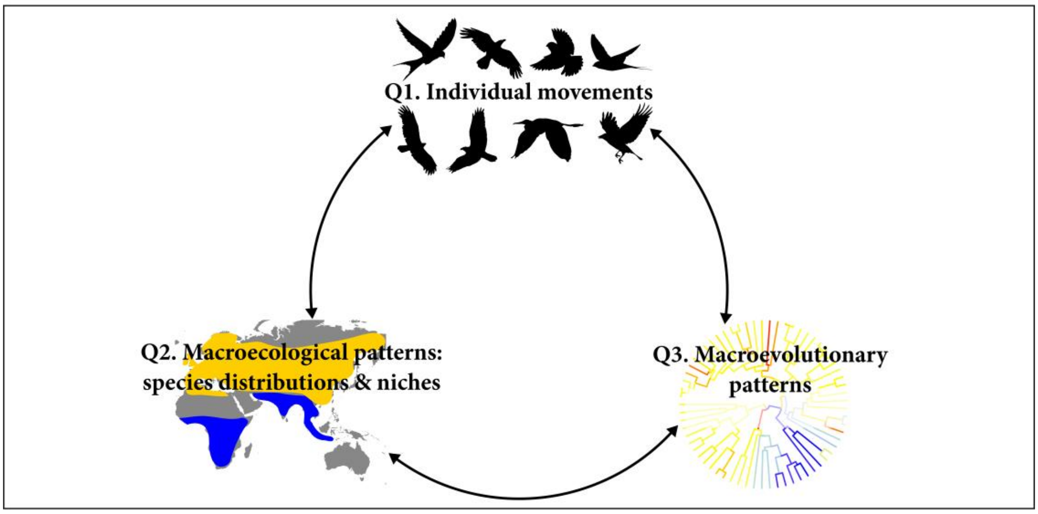
Finally, I examine how we can best take migration into account for accurate, comparable quantification of climatic niches across many bird species (Q1 iii). To this end, using Australian aviafauna as a case study, I investigate how well existing distribution datasets represent temporal dynamics by comparing seasonal patterns of species richness obtained from point-occurrence data with the seasonal patterns from range maps and go on to assess the consequences for niche quantification. Given the existing diversity of movement behaviour, the range of possible methods for quantifying climatic niches and data availability I make recommendations regarding how to best quantify climatic niches inhabited by birds.

1.7.2 Do migratory species track specific climatic conditions across seasons?

In the second chapter of my thesis (Appendix 2), I test the hypothesis that migratory bird species are moving to track specific climatic conditions (Q2). Although previous studies have examined seasonal niche overlap of migratory birds, they have all focused on the extreme examples of long-distance migrants. By making use of the new classification of migratory behaviour I developed in the first chapter, I am able to incorporate into the analysis a number of species with a greater diversity of migration behaviour. No previous study has addressed this question by looking at such a diversity of migratory behaviour. I quantify climatic niches of birds following recommendations from Chapter 1, taking into account the conditions experienced throughout the whole year (breeding and non-breeding season), and subsequently I calculate the overlap between climatic niches in each season (i.e. the degree of similarity).

If migratory birds are moving to track climatic conditions, it might be expected that migration would result in a high degree of overlap between seasonal niches. To statistically test whether migrants are tracking climatic conditions it is necessary to be able to compare niche overlap values observed in migratory species against appropriate null models. In keeping with existing studies, I first compare the seasonal niche overlap of migrants with the overlap that species would experience if they did not migrate but stayed in either their breeding or non-breeding range. However, this is only one part of the question (why do migrants migrate?)

A: Research questions



B: Scales of investigation

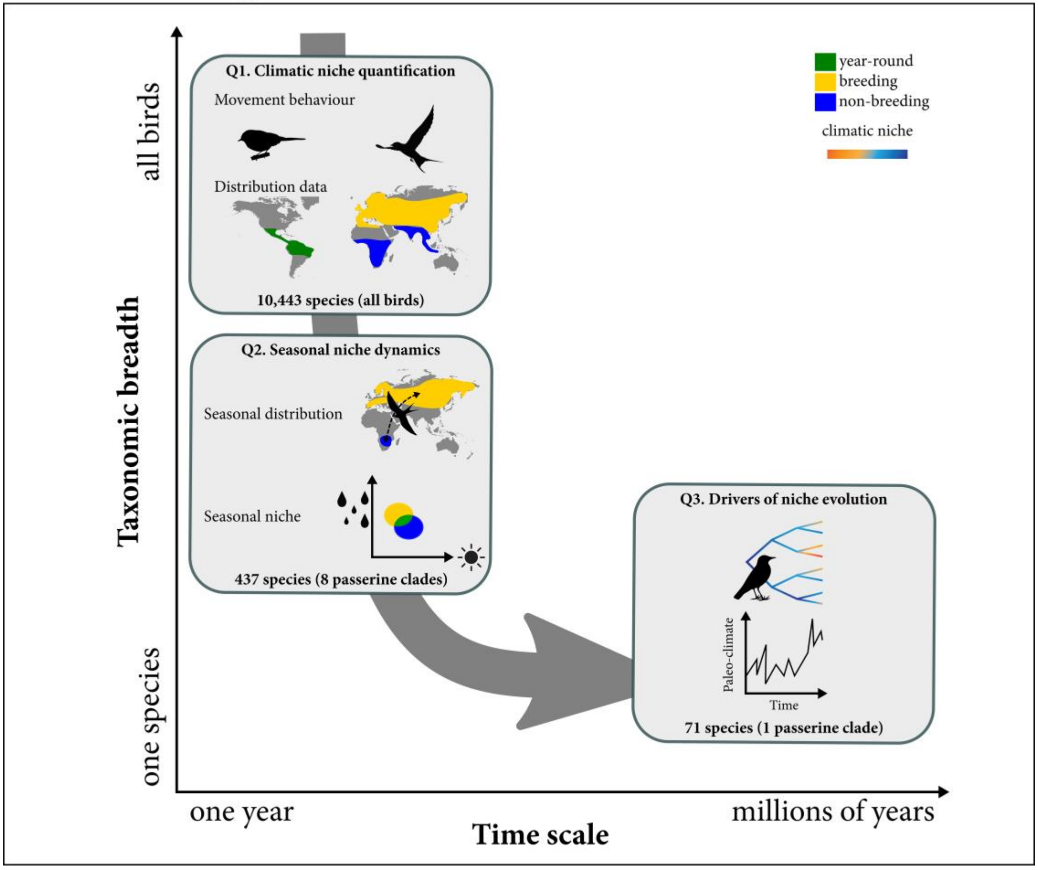


Figure 1: The overall aim of my thesis is to examine the ecological and evolutionary dynamics of climatic niches. Panel A illustrates the different aspects of biology that each chapter addresses. Panel B shows the taxonomic and temporal scales at which each study is conducted. In the first chapter I examine movement behaviour across all bird species and ask what distribution data is appropriate for niche quantification (Q1). In the second chapter I examine macroecological patterns in climatic niches in order to test whether migratory birds are moving to track seasonal climatic conditions (Q2). In the third chapter I investigate the evolutionary dynamics of climatic niches in order to test whether paleo-climatic conditions drive niche evolution (Q3).

and it does not provide insight into why some species do not migrate. Therefore, I additionally compare the seasonal niche overlap of closely related migratory and resident species. If migrants are tracking climatic conditions, I expect them to have higher seasonal niche overlap than closely related resident species.

Furthermore, as there is a lack of consensus across previous studies, with some studies detecting niche tracking whilst others finding no evidence in support of the idea, I also incorporate breeding location into the analyses to determine whether there are any geographic trends in niche tracking. I predict that migratory species breeding in highly seasonal environments (i.e. temperate regions) are more likely to migrate to track climatic conditions than are species breeding in the tropics. Finally, I control for potential confounding variables (clade and range size) in the analyses.

1.7.3 Is there a relationship between paleo-climatic conditions and rates of climatic niche evolution?

In the third chapter (Appendix 3), I test the hypothesis that there is a relationship between paleo-climatic conditions and rates of climatic niche evolution (Q3). Previous studies have suggested that large shifts in the climatic niches correspond with major changes in the climatic conditions, suggesting that climate could be a driver of niche evolution. However, owing to a lack of terrestrial paleo-climatic data with high temporal and spatial resolution, no one has explicitly tested for a relationship between climate and rates of niche evolution. To test this hypothesis, I make use of methods that infer paleo-climatic conditions for the past 20 million years from fossil data of mammalian herbivores. There exists a functional relationship between tooth structure and climate. Therefore the distribution of dental functional traits in any location reflects the type of plant foods available, which in turn reflects the ambient climate (Fortelius et al. 2014). These ambient climate conditions inferred from the fossil record are combined with rates of climatic niche evolution that I infer from combining current estimates of climatic niches with molecular phylogenies.

I quantify the climatic niches (thermal and precipitation niche) of extant species following recommendations from the previous chapters using seasonal distribution data. Combining these niche quantifications, phylogeny and evolutionary models, I infer the rates of niche change evolution across the phylogeny using evolutionary models. On the basis of these findings, mean rates of niche change across the whole tree, through time are calculated. Absolute terrestrial climatic conditions and rates of paleo-climatic change for the last 20 million years are inferred from fossil proxies for the regions where the studied bird species occur today.

Using the rates of niche change inferred using evolutionary models in combination with terrestrial paleoclimatic estimates inferred from the mammal fossil record, I test for (i) a relationship through time between paleoclimate averages and mean evolutionary rates of climatic niches (ii) a relationship between rates of paleo-climatic change with mean evolutionary rates of climatic niches. For both (i) and (ii) these relationships are tested for two aspects of climate (mean annual temperature and precipitation) separately and for four aspects of climatic niche (precipitation niche and the three temperature variables).

2 STUDY SYSTEM

Birds represent an appropriate study group for understanding the macroecological and evolutionary dynamics of climatic niches for three main reasons. Firstly, a large number of bird species (approximately 20%) are seasonal migrants, occupying different geographic locations in each season. The study of migratory birds therefore provides a good opportunity to test the drivers of species distributions. Secondly, birds, are the largest and most widespread class of terrestrial vertebrates, found almost everywhere in the world. As such, they occupy a huge variety of climatic conditions making it an exciting group to explore the evolutionary dynamics of climatic niches. Finally, birds are an appropriate system for these analyses because they are a very well-studied group. Comprehensive and relatively accurate data is available on the ecology, behaviour and distribution of birds. For example, the Global Biodiversity Information facility (GBIF, < www.gbif.org >) currently has more than 800 million point occurrence records for birds worldwide whilst the IUCN has compiled range maps available for all known bird species (BirdLife International 2016). For macroecological and evolutionary studies it is particularly important that we understand how species are related to each other. The large amount of DNA sequence data available for birds allows ecological traits to be examined within a comprehensive phylogenetic framework.

Studying the ecological and evolutionary dynamics of climatic niches for the more than 10,000 species of extant birds was beyond the scope of this thesis. For this reason, in the second chapter I focus on 437 species from eight monophyletic clades of passerine birds (order Passeriformes). The Passeriformes are the largest order of birds, representing more than half of all bird species and have a cosmopolitan distribution, occupying all continents except Antarctica. Sampling from within this group therefore represents a good compromise, reducing study species to a tractable number whilst still including birds which occupy diverse geographic locations and consequently climatic conditions. A second reason for focussing on the Passeriformes is that although the phylogeny of birds is relatively well resolved, the earliest diverging branches of the phylogeny remain contentious (Jarvis et al 2014).Within Passeriformes, relations are relatively well resolved among families and genera.

The eight clades were selected from across the Passeriformes so that each included at least 30% non-resident species, had similar species richness (approximately 50-80 species each) and comprised species for which there is also a good knowledge of the phylogenetic relationships. The resultant clade selection was as follows: Xolmiini tribe of Tyrannidae (tyrant flycatchers), Vireonidae (vireos), genus *Corvus* of the Corvidae (crows and ravens), Hirundinidae (swallows and martins), genus *Turdus* of Turdidae (thrushes), *Oenanthe*-

Monticola clade of the Muscipapidae (wheatears, chats and allies), *Setophaga-Myiothylpi*s subclade of Parulidae (American wood-warblers) and Cardinaliade (cardinals, buntings, grosbeaks and allies).This selection of clades provides the second chapter with a global representation of the passerine birds.

To test the relationship between paleo-climatic change and climatic niche evolution in the third chapter I my focus is on a monophyletic clade comprising 71 species from closely related genera of Old-World flycatchers (Muscicapidae, subfamily Saxicolinae). This clade comprises the wheatears, rock thrushes, chats and stonechats, and is hereafter referred to as the wheatear-chat clade. Species in this group are widely distributed across Asia, Africa and Europe, occupying a variety of different habitats and climatic conditions. In particular some lineages are found in very dry desert regions indicating that precipitation tolerance might have evolved rapidly in these lineages. Reducing the taxonomic scale for this final chapter allows a more detailed understanding of the evolution of this one group. As well as being an interesting group ecologically, the wheatear-chat clade is an appropriate choice for practical reasons. In this study paleo-climatic conditions are inferred from fossil data. Uneven preservation has resulted in geographic biases in the fossil record. In particular, although data is available for North America and Europe- and to a limited extent in Africa and Asia- hardly any exist in South America and Australia. As climatic niche evolution is expected to be driven by local climatic conditions, clade selection was therefore restricted to using one which does not have large parts of its distribution in South America and Australia.

3 METHODOLOGICAL APPROACHES

Throughout this thesis I quantify climatic niches using a correlative approach in which distribution and climatic data are combined. The majority of previous studies that have quantified the climatic niches of birds from distribution data have used the breeding range only, ignoring the temporal dynamics of migratory species (Pigot et al. 2010, Cooney et al. 2016, but see; Joseph and David Stockwell 2000, Laube et al. 2015). In order to take into account the seasonal dynamics of migratory birds, throughout this thesis I quantified climatic niches using seasonal range maps and corresponding climate data. The advantage of the methods I have developed is that they characterise climatic niches in a way that ensures the comparability of different types of birds (i.e. migratory or resident species).

I obtained distribution data from a variety of sources. For the study of Australian avifauna in chapter 1 (Appendix 1) I compare seasonal distribution data from range maps with those from point occurrence data. Australia was an ideal region for this case study as a coherent dataset of temporally explicit point occurrence data exists with the Atlas of Australian birds (Barrett et al. 2003). However, structured spatially and temporally explicit point occurrence data, such as that available from the Atlas of Australian birds is not commonplace (Meyer et al. 2015). In the second two studies (Appendices 2 and 3) point occurrence data that were comprehensively sampled both taxonomically and geographically were not available for the study species. Therefore, in the final two studies, climatic niches were quantified using seasonal range maps gridded to a 1 degree resolution. Although such extent-of-occurrence data are not ideal for quantifying climatic niches (Graham and Hijmans 2006), they represent the most consistent and accurate coverage of species' ranges that are currently available at a global scale and across a such large number of species.

Throughout, I have extracted climate data for niche quantification that coincides temporally and geographically with each species' seasonal distribution (i.e. when a species is in its breeding range and when is in the non-breeding range). As breeding time is species-specific, I determined the peak breeding months for all 437 species using information from the literature (mainly the Handbook of the Birds of the World (HBW) Alive website < www.hbw.com > (del Hoyo et al., 2019) , accessed until January 2019, see Appendix 2, Supplementary material for a complete list). The three non-breeding months for each species are defined as the three months beginning six months after the breeding season, as an arbitrary, but globally consistent measure across all species (Laube et al. 2015). As the geographic distribution of migratory species is poorly known outside of the breeding and non-breeding season, the annual niche that I have quantified for all species reflects the conditions experienced across these six months rather than the full year. Although this means that I did not include all conditions experienced by both migratory and resident species, this approach should represent the range of the conditions that the species experience throughout the year. To ensure comparability, climatic niches were quantified in the same manner for migratory and resident species.

In the second two studies (Appendix 2 and 3) global monthly climate layers are averaged across the same grid cells as the occurrence data. Climate datasets are selected so that they include ecologically relevant variables in the analysis. For example, in Chapter 2 (Appendix 2) climate data are obtained from the CliMond *raw climate data* dataset (averages from 1961-1990, 10 minute resolution) (Kriticos et al. 2012). This dataset was chosen because it contains a greater number of monthly climate variables than other comparable datasets. The following six climatic variables for each month are used: minimum and maximum of daily temperatures averaged within each month; total monthly precipitation; mean daily humidity of each month; and mean daily relative humidity at 9am and at 3 pm for each month. These variables were chosen as ecologically relevant descriptors of global climate including extremes of temperature and water availability (Petitpierre et al. 2017). For Chapter 3 (Appendix 3) monthly climatic data was obtained from the WorldClim *raw climate data* dataset (averages from 1970-2000, resolution 10 minute) (Fick and Hijmans 2017). This dataset was chosen as it comprises mean monthly temperature data (not available in CliMond). The following four climatic variables for each month were obtained: minimum, maximum and average daily temperatures within each month and total monthly precipitation; hereafter referred to as Tmin, Tmax, Tmean and Precipitation respectively. I chose to investigate evolution of these four aspects of climatic niches as they are most likely to be related to the climatic variables that I was able to infer from the fossil record (temperature and precipitation).

3.1 Q1: The impact of migration on climatic niche quantification

To assess the relative impact of migration on climatic niche quantification from distribution data (Q1, appendix 1), I assessed the prevalence and diversity of migratory behaviour across all 10,443 known extant bird species. The migratory categories used followed Newton (2008) with some modifications. Species are categorised into four main types of movement behaviour based on descriptions from the HBW species: 1) directional migrants, 2) dispersive migrants, 3) nomadism, and 4) residency (Appendix 1, Table 1). Briefly, migrants are defined as those which make regular seasonal movements, either in a consistent direction between breeding and non-breeding sites (directional) or in any geographic direction from the breeding sites (dispersive). Nomadic species are defined as individuals making irregular (non-seasonal) movements that vary between years. Finally, resident species are those which make no major movements. For full definitions see Appendix 1, Table 1.

Classification of migratory behaviour into discrete categories is complicated by intraspecific variation. It is not uncommon for individuals or populations of a species to exhibit different migratory behaviours. Therefore, in order to take into account this intraspecific variation, the four movement types are further divided into subcategories; full, partial and local, depending on the extent to which these movements occur within the species. When all members of a species perform the same movement behaviour it is classified as fully migratory or fully nomadic. However for species in which just some parts of the populations move, species are categorised as partially migratory or nomadic. Finally, if movements only take place at a local scale, species are classified as locally migratory or nomadic. The advantage of this classification system is that it allows for species to be classified into multiple migratory categories if they display multiple behaviours. Species are assigned to a final single overall movement category based on the knowledge of intraspecific variation in our initial classification using a consistent rationale.

Finally using Australian avifauna as a case study, I assess the ability of seasonal range maps and point occurrence data to detect spatial patterns in seasonal species richness. As climatic niches are quantified from distribution data, the ability to detect seasonal patterns of species richness was assumed to be a proxy for detecting seasonal patterns in climatic niches, simultaneously across many species. To this end I obtained extent-of-occurrence range maps from BirdLife International and Natureserve (BirdLife International and NatureServe, <www.birdlife.org>) and resampled them into an equal area grid with cells of 1 degree longitudinal and varying latitudinal extent for Australia, mapped with a Behrmann projection. I obtained temporally explicit point-occurrence data from the New Atlas of Australian Birds (Barrett et al. 2003).These point-occurrences are sampled into the same equal area grid as the range maps. In order to compare the seasonal differences in the spatial patterns of species richness between the two data sources the point occurrence data is split into time periods corresponding to the seasonal range maps.

The final analyses were carried out on the 598 species present in both datasets. For each dataset I calculated species richness in each 1-degree grid cell for each season separately. Additionally, I calculated the difference in species richness between seasons as well as the proportion of species that differ between seasons. In order to determine whether the two datasets detected similar degrees of seasonality in species richness I tested the correlation between the seasonal differences in species richness for each dataset. As patterns in point occurrence records may be unduly influenced by sampling effort, all analyses were additionally carried out using cells for which sampling effort was high (>100 records in each season).

3.2 Q2: Do migratory species track specific climatic conditions across seasons?

3.2.1 Seasonal niche overlap

To answer question two (Are migratory birds tracking climatic conditions? Appendix 2) overlap between the seasonal (i.e. breeding and non-breeding) niches is calculated for migratory and resident species. For migratory species, niche overlap is also calculated for two hypothetical scenarios: (1) the overlap that would result if a species stayed in the breeding range for the whole year, (2) the overlap that would result if a species stayed in the non-breeding range for the whole year.

I calculated niche overlap following the recommendations of Broennimann et al. (2012). This approach uses principal component analysis (PCA) to incorporate all six climatic variables used and create a two-dimensional climatic space within which niche overlap can be calculated. In order to calculate the overlap of occurrence points within this two dimensional climatic space, the entire climatic space was gridded. The occurrences of each species in climatic space can then be converted into densities within this grid. The major strength of this method is it accounts for the different availability of climatic conditions in each season by the calculation of “climate occupancy values” (Broennimann et al. 2012). The overlap between breeding and non-breeding niches was subsequently calculated for each species based on the climatic occupancy values using Schoeners D, a measure that varies between 0 (no overlap) and 1 (complete overlap) (Warren et al. 2008).

3.2.2 Comparative analyses

To answer question 2 (Appendix 2) I take a comparative approach in which I use statistical analyses to make comparisons across multiple species. When, making comparisons across many species issues of non-independence may arise. This could result in detection of relationships, on the basis on non-independent points. Conversely, relationships may be masked by phylogenetic differences across groups (Harvey and Pagel 1991). In order to control for this I take into account the relationship between species using two methods; (1) I include clade as a random effect in linear mixed effects models,(2) to control for phylogenetic relationships within clades more explicitly than the mixed-effects models, I additionally fit models using phylogenetic least-squares regression analysis (PGLS; Martins and Hansen 1997).

3.3 Q3: Is there a relationship between paleo-climatic conditions and rates of climatic niche evolution?

3.3.1 Rates of climatic niche change

Rates of climatic niche change were reconstructed from the inferred climatic niches of extant species combined with their phylogeny. Again, I quantify the climatic niche from distribution data in combination with climatic data, taking into account the seasonal dynamics of species and climate. Phylogenetic relationships within the group were obtained from Phillips et al. (2018). This study obtained sequence data for 65 of the 71 species from my study clade (see Appendix, 3 supplementary material for full list) and estimates the phylogeny using Beast version 2.4.4 (Bayesian Evolutionary Analysis Sampling Trees, Bouckaert et al. (2014). Reconstruction of rates of niche of evolution were carried out on a dated maximum clade credibility tree (MCC).

I estimate the rates of niche change across the phylogeny by fitting evolutionary models. Specifically, I use a variable rates model in the software BayesTraits, version 2 (Venditti et al. 2011; available from http://www.evolution.rdg.ac.uk/). The advantage of this model over other evolutionary models is that it allows for the rates of niche evolution to vary across the tree and is therefore able to identify areas of the phylogeny where the rates of niche evolution differ significantly. For each climatic variable, I ran two independent MCMC chains for 1 billion iterations each and retained 10,000 samples from each. All analyses were carried out on the 20,000 pooled posterior trees to take into account uncertainty in the inferred rates of change across the phylogeny. I summarize the results by calculating (1) the mean rate and (2) the probability of a rate shift over all the posterior samples for each node in the tree. In order to calculate how the rates of niche change varied through time, I followed Cooney et al. (2016) and calculated the mean rate of niche change for all the branches at successive bins across the tree. The time bins used were selected to correspond to the time bin scheme used for paleo-climatic inferences from the fossil record (see below).

3.3.2 Paleo-climatic inferences from the fossil mammal record

Owing to a lack of paleo-climatic data with high spatial and temporal resolution, previous studies have had to rely on global marine temperature curves (i.e. Zachos et al. 2008). However, species are more likely to respond to the variation in local terrestrial climatic conditions than global averages. Further, studies have mainly been limited to examining temperature variables even though other climatic variables such as precipitation are important to species (IPCC 2014, La Sorte et al. 2019). In this study I adopt a method used by paleobiologists to infer climatic conditions (mean annual temperature and precipitation) for the past 20 million years. The method infers climatic conditions on the basis of a functional relationship between tooth structure of mammalian herbivores and climate. The distribution of dental functional traits reflects the type of plant foods available, which in turn reflects the ambient climatic conditions (Fortelius et al. 2014). Put simply, when the climatic conditions are hot and dry, the mammalian community is dominated with herbivores with high crowned teeth (like those of horses and cows), which enables them to eat tough fibrous material. The functional relationship between tooth structure of mammalian herbivores and climate has been confirmed for present day conditions (Liu et al. 2012, Fortelius et al. 2014). Here I make use of the mammal fossil record to examine the distribution of dental functional traits through time and reconstruct past climatic conditions. The mammal fossil record has relatively good spatial and temporal resolution, particularly in the old world. This allows terrestrial estimates of precipitation and temperature through time at a temporal resolution that is more likely to represent the actual conditions experienced by the study species.

4 MAIN RESULTS AND DISCUSSION

4.1 Quantification of climatic niches in birds: adding the temporal dimension (Appendix 1).

The principal aim of this thesis was to address three questions relating to niche quantification in birds. I first sought to assess the impact of migration on climatic niche quantification from distribution data (Q1 i). To this end I categorised the migratory behaviour across all 10,443 extant bird species. In the final species-level categorisation, 8241 (78.9%) of all bird species were classified as resident. In keeping with previous estimates (Cox 2010, Rolland et al. 2014), 2079 (19.9%) of species were classified as migratory (either performing regular seasonal movements in a consistent direction between breeding and non-breeding sites (directional migration, 15.4%) or in any geographic direction from breeding sites (dispersive migration, 4.5 %). Only 103 (1%) of all species were categorised as nomadic, making irregular movements that vary between years. These final classifications mask some of the full diversity of movement behaviours exhibited by birds. However, in addition to this final classification the database includes information on intraspecific variation in movement behaviour. This is reflected by assigning species that exhibit several different movement behaviours to multiple categories. Intraspecific variation in movement behaviour was found to be very common with 1950 (18.7%) of all species exhibiting more than one type of behaviour in the partial subcategory (Appendix 1, Figure 1). This classification scheme is the first to classify movement behaviour in a consistent manner across all 10,443 extant bird species. Further, it is novel in its inclusion of movement behaviour below the species level classification. This classification can be used to check the detailed movement behaviour of species and determine what occurrence data are sufficient to quantify the climatic niches of study species, depending on the geographic and taxonomic scale of the study.

Second, by reviewing the literature I identified four main methods in which climatic niches of birds have been quantified in previous studies (Q1 ii). These four approaches varied depending on the type of distribution data and climatic datasets used. I then assessed the ability of each of these approaches to quantify the climatic niches of birds displaying each type of the four movement behaviours identified in part 1.

The majority of studies that have quantified climatic niches of birds have used distribution data of breeding ranges and annual climatic data only, despite the known seasonal dynamics of many species (Appendix 1, Table 2: Approach 1). This approach is appropriate if the study is limited to bird species that are not migratory or nomadic, as it is able to capture the full range of climatic conditions that a resident species experiences throughout the year. However, this approach is not appropriate for migratory species as it includes the climate at the breeding site during the non-breeding season, when the species is not present, resulting in a high probability of mischaracterising the climatic niche. Secondly, this approach is unable to capture the full range of climatic conditions that migratory species experience, as it does not include the conditions experienced outside of the breeding range.

Three studies were found to avoid the challenge presented by the movement behaviours of birds by quantifying climatic niches of species for just a single season. This was most commonly the breeding season (Appendix 1, Table 2: Approach 2; Barbet-Massin et al. 2009, Barnagaud et al. 2012, Pearman et al. 2014). Climatic niches quantified using this approach are more comparable between migratory and resident species than those derived using approach 1. However this approach only quantifies a temporal subset of a species' climatic niche.

An increasing number of studies have begun to explicitly consider the temporal and spatial dynamics of migratory species into the quantification of climatic niches (Laube et al. 2015, Gómez et al. 2016, Zurell et al. 2018). Distribution maps comprising separate breeding and non-breeding range maps for migratory species such as those available from BirdLife international have been used in combination with monthly climatic data in order to quantify climatic niches considering the distribution of species in two seasons (Appendix 1, Table 2: Approach 3a). This approach is not able to capture the climatic conditions experienced during migratory passage, but should still reflect the climatic niche of seasonal long-distance migrants. During migratory passage, many bird species pass quickly through unsuitable areas that arguably should not be considered part of their climatic niche (La Sorte et al. 2016).

For species with more complex migratory patterns (e.g. loop migrants: Klaassen et al. 2010) or those which make stopovers (Bairlein 1987) the difference between conditions experienced in breeding and non-breeding sites should be considered when quantifying the climatic niche. Similarly, climatic niches quantified using the distribution of species within two seasons are unlikely to accurately characterise the climatic niches of nomadic species which have no core breeding and non-breeding distributions. For each movement type identified in part (i) I make recommendations of appropriate methods for niche quantification (Appendix 1).

Finally, using Australian avifauna as a case study I assessed the ability of temporally explicit point-occurrence data and seasonal range maps to detect seasonal patterns in species distributions (Q1 iii). More pronounced seasonal differences in the spatial distribution of species richness were observed in the point occurrence data than the seasonal range maps (Appendix 1, Figure 3). This difference could in part be driven by variations in sampling effort. However, the difference in seasonality captured by the two datasets was even more pronounced in grid cells where sampling effort was high. I used point occurrence data to detect the nomadic movement patterns of species, for example the budgerigar (*Melopsittacus undulates*) (Appendix 1, Figure 4a). Although this nomadic movement pattern of this species has long been postulated (Nix 1974, Griffioen and Clarke 2002) is it is not evident from seasonal range maps in which a only year-round distribution is available (Appendix 1, Figure 4a). We do not have perfect knowledge of species distributions to determine which data are best able to detect seasonal differences in the distribution of species. However, this comparison is able to highlight what each dataset is and is not able to capture. In particular, seasonal range maps were shown to be of limited value when studying nomadic species. For these species temporally explicit point occurrence data are required to accurately document movement patterns. Despite the clear advantages of point-occurrence data these data are not without problems because of globally uneven sampling efforts. They are often a biased representation of species distribution (Meyer et al. 2015, Amano et al. 2016) and as such require appropriate methods of correction (Fourcade et al. 2014).

Conclusions & future directions

Altogether, my first study (Appendix 1) represents an important and timely contribution to the field. I provide a framework recommending the occurrence data appropriate for quantifying climatic niches of birds depending on migratory behaviour and the spatial and temporal focus. The classification of birds compiles migratory behaviour in a consistent manner across all bird species for the first time, which I hope will become a key resource more generally in the study of the ecology and evolution of migration. Further, in outlining the data and methods that would form best practice for niche quantification- even if not yet available- the results help direct the field towards collection of appropriate data and development of methods that make best use of it.

To categorise the movement behaviour of birds, I made use of descriptions of movement behaviour from *The Handbook Of The Birds Of The World* (del Hoyo et al. 2019), a reliable source, considered to be one of the most complete reference work on birds. However, relatively little is still known about the movement behaviour of birds. Although data derived from new tracking techniques are rapidly accumulating across many species (Bridge et al. 2011, Kays et al. 2015) it is unlikely that tracking can solve problems of taxonomic coverage. The development of statistical methods that will allow the use of occurrence data from citizen science offers a promising direction for gaining a better understanding of movement behaviour of species at and below the species level (Johnston et al. 2019).

4.2 Seasonal niche dynamics in passerine birds: Do migratory species track specific climatic conditions? (Appendix 2)

The second aim of my thesis was to understand whether migratory birds are tracking specific climatic conditions. Mixed support was found for the hypothesis that migratory species move to track climatic conditions between seasons. Evidence of niche tracking depended on three main factors: i) the perspective in which the question was examined (i.e. from the perspective of the individual migrant or in comparison to resident species), ii) the direction of migration (i.e. whether the species is moving from the breeding or non-breeding site) and, to a lesser degree (iii) geographic location (i.e. whether a species breeds in the tropics or not).

My first expectation was that the overlap between seasonal climatic niches (i.e. breeding vs. non-breeding) experienced by migrants would be greater than the hypothetical seasonal niche overlap that would arise if a migratory species did not migrate (i.e. stayed in the breeding or non-breeding range year-round), when controlling for range size and phylogeny (Laube et al. 2015). Partly in accordance with this expectation, I found that migratory species tracked their climatic niche between seasons if species were compared to a hypothetical situation in which they did not migrate, but only when moving away from the breeding ranges (Appendix 2, Figure 2a, c). These results did not show any geographic variation and were consistent regardless of whether the species were tropical or non-tropical breeders. My second expectation was that migrants would experience higher overlap between breeding vs. non-breeding climatic niches than resident species. In contrast to this expectation, I found that migratory species tracked their seasonal niches to a much lower degree than resident species within the same clade (Appendix 2, Figure 3). I found that as a result of moving huge distances, migratory birds occupy less similar niches in each season that resident species which remain in one location year-round.

The evidence for niche tracking regarding expectation one was found to be asymmetric with migration away from the breeding range significantly increasing seasonal niche overlap (indicating niche tracking) but migration away from the non-breeding range not (Appendix 2, Figure 2, a & c vs b and d). In the tropics, migration away from the breeding range resulted in a significant reduction in niche overlap (Appendix 2, Figure 2d). Together these results indicate that the drivers of migration may differ depending on direction. Climate, or factors correlated with climate are likely to drive movement away from the breeding range. However, the drivers for migration away from the non-breeding range seem likely to be factors other than climate, such as seeking lower nest predation.

Finally, in regard to both of my expectations the evidence for niche tracking was found to differ significantly depending on the location of the breeding range. These results suggest that different drivers of migration might operate in and outside of the tropics. For migratory species breeding in the tropics, I found no evidence for seasonal climatic niche tracking, suggesting that migration here is driven by factors other than climate. In the tropics, where seasonal fluctuations in climate are overall much less pronounced, biotic interactions such as competition and predation may be more important for species occurrence than the abiotic environment (Schemske et al. 2009, Faaborq et al. 2010).

Conclusions and further directions

In this second study I found some evidence that migratory species move to track seasonal climatic niches even though the results were mixed and migrants never tracked climatic niches perfectly. These results imply that migratory species show a degree of flexibility in their climatic niches as they are found occupying slightly different conditions throughout the year. Previously, migratory species have been considered particularly vulnerable to climate change because they are at risk of climatic conditions becoming unsuitable at their breeding site, non-breeding site as well as the impact this could have on migration (Zurell et al. 2018). My findings, however, suggest that migratory birds may have an unexpected degree of resilience to changing conditions.

As limited evidence was found in support of migratory species moving to track seasonal climatic niches, my results suggest that migration did not evolve to simply track climatic conditions. Instead migratory species may move to track factors correlated with climate, for example resource availability. This idea is supported by other studies (e.g. Somveille et al. 2015, Thorup et al. 2017). Finally, the finding that migratory birds do not perfectly track climatic conditions between seasons has important practical implications. It confirms that accurate, complete quantification of climatic niches of migratory birds requires consideration of the conditions they experience throughout their entire range.

The work also opens avenues for further research. For example, as I find (contrary to expectations) that migrants never achieve the same levels of overlap between seasonal climatic niches as resident species I propose that this could indicate that resident species' ranges are generally placed in regions with less seasonal climatic variation than migratory species. This would be interesting to investigate further, using more highly-resolved distribution data such as point records (Eyres et al. 2017; Appendix 1), particularly to understand why some species are partially migratory, with some individuals moving and others remaining in the same region year-round (Fiedler 2005, Fandos and Tellería 2019).

Finally, to determine whether both migration away from the non-breeding site and migration in the tropics are driven by biotic interactions such as competition for resources and predation, it would be of interest to quantify and compare these factors for migrants in their breeding and non-breeding range. Biotic interactions are difficult to study directly, particularly at this scale. However competition for resources could be measured indirectly by the use of available ecomorphological trait data, which links a species' morphology to its role in an ecosystem (Leisler and Winkler 1991, Bock 1994).

4.3 Is there a relationship between climatic conditions and rates of climatic niche evolution in the Wheatears? (Appendix 3)

The final aim of my thesis was to test whether there is a relationship between climate and inferred rates of niche change through time. For the study clade- wheatear chats - estimated mean rates of niche change for both precipitation and temperature niche increased over time, indicating that niches changed faster closer to the present day and were therefore not conserved (Appendix 3, Figure 1 C & D). In addition, I identified four significant shifts in precipitation niche across the wheatear-chats (Appendix 3, Figure B). However, in contrast to theoretical expectations - that surviving species would have adapted to changing climatic conditions through time - I found no relationship between the inferred rates of climatic niche change and either absolute climate values or rates of climate change (Appendix 3, Figure 3). This result suggests that climatic niche evolution may not be directly driven by either ambient climate or changes in climatic conditions.

These results indicate that members of the wheatear chat clade do not appear to have changed their niche in order to adapt to changes in climatic conditions (both temperature and precipitation) through time. Alternatively, the species may have altered their geographic distribution or behaviour in order to cope with changing environmental conditions (Phillimore et al. 2016, Virkkala and Lehikoinen 2017, Nogués-Bravo et al. 2018). Given the high mobility of birds, it is likely that instead of adapting their niches they buffer climatic changes through adaptive behaviour such as large scale movements or small scale habitat and micro-habitat choices (Keppel et al. 2017). Responses of this nature have been directly observed to occur in birds in response to climate change occurring over the past 25 years (Gillings et al. 2015, Massimino et al. 2015).

My results indicate that for birds, organisms that are highly mobile, other factors such as resource availability or competition may be important for driving niche dynamics (Pitteloud et al. 2017). This finding is consistent with previous studies which show that climatic conditions do not strictly determine species distributions (Khaliq et al. 2014) and studies that indicate that habitat and resources are more important than climate for determining bird occurrences (Laube et al. 2015, Teitelbaum et al. 2016). Finally, this result is consistent with studies that show that at narrow phylogenetic extents (such as one clade), biotic interactions are the most important determinant of species distributions (Barraclough and Vogler 2017).

My result appears to be in direct contrast with those of other studies pointing towards associations between climate change and rate of climate niche changes. However, this seemingly unexpected result might reflect a taxonomic bias in the literature. The majority of previous studies examining niche dynamics have focussed on terrestrial non-volant organisms, e.g. 38 out of the nearly 40 empirical studies reviewed by Pearman et al. (2008). The response of birds to changing climatic conditions might be systematically different owing to their high mobility. The response of birds might be expected to be more similar to marine organisms because movement in the marine realm is also much less restricted than in terrestrial environments. Consistent with my results for birds, the few studies examining niche dynamics in marine taxa have found that niches are relatively stable even when faced with significant environmental change (e.g. Stigall 2012, Saupe et al. 2014).

Although I have found no relationship between regional averages of climatic conditions and rates of niche change, it is not possible to dismiss other aspects of climate. For example rates of niche change might be driven by extreme events or changes in variability rather than changes in average conditions (Greenville et al. 2012). Moreover, I investigated the relationship between rates of niche change and average climatic conditions across a very broad geographic range. If niche changes are instead driven by heterogeneous local climatic conditions any such relationship would not be detected by a study at the scale of the present one.

