

**AVIAN RANGE DYNAMICS:
TRAITS, BIOTIC INTERACTIONS AND NICHES
IN CHANGING ENVIRONMENTS**

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*“When we try to pick out anything by itself,
we find it hitched to everything else in the Universe.”*

John Muir (1911)

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1 ZUSAMMENFASSUNG

1.1 Hintergrund und Zielsetzung

Das geographische Verbreitungsgebiet von Arten ist ein fundamentales Struktur gebendes Merkmal der biologischen Welt. In Teilen selbst für Gelegenheitsbeobachter zugänglich, führt das Wahrnehmen und Beschreiben der geographischen Verbreitung von Arten unvermeidlich zu Fragen über die treibenden Faktoren, die sie bestimmen. Warum Arten so verteilt sind wie sie sind, ist seit langem eine der zentralen Fragen in Ökologie, Biogeographie und Evolution (Wallace, 1876; MacArthur, 1972; Gaston, 2003). Der Anbruch des Anthropozäns stellt diese Frage mit neuer Dringlichkeit (Crutzen, 2002). Wurden geographische Artverbreitungen zuvor durch die Dynamik der natürlichen Welt bestimmt, so sind menschliche Aktivitäten jetzt der dominante Faktor, der sie auf jedem Maßstab von der lokalen Umgebung bis hin zum gesamten Erdsystem formt (Ladle & Whittaker, 2011). Die menschliche Fähigkeit, globalen Wandel auszulösen und zu beschleunigen, übertrifft jedoch unser Verständnis der Auswirkung auf Artverbreitungen und unsere Fähigkeit, die Konsequenzen unserer gesellschaftlichen Entscheidungen für die Verteilung von Biodiversität vorherzusagen (White, 1967; Chapin *et al.*, 2000). Gegenwärtig verändern sich, im Wesentlichen als unbeabsichtigtes Nebenprodukt menschlicher ökonomischer Aktivitäten und Populationsdynamik, die geographischen Verbreitungsgebiete von Arten mit entscheidender Bedeutung in der Land- und Forstwirtschaft, als Krankheitsvektoren oder als Teil der biologischen Systeme, die Ökosystemfunktionen bereitstellen (MEA, 2005a; Parmesan, 2006). Die steigende Besorgnis über invasive Arten zeigt auf, dass der menschliche Einfluss auf Artverbreitungen oft unbeabsichtigt und unsere Fähigkeit zur zielgerichteten Kontrolle von Verbreitungen begrenzt ist (Elton, 1958; Pimentel *et al.*, 2001). Daher ist es entscheidend, dass wir unser Verständnis über die Dynamiken, aus denen die geographische Verbreitung von Arten erwachsen, verbessern (Davis *et al.*, 1998).

Die Dynamik von Artverbreitungen zu verstehen ist eine Herausforderung, da geographische Artverbreitungen von einer Vielzahl interagierender Faktoren beeinflusst werden (MacArthur, 1972). Über die grundlegende Idee hinaus, dass Umweltbedingungen die Verbreitung von Arten begrenzen, hängt das Vorkommen einer Art an einem bestimmten geographischen Punkt auch davon ab, ob dieser Punkt der Art prinzipiell zugänglich ist und

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welche biologische Gemeinschaft dort bereits besteht (Pulliam, 2000; Soberon, 2007). Es wurde vorgeschlagen, die relative Bedeutung dieser Aspekte sei skalenabhängig: abiotische Bedingungen wie z.B. Klima und Ausbreitungsbeschränkungen, die sich aus der Geschichte einer Art ergeben, sind im Wesentlichen auf großer räumlicher Skala relevant, wohingegen biotische Interaktionen zunehmend auf kleiner Skala an Bedeutung gewinnen (Pearson & Dawson, 2003; Guisan & Rahbek, 2011). In jedem Fall kann das geographische Verbreitungsgebiet einer Art von ihren gegenwärtigen Merkmalen, wie Habitatwahl und Ausbreitungsfähigkeit, von ihrer evolutionären und biogeographischen Geschichte, von der raumzeitlichen Dynamik ihrer bevorzugten Umweltbedingungen sowie von den Merkmalen und der Geschichte anderer Arten beeinflusst werden (Newton, 2003; Price & Kirkpatrick, 2009). Noch haben wir kein kohärentes Bild davon, wie diese Faktoren interagieren, von ihrer relativen Bedeutung oder davon, wie diese Beziehungen zwischen verschiedenen Taxa variieren.

Während viele Studien den Einfluss einzelner Faktoren auf einzelne Arten dokumentieren, gab es erst im letzten Jahrzehnt Fortschritte in der Bioinformatik, die es uns ermöglichen durch die Integration multipler Faktoren in derselben Analyse und das Untersuchen von Mustern auf großen räumlichen Skalen über viele Arten hinweg die Dynamik von Artverbreitungen besser zu verstehen (Brown, 1995; Gaston, 2003; Brooker *et al.*, 2007). Heute haben Forscher nie dagewesenen Zugang zu Daten über die Verbreitung, Ökologie und Evolution von Arten, zu Daten, die die Umweltbedingungen der gesamten Erdoberfläche beschreiben und zu den bioinformatischen Werkzeugen, um diese Informationen zu organisieren, zu analysieren und zu integrieren (z. B. Graham *et al.*, 2004; Rangel *et al.*, 2006; Kozak *et al.*, 2008). Dies hat zu einer raschen methodischen Entwicklung in Bereichen wie der Artverbreitungsmodellierung (Guisan & Thuiller, 2005; Elith *et al.*, 2006) geführt, die ihrerseits eine Neubetrachtung des klassischen Konzepts der ökologischen Nische (Grinnell, 1917; Elton, 1927; Hutchinson, 1957) und eine Diskussion über die Integration der durch die neuen Methoden inspirierten konzeptionellen Ideen in die Niscentheorie (Pulliam, 2000; Soberon, 2007; Pearman *et al.*, 2008; Colwell & Rangel, 2009; Wiens *et al.*, 2010) angeregt hat. Artverbreitungsmodelle sind weiterhin für das Verstehen der Dynamik von Artverbreitungen von großem Wert, doch haben sie, wie jedes wissenschaftliche Werkzeug, bisweilen wissenschaftliches Denken auch eingeschränkt: durch den Fokus auf große raumzeitliche Skalen und das Klima als treibenden Faktor sowie durch

die Verwendung von Algorithmen, die Artverbreitung als präzise definierte, statische Entitäten behandeln und die ebenso statische Nischen berechnen (Araújo & Guisan, 2006; Fisher *et al.*, 2010; Franklin, 2010).

Mit dieser Doktorarbeit versuche ich, einen Beitrag zu unserem in Entwicklung begriffenen Verständnis der multiplen Faktoren, die Artverbreitungsgebiete beeinflussen, zu leisten. Ich verwende Methoden aus Bioinformatik, Statistik und GIS (Geoinformationssysteme) und kombiniere Daten zu Verbreitungsgebieten, Merkmalen, Ökologie, Evolution sowie der gegenwärtigen und vergangenen Umwelt, um unser Verständnis der Mechanismen, welche Größe, Position und Dynamik von Verbreitungsgebieten bestimmen, zu verbessern. Ich versuche ebenfalls, konzeptionell über die klassische Artverbreitungsmodellierung hinauszugehen, indem ich die raumzeitliche Dynamik des verfügbaren Nischenraums und die dynamische Natur der Nischenanforderungen berücksichtige und somit die gegenwärtige Diskussion über Nischentheorie um eine zusätzliche Perspektive bereichere. Taxonomisch konzentriere ich mich auf die Dynamik der Verbreitungsgebiete von Vögeln, spezifisch von europäischen Singvögeln in Kapitel 3 und der Gattung *Sylvia* in Kapitel 4 und 5.

Als ein Modellsystem, um die treibenden Faktoren von Artverbreitungen zu untersuchen, haben Vögel einige bedeutende Vorteile. Vögel haben schon immer die Aufmerksamkeit von Amateuren, Naturforschern und Ökologen auf sich gezogen und sind somit eine der am besten untersuchten Organismengruppen. Der Reichtum an Informationen zu Verbreitung, Ökologie und Evolution der Vögel erlaubt es, das Potential bioinformatischer Methoden voll auszuschöpfen. Europäische Singvögel im Besonderen bieten uns die Gelegenheit, entscheidende Merkmale wie die Ausbreitungsfähigkeit von morphologischen Messungen abzuleiten (Dawideit *et al.*, 2009). Die Gattung *Sylvia* (Grasmücken) verbindet eine immense Variation in Größe und Konfiguration von Verbreitungsgebieten mit einer langen Tradition von Studien zu biotischen Interaktionen innerhalb der Gattung (z. B. Cody & Walter, 1976; Martin & Thibault, 1996; Pons *et al.*, 2008) und zeigt das volle Spektrum von Migrationsverhalten, das bei Vögeln generell zu beobachten ist (Shirihai *et al.*, 2001). Die Gattung ist somit ideal geeignet, um die Beziehung zwischen biotischen Interaktionen, Zugverhalten und Artverbreitungsdynamik zu untersuchen. Meine Untersuchungen sind in drei eigenständige Kapitel gegliedert:

1.2 Zu einem mechanistischeren Verständnis von Artmerkmalen und Verbreitungsgebietsgrößen (Kapitel 3)

Ein wichtiger, ungelöster Fragenkomplex in der Makroökologie ist, die immense interspezifische Variation in der Größe geographischer Verbreitungsgebiete zu verstehen. Während man davon ausgeht, dass Artmerkmale wie Fekundität und Körpergröße einen Effekt auf Verbreitungsgebietsgrößen haben, fehlt ein allgemeines Verständnis davon, wie Verbreitungsgebietsgrößen von mehreren Merkmalen gemeinsam beeinflusst werden. Hier haben wir den Einfluss einer Vielzahl von Artmerkmalen auf die Größe der globalen Verbreitungsgebiete europäischer Singvögel getestet, um die möglichen Mechanismen hinter makroökologischen Zusammenhängen besser zu verstehen.

Wir haben den Effekt von Lebensgeschichtsmerkmalen (Fekundität, Ausbreitungsfähigkeit), ökologischen Merkmalen (Habitatnische, Nahrungsnische, Zugverhalten, Flexibilität im Zugverhalten) und morphologischen Merkmalen (Körpergröße) auf die globale Verbreitungsgebietsgröße von 165 europäischen Singvögeln beurteilt. Wir identifizierten Hypothesen zur Beziehung von Artmerkmalen und Verbreitungsgebietsgrößen aus der Literatur und verwendeten die Methodik der Pfadanalyse, um sie zu testen.

Fekundität, Ausbreitungsfähigkeit, Habitatnischenbreite und Nahrungsnischenposition hatten einen direkten positiven Effekt auf die Verbreitungsgebietsgröße. Zugverhalten hatte einen indirekten positiven Effekt via Ausbreitungsfähigkeit. Körpergröße hatte einen starken, direkten positiven Effekt, der durch indirekte negative Effekte über mehrere andere Merkmale reduziert wurde.

Die Größe der globalen geographischen Verbreitungsgebiete europäischer Singvögel wurde von Lebensgeschichtsmerkmalen (Fekundität und Ausbreitungsfähigkeit), ökologischen Merkmalen (Habitatnischenbreite, Nahrungsnischenposition und Zugverhalten) und von Körpergröße beeinflusst. Artmerkmale beeinflussten Verbreitungsgebietsgrößen auf direktem und indirektem Weg. Insbesondere der Einfluss von Körpergröße war mit positiven und negativen Effekten über verschiedene Pfade sehr komplex. Die Größe von Verbreitungsgebieten ist sehr wahrscheinlich auch von anderen Faktoren als von Artmerkmalen abhängig. Wir konnten zeigen, dass es notwendig ist, den direkten und indirekten Einfluss einer Vielzahl von Merkmalen zu entwirren, um die Mechanismen, auf denen makroökologische Beziehungen beruhen, aufzuklären.

1.3 Konkurrenz und Ausbreitungsfähigkeit interagieren bei der Bestimmung der geographischen Verbreitung von Vögeln (Kapitel 4)

Es ist weiterhin eine Herausforderung für Ökologie und Evolutionsbiologie, die Faktoren zu verstehen, welche die geographische Verbreitung von Arten beeinflussen. Insbesondere besteht wenig Konsens darüber, ob biotische Interaktionen wie interspezifische Konkurrenz Verbreitungsgebiete bestimmen. Wir untersuchen Einflüsse von Konkurrenz, Ausbreitungsfähigkeit, das Alter eines Taxons und Habitatverschiebungen seit dem letzten glazialen Maximum auf das Ausmaß, in dem Arten der Vogelgattung *Sylvia* in allen Regionen mit geeigneten Umweltbedingungen vorkommen (d. h. range filling).

Wir haben range filling in der Vogelgattung *Sylvia* unter Verwendung von Boosted Regression Trees und Ridge-Regression quantifiziert. Mittels multipler Regression haben wir für die Effekte von intragenerischer Konkurrenz, Ausbreitungsfähigkeit, Alter des Taxons und Habitatverschiebung seit dem letzten glazialen Maximum auf range filling getestet. Um verschiedene Hypothesen widerzuspiegeln, wie lokale Konkurrenz die Dynamik von Verbreitungsgebieten auf großer räumlicher Skala beeinflussen könnte, haben wir unterschiedliche Methoden verwendet, um potentielle Signale von Konkurrenz auf der Skala des Verbreitungsgebiets zu quantifizieren.

Grasmücken mit hoher Ausbreitungsfähigkeit zeigten höheres range filling, aber nur wenn Konkurrenz in Gebieten mit weniger geeignetem Habitat innerhalb ihres potentiellen Verbreitungsgebietes niedrig war. Das Alter eines Taxons und Habitatverschiebung seit dem letzten glazialen Maximum hatten keinen konsistenten Effekt.

Wir konnten somit zeigen, dass die Verbreitungsgebiete von Grasmücken mit hoher Wahrscheinlichkeit durch den simultanen, interaktiven Effekt von Konkurrenz und Ausbreitungsfähigkeit geformt werden. Wenn biotische Interaktionen wie Konkurrenz generell die Fähigkeit von Arten beeinflussen, auf der kontinentalen Skala neue Gebiete zu kolonisieren, wird es in der Tat eine Herausforderung sein, den Effekt von Klimawandel auf Biodiversität vorherzusagen.

1.4 Nischenverfügbarkeit in Zeit und Raum: Vogelzug der Grasmücken (Kapitel 5)

Im Kontext neuer Fortschritte in der ökologischen Nischenmodellierung sind sowohl die Umwelt als auch die ökologische Nische einer Art als statische Entitäten behandelt und quantifiziert worden. In der Realität sind aber sowohl die Umwelt als auch die Nischenanforderungen einer Art auf einer Vielzahl von Skalen dynamisch. Wir schlagen ein konzeptionelles System vor, das berücksichtigt, wie die realisierte Nische und geographische Verbreitung von Arten durch die entkoppelte raumzeitliche Verfügbarkeit unterschiedlicher Umweltbedingungen und durch Veränderungen der Nischenanforderungen über die Lebenszeit eines Organismus geformt werden.

Das Testen der aus dem konzeptionellen System abgeleiteten Vorhersagen am Beispiel des Vogelzugs der Grasmücken ergab neue Erkenntnisse: Das Verfolgen der Klimanische im geographischen Raum war höchstwahrscheinlich nicht die treibende Kraft für Migration in der Gattung und steht potentiell im Konflikt mit dem Verfolgen der Landnutzungsnische. Die Nischen der Grasmücken waren während der Brutsaison schmaler, was zeigt, dass Nischenanforderungen zeitlich dynamisch sein können. Wir legen nahe, dass die Berücksichtigung dynamischer Umwelten und Nischenanforderungen zu einer entscheidenden Verbesserung unseres Verständnisses der treibenden Faktoren hinter der Bewegung von Organismen im Raum und der Dynamik ihrer Nischen und Verbreitungsgebiete führt.

1.5 Schlussfolgerungen

In der vorliegenden Doktorarbeit habe ich versucht, unser gegenwärtiges Verständnis der Dynamik von Vogelverbreitungsgebieten durch die Modellierung mutmaßlicher Mechanismen, die Integration multipler Faktoren in einer einzigen Analyse und durch die Entwicklung neuer konzeptioneller Ideen zu erweitern. Zu diesem Zweck habe ich Datensätze aus Ökologie, Evolution und den Erdwissenschaften kombiniert und moderne statistische Werkzeuge wie Geoinformationssysteme, statistische Programmierumgebungen, Pfadanalyse, Boosted Regression Trees, Ridge-Regression, Bootstrapping, Kerndichteschätzer und Nischenmetrik eingesetzt.

Es ergeben sich folgende Hauptkenntnisse, wobei es wichtig ist zu betonen, dass ihre Validität durch die notwendige Beschränkung auf Singvögel als Modellsystem auf diese Gruppe beschränkt bleibt, bis sie für andere Taxa bestätigt oder widerlegt werden können: (i) Artmerkmale können keinen Großen Anteil der Variation in Verbreitungsgebietsgrößen erklären, aber sie spielen eine wichtige Rolle. Mehrere Artmerkmale beeinflussen Verbreitungsgebietsgröße auf komplexe Weise, sowohl direkt als auch indirekt über andere Merkmale. (ii) Ob Arten in der Lage sind, geeignete Areale auf großen räumlichen und zeitlichen Skalen zu kolonisieren, hängt von mehreren, interagierenden Faktoren ab. Entgegen bestehender Vorstellungen (Pearson & Dawson, 2003; Guisan & Rahbek, 2011) könnten biotische Interaktionen Verbreitungsgebiete auf kontinentaler Skala beeinflussen, wobei ihre Effekte sehr wahrscheinlich von der Habitatgüte modifiziert werden. (iii) Die Nischen und Verbreitungsgebiete von Arten sind dynamische Entitäten, die von der raumzeitlichen Verfügbarkeit von Umweltbedingungen abhängen. Die Verfügbarkeit solcher Umweltbedingungen kann für verschiedene Nischendimensionen asynchron sein, was Arten vor komplexe Optimierungsprobleme stellt, wenn sie versuchen, Umweltbedingungen im geographischen Raum zu verfolgen. Die Nischenanforderungen von Arten können über ihren Lebenszyklus hinweg variieren. Zusammenfassend kann die frühe Vorstellung, dass Verbreitungsgebiete nur von wenigen Faktoren bestimmt sind (z. B. Twomey, 1936), widerlegt werden. Die Prozesse, welche die Größe, Position und Dynamik von Verbreitungsgebieten bestimmen, sind hochkomplex und involvieren multiple, interagierende Triebkräfte. Wir stehen erst am Beginn der Entwicklung eines kohärenten, umfassenden Verständnis der Dynamik von Artverbreitungsgebieten.

Im Hinblick auf zukünftige Forschung gibt es einige Bereiche, in denen die Berücksichtigung zusätzlicher Komplexität unser Verständnis von Artverbreitungen voranbringen kann. Diese sollten insbesondere bei der Vorhersage der Verschiebung von Artverbreitungen durch globalen Wandel Berücksichtigung finden: (i) Es gibt immer noch viele ungenutzte Möglichkeiten der Integration multipler Triebkräfte der Dynamik von Artverbreitungsgebieten in einer einzigen Analyse (Botkin *et al.*, 2007), wofür sich z. B. Bayesische Methoden anbieten (Ellison, 2004; Choy *et al.*, 2009). (ii) Welche Faktoren die Verbreitung von Arten bestimmen, variiert im geographischen Raum (z. B. Barnes, 1957, Gross & Price, 2000). Die Berücksichtigung solcher Variation z. B. durch geographisch gewichtete Regression erscheint vielversprechend (Austin, 2007). (iii) Die Annahme, dass

1 Zusammenfassung

Artverbreitungen auf großer räumlicher Skala nicht durch biotische Interaktionen bestimmt werden, sollte mit großer Vorsicht betrachtet werden. Es erscheint ratsam, biotische Interaktionen besser in bestehende Methoden zu integrieren, was bedeuten könnte, dass die Verschiebung des Verbreitungsgebietes einer Art nicht in Isolation von anderen Arten modelliert werden kann (Keith *et al.*, 2008; Baselga & Araújo, 2009). (iv) Wenn Nischenanforderungen dynamisch sind, sollten die Nischen und Verbreitungsgebiete zu verschiedenen Stadien im Lebenszyklus einer Art getrennt betrachtet und modelliert werden (Doswald *et al.*, 2009; Jackson *et al.*, 2009). (v) Wie Arten mit der raumzeitlichen Desynchronisation verschiedener Nischendimensionen umgehen, kann uns helfen zu verstehen, wie Arten auf das vorhergesagte zukünftige Auftreten neuer Klimaregimes reagieren könnten (Williams *et al.*, 2007). (vi) Das in Kapitel 5 vorgeschlagene konzeptionelle System könnte auch zur Betrachtung der Veränderung von Nischen und Artverbreitungen im Verlauf der Evolution, z. B. im Kontext von Nischenkonservatismus verwendet werden (Wiens & Graham, 2005; Crisp *et al.*, 2009).

Die Dynamik von Artverbreitungen ist komplex. Im Rahmen von Wissenstransfer zu betonen, was wir gegenwärtig über die Auswirkungen von globalem Wandel auf Biodiversität nicht wissen und nicht vorhersagen können, könnte den gesellschaftlichen Diskurs über Risikoakzeptanz und Planung unter Einbeziehung von Unsicherheit anregen (Dasgupta, 2008; CCSP, 2009; Dawson *et al.*, 2011).

2 INTRODUCTION

2.1 Background

The geographic range of species is a fundamental property structuring the biological world. Accessible and observable in parts even to the casual naturalist, noticing and recording the geographic distribution of species leads inevitably to asking questions about the driving forces that shape it. Why species are distributed in the way they are has long been recognised as a central question in ecology, biogeography and evolution (Wallace, 1876; MacArthur, 1972; Gaston, 2003).

The rise of the Anthropocene poses this question with new urgency (Crutzen, 2002). If geographic ranges of species have previously been set by dynamics inherent to the natural world, human activity is now the dominant agent shaping them at every scale from the local patch to the whole Earth system (Ladle & Whittaker, 2011). However, the human ability to trigger and accelerate global change exceeds our understanding of how this will alter species ranges and our ability to predict the consequences of societal decisions for the distribution of biodiversity (White, 1967; Chapin *et al.*, 2000). Largely as an inadvertent by-product of human economic activities and population dynamics, the geographic ranges of species that are crucially important to humans in agriculture and forestry, as disease vectors or as part of the biological systems that maintain ecosystem functions, undergo far-reaching change (MEA, 2005a; Parmesan, 2006). The increasing concern over invasive species highlights that the human impact on species' ranges is often far from deliberate and that our ability to purposefully control their distribution is limited (Elton, 1958; Pimentel *et al.*, 2001). Therefore, it is imperative that we enhance our understanding of the dynamics that give rise to species' geographic distributions (Davis *et al.*, 1998).

Understanding range dynamics is challenging because geographic ranges depend on and are influenced by a multitude of interacting drivers (MacArthur, 1972). Beyond the fundamental idea that environmental conditions limit species distributions, whether a species occurs in a particular geographic location also depends on whether that area is in principle accessible to the species and on the biological community already present (Pulliam, 2000; Soberon, 2007). It has been suggested that the relative importance of these aspects is scale-dependent, such that abiotic conditions like climate and dispersal limitations resulting from a

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species' history primarily govern distributions at large spatial scales whereas biotic interactions gain increasing importance at smaller scales (Pearson & Dawson, 2003; Guisan & Rahbek, 2011). In any case, a species' geographic range can be influenced by its present traits, such as habitat preference and dispersal ability, by its evolutionary and biogeographic history, by the spatio-temporal dynamics of its preferred environmental conditions and by the traits and history of co-occurring species (Newton, 2003; Price & Kirkpatrick, 2009). At present, we do not have a coherent understanding of how these different drivers interact, of their relative importance and of how these relationships change across a broad range of taxa.

While many studies document the impact of single factors on the range of individual species, the past decade has seen bioinformatic advances that give us the opportunity to better understand range dynamics by integrating multiple drivers in the same analysis and examining patterns across many species at large spatial scales (Brown, 1995; Gaston, 2003; Brooker *et al.*, 2007). Today, researchers have unprecedented access to data on species distributions, ecology and evolution, to data describing environmental conditions on the entire Earth's surface and to the bioinformatic tools to manage, analyse and integrate this information (e.g. Graham *et al.*, 2004; Rangel *et al.*, 2006; Kozak *et al.*, 2008). This has led to the rapid methodological development of fields such as species distribution modelling (Guisan & Thuiller, 2005; Elith *et al.*, 2006) which has in turn stimulated a re-examination of the seminal concept of the ecological niche (Grinnell, 1917; Elton, 1927; Hutchinson, 1957) and an ongoing discussion about how to integrate conceptual ideas inspired by the new approaches into niche theory (Pulliam, 2000; Soberon, 2007; Pearman *et al.*, 2008; Colwell & Rangel, 2009; Wiens *et al.*, 2010). While species distribution models continue to be of great value for understanding range dynamics, they have, like any scientific tool, sometimes also constrained scientific thought by focusing on large spatio-temporal resolutions and on climate as a determinant of ranges and by using algorithms that treat geographic ranges as precisely defined, static entities and that quantify an equally static niche (Araújo & Guisan, 2006; Fisher *et al.*, 2010; Franklin, 2010).