Finally, there are possible methodological explanations as to why I might not have found a relationship between climatic conditions and niche evolution. Although I have a very substantial set of paleo-climatic data, it is still relatively small (in terms of number of climatic estimates for each time bin and continent). I was consequently only able to infer climatic conditions at quite a coarse temporal resolution. This small sample size severely limited the statistical power of my analyses.

Conclusions and further directions

This study has gone beyond previous studies, by using terrestrial paleo-climatic data that is relevant to the study organism to explicitly test whether there is a relationship between paleo-climatic conditions and clade-wide rates of niche evolution through time. Paleo-climatic conditions do not appear to drive climatic niche evolution, at least at the taxonomic and geographic scale of this study. This finding suggests that birds, as highly mobile organisms, find it easier to buffer changes in climatic conditions through behavioural adaptions than through genetic adaptations to the novel environment. This is an exciting discovery as it is consistent with studies which show that over the past few decades, birds have been shifting their distribution in order to cope with current rapid climate change. Here, we suggest that highly mobile species might respond in a similar manner on a much larger time scale (many millions of years).

As I propose that the lack of relationship between climate and niche change may be explained by the high mobility of the species studied, further investigation into the relationship between mobility and rates of niche change across realms would be of value to confirm or reject this implication.

5 CONCLUSIONS AND SYNTHESIS

My study highlights the importance of temporal dynamics in niche space occupied by species of birds across ecological (i.e. seasonal) and evolutionary timescales. Given current changes in climatic conditions, understanding the relationship between species and climate is of high importance. To this end, quantification of the climatic niches from distribution data has been an increasingly important tool. However, questions of how migration affects accurate niche quantification, occupancy of niche space throughout the year, and how niches change over evolutionary timescales have so far received relatively little attention.

I studied climatic niches at a variety of taxonomic and temporal scales in order to gain a greater understanding of the temporal dynamics of climatic niches. For example, in chapter 1 I examined the movement behaviour at and below the species level. In the second chapter I looked at how those movement patterns shape macroecological patterns and finally in the third chapter, I examined the macroevolutionary patterns of climatic niches. Although the study of macroecological and evolutionary patterns is useful, it is important to examine the underlying mechanisms to better understand the processes shaping these patterns. My work provides potential explanations for the macroecological and evolutionary patterns observed based on the inclusion of information of movement behaviour. Future macroecological and evolutionary studies would benefit from more explicitly incorporating data of this type.

On the basis of the temporal scale of dynamics examined, the main findings of my research can be divided into two kinds: i) ecological and ii) evolutionary. Firstly, in chapter 1 I provide tools and recommendations of how to quantify climatic niches of highly mobile taxa. In chapter 2, by comparing the climatic niche occupied by migratory species in each season I show that migratory species do not occupy identical conditions in each part of their range. This result suggests that migratory birds are more flexible in their climate tolerances, and therefore potentially less vulnerable to climate change than would be predicted from previous studies that only examine tolerances in the breeding season. Practically, this finding highlights that if we are to fully characterise the climatic niches of taxa containing highly mobile species such as birds, it is important to consider the climatic conditions experienced by a species in each part of its range. This finding further highlights the importance of the recommendations made in chapter 1. I hope by outlining the data and methods that would form best practice for niche quantification, future studies will make use of the tools to incorporate these dynamics.

Secondly, by inferring past climatic conditions and rates of niche evolution I found that although climatic niches are dynamic through time, rates of climatic niche evolution are not driven by climatic conditions. These results indicate that in the face of changing climatic conditions, birds might more commonly respond by moving rather than adapting their climatic niche. However, it is important to note that the current speed of climate change is much quicker than any of the changes in my study period (20 million years ago until 2 million years ago), and consequently species might not be able to move fast enough to avoid climatic conditions outside of their current tolerance range (Devictor et al. 2008).

Overall, the results at both temporal scales suggest that climate is not the sole determinant of bird distribution. These findings give some reason to be optimistic about how birds will be affected by changing climatic conditions. However, it follows that other factors are also important drivers of the distribution of birds. For example, biotic interactions that drive migration (McKinnon et al. 2010), and the search for resources (Thorup et al. 2017). Climate change may still have negative impacts on birds through changes in the distribution of these factors in both space and time (e.g. increased competition, decreases in resource availability, and trophic mismatches). Such indirect effects have already been observed (Alexander et al. 2015, Burgess et al. 2018).

6 FUTURE OPPORTUNITIES

My findings that migratory birds are able to cope with different climatic conditions in each season, as well as over the course of millions of years, suggest that birds are relatively plastic in their climatic niche either through adapting behaviour or making large scale movements. In response to changing climatic conditions phenotypic plasticity allows species to respond quickly without genetic modifications. In regard to the current speed on climate change, understanding phenotypic plasticity is particularly relevant. Therefore, future studies investigating this would be of great interest. In particular investigating whether this plasticity is the result of high mobility or rather other behavioural adaptations.

The conclusions of this thesis are based on climatic niches quantified from broad-scale distribution data. Climatic niches quantified using this approach are considered a reasonable approximation of species' fundamental niche (Wisz et al. 2013), however in reality it is unlikely that this method is able to accurately capture the full range of climatic conditions that a species is able to tolerate. To this end, future studies should apply new methods in species distribution modelling such as the use of hybrid models which take account of the physiological tolerances of species in order to provide more realistic estimates of the climatic niche (Zurell et al. 2016). Increased availability of point occurrence data and advances in methods to correct for biases will lead to a more accurate knowledge of species distribution, the use of microhabitats not detected by range maps, and consequently the climatic niche of species.

Secondly, although niche estimates based on broad presence-absence maps are able to represent the conditions that adults are able to tolerate fairly accurately, these methods are less able to detect the conditions important for survival of eggs and chicks, which is vital to the success of species. To address this, studies looking at the long-term population trends of species in relation to changing climate would provide us with key additional information on the role of climate on limiting the distributions of species.

Overall, my work provides an analytical framework for examining the temporal dynamics of climatic niches which provides insights into the relationship between birds and climate. Further, the framework developed can continue to be applied as new methods and data become available in order to address similar questions relating to niche evolution.

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APPENDIX I: Quantification of climatic niches in birds: adding the temporal dimension

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    Review of the literature **AE** 100%
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(3) Preparation of figures/ tables:
    AE prepared all figures and tables in the manuscript and supplementary materials
(4) Data analyses and interpretation of results:
    AE interpreted migratory database
    AE conducted analysis of Australian avifauna data with input from SAF and KBG
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Quantification of climatic niches in birds: adding the temporal dimension

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Quantification of the climatic niche from geographic occurrences is an increasingly important tool for studying species' relationships to their environment, for example to predict responses to climate change. However, as the geographic distributions of birds are seasonally dynamic, they pose a challenge to carrying out comparable and appropriate quantification of climatic niches. In this review, we first assess how relevant seasonal dynamics are across birds as a whole by compiling a database of migratory behaviour for 10 443 bird species. Second, we examine how studies have quantified climatic niches of birds. Finally, using Australia as a case study, we investigate how well existing distribution datasets represent temporal dynamics by comparing seasonal patterns of species richness obtained from point-occurrence data with those from range maps and assess the consequences for niche quantification. We provide a consistent classification of migratory behaviour across all birds, and find that a huge variety exists between and within species that should be considered when quantifying climatic niches. Despite this, our review of the literature revealed that seasonal dynamics have often not been accounted for. For future studies, we provide a framework for selecting appropriate occurrence data depending on migratory behaviour and data availability. Our comparison of seasonal species richness patterns obtained from extent-of-occurrence range maps and point-occurrence data suggests that range maps are less able to detect temporal dynamics of bird distributions than point-occurrence data. We conclude that seasonally explicit range maps combined with climatic data for the corresponding time period can be used to adequately quantify climatic niches for resident birds, but are not adequate to quantify the climatic niches of migratory and nomadic species. Therefore, consistent quantification of climatic niches across all birds requires temporally explicit occurrence points. As such, increasing the availability of occurrence data and methods correcting biases should be a priority.

Quantification of the climatic niche – the set of climatic conditions under which a species is able to survive, reproduce and persist (Pearson and Dawson 2003, Soberón 2007) – has become an increasingly important and popular method when studying species' relationships to their abiotic environment, for example to understand the ecology and evolution of climatic niches. Climatic niches can be directly quantified by experimental measurement of individual physiological tolerances (Diamond et al. 2012, Khaliq et al. 2014); however, as obtaining physiological data is expensive and time-consuming these data only exist for a few species. Instead, a correlative approach is most commonly used to quantify climatic niches whereby the species' observed distribution is combined with climatic data (Araújo and Peterson 2012). Methods such as species distribution modelling (SDM) or ordination techniques can then be used to describe the relationship between a species and climate either in climatic or geographical space (Guisan and Zimmermann 2000, Thuiller et al. 2004). Climatic niches quantified with these methods have been applied to a wide range of interesting questions (reviewed by Engler et al. 2017): to explain current distribution patterns (Moreno-Letelier et al. 2014); to predict species distribution in new climatic conditions (Peterson et al. 2002, Hof et al. 2011) or geographical areas (Peterson 2003); to study niche evolution (Schnitzler et al. 2012); and to support conservation (Zhang et al. 2012). Studies of climatic niches are not limited to merely studying the influence of climate on single species. Climatic niches can be studied across many species due to the increasing availability of detailed global distribution datasets for many species, for example occurrence points from the Global Biodiversity Information Facility (GBIF <www.gbif.org>) or extent-of-occurrence species distributions such as from the IUCN Red List of Threatened Species (IUCN <www.iucnredlist.org>) or BirdLife International and NatureServe (BirdLife <www.birdlife.org>). Such macroecological and macroevolutionary studies are important to help understand the general patterns and fundamental processes that influence climatic niches (Böhning-Gaese 2005, Gaston and Blackburn 2007). However, in order for these studies to be meaningful, climatic niches need to be quantified in a way that is consistent across many different species.

A common criticism of quantifying climatic niches from geographical distributions is that the approach is rarely able to identify the full range of climatic conditions in which the species is able to survive, reproduce and persist, i.e. the fundamental climatic niche (Hutchinson 1957, Soberón 2007). In practice, factors such as biotic interactions (Davis et al. 1998) and dispersal limitation (Pulliam 2000, Pigot and Tobias 2015) usually limit a species' actual distribution to a subset of the climatic conditions in which it could theoretically persist, i.e. the realised climatic niche (Hutchinson 1957, Soberón and Peterson 2005). This has implications for comparative studies, because for each species, the realised niche quantified from distribution data will be a more or less accurate representation of the fundamental niche. However, recent advances in modelling species distributions have begun to address this problem by incorporating factors such as dispersal (Génard and Lescourret 2013), biotic interactions (Kissling et al. 2010, Wisz et al. 2013), adaptation (Hällfors et al. 2015), population dynamics (Heinrichs et al. 2010), and multiple drivers and their interactions (Hof et al. 2011).

In this review, we focus on another important factor influencing niche occupancy and quantification: short-term temporal dynamics in species distributions and how well they are reflected in the available distribution data which are commonly used in niche quantification. Quantifying climatic niches from distribution data crucially depends on knowing the precise spatial and temporal occurrence of species and the corresponding climatic conditions at those spatial locations and times. Because birds are highly mobile they represent an interesting, yet challenging, group in which to study climatic niches. Although many species are resident and their distribution can be assumed to be stable throughout a year, migration is a widespread and diverse phenomenon in birds, with almost one fifth of all bird species showing some degree of migratory behaviour (Kirby et al. 2008). Therefore, in order to accurately quantify climatic niches in birds it is necessary to take into account the dynamic nature of their distributions and the climatic conditions, within and between years (Laube et al. 2015). The true challenge that needs to be addressed is to know which climatic conditions migratory species experience at different times in each part of their dynamic distribution.

The wide variety of migratory behaviours found both between and within bird species has important implications for what kind of data and methods are required in order to achieve a consistent quantification of climatic niches across many species. For example, the Alaskan breeding population of the northern wheatear *Oenanthe oenanthe* travels almost 15 000 km each year to winter in eastern Africa (Bairlein et al. 2012). To quantify the climatic niche of such highly migratory species it is necessary to consider the climatic conditions experienced at their breeding sites, along their migratory flyways and at stopover sites, and at their non-breeding sites. Complete knowledge of these detailed, temporally explicit occurrence points is currently restricted to a few species (Teitelbaum et al. 2016, Thorup et al. 2017), although data derived from new tracking techniques are rapidly accumulating across many species (Bridge et al. 2011, Kays et al. 2015). For the majority of species, seasonally distinct extent-of-occurrence distributions are available that show the breeding range and the core non-breeding areas, and which can be used to quantify breeding and non-breeding climatic niches of seasonal migrants (Laube et al. 2015). However, nomadic species such as the budgerigar *Melopsittacus undulatus* move and breed opportunistically throughout their range and have unpredictable year-to-year movements (Allen and Saunders 2002, Newton 2008), meaning that more detailed temporally explicit distribution data are needed across several years to quantify their climatic niches appropriately (Reside et al. 2010, Schidelko et al. 2013). In many species, intraspecific variation in migratory behaviour adds an additional challenge to quantifying climatic niches in birds. For example, resident populations of the blackcap *Sylvia atricapilla* are found in southern Europe whilst populations breeding in northern Europe are long-distance migrants moving to south of the Sahara (Fiedler 2005). To quantify climatic niches in these species it is important to study the movement patterns of their individual populations, as is done in the "flyway approach" used in conservation (BirdLife International 2010), and occurrence data for SDMs should ideally be temporally explicit and include abundances and subspecies identities (Howard et al. 2014).

Despite the fact that birds are relatively well studied and are one of the best-known class of organisms (Orme et al. 2006, Jetz et al. 2012), comprehensive, temporally explicit, and spatially fine-scale occurrence records are not available for the majority of species (Meyer et al. 2015). In particular, point-occurrence data for the tropics are sparse, meaning that the wintering ranges of many migratory species are comparatively poorly known (Wisz et al. 2007). In practice, the distribution data used for macroecological studies of multiple bird species usually ignore temporal dynamics and focus either exclusively on breeding (Orme et al. 2005, Holt et al. 2013) or, more rarely, wintering ranges (Wisz et al. 2007, Barbet-Massin et al. 2009). Although some studies have begun to address this by utilising seasonal extent-of-occurrence distributions (Boucher-Lalonde et al. 2014, Laube et al. 2015), the vast majority of studies leave the question of how to quantify climatic niches in migratory birds unanswered.

We aim to 1) assess the potential consequences of short-term temporal dynamics in species distributions on niche quantifications across many species using distribution data; 2) examine how current studies of climatic niche ecology and evolution have quantified the climatic niche of birds; and 3) assess how well existing distribution datasets represent the dynamic distributions and consequently the climatic niche of birds. In order to understand the type of distribution data required to quantify climatic niches in a consistent way across multiple species of birds, we first provide a classification of the different types of migratory behaviour exhibited by birds, and briefly summarise current knowledge about how many species show which type and to what extent intraspecific variation occurs. Given this knowledge, we then describe the ideal datasets needed to quantify climatic niches in birds of each migratory behaviour type, and review the datasets that have been used to date. Finally, we ask whether climatic niches in birds can be studied with our existing datasets given the complexity of migratory behaviour. We use Australia as a case study, because it is a biogeographically distinct continent for which comprehensive temporally explicit occurrence data points are available. To assess the ability of available seasonal distribution data to capture the dynamic distribution of migratory birds, we compare species richness patterns across Australia obtained from seasonal extent-of-occurrence distribution data with those from temporally explicit occurrence points. To illustrate the importance of including movement behaviour on niche quantification we characterise the climatic niche of one example nomadic species with and without taking into account movements throughout the year. We conclude that some existing datasets can be well utilised to quantify climatic niches across many species of birds that exhibit a variety of migratory behaviour, but that to date there has been a lack of awareness concerning what is, and what is not actually captured by distribution data.

Migratory behaviour in birds: how extensive is it?

Although migration is known to be a widespread phenomenon in birds, the consequences of these short-term temporal distribution dynamics for the quantification of niches from distribution data are less clear. Laube et al. (2015) recently provided a conceptual framework which uses separately mapped breeding and non-breeding ranges to quantify the climatic niches of birds taking into account the different climatic conditions experienced in two seasons, and applied this to the *Sylvia* warblers. This framework is based conceptually on the archetypal image of bird migration, in which the whole population moves from a breeding area to a separate non-breeding region. The question of how widely applicable this method is for quantifying climatic niches across the range of migratory behaviours that exist in birds has, however, not yet been addressed. Here, we assess how many species actually show classic migratory behaviour with a new classification of all extant birds into different categories of movement behaviour, with a focus on distinguishing types of behaviour that have consequences for niche quantification from occurrence data.

We follow other avian studies and use the term migration to refer to seasonal migration, i.e. regular return movements causing individual birds to be found in different locations over the course of one year (Newton 2008, Egevang et al. 2010). As an extreme example, the bar-tailed godwit *Limosa lapponica* can fly non-stop for more than 10 000 km, switching continents between seasons (Battley et al. 2012). Migration excludes everyday routine movements that occur within the home range (e.g. daily foraging in search of resources) and one-way dispersal movements by juveniles (natal dispersal) and adults (breeding dispersal). This 'classic' definition of migration only represents one extreme of a huge variety of types of movement behaviour. For example, other species seasonally disperse from their breeding sites into different directions to spend the non-breeding season in sometimes far removed locations, (e.g. the wandering albatross, *Diomedea exulans*, Croxall et al. 2005). Other species move along elevational gradients but not in a consistent geographic direction to spend the colder seasons at lower elevations often within the breeding distribution (e.g. the American dipper *Cinclus mexicanus*, Gillis et al. 2008). Still other species exhibit seasonal migration only in years with unusually low food availability (e.g. the waxwing *Bombycilla garrulus,* Svardson 1957), or exhibit nomadic behaviour like the budgerigar, which is characterized by non-seasonal, irregular movements (Allen and Saunders 2002). Classifications of migratory versus non-migratory species to date have widely differed because of this wide variety of movement behaviours between and within species. For example, Cox (2010) estimated that 26.2% of bird species perform regular seasonal movements from breeding to non-breeding sites. In contrast, global studies such as Rolland et al. (2014) define species as migratory where regular movements beyond the breeding ranges have been mapped according to the BirdLife global distribution database, treating 18.5% of bird species as migratory, a difference that equates to more than 700 species. As such, the proportion of species for which migratory behaviour impacts niche quantification from distribution data is unknown.

In order to determine the full extent of migratory behaviour and to understand the types of distribution data that are required to quantify climatic niches in a consistent way across multiple species of birds, we classified movement behaviour for all 10 443 extant species on the IOC species list ver. 3.1 (Gill and Donsker 2012). Our classification follows Newton (2008) with slight modifications (Table 1), and we used the descriptions of migratory behaviour from the Handbook of Birds of the World (HBW, del Hoyo et al. 1992–2013 and updates on the Handbook of the Birds of the World Alive website <www.hbw.com>, accessed until September 2016). We categorised birds into four main types of movement behaviour: 1) directional migration, 2) dispersive migration, 3) nomadism and 4) residency (as defined in Table 1). However, a characteristic problem of classifying migratory behaviour is that it is not uncommon for individuals or populations of a species to exhibit different migratory behaviour. Therefore the three main types of movement behaviour, 1) directional migration, 2) dispersive migration and 3) nomadism, were further subdivided into the three subcategories full, partial and local, depending on the extent to which these movements occur within the species (Table 1). When all individuals and populations of a species move, the species was categorised as fully migratory (1 or 2) or fully nomadic (3). For species in which just some populations or parts of populations move, species were categorised as partially migratory or partially nomadic. Finally, if the movements only occurred at a local scale, they were classified as locally migratory or locally nomadic. To some degree the distinction between partial and local movements was arbitrary, but it follows a long-standing tradition in the migration literature and an effort was made to provide an objective classification based on the description phrasing found in the sources (see Supplementary material Appendix 1 for examples). Species classified as resident (4) were divided into the subcategories full and partial only (Table 1).

Intraspecific variation in movement behaviour was reflected by classifying species which exhibit several different movement behaviours into multiple categories (Fig. 1). For example, the blackcap, which has resident as well as migratory populations (Fiedler 2005), was classified as partially resident and partially migratory. Note that we used partial migration to flag two quite different scenarios: 1) when populations of a species exhibit different behaviours

Table 1. Definition of large-scale movement behaviour categories in birds, modified from Newton (2008). We also indicate whether extent-of-occurrence range maps are expected to show seasonally distinct distribution areas for species in each category. Note that species with intraspecific variation in movement behaviour were initially assigned multiple categories, so the number of species in each category refer to 1) the species classified in the given behaviour category on the species level in this study (this column adds up to the total 10 443 classified species) and 2) the additional species that exhibited the given behaviour but were finally assigned other categories on the species level (see main text and Fig. 1).

Movement behaviour	Definition	Subcategory	Distinct seasonal areas mapped	Number of species in category	Additional number of species exhibiting this behaviour
Directional migration	Individuals make regular return movements that are clearly seasonal and geographically directional, i.e. they move every year from specific breeding grounds to specific non-breeding locations. Movements have a clear latitudinal or longitudinal directionality (e.g. full long-distance migration).	full	yes	529	0
		partial	yes or no	1083	0
		local	usually no	0	327 dispersive migratory, nomadic, and resident species
Dispersive migration	Individuals make regular post-breeding movements in any geographical direction from breeding sites, i.e. movements are clearly seasonal but have no consistent latitudinal or longitudinal directionality (e.g. typical seabird migration, altitudinal migration).	full	usually yes	82	0
		partial	yes or no	385	733 directional migratory, nomadic, and resident species
		local	no	0	1519 directional migratory, nomadic, and resident species
Nomadism	Individuals make irregular movements from one area to another, residing for a time wherever food is temporarily plentiful and breeding if possible. Movements are not clearly seasonal and not directional, because the areas successively occupied may lie in various directions from one another and can vary from year to year.	full	yes or no	32	0
		partial	yes or no	71	259 migratory and resident species
		local	no	0	226 migratory and resident species
Residency	Individuals are sedentary and do not make major regular or irregular movements.	full	no	7830	0
		partial	yes or no	411	1416 migratory and nomadic species
Unknown	There is not enough information to classify migratory behaviour as above.	–	usually no	20	922 migratory, nomadic, and resident species flagged as uncertain

(e.g. spatially separated resident and migratory populations), and 2) when individuals within the same population exhibit different behaviours. We were unable to distinguish these cases from the sources, and the different scenarios would not affect quantification of species-level climatic niches. A species classified as fully migratory in any one of the three migratory categories was allowed to be classified as locally migratory in any of the other categories, but not as partially. These data were classified in as objective a way as possible by a single person (the full dataset and a detailed description of procedures are publicly available from dx.doi.org/10.12761/SGN.2017.10058). 1792 species (17.2% of the 10 443 classified species) displayed several different movement behaviours and were therefore classified into multiple categories (Fig. 1).

To assign each species as a whole to a final single movement category, we used the knowledge of intraspecific variation captured by our initial classification and given in species descriptions (del Hoyo et al. 1992–2013 and updates on the Handbook of the Birds of the World Alive website <www.hbw.com>, accessed until September 2016) according to the following conditions (note that these final species-level movement assignments cannot be derived from Fig. 1 directly, but the number of species classified to each final movement category are given below and in Table 1). Species that showed partial directional migration were always assigned as 'directional migratory' overall, even if only a small proportion of individuals performed the directional migration and most individuals or populations were resident, nomadic, or dispersive migrants. Locally migratory and/or locally nomadic behaviour was disregarded in the species-level assignment. As such, species which were described as fully resident with locally dispersive migration had a final species-level categorisation as resident. Finally, we classified some partially dispersive and partially resident species, as well as some partially nomadic and partially resident ones, as overall resident where those partial movements comprised a very small proportion of individuals or were not performed over geographic distances commonly mapped in extent-of-occurrence distribution data. Consequently, our final definition of species-level residency was quite wide and included species which have local movements (directional, dispersive or nomadic) and many altitudinal migrants that move seasonally in elevation within the breeding range.

In the final species-level categorisation, 8241 species (78.9% of all species) were classified as resident (Table 1).

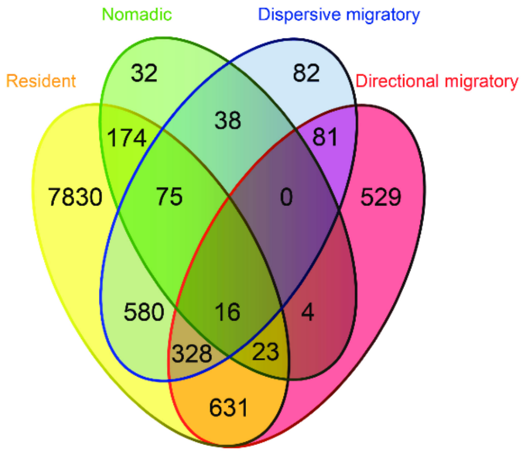

Figure 1. Classification of 10 443 extant bird species into movement behaviour categories (full and partial behaviour). Species which exhibit more than one type of movement behaviour were classified into multiple categories, so the overlap between different movement categories reveals the prevalence of intraspecific variation in birds. The diagram shows the number of species falling into each of the 15 possible unique combinations of the four types of movement behaviour. Only partial or full movements are considered here; species which only showed local movement behaviour were not considered to belong to that category. The 20 species classified as having unknown movement behaviour are not included in the figure.

As these species have distribution patterns that do not change significantly throughout the year, it can be assumed that climatic niches can be fairly accurately quantified using annual distributions without having to consider seasonal movement dynamics. Consistent with some previous estimates, 2079 species (19.9% of all species) were classified as migratory either performing regular seasonal movements in a consistent direction between breeding and non-breeding sites (directional migration, 15.4%) or in any geographical direction from breeding sites (dispersive migration, 4.5%). Because the majority of these species will have seasonally distinct extent-of-occurrence distributions mapped (Table 1), it is possible to quantify their climatic niches using the breeding and non-breeding distributions as in (Laube et al. 2015). This framework should be able to reflect the climatic niche of these species fairly well. Only 103 species (1.0% of all species) were categorised as nomadic, making irregular movements that vary between years and consequently requiring more detailed point-occurrence data over many years to quantify climatic niches. Not only would the distribution dynamics of these species not be fully represented by looking at their distributions in two seasons, but nomadic species are also normally mapped as occurring year-round in existing global datasets. Under the Laube et al. (2015) framework, this could lead to the false assumption that they experience the climate in the entire mapped distribution in all seasons, resulting in inappropriate niche quantification. We were unable to classify migratory behaviour for only 20 species due to lack of information.

These final categorisations, however, hide the true diversity of movement behaviours exhibited by birds, which is demonstrated in the full initial classification into multiple categories (Fig. 1). Intraspecific variation in movement behaviour was found to be very common, with 1950 species (18.7% of all species) exhibiting more than one type of behaviour in the partial subcategory (Fig. 1). Of the 8241 species which were categorised as resident in the final species-level categorisation only 6215 (75.4%) are fully resident species (in which all individuals are sedentary and do not make any movements, not even local ones): 24.6% of species that were classified as species-level resident also display a variety of partial and local movements. However, as the movements made by these species are likely to be at spatial scales smaller than those detected by the classic extent-of-occurrence range maps, niche quantification of these species using year-round range data is appropriate if environmental data is sampled to the same crude spatial scale as the range maps (Guisan and Thuiller 2005). More significantly, only 29.4% of migratory species (611 species) were found to be fully migratory, with all individuals and populations performing regular seasonal movements. For example, many species are partially migratory and partially nomadic (Fig. 1). The consequence of this common intraspecific variation in movement is that the number of species for which the climatic niche cannot be reasonably quantified using distribution data in two seasons may be much greater than is suggested by our final species-level classification of discrete movement categories (Table 1).

Quantifying climatic niches of birds from distribution data depends on knowing the precise spatial and temporal occurrence of species and the corresponding climatic conditions at those spatial locations and times. The temporal and spatial resolution of data required to do this varies depending on the movement patterns of the species. Our classification of movement behaviour demonstrates that across birds, a huge variety of complex movement behaviour occurs both between and within species (Fig. 1). It is therefore important to first check the movement behaviour with our detailed classification or more specific literature, and use this knowledge to determine what occurrence data are sufficient to quantify the climatic niches of the study species. In the next section, we review existing studies of climatic niche quantification in birds and more specifically discuss the data required for quantifying the climatic niches of birds with different types of movements.

Climatic niche quantification in birds: what kinds of data have been used?

For an overview of how existing literature has quantified climatic niches in birds with regard to movement behaviour, we reviewed studies focussing on those quantifying climatic niches across multiple species. We then classified these into four sets of approaches depending on which kind of distribution and climatic datasets the niche quantifications were based on (Table 2). Here, we discuss the ability of each of these approaches to quantify the climatic niche of species displaying each type of the four movement behaviours outlined in Table 1 and described in the text. We conclude by

Table 2. Typical examples of studies quantifying climatic niches in birds, key parameters of the study, and our categorisation of these studies according to occurrence and climatic data used for niche quantification. Within categories, studies are sorted by declining number of species in the study. Unless stated otherwise, the proportion of species classified as migratory follows the classification of the study. When migratory behaviour was not provided, we quantified the proportion from the species descriptions in the Handbook of the Birds of the World where possible (indicated by *); if not possible, the number of migratory species was estimated as ~ 20% (indicated by **). SDM = species distribution modelling.

	Study	No. of species	Migratory species (no. and proportion)	Geographic scale	Niche representation	Study topic
Approach 1: treat all species as residents: Breeding range and annual climate	Cooney et al. 2016	7657	1531 species (20%**)	global	ordination	evolution of climatic niches
	Pigot et al. 2010	7484	1497 species (20%**)	global	summary statistics	understanding current species distribution
	Huntley et al. 2008	431	86 species (20%**)	Europe	SDM	predicting future species distribution
	Title and Burns 2015	285	57 species (20%**)	Central and South America	SDM	evolution of climatic niches
	Beale et al. 2008	100	57 species (57%)	Europe	SDM	understanding current species distribution
	Stralberg et al. 2009	60	20 species (33%)	California	SDM	predicting future species distribution
	Nyári and Reddy 2013	29	0 species (0%*)	(southeast) Asia	SDM	evolution of climatic niches
Approach 2: quantify one season: weasonal range and seasonal climate	Pearman et al. 2014	405	81 species (20%**)	Europe	ordination	evolution of climatic niches
	Barnagaud et al. 2012	74	56 species (75%*)	Europe	summary statistics	understanding current species distribution
	Barbet-Massin et al. 2009	64	64 species (100%)	Afro-palearctic (Africa)	SDM	predicting future species distribution.
Approach 3: quantify seasonal climatic niches a) using seasonal range maps b) using temporally explicit occurrence points	Boucher-Lalonde et al. 2014	625	625 species (100%)	Americas	summary statistics	understanding migration
	Laube et al. 2015	26	13 species (50%)	Europe, Africa and western Asia.	ordination	understanding migration
	Papeş et al. 2012	1	1 species (100%)	tropics	SDM	understanding migration
	Gómez et al. 2016	103	49 species (48%)	Americas	ordination	understanding migration/ evolution of climatic niches
	Nakazawa et al. 2004	21	21 species (100%)	Americas	SDM	understanding migration
	Martinez-Meyer et al. 2004	9	5 species (56%)	North America and Northern South America	SDM	evolution of climatic niches
	Joseph and Stockwell 2000	1	1 species (100%)	South America	SDM	understanding migration

describing the ideal temporal resolution of data needed to quantify the climatic niches for each of the different types of movement behaviour.

Despite the known seasonal dynamics of many bird species, the majority of studies that have quantified the climatic niches of birds used geographic distribution data of breeding ranges and annual climatic data (Table 2, approach 1). This approach is appropriate if the research is limited to subsets of bird species that do not include any migrants or nomads (Nyári and Reddy 2013) since it includes all the climatic conditions that a resident tolerates throughout the year. However, for migratory species this approach includes the climate at the breeding sites in the non-breeding season, when migratory individuals are not present there, posing a high risk of overestimating the climatic niche. Secondly, as many migratory species have been shown to inhabit very different climatic niches from season to season (Martinez-Meyer et al. 2004, Boucher-Lalonde et al. 2014, Laube et al. 2015), this approach is unable to quantify the full range of climatic conditions experienced by migratory species because it does not include the conditions which the birds experience during the non-breeding period (Laube et al. 2015). In the rare occasions when migratory birds track a specific set of climatic conditions throughout the year, as for example in the case of Swainson's flycatcher *Myiarchus swainsoni* (Joseph and Stockwell 2000), breeding ranges can be used to accurately quantify the climatic niche of migratory species. However, knowledge of the climatic conditions in the non-breeding ranges is required to come to this conclusion in the first place. Finally, even for many overall resident species which exhibit some local or partial movement behaviour (1990 species), year-round extent-of-occurrence distributions can be misleading in niche quantifications, if the spatial scale used is so fine that local temporal dynamics should be taken into account.

Some studies have avoided the challenge of seasonal movement by quantifying the climatic niche of species for just a single season (Table 2, approach 2), most commonly the breeding season. For example, Pearman et al. (2014) quantified the climatic niche during breeding by extracting climate data for each species' breeding distribution exclusively for the months in which a species breeds. Since climatic niches quantified using this approach are equivalent for migratory and resident species (both only quantify the breeding niche), they are more comparable than those quantified using approach 1. However, by looking at only the breeding or non-breeding range, only a subset of a species' climatic niche is studied. It is unlikely that a species' response to climate change can be accurately predicted if its climatic niche is only quantified for one seasonal part of the range. For migratory species, it is essential that we understand how both the breeding and non-breeding range are affected, as both are important to ensure the survival of the species (Taylor and Hall 2012, Iwamura et al. 2013).

Other studies of climatic niches in birds are beginning to explicitly consider the temporal and spatial dynamics of migratory species (Laube et al. 2015). Typical field guides for most regions of the planet, as well as the BirdLife International or HBW Alive global distribution maps compiled from these, comprise separate breeding and non-breeding extent-of-occurrence ranges for migratory species, and such datasets have been used in combination with monthly climatic data to quantify climatic niches considering separate species distributions in two seasons (Table 2, approach 3a) (Boucher-Lalonde et al. 2014, Laube et al. 2015). Climatic niches quantified across two seasons should reflect the climatic niches of seasonal long-distance migrants fairly well despite the fact that two seasons are not able to capture the climatic conditions experienced during migratory passage. During migratory passage, many birds quickly pass through unsuitable areas (La Sorte et al. 2016) and so arguably these conditions should not be considered as part of their climatic niche. However, for species with more complex migratory patterns such as loop migrants (Klaassen et al. 2010), the conditions experienced during passage should be included when quantifying the climatic niche because a large proportion of time is spent in passage. Similarly, climatic niches quantified using the distributions within two seasons are unlikely to fully reflect the climatic niches of nomadic species, which have no core breeding and non-breeding seasonal distributions.

Finally, some studies have used temporally explicit occurrence points and split them into two (Martinez-Meyer et al. 2004, Nakazawa et al. 2004, Engler et al. 2014, Gómez et al. 2016) or three (Papeş et al. 2012) time periods in order to quantify seasonal climatic niches (Table 2 approach 3b). This is probably the ideal method as it is based on much more detailed information of species distributions than extent-of-occurrence maps. Importantly, with temporally explicit point data climatic niches could in theory be quantified at a much finer temporal resolution, which would solve many of the issues mentioned above, as the temporal resolution could be matched to the species' overall migratory behaviour type and the spatial resolution of available occurrence data. Very few studies have used temporally explicit occurrence points to quantify the climatic niche at a finer temporal resolution. For example, Joseph and Stockwell (2000) quantified the monthly climatic niche of a single species (Swainson's flycatcher). However, it is not currently feasible to use data of this quality for studies across many species on a global scale, as these data are rare and often specific to selected species or regions (Hof et al. 2015). New tracking technologies should allow this type of approach to be applied across more species in the future (Bridge et al. 2011).

To quantify the climatic niches of bird species which have dynamic distributions in space and time it is important to know which climatic conditions are experienced at different times, in each part of their distribution. Depending on the movement behaviour, different spatial and temporal resolution of distribution data will be adequate to quantify the niche. We suggest the following procedure when quantifying the climatic niches of birds from occurrence data based on the movement behaviour of the study species. First, resident species which do not make any major movements are able to have their climatic niches appropriately quantified by using breeding ranges and annual climatic data (approach 1, Table 2). Some species classified as resident in our classification scheme make partial or local movements (for example altitudinal migrants). For global studies, or studies with a large spatial extent, resident species with partial or local movements may have their niches appropriately quantified using approach 1. However, for studies at a finer scale, or those interested in understanding local movements or dynamic occurrence in mountains, temporally explicit occurrence points (approach 3b, Table 2) are more appropriate. Second, migratory species which move between seasonally and geographically distinct breeding and non-breeding areas require information on distribution and climate for both parts of their range to appropriately quantify their climatic niches, whether they are directional or dispersive migrants (approach 3a, Table 2). Third, for species with more complex movement patterns such as loop migrants or nomads, temporally explicit occurrence points and climatic data are required to capture the climatic conditions that are experienced throughout the year (approach 3b, Table 2). For migratory species where there are no distinct seasonal distributions mapped in global databases, the spatial scale of niche quantification should be considered carefully: if year-round distributions are provided because of partial migration within the species' breeding range, temporally explicit occurrence points (ideally with abundance data; approach 3b) will provide a much better reflection of the species' climatic niche at a higher spatial resolution. In many cases, seasonal distributions might not be mapped for migratory species due to lack of knowledge, as is reflected in the fact that we flagged 404 species as uncertain in our movement classification; then, approach 1 is probably the only option, but the study should explicitly discuss the large uncertainty of the occurrence data and be performed at a coarse spatial resolution. Thus, when studying climatic niches across many bird species that collectively exhibit the full range of movement behaviours as classified in Table 1, only temporally explicit occurrence data (approach 3b) are able to quantify climatic niches in a consistent way across all species.

As the optimal data for quantifying climatic niches across many species of birds are not currently available, studies across many species might need to be pragmatic and focus on more easily modelled species and clades. Because seasonally distinct extent-of-occurrence range maps exist for the majority of migratory bird species, and as the vast majority of species classified as non-residents in our scheme were seasonal migrants rather than nomadic, quantifying the climatic niche in two seasons (Laube et al. 2015) represents the most appropriate approach that can currently be applied across most species. Nevertheless, when quantifying climatic niches across many species it is important to be aware of the movement behaviour exhibited by the study species and to explicitly discuss the ability of the data to quantify climatic niches in terms of uncertainty as well as spatial and temporal resolution. To assess the implications of using the different available datasets to quantify climatic niches, we next use a case study to demonstrate how strongly patterns across many species can differ between different data sources.

Australian case study: what kind of data could be used?

Two of the most commonly used types of data to study species distribution are extent-of-occurrence range maps and point occurrence data from surveys or opportunistic observations (Graham and Hijmans 2006). Much work has already been devoted to highlighting the limitations of each of these types of distribution data (Hurlbert and White 2005, Rondinini et al. 2006, La Sorte and Hawkins 2007). Extent-of-occurrence range maps, which typically incorporate expert knowledge from a wide range of sources represent the outer limits of a species' distribution, including areas that may not be occupied, potentially overestimate species distribution (Jetz et al. 2008). In contrast, point-occurrence data exhibit spatial, temporal and taxonomic biases (Yesson et al. 2007) and likely underestimate and misrepresent species distribution (Rondinini et al. 2006). However, at low spatial resolutions which are typically used for global studies, species distribution patterns obtained from range maps and point-occurrence data are largely congruent (Graham and Hijmans 2006, Hurlbert and Jetz 2007). Because of this, and because global extent-of-occurrence range maps are available for many species, range maps have been the primary type of data for broad-scale global studies of species distribution.