In this thesis, I try to contribute to our emerging understanding of the multiple drivers that govern species distributions. I use bioinformatics, statistics and GIS (geographic information systems) methods and combine data on ranges, traits, ecology, evolution and the past and present environment to inform our thinking about the mechanisms that determine the size, location and dynamics of species ranges. I also attempt to conceptually go beyond the classic

species distribution modelling approach by considering the spatio-temporal dynamics of available niche space and the dynamic nature of niche requirements and to thus add another perspective to the current debate about niche theory.

Taxonomically, I focus on the range dynamics of birds, specifically European passerines in chapter 3 and the genus *Sylvia* in chapter 4 and 5. As a model system to explore the drivers of species distributions, birds have several key advantages. They have always attracted the attention of amateurs, naturalists and ecologists and are thus one of the best-studied groups of organisms. The wealth of information on bird distributions, traits, ecology and evolution allows us to use bioinformatic methods to their fullest advantage. European passerines, in particular, provide us with an opportunity to gauge crucial traits, such as dispersal ability, from morphological measurements (Dawideit *et al.*, 2009). The genus *Sylvia* combines large variation in the size and configuration of ranges with a long tradition of studies investigating intrageneric biotic interactions (e.g. Cody & Walter, 1976; Martin & Thibault, 1996; Pons *et al.*, 2008) and also exhibits the full spectrum of migratory behaviours seen in birds generally (Shirihai *et al.*, 2001). It is thus ideally suited to investigate relationships between biotic interactions, migration and range dynamics.

2.2 Structure and aims of the thesis

I have organised the research carried out as part of this thesis into three major chapters. Each chapter is self-contained and structured in the style of a journal publication, with an abstract followed by the sections introduction, methods, results and discussion. All references and supplementary information are given in a common reference list and appendix at the end of the thesis. The main research chapters are followed by one final chapter containing a general synthesis and conclusions.

In chapter 3, I aim to improve our understanding of how species' traits interact to influence the size of geographic ranges. I follow a macroecological approach, focusing on patterns across many taxa at large spatial scales. Here, I consider the global range sizes of 165 European passerine species. I relate range size to multiple traits of these bird species in a path model, which allows me to consider complex interactions among traits as well as the direct and indirect effects of traits on range size. The aim here is to include a multitude of life-history, ecological and morphological traits and link them to range size in a way that reflects putative mechanistic relationships reported in the literature. This provides us with an

2 Introduction

opportunity to assess the relative importance of different traits and gain a better understanding of how they influence ranges. This chapter builds partly upon the diploma thesis of Heiko Korntheuer, who took the morphological measurements of bird museum specimens, conducted a preliminary analysis relating species' traits to their occupancy in Europe and wrote this preliminary analysis into a manuscript draft. I have related the trait data to the global ranges of the species, refined the statistical methodology, calculated new path models, incorporated a new phylogeny to test for potential bias due to relatedness and rewritten the manuscript. Katrin Böhning-Gaese provided data on species' traits other than dispersal ability while Carsten Rahbek provided data on the species' global geographic ranges. Monika Schwager, Sven Trautmann and Katrin Böhning-Gaese contributed to the study design and manuscript.

In chapter 4, I aim to elucidate to what extent biotic interactions, species' traits, the evolutionary history of species and the spatio-temporal history of the environment can prevent species from colonising potentially suitable habitat. Here, I narrow the taxonomic focus on the genus *Sylvia*, which allows me to consider potential biotic interactions that have been reported for the genus from local studies. I use advanced GIS and species distribution modelling techniques to estimate the potential ranges of the *Sylvia* warblers for the present and the last glacial maximum. I then relate potential intrageneric competition, dispersal ability, taxon age and the amount of shift in the geographic location of potential habitat since the last glacial maximum to range filling, i.e. the percentage of the present potential range that the species actually occupy. For this chapter, I have collated the data from different sources, conducted all GIS, statistical and species distribution modelling analyses and drafted the manuscript. Katrin Böhning-Gaese and Catherine H. Graham contributed to the study design and manuscript writing.

In chapter 5, I aim to enrich the current debate about new extensions of niche theory by a perspective that focuses on the highly dynamic nature of niches and ranges. I present a conceptual framework for how the spatio-temporal dynamics in the environmental conditions available to a species may affect its niche, its distribution and its movements in geographic space. I also highlight the potentially dynamic nature of niche requirements over a species' life-cycle. From this framework, I derive predictions for the relationship between niches and spatio-temporal range dynamics and then test these predictions using migration in *Sylvia* warblers as a model system. To this end, I make use of new methods to quantify the

characteristics of species' niches. I have developed the framework, conducted all analyses and drafted the manuscript. Catherine H. Graham and Katrin Böhning-Gaese contributed to the study design and manuscript writing.

CHAPTER 3

TOWARDS A MORE MECHANISTIC UNDERSTANDING OF TRAITS AND RANGE SIZES



Poecile cinctus

Submitted to an international journal of ecology as:

Laube, I., Korntheuer, H., Schwager, M., Trautmann, S., Rahbek, C. & Böhning-Gaese, K.

(submitted) Towards a more mechanistic understanding of traits and range sizes.

3.1 Abstract

An important, unresolved question in macroecology is to understand the immense interspecific variation in geographic range sizes. While species' traits such as fecundity or body size are thought to affect range sizes, a general understanding on how multiple traits jointly influence them is missing. Here, we test the influence of a multitude of species' traits on range sizes of European passerine birds in order to better understand possible mechanisms behind macroecological relationships. We evaluated the effect of life-history traits (fecundity, dispersal ability), ecological traits (habitat niche, diet niche, migratory behaviour, migratory flexibility) and a morphological trait (body size) on global range sizes of 165 European passerines. We identified hypotheses from the literature relating traits to range size and used path analysis to test them. Fecundity, dispersal ability, habitat niche breadth and diet niche position had a direct positive effect on range size. Habitat niche breadth also had an indirect positive effect via fecundity. Migratory behaviour had an indirect positive effect via dispersal ability. Body size had a strong positive direct effect which was reduced by negative indirect effects via several other traits. Geographic range sizes of European passerines were influenced by life-history traits (fecundity and dispersal ability), ecological traits (habitat niche breadth, diet niche position and migratory behaviour) and by body size. Traits influenced range size both directly and indirectly. Body size effects were particularly complex with positive and negative effects acting over different pathways. We show that it is necessary to disentangle the direct and indirect influence of multiple traits on range size to better elucidate the mechanisms that generate macroecological relationships.

3.2 Introduction

One of the fundamental traits of a species is the size of its geographic range (Brown *et al.*, 1996; Gaston & Fuller, 2009). Range size influences patterns of species diversity (Jetz & Rahbek, 2002; Soberon & Ceballos, 2011) and species with small ranges have a higher extinction probability (Brown, 1995; Lee & Jetz, 2011) making range size one of the most important criteria for classifying the threat status of a species (IUCN Red List classification, IUCN, 2001).

Interspecific range size variation can cover several orders of magnitude, even between close relatives (Brown *et al.*, 1996). Yet, our understanding of the mechanisms that are

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responsible for this immense variation is limited (Lester *et al.*, 2007). Among the most important factors that influence range size are species' traits. Life-history traits, such as birth rate and dispersal ability (Holt *et al.*, 1997; Böhning-Gaese *et al.*, 2006), ecological traits, particularly habitat niche and diet niche (Brown, 1984; Gregory & Gaston, 2000) as well as migratory behaviour (Gaston & Blackburn, 1996) and morphological traits such as body size (Brown, 1995) have been shown to influence range sizes.

Brown *et al.* (1996) emphasised that several traits might influence range size simultaneously in a complex way, through direct as well as indirect effects. For example, large body size in birds may directly increase range size because of body size-dependent spatial interactions with resources and the environment (Brown, 1984). On the other hand, large-bodied species have lower fecundity which might lead to reduced range size (Gaston *et al.*, 1997; Böhning-Gaese *et al.*, 2000). Finally, large-bodied birds are less likely to be migratory (Hedenström, 2008) and thus might have lower dispersal ability and hence smaller ranges compared to small-bodied birds (Holt *et al.*, 1997; Dawideit *et al.*, 2009). The relative importance of traits can only be assessed by multiple analyses. Also, the apparent statistical significance of traits in individual tests may be caused by correlations with other, non-tested traits (Shipley, 2000). Nonetheless, in most studies, traits have been tested individually.

For a more mechanistic understanding of the relationships between life-history traits, ecological traits, morphological traits and range size, as many traits as possible should be tested simultaneously and interactions among traits should be considered. One option for testing the direct and indirect effects of traits on a response variable is structural equation modelling, in particular path analysis (Mitchell, 1992; Shipley, 2000). Such models, while based on examination of correlational patterns (Shipley, 2000), have been used successfully to evaluate factors that directly or indirectly influence macroecological patterns such as species richness (Kissling *et al.*, 2007; Qian & Kissling, 2010) or extinction risk (Lee & Jetz, 2011).

Here, we tested the most comprehensive set of traits to date for their direct and indirect effects on the geographic range sizes of birds. We used birds in this analysis because traits and range sizes of birds are well documented and a number of studies have already tested individual relationships on which we can base a priori hypotheses (e.g. Gaston *et al.*, 1997; Böhning-Gaese *et al.*, 2006; Hurlbert & White, 2007). We incorporated traits reflecting the life history (annual fecundity, dispersal ability), ecology (habitat niche breadth, diet niche breadth and position, migratory behaviour and flexibility) and morphology (body size) of

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birds into our analysis.

We identified the following a priori hypotheses in the literature about the potential mechanistic relationships between these traits and range sizes of birds (see methods for details): High annual fecundity and high dispersal ability lead to larger range sizes (Blackburn *et al.*, 2006; Böhning-Gaese *et al.*, 2006). Broader habitat niches and broader diet niches cause larger range sizes both directly and also indirectly via increasing annual fecundity (Brown, 1984; Hurlbert & White, 2007). Species with a diet niche position at higher trophic levels have smaller ranges (Gaston, 1994). There is a direct effect of migratory behaviour on range sizes, for which both negative and positive relationships have been postulated in the literature (Gaston & Blackburn, 1996; Bensch, 1999). Migratory behaviour also influences range size indirectly via dispersal ability because migrants tend to be better dispersers which in turn increases range size (Baldwin *et al.*, 2010). Species with higher migratory flexibility have larger ranges (Keitt *et al.*, 2001). Larger body size directly leads to larger range size (Brown, 1984). Additionally, body size is linked indirectly to range size via migratory behaviour, with large bodied birds being less frequently migratory, and via annual fecundity, which is lower in large-bodied bird species (Böhning-Gaese *et al.*, 2000; Hedenström, 2008). We incorporated these hypotheses into a path model and estimated the strength of the direct and indirect effects of species' traits on range sizes.

3.3 Methods

3.3.1 Study species and area, geographic range sizes

We analysed the relationship between traits and global breeding range sizes of 165 European passerine bird species (see Appendix 1). The analysis was restricted to passerines because they share a similar body plan and because dispersal ability can be quantified comparatively easily from morphology (Dawideit *et al.*, 2009).

Global breeding range sizes of birds were calculated using data from a comprehensive global geographic bird range database at a resolution of $1^\circ \times 1^\circ$ (version 30/06/2009). The geographic breeding range of each species was mapped following the approach described in Rahbek and Graves (2000, 2001). Maps represent a conservative extent-of-occurrence based on museum specimens, published sight records and spatial distribution of habitats, which have subsequently been validated by ornithological experts. Range size was quantified as the sum

of the areas of all grid cells a species occupied. We considered only the land surface area of grid cells in square kilometres after applying a Behrmann global equal-area projection.

3.3.2 Species traits

The following traits and their potential relationships with range size have been derived from the literature. We use the traits and their relationships among each other and to range size to define a priori hypotheses on paths in the path diagrams (Fig. 3.1).

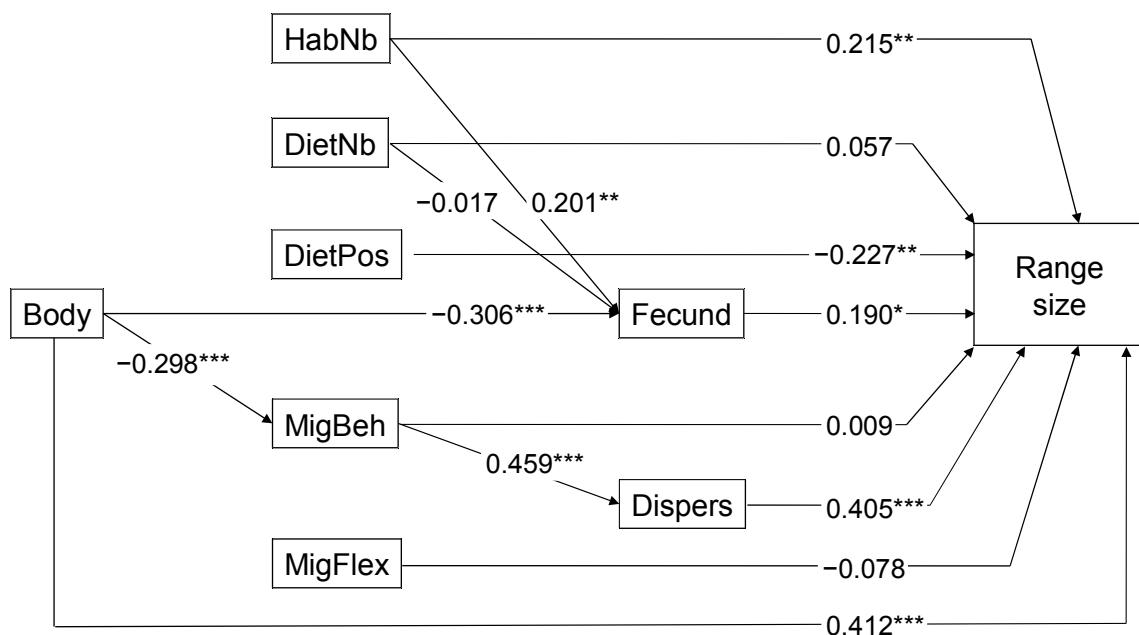


Figure 3.1: Path diagram for path model relating avian traits to global range size (NFI = 0.88, GFI = 0.95, $n = 165$). Path coefficients and significance levels: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Body = log(body mass), HabNb = habitat niche breadth, DietNb = diet niche breadth, DietPos = diet niche position, MigBeh = migratory behaviour, MigFlex = migratory flexibility, Fecund = log(annual fecundity), Dispers = log(dispersal ability).

Annual fecundity

High annual fecundity (e.g. large clutches, many broods per year) may cause large geographic ranges as it could lead to high local abundances (Blackburn *et al.*, 2006) which are often correlated with large range sizes (Brown, 1984; Blackburn *et al.*, 1996; Gaston *et al.*, 1997;

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Borregaard & Rahbek, 2010; direct path from annual fecundity to range size in Fig. 3.1). We quantified annual fecundity as the product of clutch size times the number of clutches per year using data from Ehrlich *et al.* (1994). For *Sturnus unicolor* the number of clutches per year was taken from Birds of the Western Palearctic interactive (BWPi, 2006) because data were missing in Ehrlich *et al.* (1994). For analysis, fecundity was \log_{10} -transformed.

Dispersal ability

Range filling, i.e. the ratio of realised to potential range size, can be limited, amongst other factors, by dispersal ability (Svenning & Skov, 2004). Accordingly, a positive relationship between dispersal ability and geographic range size has been shown in several studies (e.g. Dennis *et al.*, 2000; Böhning-Gaese *et al.*, 2006; direct path in Fig. 3.1).

We quantified dispersal ability as the quotient of Kipp's distance (tip of the first primary to tip of the wing) and bill depth (measured at the proximate edge of the nostrils). This measure has been shown to be the best morphological predictor of dispersal ability in European passerines (Dawideit *et al.*, 2009). We aimed to measure Kipp's distance and bill depth for at least eight museum specimens per species. However, this was not always possible (mean: 7.26 specimens; range: 1–12 specimens). We took care to select adult, non-moulting specimens from localities as close as possible to the centre of the European geographic range and whose time of death was between April and July to avoid measuring wintering individuals. If fewer than eight suitable individuals were available, we relaxed the criteria on locality and time of death. For species that Svensson (1992) describes as sexually dimorphic we measured, if possible, four individuals per sex. For species with more than one subspecies in Europe, we measured the nominate species, as it is usually the most widespread. For species where subspecies had geographic ranges of similar size, we took measures of individuals from both and calculated the mean. All measurements were taken by the same person (H. Korntheuer). When calculating averages across specimens, we first calculated the quotient of \log_{10} (Kipp's distance) and \log_{10} (bill depth) for each individual and then averaged over individuals.

Habitat niche breadth

Habitat niche breadth may be positively related to range size (e.g. Hurlbert & White, 2007; Carrascal *et al.*, 2008) as species that tolerate a wider range of conditions are able to colonise larger geographic areas (Brown, 1984; Gaston *et al.*, 1997; direct path in Fig. 3.1). Habitat

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niche breadth is also expected to increase fecundity and hence indirectly increase range size (indirect path from habitat niche breadth to fecundity in Fig. 3.1) as species that are able to live under a wide variety of conditions and use a broad range of resources should also be able to obtain more resources locally and raise more young (Brown, 1984; Gaston *et al.*, 1997).

To quantify habitat niche breadth, the habitat use of a species was converted to a habitat gradient from closed forest to open country with values of 1 (closed forest), 2 (open forest), 3 (forest edge), 4 (orchards, gardens), 5 (shrub land), 6 (open country with single trees or shrubs, e.g. agricultural land with hedgerows), and 7 (open country without trees or shrubs, e.g. structurally simple arable land) using data from Ehrlich *et al.* (1994). A species was assigned up to three different values along this habitat gradient (Böhning-Gaese & Oberrath, 2003). Habitat niche breadth was calculated as the difference between the maximum and minimum value.

Diet niche breadth

Analogous to habitat niche breadth, species which use a broad range of food sources might be more widespread than more specialised species (direct path in Fig. 3.1). In addition, a broad diet niche may lead to increased fecundity, causing an indirect positive effect of diet niche breadth on range size (Brown, 1984; indirect path from diet niche breadth to annual fecundity, Fig. 3.1). Diet niche breadth was quantified by taking into account the range of utilised food sources. We classified all species as herbivorous, insectivorous or omnivorous using data from Ehrlich *et al.* (1994; Böhning-Gaese *et al.*, 2000). We assigned species that were either herbivorous or insectivorous a diet niche breadth of 1 (38 species), species that were herbivorous and insectivorous a value of 2 (120 species), and omnivorous species a value of 3 (7 species).

Diet niche position

We used the trophic level of a species as a measure of its diet niche position. Species at higher trophic levels are faced with lower food biomass and, consequently, might have lower local abundance and hence smaller range sizes than species at lower trophic levels (Gaston, 1994; direct path in Fig. 3.1). We defined the diet niche position of herbivorous species as 1 (29 species), of species that were herbivorous and insectivorous or that were omnivorous as 2 (35 species), and of insectivorous species as 3 (101 species). Note that no true carnivores (vertebrate-eating species) were included in this study. Inclusion of these species might give

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results that differ from the above hypothesis, as many carnivorous species (especially birds of prey) appear to have rather large geographic ranges (del Hoyo *et al.*, 1994).

Migratory behaviour

Equivocal results have been found for the effect of migratory behaviour on ranges size. On the one hand, migratory birds have been shown to have smaller geographic ranges than non-migrants, potentially because migrants are limited in extending their geographic ranges along a longitudinal axis within the Holarctic due to constraints caused by their migratory behaviour (Böhning-Gaese *et al.*, 1998; Bensch, 1999). On the other hand, long distance migrants have been shown to have larger geographic ranges than sedentary birds in Anseriformes (Gaston & Blackburn, 1996). Here we tested for a potential direct effect of migratory behaviour, as well as for an indirect effect via dispersal ability (Fig. 3.1) because migratory birds show ecomorphological adaptations to long-distance flight also resulting in better dispersal ability (Winkler & Leisler, 1992; Dawideit *et al.*, 2009, Baldwin *et al.*, 2010). We classified the migratory behaviour of a species as 1 (residents, 51 species), 2 (short-distance migrants, with the centre of their non-breeding grounds south of the breeding grounds but north of the Sahara, 51 species), or 3 (long-distance migrants with the centre of their wintering grounds south of the Sahara, 63 species; Böhning-Gaese *et al.*, 2000).

Migratory flexibility

Species with flexible migratory behaviour are more successful invaders than those with a fixed migratory programme (Sol & Lefebvre, 2000). Higher invasion success might lead to larger geographic ranges (Keitt *et al.*, 2001; direct path from migratory flexibility to range size in Fig. 3.1). For migratory flexibility we differentiated between species with an invariable migratory behaviour (value 0, residents or long-distance migrants, 114 species) and species with a flexible migratory behaviour (value 1, short-distance migrants, 51 species). Resident birds and long-distance migrants were classified very conservatively (Böhning-Gaese *et al.*, 2000) and included only species with no intraspecific variation in migratory behaviour within Europe, consequently defining all species *with* intraspecific variation in migratory behaviour as short-distance migrant.

Body size

Larger species interact with their environment at larger spatial scales than smaller species. Thus, smaller organisms are able to attain higher densities in small ranges, while larger ones tend to have less dense, more widely distributed populations (Brown, 1984; 1995; direct path in Fig. 3.1). We also expected species with large body size to be less migratory (indirect path to migratory behaviour; Fig. 3.1) because large birds may need more time to raise their young and to moult and hence have less time for migration and because body size constrains flight speed during flapping flight, the most common flight style of passerines (Hedenström, 2008). Furthermore, large bird species tend to have low fecundity (Böhning-Gaese *et al.*, 2000; indirect path to fecundity in Fig. 3.1). We used body mass as a measure of body size (Clark; 1979). Data were taken from BWPi (BWPi, 2006) and were \log_{10} -transformed.

3.3.3 Statistical analyses

Path analyses

In path analysis (Mitchell, 1992; Shipley, 2000), supposed mechanistic relationships between variables are delineated in a path diagram (Fig. 3.1). Direct effects are measured by the standardised partial regression coefficient (in the following path coefficient) for the direct link between a predictor variable and a response variable. Indirect effects are calculated by multiplying the path coefficients along a path between a predictor and a response variable, and then adding these products for all possible paths between the two, excluding the direct effect (Mitchell, 1992). We used the a priori hypotheses described above to define paths between species' traits and geographic range size (Fig. 3.1). We allowed correlations between predictors if they were significantly correlated ($|r| \geq 0.15$; $P < 0.05$, $n = 165$) and if there was no information in the literature on traits and range size regarding the potential direction and cause of the correlation (Shipley, 2000). We thus fitted correlations between diet niche breadth and (i) dispersal ability, (ii) migratory behaviour, (iii) habitat niche breadth, (iv) diet niche position and (v) body weight, between migratory flexibility and (i) fecundity, (ii) habitat niche breadth, between diet niche position and (i) dispersal ability, (ii) migratory behaviour, as well as between habitat niche breadth and dispersal ability (all $|r| < 0.55$). For clarity's sake, these correlations were omitted from Fig. 3.1. In addition, we examined generalised variance inflation factors from a linear model containing all predictors to assess the potential effect of

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multicollinearity on parameter estimates. The path model was evaluated using the normed fit index (NFI) and the goodness-of-fit index (GFI) (Bentler & Bonett 1980, Arbuckle, 2008). Path analyses were calculated using AMOS (Arbuckle, 2008).

Phylogenetic relatedness

Individual species do not necessarily represent independent data points, as closely related species tend to have more similar traits than distantly related species (Harvey & Pagel, 1991). To check for potential statistical issues arising from phylogenetic non-independence, we tested the residuals from a multiple regression of range size against all species trait variables (corresponding to the direct effects in the path model in Fig. 3.1) for phylogenetic autocorrelation. We used a published supertree for European birds (Thuiller *et al.*, 2011) which contains all of our study species except for *Sitta whiteheadii* and *Anthus petrosus*. All analyses were conducted in R 2.12.2 (R Development Core Team, 2011). We tested for phylogenetic signal in the residuals using the Abouheif test (Abouheif, 1999) with 999 randomisations as implemented in the package *adephylo* (Jombart *et al.*, 2010) and by calculating Pagel's λ , a maximum-likelihood based measure of phylogenetic signal (Pagel, 1997), and testing for a significant difference to a lambda of zero (no phylogenetic structure), as implemented in the package *CAICR* (Freckleton, 2009).

3.4 Results

The path model ($n = 165$ species) adequately described the data structure (NFI = 0.88, GFI = 0.95), yet the variables included in the model explained only $R^2 = 0.25$ of the interspecific variation in global range size. Species with higher fecundity, better dispersal ability, broader habitat niches, lower trophic level and larger body size had larger ranges (Fig. 3.2a–e). Habitat niche breadth had a positive effect on annual fecundity while body size had a negative effect. Body size had a negative effect on migratory behaviour and migratory behaviour positively affected dispersal ability (Fig. 3.1). Generalised variance inflation factors for all predictors were smaller than 2.7, indicating that parameter estimates were not affected by multicollinearity.

The standardised total effect size of each trait on range size could be split into direct and indirect effects (Table 3.1). The strong total effect of habitat niche breadth on range size was mostly caused by a direct positive effect on range size and only a weak indirect positive effect

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through annual fecundity. In contrast, the total effect of migratory behaviour on range size was driven by a stronger indirect effect through dispersal ability, and a weak direct effect. The total effect of body size on range size was complex; its strong positive direct effect was counteracted slightly by two indirect negative effects, one via fecundity and the other via migratory behaviour and dispersal ability (Fig. 3.1), but still resulted in a significant positive total effect.