Although many studies have focussed on general limitations of both extent-of-occurrence maps and point-occurrence data, the impact that seasonal migration might have on the ability of these data to accurately represent species distribution has not yet been addressed. Here we compare seasonal species richness patterns for the birds of Australia using seasonal extent-of-occurrence range maps with those calculated from temporally explicit point localities, to determine how well these two data types are able to detect seasonal patterns in species distribution. We calculate the difference in species richness between seasons as a simple measure of overall seasonality captured by the occurrence datasets across many species. If each dataset is able to detect the same amount of seasonal difference in species richness, we would expect high correlation between the seasonal differences across grid cells. Alternatively, if one data type captures an overall higher amount of seasonal variation, we can assume that these data would be more appropriate for niche quantification of species with seasonal movement behaviour. Finally, we compare the climatic niche characterised for an example nomadic species, the budgerigar *M. unulatus* using extent-of-occurrence range maps, with that using temporally explicit point-occurrence data from the Australian Atlas. Australia is the ideal case study for such comparisons, firstly because it is a geographically separate unit with a comparatively low number of long-distance migrants where complex movement behaviours are known to occur, and secondly because a coherent dataset of temporally explicit occurrence points exists with the Atlas of Australian Birds (Barrett et al. 2003).

Methods

We compared seasonal differences in species richness for terrestrial bird species found in Australia from 1) extent-of-occurrence range maps where distributions are classified as breeding, non-breeding and year round; with those calculated from 2) temporally explicit species occurrences.

Extent-of-occurrence range maps were obtained from BirdLife International and Natureserve (BirdLife International and NatureServe 2015, downloaded from <www.birdlife.org> in July 2016). Taxonomy was matched to the IOC taxonomy list ver. 3.1 (Gill and Donsker 2012) and data was cleaned to exclude marine, taxonomically non-valid and extinct species. Additionally areas were excluded where species were classified as introduced, vagrant or unknown seasonality (see appendix for full description of cleaning steps). The range maps were resampled into an equal area grid with cells of 1° longitudinal and varying latitudinal extent, mapped with a Behrmann projection (Orme et al. 2005). In total, the BirdLife range maps included 603 species present in Australia for at least one season.

Temporally explicit point-occurrence data was obtained from the New Atlas of Australian birds (Barrett et al. 2003, with updates available online; <http://birdata.birdlife.org.au/>). For this analysis we used over 9 million species-by-location records for the time period starting in September 1998 and ending in August 2012. Taxonomy was matched to the same taxonomy as the occurrence data above (Gill and Donsker 2012), marine species were omitted and the data was cleaned by removing erroneous surveys with inconsistent or ambiguous date and time information. The occurrence points were resampled into the same equal area grid as above (Orme et al. 2005). As we aimed to compare seasonal differences in species richness between data sources, it was important that each data source has seasonal distribution data representing equivalent seasons. Although the point-occurrence data were temporally explicit and can therefore theoretically be split into any seasons desired, the global seasonal range maps were only available for 'breeding' and 'non-breeding' seasons. As such, in order to obtain seasonal point-occurrence data which was comparable with seasonal distribution data available from extent-of-occurrence range maps we divided the occurrences into those corresponding to Austral summer (September–February) and Austral winter (March–August), see appendix for details on additional cleaning steps and season assignment. The final cleaned seasonal point-occurrence dataset consisted of 602 species and 7 223 351 species-by-grid cell occurrences.

The following analyses were carried out using the 598 species common to both datasets. For each dataset we calculated the number of species in each cell for each season separately (Austral summer and winter). Following Somveille et al. (2013), we also calculated the difference in species richness between seasons (number of species in Austral winter minus number of species in summer) and the proportion of species that differ among seasons (difference in species richness, divided by the total number of species occurring annually). To determine whether the two datasets were able to detect similar amounts of seasonality in species richness, we tested the correlation between the seasonal differences in species richness obtained from each dataset for all cells which had species occurrences in both seasons. Cells without any species were excluded from this analysis because it is unclear whether they truly represent an absence of species or are instead a result of low sampling effort in some Atlas cells. Additionally, if both datasets have no species, including these cells in the analysis would overinflate the degrees of freedom. In addition, we also tested the correlation between seasonal differences in species richness obtained from both datasets for cells for which sampling effort was high (> 100 records in each season), to determine whether any differences detected were an artefact of poor sampling effort.

The climatic niche of the budgerigar was quantified separately using two data sources; 1) the extent-of-occurrence distribution from BirdLife International and 2) the temporally explicit distribution data from the Australian Atlas which was cleaned and divided into monthly occurrence data (details in the Supplementary material Appendix 1). For comparability between point-occurrence data and range maps, both datasets were sampled into the same equal area grid as above (Orme et al. 2005) and only grid cells that occurred in both datasets were included in the niche quantification. Monthly total precipitation and monthly mean temperature data were obtained from the WorldClim ver. 1.4 dataset (averages from 1960–1990, 30 arc seconds resolution) (Hijmans et al. 2005). As the extent-of-occurrence range maps show the budgerigar staying in the same location all year round (Fig. 4A), the climatic niche was quantified using climatic data for all months of the year for the entire annual distribution. In contrast, the annual climatic niche for the point-occurrence data was characterised taking into account the changing distribution each month. As a measure of niche similarity, we calculated the overlap between the two niches characterised following the methods of Broennimann et al. (2012) using Schoener's D and niche breadth was calculated following Laube et al. (2015). For a full explanation of niche characterisation methods see appendix.

Data deposition

Data available from <http://dataportal-senckenberg.de/database/>. (Eyres et al. 2017).

Results

Species richness was systematically lower according to point-occurrence data than from the range maps (Fig. 2). The two datasets were found to detect hugely different amounts of seasonal variability in species richness (Fig. 3): there was a low correlation between the seasonal differences in species richness for the two datasets (Pearson's correlation coefficient $r = 0.45$, $n = 799$ grid cells, Fig. 3A–B). The difference in species richness between seasons was found to be systematically greater using point-occurrence data, even when the total number of species within grid cells was accounted for by investigating proportional differences (Fig. 3C–D). In the south west and south east coastal regions of Australia where sampling effort was high (Fig. 2E–F), there were even stronger differences between the seasonality captured by the range map and point-occurrence data (Pearson's correlation coefficient $r = 0.23$, $n = 219$ grid cells, including only those which have > 100 records in each season).

Range map data for the budgerigar *Melopsittacus undulatus* shows that the distribution remains unchanged throughout the year with no seasonal movements (Fig. 4A). However, the point-occurrence data shows that the budgerigar makes movements within the year (for simplicity shown as the distribution across two seasons, Fig. 4B). Although there is large overlap between the climatic niche characterised for the budgerigar using the annual range map and the niche characterised taking into account annual movements ($D = 0.7$), niche breadth calculated from annual range map is larger than the niche characterised from monthly distribution across a year (Shannon diversity = 6.9 rather than 6.5) (Fig. 4C).

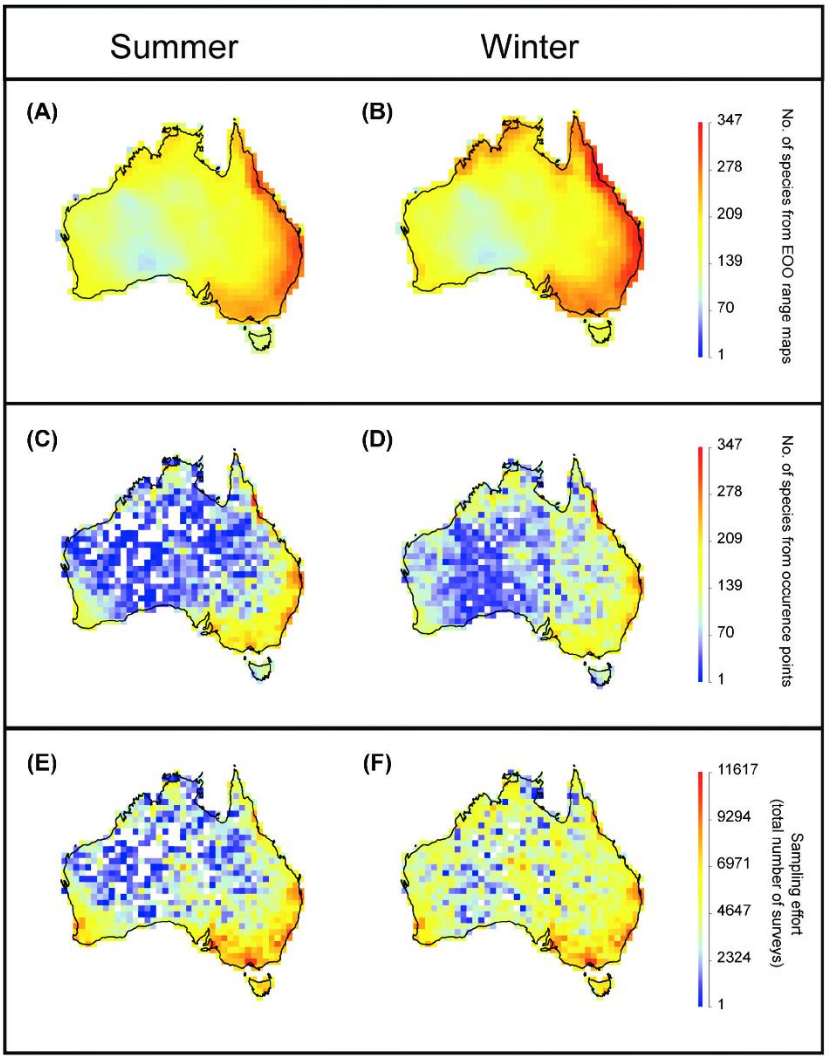

Figure 2. Comparison of seasonal species richness obtained from the extent-of-occurrence (EOO) range maps (A and B) with temporally explicit point-occurrence data (C and D). Sampling effort (the total number of surveys in each season) is shown for the point-occurrence data (E and F). Both datasets include the same 598 species, and were resampled into an equal area grid mapped with a Behrmann projection. Species richness is systematically higher according to the range maps than the point-occurrence data.

Discussion

Our comparison of seasonal range map data with point-occurrence data obtained from the New Australian Atlas highlights some potential shortcomings of both datasets. Consistent with previous studies, species richness was found to be systematically higher according to range maps than according to point-occurrence data (Hurlbert and Jetz 2007, Jetz et al. 2008). This indicates that extent-of-occurrence range maps overestimate species distributions, that point data underestimate species distributions, or both. In areas with poor sampling, point-occurrence data likely underestimate distributions (Graham and Hijmans 2006).

More importantly to our question, the point-occurrence data detected greater absolute and proportional seasonal differences in species richness than the range maps. Although this difference could be driven by sampling effort associated with survey data, across grid cells with high sampling effort we found even more substantial differences between the seasonality captured by range maps and point-occurrence data. This indicates that if sampling effort is high, point-locality data are superior to extent-of-occurrence maps at detecting seasonal variation in bird distributions. Specifically, the point-occurrence data were able to show that many species move from the coastal regions to the centre of Australia for Austral winter, or escape hot summer temperatures in the interior by moving to coastal regions in summer. This

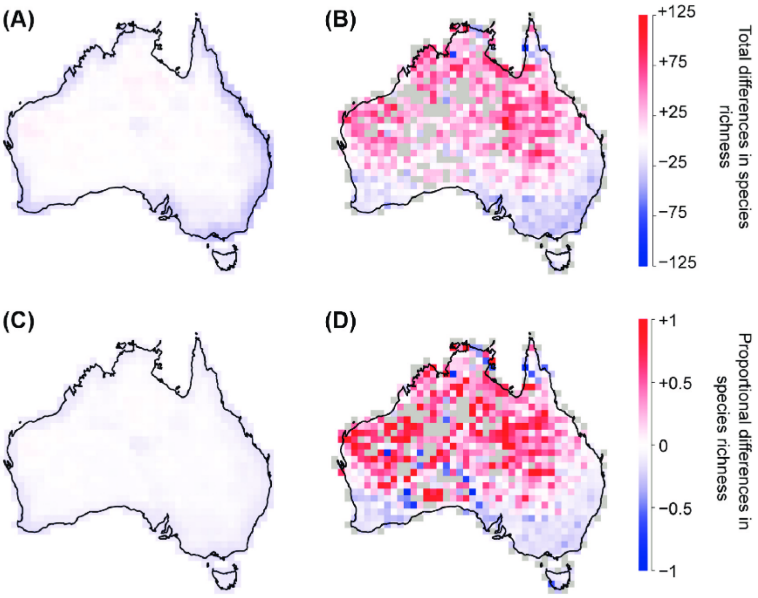

Figure 3. Comparison of seasonal differences in species richness obtained from extent-of-occurrence range maps with temporally explicit point-occurrence data. Total differences in species richness (number of species in Austral winter minus that in Austral summer) for range maps (A) and for point-occurrence data (B); and proportional differences for range maps (C) and point-occurrence data (D). Positive values (in red) indicate areas that contain more species in winter, and negative values (in blue) indicate areas with more species in summer. Cells which had no surveys in one or both season are shown in grey. Both datasets include the same 598 species, and were resampled into an equal area grid mapped with a Behrmann projection. Point-occurrence data are able to detect greater seasonality.

movement pattern has long been postulated and has been previously detected with Atlas data (Nix 1974, Griffioen and Clarke 2002), however it has not been evident from seasonal range maps (Somveille et al. 2013). Analyses that take sampling effort explicitly into account are needed to ascertain whether this pattern reflects seasonal movement patterns.

These results have important implications for the quantification of climatic niches from distribution data. As extent-of-occurrence maps were unable to detect seasonal changes in distributions that were detected from temporally explicit occurrence data split into two seasons, niche quantification from seasonal range maps could be quite misleading and include climatic conditions at sites and times where species are not actually present. This is demonstrated by our characterisation of climatic niches for the budgerigar which indicate overestimation can occur when movements are not taken into account. Importantly, this overestimation will vary depending on the movement patterns of the species making niche quantifications incomparable between species. As extent-of-occurrence range maps are known to overestimate distribution and point-to-grid data tends to underestimate species distribution (Graham and Hijmans 2006), it is possible that some of the difference in niche size is attributable to the difference between data sources. However, at large scales these two data sources provide largely congruent estimations of species distribution (Graham and Hijmans 2006). In addition, by only including grid cells which are occupied in both data sources, we minimise this possibility.

Because nomadic species make up a comparatively large proportion of the birds of Australia, our comparisons of seasonal species richness potentially overemphasise the problems of using range maps to characterise seasonal climatic niches. Although nomadic species only represent 0.9% of bird species overall (Table 1), they can be more or less relevant depending on the study species or the study area. For example, nomadic species are particularly prevalent in semi-arid ecosystems (Dean 1997). It is therefore still important to be aware of how many, and which species will not have their distribution dynamics accurately represented by certain datasets. Similar problems are expected for niche quantification of the many altitudinal migrants, the vast majority of which have year-round range maps in global datasets. Future studies should investigate how much of the discrepancy between point-occurrence data and range maps that we detected can be attributed to nomadic, dispersive, and mostly resident species.

It is not possible to clearly determine which data are best able to detect seasonal differences in species distribution because we do not have perfect knowledge of species distributions in each season. However, our comparisons of seasonal extent-of-occurrence maps with temporally explicit occurrence data highlight some potential shortcomings of both datasets and enables a better understanding of what each data type can capture. Most significantly, we show that the extent-of-occurrence maps were unable to detect seasonal changes in distributions that were detected by using temporally explicit point-occurrence data split into

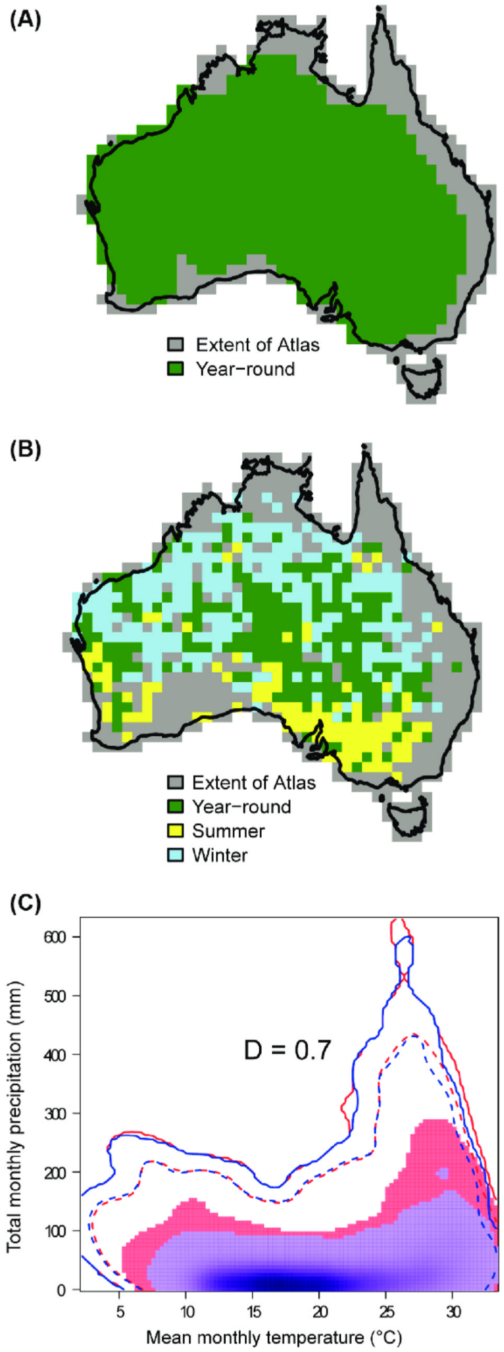

Figure 4. Comparison of the distribution of the budgerigar *Melopsittacus undulates*, a nomadic species, from extent-of-occurrence range maps (EOO) (A) with that from temporally explicit point-occurrence data (for simplicity depicted in two seasons only) (B), and (C) comparison of annual climatic niches quantified from EOO range maps and from monthly point-occurrence data. Range maps and point data were sampled into an equal area grid mapped with a Behrmann projection. The range map shows a year-round range only, whilst seasonal point-occurrence

two seasons. Secondly, extent-of-occurrence maps are often inappropriate for detecting movement patterns, particularly for nomadic species such as the budgerigar. For these species, temporally explicit occurrence data like that of the Australian Atlas, ideally at a temporal resolution appropriate to the species rather than our simple two-season and monthly approaches, are required to accurately document distribution patterns, and consequently characterise climatic niches. However, despite the clear advantages that point-occurrence data provide for detecting the movement patterns of birds these data are not without problems. Unstructured point-occurrence data coming from opportunistic observations, as well as more structured surveys are often a biased representation of species distribution (Yesson et al. 2007, Kamp et al. 2016). Unless appropriate methods are employed to correct for temporal, spatial and taxonomic biases, these data can lead to an inaccurate knowledge of a species distribution and consequently the climatic niche (Fourcade et al. 2014).

Conclusions

The quantification of climatic niches across many species is essential to understand the general patterns and fundamental processes that influence the relationship between organisms and the environment. The distributions of birds, which are much more dynamic than many other taxa, pose a particular challenge to comparable and appropriate quantification of climatic niches. In this review, we have highlighted challenges and potential solutions for quantification of climatic niches across many species of birds. Our first finding is that across birds, a huge variety of complex movement behaviours occur both between and within species. The spatial and temporal resolution of distribution data that is required to quantify climatic niches varies depending on the movement behaviour of the study species and must be considered before carrying out niche quantification. As such, our classification of movement behaviour in birds with a focus on distinguishing types of behaviour that have consequences for niche quantification from occurrence data not only reveals the extent of movement behaviour in birds, but also provides a useful tool for determining the type of distribution data that should be used for study species.

Secondly, our review of the literature found that despite the huge variety of movement behaviour revealed by our classification, the distribution dynamics of birds have often not been accounted for. A major limiting factor for

Figure 4. (Continued)
data show seasonal north–south movements (for B, point data were cleaned and categorized into two seasons as described in the appendix). In C, red polygon shading represents the climatic niche quantified from extent-of-occurrence range maps (occurrence in every month of the year), and blue represents the climatic niche quantified from monthly point-occurrence data (note, this niche is entirely within the niche characterised from range maps and therefore purple). The density of occurrence in environmental space of the point-occurrence data is shown in grey. Solid and dashed contour lines illustrate respectively, 100% and 75% of the available climatic space for each niche comparison: red, all grid cells in every month of the year; blue all point-data sampled in the Atlas (monthly points in grid cells).

incorporating seasonal dynamics into the quantification of the climatic niches of birds from distribution data is the availability of suitable data across many species. Temporally explicit point-occurrence data are not currently available for all bird species, but seasonal extent-of-occurrence range maps are available for many, allowing climatic niches of birds to be quantified taking into account the distribution at two different times of the year. We provide a framework recommending the occurrence data appropriate for quantifying climatic niches of birds depending on migratory behaviour and the spatial and temporal focus.

Finally, using Australia as a case study we show the limitations of many current distribution datasets for quantifying the climatic niches of birds exhibiting a wide diversity of migratory behaviour. Although seasonal extent-of-occurrence range maps are theoretically appropriate to quantify climatic niches for many species, we find that they have serious limitations, particularly for highly mobile species. Due to the lack of appropriate data for quantifying climatic niches across many species of birds that exhibit a variety of migratory behaviours, we stress the importance of transparently communicating what can really be captured by quantifying climatic niches from the available datasets. Closing the gaps in the availability of temporally explicit point-occurrence data is important if we are to accurately quantify climatic niches in a consistent way across all birds. Large-scale datasets of occurrence data at fine temporal and geographic resolution from national atlas projects, such as the New Atlas of Australian Birds or opportunistically sampled data such as GBIF (Global Biodiversity Information Facility <www.gbif.org>) or eBird (<http://ebird.org>) represent an exciting potential alternative to focussing on two seasons. Of course, point-occurrence data come with a range of potential biases that need to be considered, especially uneven sampling effort in space and time and a higher potential of underestimating species' distributions compared to extent-of-occurrence range maps, which usually overestimate distributions. It is therefore also important that we are aware of the possible biases in distribution data and continue developing and testing methods of correction. With appropriate methods these large data sets will increase accessibility to temporally explicit occurrence data which can be combined with climatic data with a fine temporal and spatial resolution to quantify climatic niches at a temporal scale appropriate to the species or research question.

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Supplementary material (Appendix jav-01308 at <www.avianbiology.org/appendix/jav-01308>). Appendix 1.

Journal of Avian Biology

Quantification of climatic niches in birds: adding the temporal dimension

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Supplementary material

Appendix 1

Text A1

<u>*Methods for compa*rison of seasonal differences in species richness for terrestrial bird species found in Australia:</u>

We compared seasonal differences in species richness for terrestrial bird species found in Australia from i) extent-of-occurrence range maps where distributions are classified as breeding, non-breeding and year round; with those calculated from ii) temporally explicit species occurrences.

Extent-of-occurrence range maps were obtained from BirdLife International and Natureserve (BirdLife International & NatureServe. 2015, downloaded from www.birdlife.org in July 2016). This dataset includes distribution polygons for virtually all bird species across the globe. Only polygons coded as presence 1 or 2 (extant and probably extant), origin 1 or 2 (native or reintroduced) and seasonality 1, 2 or 3 (resident, breeding season or non-breeding season) were included in this analysis, excluding areas where species were classified as extinct, introduced, vagrant, on passage or unknown seasonality. Taxonomy was matched to the IOC taxonomy list version 3.1 (Gill and Donsker 2012) and marine and taxonomically non-valid species were removed. The range maps were resampled into an equal area grid with cells of 1° longitudinal and varying latitudinal extent mapped with a Behrmann projection (Orme et al. 2005). Species were scored as present in a grid cell if its range map overlapped any part of the grid cell.

As we aimed to compare seasonal differences in species richness between two data sources, it was necessary to have seasonal distribution data for the same seasons. Although the point-occurrence data were temporally explicit and can therefore theoretically be split into any seasons desired, the global seasonal range maps were only available for "breeding" and "non-breeding" seasons. Many long-distance migrants move from the Northern hemisphere to "winter" in the Southern hemisphere and are therefore present in Australia in Austral summer. As such, we could not assume that breeding ranges obtained from this global database of range maps mean that a species is present in Australia during Austral summer, or that a species which has its non-breeding range in Australia is present there during Austral winter. Therefore, for species which had occurrences coded as seasonal (breeding or non-breeding) we checked whether species were present in Australia during Austral winter or summer and corrected seasonality accordingly. In total, the BirdLife range maps included 603 species present in Australia for at least one season.

Temporally explicit point-occurrence data was obtained from the New Atlas of Australian birds (Barrett et al. 2003, with updates available online; http://birdata.birdlife.org.au/). For this analysis we used over 9 million species-by-location records for the time period starting in September 1998 and ending in August 2012. The seasonal range maps with which we sought to compare these data represent an expert's view of the dominant patterns of seasonal species distribution, excluding areas where species occasionally occur in each season. For this reason we do not use raw seasonal point-occurrence data which might hide seasonal patterns, and instead we cleaned the data so that it shows the dominant patterns of seasonal distribution (Chapman 2005). Data were first cleaned by removing erroneous surveys with inconsistent or ambiguous date and time information. Taxonomy was matched to the same taxonomy as the occurrence data above (Gill and Donsker 2012), and marine species were removed from the dataset. The occurrence points were resampled into the same equal area grid as above (Orme et al. 2005).

To obtain seasonal distribution data we divided the occurrences into those corresponding to Austral summer (September-February) and Austral winter (March-August). Ideally seasonal distribution data would be determined depending on breeding and wintering dates for each species individually. However, this information is not available or not known for all species, and we were interested in capturing the rough seasonal pattern in direct comparison to the simple seasonal division made by extent-of-occurrence range maps. Records from the 14 days at the end of each season were omitted to avoid edge effects, leaving 15th September-14th February (or 15th in leap years) and 15th March to 17th August as the final breeding and non-breeding seasons, respectively. We calculated sampling effort for each grid cell as the total number of surveys in each season from the cleaned dataset.

It is widely recognised that survey data is often affected by erroneous records (Kelling et al. 2015). Therefore, to clean the data further, we manually removed species occurrences known to be introduced or vagrant. We then used a simple algorithm to remove additional records that were probably vagrant or erroneous; in cells which had more than 20 surveys in a season, a species occurrence was removed if there was only one survey recording the species in that season. For cells which had less than 20 surveys in a given season, all records were kept.

Although the cut-off of 20 surveys is arbitrary, the aim was to reduce the overestimation of seasonal differences likely to occur in the raw point-occurrence data in cells with very few surveys. The resulting exclusion of such records meant that any remaining detected differences in seasonal pattern between range map and point-occurrence data are, if anything, conservative. These steps removed 52,940 occurrences from the final dataset. The final cleaned dataset consisted of 602 species and 7,223,351 species-by-grid cell occurrences.

To assign final seasons to each grid cell where a species was present, we used a simple threshold approach. If all of the occurrences recorded for a species in a given grid cell belonged to one season (Austral summer or winter), that season was assigned to the cell. However, if a species was recorded to occur in both seasons in a given cell, we calculated seasonal reporting rates (the number of surveys in the given grid cell and season that recorded the species, divided by the total number of surveys in the given cell and season). The species' occurrence in the grid cell was assigned only one season if the ratio of reporting rates was more than 10:1 for that season, else the grid cell occurrence was assigned both seasons (year-round). Again, although this decision on a particular ratio was arbitrary, the procedure ensured that very few mobile individuals did not hide the seasonal distribution patterns of the species as a whole.

For the 598 species common to both datasets, we calculated the number of species in each cell for each season separately (Austral summer and winter) for each dataset. Following Somveille et al. (2013), we also calculated the difference in species richness between seasons (number of species in Austral winter minus number of species in summer) and the proportion of species that differ among seasons (difference in species richness, divided by the total number of species occurring annually). To determine whether the two datasets were able to detect similar amounts of seasonality in species richness, we tested the correlation between the seasonal differences in species richness obtained from each dataset for all cells which had species occurrences in both seasons. Cells without any species were excluded from this analysis because it is unclear whether they truly represent an absence of species or are instead a result of low sampling effort in some Atlas squares. Additionally, if both datasets have no species, including these cells in the analysis would overinflate the degrees of freedom. In addition, we also tested the correlation between seasonal differences in species richness obtained from both datasets only for cells for which sampling effort was high (>100 records in each season), to determine whether any differences detected were an artefact of poor sampling effort.

Methods for characterising and comparing the climatic niche of the Budgerigar (Melopsittacus undulatus) using year-round and monthly distribution data.

The climatic niche of the Budgerigar was quantified separately using year-round extent-of-occurrence range maps from BirdLife international (BirdLife International & NatureServe. 2015) and point-occurrence data from the Australian Atlas split into monthly point-occurrence data (Barrett et al. 2003, with updates available online; http://birdata.birdlife.org.au/). The general method is summarised in figure A1 and follows that of Broennimann et al. (2012) to characterise niches and estimate the overlap between the two niches quantified using the two different data sources. The approach uses gridding and kernel density smoothing to calculate the density of species occurrences in climatic space (Fig 4C). The total climatic space available to the species is also converted to densities of climatic availability and used to correct species occurrence densities for climate availability. For the extent-of-occurrence range maps the available climate space was defined as the climate for all months of the year for all of the grid squares within Australia. For the point-occurrence-data it was defined using the distribution of all surveys in the Australian Atlas i.e. the subset the subset of Australian grid cells where surveys were conducted, in only the months with at least one survey.

Species distribution data:

The extent-of-occurrence range map for the budgerigar (BirdLife International & NatureServe. 2015) was resampled into the grid as described for the species richness maps in the main manuscript. For the niche comparison (Fig 4C), the Australian atlas point occurrence data (>9 million records between 1998 and 2012) were cleaned as follows; incidental surveys were excluded and surveys which fell into more than one calendar day or had unambiguous date information were omitted. Following filtering 10,255 point occurrences remained where the budgerigar was recorded and 429,678 for all species across the entire continent). These were then divided into monthly point-occurrence data using the survey date. Monthly point-occurrence data was resampled into the same equal area grid cells as above. For niche quantification only grid squares were included which were present in both datasets. This was done to make the two datasets more fairly comparable and to ensure that any differences in niches detected using each method can be attributed to whether or not temporal dynamics in distribution are considered, and to exclude the possibility that they simply reflect the widely acknowledged differences between point data and extent-of-occurrence range maps.

Climate data:

Monthly mean temperature data and total monthly precipitation data were obtained from WorldClim (Version 1.4, average of 1960-1990, resolution of 30 seconds) (Hijmans et al. 2008). These were resampled to the same 1 degree x 1 degree grid as the range maps by averaging across the pixels contained in each 1 degree x 1 degree grid square using ArcGIS.

Niche overlap and breadth

Niche overlap between the niches characterised using the two methods was calculated on the environmental occupancy values using Schoener’s D (Broennimann et al. 2012). D varies from 0 (no overlap) to 1 (perfect overlap). Niche breadth was calculated following Laube et al. (2015). The environmental occupancy values were converted into proportions of the species total environmental occupancy and the Shannon diversity index was calculated for each niche characterisation.

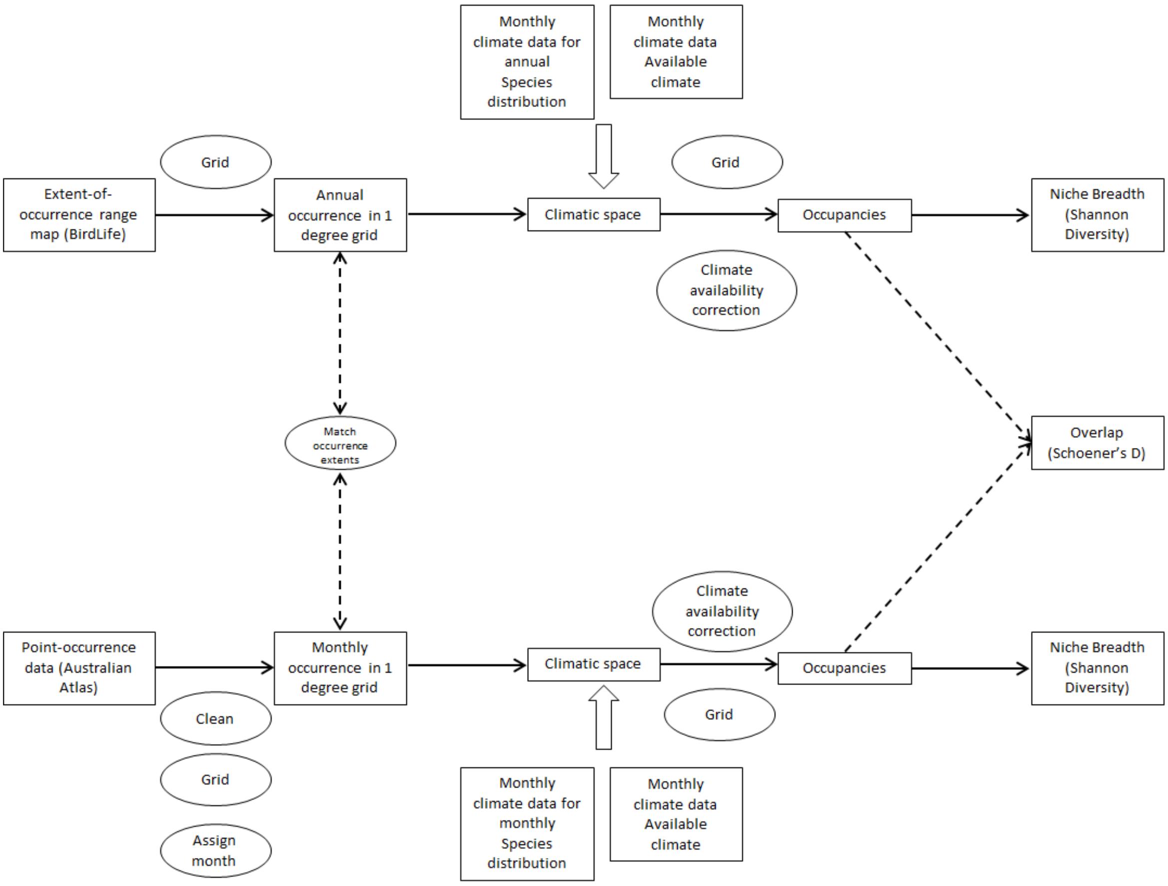

Figure A1

Overview of niche characterisation methods. Modified from (Petitpierre et al. 2012)

Table S1. Example species demonstrating the classification of different movement behaviours on the intraspecific and species levels. The main categories (directional migratory, dispersive migratory, nomadic, resident) were subdivided into full, partial, and local. Additionally, altitudinal and irruptive behaviour were flagged, as was uncertainty in deciding among categories (due to poor knowledge about movements or distributions). Typical movement descriptions for each species (usually added as comments in the database) are given below the table. Examples were chosen to represent a variety of movement strategies and marine and terrestrial birds, and are grouped according to families: Anatidae (ducks, geese, swans), Diomedeidae (albatrosses), Phalacrocoracidae (cormorants), Psittacidae (parrots), Cinclidae (dippers), Bombycillidae (waxwings), and Phylloscopidae (leaf warblers; formerly part of Sylviidae, Old World warblers).

	Directional migration			Dispersive migration			Nomadism			Residency		Altitudinal	Irruptive	Unknown	Uncertain	Species-level category
Species	Full	Part.	Local	Full	Part.	Local	Full	Part.	Local	Full	Part.					
Anser albifrons	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	migratory
Anser anser	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	migratory
Anseranas semipalmata	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	dispersive
Thalassornis leuconotus	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	resident
Thalassarche chlororhynchos	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	dispersive

Phalacrocorax carbo	0	1	0	0	1	0	0	1	0	0	1	0	0	0	0	migratory
Phalacrocorax capillatus	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	dispersive
Phalacrocorax capensis	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	resident
Neopsephotus bourkii	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	nomadic
Melopsittacus undulatus	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	nomadic
Neophema chrysogaster	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	migratory
Neophema pulchella	0	0	0	0	0	1	0	0	1	1	0	0	0	0	0	resident
Neophema splendida	0	0	1	0	0	0	0	1	0	0	1	0	1	0	1	nomadic
Charmosyna diadema	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	unknown
Cinclus cinclus	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	migratory
Cinclus mexicanus	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	resident

Table S1, continued.

Species	Directional migration			Dispersive migration			Nomadism			Residency		Altitudinal	Irruptive	Unknown	Uncertain	Species-level category
	Full	Part.	Local	Full	Part.	Local	Full	Part.	Local	Full	Part.					
Bombycilla garrulus	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	migratory
Phylloscopus ibericus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	migratory
Phylloscopus canariensis	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	resident
Phylloscopus collybita	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	migratory
Phylloscopus affinis	0	1	0	0	1	0	0	0	0	0	0	1	0	0	0	migratory
Phylloscopus pulcher	0	0	0	0	1	0	0	0	0	0	1	1	0	0	0	dispersive

Anser albifrons (Greater White-fronted Goose): migratory.

Anser anser (Greylag Goose): a few populations sedentary, mostly migratory moving S in winter.

Anseranas semipalmata (Magpie Goose): not truly migratory but wanders extensively in relation to food and water availability, dispersing widely in wet season and tends to concentrate in dry season, usually resident in one larger area but seasonal movements following environmental variation.

Thalassornis leuconotus (White-backed Duck): mostly sedentary, with some local or semi-nomadic movements largely related to availability of water and perhaps more general post-breeding dispersal in some regions as water levels drop.

Thalassarche chlororhynchos (Atlantic Yellow-nosed Albatross): disperses over S Atlantic Ocean in non-breeding season.

Phalacrocorax carbo (Great Cormorant): sedentary or dispersive throughout most of range, N populations are migratory or partly migratory, Australian ones nomadic and dispersive related to flooding and drought.

Phalacrocorax capillatus (Japanese Cormorant): dispersive, in Japan winters in warm regions and returns to colonies in April.

Phalacrocorax capensis (Cape Cormorant): mostly sedentary but extensive post-breeding dispersal offshore in winter.

Neopsephotus bourkii (Bourke’s Parrot): nomadic, often remaining in an area for many years and then disappearing.

Melopsittacus undulatus (Budgerigar): fairly nomadic according to availability of water and seeding grass, but some populations relatively predictable on seasonal basis in areas where food supply is regular or stable, especially in S of range.

Neophema chrysogaster (Orange-bellied Parrot): migratory (austral migrant Tasmania-Australia).

Neophema pulchella (Turquoise Parrot): apparently mainly sedentary but with local post-breeding dispersal and irregular local movements probably in response to rainfall.

Neophema splendida (Scarlet-chested Parrot): probably nomadic and certainly irruptive, presumably in response to favourable climate, some more regular seasonal movements noted in SE Australia.