Both tests on the potential influence of phylogenetic relatedness confirmed that there were no significant phylogenetic signals in the multiple regression residuals (Abouheif test: $P = 0.057$; Likelihood ratio test for $\lambda = 0$: $P = 1$), indicating analyses of the data with non-phylogenetic methods were appropriate. Hence, our results were not affected by the phylogenetic relatedness of the species.

Table 3.1: Standardised total effects, direct effects and indirect effects of bird traits on global range sizes of 165 European passerine species. The correlation between predictor and response variable, the total effect, can be split up into direct effects and indirect effects via other dependent variables. Direct effects are measured by the standardised partial regression coefficients between a predictor variable and a response variable (i.e. the direct link). Indirect effects are calculated by adding the products of all path coefficients over all paths between a predictor and a response variable, excluding the direct effect (Mitchell, 1992).

Bird traits	Total effect	Direct effect	Indirect effect
Fecundity	0.190	0.190	NA
Dispersal ability	0.405	0.405	NA
Habitat niche breadth	0.253	0.215	0.038
Diet niche breadth	-0.060	-0.057	-0.003
Diet niche position	-0.227	-0.227	NA
Migratory behaviour	0.195	0.009	0.186
Migratory flexibility	-0.078	-0.078	NA
Body size	0.295	0.412	-0.117

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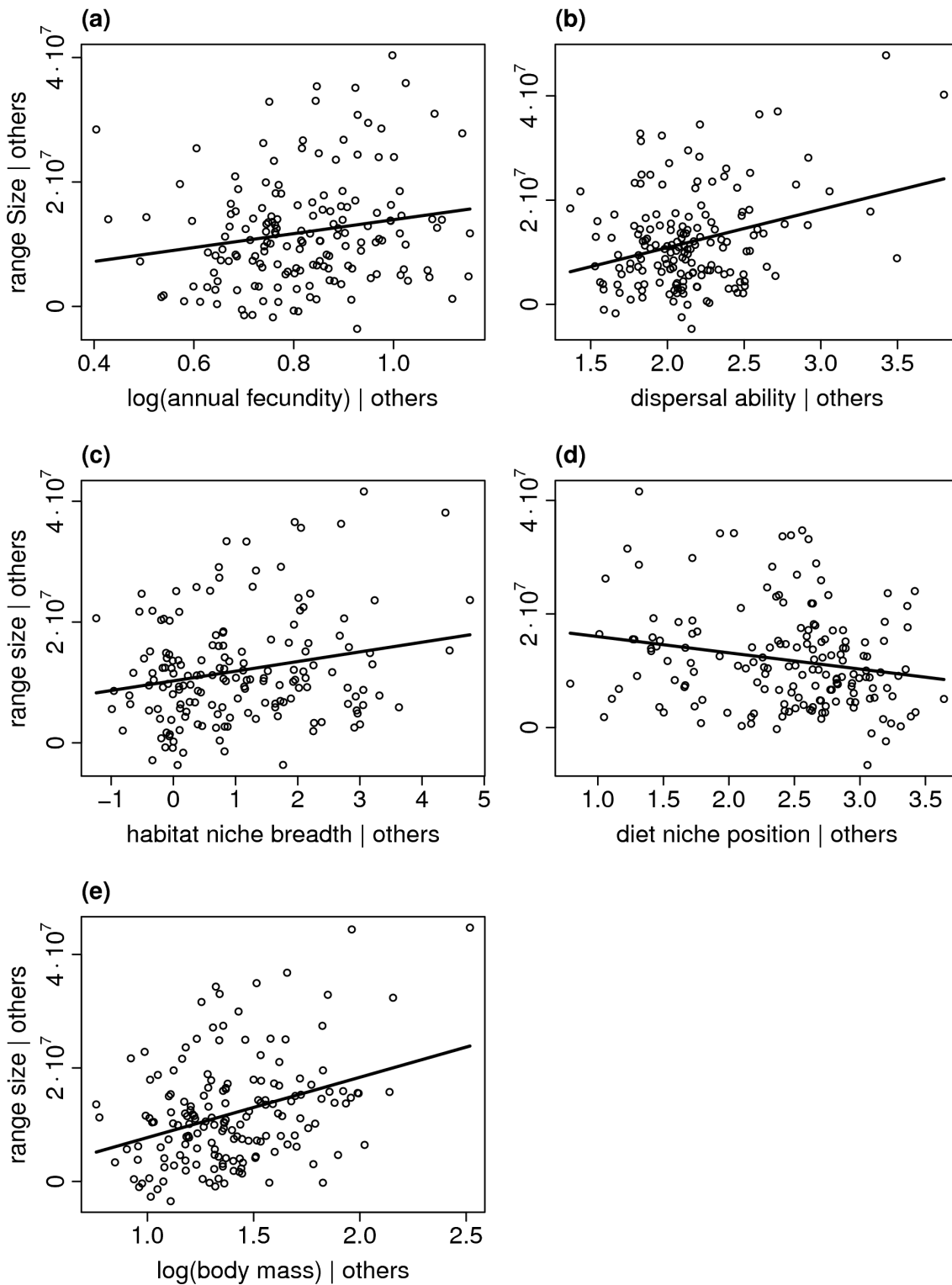


Figure 3.2: Leverage plots after Sall (1990) of bird traits with a significant direct effect on global range size: (a) log(annual fecundity), (b) dispersal ability, (c) habitat niche breadth, (d) diet niche position, (e) log(body mass), calculated from a multiple regression.

3.5 Discussion

We tested the direct and indirect effects of a multitude of traits on the global breeding range sizes of European passerine birds. Path analyses revealed direct effects of fecundity, dispersal ability, habitat niche breadth, diet niche position and body size, as well as indirect effects of habitat niche breadth, migratory behaviour and body size on global range sizes.

Species which raised more offspring per year had larger geographic ranges (Table 3.1, Fig. 3.1). These results confirmed earlier studies that found positive relationships between fecundity and range size (e.g. Blackburn *et al.*, 1996, Gaston *et al.*, 1997). High fecundity might be linked to large range sizes through higher local abundance (Brown, 1984; Blackburn *et al.*, 2006). As a consequence, populations in sink habitats might be “rescued” through regular immigration from source habitats with the result that, on average, a larger proportion of habitat patches might be occupied (Gaston, 2003).

Better dispersers had larger geographic ranges. Poor dispersal ability may lead to a larger proportion of potentially suitable habitat remaining unoccupied (Lester *et al.*, 2007). Also, good dispersers should be able to sustain sink populations at longer distances to source populations than poor dispersers. Even for mobile species such as birds and when multiple traits are tested simultaneously, dispersal ability has an influence on range size (Böhning-Gaese *et al.*, 2006). This suggests that not only trees, amphibians, and reptiles (Svenning & Skov, 2004; Araújo *et al.*, 2008) but also birds might not have fully recolonised their potential geographic range since the last glacial period 20,000 years ago. It appears that, in the face of anthropogenic climate change, at least some bird species might not be mobile enough to track spatial shifts in their climate niche (Devictor *et al.* 2008).

As shown by other studies (Hurlbert & White, 2007; Carrascal *et al.*, 2008), habitat niche breadth had a positive direct effect on range size, reflecting that the habitat niche directly constrains the area which can be colonised by a species. Species with a broad habitat niche also had higher fecundity, resulting in an additional positive indirect effect of habitat niche breadth on range size. Species with broader habitat niches should find the optimal conditions for reproduction more frequently, achieving on average higher fecundity in a given area (Brown, 1984; Gaston *et al.*, 1997).

Contrary to habitat niche breadth, diet niche breadth did not have an effect on range size. Different food sources can occur side by side in the same site, while habitat types cannot. Therefore, it is not surprising that diet niche breadth is less limiting for a species’ range size

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than habitat niche breadth. Furthermore, in regions intensively used and modified by humans, the ability to use anthropogenic food sources might be more important in determining range size than diet niche breadth (Böhning-Gaese & Oberrath, 2001). Finally, our classification of diet niche breadth was rather broad and data taking the relative consumption of finer classified diet items into account might give different results.

Bird species of higher trophic level had smaller geographic ranges. This suggests that herbivorous birds indeed have more food biomass available than insectivores and are hence able to reach higher abundances and find enough food to sustain their populations in more places than insectivores. We detected a positive indirect effect of migratory behaviour on range size, mediated via dispersal ability while migratory flexibility had no effect. This link between migratory behaviour and dispersal ability has been described previously for Passerines (Winkler and Leisler, 1992; Dawideit *et al.*, 2009).

By combining the traits in a path model it was possible to assess direct and indirect effects on range sizes. The benefit of such an analysis was best illustrated for habitat niche breadth, which had both direct and indirect effects on range size, by the presence of an indirect effect of migratory behaviour on range size in the absence of a significant direct effect and by body size showing direct and indirect effects influencing range size in opposite directions. The strong positive direct effect of body size on range size was moderated by two indirect negative effects, one via fecundity and the other via migratory behaviour and dispersal ability. The relationship between body size and range size has always been a matter of debate with published positive (Carrascal, 2008), negative (Glazier, 1980), triangular (Brown & Maurer, 1987) and non-significant relationships (Virkkala, 1993). The present study demonstrates that a potential reason for these complex patterns might be the heterogeneity in mechanisms by which body size affects range size. Depending on the spatial scale of the analysis, the set of species analysed and other traits included in the study, this might result in positive, negative or no total effect of body size on range size.

Both life-history traits, three out of five ecological traits and one morphological trait showed significant direct or indirect effects on range size. Range size thus depended on the life history, ecology and morphology of species and ecological and morphological traits acted both via direct and indirect pathways. This underlines that range size is concurrently influenced by several traits via a number of different, simultaneously acting mechanisms.

Given that our path model was able to account for only a fraction of the total variability in

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range sizes, it is clear that important predictors were lacking from the model. We could not test three potentially important species' traits in the model due to insufficient data: High relative brain size can influence the success of a species in a novel environment and the probability of exploiting novel food sources (Sol *et al.*, 2005) and may hence lead to large geographic ranges. Another trait that might influence range size is the position of a species' habitat niche: Species that prefer widespread habitats have larger geographic ranges than species preferring rare habitat types (Gregory & Gaston, 2000; Hurlbert & White, 2007). Evolutionary age may also affect avian range size, with ranges increasing rapidly after speciation and then gradually declining again (Webb & Gaston, 2000). Furthermore, since our path model focused only on species' traits, it does not incorporate a number of important factors which might also influence geographic range size: the climatic and geologic history of a species' habitat, the history of a species' distribution in space or biotic interactions with other species such as mutualism and pathogens (Orme *et al.*, 2006; Soberon & Ceballos, 2011).

In this study, we demonstrated how multiple, interacting traits have direct and indirect effects on range size. While our results apply to passerines, other bird groups may show different relationships between species' traits and range size. Birds of prey, for example, have a high trophic level but frequently very large ranges. Looking beyond birds, it might be worthwhile to carry out similar studies with other groups of organisms for which similarly good data on traits and range sizes exist, e.g. mammals, amphibians, reptiles, butterflies or plants. For example, it has long been noted that, on average, birds generally have larger geographic ranges than mammals (Anderson, 1984), which might be explained by different direct and indirect effects of traits on the range sizes of the two groups. We expect that for other groups of organisms, other traits might prove to be important. For less mobile species, e.g. reptiles or plants, one may expect dispersal ability to have an even stronger effect than for birds, whereas for butterflies, diet niche breadth (of the larval stages) might potentially prove to be essential. While our path model represents a good hypothesis for how the species' traits we measured influence range sizes, it is clear that those traits cannot fully explain interspecific range size variation. We suggest that it is necessary to disentangle the direct and indirect influence of multiple other species traits and of factors related to the biogeographical and evolutionary history of species in order to better elucidate the mechanisms that generate macroecological range size patterns.

CHAPTER 4

COMPETITION AND DISPERSAL ABILITY INTERACT TO DETERMINE GEOGRAPHIC RANGES OF BIRDS



Sylvia curruca

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4.1 Abstract

Understanding the factors that influence the geographic ranges of species remains a challenge in ecology and evolutionary biology. In particular, little consensus exists as to whether geographic ranges of species are determined by biotic interactions such as interspecific competition. We evaluated how competition, dispersal ability, taxon age and habitat shift since the last glacial maximum influenced the extent to which species in the bird genus *Sylvia* occur in all areas predicted as environmentally suitable (i.e. range filling).

We quantified range filling in the bird genus *Sylvia* using boosted regression trees and ridge regression. We tested for effects of intrageneric competition, dispersal ability, taxon age and habitat shift since the last glacial maximum on range filling using multiple regression. We explore several ways to quantify potential signals of competition at the range scale to reflect different hypotheses about how local competition might scale up to influence large-scale range dynamics.

Sylvia warblers with higher dispersal ability showed higher range filling, but only if competition in less suitable habitats within their potential range was low. Taxon age and habitat shift since the last glacial maximum had no consistent effect.

We show that *Sylvia* ranges are likely shaped by the simultaneous, interactive effect of both competition and dispersal ability. If biotic interactions, like competition, generally influence the ability of species to colonise and occupy habitat at the continental scale, predicting the impact of climate change on biodiversity will be challenging.

4.2 Introduction

Identification of the factors that determine species' geographic ranges has long fascinated ecologists, biogeographers and evolutionary biologists (Dobzhansky, 1950; MacArthur, 1972; Gaston, 2003). While a series of abiotic and biotic factors acting across spatial and temporal scales can influence ranges, knowledge of the specific mechanisms that shape ranges has long remained elusive. This is partly because research has generally focused on only one or two factors at a time. Illuminating the relative importance of and the interactions among different determinants requires integrative analysis (Brooker *et al.*, 2007; Munguia *et al.*, 2008). Here we evaluate in the bird genus *Sylvia* how biotic interactions, dispersal ability, taxon age and current and historic climate conditions influence the extent to which a species occurs in all

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environmentally suitable habitat. We show that ranges are likely shaped by the simultaneous, interactive effect of both competition and dispersal ability and that biotic interactions do influence biogeographic patterns at the continental scale.

Determining if all environmentally suitable habitat is occupied by a species and why such habitat is not occupied can yield new insights into the processes that shape geographic ranges (Pulliam, 2000; Soberon, 2007). In the context of this study, we define environmentally suitable habitat as areas with environmental conditions (such as temperature, precipitation and vegetation structure) that are similar to the area where the species is currently present. The sum of all such environmentally suitable areas is the potential range (Gaston, 2003; Soberon, 2007), which may or may not be occupied by the focal species. The ratio of actual range size to the size of this potential range has been previously defined as range filling (Gaston, 2003; Svenning & Skov, 2004). Species distribution models have been used to estimate potential ranges and examine patterns of range filling in woody plants (Svenning & Skov, 2004; Schurr, 2007; Paul *et al.*, 2009), birds (Graham *et al.*, 2010) and mammals (Munguia *et al.*, 2008). The main drivers of range filling at large spatial scales, i.e. across whole continents, are thought to be biotic interactions, dispersal ability, taxon age and historic climate change (Brooker *et al.*, 2007; Munguia *et al.*, 2008).

Biotic interactions have long been considered a potential force in setting range limits (Dobzhansky, 1950; Jaeger, 1971; Bullock *et al.*, 2000; Case *et al.*, 2005; Price & Kirkpatrick, 2009). Competition results in loss of energy through direct antagonistic interactions and restricted access to space and food and thus, may negatively affect individual reproductive output. The aggregate effect of competition over many individuals may limit population size and successful establishment in a given area, potentially to the extent where population growth is negative and the species is excluded by its competitors. As a result, competition may affect range filling through competitive exclusion or inhibitory priority effects (Fukami *et al.*, 2005; Philpott, 2010). Moreover, the influence of competition on species' ranges is contingent on abiotic conditions (Dunson & Travis, 1991; Gómez-Mestre & Tejedo, 2002), with the impact of competition typically being stronger at range edges where habitat is less suitable (Cunningham *et al.*, 2009; Moore, 2009).

Assessing the influence of competition, and biotic interactions generally, over large geographic extents is fraught with practical difficulties. Biotic interactions are events between individuals and, consequently, have mainly been documented on local to regional scales over

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short time periods (e.g. Catchpole, 1978; Robinson & Terborgh, 1995; Lovette & Hochachka, 2006, Jankowski *et al.*, 2010). It remains a crucial question if local-scale interactions translate to broader scale distributions and if their effects can be detected at a large scale (Connor & Bowers, 1987, Heikkinen *et al.*, 2007). For instance, Gotelli *et al.* (2010) identified a broad scale signature of competition by showing large-scale spatial segregation of congenics and foraging guilds of Danish avifauna even when controlling for habitat availability. They suggested that this pattern might be due to a combination of competitive interactions, such as interspecific territoriality, and conspecific attraction.

Dispersal has long been regarded as a crucial process determining the colonization of environmentally suitable habitat (Bullock *et al.*, 2002). Species with greater dispersal ability should show higher range filling. When considering large spatial extents, such as continents, range filling can also be influenced by constraints on the time available for dispersal, such that evolutionary younger species should show lower range filling than older species of similar dispersal ability (Gaston, 2003; Böhning-Gaese *et al.*, 2006). Mixed support has been obtained for taxon age and dispersal hypotheses (Svenning & Skov, 2004; Schurr, 2007; Munguia *et al.*, 2008; Paul *et al.*, 2009). Finally, variation in range filling may be a result of historical processes related to climate and geography. Species that were forced to track their preferred habitat across continents due to climate fluctuations associated with glacial cycles should have low range filling (Svenning & Skov, 2004; Munguia *et al.*, 2008). Interactions among the four potential drivers of range filling are ecologically plausible. For instance, dispersal ability, taxon age and habitat shift due to past climate change, may have little effect if range filling is constrained by competition (Price & Kirkpatrick, 2009), but such interactions have never been evaluated.

Here we evaluate all four potential drivers of range filling and their interactions to understand which factors shape geographic ranges. We also explore different ways to capture the potential large-scale signal of competition in order to understand how the influence of competition on range dynamics is contingent on habitat suitability. The group that we use to illustrate the advantage of such a comprehensive approach is the bird genus *Sylvia*. The *Sylvia* warblers (*sensu* Böhning-Gaese *et al.*, 2003), a genus of twenty-six species of primarily insectivorous passerines, are ideally suited for studies of range filling due to the extensive evidence for local competitive interactions within the genus (e.g. Cody & Walter, 1976; Cody, 1978; Garcia, 1983; Martin & Thibault, 1996; Elle, 2003; Pons *et al.*, 2008).

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The *Sylvia* warblers exhibit great intrageneric ecological similarity; all members of the genus are primarily insectivorous foliage gleaners with a preference for deciduous, woody vegetation, in which they build simple, cup-shaped nests (Shirihai et al., 2001). This shared ecology is reflected in the intrageneric similarity of morphological traits such as the size and shape of bill, feet and body size (Shirihai et al., 2001). Accordingly, investigations of biotic interactions and habitat selection along habitat gradients find extensive overlap in fine-scale habitat utilization and foraging niche, leading to local-scale intrageneric competition that may influence range filling. Field observations and removal experiments demonstrate co-occurrence and interactions at the scale of individual territories (e.g. Cody & Walter 1976, Elle, 2003, Pons et al. 2008), interspecific territoriality (Cody & Walter, 1976; Cody, 1978, Garcia, 1983), shifts in habitat utilization in the presence of congeners (Garcia, 1983, Martin & Thibault 1996) and priority effects with regard to timing of migration (Garcia, 1983). Thus, *Sylvia* warblers provide the opportunity to test if local-scale competition scales up to influence range filling over larger areas.

Another advantage of using the genus *Sylvia* as a study system is the wealth of geographic, ecological, morphological, and phylogenetic information available (Shirihai et al., 2001; Böhning-Gaese et al., 2003; 2006). They exhibit large variation in range size (4,400–2,975,000 km²) and in the number of overlapping ranges (one to nine species, Fig. 4.1a). Studies on how *Sylvia* species vary morphologically across their range have resulted in detailed knowledge about range boundaries, particularly for the Eurasian breeding ranges (Shirihai et al., 2001). *Sylvia* wing morphology gives an indication of the intrageneric variation in dispersal ability (Böhning-Gaese et al., 2006, Dawideit et al., 2009). Finally, hybridization seems not to be important for limiting range expansion in the genus as there are no major hybrid zones (Shirihai et al., 2001).

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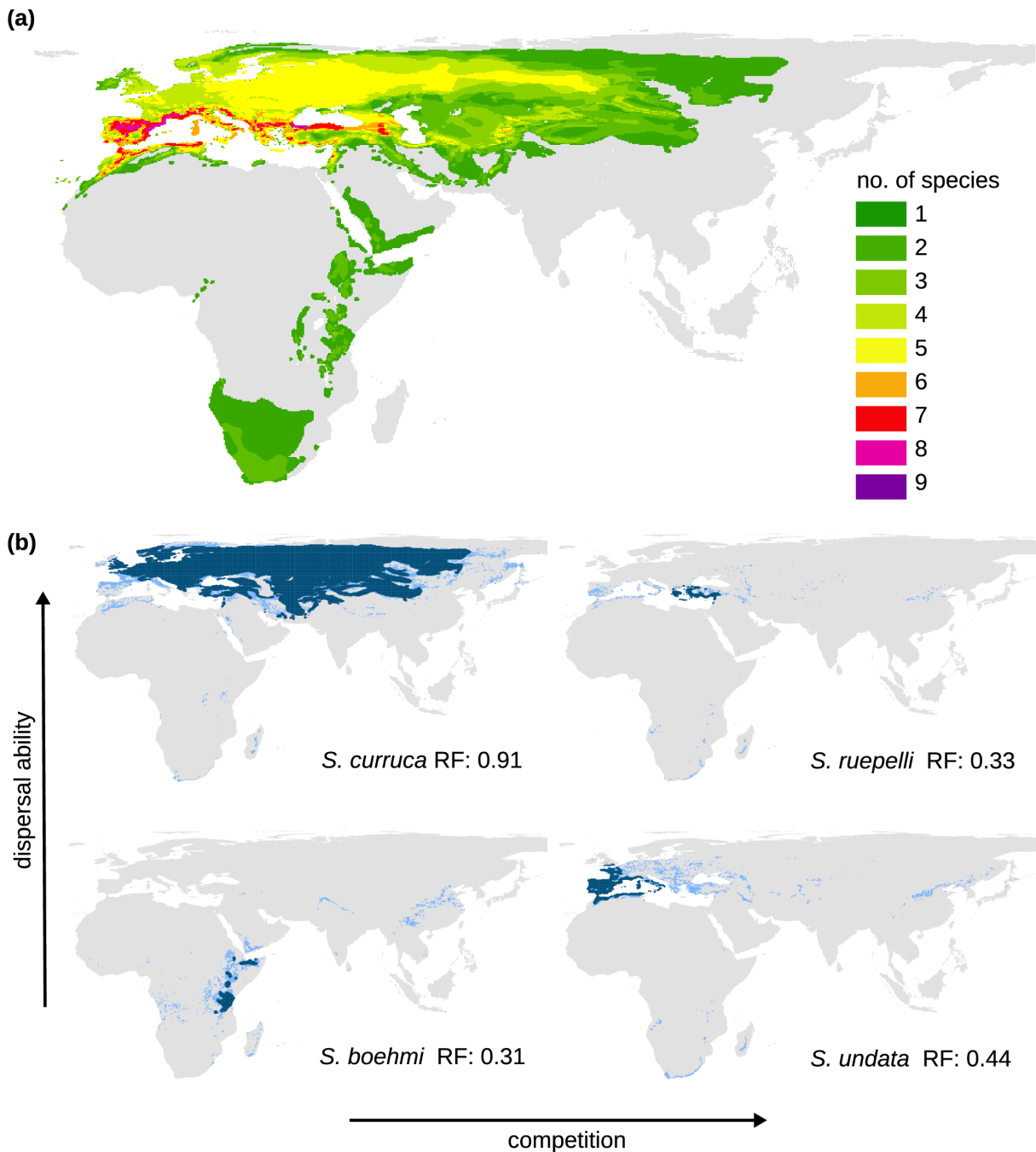


Figure 4.1: (a) Species richness of *Sylvia* warblers based on their breeding ranges. Only the 23 species included in the range filling analysis are shown. (b) Range filling of selected *Sylvia* warblers. Arrows indicate direction of increasing dispersal ability and increasing intrageneric competitive pressure. Dark blue: observed range, light blue: potential range estimate based on 10% range map conversion threshold and boosted regression trees. RF = range filling.

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Given the local-scale evidence for competition among members of the genus, we expect to see lower range filling in *Sylvia* species where a large amount of potentially suitable habitat is occupied by many congeners. If the effect of competition is independent of habitat suitability, we might expect the presence of congeners throughout a species' range to impact negatively on species persistence, which might result in a decreased capacity of that species to expand its range. When this is the case, the mean number of congeners in the total potential range should affect range filling. Alternatively, we might assume that the effect of competition on large-scale range dynamics is exacerbated when habitat suitability for the focal species is low (Case & Taper, 2000). Less suitable habitat might increase resource limitation which in turn could limit population sizes and might also force species to use a broader range of resources, leading to increased niche overlap and competition with congeners. In this case, the number of congeners in highly suitable habitat could be irrelevant for testing the potential effects of competition, since such habitat might allow coexistence. Therefore, we expect the presence of congeners to influence range dynamics at larger scales particularly where habitat is less suitable. Given that some *Sylvia* species successfully colonised large extents of suitable habitat in Northern Eurasia that have only become available after the last glacial maximum, we do not expect a strong effect of taxon age or habitat shift since the last glacial maximum on range filling. Finally, we expect greater range filling in species with higher dispersal ability. This study is the first to use a quantitative, comparative approach to determine how biotic interactions, dispersal ability, taxon age, habitat shift since the last glacial maximum (LGM) and their interactions influence range filling.

4.3 Methods

4.3.1 Data

For data on the distribution of the *Sylvia* species we used breeding range maps from a monograph (Shirihai *et al.*, 2001), except for *S. abyssinica* who was identified as a member of the genus more recently (Böhning-Gaese *et al.*, 2003) and whose breeding range was taken from (Fry *et al.*, 2000). The range maps in Shirihai *et al.* (2001) are based on a combination of expert knowledge with an extensive collation of point records and represent the most comprehensive compilation of knowledge about global *Sylvia* warbler distributions available to date. We restricted our analysis to the breeding ranges because the breeding season is a

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critical life-cycle stage for population persistence where habitat requirements of the species are likely to be most exacting (Pulliam, 2000). The breeding range maps show a high amount of spatial detail and were thus gridded at a resolution of 25 km × 25 km and converted into presences and absences. Given that the decision on how much of a range must be present in a grid cell for a species to be considered present is somewhat arbitrary, we conducted all analyses for two range map conversion thresholds: 10% and 50% present. We excluded *S. melanothorax* and *S. balearica* from the analyses since their very low prevalence, i.e. the proportion of grid cells in the study region they occupy (Manel *et al.*, 2001), rendered them unsuitable for modelling at the continental scale and no reliable range filling values could be obtained for them.

We used environmental data from all biogeographic realms currently inhabited by *Sylvia* warblers: Palearctic, Afrotropic and Indo-malay (Olson *et al.*, 2001). We included the Indo-malay region because three *Sylvia* species have extensive wintering ranges there. Hence, this realm is accessible and suitable for *Sylvia* warblers and should not be excluded a priori as potential habitat. All environmental data were resampled to the same 25 × 25 km grid as the gridded range maps. Our choice of environmental data was informed as much as possible by *Sylvia* ecology and behaviour. We used mean temperature and total precipitation to represent abiotic constraints (time period 1961–90, CRU CL 2.0; <http://www.cru.uea.ac.uk/cru/data/tmc.htm>, New *et al.*, 2000) and the normalised difference vegetation index (NDVI) to reflect plant productivity (time period 1982–1999; Global Land Cover Facility; <http://glcf.umiacs.umd.edu/data/gimms/>; Tucker *et al.*, 2005). NDVI correlates with green biomass and net primary plant productivity (e.g. Chong *et al.*, 1993) and may thus be linked to the availability of bird food resources, in particular insects, in the breeding season (Hurlbert, 2004). We used the mean values of these variables for the three peak breeding months for each species for modelling (Heikkinen *et al.*, 2006). The breeding season for each species was defined based on information collated from the literature (Urban *et al.*, 1997; Fry *et al.*, 2000; Shirihai *et al.*, 2001; Bauer *et al.*, 2005). Further, since habitat choice of *Sylvia* warblers is strongly affected by vegetation type and structure (Shirihai *et al.*, 2001), we also used data on vegetation cover using the UMD Land Cover Classification data (<http://glcf.umiacs.umd.edu/data/landcover/>; 1 km pixel resolution, Hansen *et al.*, 2000). We distinguished between open shrub-land, closed shrub-land, wooded grassland, woodland and non-needleleaf forest and calculated the proportion of each of these classes for each grid cell.

4.3.2 Species distribution models and range filling

Quantifying range filling requires an estimate of a species' potential range. For each *Sylvia* species, we fitted species distribution models combining the climate, remote-sensing and classified land-use data for each grid cell with the range maps and projected them onto the geographic realms where *Sylvia* warblers presently occur, i.e. the Palearctic, Afrotropic and Indo-malay. The sum of the grid cells predicted as suitable for the species by the distribution model represents an estimate of the potential range. To assess the sensitivity of our results to the modelling method, we used two different species distribution modelling algorithms: boosted regression trees, which can fit very complex relationships in a data-driven, iterative approach and ridge regression, where fitted relationships are explicitly specified and typically simpler.

Boosted regression tree models are built in an iterative procedure, where multiple regression trees (i.e. models that relate the probability of a species' presence to environmental conditions by recursive binary splits; Hastie *et al.*, 2001), are combined in a linear fashion and subsequent regression trees focus on the residuals of the previous model so as to minimise a loss function such as deviance (Elith *et al.*, 2008). The process of building and combining the collection of regression trees is called "boosting" (Friedman *et al.*, 2000). As a result, boosted regression trees fit complex non-linear effects and interactions in a data-driven fashion. We fitted models using a bag fraction (the proportion of data drawn randomly at each iterative step) of 0.5 and a tree complexity of seven. Learning rate (the contribution of each tree to the final model) was adjusted according to the number of presences for each species (< 100 presences: 0.001, < 1000 presences: 0.01, < 10,000 presences: 0.02, > 10,000 presences: 0.05). The optimal number of trees was estimated using 10-fold cross validation to calculate predictive deviance on models of increasing complexity, yielding final models with 2000–8000 trees. To evaluate the final models, we used 10-fold cross validation with each of ten data subsets having the same prevalence as the original data and report cross-validated AUC and percentage of deviance explained.

Ridge regression is a logistic regression technique where model complexity is constrained through a penalty term to avoid over-fitting (Reineking & Schröder, 2006). In this method the generalization ability of the logistic regression model is optimised to enhance the fit on the training data by increasing model complexity only when the resulting decrease in variance outweighs the increase in bias. The ridge or penalised maximum likelihood method uses the

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sum of the squared values of the parameter estimates to quantify model complexity (Harrell, 2001). Ridge regressions were fitted using restricted cubic splines with three nodes for temperature, precipitation and NDVI. The five land cover variables were fitted as linear terms. For each model, we estimated the best penalty value by optimizing a modified AIC (Harrell, 2001). To evaluate the final models, we used a bootstrap resampling procedure (Efron, 1983) with one thousand replicates and report validated $R^2_{\text{Nagelkerke}}$ and AUC as performance measures. Bootstrap samples were generated by randomly selecting grid cells with replacement while keeping the same prevalence and total number of grid cells as the original dataset. For each resampling run, we refitted the model on the bootstrap sample and calculated the difference in performance measures between the bootstrap sample and the original data. This difference is an estimate of statistical optimism i.e. the tendency of a model to have better predictive accuracy when evaluated using the training data as opposed to new data (Steyerberg, 2009). Subtracting the average optimism over all resampling runs from the performance of the model fitted and evaluated on the original data then gives the final internally validated performance value (Harrell, 2001).

We acknowledge recent criticism of AUC as a measure of evaluation for species distribution models (Lobo *et al.*, 2008). The prevalence of our species in the study area is low (based on 50% range map conversion threshold: min = 0.0004, 25% quartile = 0.0006; median = 0.014, 75% quartile = 0.037, max = 0.231). This might lead to an overestimation of AUC values. Yet, we note that AUC values are not significantly lower for species with higher prevalence ($r > -0.4$, $P > 0.06$ for all algorithms and range map conversion thresholds). Also none of our hypotheses and tests is based on AUC values and, thus, we do not expect that potentially overestimating model performance should bias our results.

The output of our species distribution models is a continuous probability. Since we were interested in the size of a species' potential range, it was necessary to define a threshold to convert the continuous output into a binary classification of "suitable" versus "unsuitable" habitat. To assess the sensitivity of our results to varying this threshold, we calculated our analyses for three different threshold rules identified as best practice by a comprehensive comparative study, Liu *et al.* (2005). We present results for setting the threshold so that specificity equals sensitivity in the main text and provide results for two additional threshold rules (threshold = mean occurrence probability; threshold = observed prevalence) in appendix 2 to demonstrate that our results were robust to the choice of threshold rule.

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Modelling was carried out in R (version 2.5.1, R Development Core Team 2011) using published code and libraries (Harrell, 2001; Elith *et al.*, 2008; Freeman & Moisen, 2008). For each *Sylvia* species, we calculated range filling as the area of the range from the range map (realised range) divided by the area predicted as presence by the species distribution model (potential range).

4.3.3 Potential determinants of range filling

Competition

We measured competition in two ways: first, the mean number of congeneric species in grid cells in the unoccupied parts of the potential range and second, the mean number of congeneric species per grid cell in subsets of the potential range (i.e. both occupied and unoccupied) based on habitat suitability. The first approach measures the potential role of competition in preventing the *Sylvia* warblers from extending their ranges into the unoccupied parts of the potential range. We expect lower range filling for species with a high mean number of congenics in those parts of their potential range. The second approach measures how the potential impact of local competition on large-scale distributions is affected by habitat suitability. We expect range filling to be more strongly impacted by competition in areas of lower habitat suitability. To explore this issue, we repeated our analyses using the mean number of congenics in all of the potential range, the least suitable 50% of the potential range and the least suitable 25% of the potential range. Habitat suitability was quantified as the continuous output of the boosted regression trees and ridge regressions used to identify the species' potential ranges.

Both our approaches to measure competition assume that the presence of several *Sylvia* species in a grid cell signifies an increased chance that those species will interact locally. There are several potential issues with this assumption. First, the number of congenics in a cell could simply represent habitat heterogeneity; in more heterogeneous cells *Sylvia* warbler species could occur as spatially segregated populations in different habitats within the cell and, therefore, not compete. This is unlikely because habitat preferences of *Sylvia* warblers are similar (Shirihai *et al.*, 2001) and local co-occurrence and use of the same habitat is well documented in *Sylvia* warblers, even in small areas (e.g. Elle, 2003: 2 species, 1.28 km²; Pons *et al.*, 2008: 3 species, 0.16 km²; Cody & Walter, 1976: 4 species, 0.03 km²). Second, using the mean number of congenics in a given area as a measure of local competitive interactions

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involves the simplifying assumption that all co-occurring congeners are equally important competitors of a given focal species. While the importance of competitive interactions among *Sylvia* warblers may vary (e.g. Schaefer & Barkow, 2004), competition has been documented for numerous different species pairs. Further, co-occurrences of large numbers of congeners mainly reflect combinations of temperate and Mediterranean species (Fig. 4.1a) for which evidence for intrageneric competition is strongest (e.g. Cody & Walter, 1976; Cody, 1978; Garcia, 1983; Martin & Thibault, 1996; Elle, 2003; Pons *et al.*, 2008). Hence, the mean number of congeners likely provides a useful measure of variation in competitive pressure even though it does not explicitly incorporate differences in interactions strength within the genus. Finally, *Sylvia* warblers may compete with birds outside the genus. While information on competitive interactions between *Sylvia* warblers and other bird genera is far from complete, particularly for the tropics, we are not presently aware of an important extrageneric competitor. Given that we have evidence for local-scale intrageneric competition and that we can assume that competition should be most severe within the genus where foraging behaviour and morphology are most similar (Gotelli *et al.*, 2010), we focus on intrageneric competition among the *Sylvia* warblers.

Dispersal ability

To quantify the dispersal ability of each species, we took an ecomorphological approach. We use morphological traits that are related to natal dispersal distance in passerines and have been previously identified as the most useful surrogate measure for dispersal ability in this group (Dawideit *et al.*, 2009): Kipp's distance (distance between tip of the first secondary and tip of the longest primary/wing tip with the wing folded) divided by bill depth. Birds with high Kipp's distance have more pointed wings which makes forward flight faster and more efficient (Rayner, 1988; Norberg, 1989; Leisler & Winkler, 2003). Shallow bill depth is indicative of insectivorous migratory birds which tend to have larger dispersal distances (Peach *et al.*, 2001; Dawideit *et al.*, 2009).

Taxon age

As an estimate of the age of each *Sylvia* species, we used data from a time-calibrated phylogeny (Böhning-Gaese *et al.*, 2006). Since we had no genetic data for *S. deserti*, we omitted this species from our analyses. Taxon age in mya was log-transformed to satisfy distributional assumptions of regression analysis. We acknowledge that taxon age as defined

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from nodes in a phylogenetic tree may underestimate the true age of a species, e.g. where it persists after giving rise to daughter species (Webb & Gaston, 2000).

Habitat shift since LGM

In order to assess how much the geographic position of a species' preferred habitat has shifted since the late Pleistocene, we fitted species distribution models to current data and projected them back to LGM. Specifications are the same as for species distribution models used to quantify range filling, but with two exceptions:

First, to project models back in time we had to restrict the analyses to variables that were available for both time periods. Hence, for these models we used only temperature and precipitation for the present (1960–1990) and for the last glacial maximum (21,000 BC) and no data on NDVI or vegetation cover. Since estimations of past climate vary with the general circulation model (GCM) used, we conducted the analyses with data from two different GCMs, the community climate system model (CCSM) and the model for interdisciplinary research on climate (MIROC). Layers from the Paleoclimate Modelling Intercomparison Project Phase II (PMIP2; <http://pmip2.lsce.ipsl.fr/>) (Braconnot *et al.*, 2007) were downscaled using the projected change in temperature or precipitation derived from the difference between GCM output for the past and present as applied to WorldClim current climate (see <http://www.worldclim.org/downscaling>). Second, as breeding phenology in the past is unknown, we used yearly means of the climate variables for both the present and the LGM instead of averaging over the three peak breeding months. We acknowledge that projecting species distribution models back in time involves a number of simplifying assumptions. However, understanding the impact of habitat shift on range filling requires exploring variation in spatial shifts in temperature and precipitation regimes at the continental scale. Our conclusions are therefore robust to uncertainty in the spatial delineation of past species ranges at higher resolutions.

We quantified habitat shift since LGM as the area of geographic non-overlap between the past potential range and the present potential range as predicted from the above species distribution models divided by the combined area of both potential ranges.

Statistical Analysis

We used multiple regression to assess the influence of competition, dispersal ability, taxon age and habitat shift since LGM on range filling. We started with a model containing the four predictors as linear terms and checked for non-linearity in the relationships by examining smoothed scatterplot matrices and ceres plots (Fox, 1997). We tested in the models successively all two-way interaction terms in addition to the linear terms and kept those in the model that were significant (Crawley, 2007). In addition, we examined the results of a model selection procedure based on AICc, exploring all models that complied with the principle of marginality (Fox, 1997). This analysis demonstrated that the AICc of our final regression models (Table 4.1) deviated by less than two from the model with the lowest AICc and thus belong in the group of equally well supported best models (Burnham & Anderson, 2002; see Appendix 3). P-values for individual t-tests in multiple regressions were adjusted for multiple inference to control for inflation of type I error (Hothorn *et al.*, 2008). We tested for phylogenetic signal in the residuals of the final model using Moran's I and the phylogenetic distance matrix A (Pavoine *et al.*, 2008). All analyses were conducted in R (version 2.12.2, R Development Core Team 2011) using published code and libraries (Fox, 2003; Dray & Dufour, 2007; Hothorn *et al.*, 2008; Pavoine *et al.*, 2008).

4.4 Results

Species distribution models for the *Sylvia* warblers were well validated (mean \pm standard deviation over all models; boosted regression trees, % deviance explained = 57.27 ± 18.40 , AUC = 1st quartile: 0.979, median: 0.984, 3rd quartile: 0.987; ridge regressions, $R^2_{\text{Nagelkerke}} = 0.44 \pm 0.12$, AUC = 1st quartile: 0.939, median: 0.955, 3rd quartile: 0.964).

Estimates of range filling for *Sylvia* species varied from 0.22 to 0.91 (see Appendix 4). Long-distance migrants breeding in North-Western Eurasia like *S. curruca*, *S. borin* and *S. communis* filled a large proportion of their potential range, while the lowest range filling values were shown by the North African short-distance migrant *S. deserticola* and the African residents *S. lugens* and *S. boehmi*.

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Range filling was strongly influenced by the interaction between dispersal ability and competition (Fig. 4.2, Table 4.1). Dispersal ability had a positive effect on range filling only for those *Sylvia* species that had few competitors in their unoccupied potential range (Fig. 4.2). Taxon age had no consistent effect on range filling (Table 4.1). Older *Sylvia* species showed higher range filling than younger species in only 25% of model realizations. (Fig. 4.3c, Table 4.1). Habitat shift since LGM had no effect on range filling (Fig. 4.3d, Table 4.1). These results were robust to modelling decisions, such as threshold used to convert range maps to presences and absences, model algorithm and LGM general circulation model (see methods; Table 4.1). None of the final regression models showed phylogenetic signal in the residuals. The effect of the interaction of competition and dispersal on range filling depended on the habitat suitability of the area considered for the assessment of competition (Table 4.2, Appendix 3). Range filling was most strongly related to competition in areas of low habitat suitability (Table 4.2, Appendix 3).

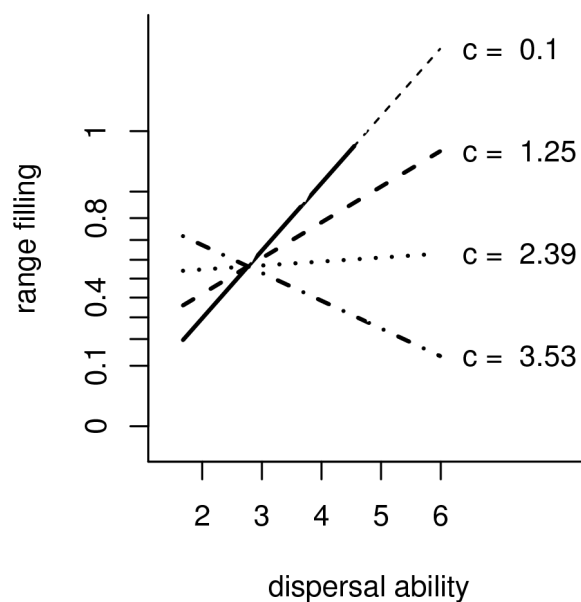


Figure 4.2: Interactive effect of dispersal ability and competition on range filling, calculated with 10% range map conversion threshold, boosted regression trees, and CCSM climate model (Table 4.1, line 1). Shown are regression lines illustrating the effect of dispersal ability on range filling for different levels of competition (Fox, 2003). Regression line slopes for competition levels 2.39 and 3.53 are not significantly different from zero. c = competition.

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Table 4.1: Effects of competition in the unoccupied parts of the potential range, dispersal ability, taxon age, habitat shift since LGM and the interaction between dispersal ability and competition on range filling. Multiple regressions for different range map conversion thresholds, model algorithms and past climate models. BRT = boosted regression trees; ridge = ridge regression. Shown are standardised partial regression coefficients, standard errors (in parentheses), significances adjusted for simultaneous inference and whole model R^2 and significances. Response $\text{asin}(\sqrt{x})$ transformed. $n = 23$.

range map conversion threshold	model algorithm	past climate model	competition	dispersal ability	log (taxon age)	habitat shift since LGM	dispersal ability × competition	model R^2
10%	BRT	CCSM	-0.43 (0.20)	0.42 (0.18)	0.49 * (0.16)	0.14 (0.16)	-0.72 ** (0.20)	0.68 **
10%	BRT	MIROC	-0.47 (0.19)	0.45 (0.17)	0.49 * (0.15)	0.24 (0.15)	-0.71 ** (0.18)	0.71 ****
10%	Ridge	CCSM	-0.33 (0.13)	0.48 ** (0.11)	0.33 (0.12)	-0.32 (0.12)	-0.66 *** (0.13)	0.85 ****
10%	Ridge	MIROC	-0.43 * (0.13)	0.49 ** (0.11)	0.31 (0.13)	-0.26 (0.11)	-0.64 ** (0.13)	0.84 ****
50%	BRT	CCSM	-0.46 (0.22)	0.49 (0.20)	0.41 (0.18)	0.09 (0.18)	-0.62 * (0.21)	0.61 **
50%	BRT	MIROC	-0.52 (0.21)	0.52 (0.19)	0.42 (0.17)	0.22 (0.16)	-0.62 * (0.2)	0.64 **
50%	Ridge	CCSM	-0.33 (0.15)	0.49 ** (0.12)	0.34 (0.12)	-0.34 (0.14)	-0.70 *** (0.14)	0.83 ****
50%	Ridge	MIROC	-0.45 * (0.14)	0.49 ** (0.12)	0.30 (0.13)	-0.22 (0.13)	-0.68 ** (0.14)	0.81 ****

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

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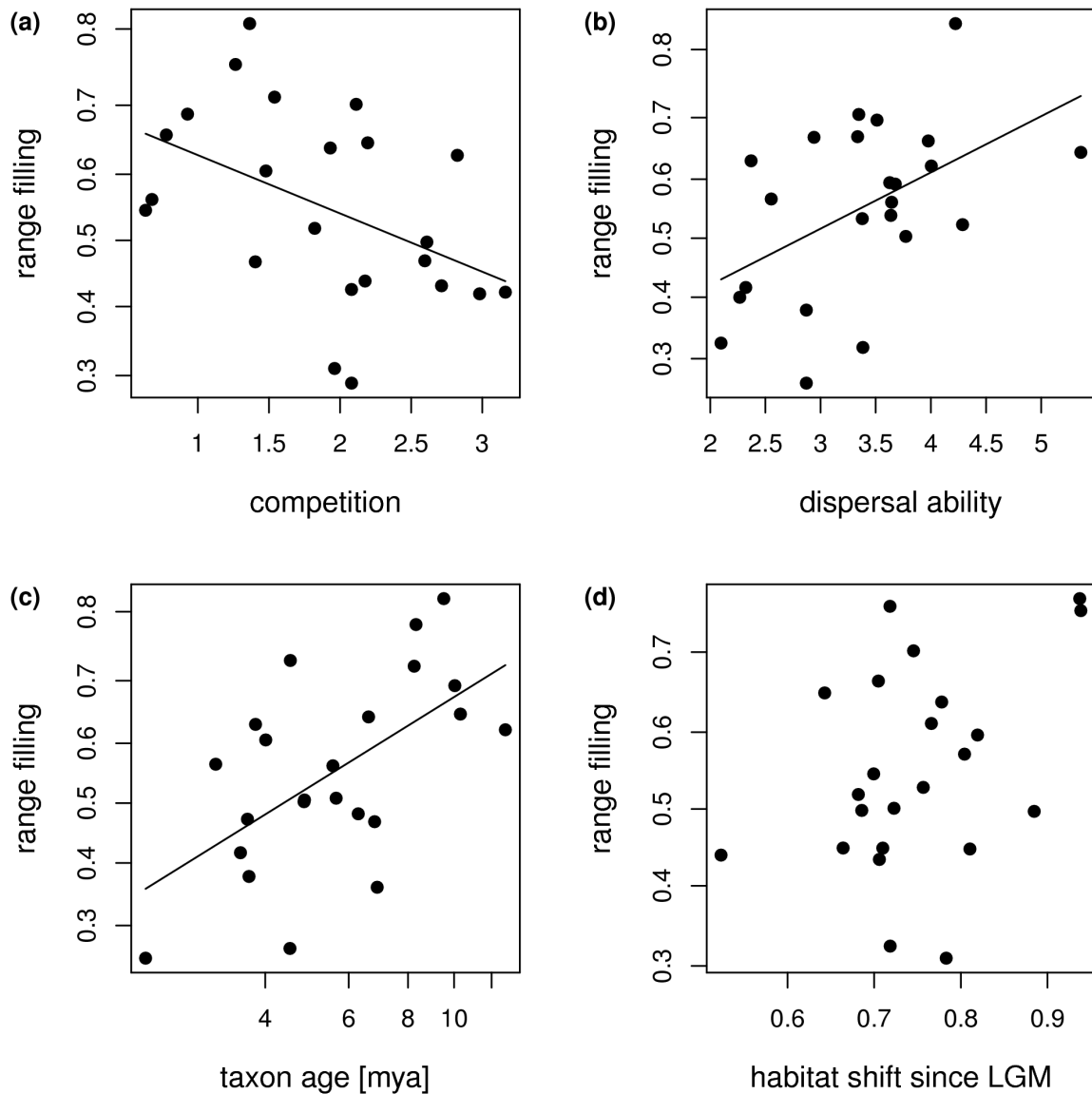


Figure 4.3: Effect of (a) competition, (b) dispersal ability, (c) taxon age and (d) habitat shift since LGM on range filling for the multiple regression model ($n = 23$) based on 10% range map conversion threshold, boosted regression trees and CCSM climate model and (Table 4.1, line 1). Leverage plots after Sall (1990).

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Table 4.2: Effect of habitat suitability on the relationship between competition and range filling. Habitat suitability = subset of the potential range used to estimate competition, Multiple regressions based on boosted regression trees, 10% range map conversion threshold and CCSM past climate model. Shown are standardised partial regression coefficients, standard errors (in parentheses), significances adjusted for simultaneous inference and whole model R^2 and significances. Response $\text{asin}(\sqrt{x})$ transformed. $n = 23$.

habitat suitability	competition	dispersal ability	log (taxon age)	habitat shift since LGM	dispersal ability × competition	model R^2
all habitat	-0.40 (0.33)	0.47 (0.23)	0.60 * (0.19)	0.17 (0.22)	-0.73 (0.31)	0.58 **
least suitable 50%	-0.44 (0.31)	0.47 (0.22)	0.63 * (0.18)	0.20 (0.21)	-0.77 ° (0.30)	0.61 **
least suitable 25%	-0.53 (0.25)	0.48 ° (0.19)	0.59 * (0.17)	0.20 (0.18)	-0.85 * (0.25)	0.67 **

° $P < 0.1$; * $P < 0.05$; ** $P < 0.01$.