Charmosyna diadema (New Caledonian Lorikeet): Red List status CR (critically endangered) but may be extinct, known from only 2 specimen, last recorded with certainty in 1913 but reports in 1950s and 1970s.

Cinclus cinclus (White-throated Dipper): resident with post-breeding descent from high altitudes, more migratory in N where migrates S in winter, some partially migratory populations.

Cinclus mexicanus (American Dipper): resident with local movements, some altitudinal movement between breeding and non-breeding areas.

Bombycilla garrulus (Bohemian Waxwing): partial migrant, withdraws from large part of breeding range in winter towards S, renowned for periodic irruptive movements, large flocks sometimes reaching areas well outside normal wintering grounds.

Phylloscopus ibericus (Iberian Chiffchaff): migratory, non-breeding range imperfectly known.

Phylloscopus canariensis (Canary Chiffchaff): sedentary.

Phylloscopus collybita (Common Chiffchaff): mostly migratory, some populations largely altitudinal migrants, small numbers remain in parts of N range.

Phylloscopus affinis (Tickell’s Leaf Warbler): migratory and altitudinal migrant, moves short to medium distances to lower levels into non-breeding areas S of breeding range.

Phylloscopus pulcher (Buff-barred Warbler): altitudinal migrant, making post-breeding movement to lower levels, many within breeding range but also some to an area S of breeding range.

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APPENDIX II: The effects of seasonal migration on climatic niches in passerine birds

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Title: **The effects of seasonal migration on climatic niches in passerine birds**

Status:

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Author contributions:

(1) Development and planning:

AE 80%, SAF 10%, KBG 10%

(2) Preparation and collection of data:

Range maps were compiled by SAF 50%, CR 30%, DO 10% & KBG 10%

AE collected breeding month data

AE prepared and processed all climatic and phylogenetic datasets

(3) Preparation of figures/ tables:

AE prepared all figures and tables in the manuscript and supplementary materials

(4) Data analyses and interpretation of results:

AE performed all statistical analyses 90% with input from SF 10%

AE interpreted results 90% with input from SF and KBG (in total 10%)

(5) Preparation of manuscript:

AE 90%, SAF & KBG 10% in total

Title: The effects of seasonal migration on climatic niches in passerine birds

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Key words: Passeriformes, tropics, macroecology, seasonal migration, comparative analysis, non-breeding

ABSTRACT

The question of whether migratory birds track a specific climatic niche by seasonal movements has important implications for understanding the evolution of migration, the factors affecting species' geographic distributions and the responses of migratory species to past or future climate change. Despite much research on bird migration, previous studies have produced mixed results. Further to this lack of consensus, whether species migrate to track climate is only one half of the question, with the other half being why residents remain in the same geographic range year-round. Here, we test for seasonal overlap in climatic niches across 437 closely related migratory and resident species from eight clades of passerine birds, using a new global dataset of breeding and non-breeding geographic ranges. In addition, we controlled for two biogeographic factors (tropical vs. non-tropical breeding location and range size). Partly in accordance with the expectation of niche tracking, we found that the seasonal overlap of breeding vs. non-breeding climatic conditions in migratory species was greater than the overlap they would experience if they did not migrate. However, this was only the case for species breeding outside of the tropics and only for migration away from the breeding range. In direct contrast to expectations of niche tracking, migratory species experienced lower seasonal climatic niche overlap than resident species, with significant differences between tropical and non-tropical breeding species. Our study suggests that movements away from breeding ranges in more seasonal non-tropical environments may be driven by climatic variation; however, different factors may drive seasonal movements in the climatically more stable tropical regions. We conclude that the drivers of migration might vary across different regions and between departure from breeding and non-breeding ranges, and offer some explanation as to the variable results of previous studies.

INTRODUCTION:

The world-wide spectacle of animal migration has fascinated people for thousands of years (Thompson, 1907). One hypothesis proposed to explain the seasonal movements of migratory species is that they track preferred climatic conditions (Joseph and Stockwell 2000). However, despite the considerable attention that has been given to migration (Greenberg and Marra 2005), it remains unclear to what degree species track specific climatic conditions by seasonal movements. This question has important implications for understanding the evolution of migration (Nakazawa et al. 2004); the factors affecting species' distribution (Boucher-Lalonde et al. 2013); and the responses of species to past or future climate change (Thomas et al. 2004). These questions are particularly relevant for birds as ~20% of all species are migratory, changing distribution throughout the year (Kirby et al. 2008, Eyres et al. 2017). In this study, we investigate the relationship between migratory behaviour and the climatic conditions occupied by different species in each season using a phylogenetic comparative framework.

Climatic conditions are dynamic with one notable pattern of climatic variation being seasonal variations, which are most pronounced in temperate regions. Migratory species might be expected to move to track climatic conditions directly if they cannot tolerate physiologically tolerate seasonal variations in climate (Joseph and Stockwell 2000, Somveille et al. 2015). Although birds can regulate their internal body temperature independent of ambient conditions, this is energetically expensive and there are limits to the climatic conditions under which a species is able to survive (Khaliq et al. 2014). As well as direct physiological limitations, migrants might track climatic conditions in order to pursue seasonally available resources (Greenberg and Marra 2005, Luis Tellería et al. 2008, Thorup et al. 2017). Alternatively, migratory species may occupy different climatic conditions in each season if they move to avoid extreme climatic conditions rather than to track specific conditions (Newton 2008), have different seasonal requirements (Spencer 1982), or because movement is driven by factors other than climate e.g. nest predation (McKinnon et al. 2010). To assess whether seasonal migrants track the climatic conditions in their breeding grounds when moving to non-breeding grounds, and vice versa studies have increasingly used the climatic niche concept (Boucher-Lalonde et al. 2013, Laube et al. 2015). This describes the climatic conditions within which a species can maintain a viable population (Pearman et al. 2008, Bonetti and Wiens 2014).

Mixed support has been found for climatic niche-tracking. For example, although Joseph and Stockwell (2000) found that the Swainson's flycatcher tracks its niche throughout the year, subsequent studies have shown that this is not the case for all migratory species (Nakazawa et al. 2004, Martinez-Meyer et al. 2004, Zurell et al. 2018). Migratory species in the family Parulidae (American wood-warblers) were found to track their niche to a greater extent than resident species (Gómez et al. 2016). As these studies were carried out on different groups of birds, in different geographic regions, using a variety of different methods, generalisation is difficult and the reasons behind the observed variation in niche tracking across species remain unclear.

Most previous studies have tested the ability of migratory birds, in particular long-distance migrants (Boucher-Lalonde et al. 2013, Somveille et al. 2015, Zurell et al. 2018), to track a niche across seasons by comparing to a null expectation. A variety of null expectations have been used, for example by comparing whether the niche overlap is greater than if species did not migrate but stayed in each of their seasonal ranges (Laube et al. 2015), if species migrated to a random location (Zurell et al. 2018) or if species migrated to seasonal ranges derived from a simulation model controlling for the migration options available to each species (Somveille et al. 2018). Although these comparisons provide important information about niche tracking from the perspective of each migratory species, they do not determine why other species do not migrate. In contrast to migrants, resident species stay in one location and tolerate the entire annual range of climatic conditions in their breeding regions (Soberón 2007). Seasonal migration has evolved multiple times in birds as a whole, and many genera and families actually include closely related migratory and resident lineages (Winger et al. 2014, Phillips et al. 2018). Therefore, whether species migrate to track seasonal climate is only one side of the question, with the other being to what degree resident species do not track seasonal climate.

A comparison of the occurrence-climate relationships among migratory and closely related resident species in a phylogenetic comparative framework therefore adds an important additional perspective of shared biogeographic history. This perspective has been largely absent from the literature so far (but see Gómez et al. 2016). In this study, we explicitly test for the influence of breeding location on seasonal niche tracking both within migratory birds and across migratory and resident species. We do so using a large dataset comprising 437 extant species in eight passerine clades found across the world (Supplementary materials, Figure S1) and controlling for geographic range size and phylogenetic effects. In addition, we use a consistent new classification of migratory behaviour (Eyres et al. 2017), which is based on descriptions of migratory behaviour and includes a greater diversity of movement types (i.e. both short and long distance migrants) than previous studies (Zurell et al. 2018). Further, we quantify seasonal niche overlap from geographic occurrences using a new database containing up-to-date maps of species' breeding and non-breeding distributions. We apply and compare these two methods using a phylogenetic comparative framework and focus particularly on two biogeographic factors.

First, the degree to which species track climatic conditions is expected to vary with breeding location because climate seasonality increases with latitude (Archibald et al. 2010). The combined analysis of tropical and non-tropical breeding species may therefore obscure any signal of climatic niche tracking (Zurell et al. 2018), so we control for the effects of breeding location (within vs outside the tropics). Second, most previous studies have not taken geographical range size into account in analyses of niche tracking. Within long-distance migrants, range size has been shown to be significantly positively related to seasonal niche overlap (Zurell et al. 2018). Therefore, we control for range size in our analyses.

To test the hypothesis that migratory species move to track seasonal climatic niches we checked the following expectations:

1. If migrants track seasonal climatic niches we expect the overlap between seasonal climatic niches (i.e. breeding vs. non-breeding) experienced by migrants to be greater than the hypothetical seasonal niche overlap that would arise if a migratory species did not migrate (i.e. stayed in the breeding or non-breeding range year-round; blue species in Fig. 1a, b), when controlling for range size and phylogeny (Laube et al. 2015). In addition, we expect an effect of breeding location: the previous expectation should hold more strongly for species breeding outside the tropics, but the observed and hypothetical seasonal niche overlap might not differ for species breeding in the tropics where climatic conditions remain relatively stable year-round.
2. If migrants track seasonal climatic niches we expect higher overlap between breeding vs. non-breeding climatic niches for migratory species than for resident species (contrast blue and red species in Fig. 1a, b), when accounting for range size and phylogeny (Gómez et al. 2016). In addition, we expect an interaction between breeding location and migratory behaviour: Migrants might have larger seasonal overlap than residents only if breeding in non-tropical regions due to the stronger climatic seasonality there. No difference in seasonal niche overlap is expected between migrants and residents

breeding in the tropics if climatic conditions remain relatively stable year-round there.

METHODS

We selected eight monophyletic clades from across the Passeriformes that contained a mixture of migratory and resident species and were distributed globally (Table 1 & Figure S1). Each clade was selected to have similar orders of species richness (approximately 50-80 species each) and at least 30% non-resident species. Species names followed IOC taxonomy V 3.1 (Gill and Donsker 2012). Classification of migratory behaviour followed Eyres et al. (2017).

For each species, we characterised the breeding and non-breeding climatic niches using seasonal distribution and climate data. Breeding time is species-specific so we determined the three peak breeding months for each species individually using information from the literature (del Hoyo et al., 2019, and others; see Table S1 for details). Where no information was available on the breeding months, these were chosen using information from con-generic species breeding in the same geographic region (31 of 437 species in the final analyses, for details, Supplementary materials, Table S1). The three non-breeding months for each species were defined as 6 months later than the breeding season, a somewhat arbitrary decision given the different degree of climatic seasonality and migratory timing in different regions and species, but chosen to be globally consistent across all species.

Range maps and climatic datasets

To characterise climatic niches, geographic distributions for the breeding season were obtained from the *Copenhagen global avian distributional database* (Holt et al. 2013). This is an extensive database mapping a conservative extent-of-occurrence during the breeding season at a 1° latitudinal-longitudinal resolution for each species based on museum specimens and published sight records and validated by ornithological experts. Non-breeding distributions of migratory species were obtained as extent-of-occurrence polygons from the *GeoMiB database (Geographic distributions of migratory birds* v. 1.1 compiled by us, see supplementary information for more details) and sampled to the same resolution as the breeding ranges. Species occurrences were therefore seasonal presences in 1° latitude-longitude grid cells where species were recorded in the Copenhagen database (breeding and year-round, with the difference among the two determined from the GeoMiB range maps) or where >5% of the grid cell was covered by species' range maps from the GeoMiB database (non-breeding). Although such extent-of-occurrence data are not ideal for quantifying climatic niches (Graham and Hijmans 2006), they represent the most consistent and accurate coverage of species' ranges that are currently available at a global scale and across a large number of species (Meyer et al. 2015).

Monthly climate data for all zoogeographic realms (Holt et al. 2013) inhabited by the study species (Figure S1) were obtained from the CliMond *raw climate data* dataset (averages from 1961-1990, 10' resolution) (Kriticos et al. 2012) and averaged into the same grid as the occurrence data. The following climatic variables for each month were used: minimum and maximum of daily temperatures averaged within each month, total monthly precipitation, mean daily humidity of each month, and mean daily relative humidity at 9am and at 3 pm for each month. These six climatic variables were chosen as ecologically relevant descriptors of global climate including extremes of temperature and water availability (Petitpierre et al. 2017).

Niche metrics and explanatory variables

To test expectation one (Figure 1, blue species) we quantified the climatic niche overlap of migratory species between seasons from the seasonal occurrence data and in addition for two hypothetical situations: (1) the overlap that would result if a species stayed in the breeding range for the whole year, (2) the overlap that would result if a species stayed in the non-breeding range for the whole year. To test expectation two we calculated and compared the overlap in climatic niche between seasons for resident species with that of migratory species (Figure 1, red species vs blue species, respectively).

Seasonal niche overlap was characterised following Broennimann et al. (2012). Principal component analysis (PCA) was used to incorporate information from all six climatic variables and create a two dimensional climatic space in which niche overlap could be measured. As different climatic factors might be important for determining each clade's distribution, we carried out PCA for each clade individually. The major strength of this method is that it accounts for the different availability of specific climatic conditions in the breeding and non-breeding seasons, through inclusion of not only the species-occurrences but also the climate available to the clade in each clade-wide PCA. The method takes this into account through calculation of "climatic occupancy values" (Broennimann et al. 2012, for details see Supplementary materials, Methods). The climate available to a species in a season was defined as the climate across all zoogeographic realms that the species inhabits in that season; the climate available to the clade as a whole was defined as all the zoogeographic realms that any member of the clade inhabits (see Figure 1c for an example species) (Holt et al. 2013, details in Supplementary material, Methods). The overlap between breeding and non-breeding niches was then calculated for each species based on the climatic occupancy values using Schoeners D, a measure that varies between 0 (no overlap) and 1 (complete overlap) (Warren et al. 2008).

In order to test whether the breeding location affects niche overlap between seasons, species were categorised as tropical breeding (at least 10% of the breeding range occurred between 23.5° N and 23.5° S), or non-tropical breeding. Division into these two categories was chosen rather than using a continuous latitude variable because the tropical – temperate split represents the most striking difference in climatic seasonality globally (Archibald et al. 2010). Although the threshold of 10% is arbitrary and our definition of tropical breeder is generous, this ensured that all species classified as non-tropical breeders really experienced non-tropical climatic seasonality.

Geographic range size was determined for each species as the sum of the total land area within all grid squares occupied by the species in the breeding distribution and all the grid squares occupied by the species in the non-breeding distribution (i.e. year-round distributions were counted twice, because year-round occurrences also enter the niche calculations twice, once for the breeding and once for the non-breeding months). Range size was log-transformed in all analyses because the data were not normally distributed.

Comparative analyses across species

In total, our selected clades contained 518 extant species displaying a variety of migratory behaviours: dispersive migration (n=21), directional migration (n=178), nomadism (n=1), residency (n=316) and species with unknown movement behaviour (n=2) (Table 1). We omitted dispersive migrants, defined as those where individuals make regular post-breeding movements in any geographical direction from breeding sites (Newton 2008), nomadic species (which perform non-seasonal movements) and those with unknown movement behaviour from our analyses because it is unlikely that seasonal range maps are able to accurately represent distribution patterns of these species (24 species in total). Five additional species were omitted because they lacked distribution data, whilst 51 species were additionally omitted from analyses because they had a too small range size to calculate niche metrics using our methods (see Supplementary Materials, Table S1 for full species list). Final analyses were carried out on 437 species. Eight species included in the analysis were defined as directional migrants but only had year-round distribution data available.

To determine whether geographic range size influenced seasonal niche overlap, we tested whether range size differed between categories of movement behaviour and for a relationship between range size and seasonal niche overlap using linear mixed effects models. These analyses showed significant relationships (details in Supplementary material, Methods), so geographic range size was included in all subsequent models.

To test expectation one (i.e. whether migratory species increased seasonal overlap by migrating away from their breeding or non-breeding range), we used paired t-tests to compare the overlap between observed seasonal niches with two measures of hypothetical overlap, assuming the species stayed in one of the two seasonal ranges (Laube et al. 2015). To determine whether the effect of migration was influenced by breeding location this analysis was carried out separately on tropical and non-tropical breeding species. To check that results were not unduly influenced by differences in range size we additionally constructed two linear mixed effects models in which the differences between the observed niche overlap and each hypothetical overlap were the response variables, and differences between the observed range size and the range size that occurred in each of the two hypothetical scenarios were the fixed effect. As the values for differences in seasonal range size were on a very different scale to other variables they were first scaled to be between -1 and 1 using the rescale function from the *plotrix* package (Lemon 2006). To control for phylogeny, clade was included as a random effect.

To test expectation two (i.e. whether migratory species experience higher seasonal niche overlap than closely related resident species), analyses of seasonal niche overlap across migratory and resident species were performed using linear mixed-effects models. Clade was included as a random effect to control for phylogenetic effects, with random intercepts allowed for each clade. To test whether seasonal niche overlap differed between migratory and resident species, and whether this relationship was geographically consistent, the fixed effects of migratory status (resident or migratory), breeding location (tropical or non-tropical), and geographic range size were tested on seasonal niche overlap. Our strategy for model selection was as follows: (1) We started with the maximum model including a 3-way interaction, (2) we dropped non-significant interactions, (3) we checked the impact of dropping the interaction from our model using a Chi-squared test, (4) we present minimum adequate models. Additionally, we calculated the marginal and conditional R^2 values (i.e., the variance explained by the fixed effects only and by the entire model, respectively) as a measure of goodness of fit of the final models (Nakagawa and Schielzeth 2013).

To control for phylogenetic relationships within clades more explicitly than the mixed-effect models described above which only control for clade effects, we additionally fitted equivalent models using phylogenetic generalised least-squares regression analyses (PGLS). PGLS analyses were conducted using the *caper* package in R (Orme et al. 2014) (details in Supplementary material, Methods). By matching the species available in the phylogenetic datasets to our data on niche quantification, the total number of species was reduced to 415 for these analyses.

RESULTS

Expectation 1: Seasonal niche overlap of migratory species

Overall, observed seasonal niche overlap in climate experienced by migratory species was found to vary from D=0 (no overlap) to D=0.78; 83% of the D values were lower than 0.5, indicating generally low niche tracking within migratory species. The hypothetical seasonal overlap that would be experienced by migrants if they stayed in the breeding or non-breeding ranges year-round ranged from D=0 to D=0.80 and from D=0 to D=0.83, respectively. For both cases, more than 75 % of D values were lower than 0.5.

Contrary to expectation one (Figure 1), the observed seasonal niche overlap in migratory species was not consistently greater than the hypothetical overlap if migrants were to stay in either the breeding or non-breeding range year-round, and the results did not differ strongly by breeding location (Figure 2). Instead, whether migratory species increased seasonal niche overlap by migrating was found to vary depending on whether they were migrating away from their breeding or non-breeding location. As expected under climatic niche tracking we found that observed overlap was significantly larger than hypothetical overlap if species stayed in the breeding range year-round, for both non-tropical and tropical breeding species (Figure 2a and c, paired two-tailed t-tests, p<0.001, t=7.3477, df=114 and, p=0.01, t=2.588, df=52, respectively). However, this was not the case if species stayed on the non-breeding range year-round (non-tropical breeding species: Figure 2b, paired two-tailed t-test, p=0.09, t=1.7075, df=114). In fact, the overlap for tropical breeding species was significantly smaller, if they migrated than if they stayed on the non-breeding range year-round (Figure 2d, paired two-tailed t-test, p= 0.003, t= -3.0741, df=52). We found that the seasonal difference in range size had no significant effect on any of these observed niche overlap patterns in migratory species (Supplementary material, Figure S3; linear mixed effects models, all p values >0.11).

Expectation 2: Comparison of seasonal niche overlap between migratory and resident species

Overall, seasonal overlap values for resident species varied from D=0 to D=0.89 (for comparison, migratory species varied from D=0 to D=0.78). The D values for both resident and migratory species were heavily left skewed with 71% and 83% of overlap values being lower than 0.5, respectively.

In contrast to our second expectation, migratory species overall had significantly lower niche overlap between the climate experienced during breeding and non-breeding season than resident species when controlling for clade and range size (Figure 3, Table 2). Although there was an interaction of breeding location and migratory behaviour as expected (Table 2), the effect was the opposite to initial expectations as tropical migratory species were found to differ much more in seasonal overlap from tropical resident species than non-tropical migrants vs. non-tropical residents (Figure 3). Tropical species tended to have higher overlap than non-tropical species, although this depended on range size and migratory behaviour and the main effect was not significant in the model (breeding location was only significant in interactions with range size and migratory behaviour, Table 2). As expected, species with larger range sizes had significantly larger seasonal niche overlap (Figure 3a vs 3c), but range size interacted significantly with both migratory behaviour and breeding location (table 2; for details see supplementary materials, Figure S2). Our results were consistent across the eight clades (conditional and marginal R^2 values were 38% and 37% respectively).

All results were qualitatively similar when we controlled for the effects of phylogeny below the clade level using PGLS (details in Supplementary material, Results). However, the interactions of migratory behaviour and breeding location with our control variable (range size) were no longer significant ($P = 0.08$ and $P=0.42$). Because the results are qualitatively similar but the models included fewer species we just report these in the Supplementary material, Table S2 and Supplementary material, Figure S4).

DISCUSSION

We found mixed support for the hypothesis that migratory species move to track climatic conditions between seasons. Partly in accordance with expectation one, we found that both tropical and non-tropical migratory species tracked their climatic niche between seasons if species were compared to a hypothetical situation where they did not migrate, but only when moving away from the breeding ranges. In contrast to expectation two, we found that migratory species tracked their seasonal niches to a much lower degree than resident species within the same clade. We conclude that support for climatic niche tracking in migrants varies depending on the perspective in which the question is examined (i.e. from the perspective of the individual migrant moving from breeding or non-breeding sites vs migratory species in comparison to resident species), as well as on confounding factors such as breeding location and range size.

Although we found some evidence that migratory species tracked seasonal climate, the results were mixed across the two expectations and migrants never tracked niches perfectly. As such, our results suggest that migratory species might track factors correlated with climate, and migration did not simply evolve to track climatic niches (Salewski and Bruderer 2007, Thorup et al. 2017). From the perspective of migratory species, there was evidence that they were tracking climatic niches to some degree, at least when they moved away from their breeding range. However, in comparison to resident species there was no evidence of niche tracking in migrants, inconsistent with the findings of Gómez et al. (2016). This result is predominantly driven by the fact that despite staying in the same location year-round, resident species inhabited very similar conditions in each season, possibly indicating quite broad but similar climatic niches in each season. Alternatively, it could indicate that even outside the tropics, the geographic distribution of resident species may be placed to experience as little climatic seasonality as possible. This is consistent with the overall pattern that there are relatively more migratory than resident species breeding outside the tropics than within the tropics, and could help to explain why richness of migratory species is higher in more seasonal environments (Somveille et al. 2013, 2015).

The evidence for niche tracking regarding our first expectation was found to be asymmetric, indicating that the drivers for migration may be different depending on direction. Migration away from the breeding range significantly increased seasonal climatic niche overlap but migration away from the non-breeding range did not, and in the tropics actually led to a significant reduction in niche overlap. Climate or factors correlated with climate are therefore likely to drive movement away from the breeding site, for example a decrease in available resources in the non-breeding season in temperate regions (Somveille et al. 2015). In contrast, the drivers for migration away from the non-breeding range seem likely to be factors other than climate, such as seeking lower nest predation, or higher availability of nesting sites (Cox 1968). Asymmetries have been found in previous studies which have tried to predict one season’s niche from the other, and are actually expected under some hypotheses of evolution of migration (Salewski and Bruderer 2007). For example, Martinez-Meyer et al. (2004) found that the breeding niche can be predicted from the non-breeding niche but not vice-versa in the *Passerina* buntings, whilst Nakazawa et al. (2004) observed this asymmetry occurring in both directions for Nearctic-Neotropical migratory species.

In relation to both expectations, the degree of niche tracking was found to differ significantly depending on the location of the breeding range, suggesting that there might be different drivers for migration operating in the tropics and outside of the tropics. For migratory species breeding in the tropics we found no evidence for seasonal climatic niche tracking, suggesting that migration here is driven by factors other than climate, e.g. by local weather aspects not captured well in our climate datasets (Reside et al. 2010). Biotic interactions such as competition and predation could be much more important for determining species distributions than the abiotic environment in the tropics (Schemske et al. 2009, Faaborq et al. 2010). However, some of the difference could be attributable to spatial biases in data quality: as lower-quality distribution data are expected in the tropics, especially for migratory species niche overlap may be systematically underestimated there (Yesson et al. 2007, Meyer et al. 2015).

Our results were not always consistent with previous studies. Overall, we found less evidence of niche tracking in migratory birds than Zurell et al. (2018), who examined northern-Hemisphere long-distance migrants, but more evidence than Boucher-Lalonde et al. (2013) who studied migratory and resident species across the New World. Most strikingly our results were in direct contrast to those of Gómez et al. (2016) who found that resident species experience lower seasonal overlap than migratory species in the Parulidae family. We give five possible explanations for this lack of consistency with previous studies. First, as previously discussed we found that the support for niche tracking in migrants varied depending on the perspective taken to test it. Second, as we found that niche tracking was found to vary depending on breeding location, previous studies looking at species in different geographic regions or not accounting for this geographic effect could have produced varying results.

Third, physiology might affect species' ability to track climatic conditions. For example, as flight is more energetically costly with increasing body size larger birds might be expected to track climate to a lesser degree than small birds (Alerstam et al. 2003). Zurell et al. (2018) found that traits and in particular body mass explained 12-18% of variance in tracking of niches. As we focus only on passerine species it is likely that we do not find an effect of clade (which would indicate a strong influence of phylogenetically conserved traits such as body mass), because our study species do not exhibit as great a variation in body mass as those included in Zurell et al. (2018). Fourth, we found a significant positive relationship between range size and our niche metrics, consistent with the findings of Zurell et al. (2018). Prior to that study, range size has not been controlled for when testing niche overlap across resident and migratory species, and we show it is important to consider as otherwise differences among resident and migratory species may just reflect the differences in range size of species being studied.

Finally, differences in our results with previous studies may have arisen through methodological differences. Although highly standardised, the overlap metrics from Broennimann et al. (2012) are highly sensitive to what is chosen as the available climate, and whether climatic space is gridded for individual species separately or across the entire clade. Differences might also be attributed to data quality. Here, we used new range maps which were compiled specifically to offer better estimates of the non-breeding range of migrants than those available from BirdLife International. However, range maps are more likely to overestimate the species ranges, and consequently the niche, than point occurrence data

(Hurlbert and White 2005, Graham and Hijmans 2006, Eyres et al. 2017). In addition, in contrast to previous studies, migrants were classified independent of range map data from descriptions of movement and we excluded those species which make nomadic and non-directional movements.

IMPLICATIONS AND CONCLUSIONS

Overall, we found relatively little support for seasonal niche tracking. Despite some evidence that migratory species which breed outside of the tropics leave the breeding range to track climatic conditions, seasonal niche overlap values were overall relatively low and the niche occupied by migrants was never identical between seasons. As such, for accurate quantification of the climatic niches of birds it is essential to take into account the conditions they experience in both seasons. Our results suggest that the drivers of migration might vary across different regions and between departure from breeding and non-breeding ranges, and offer some explanation as to the variable results of previous studies. Finally, as migrants do not achieve the same levels of seasonal overlap as resident species, we suggest that resident species' ranges are generally placed in less seasonal regions than migratory species. This warrants further investigation using more highly-resolved distribution data such as point records (Eyres et al. 2017), particularly to understand why some species are partially migratory, with some individuals moving and others remaining in the same region year-round (Fiedler 2005, Fandos and Tellería 2019).

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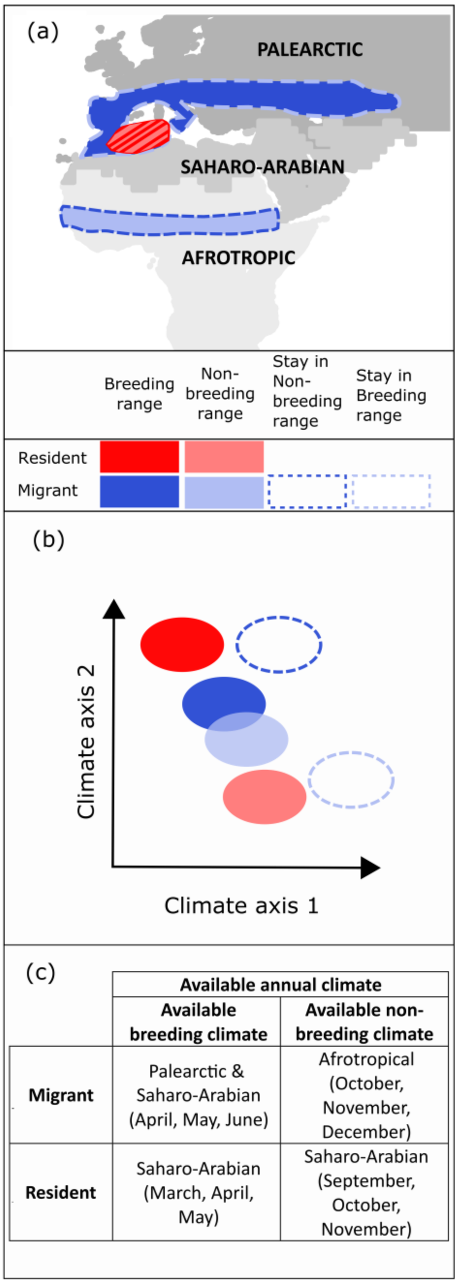

	Available annual climate	
	Available breeding climate	**Available non-breeding climate**
Migrant	Palearctic & Saharo-Arabian (April, May, June)	Afrotropical (October, November, December)
Resident	Saharo-Arabian (March, April, May)	Saharo-Arabian (September, October, November)

Figure 1. Schematic showing example non-tropical migratory and resident species: geographic distributions in breeding and non-breeding season (a), expectations of niche overlap in climatic space (b) and zoogeographic realms and months defining the climatic space available to each example species in each season (c). Expectation 1 (distributions and niches shaded in blue vs. those surrounded by dashed blue lines): If migrants track climatic conditions, it is expected that the seasonal niche overlap is greater than if they did not migrate and stayed in either the breeding or non-breeding range year-round. Expectation 2 (distributions and niches shaded in blue vs. those shaded in red): If migrants track climatic conditions, it is expected that the breeding and non-breeding niches are more similar in climatic space (higher overlap) than those of residents.

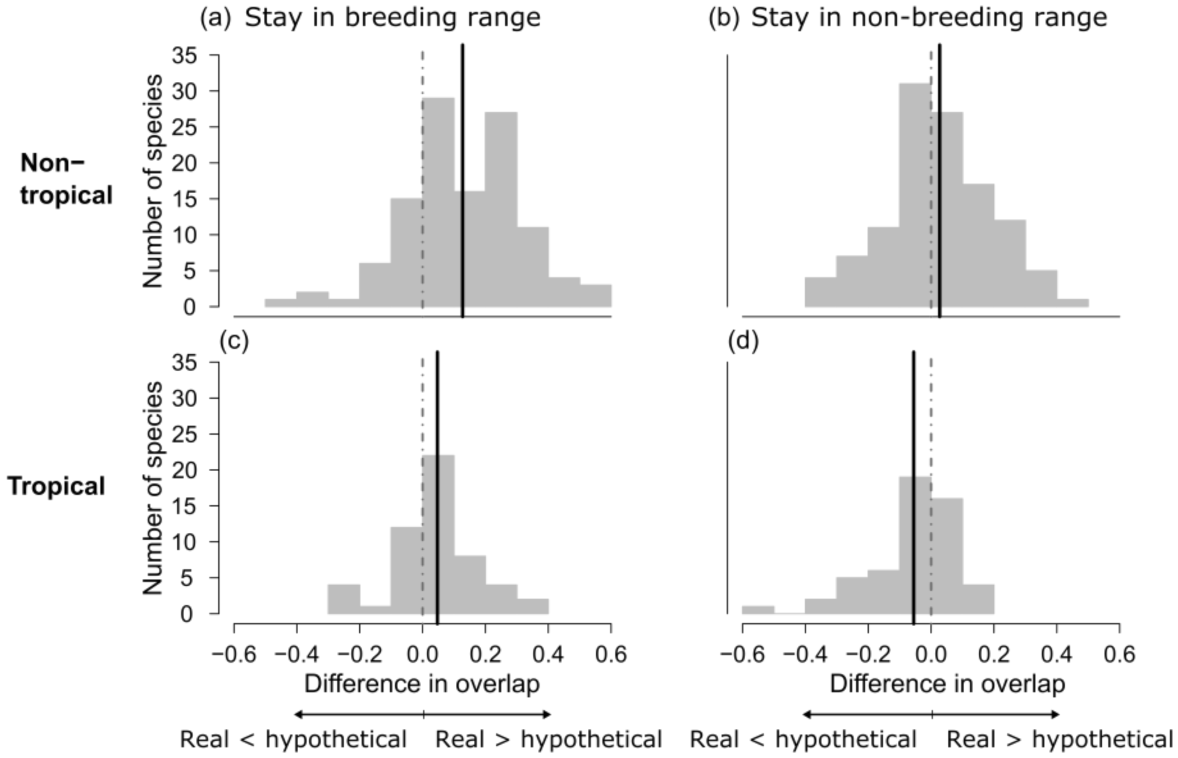

Figure 2. Frequency distributions of differences in niche overlap across migratory species, contrasting the real overlap to hypothetical overlap if migratory species did not migrate but rather stayed year-round in either the range they occupy in the breeding season (a and c) or non-breeding season (b and d). This is shown for species breeding outside of the tropics (N= 115, a and b) and species that breed at least partly (>10% of breeding range) in the tropics (N=53, c and d). Only directional migrants were considered (N= 168 species). We measured observed overlap given migration minus hypothetical overlap assuming no migration. If species track their climatic niche across seasons, positive values are expected: dotted grey line shows 0 (no difference), solid black line indicates mean difference for each scenario.

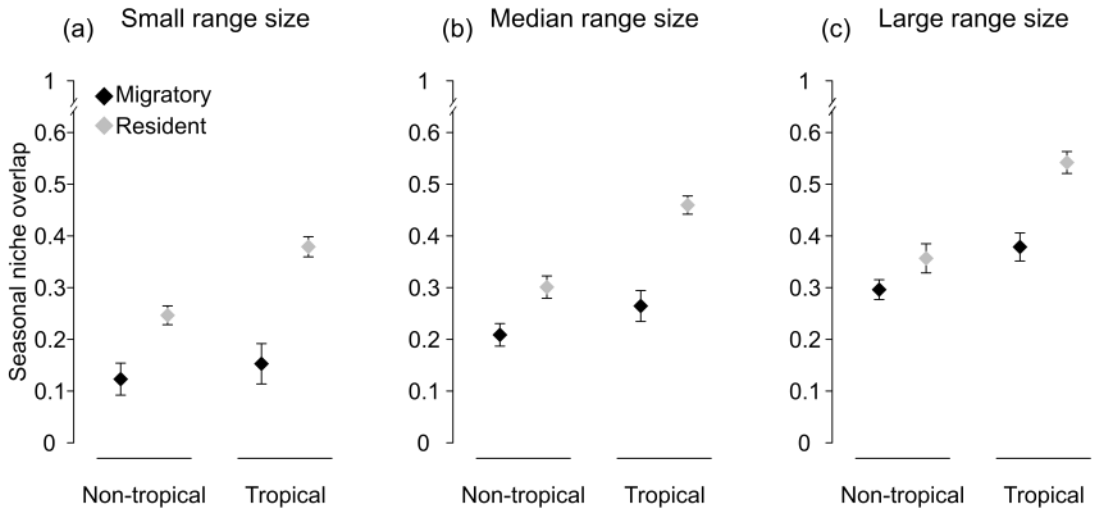

Figure 3. Predicted means and 95% confidence intervals across migratory (black) and resident (grey) species for seasonal niche overlap from linear mixed-effects models, separately for non-tropical and tropical species (tropical species have at least 10% of breeding range in the tropics). The models controlled for clade as a random effect and range size (log-transformed) as a fixed effect. Predicted means are shown at 3 example range sizes; the values for a) the 1st quartile, b) the median, and c) the 3rd quartile of log-transformed range sizes across all analysed species (N=437). Values of seasonal niche overlap can vary from 0 (no overlap) to 1 (complete overlap).

Table 1 Details of study clades. Clades are in taxonomic order following (IOC World Bird List (v 3.1) (Gill and Donsker 2012). Genera are listed by species number from highest to lowest. Migratory classification follows Eyres et al. (2017). Number of total species includes two extinct species that were not scored for migratory behaviour. For the residents and directional migrants only, we also indicate how many species are tropical breeders or non-tropical breeders. Tropical breeders are those which have at least 10% of their breeding range in tropics. Note that some species had to be excluded from niche calculations because of extremely small range sizes, so tropical and non-tropical species numbers do not add up to the clade total.

Clade	**Genera**	**Passeriform lineage**	**Total Species**	**Number of species by migratory type**					**Number of included Tropical breeders**		**Number of included Non-tropical breeders**	
				Resident	**Directional migrant**	**Dispersive migrant**	**Nomadic**	**Unknown**	**Resident**	**Directional migrant**	**Resident**	**Directional migrants**
Xolmiini Tyrant flycatchers	*Muscisaxicola, Knipolegus, Xolmis, Agriornis, Myiotheretes, Lessonia, Cnemarchus, Heteroxolmis, Hymenops, Neoxolmis, Polioxolmis, Satrapa,*	Suboscines: Tyranni, Tyrannidae	48	28	20	0	0	0	24	15	3	5
Vireonidae Vireos, Greenlets and allies	*Vireo, Hylophilus, Vireolanius, Cyclarhis*	Oscines: Corvoidea	53	40	13	0	0	0	13	3	18	10
Corvidae Crows & Ravens	*Corvus, Coloeus*	Oscines: Corvoidea	47	34	9	3	1	0	13	0	16	9
Hirundinidae Swallows & Martins	*Hirundo, Petrochelidon, Cecropis, Progne, Tachycineta, Riparia, Psalidoprocne,Notiochelidon, Ptyonoprogne, Delichon, Atticora, Phedina, Pseudochelidon, Stelgidopteryx, Alopochelidon, Cheramoeca, Haplochelidon, Neochelidon, Pseudhirundo.*	Oscines: Sylvioidea	88	32	43	12	0	1	17	28	14	11
Turdus Thrushes	*Turdus, Nesocichla, Psophocichla*	Oscines: Muscicapoidea, Turdidae	81	53	25	3	0	0	25	4	19	21
Oenanthe-Monticola Wheatears, chats and allies	*Oenanthe, Saxicola, Monticola, Myrmecocichla, Emarginata, Pentholaea, Thamnolaea, Campicoloides, Pinarochroa*	Oscines: Muscicapoidea, Muscicapidae	70	44	23	2	0	1	15	0	25	20
Setophaga-Myioborus Woodwarblers	*Setophaga, Myiothlypis, Myioborus, Basileuterus, Cardellina, Catharopeza*	Oscines: Passeroidea, Parulidae	80	50	30	0	0	0	19	0	15	27
Cardinalidae Cardinals, Grosbeaks and Allies	*Piranga, Passerina, Pheucticus, Habia,Chlorothraupis, Amaurospiza, Cardinalis, Cyanocompsa, Granatellus Caryothraustes, Cyanoloxia Periporphyrus, Rhodothraupis, Spiza.*	Oscines: Passeroidea	51	35	15	1	0	0	13	3	20	12

Table 2 Results from final linear mixed effects models with seasonal niche overlap as response variable. Migratory status (migratory vs. resident), breeding location (tropics vs. non-tropics), geographic range size (log-transformed), and their two-way interactions (indicated by *) were included as fixed effects, clade was included as a random effect. Marginal R^2 describes the proportion of variance explained by the fixed factors. The conditional R^2 describes the proportion of variance explained by the fixed effects and the random effect (clade). N= 437 species.