4.5 Discussion

Range filling in *Sylvia* warblers was strongly determined by an interaction between dispersal ability and competition. *Sylvia* species with higher natal dispersal distances filled a larger proportion of their potential range, but only when dispersal was not constrained by intrageneric competition. For example, *S. curruca* and *S. rueppelli* are both good dispersers, but only *S. curruca* has been able to colonise most of its potential habitat in Northern Europe and Central Asia where few other *Sylvia* warblers occur; *S. rueppelli* failed to invade large portions of its potential habitat in the Mediterranean where species richness of *Sylvia* warblers is highest (Fig. 4.1b). Conversely, the rather poor dispersers *S. boehmi* and *S. undata* show no marked difference in their range filling although *Sylvia* richness in the potential habitat of *S. undata* in Central Europe is much higher than for *S. boehmi* in East Africa (Fig. 4.1b).

Previous studies on range filling have not addressed competition directly even though it has long been considered an important determinant for shaping species ranges (Dobzhansky, 1950; MacArthur, 1972). Distribution patterns that concur with expected effects of

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competition at the regional scale have been found for mammals (Anderson *et al.*, 2002; Sanchez-Cordero *et al.*, 2008) and birds (Gross & Price, 2000). However, quantitative evidence of the effect of competitive interactions at larger spatial scales remains very limited (but see Heikkinen *et al.*, 2007; Gotelli *et al.*, 2010). Recently, intrageneric competition in songbirds has been found to be important for setting elevational range limits in tropical bird communities (Jankowski *et al.*, 2010). Where *Sylvia* species occur syntopically, competition frequently manifests itself as segregation at the microhabitat and diet level (Martin & Thibault, 1996; Pons *et al.*, 2008) and sometimes as interspecific territoriality (Cody & Walter, 1976; Cody, 1978; Garcia, 1983). It is conceivable that such local segregation of niches and space might allow coexistence at larger spatial scales (Wiens, 1989; Lovette & Hochachka, 2006). This seems to be the case in the core of the species' ranges, where habitat suitability is optimal for *Sylvia* warblers. Consequently, patterns of congeneric species richness across the whole potential range are not related to range filling. Nevertheless, our results indicate that the effects of intrageneric competition observed at the local scale can influence the size of the realised ranges of the species at the geographic scale when habitat suitability is low. Accordingly, congeneric species richness was increasingly related to range filling when quantified only for less suitable habitat. Range margins often have lower habitat suitability than the range core (Brown *et al.*, 1996; Sagarin & Gaines, 2002). The unoccupied parts of the potential range of *Sylvia* warblers are mainly areas with low habitat suitability located at the edge of the potential range. Hence, range filling was even more strongly related to the number of congenics in the unoccupied potential range than to the number of congenics in the least suitable 25% of the potential range. These results correspond well to recent experimental transplant studies showing that the harsher abiotic conditions at range edges lead to an increased impact of intrageneric competition on salamanders (Cunningham *et al.*, 2009) and of competition by neighbouring annuals on an annual legume (Moore, 2009). Thus, while *Sylvia* warblers engage in local-scale competitive interactions throughout their ranges (Cody & Walter, 1976; Cody, 1978; Garcia, 1983; Martin & Thibault, 1996; Elle, 2003; Pons *et al.*, 2008), this translates into consequences for large-scale distributions only in less suitable habitat.

In *Sylvia* warblers, dispersal ability had a clear effect on range filling but there was no evidence for dispersal limitation caused by historic habitat shift. A similar pattern was observed in the plant family Proteaceae, where dispersal ability influenced range filling and

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historic climate change or geographic barriers had little influence (Schurr, 2007). Conversely, for tree and mammal taxa, where range filling is primarily a result of historic constraints related to geography and climate, no effect of dispersal ability could be detected (Svenning & Skov, 2004; Munguia *et al.*, 2008). These results suggest that the effect of dispersal ability on range filling is most pronounced when dispersal has not been constrained by current or historic spatial configuration of habitats and climate.

We found no consistent tendency for older *Sylvia* warblers to fill more of their potential range than younger species. An effect of taxon age on range filling has been suggested to result mainly from the limited time for dispersal available to younger species (Paul *et al.*, 2009). Another possible explanation for a correlation between high range filling and taxon age might be that older species possess a suite of traits, such as broad environmental or habitat niches, disturbance tolerance, or high population growth rates that promotes rapid range filling and simultaneously enables the long-term survival of a taxon (Webb & Gaston, 2000). We might expect older species to be less affected by competition due to their potentially greater divergence in ecological requirements. Therefore, a third explanation for higher range filling in older species might be that those species are less affected by the presence of congeners than younger species. However, we did not find support for an interaction between taxon age and competition. Other studies relating taxon age to range filling have focused on plants, where no clear relationship has been found (Schurr, 2007; Paul *et al.*, 2009). The oldest *Sylvia* species with the highest range filling (e.g. *S. curruca*, range filling = 0.91, range size = 2,975,000 km²) must have occupied their large ranges rapidly after the last glacial maximum towards the end of the Pleistocene (Shirihai *et al.*, 2001). Hence, the *Sylvia* warblers appear not to be dispersal limited. Also, older species did not necessarily have more time for dispersal. The rapid expansion of species into Northern Eurasia may also explain why we did not find an effect of habitat shift since LGM on range filling for the *Sylvia* warblers, even though quaternary climate change clearly had an effect on the current distribution of many taxa (e.g. Svenning & Skov, 2004).

We observed an increasing disparity in range filling values based on boosted regression trees and ridge regressions for species with lower prevalence (Appendix 4). Prevalence may affect the accuracy of distribution models (e.g. Marmion *et al.*, 2009). Yet, although models for species with lower prevalence showed increasing variation in range filling between model algorithms, identification of range filling determinants was robust to modelling method. We

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also note that the validity of the hindcasting approach used to quantify habitat shift since LGM rests on the assumption of niche conservatism for *Sylvia* warblers in the last 21,000 years (Böhning-Gaese *et al.*, 2003). Further, our potential range estimates may underestimate the true extent of the geographic area suitable for the species since they are derived from realised occurrences (Pulliam, 2000). Due to being limited to bird species with strong evidence for local-scale competition, our sample size is at the lower end of what is desirable for our analysis. Hence, high model R^2 should not be taken as an indication that range filling is not determined by factors not included in our analysis. We also note that a measure attempting to capture the signal of local competition in *Sylvia* warblers at larger scales could be enhanced by detailed comparative studies on interaction strength within and beyond the genus as well as abundance information across the whole intercontinental extent of *Sylvia* distributions. While the *Sylvia* warblers are probably among the best-researched bird genera, such comprehensive information is not available and we prefer to use a measure that reflects the extent of current knowledge. If this approach results in an oversimplified measure, we would expect to find no consistent relationship with range filling. Finally, we acknowledge this is a correlational study. It would be exciting to compare our findings to results from large-scale experimentation addressing establishment success and intrageneric competitive pressure across the entire potential geographic range of several *Sylvia* species.

In sum, our results indicate that competition and dispersal ability are among the forces that determine the distribution of species at the continental scale. However, the effect of competition on range-filling is contingent on species traits and habitat suitability. We therefore strongly recommend the integration of multiple factors, including biological interactions, and the examination of potential interactions among those factors in analyses of range characteristics. We would also caution against the assumption that biotic interactions are generally not important for large-scale range dynamics. If competition generally plays a dominant role and even interacts with other factors in determining if a species is able to colonise and occupy suitable habitat at large scales, then it will, indeed, be a challenge to predict the ability of species to persist in the face of habitat shifts caused by climate change.

CHAPTER 5

NICHE AVAILABILITY IN SPACE AND TIME: MIGRATION IN *SYLVIA* WARBLERS



Sylvia borin

Will be submitted to an international journal of ecology as:

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migration in *Sylvia* warblers.

5.1 Abstract

In the context of recent advances in ecological niche modelling, both the environment and the ecological niche of a species have often been treated and quantified as static entities. In reality, the environment and species' niche requirements are dynamic on a variety of scales. We propose a conceptual framework of how species' realised niches and geographic ranges are shaped by the decoupled spatio-temporal availability of different environmental conditions and by changes in niche requirements throughout an organism's lifetime. Testing predictions derived from the framework using migration of *Sylvia* warblers yielded new insights: Climate niche tracking was unlikely to be the main driver of migration in the genus and potentially conflicted with land-cover niche tracking. *Sylvia* niches were smaller during the breeding season, demonstrating that niche requirements can be dynamic in time. We suggest that taking dynamic environments and niche requirements into account enhances our understanding of the drivers behind spatial movements of organisms and the dynamics in their niches and geographic ranges.

5.2 Introduction

Recently, there is a renewed conceptual focus in ecology on the ecological niche, partly sparked by developments in species distribution modelling (e.g. Soberon, 2007; Pearman *et al.*, 2008; Colwell & Rangel, 2009; Wiens *et al.*, 2010). In this context, both the environment and the ecological niche of a species have often been treated and quantified as static entities (Fisher *et al.*, 2010; Franklin, 2010). For example, it is common in species distribution modelling to use occurrence and environmental data averaged over long time periods, e.g. years, to estimate the realised niche of a species (e.g. Dormann *et al.*, 2010). However, in reality, the environmental conditions available to organisms are highly dynamic in space and time on a variety of scales (e.g. days, seasons, decades). These dynamics result in diverse phenomena such as the daily movements of zoo-plankton in the water column (Williamson *et al.*, 2011), annual migrations of birds, mammals, fish and insects (Milner-Gulland *et al.*, 2011), periods of dormancy in crustaceans, fungi and plants (Lubzens *et al.*, 2010), and range shifts of organisms as a consequence of climate change (Huntley *et al.*, 2006; Barbet-Massin *et al.*, 2009; Doswald *et al.*, 2009). In addition, the niche requirements of organisms also vary on a variety of temporal scales (e.g. days, seasons, ontogenetic development). How dynamic

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environments and niche requirements affect realised niches and geographic ranges of species is a central question in ecology and evolution and is critical for managing species given ongoing environmental change (Gaston, 2003; Pearman *et al.*, 2008). Here we develop a framework that can enhance our understanding of niche and range dynamics, and use *Sylvia* warblers to test predictions derived from the framework to assess its utility.

Seasonal changes in the environment have long been linked to the regular movement of organisms across geographic regions (Lack, 1954; Milner-Gulland *et al.*, 2011). Such movements have sometimes been associated with a niche tracking strategy (e.g. Martinez-Meyer *et al.*, 2004; Nakazawa *et al.*, 2004; Batalden *et al.*, 2007; Marini *et al.*, 2010). Studies using species distribution modelling to examine niche tracking have described spatio-temporal patterns in the realised niches of species, but they have not evaluated the costs and trade-offs associated with particular strategies nor have they explicitly related the observed patterns to the dynamic availability of environmental niche conditions in space and time. Previous studies have focused on migrating birds and butterflies and the extent of overlap in environmental niche dimensions between their breeding and non-breeding niches (Martinez-Meyer *et al.*, 2004; Nakazawa *et al.*, 2004; Batalden *et al.*, 2007; Marini *et al.*, 2010) and on annual temperature tracking (Joseph & Stockwell, 2000). Species often either show high overlap between breeding and non-breeding niche (“niche trackers”) or little overlap (“niche switchers”).

Previous studies on niche tracking have examined environmental niche dimensions (most often climate) that have similar spatio-temporal dynamics (Martinez-Meyer *et al.*, 2004; Nakazawa *et al.*, 2004; Batalden *et al.*, 2007; Marini *et al.*, 2010). However, the availability of different niche dimensions is not necessarily synchronised in time and space (Jimenez-Valverde *et al.*, 2009). For example, a seasonal change in local climate is not necessarily associated with corresponding changes in local land cover. Across different seasons, the same climatic conditions may be available in locations with very different land cover.

Niche requirements of organisms are usually assumed to be constant across various temporal scales. However, the subset of niche space an organism uses may vary daily, seasonally and throughout an organism’s lifetime (Batalden *et al.*, 2007; Suarez-Seoane *et al.*, 2008). For example, the niche for energetically more demanding activities, such as reproduction, may be a subset of the general survival niche (Grubb, 1977; Alerstam & Högstedt, 1982; Titeux *et al.*, 2007), or species may exhibit ontogenetic niche shifts as they

mature (Takimoto, 2003; Young *et al.*, 2005). As a result, both niche space availability and a species' niche requirements may concurrently vary in time.

5.2.1 Conceptual framework for niche dynamics in space and time

We attempt to develop a conceptual framework that incorporates the dynamic nature of niches, geographic ranges and the available environment as discussed above and which thus stimulates new questions about the drivers behind species' niche and range dynamics. Here, we consider niches both in the Grinnellian tradition, in the sense that we focus on niches as defined by broad environmental conditions (Grinnell, 1917; Soberon, 2007), and in the Hutchinsonian tradition, in the sense that we regard the niche as an entity defined in an abstract hyperspace which can be limited by biotic interactions (Hutchinson, 1957; Colwell & Rangel, 2009). Building on these traditions, we focus on realised niches quantified from large-scale occurrence data, which also reflect dispersal limitations and biotic interactions (Soberon, 2007; Colwell & Rangel, 2009). Our aim is to better understand how the dynamics in these realised niches are related to the dynamic availability of total niche space, i.e. of the availability of niche dimensions, such as environmental conditions, in time and geographic space.

To conceptualise the strategies of organisms to cope with the highly dynamic nature of available niche space, we can distinguish two extreme scenarios of how organisms might react to a change in locally available environmental conditions: 1) Organisms move in geographic space to track their favoured environmental conditions. Thus, they always stay within the specific subset of niche space they prefer (Fig. 5.1, red strategy). This strategy contributes to ecological phenomena such as diurnal vertical plankton migration or the annual migrations of ungulates in Southern Africa (Milner-Gulland *et al.*, 2011; Williamson *et al.*, 2011). 2) Alternatively, organisms stay where they are and tolerate the local change in environmental conditions. The organism's niche then has to encompass the full range of environmental conditions available locally through time (Soberon, 2007; Pearman *et al.*, 2008; Fig. 5.1, blue strategy). To endure harsh conditions in situ, organisms may even temporarily reduce their activity level, e.g. hibernation in mammals or winter dormancy in trees (Lubzens *et al.*, 2010). Intermediate strategies between these two scenarios of perfect niche tracking and no niche tracking are conceivable and have been observed (Martinez-Meyer *et al.*, 2004). Organisms incur an energy cost both for movement across regions (Alerstam *et al.*, 2003; Wikelski *et al.*, 2003) and for high environmental tolerance (DeWitt *et*

al., 1998; Caley & Munday, 2003; Auld *et al.*, 2010). Hence, it seems plausible to assume a trade-off between the ability of organisms to track niches in space and the ability to tolerate a wide variety of conditions.

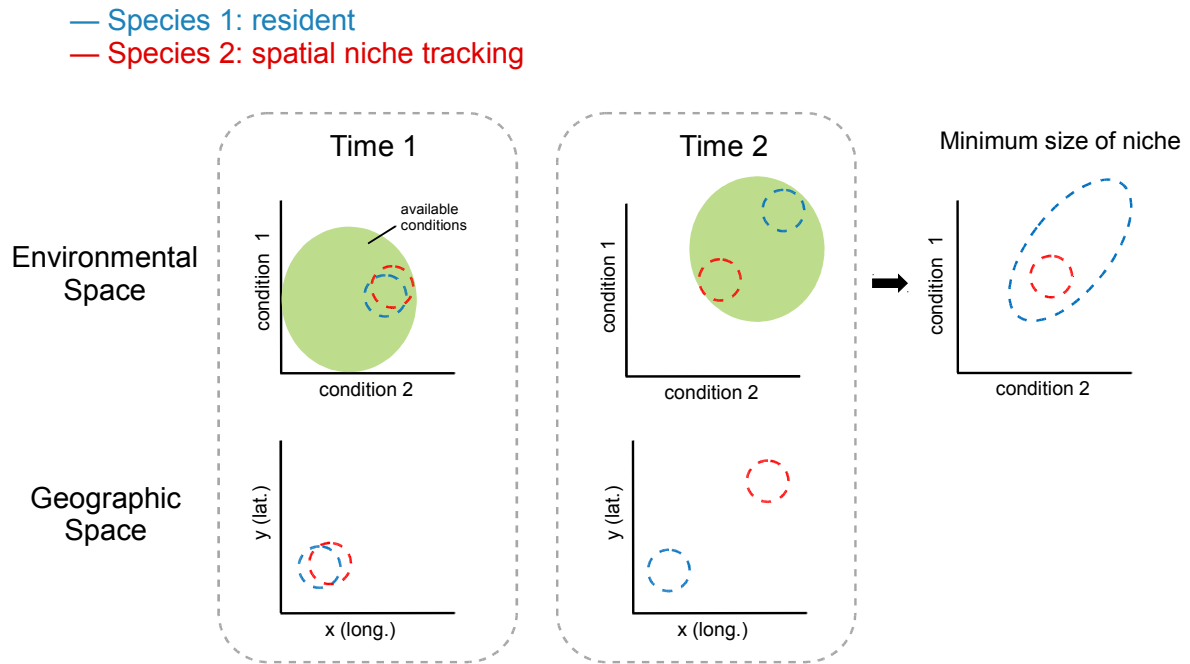


Figure 5.1: Framework illustrating organismal strategies to cope with dynamic niche space. Shown are two extreme scenarios of niche and range dynamics for a geographic region at two points in time that differ in the availability of environmental space. 1. Resident (species 1, niches and ranges shown in blue): Species staying in the same geographic location have to tolerate the local change in available environmental niche space. The species' niche then has to encompass the full range of environmental conditions available locally through time, resulting in a broad environmental niche. 2. Spatial niche tracking (species 2, niches and ranges shown in red): Species may move in geographic space to track their favoured environmental conditions. Thus, species always stay within the specific subset of environmental niche space they prefer and can have narrow niches.

This conceptual framework is relevant for a wide variety of niche dimensions, both abiotic and biotic. It can be applied to temporally highly dynamic (e.g. climate) and more static (e.g. land cover) niche dimensions at the same time and can thus be used to explore the potentially complex optimization problems faced by species due to the decoupled availability of different

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niche dimensions. Also, by allowing the shape of the niche space required by a species (Fig. 5.1, dashed circles in environmental space) to change in time, the framework can incorporate dynamic niche requirements across seasons and throughout species' life-cycles.

5.2.2 Applying the framework to animal migration

We derive four general predictions from our framework to better understand how environmental variation in space and time relates to the spatial movements and niche characteristics of organisms. We then evaluate these four predictions using migration behaviour in *Sylvia* warblers as a case study. The *Sylvia* warblers are an excellent system to evaluate variation in migration patterns as a function of species' niche characteristics and the dynamic availability of their niche in space and time. There is extensive information available on their ranges, ecology and phylogeny (e.g. Shirihai *et al.*, 2001; Böhning-Gaese *et al.*, 2003; Voelker & Light, 2011). The 26 species of *Sylvia* warblers evaluated here use a range of migration strategies including temperate and tropical residents, short-, middle- and long-distance migrants (Shirihai *et al.*, 2001). In the following, we state each of the four general prediction together with the specific question we evaluate for *Sylvia* warblers:

Trade-offs between niche breadth and migration distance:

If both strategies in Fig. 5.1, niche tracking or having a broad niche, are costly for species, then we might expect a trade-off between the amount of environmental variation a species can tolerate and migration distance. Species that move long distances should then have more constant niches throughout the year than more resident species (i.e. high niche overlap across seasons sensu Broennimann *et al.*, 2011), particularly for niche dimensions that are temporally highly dynamic such as climate. However, if niche dimensions are temporally more static (e.g. land-cover), then species moving longer distances may experience large changes in these dimensions resulting in a low overlap between different seasons. It follows that species that move long distances should have narrower total annual niches for the niche dimensions they are tracking and broader total annual niches for niche dimensions that are more static in time but vary in space.

Specific questions: Do *Sylvia* warblers that migrate longer distances between breeding and non-breeding grounds show greater niche overlap between these areas for temporally dynamic climate niche dimensions and lower overlap in static land-cover niche dimensions? Do *Sylvia* warblers with longer distances between breeding and non-breeding grounds show

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lower total annual climate niche breadth and higher total annual land-cover niche breadth? To address these questions we quantified climate and land-cover niche characteristics in both breeding and non-breeding areas for each species.

Niche tracking

If the reason for movement is niche tracking, then movement should lead to an increased niche overlap in the seasonal niches for the tracked niche dimension compared to a resident strategy.

Specific question: Is the climate niche of migrant *Sylvia* warblers more stable as a result of migration compared to if these same warblers had not migrated? To answer this question, we compared the niche overlap between the breeding and non-breeding conditions which the species actually experience to the hypothetical niche overlap resulting from staying either on the breeding or on the non-breeding grounds during the whole year.

Geographic proximity

If organisms that move in geographic space as a response to dynamic niche availability minimise the cost of movement, they should move to the nearest available geographic location with suitable conditions.

Specific question: Do migrant *Sylvia* warblers move to the closest place with suitable conditions? For this question we project environmental niche conditions into geographic space and then locate the areas with similar climate and land-cover to the observed breeding and non-breeding grounds.

Seasonal changes in niche requirements

If activities demanding high amounts of energy, such as reproduction or accumulation of body reserves before pupation or hibernation, involve more exacting energy and resource requirements, then the high energy activity niche should be equal or smaller to the survival niche, because the survival niche also incorporates seasons of comparatively lower energy and resource requirements which can be met under a broader set of environmental conditions.

Specific question: Is the breeding niche of migrant *Sylvia* warblers equal to or smaller than the survival niche? Here, we test whether niche breadth as derived from the breeding range during the breeding season is smaller or equal than the total niche breadth derived from the combination of breeding and non-breeding environmental conditions.

5.3 Methods

5.3.1 Study species

The *Sylvia* warblers are a genus of 27 primarily insectivorous passerines, occurring in Europe, Africa and western Asia. Böhning-Gaese *et al.* (2003) have classified 14 of them as residents, 4 as short-distance migrants and 9 as long-distance migrants. Migration distances in km for the *Sylvia* warblers, based on the orthodrome distance between centres of gravity for breeding and non-breeding ranges were also taken from Böhning-Gaese *et al.* (2003). Phylogenetic information on the relationship of species within the genus was taken from Voelker & Light (2011).

5.3.2 Ranges

Information on breeding and non-breeding ranges of the *Sylvia* species was taken from Shirihai *et al.* (2001), except for *S. abyssinica*, which was more identified as a member of the genus more recently (Böhning-Gaese *et al.*, 2003) and whose ranges were taken from Fry *et al.* (2000). *Sylvia dohrni*, an island endemic recently added to the genus (Voelker *et al.*, 2009), was not included in the analyses because its extremely small range precluded reliable quantification of niche characteristics. The range maps in Shirihai *et al.* (2001) combine expert knowledge with an extensive collation of point records and are the most comprehensive compilation of knowledge about *Sylvia* geographic distributions available. The range maps show a high amount of spatial detail and were thus gridded at a resolution of 25 × 25 km and converted into presences and absences. To assess whether the grid resolution affects our results, we conducted all analyses for two different range gridding thresholds (i.e. the percentage of minimum overlap between the range and a grid cell for that grid cell to be classified as presence): 10% and 50% present. Both thresholds yielded very similar results (see Appendix S1 in Supporting Information) so we report results using the 10% threshold.

5.3.3 Environmental variables

We used environmental data from all biogeographic realms currently inhabited by *Sylvia* warblers: Palearctic, Afrotropic and Indo-malay (Olson *et al.*, 2001). The data were resampled to the same 25 km × 25 km grid as the gridded range maps. We chose environmental variables based on our knowledge of *Sylvia* ecology and behaviour. We used mean temperature and

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total precipitation to represent abiotic environmental conditions (time period 1961–90, CRU CL 2.0; <http://www.cru.uea.ac.uk/cru/data/tmc.htm>, New *et al.*, 2000). These climatic variables may affect bird distributions directly via physiological survival limits, through their effects on the availability and phenology of food resources or via the abundance of competitors and parasites (Huntley *et al.*, 2006). We used the normalised difference vegetation index (NDVI; time period 1982–1999; Global Land Cover Facility; <http://glcf.umiacs.umd.edu/data/gimms/>; Tucker *et al.*, 2005) which correlates with green biomass and net primary plant productivity (e.g. Chong *et al.*, 1993) and may thus be linked to the availability of bird food resources such as insects (Hurlbert, 2004). We used the mean values of these variables for the three peak breeding and non-breeding months for each species (Heikkinen *et al.*, 2006). Peak breeding and non-breeding seasons for each species were defined based on information in the literature (Urban *et al.*, 1997; Fry *et al.*, 2000; Shirihai *et al.*, 2001; Bauer *et al.*, 2005). Since habitat choice of *Sylvia* warblers is determined by vegetation type and structure (Shirihai *et al.*, 2001), we used the UMD Land Cover Classification data (<http://glcf.umiacs.umd.edu/data/landcover/>; 1km pixel resolution, Hansen *et al.*, 2000) to reflect vegetation cover. We distinguished between open shrub-land, closed shrub-land, wooded grassland, woodland and non-needle leaf forest and calculated the proportion of each of these classes for each grid cell. These eight environmental variables have been confirmed as important for shaping broad-scale *Sylvia* distributions in several studies developing species distribution models for the genus (Wisz *et al.*, 2007; Doswald *et al.*, 2009; Barbet-Massin *et al.*, 2009).

5.3.4 Niche characteristics

Ecologists have long debated how to best measure niche overlap and niche breadth (e.g. Horn, 1966; Colwell & Futuyma, 1971; Warren *et al.*, 2008; Dormann *et al.*, 2010; Rödder & Engler, 2011). Here, we follow recommendations from Broennimann *et al.* (2011). For each species, we conducted a principal component analysis of the environmental variables described above for the whole study region (Palearctic, Afrotropic and Indo-malay) including the data from both the breeding and the non-breeding season. Depending on the question, we used either all environmental variables in the PCA or calculated separate PCAs for the three climate and five land-cover variables. The first two principal components of the PCA were used as the axes to describe the total annual environmental space, bounded by the minimum and maximum environmental values found in any of the two seasons in the whole study

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region.

For further analysis, the environmental space described by the first two PCA axes was divided into 100 x 100 regularly spaced grid cells (v_{ij}), with each cell thus representing a unique set of environmental conditions. Next, we calculated for each species and for both breeding and non-breeding seasons the density of species occurrences (o_{ij}) and the density of available environments (e_{ij}) (i.e. the number of grid cells with these environmental conditions in the whole study region during that season) in each grid cell in the environmental space. Both o_{ij} and e_{ij} were calculated using a kernel smoothing function to account for imperfect sampling of occurrences and to make the metrics independent of the number of grid cells in environmental space. Dividing o_{ij} by e_{ij} for each species and season then gave the occupancy of the environment (z_{ij}) in the grid cells in environmental space. If the environmental conditions corresponding to a grid cell were unavailable in a particular season (i.e. $e_{ij} = 0$), z_{ij} was set to zero. This procedure corrects the observed occurrences for the availability of environmental conditions in each season to ensure unbiased comparisons (Broennimann *et al.*, 2011).

Niche overlap between seasonal ranges was calculated using the D metric (Schoener, 1970; Warren *et al.*, 2008) on the occupancy values in environmental space (z_{ij}). To calculate the D metric, the absolute differences in occupancy values between the two ranges are summed, multiplied by 0.5 and then subtracted from one. The D metric varies from 0 (no niche overlap) to 1 (complete niche overlap).

To calculate niche breadth, we converted the environmental occupancy values (z_{ij}) to proportions and then calculated the Shannon index (Colwell & Futuyma, 1971). This measure of niche breadth thus takes into account both the number of occupied grid cells in environmental space and the evenness in the occupancy among those grid cells. For the comparison of breeding and annual niche breadth within each species, annual niche breadth was calculated by first summing the occupancy values (z_{ij}) for breeding and non-breeding niches in environmental space and then calculating the Shannon index on the summed proportional occupancy values.

To determine whether a species moved during migration from its breeding range to the closest non-breeding range with suitable non-breeding environmental conditions, we conducted the following five steps. First, we projected the occupancy values derived from each species' seasonal PCAs including both climate and land-cover into geographic space to

identify suitability values for each grid cell in geographic space. Second, to distinguish suitable from unsuitable areas we thresholded the suitability maps using the sensitivity equals specificity rule, as recommended by Liu *et al.* (2005) in a comparative study of thresholding rules. Third, we identified the closest suitable non-breeding area by calculating the nearest neighbour distances from all suitable non-breeding grid cells to all cells in the breeding range. Forth, we selected the suitable non-breeding grid cells that had the shortest nearest neighbour distances to the known breeding range. We selected the same number of grid cells as the number of grid cells in the known non-breeding range. Fifth, we calculated the average of the pairwise distances between all grid cells in the closest suitable non-breeding area and all grid cells in the known breeding range to obtain the minimum migration distance.

Analogously, we calculated whether a species moved from its non-breeding range to the closest breeding range with suitable breeding environmental conditions. The closest suitable breeding area was identified by calculating the nearest neighbour distances of suitable breeding grid cells to the known non-breeding range and then selecting the same number of cells as in the known breeding range with the shortest nearest neighbour distance to the known non-breeding range. To compare the minimum migration distances to the actual migration distances for each species, we did not use the migration distances obtained from Böhning-Gaese *et al.* (2003) that were used in the other analyses. Instead, we calculated actual migration distance as the average of the pairwise distances between all breeding range grid cells and all non-breeding range grid cells. This ensured maximum consistency between the quantifications of minimum and actual migration distances for this question.

All analyses were conducted in R 2.13.1 (R Development Core Team 2011) using published code and libraries (Broennimann *et al.*, 2011; Baddeley & Turner, 2005).

5.3.5 Statistical Analysis

Trade-offs between niche breadth and migration distance

We calculated linear regressions between niche overlap and movement distances and between total annual niche breadth and movement distances separately for climate and land-cover niches for all *Sylvia* warblers. Closely related species may tend to have more similar traits than distantly related species and thus species do not necessarily represent independent data points (Harvey & Pagel, 1991). To take the phylogenetic relationship between *Sylvia* warblers into account, we checked the residuals from the linear regressions for phylogenetic

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autocorrelation. We tested for phylogenetic signal in the residuals using the Abouheif test (Abouheif, 1999) with 999 randomisations as implemented in the R package *adephylo* (Jombart *et al.*, 2010) and by calculating Pagel's λ , a maximum-likelihood based measure of phylogenetic signal (Pagel, 1997), and testing for a significant difference to a lambda of zero (no phylogenetic structure), as implemented in the R package *CAICR* (Freckleton, 2009).

Niche tracking

To determine if the climate niche of migrant *Sylvia* warblers is more stable between seasons as a result of migration, we calculated the climatic niche overlap for the breeding and non-breeding grounds assuming a given warbler had not migrated and compared this overlap to the climate niche overlap the migrants actually experience. We calculated paired t-tests to compare the climate niche overlap values for these hypothetical resident strategies to the climate niche overlap the migrants actually experience between breeding and non-breeding grounds. Additionally, to examine to what extent conditions in the non-breeding range differ from the conditions available on the breeding range during the non-breeding season, we calculated the climate niche overlap between non-breeding conditions and the climate available on the breeding range during the non-breeding season.

Geographic proximity

To evaluate if migrant *Sylvia* warblers move to the closest place with suitable conditions based on niche quantifications incorporating both climate and land-cover, we used paired t-tests to compare the known migration distance with the distance from the breeding range to the closest suitable non-breeding area and the known migration distance with the distance from the non-breeding range to the closest suitable breeding area for each *Sylvia* species. We also divided the differences between known migration distance and the migration distances to the closest suitable area (i.e. distance between known breeding range and the closest non-breeding area and the known non-breeding range and the closest breeding area) by the known migration distance to obtain species-specific estimates of potential reductions in distance from adopting the shortest possible migration route.

Seasonal changes in niche requirements

To determine if the breeding niche of migrant *Sylvia* warblers is equal to or smaller than the survival niche, we calculated a paired Wilcoxon signed rank test comparing breeding niche breadth vs. total annual niche breadth for each *Sylvia* species. Niches here reflect both climate and land-cover simultaneously.

5.4 Results

Trade-offs between niche breadth and migration distance

Contrary to our prediction, movement distance between breeding and non-breeding grounds had no effect on the overlap of breeding and non-breeding climate niches ($\beta = 0.00001$, $t = -1.03$, $P = 0.31$, $R^2 = 0.04$, Fig. 5.2a) and on total annual climate niche breadth ($\beta = -0.0000002$, $t = -0.04$, $P = 0.97$, $R^2 < 0.01$, Fig. 5.2c) in *Sylvia* warblers. Land-cover niches showed the expected relationship to migration distance: *Sylvia* warblers with longer distances between breeding and non-breeding grounds did exhibit a significantly lower overlap in their land-cover niche ($\beta = -0.00008$, $t = -4.55$, $P = 0.0001$, $R^2 = 0.46$, Fig. 5.2b) and had significantly broader total annual land-cover niches ($\beta = 0.00019$, $t = 2.77$, $P = 0.01$, $R^2 = 0.24$, Fig. 5.2d). A few species migrating short distances deviated slightly from this pattern due to the size difference between their very small breeding ranges and larger non-breeding ranges (Fig. 5.2b, scatter below regression line). There was no significant phylogenetic signal in any of the regression residuals (Abouheif tests: $P > 0.052$; Likelihood ratio tests for $\lambda=0$: $P > 0.55$), indicating that our results are not affected by the phylogenetic relatedness of the species.

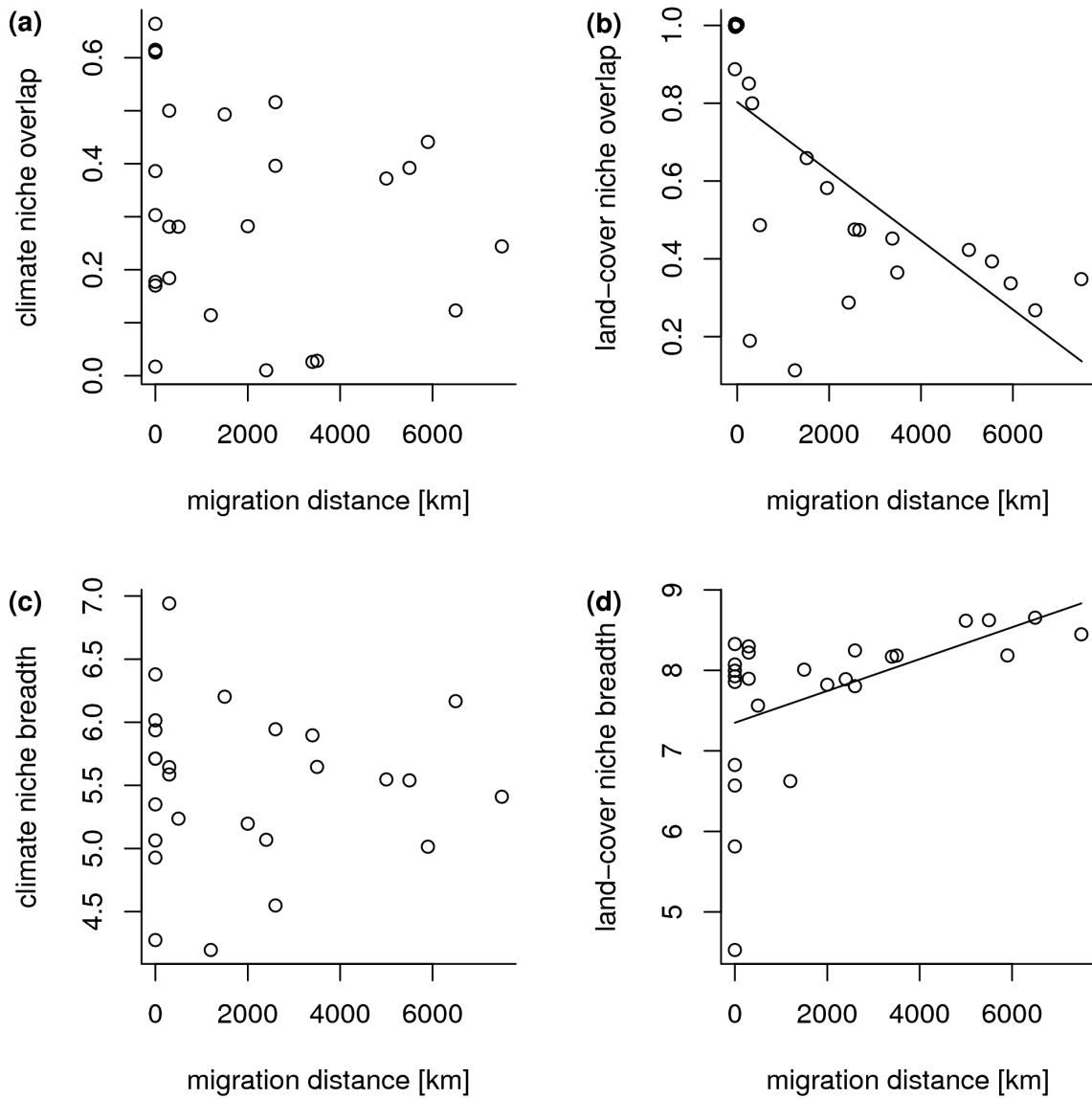


Figure 5.2: Relationship between migration distance and (a) climate niche overlap between breeding and non-breeding season, (b) land-cover niche overlap between breeding and non-breeding season, (c) total annual climate niche breadth, (d) total annual land-cover niche breadth for 26 species of *Sylvia* warblers.

Niche tracking

The climate niche overlap between breeding and non-breeding grounds for migrant *Sylvia* warblers was not significantly higher than if they had stayed either on the breeding grounds ($t = 0.59$, $df = 12$, $P = 0.56$) or on the non-breeding grounds ($t = -0.03$, $df = 12$, $P = 0.97$) year-round (Fig.5.3). Climate niche overlap between the conditions migrant *Sylvia* warblers experience on the non-breeding grounds and conditions available on their breeding grounds during the non-breeding season was low ($D = 0.15 \pm 0.25$ (mean \pm SD), $n = 13$).

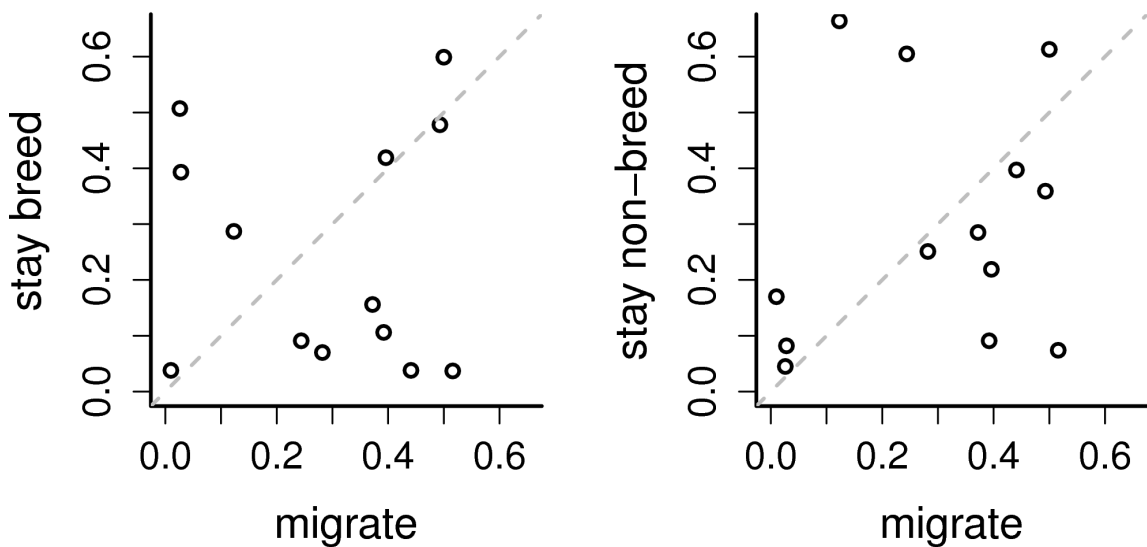


Figure 5.3: Climate niche overlap for different potential migration strategies in migrant *Sylvia* warblers. Migration does not lead to consistently higher climate niche overlap compared to resident strategies. migrate: niche overlap between breeding and non-breeding grounds actually experienced by the species, stay breed: hypothetical niche overlap resulting from staying on the breeding grounds all year, stay non-breed: hypothetical niche overlap resulting from staying on the non-breeding grounds all year, dashed grey line = identity line, $n = 13$.

Geographic proximity

Incorporating both climate and land-cover in niche quantifications, known migration distances were significantly longer than distances between the known breeding ranges and the closest suitable non-breeding area ($t = 4.55$, $df = 12$, $P = < 0.001$; Fig. 5.4). Migrant *Sylvia* warblers could migrate an average of $21 \pm 20\%$ (mean \pm SD) less distance by flying to the closest suitable non-breeding area. Similarly, known migration distances were significantly longer than the distances between the known non-breeding range and the closest suitable breeding area ($t = 5.72$, $df = 12$, $P = < 0.001$, Fig. 5.4). Potential reductions in distance for flying to the closest suitable breeding area were on average $23 \pm 18\%$ (mean \pm SD) of the species' known migration distance.

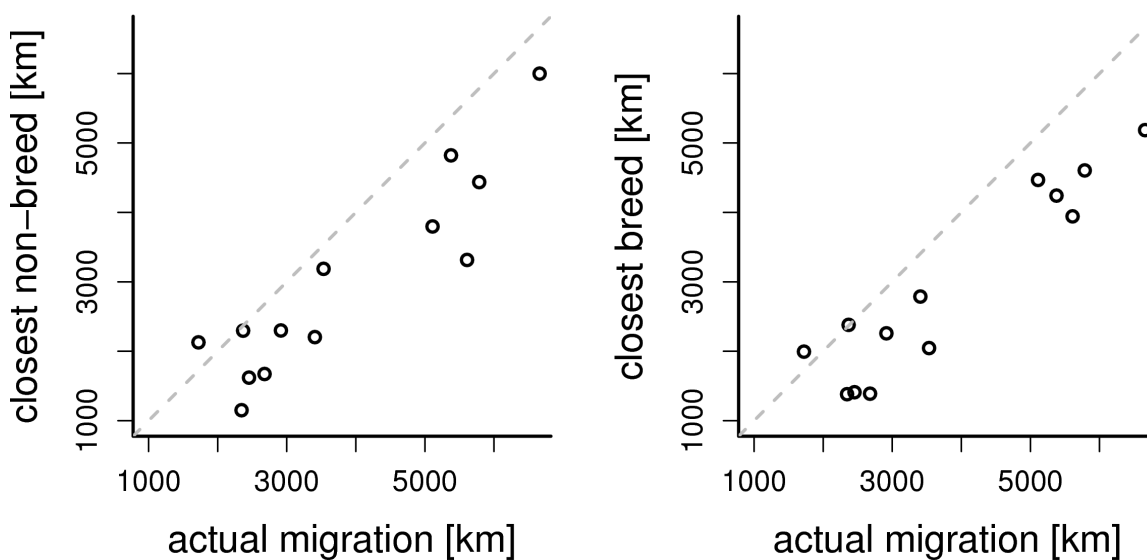


Figure 5.4: Migration distance and distance to the closest suitable non-breeding and breeding areas in migrant *Sylvia* warblers. Points below the identity line indicate actual migration distance is longer than the distance to the closest suitable areas. actual migration: average distance between known breeding and non-breeding ranges, closest non-breed: average distance between known breeding range and closest suitable non-breeding area, closest breed: average distance between known non-breeding range and closest suitable breeding area, dashed grey line = identity line, $n = 13$.

Seasonal changes in niche requirements

Taking into account both climate and land-cover, breeding niche breadth in *Sylvia* warblers was, as predicted, significantly smaller than total annual niche breadth ($W = 14$, $n = 26$, $P < 0.001$, Fig. 5.5). Note that in species whose non-breeding range is environmentally very uniform, total annual niche breadth can actually be smaller than breeding niche breadth, because including the non-breeding range decreases the evenness of occupied environments (scatter below regression line, Fig. 5.5).

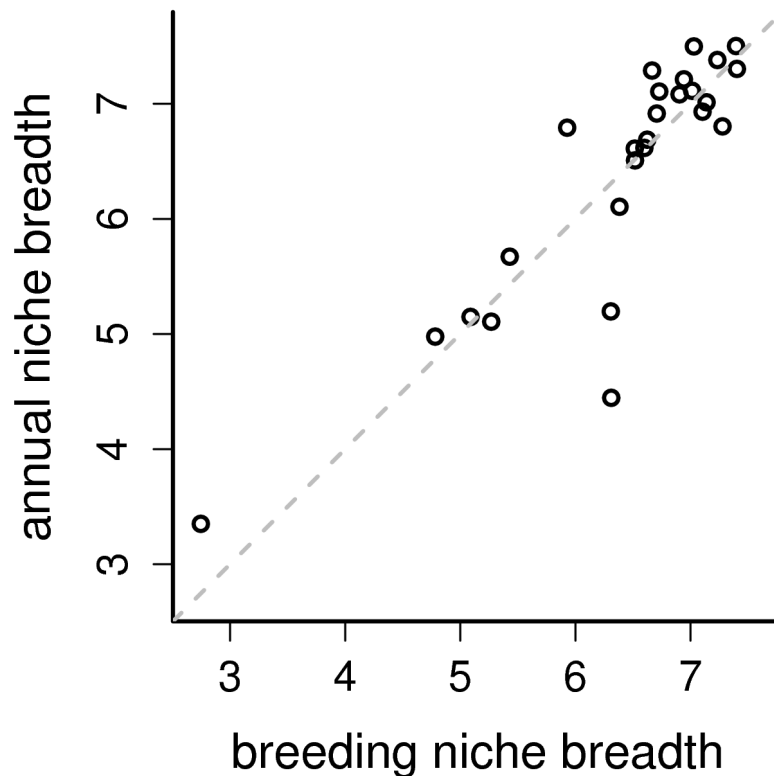


Figure 5.5: Comparison of total annual niche breadth and breeding niche breadth in *Sylvia* warblers. The majority of points above the identity line indicate breeding niche breadth is smaller than total annual niche breadth. Niche breadth incorporates both climate and land-cover. dashed grey line = identity line, $n = 26$.

5.5 Discussion

We developed a new framework to understand how organisms respond to spatio-temporally dynamic niche space (Fig. 5.1) and tested the framework on seasonal migration in *Sylvia* warblers. We showed that *Sylvia* migration does not appear to be driven by climate niche tracking and that it exposes species to greater variation in other niche dimensions such as land-cover, which are comparatively static across seasons. Niches were narrower during the breeding season, demonstrating that niche requirements can be dynamic in time. We showed that the framework is useful for testing predictions about *Sylvia* warbler migration and for stimulating new questions which can potentially be transferred to other ecological phenomena.

Trade-offs between niche breadth and migration distance

Our results indicate that *Sylvia* warblers do not compensate for the costs of a long migratory journey by closely tracking their preferred climate. However, land-cover niche breadth increased with migration distance, highlighting the decoupled spatio-temporal availability of climate and land cover. By applying our framework to examine tracking of niche dimensions other than climate we show that it may be impossible for *Sylvia* species to track both climatic and land-cover conditions at the same time. If tracking climate involves longer movement in geographic space, this would likely result in broader land-cover niches. Future research should explore how migratory behaviour is influenced by and evolves under such complex constraints, and how climate and land cover translate into reproductive output. This also raises important questions for the transferability of correlative species distribution models in space and time, which assume a constant correlation structure between environmental variables (Morin & Lechowicz, 2008; Jimenez-Valverde *et al.*, 2009).

We also note that, especially for species with large ranges, quantifying the niche at the species level ignores that subpopulations and individuals may select specific environments from the total available niche space, e.g. short-distance vs. trans-Saharan migrant subpopulations in *S. atricapilla* (Shirihai *et al.*, 2001; Doswald *et al.*, 2009), and hence might experience very different niche overlap.

Niche tracking

Migration in *Sylvia* warblers is not driven by climate niche tracking because migrating *Sylvia* warblers experienced just as much climatic variation between breeding and non-breeding grounds as they would through annual climatic variation if they were resident on either the breeding or non-breeding grounds. The low niche overlap between winter climate on the breeding and on the non-breeding grounds suggests that overwintering on the breeding grounds would require tolerating deviation from the breeding conditions in a different direction of niche space compared to migration. A resident strategy may thus expose migratory *Sylvia* warblers to cold, unproductive winters which the species may be less able to tolerate. Hence, the advantage of migration might rather be higher reproductive success and lower nest predation at higher latitudes and lower winter mortality at tropical latitudes (Böhning-Gaese *et al.*, 2000; Alerstam *et al.*, 2003; Lemoine & Böhning-Gaese, 2003; Griebeler *et al.*, 2010; McKinnon *et al.*, 2010).

Evidence for climate niche tracking between breeding and non-breeding ranges in birds has been ambiguous so far, with high overlap between breeding and non-breeding climate in some species (Joseph & Stockwell, 2000; Martinez-Meyer *et al.*, 2004; Nakazawa *et al.*, 2004; Marini *et al.*, 2010) but not in others (Martinez-Meyer *et al.*, 2004; Nakazawa *et al.*, 2004). The framework allows us to go beyond classifying bird species as “niche trackers” or “niche switchers” based solely on climate niche overlap between their breeding and non-breeding grounds. It is crucial to examine which part of the total environmental niche space is available when and where to understand whether species’ movements are indeed driven by environmental dynamics in particular niche dimensions (Reside *et al.*, 2010). By taking the spatio-temporal availability of environments into account, we can compare the niche overlap resulting from alternative hypothetical migration strategies and evaluate if an observed migration pattern minimises niche overlap.

Geographic proximity

Both during the spring and autumn migrations, *Sylvia* warblers fly, on average, 20% further than to the nearest area with suitable climate and land-cover. Hence, migration distance is likely driven by additional factors. Although we quantified niche characteristics from occurrence records and they thus reflect the realised niche, we do not explicitly address the influence of biotic interactions on occupied niche space and geographic distributions, which

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has been demonstrated for bird migration regarding diffuse competition with residents, parasitism and nest predation (Alerstam *et al.*, 2003; Lemoine & Böhning-Gaese, 2003; McKinnon *et al.*, 2010). An imperfect optimisation of migration distance could also be the result of genetic constraints on the migration routes of bird populations or of the influence of geographic barriers and the availability of stop-over sites on the cost of migrating along specific routes (Alerstam *et al.*, 2003; Doswald *et al.*, 2009).