	F	**p**	**Residual d.f.**
Migratory status	7.24	0.007	425.37
Breeding location	2.03	0.156	428.21
Range size	122.87	<0.001	418.73
Migratory status*Range size	4.43	0.036	424.96
Migratory status* Breeding location	5.97	0.015	410.75
Breeding location*Range size	4.07	0.044	428.51

Appendix 1

Supplementary methods

Niche metrics and overlap calculation

Seasonal niche overlap was quantified following the methods of Broennimann et al. (2012). Principal component analysis (PCA) was carried out to incorporate information all six climatic variables and create a two dimensional space in which niche overlap was measured. As different climatic factors might be important for determining each clade's distribution, we carried out PCA for each clade individually; PCA was carried out across each entire clade to ensure comparability across species within each clade. In order to measure seasonal niche overlap with occurrence points within the bi-dimensional climatic space characterized by the first two principal components, the entire climatic space available to a clade was gridded into a 100 x 100 cells following Broennimann et al. (2012). The occurrences of each species and the climatic space available to each species (see explanation below and figure 1c) in the season of interest were then converted into densities within this grid. To ensure our metrics were independent of the resolution of the grid, kernel density smoothing was used to generate density surfaces.

To ensure that quantification of niches was comparable across all species and accounted for availability of climatic conditions, each clade-wide PCA was carried out including not only the species occurrences but also the climate available to the clade as a whole across both seasons. Species occurrence densities were subsequently divided by the density surface of available climate to give "climatic occupancy values" (Broennimann et al. 2012). The climate available to a species in a season was defined as the climate across all zoogeographic realms that the species inhabits in that season; the climate available to the clade as a whole was defined as all the zoogeographic realms that any member of the clade inhabits (see figure 1c for an example species). Zoogeographic realms were chosen because their borders represent areas of major turnover in species' distributions and phylogenetic lineages (Holt et al. 2013), so they approximate common frontiers to dispersal processes. The overlap between breeding and non-breeding niches was then calculated for each species based on the climatic occupancy values using Schoeners D, a measure that varies between 0 (no overlap) and 1 (complete overlap)(Warren et al. 2008).

Influence of geographic range size on niche overlap

To determine whether geographic range size influenced seasonal niche overlap, we tested whether range size differed between different categories of movement behaviour and for a relationship between range size and seasonal niche overlap. A linear mixed effects model across all species accounting for clade as a random effect showed that directional migrants had on average significantly larger total geographic range sizes than resident species (log transformed range size for migrants =15.54 ± 0.14, for residents = -1.51 ± 0.14, F=121.91, df = 434.9, p<0.001). We therefore tested whether there was a significant relationship between total range size and seasonal niche overlap. Using a linear mixed effects model accounting for clade as a random effect, geographic range size had a significant positive effect on seasonal niche overlap (slope =0.06 ± 0.006, t=10.06, df=431.86, p<0.001, figure S2), showing that species with larger ranges had greater niche overlap.

Supplementary figures

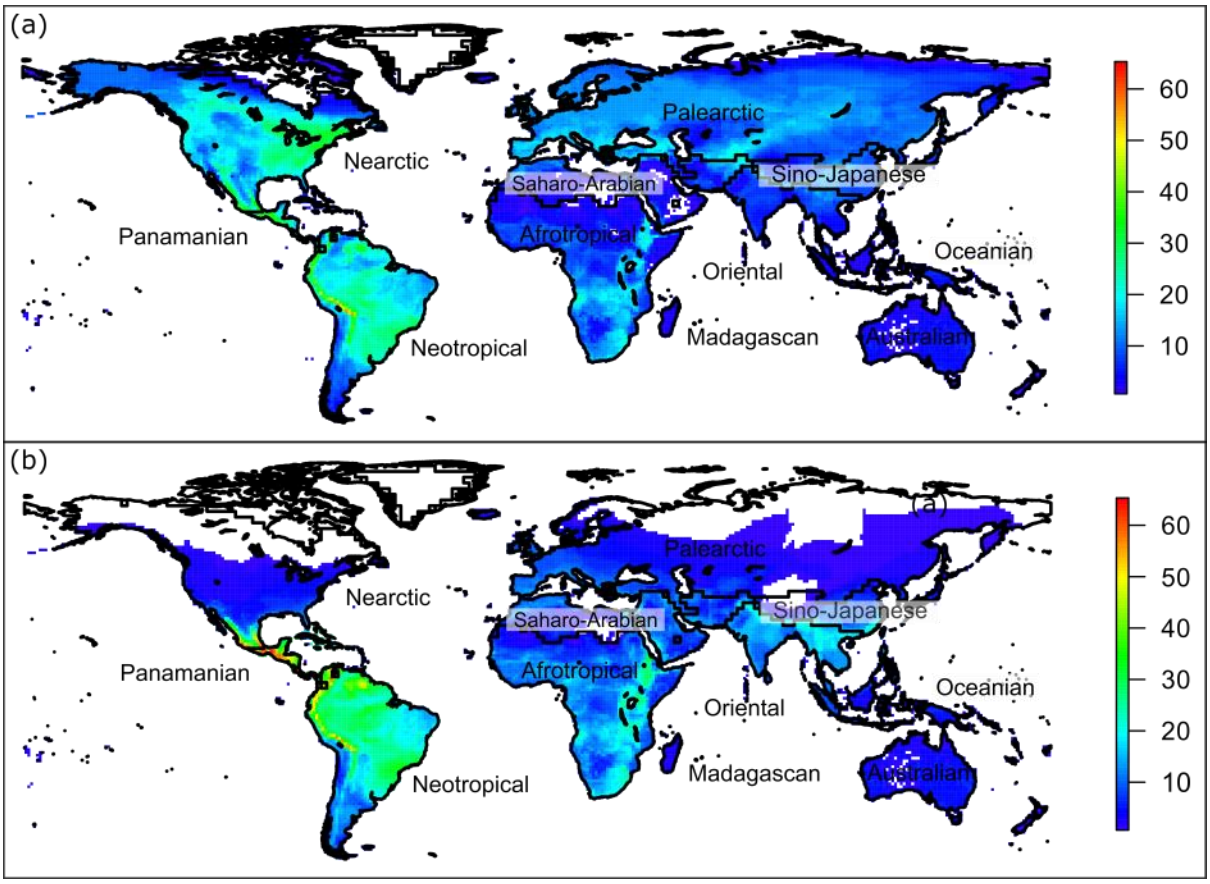

Figure S1. Species richness for the 437 species included in our final analyses. Shown for northern-hemisphere summer (a) and for northern-hemisphere winter (b). Thick lines indicate the 11 terrestrial zoographic realms (Holt et al. 2013). Our clades are distributed widely in both seasons with species present in all 11 zoographic realms.

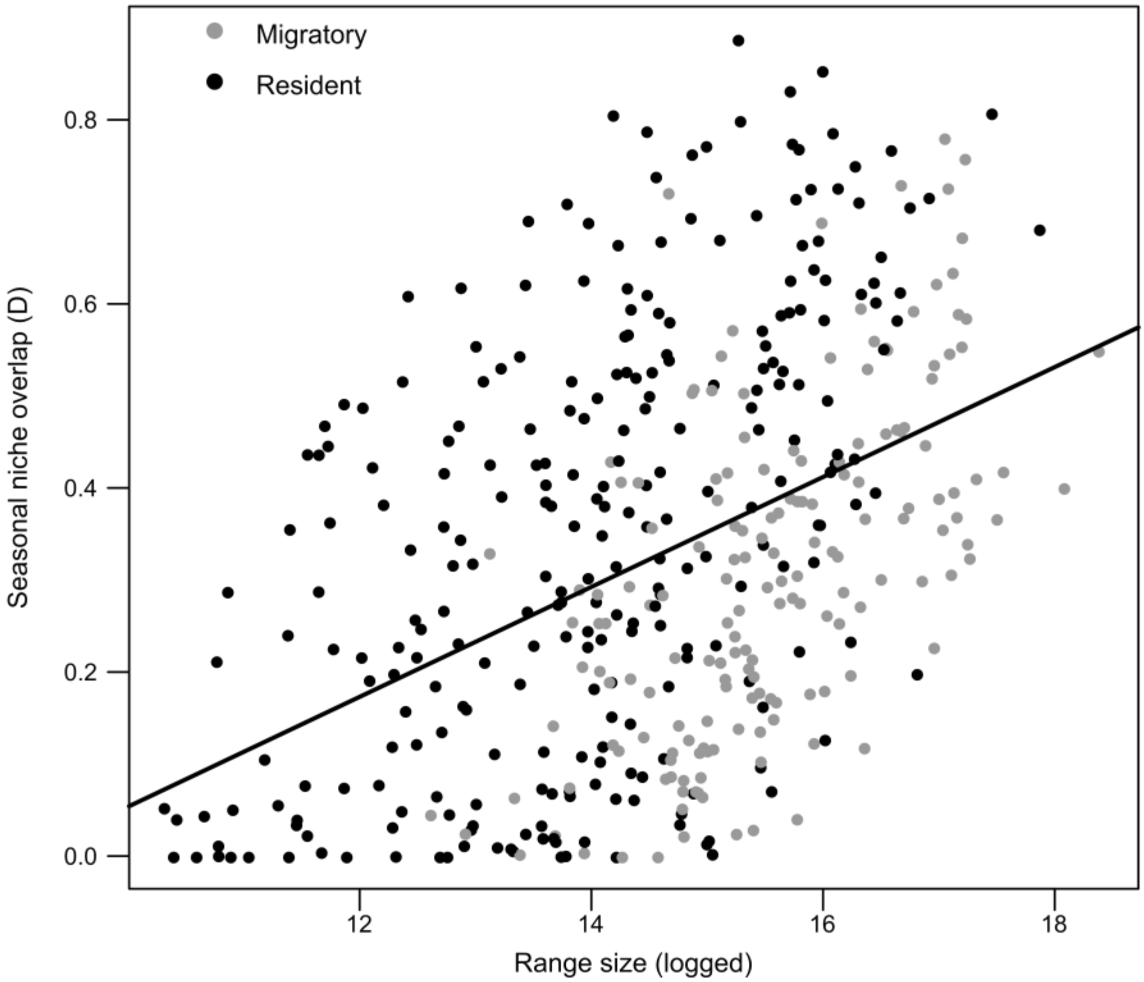

Figure S2. Relationship between seasonal niche overlap and range size across 8 clades of passerine birds (n = 437). The line shows the results of linear mixed effects models controlling for clade as a random effect. Range size was log-transformed. Niche overlap was calculated from the climatic occupancy values using Schoeners D. Migratory species (grey) had larger average range sizes than resident species (black). The relationship of niche overlap and geographic range size was less strong for resident species than for migratory species and less strong for species breeding outside of the tropics compared to those breeding in the tropics.

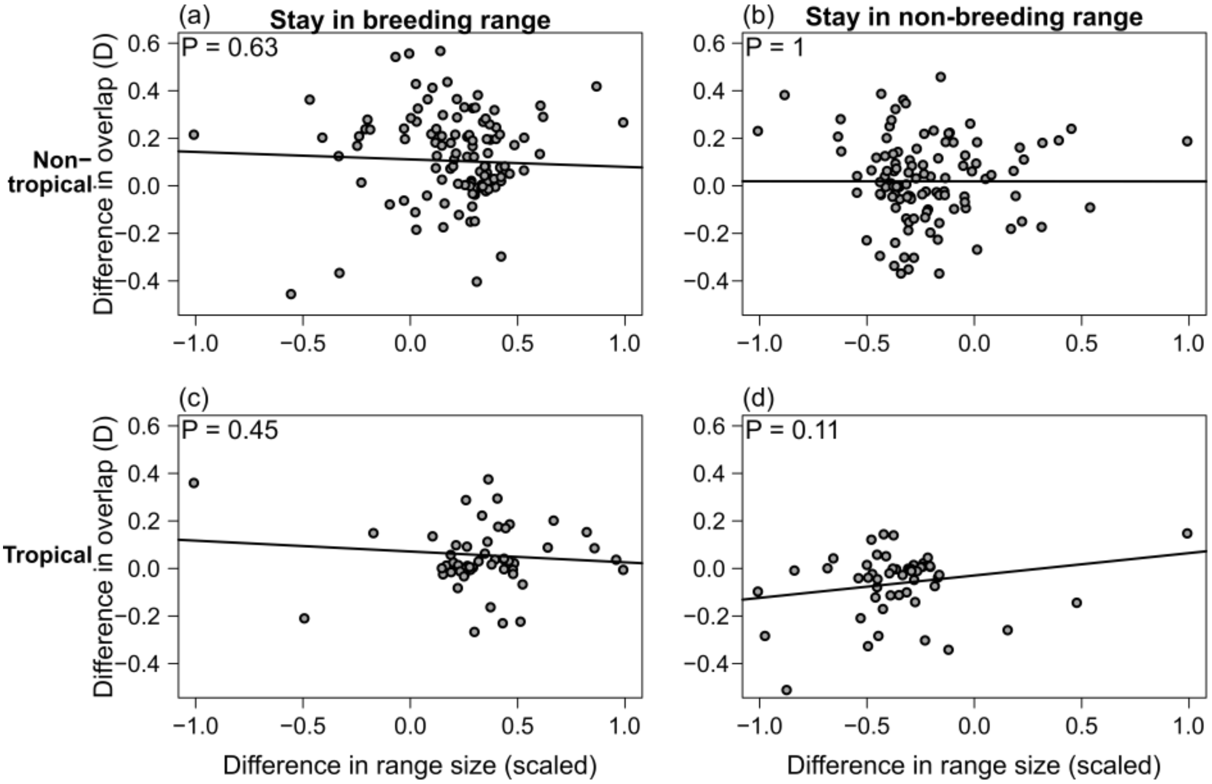

Figure S3. Results of the linear mixed effects model for differences in niche overlap, contrasting the real overlap to hypothetical overlap if migratory species stayed year round in either the range they occupy in the breeding season (left, a and c) or the non-breeding season (right, b and d) rather than migrate. Difference in range size among seasons (scaled between -1 and 1) was included as the fixed effect and clade was included as a random effect. This is shown for species breeding outside of the tropics (N=115, top, a and b) and species at least partly breeding in the tropics (N= 53, bottom, c and d). There was no relationship between difference in overlap and difference in range size. Only directional migrants were considered (N = 168).

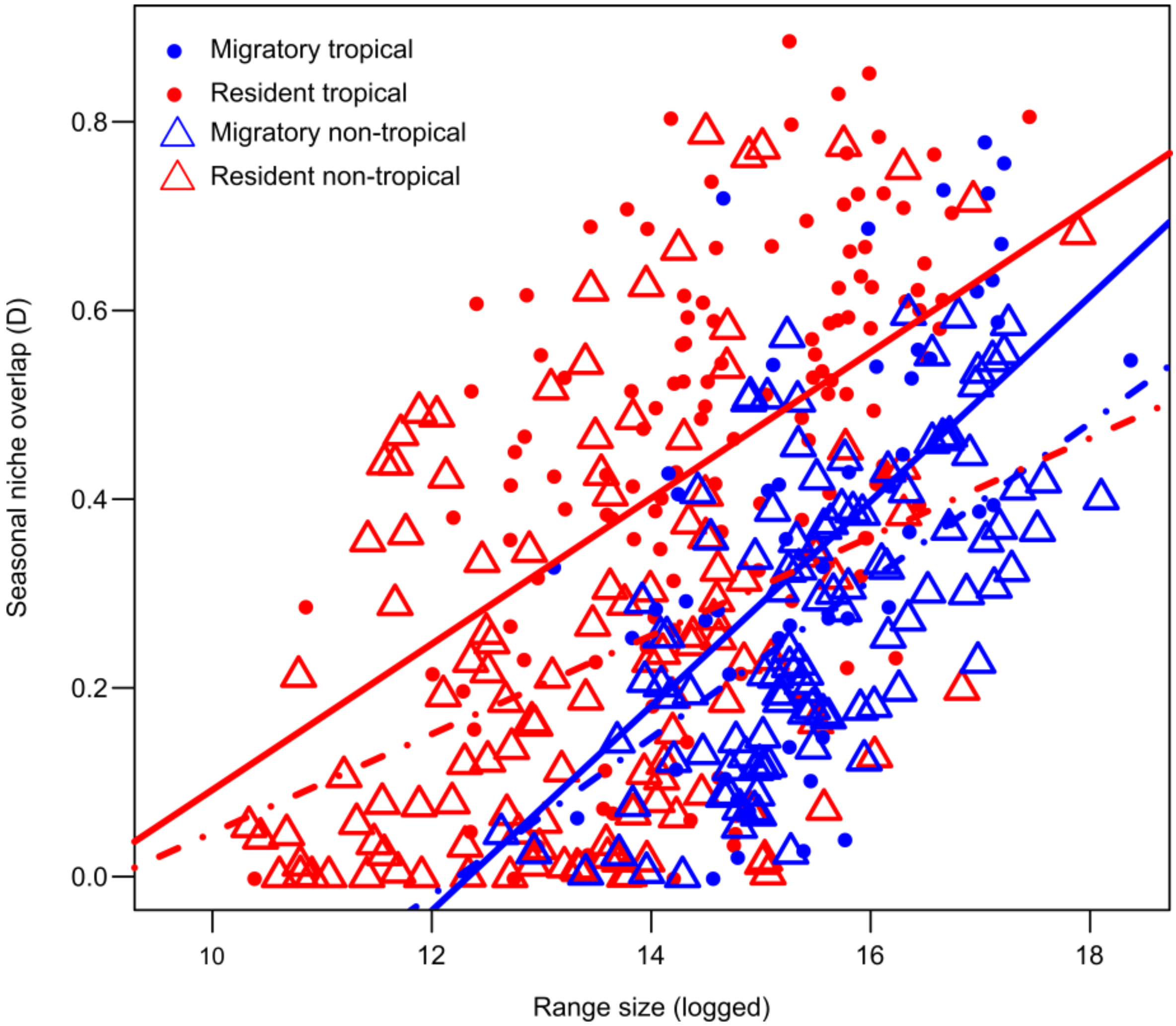

Figure S4. Results of the phylogenetic generalized lease squares analysis (PGLS) (table S2) testing the effect of migration and breeding location on seasonal niche overlap, whilst considering range size and the phylogenetic effect on these traits. Range size measures were log-transformed. Resident species are shown in red and migrants are shown in blue. Continuous lines and filled circles are used for species breeding in the tropics. Dashed lines and empty triangles depict species breeding outside of the tropics.

Supplementary Table 1. Details for all species within our 8 clades. Migratory categorization follows Eyres et al. (2017). Range size is total terrestrial range (breeding plus non-breeding). Peak breeding months are shown and source of information denoted. For species included in our study we report climatic niche values. Reason for exclusion from analyses is noted in final column.

Clade	**Species**	**Migratory behaviour**	**Breeding location**	**Range size (Km^2)**	**Peak breeding months**			**Breeding source (unless stated information comes from species description in handbook of birds of the world)**	**Annual niche breadth**	**Overlap**	**Overlap if stay in winter range**	**Overlap if stay in breeding range**	**Reason for exclusion**
Xolmiini	Agriornis_albicauda	resident	Tropical	672138	May	June	July		7.71	0.349	NA	NA	
Xolmiini	Agriornis_lividus	resident	Non-tropical	661396	October	November	December		7.83	0.104	NA	NA	
Xolmiini	Agriornis_micropterus	directional migratory	Tropical	3197380	October	November	December		8.12	0.268	0.304	0.330	
Xolmiini	Agriornis_montanus	directional migratory	Tropical	2178027	November	December	January		8.07	0.360	0.340	0.344	
Xolmiini	Agriornis_murinus	directional migratory	Tropical	2335986	October	November	December		7.84	0.022	0.096	0.020	
Hirundinidae	Alopochelidon_fucata	directional migratory	Tropical	3865948	September	October	November		6.32	0.431	0.434	0.451	
Cardinalidae	Amaurospiza_carrizalensis	resident	Non-tropical	12206	April	August	September	Subspecies of Amaurospiza_moesta	NA	NA	NA	NA	Small range
Cardinalidae	Amaurospiza_concolor	resident	Tropical	729710	May	June	July		6.96	0.190	NA	NA	
Cardinalidae	Amaurospiza_moesta	resident	Tropical	638684	April	August	September		6.11	0.277	NA	NA	
Hirundinidae	Atticora_fasciata	resident	Tropical	7141627	February	March	April		6.42	0.602	NA	NA	
Hirundinidae	Atticora_melanoleuca	resident	Tropical	2598019	February	March	April		6.22	0.465	NA	NA	
Setophaga	Basileuterus_basilicus	resident	Non-tropical	12108	April	May	June		NA	NA	NA	NA	Small range
Setophaga	Basileuterus_belli	resident	Non-tropical	667160	April	May	June		6.76	0.237	NA	NA	
Setophaga	Basileuterus_culicivorus	resident	Tropical	7031509	April	May	June		7.26	0.624	NA	NA	
Setophaga	Basileuterus_ignotus	resident	Non-tropical	8538	May	June	July		NA	NA	NA	NA	Small range
Setophaga	Basileuterus_lachrymosus	directional migratory	Non-tropical	742090	April	May	June	Close relative (Basileuterus rufifrons)	6.80	0.254	0.305	0.258	
Setophaga	Basileuterus_melanogenys	resident	Non-tropical	45398	April	May	June		6.03	0.356	NA	NA	
Setophaga	Basileuterus_rufifrons	resident	Non-tropical	1400516	April	May	June		7.26	0.227	NA	NA	
Setophaga	Basileuterus_trifasciatus	resident	Non-tropical	85173	April	May	June		5.42	0.488	NA	NA	
Setophaga	Basileuterus_tristriatus	resident	Tropical	830395	April	May	June		6.81	0.527	NA	NA	
Oenanthe	Campicoloides_bifasciatus	resident	Tropical	361313	September	October	November		5.43	0.465	NA	NA	
Setophaga	Cardellina_canadensis	directional migratory	Tropical	5761791	May	June	July		6.83	0.172	0.519	0.001	

Setophaga	Cardellina_pusilla	directional migratory	Non-tropical	10272546	May	June	July		6.83	0.327	0.259	0.043	
Setophaga	Cardellina_rubra	resident	Non-tropical	450795	May	June	July		6.73	0.017	NA	NA	
Setophaga	Cardellina_rubrifrons	directional migratory	Non-tropical	1064900	May	June	July		6.96	0.004	0.092	0.001	
Setophaga	Cardellina_versicolor	resident	Non-tropical	128599	April	May	June		6.37	0.334	NA	NA	
Cardinalidae	Cardinalis_cardinalis	resident	Non-tropical	6011247	February	March	April		7.72	0.384	NA	NA	
Cardinalidae	Cardinalis_phoeniceus	resident	Non-tropical	90334	June	July	August		5.62	0.192	NA	NA	
Cardinalidae	Cardinalis_sinuatus	resident	Non-tropical	1744390	May	June	July		7.57	0.003	NA	NA	
Cardinalidae	Caryothraustes_canadensis	resident	Tropical	3200849	February	March	April		6.92	0.528	NA	NA	
Cardinalidae	Caryothraustes_poliogaster	resident	Non-tropical	381225	April	May	June		6.74	0.426	NA	NA	
Setophaga	Catharopeza_bishopi	resident	Non-tropical	524	May	June	July		NA	NA	NA	NA	Small range
Hirundinidae	Cecropis_abyssinica	directional migratory	Tropical	13491417	March	May	June		7.00	0.780	0.813	0.800	
Hirundinidae	Cecropis_badia	resident	Non-tropical	185565	May	June	July		5.55	0.317	NA	NA	
Hirundinidae	Cecropis_cucullata	directional migratory	Tropical	3930206	October	November	December		6.14	0.418	0.291	0.227	
Hirundinidae	Cecropis_daurica	directional migratory	Tropical	23223171	May	June	July		7.38	0.369	0.173	0.161	
Hirundinidae	Cecropis_domicella	resident	Non-tropical	2556348	April	May	June		6.49	0.508	NA	NA	
Hirundinidae	Cecropis_hyperythra	resident	Non-tropical	66111	June	July	August		5.29	0.226	NA	NA	
Hirundinidae	Cecropis_semirufa	directional migratory	Tropical	9859524	April	August	December		7.00	0.530	0.669	0.735	
Hirundinidae	Cecropis_senegalensis	dispersive migratory	Tropical	13042941	April	August	December		NA	NA	NA	NA	Migratory status
Hirundinidae	Cecropis_striolata	directional migratory	Tropical	2350838	April	May	June		6.81	0.355	0.383	0.334	
Hirundinidae	Cheramoeca_leucosterna	resident	Tropical	3383270	September	October	November		6.58	0.592	NA	NA	
Cardinalidae	Chlorothraupis_carmioli	resident	Non-tropical	135461	March	April	May		6.07	0.122	NA	NA	
Cardinalidae	Chlorothraupis_frenata	resident	Tropical	372800	January	February	March	Close relative (Chlorothraupis stolzmanni)	6.72	0.230	NA	NA	
Cardinalidae	Chlorothraupis_olivacea	resident	Non-tropical	208277	January	February	March	Close relative (Chlorothraupis stolzmanni)	6.22	0.160	NA	NA	
Cardinalidae	Chlorothraupis_stolzmanni	resident	Tropical	171925	January	February	March		6.09	0.417	NA	NA	
Xolmiini	Cnemarchus_erythropygius	resident	Tropical	255508	October	November	December		6.87	0.426	NA	NA	
Corvus	Coloeus_dauuricus	directional migratory	Non-tropical	7216488	March	April	May		6.68	0.262	0.484	0.432	
Corvus	Coloeus_monedula	directional migratory	Non-tropical	18477193	April	May	June		7.22	0.325	0.280	0.247	
Corvus	Corvus_albicollis	resident	Tropical	2939935	September	October	November		6.28	0.544	NA	NA	

Corvus	Corvus_albus	resident	Tropical	19450758	April	June	September		7.22	0.806	NA	NA	
Corvus	Corvus_bennetti	nomadic	Tropical	4702793	July	August	September		NA	NA	NA	NA	Migratory status
Corvus	Corvus_brachyrhynchos	directional migratory	Non-tropical	11655107	March	April	May		6.98	0.596	0.686	0.632	
Corvus	Corvus_capensis	resident	Tropical	5152953	September	October	December		6.40	0.733	NA	NA	
Corvus	Corvus_caurinus	resident	Non-tropical	578013	April	May	June		6.08	0.016	NA	NA	
Corvus	Corvus_corax	dispersive migratory	Non-tropical	52289434	February	March	April		NA	NA	NA	NA	Migratory status
Corvus	Corvus_cornix	directional migratory	Non-tropical	18221353	February	March	April		7.36	0.339	0.382	0.485	
Corvus	Corvus_corone	directional migratory	Non-tropical	19360797	April	May	June		7.49	0.411	0.344	0.350	
Corvus	Corvus_coronoides	resident	Tropical	4181741	July	August	September		7.02	0.321	NA	NA	
Corvus	Corvus_crassirostris	resident	Non-tropical	676412	January	February	March		6.40	0.120	NA	NA	
Corvus	Corvus_cryptoleucus	dispersive migratory	Non-tropical	1903634	April	May	June		NA	NA	NA	NA	Migratory status
Corvus	Corvus_culminatus	resident	Non-tropical	2641822	May	June	July		7.16	0.099	NA	NA	
Corvus	Corvus_edithae	resident	Tropical	1463196	February	May	June		5.26	0.762	NA	NA	
Corvus	Corvus_enca	resident	Tropical	1761542	May	June	July		5.67	0.509	NA	NA	
Corvus	Corvus_florensis	resident	Non-tropical	15363	October	November	January		5.55	0.081	NA	NA	
Corvus	Corvus_frugilegus	directional migratory	Non-tropical	22423121	March	April	May		7.15	0.554	0.642	0.661	
Corvus	Corvus_fuscicapillus	resident	Tropical	101915	July	August	September	Close relative (Corvus tristis)	4.60	0.385	NA	NA	
Corvus	Corvus_hawaiiensis	resident	Non-tropical	8885	March	April	May		NA	NA	NA	NA	Extinct
Corvus	Corvus_imparatus	resident	Non-tropical	203068	April	May	June		5.37	0.039	NA	NA	
Corvus	Corvus_insularis	resident	Tropical	44623	February	March	April		4.86	0.244	NA	NA	
Corvus	Corvus_jamaicensis	resident	Non-tropical	11021	May	June	July	Gosse. The birds of Jamaica	NA	NA	NA	NA	Small range
Corvus	Corvus_kubaryi	resident	Non-tropical	696	September	November	January		NA	NA	NA	NA	Small range
Corvus	Corvus_leucognaphalus	resident	Non-tropical	58315	March	April	May		5.10	0.418	NA	NA	
Corvus	Corvus_levaillantii	resident	Non-tropical	1660244	January	February	March		6.95	0.014	NA	NA	
Corvus	Corvus_macrorhynchos	resident	Tropical	11333373	March	July	November		7.32	0.716	NA	NA	
Corvus	Corvus_meeki	resident	Non-tropical	9566	August	September	October		NA	NA	NA	NA	Small range
Corvus	Corvus_mellori	dispersive migratory	Non-tropical	1130055	August	September	October		NA	NA	NA	NA	Migratory status
Corvus	Corvus_minutus	resident	Non-tropical	17088	April	May	June		5.23	0.027	NA	NA	
Corvus	Corvus_moneduloides	resident	Tropical	16647	October	November	December		4.26	0	NA	NA	

Corvus	Corvus_nasicus	resident	Non-tropical	52771	April	May	June		4.98	0.024	NA	NA	
Corvus	Corvus_orru	resident	Tropical	5025206	January	April	November		7.13	0.428	NA	NA	
Corvus	Corvus_ossifragus	directional migratory	Non-tropical	1484475	March	April	May		5.35	0.507	0.507	0.507	
Corvus	Corvus_palmarum	resident	Non-tropical	58206	April	May	June		5.14	0.288	NA	NA	
Corvus	Corvus_rhipidurus	resident	Tropical	3534669	May	June	September		6.65	0.450	NA	NA	
Corvus	Corvus_ruficollis	directional migratory	Non-tropical	13495906	February	March	April		6.76	0.547	0.547	0.547	
Corvus	Corvus_sinaloae	resident	Non-tropical	113373	May	June	July		5.15	0.001	NA	NA	
Corvus	Corvus_splendens	resident	Tropical	4610234	April	May	June		7.11	0.127	NA	NA	
Corvus	Corvus_tasmanicus	resident	Non-tropical	226760	July	August	September		6.15	0.056	NA	NA	
Corvus	Corvus_torquatus	directional migratory	Non-tropical	3080116	February	March	April		6.38	0.375	0.375	0.375	
Corvus	Corvus_tristis	resident	Tropical	679644	July	August	September		5.91	0.403	NA	NA	
Corvus	Corvus_typicus	resident	Tropical	125938	May	June	July	Close relative (Corvus enca)	5.05	0.614	NA	NA	
Corvus	Corvus_unicolor	resident	Tropical	7108	April	May	June		NA	NA	NA	NA	Small range
Corvus	Corvus_validus	resident	Tropical	26571	May	June	July	Close relative (Corvus enca)	4.20	0.291	NA	NA	
Corvus	Corvus_violaceus	resident	Tropical	27753	May	June	July		4.78	0.051	NA	NA	
Corvus	Corvus_woodfordi	resident	Non-tropical	14820	July	August	September		NA	NA	NA	NA	Small range
Cardinalidae	Cyanocompsa_brissonii	resident	Tropical	5750072	November	December	January		7.27	0.234	NA	NA	
Cardinalidae	Cyanocompsa_cyanoides	resident	Tropical	7473561	February	March	April		7.02	0.652	NA	NA	
Cardinalidae	Cyanocompsa_parellina	resident	Non-tropical	845900	April	May	June		6.90	0.375	NA	NA	
Cardinalidae	Cyanoloxia_glaucocaerulea	directional migratory	Tropical	1307461	October	November	December		6.52	0.217	0.213	0.208	
Vireonidae	Cyclarhis_gujanensis	resident	Tropical	13369924	May	June	July		NA	NA	NA	NA	Missed out accidentally
Vireonidae	Cyclarhis_nigrirostris	resident	Tropical	280930	May	June	July		6.24	0.531	NA	NA	
Hirundinidae	Delichon_dasypus	directional migratory	Tropical	7134509	May	June	July		6.88	0.387	0.371	0.188	
Hirundinidae	Delichon_nipalense	resident	Non-tropical	952036	May	June	July		6.97	0.087	NA	NA	
Hirundinidae	Delichon_urbicum	directional migratory	Tropical	40644043	May	June	July		6.87	0.367	0.404	0.124	
Oenanthe	Emarginata_schlegelii	resident	Tropical	991696	September	October	November		5.81	0.611	NA	NA	
Oenanthe	Emarginata_sinuata	resident	Non-tropical	868832	October	November	December		5.68	0.246	NA	NA	
Oenanthe	Emarginata_tractrac	resident	Tropical	841312	September	October	November		5.76	0.568	NA	NA	
Cardinalidae	Granatellus_pelzelni	resident	Tropical	4351514	February	March	April		6.94	0.361	NA	NA	

Cardinalidae	Granatellus_sallaei	resident	Non-tropical	398666	June	July	August	Close relative (Granatellus venustus)	6.30	0.034	NA	NA	
Cardinalidae	Granatellus_venustus	resident	Non-tropical	312066	June	July	August		6.82	0.006	NA	NA	
Cardinalidae	Habia_atrimaxillaris	resident	Non-tropical	10765	February	March	April		NA	NA	NA	NA	Small range
Cardinalidae	Habia_cristata	resident	Non-tropical	72488	May	June	July		5.56	0.492	NA	NA	
Cardinalidae	Habia_fuscicauda	resident	Non-tropical	879196	April	May	June		6.57	0.255	NA	NA	
Cardinalidae	Habia_gutturalis	resident	Non-tropical	109785	February	March	April		5.99	0.120	NA	NA	
Cardinalidae	Habia_rubica	resident	Tropical	6296347	April	May	June		7.17	0.612	NA	NA	
Hirundinidae	Haplochelidon_andecola	resident	Tropical	594379	November	December	January		5.68	0.245	NA	NA	
Xolmiini	Heteroxolmis_dominicana	resident	Tropical	1193268	October	November	December		6.93	0.186	NA	NA	
Hirundinidae	Hirundo_aethiopica	dispersive migratory	Tropical	5319088	April	June	August		NA	NA	NA	NA	Migratory status
Hirundinidae	Hirundo_albigularis	directional migratory	Tropical	4553252	October	November	December		6.34	0.276	0.256	0.249	
Hirundinidae	Hirundo_angolensis	resident	Tropical	2219782	April	August	December		6.30	0.799	NA	NA	
Hirundinidae	Hirundo_atrocaerulea	directional migratory	Tropical	509541	November	December	January		5.71	0.330	0.466	0.037	
Hirundinidae	Hirundo_dimidiata	directional migratory	Tropical	3365705	August	September	October		6.46	0.276	0.249	0.353	
Hirundinidae	Hirundo_domicola	resident	Non-tropical	135795	March	April	May		6.05	0.217	NA	NA	
Hirundinidae	Hirundo_leucosoma	dispersive migratory	Non-tropical	1478308	April	May	June		NA	NA	NA	NA	Migratory status
Hirundinidae	Hirundo_lucida	resident	Tropical	2706831	August	September	October		6.90	0.163	NA	NA	
Hirundinidae	Hirundo_megaensis	resident	Non-tropical	61338	April	May	June		5.16	0.469	NA	NA	
Hirundinidae	Hirundo_neoxena	directional migratory	Tropical	4596354	August	September	October		7.19	0.689	0.685	0.690	
Hirundinidae	Hirundo_nigrita	resident	Tropical	3410894	January	July	December		6.32	0.832	NA	NA	
Hirundinidae	Hirundo_nigrorufa	resident	Tropical	760081	July	August	September		6.13	0	NA	NA	
Hirundinidae	Hirundo_rustica	directional migratory	Tropical	95573950	May	June	July		7.33	0.549	0.397	0.185	
Hirundinidae	Hirundo_smithii	directional migratory	Tropical	15916287	April	May	October		6.94	0.758	0.827	0.741	
Hirundinidae	Hirundo_tahitica	resident	Tropical	3585857	April	May	June		6.29	0.715	NA	NA	
Vireonidae	Hylophilus_amaurocephalus	resident	Tropical	1144644	December	January	February		6.96	0.107	NA	NA	
Vireonidae	Hylophilus_aurantiifrons	resident	Non-tropical	634104	July	August	September		6.54	0.079	NA	NA	
Vireonidae	Hylophilus_brunneiceps	resident	Tropical	762523	March	May	July	Close relative (Hylophilus muscicapinus)	6.19	0.264	NA	NA	
Vireonidae	Hylophilus_decurtatus	resident	Tropical	1092938	March	April	May		6.68	0.293	NA	NA	
Vireonidae	Hylophilus_flavipes	resident	Non-tropical	989357	April	May	June		6.69	0.359	NA	NA	

Vireonidae	Hylophilus_hypoxanthus	resident	Tropical	3726094	March	May	July	Close relative (Hylophilus pectoralis)	6.84	0.595	NA	NA	
Vireonidae	Hylophilus_muscicapinus	resident	Tropical	2757069	February	March	April		6.94	0.556	NA	NA	
Vireonidae	Hylophilus_ochraceiceps	resident	Tropical	6171373	April	May	June		6.99	0.711	NA	NA	
Vireonidae	Hylophilus_olivaceus	resident	Tropical	171247	May	June	July		6.22	0.359	NA	NA	
Vireonidae	Hylophilus_pectoralis	resident	Tropical	2706524	March	May	July		7.10	0.531	NA	NA	
Vireonidae	Hylophilus_poicilotis	resident	Tropical	862356	August	September	October		6.16	0.595	NA	NA	
Vireonidae	Hylophilus_sclateri	resident	Non-tropical	331096	March	May	July	Close relative (Hylophilus pectoralis)	5.90	0.188	NA	NA	
Vireonidae	Hylophilus_semibrunneus	resident	Tropical	241088	April	May	June		6.04	0.517	NA	NA	
Vireonidae	Hylophilus_semicinereus	resident	Tropical	4186330	March	May	July	Close relative (Hylophilus pectoralis)	6.91	0.638	NA	NA	
Vireonidae	Hylophilus_thoracicus	resident	Tropical	3785961	March	May	July	Close relative (Hylophilus pectoralis)	7.09	0.665	NA	NA	
Xolmiini	Hymenops_perspicillatus	directional migratory	Tropical	4359166	November	December	January		8.25	0.041	0.059	0.005	
Xolmiini	Knipolegus_aterrimus	directional migratory	Tropical	2454073	November	December	January		8.08	0.255	0.198	0.212	
Xolmiini	Knipolegus_cyanirostris	directional migratory	Tropical	2456907	November	December	January		7.06	0.139	0.138	0.071	
Xolmiini	Knipolegus_franciscanus	resident	Tropical	176899	November	December	January		6.43	0	NA	NA	
Xolmiini	Knipolegus_hudsoni	directional migratory	Tropical	2158173	November	December	January	Close relative (Knipolgus Aterrimus)	7.63	0	0.034	0.000	
Xolmiini	Knipolegus_lophotes	resident	Tropical	2550391	September	October	November		6.87	0.697	NA	NA	
Xolmiini	Knipolegus_nigerrimus	resident	Tropical	740470	September	October	November	Close relative (Knipolgus lophotes)	6.58	0.806	NA	NA	
Xolmiini	Knipolegus_orenocensis	resident	Tropical	1112688	February	March	April		6.88	0.286	NA	NA	
Xolmiini	Knipolegus_poecilocercus	resident	Tropical	2440993	July	August	September		6.95	0.489	NA	NA	
Xolmiini	Knipolegus_poecilurus	resident	Tropical	1011567	April	June	August		7.27	0.501	NA	NA	
Xolmiini	Knipolegus_signatus	resident	Tropical	433717	October	December	January		7.71	0.382	NA	NA	
Xolmiini	Knipolegus_striaticeps	resident	Tropical	1315406	November	December	January		7.44	0.035	NA	NA	
Xolmiini	Lessonia_oreas	resident	Tropical	1035068	October	November	December		7.46	0.527	NA	NA	
Xolmiini	Lessonia_rufa	directional migratory	Tropical	3376010	September	October	November		7.86	0.214	0.504	0.506	
Oenanthe	Monticola_angolensis	resident	Tropical	2443581	September	October	November		6.34	0.380	NA	NA	
Oenanthe	Monticola_brevipes	resident	Tropical	1333796	November	December	January		6.02	0.047	NA	NA	
Oenanthe	Monticola_cinclorhynchus	directional migratory	Non-tropical	1134300	May	June	July		6.69	0.207	0.108	0.119	
Oenanthe	Monticola_explorator	resident	Non-tropical	574123	September	October	November		5.54	0.626	NA	NA	
Oenanthe	Monticola_gularis	directional migratory	Non-tropical	4205882	May	June	July		5.97	0.324	0.118	0.000	

Oenanthe	Monticola_imerina	resident	Tropical	16383	November	December	January		NA	NA	NA	NA	Small range
Oenanthe	Monticola_rufiventris	directional migratory	Non-tropical	3798128	April	May	June		7.04	0.306	0.302	0.305	
Oenanthe	Monticola_rufocinereus	resident	Tropical	990103	March	May	September		5.90	0.788	NA	NA	
Oenanthe	Monticola_rupestris	resident	Tropical	730718	October	November	December		5.70	0.152	NA	NA	
Oenanthe	Monticola_saxatilis	directional migratory	Tropical	12544719	May	June	July		6.53	0.596	0.530	0.035	
Oenanthe	Monticola_semirufus	resident	Non-tropical	509587	June	July	August		6.20	0.066	NA	NA	
Oenanthe	Monticola_sharpei	resident	Tropical	347795	November	December	January		5.98	0.025	NA	NA	
Oenanthe	Monticola_solitarius	directional migratory	Tropical	24450543	April	May	June		7.27	0.585	0.349	0.313	
Xolmiini	Muscisaxicola_albifrons	resident	Tropical	413093	November	December	January		7.22	0.386	NA	NA	
Xolmiini	Muscisaxicola_albilora	directional migratory	Tropical	1689648	October	November	December		7.55	0.294	0.459	0.113	
Xolmiini	Muscisaxicola_alpinus	resident	Tropical	195225	September	October	November		6.17	0.469	NA	NA	
Xolmiini	Muscisaxicola_capistratus	directional migratory	Tropical	1870678	October	November	December		7.85	0.274	0.391	0.099	
Xolmiini	Muscisaxicola_cinereus	directional migratory	Tropical	876904	October	December	February		7.67	0.430	0.452	0.394	
Xolmiini	Muscisaxicola_flavinucha	directional migratory	Tropical	1557884	November	December	January		7.51	0.408	0.403	0.027	
Xolmiini	Muscisaxicola_fluviatilis	resident	Tropical	2229594	August	September	October		7.32	0.295	NA	NA	
Xolmiini	Muscisaxicola_frontalis	directional migratory	Tropical	986277	November	January	February		7.31	0.255	0.362	0.028	
Xolmiini	Muscisaxicola_griseus	resident	Tropical	528512	November	December	January		7.28	0.360	NA	NA	
Xolmiini	Muscisaxicola_juninensis	resident	Tropical	575418	October	November	December		7.23	0.477	NA	NA	
Xolmiini	Muscisaxicola_maclovianus	directional migratory	Tropical	2968212	September	December	February		8.01	0.507	0.531	0.300	
Xolmiini	Muscisaxicola_maculirostris	directional migratory	Tropical	2181603	November	January	February		7.79	0.411	0.399	0.349	
Xolmiini	Muscisaxicola_rufivertex	resident	Tropical	1094826	September	November	January		7.63	0.591	NA	NA	
Setophaga	Myioborus_albifacies	resident	Non-tropical	24508	April	May	June	Close relative (Myioborus ornatus)	5.80	0.012	NA	NA	
Setophaga	Myioborus_albifrons	resident	Non-tropical	64149	April	May	June		5.58	0.363	NA	NA	
Setophaga	Myioborus_brunniceps	resident	Tropical	406238	October	November	December		6.85	0.115	NA	NA	
Setophaga	Myioborus_cardonai	resident	Non-tropical	12254	April	May	June	Close relative (Myioborus ornatus)	NA	NA	NA	NA	Small range
Setophaga	Myioborus_castaneocapilla	resident	Non-tropical	159507	April	May	June	Close relative (Myioborus ornatus)	5.95	0.186	NA	NA	
Setophaga	Myioborus_flavivertex	resident	Non-tropical	13239	April	May	June		NA	NA	NA	NA	Small range
Setophaga	Myioborus_melanocephalus	resident	Tropical	516617	July	September	November		7.03	0.517	NA	NA	
Setophaga	Myioborus_miniatus	resident	Tropical	2680254	February	April	June		7.19	0.572	NA	NA	

Setophaga	Myioborus_ornatus	resident	Non-tropical	330131	April	May	June		6.11	0.544	NA	NA	
Setophaga	Myioborus_pariae	resident	Non-tropical	9163	April	May	June	Close relative (Myioborus ornatus)	NA	NA	NA	NA	Small range
Setophaga	Myioborus_pictus	directional migratory	Non-tropical	1542006	April	May	June		7.10	0.143	0.275	0.175	
Setophaga	Myioborus_torquatus	resident	Non-tropical	51762	March	April	May		6.01	0.078	NA	NA	
Xolmiini	Myiotheretes_fumigatus	resident	Tropical	645230	July	August	September		6.85	0.499	NA	NA	
Xolmiini	Myiotheretes_fuscorufus	resident	Tropical	178628	September	October	November		6.96	0.452	NA	NA	
Xolmiini	Myiotheretes_pernix	resident	Non-tropical	13239	February	April	May	Close relative (Myiotheretes striaticollis)	NA	NA	NA	NA	Small range
Xolmiini	Myiotheretes_striaticollis	resident	Tropical	1117764	February	April	May		7.77	0.669	NA	NA	
Setophaga	Myiothlypis_bivittata	resident	Tropical	758620	November	December	January		6.57	0.316	NA	NA	
Setophaga	Myiothlypis_chlorophrys	resident	Tropical	63112	May	June	July	Close relative (Myiothlypis fulvicauda)	5.90	0.447	NA	NA	
Setophaga	Myiothlypis_chrysogaster	resident	Tropical	84365	May	June	July	Close relative (Myiothlypis fulvicauda)	6.22	0.217	NA	NA	
Setophaga	Myiothlypis_cinereicollis	resident	Non-tropical	133925	April	June	July		6.43	0.258	NA	NA	
Setophaga	Myiothlypis_conspicillata	resident	Non-tropical	24155	April	May	June		5.55	0.212	NA	NA	
Setophaga	Myiothlypis_coronata	resident	Tropical	776072	May	June	July		7.15	0.431	NA	NA	
Setophaga	Myiothlypis_flaveola	resident	Tropical	4417088	October	November	December		6.90	0.361	NA	NA	
Setophaga	Myiothlypis_fraseri	resident	Tropical	123262	January	February	March		6.31	0.158	NA	NA	
Setophaga	Myiothlypis_fulvicauda	resident	Tropical	3151565	May	June	July		7.11	0.589	NA	NA	
Setophaga	Myiothlypis_griseiceps	resident	Non-tropical	11829	May	June	July		NA	NA	NA	NA	Small range
Setophaga	Myiothlypis_leucoblephara	resident	Tropical	1400119	October	November	December	Close relative (Basileuterus leucoblepharus)	6.20	0.217	NA	NA	
Setophaga	Myiothlypis_leucophrys	resident	Tropical	885842	October	November	December		6.44	0.062	NA	NA	
Setophaga	Myiothlypis_luteoviridis	resident	Tropical	642119	August	September	October		6.77	0.390	NA	NA	
Setophaga	Myiothlypis_nigrocristata	resident	Tropical	523292	May	June	July		6.70	0.416	NA	NA	
Setophaga	Myiothlypis_rivularis	resident	Tropical	4702898	February	March	April		7.17	0.496	NA	NA	
Setophaga	Myiothlypis_signata	resident	Tropical	436469	December	January	February		6.58	0.069	NA	NA	
Oenanthe	Myrmecocichla_aethiops	resident	Tropical	2903618	June	July	August		6.33	0.071	NA	NA	
Oenanthe	Myrmecocichla_formicivora	resident	Tropical	2396113	October	November	December		6.13	0.191	NA	NA	
Oenanthe	Myrmecocichla_melaena	resident	Non-tropical	217073	June	July	August		6.00	0.030	NA	NA	
Oenanthe	Myrmecocichla_nigra	resident	Tropical	4932444	March	July	November		6.70	0.786	NA	NA	

Oenanthe	Myrmecocichla_tholloni	resident	Tropical	400082	June	July	August		6.20	0.074	NA	NA	
Hirundinidae	Neochelidon_tibialis	resident	Tropical	4350340	March	April	May		6.42	0.670	NA	NA	
Xolmiini	Neoxolmis_rufiventris	directional migratory	Non-tropical	1484896	November	December	January		7.51	0	0	0.000	
Turdus	Nesocichla_eremita	resident	Non-tropical	96	October	November	December		NA	NA	NA	NA	Small range
Hirundinidae	Notiochelidon_cyanoleuca	directional migratory	Tropical	16832582	March	April	May		7.22	0.634	0.727	0.635	
Hirundinidae	Notiochelidon_flavipes	resident	Tropical	411151	July	August	September		5.97	0.428	NA	NA	
Hirundinidae	Notiochelidon_murina	resident	Tropical	975553	August	September	October		6.27	0.487	NA	NA	
Hirundinidae	Notiochelidon_pileata	resident	Non-tropical	140752	April	May	June		5.94	0.248	NA	NA	
Oenanthe	Oenanthe_albonigra	resident	Non-tropical	1205077	March	April	May		6.26	0.581	NA	NA	
Oenanthe	Oenanthe_bottae	resident	Non-tropical	509298	March	April	May		5.85	0.485	NA	NA	
Oenanthe	Oenanthe_chrysopygia	directional migratory	Non-tropical	4751993	May	June	July		6.34	0.173	0.023	0.034	
Oenanthe	Oenanthe_cypriaca	directional migratory	Non-tropical	1570563	April	May	June		NA	NA	NA	NA	Small range
Oenanthe	Oenanthe_deserti	directional migratory	Non-tropical	21439256	May	June	July		6.44	0.520	0.133	0.097	
Oenanthe	Oenanthe_dubia	unknown	Non-tropical	72896	May	June	July		NA	NA	NA	NA	Migratory status
Oenanthe	Oenanthe_familiaris	resident	Tropical	8163458	March	September	December		6.90	0.768	NA	NA	
Oenanthe	Oenanthe_finschii	directional migratory	Non-tropical	4089050	April	May	June		6.67	0.504	0.356	0.230	
Oenanthe	Oenanthe_fusca	resident	Non-tropical	1479910	April	May	June		6.30	0.069	NA	NA	
Oenanthe	Oenanthe_heuglini	dispersive migratory	Non-tropical	3747670	January	February	March		NA	NA	NA	NA	Migratory status
Oenanthe	Oenanthe_hispanica	directional migratory	Non-tropical	8243887	April	May	June		6.38	0.384	0.417	0.302	
Oenanthe	Oenanthe_isabellina	directional migratory	Tropical	23442815	April	May	June		6.55	0.534	0.322	0.239	
Oenanthe	Oenanthe_leucopyga	resident	Non-tropical	5978678	March	April	May		6.30	0.750	NA	NA	
Oenanthe	Oenanthe_leucura	resident	Non-tropical	1654812	March	April	May		5.94	0.772	NA	NA	
Oenanthe	Oenanthe_lugens	directional migratory	Non-tropical	4657457	April	May	June		6.54	0.300	0.230	0.244	
Oenanthe	Oenanthe_lugentoides	resident	Non-tropical	352627	April	May	June		5.53	0.266	NA	NA	
Oenanthe	Oenanthe_lugubris	resident	Tropical	459468	April	May	June	Close relative (Oenanthe lugens)	5.94	0.274	NA	NA	
Oenanthe	Oenanthe_melanura	resident	Non-tropical	3217034	April	May	June		6.14	0.316	NA	NA	
Oenanthe	Oenanthe_moesta	resident	Non-tropical	1294994	March	April	May		5.59	0.540	NA	NA	
Oenanthe	Oenanthe_monacha	resident	Non-tropical	1519762	April	May	June		6.62	0.314	NA	NA	
Oenanthe	Oenanthe_monticola	resident	Tropical	1856762	September	October	November		6.05	0.670	NA	NA	

Oenanthe	Oenanthe_oenanthe	directional migratory	Tropical	42940839	May	June	July		6.94	0.418	0.226	0.198	
Oenanthe	Oenanthe_phillipsi	resident	Non-tropical	596237	April	May	June		4.75	0.303	NA	NA	
Oenanthe	Oenanthe_picata	directional migratory	Non-tropical	3408303	April	May	June		6.50	0.388	0.275	0.362	
Oenanthe	Oenanthe_pileata	dispersive migratory	Tropical	6441956	June	August	October		NA	NA	NA	NA	Migratory status
Oenanthe	Oenanthe_pleschanka	directional migratory	Tropical	15564389	May	June	July		6.20	0.553	0.519	0.006	
Oenanthe	Oenanthe_scotocerca	resident	Non-tropical	771752	March	April	May		6.24	0.665	NA	NA	
Oenanthe	Oenanthe_xanthoprymna	directional migratory	Non-tropical	3082682	June	July	August		5.85	0.070	0.024	0.000	
Cardinalidae	Passerina_amoena	directional migratory	Non-tropical	3868335	June	July	August		6.99	0.193	0.004	0.006	
Cardinalidae	Passerina_caerulea	directional migratory	Non-tropical	7212397	April	May	June		7.87	0.177	0.441	0.234	
Cardinalidae	Passerina_ciris	directional migratory	Non-tropical	3225589	March	April	May		7.28	0.119	0.415	0.517	
Cardinalidae	Passerina_cyanea	directional migratory	Non-tropical	6964797	May	June	July		7.50	0.282	0.322	0.006	
Cardinalidae	Passerina_leclancherii	resident	Non-tropical	204479	May	June	July		6.46	0.012	NA	NA	
Cardinalidae	Passerina_rositae	resident	Non-tropical	20281	June	July	August		5.23	0	NA	NA	
Cardinalidae	Passerina_versicolor	directional migratory	Non-tropical	1635179	April	May	June		7.38	0.085	0.233	0.167	
Oenanthe	Pentholaea_albifrons	resident	Non-tropical	2703479	March	April	May		6.59	0.340	NA	NA	
Oenanthe	Pentholaea_arnotti	resident	Tropical	3420283	August	October	December		6.49	0.626	NA	NA	
Oenanthe	Pentholaea_collaris	resident	Tropical	507052	September	October	November	Subspecies of Myrmecocichla arnotti	5.87	0.072	NA	NA	
Cardinalidae	Periporphyrus_erythromelas	resident	Tropical	857650	February	March	April	Close relative (Caryothraustes_canadensis)	6.39	0.145	NA	NA	
Hirundinidae	Petrochelidon_ariel	directional migratory	Tropical	5284479	October	November	December		7.07	0.543	0.492	0.512	
Hirundinidae	Petrochelidon_fluvicola	dispersive migratory	Non-tropical	2923972	January	April	August		NA	NA	NA	NA	Migratory status
Hirundinidae	Petrochelidon_fuliginosa	resident	Tropical	282365	April	May	June		5.57	0.392	NA	NA	
Hirundinidae	Petrochelidon_fulva	directional migratory	Non-tropical	1165793	April	June	August		6.59	0.194	0.230	0.222	
Hirundinidae	Petrochelidon_nigricans	directional migratory	Tropical	6819245	September	October	November		7.19	0.450	0.558	0.608	
Hirundinidae	Petrochelidon_perdita	unknown	Non-tropical	3329	February	March	April		NA	NA	NA	NA	Migratory status
Hirundinidae	Petrochelidon_preussi	dispersive migratory	Non-tropical	2846429	March	April	May		NA	NA	NA	NA	Migratory status
Hirundinidae	Petrochelidon_pyrrhonota	directional migratory	Tropical	28024969	May	June	July		7.16	0.396	0.650	0.242	
Hirundinidae	Petrochelidon_rufigula	directional migratory	Tropical	1618892	July	August	September		6.22	0.071	0.076	0.068	
Hirundinidae	Petrochelidon_rufocollaris	resident	Tropical	226317	April	May	June		5.38	0.555	NA	NA	

Hirundinidae	Petrochelidon_spilodera	directional migratory	Tropical	1552061	November	January	February		6.15	0.116	0.159	0.019	
Hirundinidae	Phedina_borbonica	dispersive migratory	Tropical	687474	August	September	October		NA	NA	NA	NA	Migratory status
Hirundinidae	Phedina_brazzae	resident	Tropical	220480	July	August	September		5.70	0.034	NA	NA	
Cardinalidae	Pheucticus_aureoventris	dispersive migratory	Tropical	1580972	November	December	January		NA	NA	NA	NA	Migratory status
Cardinalidae	Pheucticus_chrysogaster	resident	Tropical	597859	March	April	May		7.13	0.689	NA	NA	
Cardinalidae	Pheucticus_chrysopeplus	directional migratory	Non-tropical	480571	June	July	August		7.24	0.023	0.023	0.013	
Cardinalidae	Pheucticus_ludovicianus	directional migratory	Tropical	7024934	June	July	August		6.70	0.442	0.204	0.000	
Cardinalidae	Pheucticus_melanocephalus	directional migratory	Non-tropical	5338176	April	May	June		7.48	0.168	0.232	0.348	
Cardinalidae	Pheucticus_tibialis	resident	Non-tropical	72474	March	April	May		6.25	0.075	NA	NA	
Oenanthe	Pinarochroa_sordida	resident	Tropical	413577	February	March	May		6.17	0.405	NA	NA	
Cardinalidae	Piranga_bidentata	resident	Non-tropical	1063149	April	May	June		7.43	0.273	NA	NA	
Cardinalidae	Piranga_erythrocephala	resident	Non-tropical	443127	May	June	July	Close relative (Piranga_hepatica)	7.34	0.020	NA	NA	
Cardinalidae	Piranga_flava	directional migratory	Tropical	5670146	October	November	December		7.53	0.416	0.403	0.397	
Cardinalidae	Piranga_hepatica	directional migratory	Non-tropical	1904246	May	June	July		7.52	0.113	0.151	0.097	
Cardinalidae	Piranga_leucoptera	resident	Tropical	1646860	May	June	July	Close relative (Piranga_hepatica)	7.03	0.327	NA	NA	
Cardinalidae	Piranga_ludoviciana	directional migratory	Non-tropical	5199162	May	June	July		7.56	0.178	0.196	0.047	
Cardinalidae	Piranga_lutea	resident	Tropical	1172864	July	September	October		7.05	0.368	NA	NA	
Cardinalidae	Piranga_olivacea	directional migratory	Tropical	5911574	May	June	July		7.03	0.150	0.486	0.009	
Cardinalidae	Piranga_roseogularis	resident	Non-tropical	165832	May	June	July	Close relative (Piranga_hepatica)	5.98	0	NA	NA	
Cardinalidae	Piranga_rubra	directional migratory	Tropical	9173932	May	June	July		7.76	0.180	0.405	0.004	
Cardinalidae	Piranga_rubriceps	resident	Tropical	355687	September	October	November		5.99	0.691	NA	NA	
Xolmiini	Polioxolmis_rufipennis	resident	Tropical	627257	December	January	February		7.38	0.183	NA	NA	
Hirundinidae	Progne_chalybea	directional migratory	Tropical	15258580	April	May	June		6.82	0.673	0.663	0.680	
Hirundinidae	Progne_cryptoleuca	directional migratory	Non-tropical	110178	May	June	July		NA	NA	NA	NA	Small range
Hirundinidae	Progne_dominicensis	directional migratory	Non-tropical	106756	April	May	June		NA	NA	NA	NA	Small range
Hirundinidae	Progne_elegans	directional migratory	Tropical	4868050	November	December	January		6.36	0.029	0.351	0.047	
Hirundinidae	Progne_modesta	resident	Tropical	7236	February	March	April		NA	NA	NA	NA	Small range
Hirundinidae	Progne_murphyi	resident	Tropical	120128	February	March	April		5.19	0.517	NA	NA	

Hirundinidae	Progne_sinaloae	directional migratory	Non-tropical	400589	April	May	June		NA	NA	NA	NA	Small range
Hirundinidae	Progne_subis	directional migratory	Tropical	18939902	April	May	June		7.05	0.379	0.658	0.337	
Hirundinidae	Progne_tapera	directional migratory	Tropical	15215419	December	January	February		7.15	0.590	0.630	0.546	
Hirundinidae	Psalidoprocne_albiceps	directional migratory	Tropical	1323761	February	June	October		6.18	0.721	0.727	0.749	
Hirundinidae	Psalidoprocne_fuliginosa	resident	Non-tropical	31827	December	January	February		4.65	0	NA	NA	
Hirundinidae	Psalidoprocne_nitens	resident	Tropical	2241219	February	May	August		6.35	0.888	NA	NA	
Hirundinidae	Psalidoprocne_obscura	dispersive migratory	Non-tropical	1561613	June	July	August		NA	NA	NA	NA	Migratory status
Hirundinidae	Psalidoprocne_pristoptera	directional migratory	Tropical	8884728	April	June	August		6.79	0.730	0.730	0.730	
Hirundinidae	Pseudhirundo_griseopyga	dispersive migratory	Tropical	6557321	June	July	August		NA	NA	NA	NA	Migratory status
Hirundinidae	Pseudochelidon_eurystomina	directional migratory	Tropical	541870	February	March	April		5.50	0.064	0.160	0.326	
Hirundinidae	Pseudochelidon_sirintarae	directional migratory	Non-tropical	23745	February	March	April		NA	NA	NA	NA	Small range
Turdus	Psophocichla_litsitsirupa	resident	Tropical	4621273	September	October	November		6.34	0.626	NA	NA	
Hirundinidae	Ptyonoprogne_concolor	resident	Non-tropical	3474295	February	July	August		7.22	0.775	NA	NA	
Hirundinidae	Ptyonoprogne_fuligula	dispersive migratory	Tropical	7244781	February	June	October		NA	NA	NA	NA	Migratory status
Hirundinidae	Ptyonoprogne_obsoleta	resident	Non-tropical	6159945	February	March	April		6.57	0.433	NA	NA	
Hirundinidae	Ptyonoprogne_rupestris	directional migratory	Non-tropical	12590933	May	June	July		7.37	0.302	0.073	0.079	
Cardinalidae	Rhodothraupis_celaeno	resident	Non-tropical	168462	April	May	June		6.27	0.136	NA	NA	
Hirundinidae	Riparia_chinensis	dispersive migratory	Non-tropical	3711768	March	July	November	Subspecies of Riparia paludicola	NA	NA	NA	NA	Migratory status
Hirundinidae	Riparia_cincta	directional migratory	Tropical	9424303	March	July	November		6.90	0.561	0.765	0.779	
Hirundinidae	Riparia_congica	resident	Tropical	194275	February	March	April		5.16	0.232	NA	NA	
Hirundinidae	Riparia_diluta	directional migratory	Non-tropical	12776449	February	March	April		7.19	0.118	0.204	0.569	
Hirundinidae	Riparia_paludicola	dispersive migratory	Tropical	7762717	March	July	November		NA	NA	NA	NA	Migratory status
Hirundinidae	Riparia_riparia	directional migratory	Tropical	72465529	May	June	July		7.25	0.400	0.576	0.159	
Xolmiini	Satrapa_icterophrys	directional migratory	Tropical	8290623	October	December	January		7.96	0.551	0.566	0.529	
Oenanthe	Saxicola_caprata	directional migratory	Tropical	9713647	March	April	June		7.29	0.465	0.486	0.534	
Oenanthe	Saxicola_dacotiae	resident	Non-tropical	2009	February	March	April		NA	NA	NA	NA	Small range
Oenanthe	Saxicola_ferreus	directional migratory	Non-tropical	5861028	April	May	June		7.08	0.430	0.306	0.342	
Oenanthe	Saxicola_gutturalis	resident	Tropical	15689	October	November	December		NA	NA	NA	NA	Small range

Oenanthe	Saxicola_insignis	directional migratory	Non-tropical	881490	June	July	August		5.47	0.143	0.003	0.000	
Oenanthe	Saxicola_jerdoni	resident	Non-tropical	563846	March	April	May		6.34	0.109	NA	NA	
Oenanthe	Saxicola_leucurus	resident	Non-tropical	809849	March	April	May		6.45	0.464	NA	NA	
Oenanthe	Saxicola_macrorhynchus	directional migratory	Non-tropical	716491	April	May	June		6.18	0.190	0.190	0.190	
Oenanthe	Saxicola_rubetra	directional migratory	Tropical	17739735	May	June	July		6.40	0.463	0.330	0.029	
Oenanthe	Saxicola_rubicola	directional migratory	NA	NA	April	May	June		NA	NA	NA	NA	No data
Oenanthe	Saxicola_sibilla	resident	Tropical	472840	August	September	October		6.08	0.277	NA	NA	
Oenanthe	Saxicola_stejnegeri	directional migratory	NA	NA	May	June	July		NA	NA	NA	NA	No data
Oenanthe	Saxicola_tectes	resident	Tropical	3038	November	December	January		NA	NA	NA	NA	Small range
Oenanthe	Saxicola_torquatus	resident	Tropical	48003261	May	July	September		7.22	0.682	NA	NA	
Setophaga	Setophaga_adelaidae	resident	Non-tropical	8892	April	May	June		NA	NA	NA	NA	Small range
Setophaga	Setophaga_aestiva	directional migratory	NA	NA	May	June	July		NA	NA	NA	NA	No data
Setophaga	Setophaga_americana	directional migratory	Non-tropical	4594806	May	June	July		6.22	0.456	0.231	0.039	
Setophaga	Setophaga_angelae	resident	Non-tropical	8892	April	May	June		NA	NA	NA	NA	Small range
Setophaga	Setophaga_auduboni	directional migratory	NA	NA	May	June	July		NA	NA	NA	NA	No data
Setophaga	Setophaga_caerulescens	directional migratory	Non-tropical	1924937	May	June	July		6.04	0.130	0.428	0.003	
Setophaga	Setophaga_castanea	directional migratory	Non-tropical	3920861	May	June	July		6.18	0.186	0.377	0.000	
Setophaga	Setophaga_cerulea	directional migratory	Tropical	3199168	May	June	July		6.70	0.065	0.429	0.000	
Setophaga	Setophaga_chrysoparia	directional migratory	Non-tropical	306461	April	May	June		6.22	0.046	0.280	0.063	
Setophaga	Setophaga_citrina	directional migratory	Non-tropical	3101941	June	July	August		5.98	0.337	0.177	0.002	
Setophaga	Setophaga_coronata	directional migratory	Non-tropical	16886961	May	June	July		7.59	0.467	0.200	0.177	
Setophaga	Setophaga_delicata	resident	Non-tropical	2113	April	May	June	Close relative (Setophaga adelaidae)	NA	NA	NA	NA	Small range
Setophaga	Setophaga_discolor	directional migratory	Non-tropical	2429167	May	June	July		5.93	0.087	0.182	0.000	
Setophaga	Setophaga_dominica	directional migratory	Non-tropical	3529783	May	June	July		6.41	0.211	0.344	0.000	
Setophaga	Setophaga_flavescens	resident	Non-tropical	2759	May	June	July		NA	NA	NA	NA	Small range
Setophaga	Setophaga_fusca	directional migratory	Tropical	4765330	May	June	July		6.78	0.205	0.536	0.003	
Setophaga	Setophaga_goldmani	resident	NA	NA	May	June	July		NA	NA	NA	NA	No data
Setophaga	Setophaga_graciae	directional migratory	Non-tropical	1617373	May	June	July		7.19	0.113	0.164	0.110	

Setophaga	Setophaga_kirtlandii	directional migratory	Non-tropical	33300	May	June	July		NA	NA	NA	NA	Small range
Setophaga	Setophaga_magnolia	directional migratory	Non-tropical	5796050	June	July	August		5.83	0.369	0.181	0.000	
Setophaga	Setophaga_nigrescens	directional migratory	Non-tropical	2686887	May	June	July		6.61	0.052	0.015	0.044	
Setophaga	Setophaga_occidentalis	directional migratory	Non-tropical	1309232	May	June	July		6.70	0.254	0.209	0.003	
Setophaga	Setophaga_palmarum	directional migratory	Non-tropical	4918077	May	June	July		6.46	0.215	0.366	0.000	
Setophaga	Setophaga_pensylvanica	directional migratory	Non-tropical	4643592	May	June	July		6.23	0.225	0.244	0.005	
Setophaga	Setophaga_petechia	resident	Tropical	19244540	April	May	June		7.71	0.199	NA	NA	
Setophaga	Setophaga_pharetra	resident	Non-tropical	11021	March	April	May		NA	NA	NA	NA	Small range
Setophaga	Setophaga_pinus	directional migratory	Non-tropical	3039324	April	May	June		6.30	0.223	0.130	0.209	
Setophaga	Setophaga_pitiayumi	resident	Tropical	9730576	March	June	August		7.43	0.706	NA	NA	
Setophaga	Setophaga_pityophila	resident	Non-tropical	21666	March	April	May		5.54	0.044	NA	NA	
Setophaga	Setophaga_plumbea	resident	Non-tropical	2437	April	May	June		NA	NA	NA	NA	Small range
Setophaga	Setophaga_ruticilla	directional migratory	Tropical	12309319	May	June	July		7.03	0.408	0.319	0.078	
Setophaga	Setophaga_striata	directional migratory	Tropical	11518441	May	June	July		7.11	0.197	0.561	0.023	
Setophaga	Setophaga_subita	resident	Non-tropical	436	April	May	June	Close relative (Setophaga adelaidae)	NA	NA	NA	NA	Small range
Setophaga	Setophaga_tigrina	directional migratory	Non-tropical	4149085	June	July	August		5.54	0.572	0.109	0.000	
Setophaga	Setophaga_townsendi	directional migratory	Non-tropical	4130350	May	June	July		7.04	0.240	0.151	0.021	
Setophaga	Setophaga_virens	directional migratory	Non-tropical	5434409	May	June	July		6.38	0.422	0.198	0.052	
Setophaga	Setophaga_vitellina	resident	Non-tropical	281	April	May	June		NA	NA	NA	NA	Small range
Cardinalidae	Spiza_americana	directional migratory	Non-tropical	5598238	May	June	July		6.97	0.293	0.238	0.001	
Hirundinidae	Stelgidopteryx_ruficollis	directional migratory	Tropical	13898140	April	May	June		6.82	0.726	0.748	0.720	
Hirundinidae	Stelgidopteryx_serripennis	directional migratory	Non-tropical	10737874	March	April	May		7.20	0.272	0.440	0.634	
Hirundinidae	Tachycineta_albilinea	resident	Non-tropical	1106031	March	April	May		6.34	0.325	NA	NA	
Hirundinidae	Tachycineta_albiventer	directional migratory	Tropical	12436158	February	March	April		6.78	0.623	0.607	0.633	
Hirundinidae	Tachycineta_bicolor	directional migratory	Non-tropical	15549291	May	June	July		6.69	0.460	0.215	0.093	
Hirundinidae	Tachycineta_cyaneoviridis	dispersive migratory	Non-tropical	12781	May	June	July		NA	NA	NA	NA	Migratory status
Hirundinidae	Tachycineta_euchrysea	resident	Non-tropical	44989	June	July	August		4.63	0	NA	NA	
Hirundinidae	Tachycineta_leucopyga	directional migratory	Tropical	4559783	October	November	December		6.89	0.331	0.325	0.124	

Hirundinidae	Tachycineta_leucorrhoa	directional migratory	Tropical	6890623	October	November	December		6.50	0.288	0.240	0.195	
Hirundinidae	Tachycineta_stolzmanni	resident	Non-tropical	92643	January	February	March		5.21	0.423	NA	NA	
Hirundinidae	Tachycineta_thalassina	directional migratory	Non-tropical	7547618	May	June	July		6.79	0.123	0.073	0.197	
Oenanthe	Thamnolaea_cinnamomeiventris	resident	Tropical	3677478	November	March	July		6.49	0.769	NA	NA	
Oenanthe	Thamnolaea_coronata	resident	Non-tropical	863167	May	June	July		6.33	0.091	NA	NA	
Turdus	Turdus_abyssinicus	resident	Tropical	1446670	March	June	August		6.43	0.695	NA	NA	
Turdus	Turdus_albicollis	resident	Tropical	8584114	October	November	December		6.61	0.584	NA	NA	
Turdus	Turdus_albocinctus	dispersive migratory	Non-tropical	640411	April	May	June		NA	NA	NA	NA	Migratory status
Turdus	Turdus_amaurochalinus	directional migratory	Tropical	8756466	February	October	December		6.89	0.367	0.371	0.209	
Turdus	Turdus_assimilis	resident	Non-tropical	984561	April	May	June		6.54	0.405	NA	NA	
Turdus	Turdus_atrogularis	directional migratory	Non-tropical	8408414	May	June	July		6.65	0.342	0.057	0.000	
Turdus	Turdus_aurantius	resident	Non-tropical	11021	May	June	July		NA	NA	NA	NA	Small range
Turdus	Turdus_bewsheri	resident	Tropical	1671	August	September	October		NA	NA	NA	NA	Small range
Turdus	Turdus_boulboul	directional migratory	Non-tropical	1448808	April	May	June		6.93	0.356	0.103	0.330	
Turdus	Turdus_cardis	directional migratory	Non-tropical	1107354	May	June	July		5.83	0.290	0.009	0.026	
Turdus	Turdus_celaenops	resident	Non-tropical	1387	April	May	June		NA	NA	NA	NA	Small range
Turdus	Turdus_chiguanco	resident	Tropical	1315594	April	May	June		6.26	0.467	NA	NA	
Turdus	Turdus_chrysolaus	directional migratory	Non-tropical	1290933	June	July	August		5.67	0.204	0.072	0.000	
Turdus	Turdus_daguae	resident	Tropical	198903	April	May	June		5.29	0.624	NA	NA	
Turdus	Turdus_dissimilis	dispersive migratory	Non-tropical	1377645	April	May	June		NA	NA	NA	NA	Migratory status
Turdus	Turdus_eunomus	directional migratory	Non-tropical	7257360	June	July	August		6.34	0.386	0.021	0.000	
Turdus	Turdus_falcklandii	resident	Non-tropical	756465	October	November	December		6.53	0.065	NA	NA	
Turdus	Turdus_feae	directional migratory	Non-tropical	356170	May	June	July		6.00	0.025	0.022	0.000	
Turdus	Turdus_flavipes	directional migratory	Tropical	1153499	November	December	January		6.06	0.284	0.291	0.272	
Turdus	Turdus_fulviventris	resident	Tropical	220011	May	June	July		5.50	0.319	NA	NA	
Turdus	Turdus_fumigatus	resident	Tropical	4514381	February	June	December		6.36	0.856	NA	NA	
Turdus	Turdus_fuscater	resident	Tropical	836001	March	April	June		6.23	0.614	NA	NA	
Turdus	Turdus_grayi	resident	Non-tropical	1111860	April	May	June		6.10	0.255	NA	NA	
Turdus	Turdus_haplochrous	resident	Tropical	119219	April	May	June	Close relative (Turdus chiguanco)	5.21	0.051	NA	NA	