Seasonal changes in niche requirements

Our findings suggest that *Sylvia* warblers only breed in a subset of their total annual niche space, which is congruent with the idea that more exacting requirements, in terms of energy, nutrients and protection from predation during reproduction, may lead to smaller niches (Grubb, 1977; Alerstam & Högstedt, 1982; Titeux *et al.*, 2007). In order to not obscure such seasonal niche shifts, species distribution models should be fitted with seasonal subsets of occurrence and environmental data (Heikkinen *et al.*, 2006). Our findings also indicate that niches should be regarded as dynamic entities over the life cycle of species and that closer examination of how niches vary during specific phases of the life cycle of organisms may be beneficial for future studies aiming to model niches and distribution (Jackson *et al.*, 2009).

Implications

We have shown that our conceptual framework (Fig. 5.1) is a useful starting point to understand how the dynamics of environmental conditions in space and time and dynamic niche requirements affect the niches and distributions of organisms. The framework goes beyond previous studies of niche tracking by taking the dynamic availability of niches in space and time into account. It is thus a useful approach to identify the niche dimensions that are crucial in shaping organisms' movements and it describes fundamental processes and constraints which are applicable to a broad range of ecological phenomena and taxa. For example, the framework could be used to test how diel vertical migration in zoo-plankton is linked to the daily variation of temperature and sunlight in the water column or to explore to what extent plant dormancy, which could be seen as an extreme case of dynamism in species' niche requirements, is a response to changes in the availability of particular niche dimensions.

The framework is relevant for predicting how species ranges will respond to long-term temporal changes in conditions caused by climate change. Tracking climate change might increasingly desynchronise species with other niche dimensions such as land-cover. Our

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results for the *Sylvia* warblers suggest they might not track the predicted shifts in their preferred climatic conditions (Barbet-Massin *et al.*, 2009; Doswald *et al.*, 2009). Applying the framework to animal migration highlights that niche tracking behaviour is complex and that assuming simple climate tracking when predicting future range shifts may be too simplistic.

Our framework is part of an emerging trend to improve the mechanistic understanding of macroecological processes through analyses of temporal dynamics (Fisher *et al.*, 2010). We suggest that future studies aiming to model niches and distribution may benefit from making use of high temporal resolution of occurrence and environmental data instead of using temporal averages as input (Heikkinen *et al.*, 2006; Jackson *et al.*, 2009). While the species distribution modelling paradigm allows the examination of niches and ranges at several individually modelled points in time, it would be interesting to explore the potential consequences of changes in niche availability and niche requirements in a dynamic model (Pagel & Schurr, 2011). Applying our framework to bird migration shows how we can significantly enhance our understanding of the drivers behind spatial movements of organisms and the dynamics in their realised niches by taking changing niche requirements throughout organism's life-cycles and the spatio-temporal availability of environments into account.

6 CONCLUSIONS

In this thesis, I have attempted to advance our current understanding of avian range dynamics by modelling putative mechanistic links, integrating multiple drivers in the same analysis, and by developing new conceptual ideas. To this end, I have combined datasets from ecology, evolution and the Earth sciences and used tools from information science such as geographic information systems, statistical programming environments, path analysis, boosted regression trees, ridge regression, bootstrapping techniques, kernel estimators and niche metrics. Corresponding to the previous three chapters, the following major findings emerge: (i) Species' traits do not account for the majority of the variation in range size, but they do play an important role. Several traits influence range size simultaneously in complex ways, both directly and indirectly through other traits. High annual fecundity, high dispersal ability, broad habitat niches, low trophic level, large body size and being migratory emerge as the most important traits leading to large global ranges in European passerines. (ii) Whether species are able to colonise potentially suitable areas at large spatial and temporal scales depends on multiple drivers that interact with each other. High dispersal ability only enables *Sylvia* warblers to fill a high proportion of their potential range if species richness of congeners in areas of low habitat suitability within their potential range is low. Contrary to previous ideas on the scale-dependence of drivers of range dynamics (Pearson & Dawson, 2003; Guisan & Rahbek, 2011), this suggests that biotic interactions may be important in shaping ranges at the continental scale and that their effect is likely contingent on habitat suitability. (iii) Species' niches and distributions are dynamic entities that depend on the spatio-temporal availability of environmental conditions. The availability of niche dimensions may be desynchronised, challenging species with complex optimisation problems when trying to track them in geographic space. Niche requirements of species may vary throughout their life-cycle. Migration in *Sylvia* warblers is not driven by climate niche tracking and results in broader land-cover niches. *Sylvia* warblers had narrower niches during the breeding season. In summary, the early idea that ranges are set by very few factors (e.g. Twomey, 1936) can be rejected. The processes that determine the size, geographic location and the dynamic of species distributions are highly complex and involve multiple interacting drivers. We are just beginning to form a coherent, comprehensive view of range dynamics.

6.1 Future research perspectives

It is important to keep in mind that, of necessity, the results in this thesis were obtained using different passerine groups as model systems. As a consequence, the validity of those results remains restricted to these model groups until confirmed or rejected for other taxa. Nevertheless, this thesis provides analysis approaches, predictions and conceptual ideas that can be applied to other groups of birds and, indeed, other taxa from all kingdoms of life. Studies integrating multiple potential drivers of range dynamics are still rare (Gaston, 2003). It is too early to comment on the likely differences in range dynamics across a broad taxonomic spectrum, but given the results from this thesis, one might formulate the cautious expectation that range dynamics in other taxa will be equally complex, but that the relative importance of different drivers is likely taxon-specific. For example, it has been noted that, on average, plants and insects have smaller geographic ranges than vertebrates (Gaston, 1994) and birds generally have larger geographic ranges than mammals (Anderson, 1984). Hypotheses involving dispersal ability, body size and habitat use have been proposed as explanations (Anderson, 1984), but this pattern has so far not been demonstrably linked to characteristics of these animal groups. Studying the questions raised in this thesis for other taxa seems a worthwhile endeavour.

Range dynamics are complex because a species' geographic distribution is an emergent property of a number of highly elaborate subsystems such as population genetics, metapopulation dynamics and community ecology; all influenced by short-term environmental dynamics, long-term environmental change and historic effects (Gaston, 2003; Newton, 2003; Böhning-Gaese *et al.*, 2006; Price & Kirkpatrick, 2009). Few of the data, patterns and potential relationships are directly observable by any individual researcher and many cannot be studied by experimentation (Brown, 1995). It appears that there might be a trade-off between breadth and depth. Studies at large spatio-temporal scales that include many species sometimes may become divorced from the local ecology and history of the individual taxa (Wiens & Donoghue, 2004). For example, for a comparative analysis of the global ranges of all European passerines as in chapter three, one has to resort to relatively broad classifications to characterise the species' habitat and diet preferences. On the other hand, detailed studies of occupancy, population dynamics and biotic interactions can be so restricted in taxonomic and geographic focus that it is hard to know how to generalise beyond regarding

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them as a collection of single case studies (Brown, 1995; Ladle & Whittaker, 2011); e.g. studies investigating intrageneric biotic interactions in *Sylvia* warblers typically cover spatial extents below 2.5 km² (e.g. Cody & Walter, 1976; Cody, 1978; Garcia, 1983; Martin & Thibault, 1996; Elle, 2003; Pons *et al.*, 2008). One fundamental challenge facing research on species distributions is to synthesise these two perspectives (Pearson & Dawson, 2003; Wiens & Donoghue, 2004; Guisan & Rahbek, 2011).

In working towards such a synthesis of breadth and depth in range dynamics, there are two current trends: one is to combine data from ecology, evolution and geoscience and the other is to integrate an increasing number of factors and more complex relationships into the same quantitative framework, which then allows us to look at the emergent properties of systems that are too complex to be anticipated by the human mind. In this thesis, I have pursued both approaches; the first approach particularly in chapters 4 and 5, and the second approach particularly in chapter 3. Two potential difficulties in further developing this line of research have become apparent: (i) Even when working with exceptionally well-studied taxa, data availability quickly becomes an issue. The Linnean and Wallacean shortfalls, the incompleteness of our knowledge of species and their distributions (Lomolino *et al.*, 2010), are acutely felt. For the *Sylvia* warblers, advances in our taxonomic knowledge have resulted in species being attributed to the genus as recently as 2009 (Voelker *et al.*, 2009) and there is a geographic bias in the quality of the information on species' ranges, with data for North Africa and the Middle East being notably poorer than for Europe (Shirihai *et al.*, 2001). Also, to fully understand the dynamic nature of avian geographic ranges we will need to build sufficiently standardised and integrated datasets about temporal changes in the abundance structure within the area we presently consider a species' geographic range and about migratory movements (Wikelski & Kays, 2011). Regarding potential drivers of range dynamics, computationally accessible quantitative information on many species' traits, such as dispersal ability or brain size, is still limited to particular bird groups, and some drivers, such as biotic interactions, are exceedingly difficult to quantify. (ii) Developing models that retain breadth (i.e. apply to many species over large scales) without losing depth (i.e. take into account the local ecology of individual species) implies higher model complexity. Hence the models need large amounts of data when we want to test hypotheses about the factors driving range dynamics. Even if we have comparatively good data for a group, we may be faced with the conundrum that the group may simply not have enough members to result in a

sample size with enough degrees of freedom to test more complex hypotheses. Purely practical constraints that are still of relevance when conducting studies on range dynamics are that preparation and integration of data from different sources into a common geographical and statistical environment can be very time-consuming and increasingly complex models may simply take a very long time to run.

Finally, I want to point out several areas where the incorporation of additional complexity has the potential to advance our understanding of species' distributions and which should be considered when trying to predict range shifts under global change: (i) There is still ample scope to integrate more of the drivers of range dynamics into one analysis (Botkin *et al.*, 2007). For example, it might be interesting to incorporate all of the species traits identified as important determinants of range size in chapter 3 into analyses similar to those presented in chapter 4, which attempt to assess how important species' traits are relative to other potential drivers of range dynamics, such as biotic interaction and historic constraints. Bayesian methods may be a promising route for the simultaneous analysis of multiple drivers as they allow for great model complexity and, by using priors, can take information into account that is difficult to integrate into other methods (Ellison, 2004; Choy *et al.*, 2009). (ii) Chapter 4 highlights that the mechanisms which facilitate or prevent colonisation of suitable habitat are contingent on the environmental conditions of the area under consideration. This is consistent with studies of range edges which demonstrate that range limits for the same species can be set by different mechanisms in different places (e.g. Barnes, 1957; Gross & Price, 2000). It may be fruitful to explore techniques such as geographically weighted regression and make more use of the capabilities of data-driven species distribution modelling methods such as boosted regression trees to visualise complex interactions (Austin, 2007; Elith *et al.*, 2008). (iii) We should be cautious about assuming that biotic interactions can be safely ignored for predicting range shifts at large scales (Brooker *et al.*, 2007). There is an increasing trend to take biotic interactions into account in species distribution modelling by using the occurrence of other species as predictors (Araújo & Luoto, 2007; Heikkinen *et al.*, 2007; Preston *et al.*, 2008). If biotic interactions are important at large scales, species cannot be modelled in isolation when trying to predict range shifts, and methods which iteratively consider shifts in several species have to be developed (Keith *et al.*, 2008; Baselga & Araújo, 2009). (iv) Chapter 5 provides an example of how the in-depth consideration of the ecology of a particular species group can stimulate the development of conceptual frameworks and ideas that are relevant for many taxa

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and ecological phenomena. The dynamic nature of niche requirements demonstrated in chapter 5 indicates that ranges for different life-cycle stages may have to be modelled separately to properly account for the associated change in species' niches (Doswald *et al.*, 2009; Jackson *et al.*, 2009). Also, understanding how species deal with spatio-temporal de-synchronisation in different niche dimensions may help us understand how they will respond to the predicted future prevalence of novel climates (Williams *et al.*, 2007). While we discuss the framework mainly in the context of short-term temporal dynamics, it can in principle be equally applied to how ranges and niches change in the course of evolution and to examine phenomena such as niche conservatism (Wiens & Graham, 2005; Crisp *et al.*, 2009). Focusing on the strategies species can develop in response to the dynamic availability of environmental conditions can potentially yield new insights into how organisms may deal with environments that are dynamic both on ecological and evolutionary time-scales (Fisher *et al.*, 2010; Pearman *et al.*, 2008).

6.2 Concluding remarks

Range dynamics are complex. Considering the scale of our ignorance and the data required to remedy it, it seems doubtful whether our ability to make meaningful predictions of the effect of global change on biodiversity will improve sufficiently within the time-frame of a few years that is relevant for political action and management decisions (MEA, 2005b; SCBD, 2010). The urgency of making wide-ranging societal decisions shaping a trajectory of global change that cannot be controlled or reversed (Hannah *et al.*, 2002; King, 2005; Stern, 2006) contrasts with the inevitably small, incremental steps and recursive discussions in which science can decipher why organisms are distributed the way they are (Ladle & Whittaker, 2011).

More research on the dynamics that give rise to species' geographic distributions is urgently needed (Davis *et al.*, 1998; MEA, 2005b; Parmesan, 2006; SCBD, 2010). Notwithstanding pressure to obtain funding in a scientific system whose members are increasingly part of the precariat, ecologists should be cautious about enabling the notion that global change impacts can be precisely predicted and managed by overstating the certainty and practical relevance of their predictions (Sutherst *et al.*, 2007; Willis & Bhagwat, 2009; Sinclair *et al.*, 2010). Equally, they should be wary of providing excuses for societal agents to postpone difficult decisions by exaggerating the imminence of results that would allow such

management (Glanz, 1988; Hulme, 2005; Sutherst *et al.*, 2007; SCBD, 2010). Highlighting what we presently do not know and cannot predict may encourage societal discourse about risk acceptance and planning under uncertainty (Dasgupta, 2008; CCSP, 2009; Dawson *et al.*, 2011).

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9 APPENDICES

Appendix 1: Study species

Table A1.1: List of 165 European passerine bird species used for analyses in chapter 3

Family	Genus	Species
Aegithalidae	<i>Aegithalos</i>	<i>caudatus</i>
Alaudidae	<i>Alauda</i>	<i>arvensis</i>
Alaudidae	<i>Calandrella</i>	<i>brachydactyla</i>
Alaudidae	<i>Calandrella</i>	<i>rufescens</i>
Alaudidae	<i>Chersophilus</i>	<i>duponti</i>
Alaudidae	<i>Eremophila</i>	<i>alpestris</i>
Alaudidae	<i>Galerida</i>	<i>cristata</i>
Alaudidae	<i>Galerida</i>	<i>theklae</i>
Alaudidae	<i>Lullula</i>	<i>arborea</i>
Alaudidae	<i>Melanocorypha</i>	<i>calandra</i>
Bombycillidae	<i>Bombycilla</i>	<i>garrulus</i>
Certhiidae	<i>Certhia</i>	<i>brachydactyla</i>
Certhiidae	<i>Certhia</i>	<i>familiaris</i>
Certhiidae	<i>Troglodytes</i>	<i>troglodytes</i>
Cinclidae	<i>Cinclus</i>	<i>cinclus</i>
Cisticolidae	<i>Cisticola</i>	<i>juncidis</i>
Corvidae	<i>Corvus</i>	<i>corax</i>
Corvidae	<i>Corvus</i>	<i>corone</i>
Corvidae	<i>Corvus</i>	<i>frugilegus</i>
Corvidae	<i>Corvus</i>	<i>monedula</i>
Corvidae	<i>Cyanopica</i>	<i>cyaneus</i>
Corvidae	<i>Garrulus</i>	<i>glandarius</i>
Corvidae	<i>Nucifraga</i>	<i>caryocatactes</i>
Corvidae	<i>Oriolus</i>	<i>oriolus</i>
Corvidae	<i>Perisoreus</i>	<i>infaustus</i>
Corvidae	<i>Pica</i>	<i>pica</i>
Corvidae	<i>Pyrrhocorax</i>	<i>graculus</i>
Corvidae	<i>Pyrrhocorax</i>	<i>pyrrhocorax</i>
Fringillidae	<i>Calcarius</i>	<i>lapponicus</i>
Fringillidae	<i>Carduelis</i>	<i>cannabina</i>
Fringillidae	<i>Carduelis</i>	<i>carduelis</i>
Fringillidae	<i>Carduelis</i>	<i>chloris</i>
Fringillidae	<i>Carduelis</i>	<i>flammea</i>
Fringillidae	<i>Carduelis</i>	<i>flavirostris</i>
Fringillidae	<i>Carduelis</i>	<i>hornemanni</i>
Fringillidae	<i>Carduelis</i>	<i>spinus</i>
Fringillidae	<i>Carpodacus</i>	<i>erythrinus</i>

Family	Genus	Species
Fringillidae	<i>Coccothraustes</i>	<i>coccothraustes</i>
Fringillidae	<i>Emberiza</i>	<i>aureola</i>
Fringillidae	<i>Emberiza</i>	<i>caesia</i>
Fringillidae	<i>Emberiza</i>	<i>cia</i>
Fringillidae	<i>Emberiza</i>	<i>cirlus</i>
Fringillidae	<i>Emberiza</i>	<i>citrinella</i>
Fringillidae	<i>Emberiza</i>	<i>hortulana</i>
Fringillidae	<i>Emberiza</i>	<i>melanocephala</i>
Fringillidae	<i>Emberiza</i>	<i>pusilla</i>
Fringillidae	<i>Emberiza</i>	<i>rustica</i>
Fringillidae	<i>Emberiza</i>	<i>schoeniclus</i>
Fringillidae	<i>Fringilla</i>	<i>coelebs</i>
Fringillidae	<i>Fringilla</i>	<i>montifringilla</i>
Fringillidae	<i>Loxia</i>	<i>curvirostra</i>
Fringillidae	<i>Loxia</i>	<i>leucoptera</i>
Fringillidae	<i>Loxia</i>	<i>pytyopsittacus</i>
Fringillidae	<i>Loxia</i>	<i>scotica</i>
Fringillidae	<i>Miliaria</i>	<i>calandra</i>
Fringillidae	<i>Pinicola</i>	<i>enucleator</i>
Fringillidae	<i>Plectrophenax</i>	<i>nivalis</i>
Fringillidae	<i>Pyrrhula</i>	<i>pyrrhula</i>
Fringillidae	<i>Serinus</i>	<i>citrinella</i>
Fringillidae	<i>Serinus</i>	<i>serinus</i>
Hirundinidae	<i>Delichon</i>	<i>urbicum</i>
Hirundinidae	<i>Hirundo</i>	<i>aurica</i>
Hirundinidae	<i>Hirundo</i>	<i>rupestris</i>
Hirundinidae	<i>Hirundo</i>	<i>rustica</i>
Hirundinidae	<i>Riparia</i>	<i>riparia</i>
Laniidae	<i>Lanius</i>	<i>collurio</i>
Laniidae	<i>Lanius</i>	<i>excubitor</i>
Laniidae	<i>Lanius</i>	<i>minor</i>
Laniidae	<i>Lanius</i>	<i>nubicus</i>
Laniidae	<i>Lanius</i>	<i>senator</i>
Muscicapidae	<i>Cercotrichas</i>	<i>galactotes</i>
Muscicapidae	<i>Erithacus</i>	<i>rubecula</i>
Muscicapidae	<i>Ficedula</i>	<i>albicollis</i>
Muscicapidae	<i>Ficedula</i>	<i>hypoleuca</i>
Muscicapidae	<i>Ficedula</i>	<i>parva</i>
Muscicapidae	<i>Luscinia</i>	<i>luscinia</i>
Muscicapidae	<i>Luscinia</i>	<i>megarhynchos</i>
Muscicapidae	<i>Luscinia</i>	<i>svecica</i>
Muscicapidae	<i>Monticola</i>	<i>saxatilis</i>
Muscicapidae	<i>Monticola</i>	<i>solitarius</i>
Muscicapidae	<i>Muscicapa</i>	<i>striata</i>
Muscicapidae	<i>Oenanthe</i>	<i>hispanica</i>
Muscicapidae	<i>Oenanthe</i>	<i>isabellina</i>

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Family	Genus	Species
Muscicapidae	<i>Oenanthe</i>	<i>leucura</i>
Muscicapidae	<i>Oenanthe</i>	<i>oenanthe</i>
Muscicapidae	<i>Oenanthe</i>	<i>pleschanka</i>
Muscicapidae	<i>Phoenicurus</i>	<i>ochruros</i>
Muscicapidae	<i>Phoenicurus</i>	<i>phoenicurus</i>
Muscicapidae	<i>Saxicola</i>	<i>rubetra</i>
Muscicapidae	<i>Saxicola</i>	<i>rubicola</i>
Muscicapidae	<i>Tarsiger</i>	<i>cyanurus</i>
Muscicapidae	<i>Turdus</i>	<i>iliacus</i>
Muscicapidae	<i>Turdus</i>	<i>merula</i>
Muscicapidae	<i>Turdus</i>	<i>philomelos</i>
Muscicapidae	<i>Turdus</i>	<i>pilaris</i>
Muscicapidae	<i>Turdus</i>	<i>torquatus</i>
Muscicapidae	<i>Turdus</i>	<i>viscivorus</i>
Paridae	<i>Cyanistes</i>	<i>caeruleus</i>
Paridae	<i>Lophophanes</i>	<i>cristatus</i>
Paridae	<i>Parus</i>	<i>major</i>
Paridae	<i>Periparus</i>	<i>ater</i>
Paridae	<i>Poecile</i>	<i>cinctus</i>
Paridae	<i>Poecile</i>	<i>lugubris</i>
Paridae	<i>Poecile</i>	<i>montanus</i>
Paridae	<i>Poecile</i>	<i>palustris</i>
Paridae	<i>Remiz</i>	<i>pendulinus</i>
Passeridae	<i>Anthus</i>	<i>campestris</i>
Passeridae	<i>Anthus</i>	<i>cervinus</i>
Passeridae	<i>Anthus</i>	<i>petrosus</i>
Passeridae	<i>Anthus</i>	<i>pratensis</i>
Passeridae	<i>Anthus</i>	<i>spinoletta</i>
Passeridae	<i>Anthus</i>	<i>trivialis</i>
Passeridae	<i>Montifringilla</i>	<i>nivalis</i>
Passeridae	<i>Motacilla</i>	<i>alba</i>
Passeridae	<i>Motacilla</i>	<i>cinerea</i>
Passeridae	<i>Motacilla</i>	<i>flava</i>
Passeridae	<i>Passer</i>	<i>domesticus</i>
Passeridae	<i>Passer</i>	<i>hispaniolensis</i>
Passeridae	<i>Passer</i>	<i>montanus</i>
Passeridae	<i>Petronia</i>	<i>petronia</i>
Passeridae	<i>Prunella</i>	<i>collaris</i>
Passeridae	<i>Prunella</i>	<i>modularis</i>
Regulidae	<i>Regulus</i>	<i>ignicapilla</i>
Regulidae	<i>Regulus</i>	<i>regulus</i>
Sittidae	<i>Sitta</i>	<i>europaea</i>
Sittidae	<i>Sitta</i>	<i>neumayer</i>
Sittidae	<i>Sitta</i>	<i>whiteheadi</i>
Sittidae	<i>Tichodroma</i>	<i>muraria</i>
Sturnidae	<i>Sturnus</i>	<i>roseus</i>

Family	Genus	Species
Sturnidae	<i>Sturnus</i>	<i>unicolor</i>
Sturnidae	<i>Sturnus</i>	<i>vulgaris</i>
Sylviidae	<i>Acrocephalus</i>	<i>arundinaceus</i>
Sylviidae	<i>Acrocephalus</i>	<i>dumetorum</i>
Sylviidae	<i>Acrocephalus</i>	<i>melanopogon</i>
Sylviidae	<i>Acrocephalus</i>	<i>paludicola</i>
Sylviidae	<i>Acrocephalus</i>	<i>palustris</i>
Sylviidae	<i>Acrocephalus</i>	<i>schoenobaenus</i>
Sylviidae	<i>Acrocephalus</i>	<i>scirpaceus</i>
Sylviidae	<i>Cettia</i>	<i>cetti</i>
Sylviidae	<i>Hippolais</i>	<i>icterina</i>
Sylviidae	<i>Hippolais</i>	<i>olivetorum</i>
Sylviidae	<i>Hippolais</i>	<i>pallida</i>
Sylviidae	<i>Hippolais</i>	<i>polyglotta</i>
Sylviidae	<i>Locustella</i>	<i>fluviatilis</i>
Sylviidae	<i>Locustella</i>	<i>luscinioides</i>
Sylviidae	<i>Locustella</i>	<i>naevia</i>
Sylviidae	<i>Panurus</i>	<i>biarmicus</i>
Sylviidae	<i>Phylloscopus</i>	<i>bonelli</i>
Sylviidae	<i>Phylloscopus</i>	<i>borealis</i>
Sylviidae	<i>Phylloscopus</i>	<i>collybita</i>
Sylviidae	<i>Phylloscopus</i>	<i>sibilatrix</i>
Sylviidae	<i>Phylloscopus</i>	<i>trochiloides</i>
Sylviidae	<i>Phylloscopus</i>	<i>trochilus</i>
Sylviidae	<i>Sylvia</i>	<i>atricapilla</i>
Sylviidae	<i>Sylvia</i>	<i>borin</i>
Sylviidae	<i>Sylvia</i>	<i>cantillans</i>
Sylviidae	<i>Sylvia</i>	<i>communis</i>
Sylviidae	<i>Sylvia</i>	<i>conspicillata</i>
Sylviidae	<i>Sylvia</i>	<i>curruca</i>
Sylviidae	<i>Sylvia</i>	<i>hortensis</i>
Sylviidae	<i>Sylvia</i>	<i>melanocephala</i>
Sylviidae	<i>Sylvia</i>	<i>nisoria</i>
Sylviidae	<i>Sylvia</i>	<i>rueppelli</i>
Sylviidae	<i>Sylvia</i>	<i>sarda</i>
Sylviidae	<i>Sylvia</i>	<i>undata</i>