Turdus	Turdus_hauxwelli	resident	Tropical	3142036	February	March	April		6.14	0.419	NA	NA	
Turdus	Turdus_helleri	resident	Non-tropical	12287	March	April	May		NA	NA	NA	NA	Small range
Turdus	Turdus_hortulorum	directional migratory	Non-tropical	3152073	May	June	July		5.79	0.086	0.009	0.000	
Turdus	Turdus_ignobilis	resident	Tropical	4077041	February	April	June		6.48	0.726	NA	NA	
Turdus	Turdus_iliacus	directional migratory	Non-tropical	18013755	April	May	June		6.74	0.366	0.513	0.154	
Turdus	Turdus_infuscatus	resident	Non-tropical	265641	May	June	July		6.02	0.112	NA	NA	
Turdus	Turdus_jamaicensis	resident	Non-tropical	11021	April	May	June		NA	NA	NA	NA	Small range
Turdus	Turdus_kessleri	dispersive migratory	Non-tropical	1701708	May	June	July		NA	NA	NA	NA	Migratory status
Turdus	Turdus_lawrencii	resident	Tropical	3103716	December	January	February		6.19	0.504	NA	NA	
Turdus	Turdus_leucomelas	resident	Tropical	7646988	November	December	January		6.68	0.552	NA	NA	
Turdus	Turdus_leucops	resident	Tropical	818871	February	March	April		6.09	0.561	NA	NA	
Turdus	Turdus_lherminieri	resident	Non-tropical	3998	April	May	June		NA	NA	NA	NA	Small range
Turdus	Turdus_libonyana	resident	Tropical	4824453	September	October	November		6.32	0.418	NA	NA	
Turdus	Turdus_ludoviciae	resident	Non-tropical	59710	May	June	July		4.80	0.003	NA	NA	
Turdus	Turdus_maculirostris	resident	Tropical	171415	January	February	March		5.40	0.271	NA	NA	
Turdus	Turdus_maranonicus	resident	Non-tropical	97899	January	February	March	Close relative (Turdus maculirostris)	5.39	0.077	NA	NA	
Turdus	Turdus_maximus	resident	Non-tropical	572862	May	June	July		6.69	0.240	NA	NA	
Turdus	Turdus_menachensis	resident	Non-tropical	116014	April	May	June		5.75	0.225	NA	NA	
Turdus	Turdus_merula	directional migratory	Non-tropical	17432667	April	June	July		7.33	0.356	0.318	0.277	
Turdus	Turdus_migratorius	directional migratory	Non-tropical	18466880	May	June	July		7.38	0.306	0.139	0.286	
Turdus	Turdus_mupinensis	resident	Non-tropical	1839448	May	June	July		6.79	0.018	NA	NA	
Turdus	Turdus_naumanni	directional migratory	Non-tropical	4290887	May	June	July		6.24	0.025	0.004	0.000	
Turdus	Turdus_nigrescens	resident	Non-tropical	48063	March	April	May		5.65	0.036	NA	NA	
Turdus	Turdus_nigriceps	directional migratory	Tropical	971453	November	December	January		6.22	0.283	0.137	0.167	
Turdus	Turdus_nudigenis	resident	Tropical	1674351	June	July	August		6.27	0.399	NA	NA	
Turdus	Turdus_obscurus	directional migratory	Tropical	9818323	May	June	July		6.54	0.331	0.516	0.000	
Turdus	Turdus_obsoletus	resident	Tropical	346795	April	May	June		5.56	0.624	NA	NA	
Turdus	Turdus_olivaceofuscus	resident	Non-tropical	839	October	November	December		NA	NA	NA	NA	Small range
Turdus	Turdus_olivaceus	resident	Tropical	496844	March	July	November		5.79	0.714	NA	NA	

Turdus	Turdus_olivater	resident	Non-tropical	472109	March	April	June		5.99	0.253	NA	NA	
Turdus	Turdus_pallidus	directional migratory	Non-tropical	4966446	May	June	July		6.54	0.197	0.135	0.001	
Turdus	Turdus_pelios	resident	Tropical	8947192	March	July	November		7.22	0.620	NA	NA	
Turdus	Turdus_philomelos	directional migratory	Non-tropical	18663870	May	June	July		6.74	0.299	0.109	0.052	
Turdus	Turdus_pilaris	directional migratory	Non-tropical	19541587	May	June	July		6.94	0.226	0.128	0.026	
Turdus	Turdus_plebejus	resident	Non-tropical	243944	March	April	May		6.32	0.208	NA	NA	
Turdus	Turdus_plumbeus	resident	Non-tropical	202446	April	May	June		5.41	0.170	NA	NA	
Turdus	Turdus_poliocephalus	resident	Tropical	1071887	April	May	June		6.02	0.743	NA	NA	
Turdus	Turdus_ravidus	resident	Non-tropical	211	-	-	-		NA	NA	NA	NA	Extinct
Turdus	Turdus_reevei	resident	Tropical	111462	January	February	March		5.64	0.195	NA	NA	
Turdus	Turdus_roehli	resident	Non-tropical	48296	July	August	September		4.58	0.050	NA	NA	
Turdus	Turdus_rubrocanus	directional migratory	Non-tropical	2025778	May	June	July		6.45	0.116	0.048	0.082	
Turdus	Turdus_ruficollis	directional migratory	Non-tropical	2841132	May	June	July		5.91	0.129	0.171	0.000	
Turdus	Turdus_rufitorques	resident	Non-tropical	161246	March	April	May	Close relative (Turdus plebejus)	6.01	0.068	NA	NA	
Turdus	Turdus_rufiventris	resident	Tropical	5128756	September	October	November		6.38	0.438	NA	NA	
Turdus	Turdus_rufopalliatus	resident	Non-tropical	491660	June	July	August		6.12	0.001	NA	NA	
Turdus	Turdus_sanchezorum	resident	Tropical	686252	December	January	February		5.62	0.393	NA	NA	
Turdus	Turdus_serranus	resident	Tropical	1108691	May	June	July		6.54	0.417	NA	NA	
Turdus	Turdus_simillimus	directional migratory	Non-tropical	1455883	April	July	September		7.17	0.181	0.222	0.190	
Turdus	Turdus_smithi	resident	Non-tropical	900040	September	October	November		5.69	0.521	NA	NA	
Turdus	Turdus_subalaris	directional migratory	Tropical	2477436	November	December	January		5.75	0.082	0.021	0.036	
Turdus	Turdus_swalesi	resident	Non-tropical	27259	May	June	July		4.79	0	NA	NA	
Turdus	Turdus_tephronotus	resident	Tropical	763404	March	April	May		5.78	0.526	NA	NA	
Turdus	Turdus_torquatus	directional migratory	Non-tropical	4927859	May	June	July		6.57	0.349	0.018	0.059	
Turdus	Turdus_unicolor	directional migratory	Non-tropical	1656266	May	June	July		6.59	0.406	0.015	0.187	
Turdus	Turdus_viscivorus	directional migratory	Non-tropical	16640278	April	May	June		6.96	0.447	0.331	0.274	
Turdus	Turdus_xanthorhynchus	resident	Non-tropical	177	October	November	December		NA	NA	NA	NA	Small range
Vireonidae	Vireo_altiloquus	directional migratory	Tropical	5214907	May	June	July		6.52	0.104	0.610	0.013	
Vireonidae	Vireo_approximans	resident	Non-tropical	28	April	May	June		NA	NA	NA	NA	Small range

Vireonidae	Vireo_atricapilla	directional migratory	Non-tropical	661500	May	June	July		6.19	0.003	0.004	0.000	
Vireonidae	Vireo_bairdi	resident	Non-tropical	856	May	June	July		NA	NA	NA	NA	Small range
Vireonidae	Vireo_bellii	directional migratory	Non-tropical	3444329	April	May	June		6.92	0.117	0.151	0.086	
Vireonidae	Vireo_brevipennis	resident	Non-tropical	272391	May	June	July		6.45	0.010	NA	NA	
Vireonidae	Vireo_caribaeus	resident	Non-tropical	28	April	May	June		NA	NA	NA	NA	Small range
Vireonidae	Vireo_carmioli	resident	Non-tropical	36508	March	April	May		5.99	0.106	NA	NA	
Vireonidae	Vireo_cassinii	directional migratory	Non-tropical	2893957	April	May	June		6.84	0.504	0.152	0.170	
Vireonidae	Vireo_crassirostris	resident	Non-tropical	34827	April	May	June		NA	NA	NA	NA	Small range
Vireonidae	Vireo_flavifrons	directional migratory	Non-tropical	5258014	May	June	July		6.38	0.136	0.241	0.019	
Vireonidae	Vireo_flavoviridis	directional migratory	Tropical	3761514	May	June	July		6.88	0.545	0.396	0.245	
Vireonidae	Vireo_gilvus	directional migratory	Non-tropical	10115569	May	June	July		7.22	0.254	0.068	0.124	
Vireonidae	Vireo_gracilirostris	resident	Tropical	19	May	June	July		NA	NA	NA	NA	Small range
Vireonidae	Vireo_griseus	directional migratory	Non-tropical	3702124	April	May	June		6.64	0.326	0.454	0.185	
Vireonidae	Vireo_gundlachii	resident	Non-tropical	110178	April	May	June		5.39	0.032	NA	NA	
Vireonidae	Vireo_huttoni	resident	Non-tropical	1795337	February	March	April		7.40	0.230	NA	NA	
Vireonidae	Vireo_hypochryseus	resident	Non-tropical	471956	June	July	August		6.47	0.000	NA	NA	
Vireonidae	Vireo_latimeri	resident	Non-tropical	7249	March	April	May		NA	NA	NA	NA	Small range
Vireonidae	Vireo_leucophrys	resident	Tropical	1174927	April	May	June		6.90	0.546	NA	NA	
Vireonidae	Vireo_magister	resident	Non-tropical	41000	May	June	July		6.03	0.056	NA	NA	
Vireonidae	Vireo_masteri	resident	Non-tropical	24559	July	August	September		5.07	0.001	NA	NA	
Vireonidae	Vireo_modestus	resident	Non-tropical	11021	April	May	June		NA	NA	NA	NA	Small range
Vireonidae	Vireo_nanus	resident	Non-tropical	52857	March	April	May		5.43	0.437	NA	NA	
Vireonidae	Vireo_nelsoni	resident	Non-tropical	306211	May	June	July		6.64	0.009	NA	NA	
Vireonidae	Vireo_olivaceus	directional migratory	Tropical	23896240	May	June	July		7.27	0.389	0.687	0.286	
Vireonidae	Vireo_osburni	resident	Non-tropical	11021	April	May	June		NA	NA	NA	NA	Small range
Vireonidae	Vireo_pallens	resident	Non-tropical	413040	April	May	June		6.76	0.305	NA	NA	
Vireonidae	Vireo_philadelphicus	directional migratory	Non-tropical	3933175	June	July	August		5.71	0.303	0.182	0.000	
Vireonidae	Vireo_plumbeus	directional migratory	Non-tropical	2647424	April	May	June		6.83	0.148	0.179	0.265	
Vireonidae	Vireo_solitarius	directional migratory	Non-tropical	6750142	April	May	June		6.76	0.390	0.423	0.145	

Vireonidae	Vireo_vicinior	directional migratory	Non-tropical	994336	April	May	June		6.34	0.075	0.064	0.219	
Vireonidae	Vireolanius_eximius	resident	Non-tropical	198008	May	June	July		6.41	0.345	NA	NA	
Vireonidae	Vireolanius_leucotis	resident	Tropical	4569658	May	June	July	Close relative (Vireolanius eximius)	7.09	0.583	NA	NA	
Vireonidae	Vireolanius_melitophrys	resident	Non-tropical	404002	May	June	July		6.41	0.020	NA	NA	
Vireonidae	Vireolanius_pulchellus	resident	Non-tropical	593882	March	April	May		6.62	0.228	NA	NA	
Xolmiini	Xolmis_cinereus	resident	Tropical	7118802	November	December	January		7.76	0.396	NA	NA	
Xolmiini	Xolmis_coronatus	directional migratory	Tropical	2401996	September	October	November		7.69	0.106	0.384	0.331	
Xolmiini	Xolmis_irupero	resident	Tropical	3670642	September	October	November		7.82	0.514	NA	NA	
Xolmiini	Xolmis_pyrope	directional migratory	Non-tropical	819837	October	November	December		7.82	0.122	0.120	0.074	
Xolmiini	Xolmis_rubetra	directional migratory	Non-tropical	1892750	October	December	February		7.93	0.071	0.100	0.029	
Xolmiini	Xolmis_salinarum	resident	Non-tropical	74157	September	October	November	Close relative (Xolmis irupero)	6.24	0	NA	NA	
Xolmiini	Xolmis_velatus	resident	Tropical	3690383	November	December	January	Close relative (Xolmis cinereus)	7.28	0.223	NA	NA	

Supplementary table 2. Results of phylogenetic generalized least squares (PGLS) analysis testing the effect of migration and breeding location on niche breadth and seasonal niche overlap, whilst considering range size and the phylogenetic effect on these traits. N= 415 species. Estimated lambda for the model = 0.083.

	F	p	df	Multiple R2	Adjusted R2
Migratory behaviour	75.60	<0.001	1	0.3766	0.3675
Breeding location	36.26	<0.001	1		
Range size (logged)	124.25	<0.001	1		
Migratory behaviour* Range size	2.98	0.08	1		
Breeding location * Range size	0.65	0.42	1		
Migratory behaviour*breeding location	6.76	0.010	1		

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APPENDIX III: Paleo-climatic change does not drive climatic niche evolution: evidence from a passerine bird clade

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Title: Climatic niche change in relation to paleo-climatic change in birds

Status:

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Author contributions:

(1) Development and planning:

AE 80%, SAF 10%, JTE, 10%

(2) Preparation and collection of data:

Phylogeny taken from the literature (100%)

Climatic niche quantification 100% **AE**

Rates of niche evolution 100% **AE**

Paleoclimate data JTE (70%), **AE** (30%)

(3) Preparation of figures/ tables:

AE prepared all figures and tables in the manuscript and supplementary materials

(4) Data analyses and interpretation of results:

AE performed all statistical analyses (90%) with input from SF (10%)

AE interpreted results (90%) with input from SF, JTE & KBG (in total 10%)

(5) Preparation of manuscript:

AE 90%, SAF, JTE & KBG (in total 10%)

Title: Paleo-climatic change does not drive climatic niche evolution: evidence from a passerine bird clade

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Key words: Macroevolution, paleobiology, trait evolution, climate change, precipitation, temperature

Abstract:

The climatic niche describes the climatic conditions in which a species can persist in both space and time. Therefore, investigating how the climatic niche evolves is vital to understanding how climate shapes biological processes. If species adapt their niche to cope with new climatic conditions, a relationship would be expected between changing climatic conditions and rates of niche change. Previous studies have observed that shifts in climatic niches appear to coincide with time periods characterised by major changes in climatic conditions. Here, we explicitly test whether there is a relationship between rates of climatic niche evolution and paleo-climatic conditions through time, using a monophyletic clade of 71 species from the Old-World flycatchers (*Muscicapidae*). We combine climatic niche quantification and dated phylogenies for to infer past rates of niche evolution, and utilize the mammal fossil record to infer terrestrial climatic conditions. Despite finding changes in the climatic niche, we find no relationship of rates of climatic niche evolution with either absolute paleo-climatic conditions or rates of paleo-climatic change. Our results indicate that at the taxonomic and geographic scale studied, climate is not a driver of climatic niche evolution, indicating that birds cope with changing climatic conditions through distributional or behavioural changes.

Introduction

The climatic niche describes the climatic conditions in which a species can maintain a viable population. It strongly influences where a species can persist in both space and time (Hutchinson 1957; Pearman et al. 2008). As such, examining how the climatic niche can change through time is vital to our understanding of speciation and extinction, and how climate shapes both past and future species' diversity patterns (Moreno-Letelier et al. 2014; Hawkins et al. 2017; Castro-Insua et al. 2018). As species evolve to adapt to novel climatic conditions, their climatic niche changes. It is especially important to know about the potential speed of niche change (i.e. the rate), which can help predict how rapidly species' are able to adapt their climatic niche in response to new conditions (Quintero and Wiens 2013a). Predictions of this sort could overcome a limitation of projecting current species distributions in response to future climate change: the majority of such projections assume that the climatic niche is conserved, ignoring the possibility of niche change and potentially overestimating the impacts of climate change (Pearman et al. 2008).

If species adapt their climatic niche in response to changes in climate, a relationship between the rates of climatic niche change and climate is expected. However, such a relationship might not be expected if organisms cope with climatic changes through behavioural adaptations such as moving to avoid unfavourable conditions. Further, no relationship would be expected if climatic niche changes are instead driven by other factors, for example biotic interactions (e.g. avoiding competition; Pitteloud et al. 2017), or key innovations allowing occupation of new climatic conditions (Arakaki et al. 2011). Although many studies have hypothesised that rates of climatic niche change are driven by climatic variations in temperature and precipitation, a lack of spatially resolved information on terrestrial environmental conditions from the deep past has largely precluded explicitly testing for a relationship (e.g. Duran and Pie 2015, Nürk et al. 2015). In this study, we used terrestrial climate estimates inferred from the fossil mammal record (Liu et al. 2012) to test for a relationship between climatic conditions and phylogenetically reconstructed rates of niche change through the middle and late Miocene and Pliocene (approx. 17.2 until 2 million years ago). As a focal case, we used a monophyletic clade of closely related genera of Old-World flycatchers (*Muscicapidae,* subfamily *Saxicolinae*) containing the wheatears, rock thrushes, chats and stonechats, hereafter the wheatear-chat clade.

There is a wide variety of indirect support for a relationship between environmental climatic conditions and change in species' climatic niches throughout earth's history. For example, the observation that species have broader climatic tolerances when living in more variable climatic conditions suggests that the breadth of species' climatic niches is driven by climatic conditions (Janzen 1967; Quintero and Wiens 2013b; Khaliq et al. 2014). This relationship has been shown both for experimentally derived physiological tolerance levels and for species' tolerances inferred from current geographic distribution patterns, both of which are assumed to be an (albeit imperfect) approximation of a species' fundamental climatic niche. Observed shifts in climatic niches of invasive species outside of their native range suggests that climatic niches can rapidly change (Broennimann et al. 2007). Finally, studies which have inferred niche change using molecular phylogenies have suggested that rapid shifts in niches coincide with periods of pronounced climatic change (Duran and Pie 2015; Nürk et al. 2015). However, in direct contrast, other studies have found no evidence for a relationship between climatic conditions and niche changes across millions of years (e.g. Schnitzler et al. 2012). As such, it remains unclear whether changes in climatic niches are driven by climate and climate change at deep phylogenetic time scales. Although there is some evidence of inferred shifts of climatic niches in single phylogenetic branches that coincide in time with periods of climate change (Evans et al. 2009; Duran and Pie 2015) to our best knowledge, no previous study has explicitly tested whether there is a general relationship through time between changes in paleo-climatic conditions and rates of change in climatic niches inferred across multiple lineages in a clade.

Different aspects of climate might be expected to affect rates of climatic niche change (see Garcia et al. 2014). For example, changes in niches could be driven by absolute climatic conditions (i.e. the actual climate values at a particular point in time). As mutation rates increase with temperature, a positive relationship would be expected between temperature and rates of climatic niche change if genetic change is correlated with phenotypic change (Oppold et al. 2016, Foucault et al. 2018). However, examination of this relationship across taxonomic levels in both plants and animals has failed to confirm this expectation (Davies and Savolainen 2006). For example, contrary to theoretical expectations based on mutation rates, Clavel and Morlon (2017) found that the evolution of body mass across virtually all birds and mammals was faster during periods of cold temperature. This suggests that the rate of trait evolution that emerges at such large phylogenetic scales (many millions of years) might be driven by underlying selection pressure rather than through the direct effect of climate on mutation rates. The upper physiological limits of climatic niches are not correlated with ambient temperatures across many extant species, but the lower limits are, suggesting that lower temperatures exert a greater selective pressure across species (Araújo et al. 2013; Khaliq et al. 2017). Further, higher recent rates of phenotypic evolution in temperate regions than in the tropics (Lawson and Weir 2014) additionally suggest that cold and dry conditions pose a stronger selection pressure than warm and moist conditions. Consequently, we could expect to find a negative relationship between rates of niche change and both temperature and precipitation.

An additional expectation would be a positive relationship of rates of climatic niche change with the rates of climate change through time. Faster climatic changes, in terms of both precipitation and temperature, are expected to impose a stronger selection pressure on climatic niches, leading to higher rates of niche change (Benton 2009; Duran and Pie 2015). However, this might only be the case up to a point. If climatic conditions change very rapidly, as is currently the case, species might not be able to adapt fast enough (Quintero and Wiens 2013a). The study of the impacts of climate change crucially depends on understanding niche changes (i.e. how plastic a species is in terms of its' tolerance of climatic conditions, and how fast evolutionary adaptation can take place) (Pearman et al. 2008).

A lack of appropriate paleo-climatic data has hindered testing for relationships with niche change. At present, studies that have related trait evolution to climatic conditions in the past have had to rely on global temperature curves derived from the marine record (Zachos et al. 2008), which are unlikely to represent regional or local terrestrial climatic conditions adequately (Clavel and Morlon 2017). Additionally, they have been limited by focussing on temperature even though precipitation is an important aspect of a species' climatic niche and precipitation conditions are expected to change significantly in the future (IPCC 2014; La Sorte et al. 2019). Here we estimated climatic conditions (mean annual temperature and precipitation) from fossil occurences of large mammalian herbivores based on a functional relationship between tooth structure and environment to infer terrestrial, regional conditions through time (Liu et al. 2012). The distribution of dental functional traits in ungulates that occur in a location reflects the type of plant foods available, which in turn reflects the ambient climate (Liu et al. 2012, see also Fortelius et al. 2014).

We predicted and tested for relationships between estimated rates of climatic niche change with i) absolute paleo-climatic conditions and ii) rates of paleo-climatic change, by comparing niche changes in both temperature and precipitation with the corresponding environmental conditions. Previous studies suggest that the rates of niche change is driven by selection pressure rather than through the effect of climate on mutation rates, and that lower extremes (cold, dry environments) exert particularly strong pressure (see above). Therefore, firstly, we hypothesised that estimated rates of niche change are negatively related to absolute temperature and precipitation, i.e. we expected to find faster rates of niche change occurring in cold dry conditions. Secondly we hypothesised that estimated rates of niche change are positively associated with the rate of experienced climate change for both temperature and precipitation. We tested these hypotheses using the wheatear-chat clade, a monophyletic clade with a broad latitudinal distribution, as a focal group. This group is a suitable clade to test these hypotheses for several reasons. Species in this group are widely distributed across Asia, Africa and Europe, occupying a variety of different climatic conditions and habitats. As well as being an interesting group ecologically, it is an appropriate choice for practical reasons. Its geographic and temporal distribution matches the areas and time period for which paleo-climatic data from the mammalian fossil record were available.

Methods:

Rates of climatic niche evolution

We investigated climatic niche evolution in a monophyletic clade comprising 71 species (following IOC taxonomy v 3.01; Gill and Donsker 2012), see supplementary materials, Table S2 for a full list of species) of Old-World flycatchers (the wheatear-chat clade). Phylogenetic relationships within the group were obtained from (Phillips et al. 2018). This study obtained and vetted sequence data for three genes (one nuclear and two mitochondrial) from GenBank (www.ncbi.nlm.nik.gov/ genbank) for 65 species, and estimated the phylogeny using Beast version 2.4.4 (Bayesian Evolutionary Analysis Sampling Trees, Bouckaert et al. (2014). Sequence data were missing or insufficient for six species. They ran four independent runs, each for 50 million generations, and combined the results post burn-in. A maximum clade credibility (MCC) tree was calculated using Tree Annotator (also in Beast version 2). Absolute dates were derived based on a *Luscinia* fossil (Jenõ and János 2012). All subsequent analyses were carried out on the resulting dated MCC tree. Although it is possible that this tree is not the true representation of all relationships within the group, the majority of branches were strongly supported in the Bayesian analysis, and relationships and dates were mostly consistent with previous phylogenetic studies (supplementary figure 1; also see discussion (Phillips et al. 2018).

Rates of climatic niche change were reconstructed from the inferred climatic niches of extant species combined with their phylogeny. Ideally, the fundamental climatic niche would be determined from physiological tolerance data (Pearman et al. 2008), but despite birds being a well-studied group of organisms, physiological data are not available for the vast majority of species, including the majority of the wheatear-chat clade (Khaliq et al. 2014). Therefore, realized climatic niches were quantified using climatic conditions within the geographical range maps of species distribution. For the studied clade, we could not use available point occurrence data as these have not been sampled comprehensively across all species and within most species' geographic ranges (Meyer et al. 2015). Despite limitations, at such broad scales, extent-of-occurrence range maps are considered to capture a reasonable approximation of a species' fundamental niche (Kearney et al. 2010; Wisz et al. 2013). Due to a lack of good data for bird distributions outside of the breeding range, many previous studies have quantified climatic niches using the breeding range only. Using this approach may mean that the climatic niches of migratory species are misrepresented and not comparable with those of resident species (Eyres et al. 2017). As 22 out of the 65 species included in our analyses are classified as migratory following Eyres et al. (2017), we make use of a new database of non-breeding ranges of migratory bird species to ensure that our niche quantifications take into account conditions experienced by species in both their breeding and non-breeding range. Geographic distributions for the breeding season were obtained from the *Copenhagen global avian distributional database* (Holt et al. 2013). This is an extensive database mapping a conservative extent-of-occurrence during the breeding season at a 1° latitudinal-longitudinal resolution for each species based on museum specimens and published sightings validated by ornithological experts. Non-breeding distributions of migratory species were obtained as extent-of-occurrence polygons from the *GeoMiB database (Geographic distributions of migratory birds* v. 1.1 compiled by us, see Phillips et al. (2018) for more details) and sampled to the same resolution as the breeding ranges. Species occurrences were therefore seasonal presences in 1° latitude-longitude grid squares where species were recorded in the Copenhagen database (breeding and year-round, with the difference among the two determined from the GeoMiB range maps) or where >5% of the grid square was covered by species' range maps from the GeoMiB database (non-breeding). The combination of these two datasets ensured high consistency of maps across the focal species and the highest possible quality for geographic extent-of-occurrence range maps in both seasons of the year.

In order for niche quantification to represent the climatic conditions of a migratory species, we used the climate data for the season when each species is present in a particular part of their range (i.e. when a species is in its breeding range and when is in the non-breeding range). As breeding time is species-specific, we determined the peak breeding months for each species individually using information from the literature (the Handbook of the Birds of the World (HBW) Alive website < www.hbw.com > (del Hoyo et al., 2019) , accessed until January 2019), see supplementary materials for full list. The three non-breeding months for each species were defined as six months later than the breeding season, which is somewhat arbitrary, but was chosen to be globally consistent across all species (Laube et al. 2015). As the geographic distribution of migratory species is poorly known outside of the breeding and non-breeding season, our annual niche quantification for all species reflects the conditions experienced across these six months rather than the full year. This approach should capture the range of conditions that the species experience throughout the year. To ensure comparability across species, climatic niches were calculated in the same way for residents and migrants.

Monthly climatic data was obtained from the WorldClim *raw climate data* dataset (averages from 1970-2000, resolution 10 minute; Fick and Hijmans 2017). The following four climatic variables for each month were obtained: minimum, maximum and average daily temperatures within each month and total monthly precipitation, hereafter referred to as Tmin, Tmax, Tmean and Precipitation, respectively. We chose to investigate the rates of change of these four aspects of climatic niches as they are most likely to be related to the climatic variables that we were able to infer from the fossil record (temperature and precipitation). Climate data were averaged across the same grid cells as the occurrence data. As a measure of average climatic conditions that species are exposed to, highest density values from the entire distribution of grid square values that species experience across their entire range throughout the six months (breeding and non-breeding) were determined from density plots using the *hdr* function from the R package *hdrcde* (Hyndman et al. 2013) for each of the four climatic variables. These highest-density values were used rather than the mean because climatic conditions tolerated by species are often not normally distributed (Evans et al. 2009), and the values were subsequently assumed to be representative of the central niche position for each species.

We calculated rates of climatic niche change for each of the four climatic variables for two time bin schemes (which match the time bins of the paleo-climate data, see below for further details) as follows; 1) within time bins to match the absolute paleoclimate values and 2) between the midpoints of subsequent time bins to match the rates of paleo-climatic change. We assume that the fundamental climatic niche is captured by our niche position quantification from geographic range maps, and therefore follow previous studies in considering the evolutionary rates of change in these inferred climatic niches as a meaningful approximation of climatic niche evolution (Schnitzler et al. 2012; Title and Burns 2015; Cooney et al. 2016), although we realize that these assumptions might be contentious and that any observed climatic niche is not necessarily an evolving species trait (Dormann et al. 2010; Soberón and Peterson 2011). Rates of niche change were estimated using the variable rates model in the software BayesTraits, version 2 (Venditti et al. 2011; available from http://www.evolution.rdg.ac.uk/) a method which is limited to a single phylogenetic tree. The model was run using default priors and two independent MCMC chains for 1 billion iterations each. For each climatic variable we carried out two independent runs and combined the post-burn-in results for the final analysis. From each chain we retained every 100,000th tree post burn-in (10,000 samples). All subsequent analyses were carried out on the pooled 20,000 posterior trees from both chains to account for uncertainty in the inferences of rates of change across the phylogeny.

To calculate how the rates of niche change varied across time, we followed Cooney et al. (2016) and summarised the results of the combined runs by calculating the mean evolutionary rate across all of the posterior trees in each time bin. For each time bin, we calculated the weighted mean rate of evolution across all branches present in the time bin in question. The branches were weighted by the proportion of the time bin that they covered (so a branch which is present for the whole time bin has more weight than one which is only present for part of the time bin). This was carried out for each posterior tree and then averaged across trees. In addition, to test for significant shifts on particular branches or clades, we calculated the probability of a rate shift across all posterior trees for each node in the tree.

Fossil Mammal data and Paleo-climatic conditions

We estimated paleo-climatic conditions (temperature and precipitation) from the mammal fossil record for the Neogene (i.e. Miocene and Pliocene, ~ 23- 2 million years ago (Mya)). Because the glacial-interglacial oscillations in the Pleistocene were not well resolved in the continental mammal records we used, we did not include the last ~2 million years (i.e. Pleistocene) in our analyses.

We extracted geo-referenced and dated fossil records for herbivorous large mammals (Orders: Artiodactyla, Perissodactyla, Primates, Proboscidea) from the NOW database (NOW, the New and Old Worlds Database of Fossil Mammals, www.helsinki.fi/science/now/) for the continents in which the study clade is distributed (Europe, Asia and Africa). Mean annual precipitation (MAP) and temperature (MAT) were estimated from the composition of the herbivore communities present at each unique combination of spatial location and age-estimate (hereafter referred to as locality) following Liu et al. (2012). This is a linear regression method which estimates MAT and MAP for each locality based on the dental traits of the herbivore assemblage. Negative precipitation values were corrected to zero. In total, MAT and MAP were estimated for 1735 unique fossil localities. To incorporate a measure of uncertainty in each of these point values, we calculated the minimum and maximum possible value using the error term in the regression analyses used to derive climatic estimates (Liu et al. 2012).

We used the MN (Mammal Neogene) temporal units as provided in the NOW database. To estimate assignment uncertainty of these biozones, we used two different methods. Our first approach (hereafter “strict” assignment) was to assign records to MN zones based on the absolute minimum and maximum age estimate given in the source data. If both the minimum and maximum time estimate lay within an MN zone it was assigned to that zone. 1157 fossil localities were assigned using this approach. For the second approach (hereafter, mid-point assignment), the mean age of each record was calculated from the minimum and maximum age estimates. A locality was assigned to the MN zone if the mean age fell into that MN zone, regardless of whether the whole time span was unambiguously within one MN zone or not (all 1735 records were assigned in this approach). We carried out all analyses separately for these two different methods. MN 1 and 2 had very few fossil localities; we therefore combined them into an MN 1-2 time bin for all following analyses.

Directly averaging paleo-climate records across the entire geographic region for each time bin would not take into account the spatial variation in sampling or the uncertainty in climate inferences. Therefore, we gridded the entire region using a 1-degree grid and summarised the records that fell into each grid square. Average MAP and MAT and a measure of uncertainty for each grid square by time bin combination were subsequently derived following Fritz et al. (2016). First a frequency distribution of climatic values was produced for each unique combination by binning the climatic range between the minimum and maximum estimates climate values in the grid square and time bin (MAT and MAP) into bins of 0.01°C or 1mm/year respectively. The average climatic value assigned to a grid square was the highest density point of this frequency distribution. As a measure of uncertainty within a grid square we also extracted the upper and lower limits of the credibility interval containing 50% of the binned values. For the two datasets, i.e. strict and mid-point stratigraphic stage allocation, between 404 and 589 grid square-by-time bin combinations for the two stratigraphic stage allocations contained only one record for either temperature or precipitation. In these cases, the mean value was calculated as the average of the min and max and the limits of the 50% interval were approximated as the mean ± 1 standard deviation. The standard deviation was calculated as the total range (maximum – minimum) divided by 4 (Fritz et al. 2016).

The number of grid squares containing fossil localities varied within each continent (i.e. Africa, Europe, and Asia) and among time bins. To ensure that estimated climatic conditions through time were not unduly influenced, we first calculated climatic averages for each continent, and then averaged these to get an estimate for the entire study region. The average climate value for each continent in each time bin was calculated as the weighted mean of all the grid squares in a continent. The value from each grid square was weighted by its uncertainty estimate (the inverse of the size of the 50% credibility interval) in order to account for heterogeneity of uncertainty of climatic estimates in each grid square; continental averages were obtained from the terrestrial values in each time bin for which a climate value was available for more than one grid square.

Rates of paleo-climatic change were calculated as the absolute difference in climatic conditions between successive time bins, divided by time, i.e. the difference between the mid points of successive time bins. Rates were first calculated for each continent separately and rates for the whole region were subsequently calculated as the average of those values based on more than one grid square.

Using these methods, overall, paleo-climatic conditions for the past ~22 million years were estimated from 1735 and 1157 fossil localities using the mid-point and strict assignment methods, respectively. Overall the point-records were distributed across 469 grid cells. When assigned to MN zones using the two methods (strict and mid-point assignment) they occupied 538 and 872 unique grid square by time bin combinations, respectively. The smallest number of grid squares containing fossil data for a time bin was 36 and 44 (for the strict fossil assignment and mid-point assignment, respectively), whilst the greatest number of grid cells containing fossil data for a time bin was 118 and 194 (for strict and mid-point assignment, respectively). Although there were differences between climatic conditions estimated from the two time bin schemes they did not result in fundamentally different results of subsequent analyses. As such we present results from the mid-point assignment in the main text and the results from the strict fossil assignment in the supplement.

Statistical analyses

We tested for (i) a relationship through time between paleoclimate averages and mean rates change of climatic niches in each time bin, and for (ii) a relationship between rates of paleo-climatic change with mean rates of change in climatic niches among subsequent time bins. For both relationships we tested for two aspects of climate (mean annual temperature and precipitation, separately) and for four aspects of climatic niches (precipitation niche and the three temperature variables). We first tested for temporal auto-correlation using the auto-correlation function ACF in R and found a significant correlation for time lag one for all analyses. To test our hypotheses, we therefore used generalized least squares (GLS) models which accounted for the temporal structure through first order autoregressive models, taking correlation among subsequent time bins into account.

Results:

Rates of climatic niche evolution

The phylogeny (Phillips et al. 2018) was relatively well resolved with only seven nodes in which the posterior support lay below 0.9 (Supplementary Figure S1). Using this phylogeny, it was possible to map potential changes in temperature and precipitation niches across the tree (Fig 1A & B and Supplementary Figure S2). There was little difference between the results for the three aspects of temperature niche (Tmin, Tmean and Tmax). Hence, we present the results from Tmin in the main text and the rest in the supplement. No significant branch or clade shifts in inferred rates of climatic niche change were detected for the temperature niche using any of the three temperature variables (Fig 1A for Tmin & Fig S2 A & B for Tmax and Tmean). The inferred rates of temperature niche change did not vary significantly between any of the branches or clades. The average rates of temperature niche change across the whole tree showed a slight overall positive trend through time (Fig 1C & Supplementary Figure S2 C & D) indicating that temperature niche evolution became faster closer to the present.

In contrast to temperature, we identified four significant shifts in inferred rates of change in precipitation niche within the phylogeny (Fig. 1B). Significant shifts were found in the branch leading to the *Oenanthe- Myrmecocichla* split, within *Oenanthe*, within *Myrmecocichla* and finally within the branch leading to *Saxicola*. All four of these shifts were to faster rates of niche evolution (Fig 1B). Average rates of precipitation niche change across the whole tree through time show a slight overall positive trend with rates increasing through time (Fig 1D). There was also a slight peak in the rate of change for precipitation niche around 12 Mya (Fig 1D). Overall, estimated rates of change in precipitation niche were more variable than those of the temperature niche.

Paleo-climatic conditions

Mean annual temperature was variable through time, with temperature ranging from a low of ~14°C to a high of + 22°C (Fig. 2A). We observed stronger temporal patterns in the precipitation record than in temperature record with precipitation values varying more than two fold between lows of ~700mm and highs of ~1700mm (Fig 2A). Rates of paleo-climatic change for both temperature and precipitation were found to be very variable (Fig 2B). The rates of both temperature and precipitation change were found to peak between MN 5 and MN 6. Results for paleo-climate using the strict assignment of MN zones were highly similar (Figure S3).

Relationship between paleo-climate and rates of niche evolution

We found no significant relationship between absolute paleo-climatic conditions and rates of evolution of the climatic niche for any of the temperature and precipitation variables (Fig 3A & B, Table 1). Although not significant, the relationship between precipitation and rates of change in precipitation niche showed the expected direction (negative estimated coefficient, Table 1). This was also the case for the relationship between temperature and the rates of change in one of the temperature niche measures (Tmean; Table 1). However, for Tmin and Tmax, contrary to expectations positive (non-significant) relationships were found (Table 1).

We also found no significant relationship between rates of paleo-climatic change and rates of evolution of the climatic niche for both temperature and precipitation (Fig 3C & D, Table 1). Although not significant, the relationship of rates of niche change with rates of paleo-climatic change showed the expected direction (positive coefficient estimate) for precipitation, Tmin, and Tmean, but not for Tmax (Table 1). These results were robust across three measures of temperature niche and one measure of precipitation niche using two methods of time-bin assignment (see Table S2 in supplement).

Discussion:

Using methods from paleobiology, we reconstructed terrestrial precipitation and temperature through time in order to test whether there is a relationship between ambient climate and inferred rates of niche change in a clade through time. Our paleo-climatic inferences match well-known trends that characterize the late Neogene (see e.g. Fortelius et al. 2014). For the study clade, estimated mean rates of niche change for both precipitation and temperature niche increased over time, indicating that niches changed faster closer to the present and were therefore not conserved. In addition, we found four significant shifts in precipitation niche across the wheatear-chat phylogeny. Contrary to theoretical expectations - that surviving species would have adapted to changing climatic conditions through time - we find no relationship between the inferred rates of climatic niche change and either absolute climate values or rates of climate change. This suggests that climatic niche evolution may not be directly driven by either ambient climate or changes in climatic conditions.

Despite the changes in climatic niche observed for our focal clade, the old-world flycatchers do not appear to have changed their niche in order to adapt to the changes in climatic conditions (both temperature and precipitation) for the period of interest. These results suggest that the species may instead have altered their geographic distributions or behaviour in order to cope with environmental change (Virkkala and Lehikoinen 2017; Nogués-Bravo et al. 2018). Considering the high mobility of birds, it is highly likely that instead of adapting their niches they buffer climatic change through adaptive behaviour such as large-scale movements or small-scale habitat and micro-habitat choices (Keppel et al. 2017). This is particularly relevant to this study clade, as a disproportionate number of species (>30%) are migratory, and therefore highly mobile. Indeed, range shifts and expansions have already been observed in birds in response to current and ongoing climate change (Gillings et al. 2015; Massimino et al. 2015) and in mammals in response to past changes (Eronen and Rook 2004). For mobile organisms, such as birds, other factors such as habitat, resources and competition may be more important for niche dynamics (Jønsson et al. 2012; Pitteloud et al. 2017). This supports previous work of Khaliq et al. (2014) who showed that the thermal tolerance limits of many bird species do not match ambient climatic conditions, indicating that environmental climatic conditions do not strictly limit species' distributions. Our results are furthermore consistent with previous studies which show that habitat and resources are often more important than climate for determining bird occurrence (Laube et al. 2015; Somveille et al. 2015; Teitelbaum et al. 2016) and studies which show that at narrow phylogenetic extents (such as ours) biotic interactions such as competition are more important than climatic factors at for determining bird occurrences (Barraclough and Vogler 2017; Graham et al. 2018).