Appendix 2: SDM threshold sensitivity analysis

Table A2.1: Effects of competition in the unoccupied parts of the potential range, dispersal ability, taxon age, habitat shift since LGM and the interaction between dispersal ability and competition on range filling. Multiple regressions for different range map conversion thresholds, model algorithms and past climate models. Species distribution model output was converted from continuous probabilities into binary output using the **mean probability value as threshold**. BRT = boosted regression trees; ridge = ridge regression. Shown are standardised partial regression coefficients, standard errors (in parentheses), significances adjusted for simultaneous inference and whole model R^2 and significances. Response $\text{asin}(\sqrt{x})$ transformed. $n = 23$.

range map conversion threshold	model algorithm	past climate model	competition	dispersal ability	log (taxon age)	habitat shift since LGM	dispersal ability × competition	model R^2
10%	BRT	CCSM	-0.35 (0.16)	0.61 ** (0.13)	0.33 (0.12)	-0.28 (0.13)	-0.52 * (0.15)	0.83 ***
10%	BRT	MIROC	-0.44 (0.16)	0.60 ** (0.14)	0.33 (0.13)	-0.18 (0.13)	-0.57 ** (0.15)	0.80 ***
10%	Ridge	CCSM	-0.44 * (0.15)	0.45 * (0.13)	0.24 (0.13)	-0.16 (0.13)	-0.63 * (0.16)	0.81 ***
10%	Ridge	MIROC	-0.51 ** (0.14)	0.46 * (0.13)	0.23 (0.13)	-0.09 (0.11)	-0.63 ** (0.17)	0.81 ***
50%	BRT	CCSM	-0.46 * (0.18)	0.60 ** (0.12)	0.32 (0.12)	-0.21 (0.14)	-0.58 ** (0.14)	0.82 ***
50%	BRT	MIROC	-0.56 (0.18)	0.59 ** (0.13)	0.32 (0.12)	-0.11 (0.14)	-0.63 ** (0.15)	0.80 ***
50%	Ridge	CCSM	-0.50 * (0.15)	0.44 * (0.13)	0.25 (0.13)	-0.11 (0.13)	-0.67 ** (0.15)	0.81 ***
50%	Ridge	MIROC	-0.55 ** (0.14)	0.46 * (0.13)	0.24 (0.13)	-0.04 (0.11)	-0.67 ** (0.15)	0.80 ***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table A2.2: Effects of the competition in unoccupied parts of the potential range with the least suitable habitat, dispersal ability, taxon age, habitat shift since LGM and interaction between dispersal ability and competition on range filling. Multiple regressions for different range map conversion thresholds, model algorithms and past climate models. Species distribution model output was converted from continuous probabilities into binary output using the **observed prevalence value as threshold**. BRT = boosted regression trees; ridge = ridge regression. Shown are standardised partial regression coefficients, standard errors (in parentheses), significances adjusted for simultaneous inference and whole model R^2 and significances. Response $\text{asin}(\sqrt{x})$ transformed. $n = 23$.

range map conversion threshold	model algorithm	past climate model	competition	dispersal ability	log (taxon age)	habitat shift since LGM	dispersal ability \times competition	model R^2
10%	BRT	CCSM	-0.35 (0.16)	0.61 ** (0.13)	0.33 (0.12)	-0.28 (0.13)	-0.53 ** (0.15)	0.83 ***
10%	BRT	MIROC	-0.44 (0.16)	0.60 ** (0.14)	0.33 (0.13)	-0.18 (0.13)	-0.57 ** (0.15)	0.80 ***
10%	Ridge	CCSM	-0.44 * (0.15)	0.45 * (0.13)	0.24 (0.13)	-0.16 (0.13)	-0.63 ** (0.14)	0.81 ***
10%	Ridge	MIROC	-0.51 ** (0.14)	0.46 * (0.13)	0.23 (0.13)	-0.09 (0.11)	-0.63 ** (0.15)	0.81 ***
50%	BRT	CCSM	-0.46 (0.18)	0.60 ** (0.12)	0.32 (0.12)	-0.22 (0.14)	-0.58 * (0.16)	0.82 ***
50%	BRT	MIROC	-0.56 * (0.18)	0.59 ** (0.13)	0.32 (0.12)	-0.11 (0.13)	-0.63 ** (0.17)	0.80 ***
50%	Ridge	CCSM	-0.50 * (0.15)	0.44 * (0.13)	0.25 (0.13)	-0.11 (0.13)	-0.68 ** (0.15)	0.81 ***
50%	Ridge	MIROC	-0.55 ** (0.14)	0.46 * (0.13)	0.24 (0.13)	-0.04 (0.11)	-0.68 ** (0.15)	0.80 ***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

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Table A2.3: Best models (corrected AIC difference of less than 2 from best model) for multiple regressions focusing on competition in the unoccupied parts of the potential range and for different range map conversion thresholds, model algorithms and past climate models. Species distribution model output was converted from continuous probabilities into binary output using the **mean probability value as threshold**. d = dispersal ability; a = log (taxon age); c = competition; h = habitat shift since LGM; BRT = boosted regression trees; ridge = ridge regression; x = variable or interaction term included in model.

range map conversion threshold	model algorithm	past climate model	d	a	c	h	d:a	d:c	d:h	a:c	a:h	c:h	AICc	
10%	BRT	MIROC	x	x	x			x					-8.39	
			x	x	x	x		x						-6.62
10%	BRT	CCSM	x	x		x	x		x				-10.56	
			x	x	x	x		x					-9.78	
			x	x		x			x					-8.58
50%	BRT	MIROC	x	x	x			x				-9.8		
50%	BRT	CCSM	x	x	x				x				-9.8	
			x	x		x	x			x				-9.72
			x	x	x	x		x						-8.71
10%	Ridge	MIROC	x	x	x	x		x	x				-17.61	
			x		x			x						-17.36
			x	x	x			x						-17.1
10%	Ridge	CCSM	x	x	x	x		x	x				-17.41	
			x		x			x						-17.36
			x	x	x			x						-17.1
50%	Ridge	MIROC	x	x	x			x					-17.46	
			x	-	x			x						-17.15
50%	Ridge	CCSM	x	x	x			x					-17.46	
			x	-	x			x						-17.15

Table A2.4: Best models (corrected AIC difference of less than 2 from best model) for multiple regressions focusing on competition in the whole potential range and for different range map conversion thresholds, model algorithms and past climate models. Species distribution model output was converted from continuous probabilities into binary output using the **observed prevalence value as threshold**. d = dispersal ability; a = log (taxon age); c = competition; h = habitat shift since LGM; BRT = boosted regression trees; ridge = ridge regression; x = variable or interaction term included in model.

range map conversion threshold	model algorithm	past climate model	d	a	c	h	d:a	d:c	d:h	a:c	a:h	c:h	AICc	
10%	BRT	MIROC	x	x	x			x					-8.49	
			x	x	x	x		x						-6.66
10%	BRT	CCSM	x	x		x	x		x				-10.62	
			x	x	x	x		x						-9.85
50%	BRT	MIROC	x	x	x			x					-9.87	
50%	BRT	CCSM	x	x	x				x					-9.87
			x	x		x	x			x				-9.85
			x	x	x	x		x						-8.8
10%	Ridge	MIROC	x	x	x	x		x	x				-17.61	
			x		x			x						-17.36
			x	x	x			x						-17.1
10%	Ridge	CCSM	x	x	x	x		x	x				-17.41	
			x		x			x						-17.36
			x	x	x			x						-17.1
50%	Ridge	MIROC	x	x	x			x					-17.46	
			x		x			x						-17.15
50%	Ridge	CCSM	x	x	x			x					-17.46	
			x		x			x						-17.15

Appendix 3: Akaike model selection & full model regression results for all habitat suitability levels

Table A3.1: Effects of competition **in the potential range**, dispersal ability, taxon age, habitat shift since LGM and the interaction between dispersal ability and competition on range filling. Multiple regressions for different range map conversion thresholds, model algorithms and past climate models. BRT = boosted regression trees; ridge = ridge regression. Shown are standardised partial regression coefficients, standard errors (in parentheses), significances adjusted for simultaneous inference and whole model R^2 and significances. Response $\text{asin}(\sqrt{x})$ transformed. $n = 23$.

range map conversion threshold	model algorithm	past climate model	competition	dispersal ability	log (taxon age)	habitat shift since LGM	dispersal ability × competition	model R^2
10%	BRT	CCSM	-0.40 (0.33)	0.47 (0.23)	0.60 * (0.19)	0.17 (0.22)	-0.73 (0.31)	0.58 **
10%	BRT	MIROC	-0.51 (0.29)	0.54 (0.22)	0.61 * (0.17)	0.31 (0.19)	-0.77 * (0.27)	0.63 **
10%	Ridge	CCSM	-0.30 (0.21)	0.68 ** (0.17)	0.54 * (0.15)	-0.46 * (0.15)	-0.75 * (0.22)	0.75 ***
10%	Ridge	MIROC	-0.40 (0.23)	0.70 * (0.20)	0.49 * (0.17)	-0.28 (0.15)	-0.63 (0.25)	0.68 **
50%	BRT	CCSM	-0.29 (0.37)	0.45 (0.26)	0.53 (0.21)	0.05 (0.25)	-0.56 (0.34)	0.50 *
50%	BRT	MIROC	-0.48 (0.33)	0.54 (0.25)	0.57 * (0.20)	0.25 (0.22)	-0.67 (0.31)	0.53 *
50%	Ridge	CCSM	-0.19 (0.23)	0.65 * (0.18)	0.54 * (0.16)	-0.49 (0.17)	-0.68 * (0.24)	0.71 ***
50%	Ridge	MIROC	-0.31 (0.25)	0.66 * (0.21)	0.48 (0.18)	-0.26 (0.17)	-0.55 (0.26)	0.63 **

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

Table A3.2: Effects of competition in the 50% of the potential range with the least suitable habitat, dispersal ability, taxon age, habitat shift since LGM and the interaction between dispersal ability and competition on range filling. Multiple regressions for different range map conversion thresholds, model algorithms and past climate models. BRT = boosted regression trees; ridge = ridge regression. Shown are standardised partial regression coefficients, standard errors (in parentheses), significances adjusted for simultaneous inference and whole model R^2 and significances. Response $\text{asin}(\sqrt{x})$ transformed. $n = 23$.

range map conversion threshold	model algorithm	past climate model	competition	dispersal ability	log (taxon age)	habitat shift since LGM	dispersal ability × competition	model R^2
10%	BRT	CCSM	-0.44 (0.31)	0.47 (0.22)	0.63 * (0.18)	0.20 (0.21)	-0.78 (0.30)	0.61 **
10%	BRT	MIROC	-0.56 (0.27)	0.55 (0.21)	0.64 ** (0.17)	0.34 (0.18)	-0.82 * (0.26)	0.66 **
10%	Ridge	CCSM	-0.50 * (0.14)	0.52 ** (0.10)	0.42 * (0.11)	-0.33 * (0.11)	-0.92 *** (0.15)	0.87 ***
10%	Ridge	MIROC	-0.60 ** (0.14)	0.53 ** (0.11)	0.40 * (0.12)	-0.24 (0.11)	-0.91 *** (0.16)	0.85 ***
50%	BRT	CCSM	-0.32 (0.34)	0.45 (0.25)	0.54 (0.20)	0.06 (0.23)	-0.60 (0.31)	0.56 *
50%	BRT	MIROC	-0.49 (0.31)	0.54 (0.24)	0.58 * (0.19)	0.26 (0.21)	-0.69 (0.28)	0.56 *
50%	Ridge	CCSM	-0.46 (0.16)	0.53 ** (0.11)	0.42 * (0.12)	-0.38 (0.14)	-0.94 *** (0.17)	0.85 ***
50%	Ridge	MIROC	-0.60 * (0.17)	0.53 ** (0.13)	0.38 (0.13)	-0.21 (0.13)	-0.90 ** (0.19)	0.81 ***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

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Table A3.3: Effects of competition in the 25% of the potential range with the least suitable habitat, dispersal ability, taxon age, habitat shift since LGM and the interaction between dispersal ability and competition on range filling. Multiple regressions for different range map conversion thresholds, model algorithms and past climate models. BRT = boosted regression trees; ridge = ridge regression. Shown are standardised partial regression coefficients, standard errors (in parentheses), significances adjusted for simultaneous inference and whole model R² and significances. Response asin(sqrt(x)) transformed. *n* = 23.

range map conversion threshold	model algorithm	past climate model	competition	dispersal ability	log (taxon age)	habitat shift since LGM	dispersal ability × competition	model R ²
10%	BRT	CCSM	-0.53 (0.25)	0.48 (0.19)	0.59 * (0.17)	0.20 (0.18)	-0.85 * (0.25)	0.67 **
10%	BRT	MIROC	-0.60 (0.23)	0.53 * (0.18)	0.58 ** (0.15)	0.31 (0.16)	-0.86 ** (0.22)	0.71 ***
10%	Ridge	CCSM	-0.50 ** (0.14)	0.45 ** (0.11)	0.38 * (0.11)	-0.25 * (0.11)	-0.84 *** (0.14)	0.87 ***
10%	Ridge	MIROC	-0.56 ** (0.13)	0.44 ** (0.11)	0.37 * (0.12)	-0.20 (0.10)	-0.84 *** (0.15)	0.86 ***
50%	BRT	CCSM	-0.42 (0.28)	0.45 (0.21)	0.51 (0.18)	0.09 (0.20)	-0.72 (0.27)	0.58 **
50%	BRT	MIROC	-0.54 (0.26)	0.50 (0.20)	0.52 * (0.17)	0.25 (0.19)	-0.76 * (0.25)	0.61 **
50%	Ridge	CCSM	-0.49 * (0.15)	0.45 ** (0.10)	0.37 * (0.11)	-0.30 (0.12)	-0.91 *** (0.15)	0.87 ***
50%	Ridge	MIROC	-0.59 ** (0.14)	0.44 ** (0.11)	0.35 * (0.12)	-0.19 (0.12)	-0.90 *** (0.16)	0.85 ***

P* < 0.05; *P* < 0.01; ****P* < 0.001

Table A3.4: Best models (corrected AIC difference of less than 2 from best model) for multiple regressions focusing on competition in the **unoccupied parts of the potential range** and for different range map conversion thresholds, model algorithms and past climate models. d = dispersal ability; a = log (taxon age); c = competition; h = habitat shift since LGM; BRT = boosted regression trees; ridge = ridge regression; x = variable or interaction term included in model.

range map conversion threshold	model algorithm	past climate model	d	a	c	h	d:a	d:c	d:h	a:c	a:h	c:h	AICc
10%	BRT	MIROC	x	x	x			x					-11.59
			x	x	x	x		x					-10.83
			x	x	x			x		x			-10.23
10%	BRT	CCSM	x	x	x			x					-11.59
			x	x	x			x		x			-10.23
			x	x	x	x		x	x			x	-10.11
50%	BRT	MIROC	x	x	x			x					-8.02
			x	x	x			x		x			-7.31
			x	x	x	x		x					-6.07
50%	BRT	CCSM	x	x	x			x					-8.02
			x	x	x			x		x			-7.31
10%	Ridge	MIROC	x	x	x	x		x					-18.32
			x		x			x					-16.93
10%	Ridge	CCSM	x	x	x	x		x				-20.16	
50%	Ridge	MIROC	x		x			x					-15.83
			x	x	x			x					-15.68
			x	x	x	x		x					-15.16
50%	Ridge	CCSM	x	x	x	x		x				-18.58	

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Table A3.5: Best models (corrected AIC difference of less than 2 from best model) for multiple regressions focusing on competition in the **whole potential range** and for different range map conversion thresholds, model algorithms and past climate models. d = dispersal ability; a = log (taxon age); c = competition; h = habitat shift since LGM; BRT = boosted regression trees; ridge = ridge regression; x = variable or interaction term included in model.

range map conversion threshold	model algorithm	past climate model	d	a	c	h	d:a	d:c	d:h	a:c	a:h	c:h	AICc			
10%	BRT	MIROC	x	x									-6.1			
			x	x	x		x	x						-5.94		
			x	x	x				x			x		-5.71		
					x										-5.18	
					x	x						x			-5.13	
			x	x	x				x						-5.08	
			x	x				x							-5.07	
					x	x										-4.54
			x	x	x	x				x						-4.27
			x	x				x				x				-4.16
10%	BRT	CCSM	x	x	x	x	x		x		x	x	-7.52			
			x	x										-6.1		
			x	x		x				x				-5.98		
			x	x	x		x		x					-5.94		
			x	x	x				x			x		-5.71		
50%	BRT	MIROC	x	x									-4.89			
				x	x						x			-4.69		
				x										-4.45		
			x	x			x							-4.14		
			x	x	x				x			x		-3.99		
			x	x	x		x		x					-3.31		
		x	x									-3.08				
50%	BRT	CCSM	x	x	x	x	x		x		x	-7.13				
10%	Ridge	MIROC	x	x		x	x		x			-7.88				
10%	Ridge	CCSM	x	x		x	x		x			-10.48				
50%	Ridge	MIROC	x	x		x	x		x			-5.27				
50%	Ridge	CCSM	x	x		x	x		x			-8.79				

Table A3.6: Best models (corrected AIC difference of less than 2 from best model) for multiple regressions focusing on competition in the **50% of the potential range with least suitable habitat** and for different range map conversion thresholds, model algorithms and past climate models. d = dispersal ability; a = log (taxon age); c = competition; h = habitat shift since LGM; BRT = boosted regression trees; ridge = ridge regression; x = variable or interaction term included in model.

range map conversion threshold	model algorithm	past climate model	d	a	c	h	d:a	d:c	d:h	a:c	a:h	c:h	AICc		
10%	BRT	MIROC	x	x	x			x		x			-7.24		
			x	x	x		x	x						-7.16	
			x	x	x				x					-6.26	
			x	x	x	x			x						-6.18
			x	x											-6.1
10%	BRT	CCSM	x	x	x	x	x		x		x	x	-7.85		
			x	x	x			x			x			-7.24	
			x	x	x		x	x						-7.16	
			x	x	x				x					-6.26	
			x	x	x	x	x			x			x		-6.2
			x	x											-6.1
50%	BRT	MIROC	x	x	x			x			x			-4.96	
			x	x										-4.89	
					x	x						x			-4.52
					x										-4.45
			x	x				x							-4.14
			x	x	x		x	x							-3.92
50%	BRT	CCSM	x	x	x	x	x		x		x	x	-8.48		
10%	Ridge	MIROC	x	x	x	x		x					-20.16		
			x	x	x				x					-18.34	
10%	Ridge	CCSM	x	x	x	x		x					-23.9		
50%	Ridge	MIROC	x	x	x				x					-15.42	
			x	x	x	x			x			x		-14.69	
			x	x	x	x			x					-14.4	
			x	x	x		x	x						-13.48	
50%	Ridge	CCSM	x	x	x	x		x					-19.89		

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Table A3.7: Best models (corrected AIC difference of less than 2 from best model) for multiple regressions focusing on competition in the **25% of the potential range with least suitable habitat** and for different range map conversion thresholds, model algorithms and past climate models. d = dispersal ability; a = log (taxon age); c = competition; h = habitat shift since LGM; BRT = boosted regression trees; ridge = ridge regression; x = variable or interaction term included in model.

range map conversion threshold	model algorithm	past climate model	d	a	c	h	d:a	d:c	d:h	a:c	a:h	c:h	AICc		
10%	BRT	MIROC	x	x	x	x		x					-10.16		
				x	x	x			x					-9.65	
				x	x	x			x			x			-8.92
				x	x	x		x	x						-8.19
10%	BRT	CCSM	x	x	x			x					-9.65		
				x	x	x			x		x			-8.92	
				x	x	x		x	x					-8.19	
50%	BRT	MIROC	x	x	x			x			x		-6.48		
				x	x	x			x					-6.05	
				x	x	x		x	x					-4.96	
				x	x									-4.89	
50%	BRT	CCSM	x	x	x	x	x		x		x	x	-8.56		
10%	Ridge	MIROC	x	x	x	x		x					-21.33		
				x	x	x			x					-20.92	
10%	Ridge	CCSM	x	x	x	x		x					-22.52		
				x	x	x			x					-20.92	
50%	Ridge	MIROC	x	x	x			x					-20.3		
				x	x	x	x		x					-19.14	
50%	Ridge	CCSM	x	x	x	x		x					-22.61		

Appendix 4: Range filling estimates for different *Sylvia* species and distribution modelling methods

Table A4.1: Range filling estimates for different *Sylvia* species distribution modelling methods. BRT = boosted regression trees; Ridge = ridge regression.

species	10% range map conversion threshold		50% range map conversion threshold	
	BRT	Ridge	BRT	Ridge
<i>S. [curruca] curruca</i>	0.91	0.74	0.91	0.72
<i>S. communis</i>	0.89	0.67	0.88	0.68
<i>S. borin</i>	0.86	0.62	0.85	0.62
<i>S. atricapilla</i>	0.85	0.58	0.83	0.57
<i>S. [sarda] sarda</i>	0.78	0.05	0.77	0.06
<i>S. nisoria</i>	0.74	0.44	0.72	0.42
<i>S. subcaeruleum</i>	0.69	0.25	0.69	0.26
<i>S. [nana] nana</i>	0.65	0.35	0.66	0.35
<i>S. layardi</i>	0.63	0.06	0.65	0.06
<i>S. melanocephala</i>	0.58	0.17	0.53	0.18
<i>S. [hortensis] hortensis</i>	0.45	0.10	0.42	0.07
<i>S. leucomelaena</i>	0.45	0.16	0.51	0.16
<i>S. mystacea</i>	0.45	0.15	0.48	0.13
<i>S. undata</i>	0.44	0.13	0.40	0.13
<i>S. cantillans</i>	0.41	0.11	0.37	0.11
<i>S. conspicillata</i>	0.41	0.11	0.35	0.11
<i>S. [hortensis] crassirostris</i>	0.39	0.13	0.40	0.11
<i>S. buryi</i>	0.38	0.07	0.41	0.07
<i>S. abyssinica</i>	0.36	0.10	0.31	0.06
<i>S. rueppelli</i>	0.33	0.04	0.38	0.04
<i>S. boehmi</i>	0.31	0.06	0.31	0.06
<i>S. lugens</i>	0.31	0.06	0.32	0.05
<i>S. deserticola</i>	0.22	0.05	0.20	0.05

Appendix 5: Gridding threshold sensitivity analysis

Results of analyses in chapter 5 using a 50% gridding threshold (i.e. the percentage of minimum overlap between the range polygon and a geographic grid cell for that grid cell to be classified as presence) for the *Sylvia* ranges.

Trade-offs between niche breadth and migration distance

Table 5.1: Relationship between migration distance and different niche characteristics. Given are β , t , P , R^2 from simple regression analyses. Significant relationships are printed in bold. No phylogenetic signal in any regression residuals (all Abouheif tests: $P > 0.06$, all Likelihood ratio tests for lambda=0: $P > 0.53$). $n = 26$.

Niche characteristic	β	t	P	R^2
climate niche overlap between breeding and non-breeding season	0.00001	-0.89	0.38	0.03
total annual climate niche breadth	-0.0000006	0.01	0.99	< 0.01
land-cover niche overlap between breeding and non-breeding season	-0.00009	-4.36	< 0.001	0.44
total annual land-cover niche breadth	0.0002	2.73	0.01	0.24

Niche tracking

Table 5.2: Climate niche overlap for different potential migration strategies in migrant *Sylvia* warblers. stay breed: hypothetical climate niche overlap resulting from staying on the breeding grounds all year, stay non-breed: hypothetical climate niche overlap resulting from staying on the non-breeding grounds all year, Given are t , df , p , from paired t-tests.

Climate niche overlap between breeding and non-breeding season vs.	t	df	P
stay breed:	0.70	12	0.50
stay non-breed:	-0.08	12	0.94

Climate niche overlap between the conditions migrant *Sylvia* warblers experience on the non-breeding grounds and conditions available on their breeding ranges during the non-breeding season was low ($D = 0.14 \pm 0.25$ (mean \pm SD), $n = 13$).

Geographic proximity

Table 5.3: Migration distance and distance to the closest suitable non-breeding and breeding areas in migrant *Sylvia* warblers. Area suitability incorporates both climate and land-cover. actual migration: average distance between known breeding and non-breeding ranges, closest non-breed: average distance between known breeding range and closest suitable non-breeding area, closest breed: average distance between known non-breeding range and closest suitable breeding area, Given are t , df , P , from paired t-tests and potential savings in distance for the shortest possible route as a percentage of actual migration distance.

Actual migration distance vs.	t	df	P	potential savings (mean \pm SD)
closest non-breed:	4.36	12	< 0.001	21 \pm 20 %
closest breed:	6.01	12	< 0.001	25 \pm 18 %

Seasonal changes in niche requirements:

Breeding niche breadth in *Sylvia* warblers was significantly smaller than total annual niche breadth (paired Wilcoxon signed rank test, $W = 15$, $n = 26$, $P < 0.001$).

CURRICULUM VITAE

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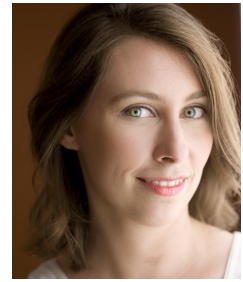
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