Our results appear in contrast with those of other studies pointing towards associations between climate change and rate of climate niche changes. This might reflect a taxonomic bias in the literature. The majority of previous studies examining niche dynamics have focussed on terrestrial non-volant organisms, e.g. 38 out of the nearly 40 empirical studies reviewed by Pearman et al. (2008). However, the response of birds to changing climatic conditions might be systematically different due to their high mobility, and could be expected to be more similar to marine organisms because movement in the marine realm is also much less restricted than in terrestrial environments. Consistent with our results for birds, the few studies that have examined niche dynamics in marine taxa have found that niches are relatively stable even when faced with significant environmental change (e.g. Stigall 2012, Saupe et al. 2014).

However, solely based on our results we cannot dismiss other aspects of climate, such as changes in seasonality or the emergence of novel climates, as unimportant to birds. Instead of average conditions, rates of niche change might be rather affected by extreme events (Greenville et al. 2012; Grant et al. 2017). For example, although we do not find a relationship between precipitation conditions and rates of inferred niche change through time, we do observe a sudden drop in precipitation around 12Mya (which is also seen as an increase in rate of precipitation change), which appears to coincide with a peak in the rates of precipitation niche change. Hence, some of the niche changes may be driven by climate change, but our results imply that this is not consistent over time. Further, we examined whether there is a relationship between rates of niche change and average climatic conditions across a very broad geographic range. If highly heterogeneous local climatic conditions are driving rates of niche change we might fail to find a relationship at this scale. Finally, we tested for a relationship between climate and mean clade-wide rates of niche change. If some lineages respond to climate and others do not, or if lineages respond in opposing ways, we would not detect this by looking at average rates.

As well as these mechanistic explanations, there are methodological reasons why we might not find a relationship between climatic conditions and niche evolution. Although we have a very reasonable set of paleo-climatic data for a paleo-study, it is still relatively small (in terms of number of climatic estimates for each time bin and continent). As a consequence we can only infer climatic conditions at a coarse temporal resolution, which subsequently severely limits our statistical power. It is also worth noting that a major caveat of studies reconstructing rates of climatic niche evolution is that the results are highly dependent on the method used to characterize climatic niches (Budic and Dormann 2015). Finally, it is assumed that the spatial distribution of species is able to represent the full range of climatic conditions that a species is able to survive under (i.e. its fundamental niche). However, it is likely that other factors such as competition and dispersal limitations also shape species' distributions (Soberón 2007), meaning that we likely underestimated the fundamental climatic niche possibly decreasing the chance of finding a relationship.

Conclusions

Here, we have gone beyond previous studies by using terrestrial paleo-climatic data that are relevant to the study organism, and by explicitly testing whether there is a relationship between paleo-climatic conditions and clade-wide rates of climate niche evolution through time. At this taxonomic and geographic scale, paleo-climatic conditions do not appear to drive climatic niche evolution. We suggest that birds, as highly mobile organisms, find it easier to buffer changes in climatic conditions through behavioural adaptions than through genetic adaptations to the novel environment. These results suggest that highly mobile species have a different strategy for coping with changing climatic conditions than those with limited movement ability. Further investigation into the relationship between mobility and rates of niche change across realms, e.g. in highly mobile marine organisms, would be of value to confirm or reject this implication.

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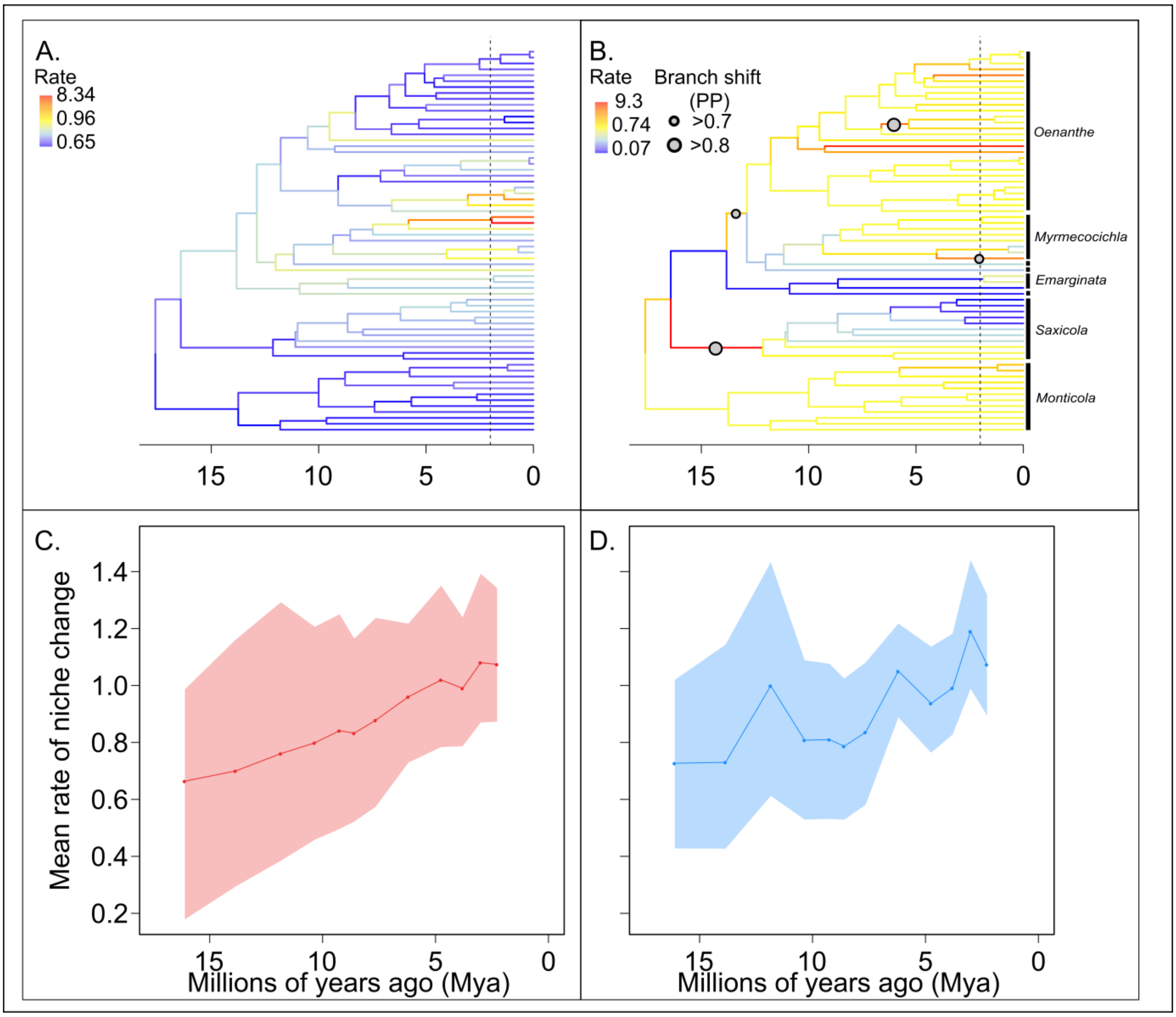

Figure 1. The consensus phylogeny for Wheatears and Chats (n= 65 species) coloured by estimates of the mean rates of trait evolution for climatic niche aspects (A-B) and mean rate of evolution through time calculated from 20,000 samples from a BayesTraits analysis (C-D) for minimum temperature (A & C) and precipitation (B & D). Rate values were logged for visualisation. Grey circles show rate shifts inferred on individual internal branches, with the relative size of each circle indicating the posterior probability (PP) of a rate shift. Mean rate of climatic niche evolution (C &D) with 95% confidence intervals (shaded region) were calculated for each time period as the weighted average of all branches which are present in a time period.

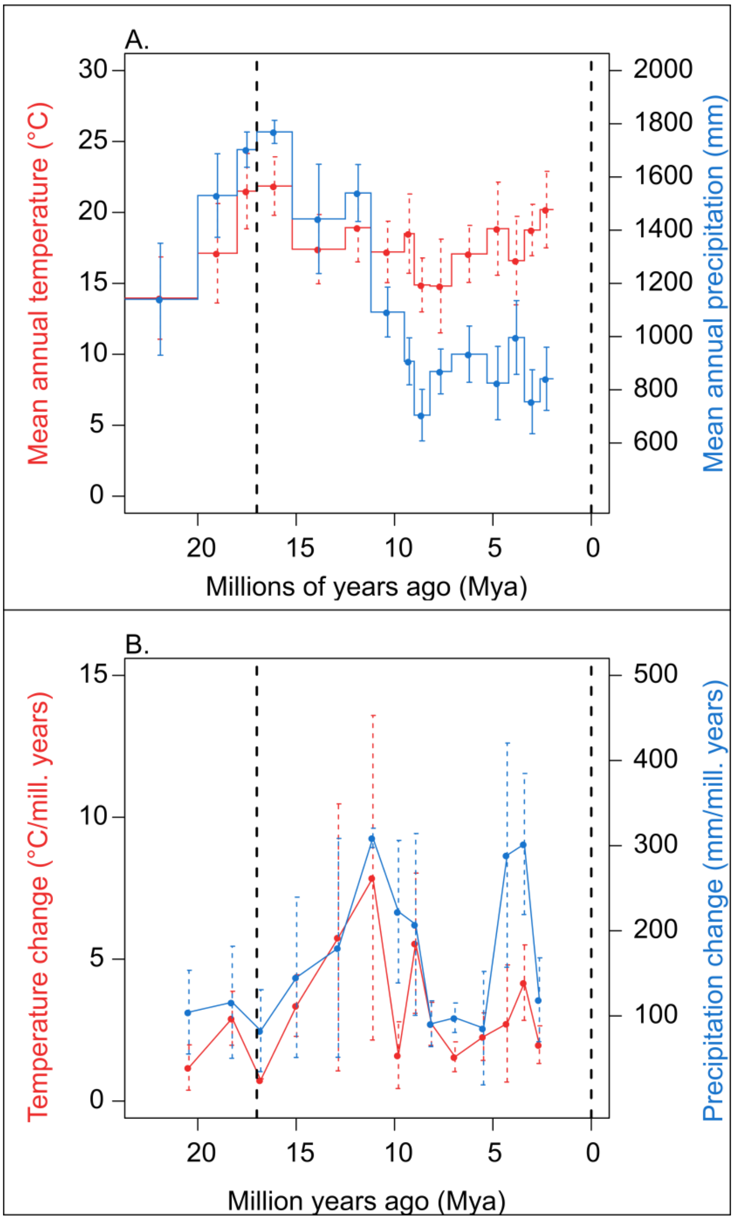

Figure 2. Absolute paleo-climatic values (A) and inferred rates of paleo-climatic change through time (B) for mean annual temperature (red) and precipitation (blue) inferred from the full mammalian fossil record (mid-point assignment) in the Neogene (time bins based on Mammal Neogene (MN) zones). Rates of climatic change were calculated between successive time bins. Both absolute climate and rates of climate change were representative of climatic conditions for the whole region (Asia, Africa and Europe). Dashed black lines denote the temporal extent of evolution in study clade. Error bars for absolute climate variables (A) were calculated as the mean of the standard errors for each region. As a measure of regional variability in rates values (B) we calculated the standard error of the rates between regions.

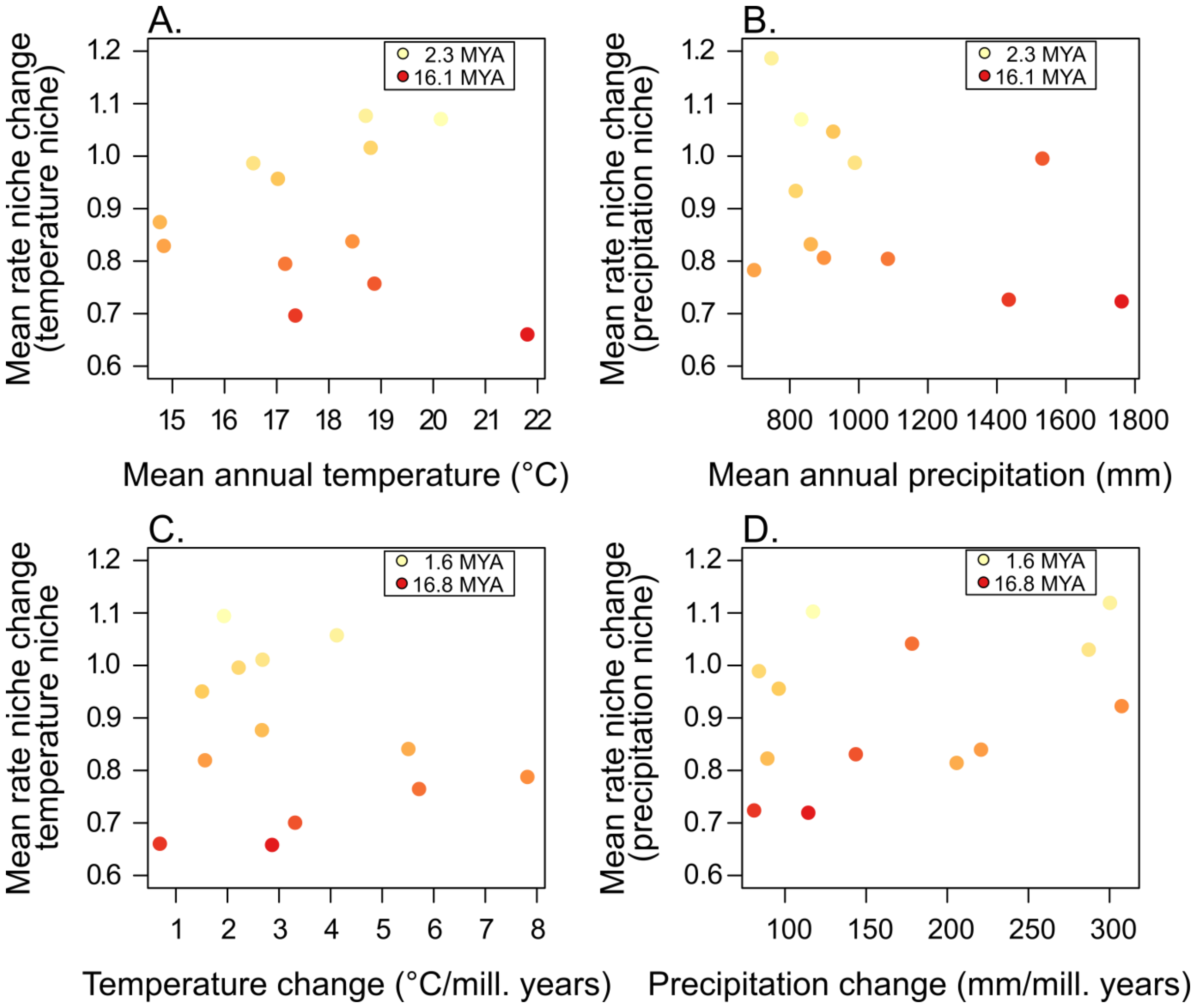

Figure 3. Relationship between paleo-climatic conditions and rates of niche evolution for absolute paleo-climate values (A-B) and rates of paleo-climate change (C-D), calculated for two aspects of climate and climatic niche; temperature (A ,C) and precipitation (B,D) respectively. To highlight the temporal structure of the data points are coloured by the midpoint age of MN zones. Paleo-climatic conditions were calculated using the full fossil data set (mid-point assignment method).

Table 1. Results from the final GLS models testing for a relationship between rates of climatic niche evolution with a) absolute paleo-climatic conditions and b) rates of paleo-climatic conditions. Response variables were rates of climatic niche evolution (either temperature variables or precipitation) inferred based on phylogeny for the wheatear-chat clade. In the first two models absolute paleo-climatic values (MAT and MAP, respectively) were included as fixed effects. In the second two models the rates of paleo-climatic change in MAT and MAP were used as respective fixed effects. Paleo-climatic conditions were calculated using the full fossil data set (mid-point assignment method). Temporal autocorrelation in the data structure was accounted for in the GLS model.

	Coefficient	**Pseudo R2**	**AIC**	**F**	**P**	**Autocorrelation parameter (Phi1)**
(a) Absolute paleo-climate values						
Tmin	0.00235	0.0027	-24.0	0.070	0.797	0.833
Tmean	-0.000281	0.00026	-27.3	0.00136	0.971	0.847
Tmax	0.000334	0.00383	-28.9	0.00228	0.963	0.861
Precipitation	-0.0001	0.176	-10.0	0.997	0.342	0.305
(b) Rates of paleo-climatic change						
Tmin	0.000458	0.0187	-31.0	0.00975	0.923	0.892
Tmean	0.00054	0.0317	-37.0	0.0273	0.872	0.926
Tmax	-0.000952	0.0331	-32.9	0.410	0.535	0.918
Precipitation	0.000379	0.147	-15.3	1.04	0.329	0.622

Supplementary material for Eyres et al. Paleo-climatic change does not drive climatic niche evolution: evidence from a passerine bird clade

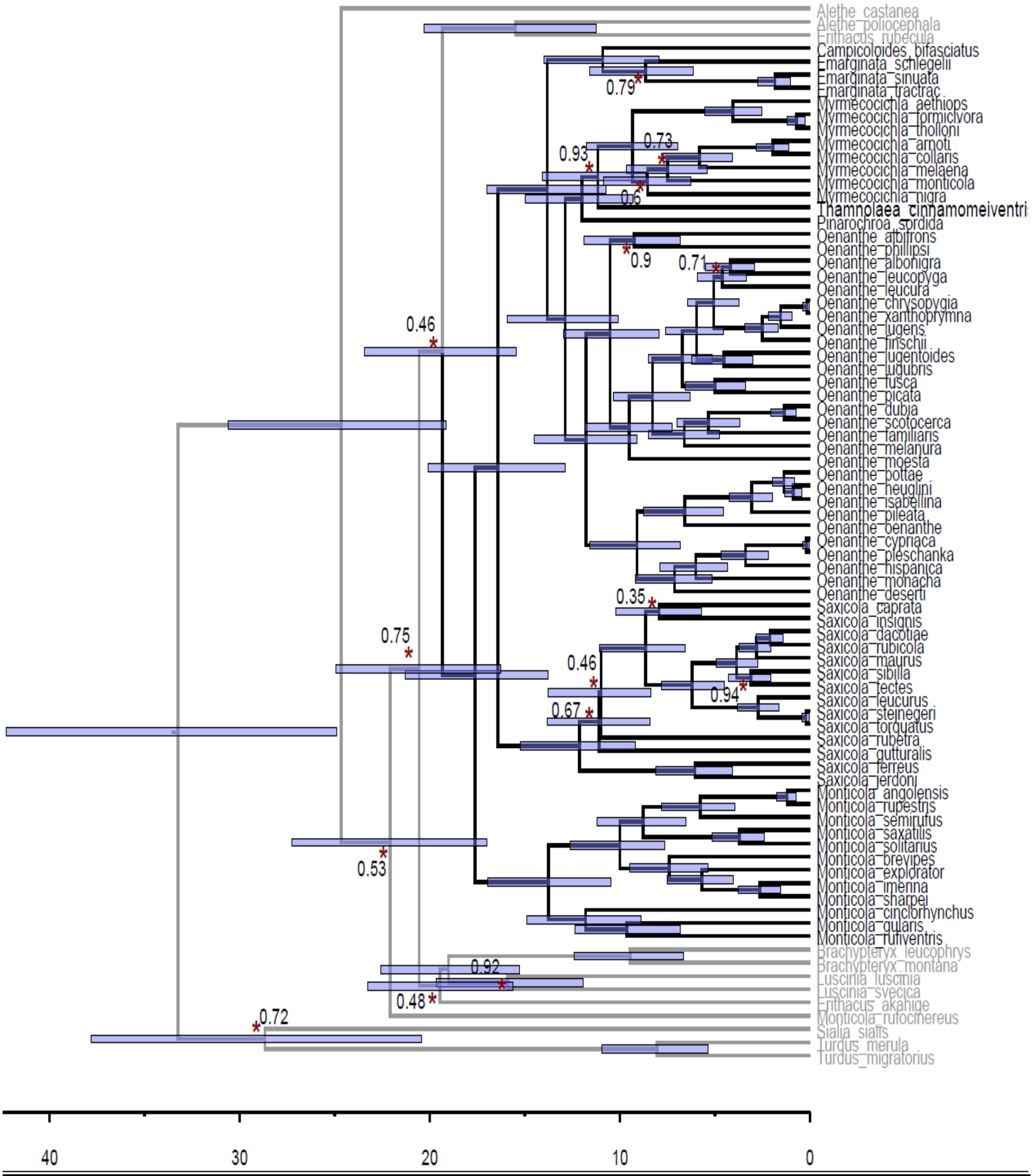

Figure S1.Maximum clade credibility tree for the wheatear-clade as obtained in a BEAST analyses (figure modified from Phillips et al. in review). Provided are node bars (blue) showing the 95% height range of each internal node within the phylogeny. Nodes with a posterior probability below 0.95 are indicated with an asterisk (*) and a support value. Time axis is in millions of years ago (Mya). Outgroups to the clade are shown in grey.

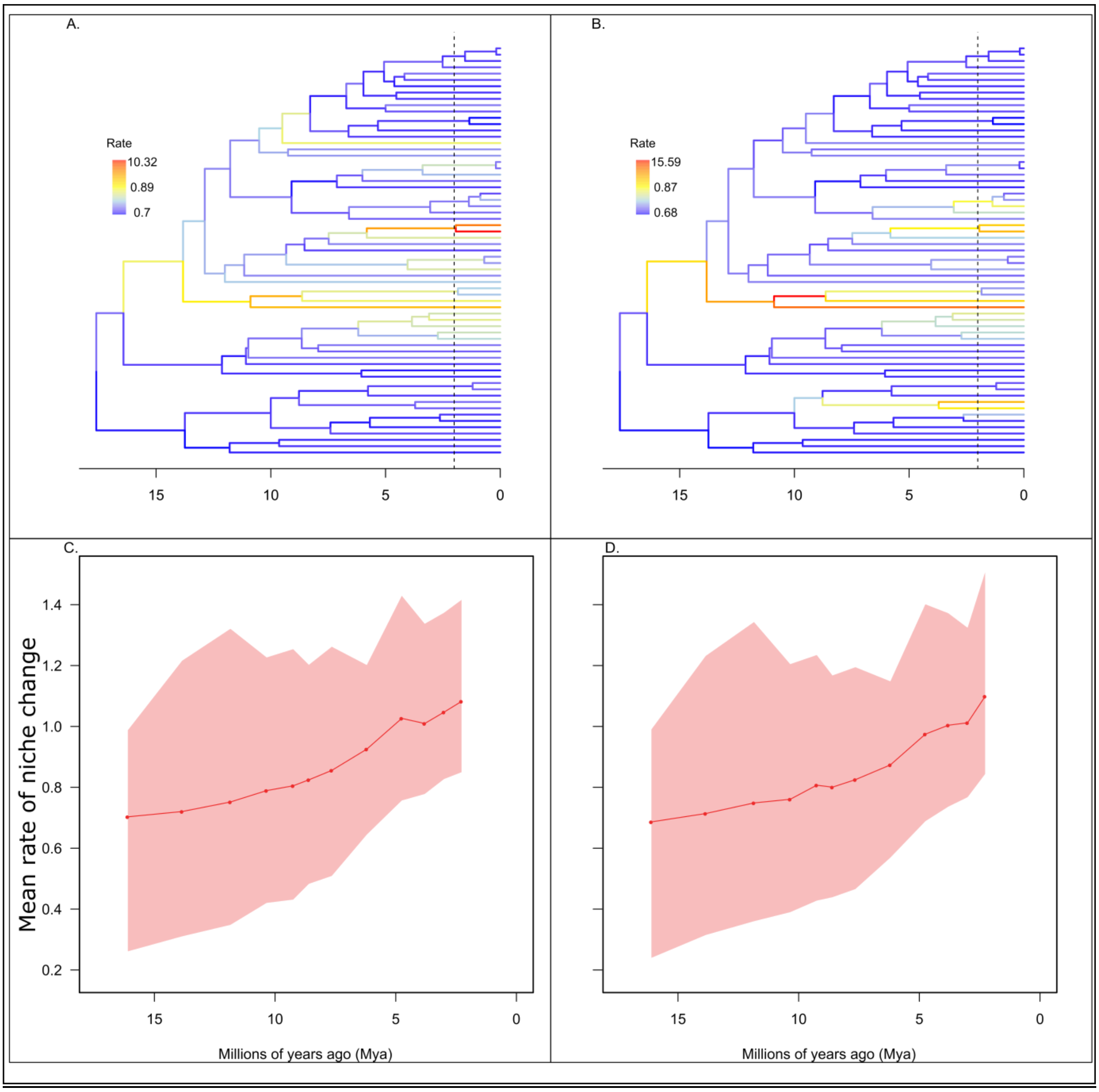

Figure S2. The consensus phylogeny for Wheatears and Chats (n= 65 species) coloured by estimates of the mean rates of trait evolution for climatic niche traits and mean rate of evolution through time calculated from 20,000 samples from a BayesTraits analysis for mean temperature (A & C) and maximum temperature (B & D). Rate values were logged for visualisation. Mean rate of climatic niche evolution (C &D) with 95% confidence intervals (shaded region) were calculated for each time period as being the weighted average of all branches which are present in a time period.

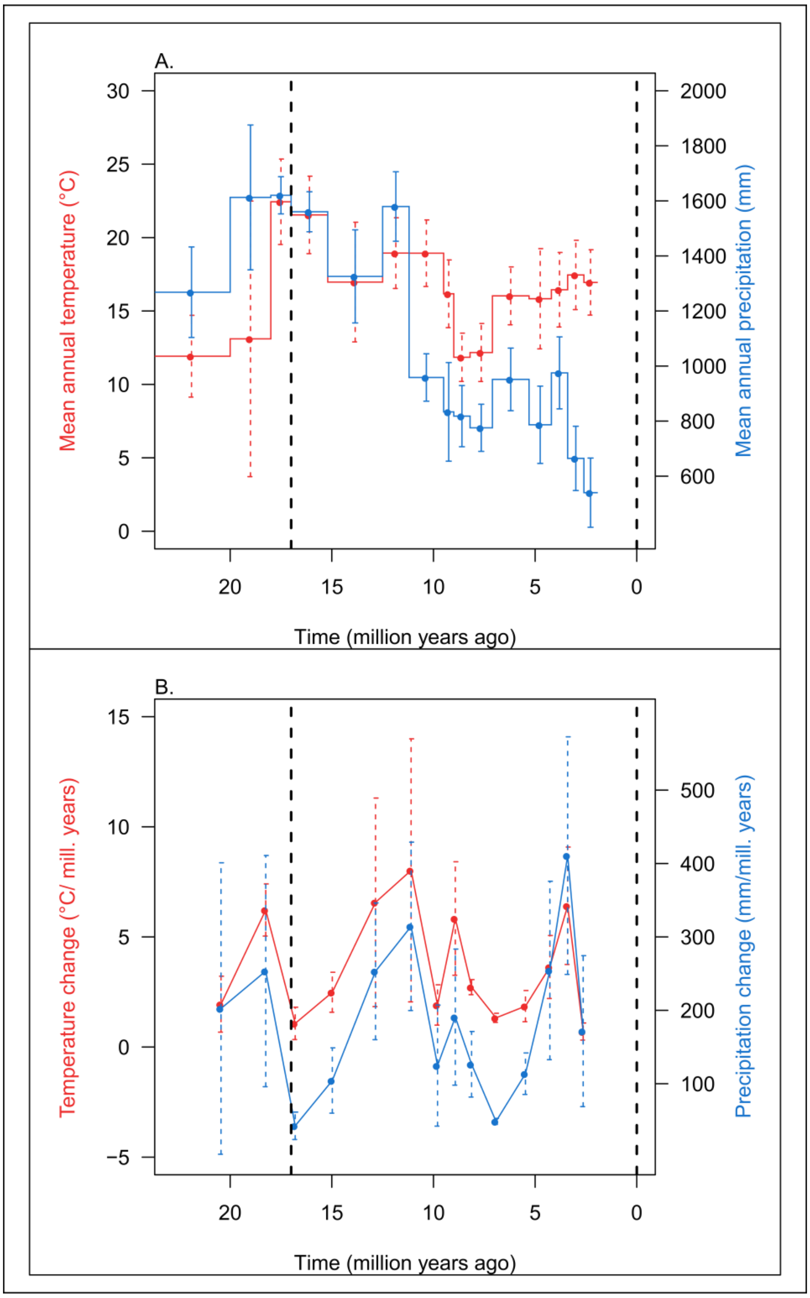

Figure S3. Absolute paleo-climatic values (A) and inferred rates of climatic change through time (B) for mean annual temperature (MAT) (red) and precipitation (MAP) (blue) inferred using only fossils that could unambiguously assigned to a mammal Neogene time zone (strict assignment) in the Neogene (time bins based on Mammal Neogene (MN) zones). Rates of climatic change calculated between successive time bins. Both absolute climate and rates of climate change are representative of climatic conditions from for the whole region (Asia, Africa and Europe) equally. Dashed lines denote the temporal extent of study clade. Error bars for Absolute climate variables (A) were calculated as the mean of the standard errors for each region. As a measure of regional variability in rates values (B) we calculated the standard error of the rates between each region.

Table S1. Results from the final GLS models testing for a relationship between rates of climatic niche evolution with a) absolute paleo-climatic conditions and b) rates of paleo-climatic conditions. Response variables were rates of climatic niche evolution (either temperature variables or precipitation) inferred based on phylogeny for the wheatear-chat clade. In the first two models absolute paleo-climatic values (MAT and MAP, respectively) were included as fixed effects. In the second two models the rates of paleo-climatic change in MAT and MAP were used as respective fixed effects. Paleo-climatic conditions were calculated using only the fossil data which unambiguously feel into MN zones (strict assignment method). Temporal autocorrelation in the data structure was accounted for in the GLS model.

	Coefficient	**Pseudo R2**	**AIC**	**F**	**P**	**Autocorrelation parameter (Phi1)**
(a) Absolute paleo-climate values						
Tmin	0.000548	0.0944	-23.9	0.00459	0.947	0.835
Tmean	-0.000564	0.0612	-27.3	0.00658	0.937	0.846
Tmax	-0.000952	0.0463	-28.9	0.0222	0.885	0.861
Precipitation	-0.000115	0.178	-10.0	0.882	0.370	0.243
(b) Rates of paleo-climatic change						
Tmin	0.000496	0.0503	-31.0	0.0163	0.901	0.893
Tmean	0.000291	0.0638	-37.0	0.0110	0.918	0.926
Tmax	-0.00228	0.0651	-32.9	0.459	0.512	0.916
Precipitation	0.000371	0.210	-16.7	2.50	0.142	0.694

Table S2: List of study species and peak breeding months determined from descriptions in the Handbook of birds of the world (del Hoyo et al. 2019). Taxonomy follows IOC v 3.1 (Gill and Donsker 2012).

Species (IOC v3.1)	Peak breeding months		
Oenanthe oenanthe	May	June	July
Oenanthe pileata	June	August	October
Oenanthe bottae	March	April	May
Oenanthe heuglini	January	February	March
Oenanthe isabellina	April	May	June
Oenanthe monacha	April	May	June
Oenanthe deserti	May	June	July
Oenanthe hispanica	April	May	June
Oenanthe cypriaca	April	May	June
Oenanthe pleschanka	May	June	July
Pentholaea albifrons	March	April	May
Oenanthe phillipsi	April	May	June
Oenanthe moesta	March	April	May
Oenanthe melanura	April	May	June
Oenanthe familiaris	March	September	December
Oenanthe scotocerca	March	April	May
Oenanthe dubia	May	June	July
Oenanthe fusca	April	May	June
Oenanthe picata	April	May	June
Oenanthe leucura	March	April	May
Oenanthe lugubris	April	May	June
Oenanthe leucopyga	March	April	May
Oenanthe albonigra	March	April	May
Oenanthe finschii	April	May	June
Oenanthe lugens	April	May	June
Oenanthe lugentoides	April	May	June
Oenanthe xanthoprymna	June	July	August
Oenanthe chrysopygia	May	June	July
Myrmecocichla nigra	March	July	November
Myrmecocichla aethiops	June	July	August
Myrmecocichla tholloni	June	July	August
Myrmecocichla formicivora	October	November	December
Myrmecocichla melaena	June	July	August
Oenanthe monticola	September	October	November
Pentholaea arnotti	August	October	December
Pentholaea collaris	September	October	November
Thamnolaea cinnamomeiventris	November	March	July

Thamnolaea coronata	May	June	July
Pinarochroa sordida	February	March	May
Emarginata sinuata	October	November	December
Emarginata schlegelii	September	October	November
Emarginata tractrac	September	October	November
Campicoloides bifasciatus	September	October	November
Saxicola rubetra	May	June	July
Saxicola macrorhynchus	April	May	June
Saxicola insignis	June	July	August
Saxicola dacotiae	February	March	April
Saxicola rubicola	April	May	June
Saxicola maurus	May	June	July
Saxicola stejnegeri	May	June	July
Saxicola torquatus	May	July	September
Saxicola sibilla	August	September	October
Saxicola tectes	November	December	January
Saxicola leucurus	March	April	May
Saxicola caprata	March	April	June
Saxicola jerdoni	March	April	May
Saxicola ferreus	April	May	June
Saxicola gutturalis	October	November	December
Monticola semirufus	June	July	August
Monticola rupestris	October	November	December
Monticola explorator	September	October	November
Monticola brevipes	November	December	January
Monticola angolensis	September	October	November
Monticola saxatilis	May	June	July
Monticola rufocinereus	March	May	September
Monticola solitarius	April	May	June
Monticola rufiventris	April	May	June
Monticola cinclorhynchus	May	June	July
Monticola gularis	May	June	July
Monticola imerina	November	December	January
Monticola sharpei	November	December	January

References

del Hoyo, J., A. Elliott, J. Sargatal, D. A. Christie, and E. de Juana. 2019. HBW Alive: Handbook of the Birds of the World Alive.

Gill, F., and D. Donsker. 2012. IOC World Bird Names (version 3.1).

APPENDIX IV: Curriculum vitae

Alison Eyres

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Senckenberg Biodiversity and Climate Research Centre
Senckenberganlage 25
60325, Frankfurt am Main
Germany

EDUCATION

11/2014- **PhD Student**
Senckenberg Biodiversity and Climate Research Centre (SBiK-F) and Goethe University, Frankfurt am Main, Germany.

Thesis title: Macroecology and Evolution of Climatic niches in Birds
Supervisors: Dr Susanne Fritz & Professor Katrin Böhning-Gaese

2013 – 2014 **MSc Plant Diversity and Systematics** (graduated with distinction)
School of Biological Sciences, University of Reading, UK

Thesis title: Climatic niche evolution in the genus *Hypericum*
Supervisors: Professor Alastair Culham (University of Reading) & Dr. Mark Carine (NHM)

2007 – 2010 **Bachelor of Arts, Biological Sciences with Honours** (2.1)
University of Oxford, UK

RESEARCH EXPERIENCE

June- August 2013 **Leonardo Da Vinci mobility funded placement**
University of Evora, Portugal

- *Tyto*Tagus project: Studying Barn Owl dispersal

2012 – 2013 **Senior Research Technician**
Department of Life Sciences, University of Warwick, UK

- Investigating plant pathogen interactions

2011 -2012 **Senior Research Technician**
Department of Life Sciences, University of Warwick, UK

- Cell specific gene expression in *A. thaliana*

ADDITIONAL EXPERIENCE

01-03 2019 **Walker publishing, UK - Amazing World of Plants (children's book)**

- Reviewing, editing and writing additional text and captions

LANGUAGE SKILLS

English: Native speaker

German: good working knowledge (4+ years living in Germany)

COMPUTING SKILLS

Writing R-based code for data management, statistical analysis, graphical representation, spatial data manipulation, species distribution modelling (BIOMOD) and phylogenetic analyses; spatial data manipulation using ArcGIS; phylogenetic analysis using BEAST, Mesquite, Bayes traits and in R.

PUBLICATIONS

1. Huang, S, Meijers, J.M, **Eyres, A**, Mulch, A and Fritz, S.A . 2019. Unravelling the history of biodiversity in mountain ranges through integrating geology and biogeography. Journal of Biogeography.
2. **Eyres, A.**, Böhning-Gaese, K. and Fritz, S. A. 2017. Quantification of climatic niches in birds: Adding the temporal dimension. - J. Avian Biol.
3. Bowden, S. D., **Eyres, A.**, Chung, J. C. S., Monson, R. E., Thompson, A., Salmond, G. P. C., Spring, D. R. and Welch, M. 2013. Virulence in Pectobacterium atrosepticum is regulated by a coincidence circuit involving quorum sensing and the stress alarmone, (p)ppGpp. - Mol. Microbiol. 90: 457–471.
4. Grønlund, J. T., **Eyres, A**., Kumar, S., Buchanan-Wollaston, V. and Gifford, M. L. 2012. Cell specific analysis of Arabidopsis leaves using fluorescence activated cell sorting. - JoVE: 1–7.

PUBLICATIONS IN REVIEW

1. **Eyres, A.**, Böhning-Gaese, K. ,Eronen, J. , and Fritz, S.A. Paleo-climatic change does not drive climatic niche evolution: evidence from a passerine bird clade. Submitted to Evolution August 2019.

2. **Eyres, A.**, Böhning-Gaese, K., Orme, C.D.L., Rahbek, C., and Fritz, S. A. The effects of seasonal migration on the climatic niche of passerine birds. Submitted to Ecography August 2019.

CONFERENCE CONTRIBUTIONS

1. Huang, S. 2019. The relationship between extinction and climate change in space and time. International Biogeography Society Conference. Malaga (oral). In place of Huang, S.
2. **Eyres, A.,** Eronen, J., Fritz, S.A 2019. Climatic niche evolution and paleo-climatic change in the Wheatears and Chats. International Biogeography Society Conference. Malaga (poster)
3. **Eyres, A.,** Böhning-Gaese, K., Fritz, S.A. 2017 The effects of seasonal migration on the climatic niches of passerine birds. BES Ecology Across Borders Conferences. Ghent, Belgium (oral).

4. **Eyres, A.,** Böhning-Gaese, K., Fritz, S.A. 2017 Climatic niches in space and time: seasonal dynamics in migratory birds. International Biogeographic Society Conference. Tucson, USA (oral).
5. **Eyres, A.,** Böhning-Gaese, K., Fritz, S.A. 2017 Quantification of Climatic niches in birds: adding the temporal dimension. 1st Joint Meeting of Young Ornithologists. Vienna, Austria (oral).
6. **Eyres, A.,** Böhning-Gaese, K., Fritz, S.A. 2015 Climatic niches in time and space: seasonal dynamics in migratory birds. EU Macro. Copenhagen, Denmark (poster).

SERVICE TO DISCIPLINE

1. Reviewed for Journal of Avian Biology, Systematic Biology and Journal of Biogeography
2. Student helper at BES Ecology Across Borders. Ghent, Belgium.
3. Coordinator of weekly working group meeting for three research groups (Senckenberg Biodiversity and Climate Research Institute, 2015-2016)

PROFESSIONAL MEMBERSHIPS

British Ecological Society, International Biogeography Society