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The Responses of Species to Novel Climates

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Faculté de biologie
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The Responses of Species to Novel Climates

Thèse de doctorat ès sciences de la vie (PhD)

présentée à la

Faculté de biologie et de médecine
de l'Université de Lausanne

par

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The responses of species to novel climates

Lausanne, le 9 février 2024

pour le Doyen
de la Faculté de biologie et de médecine

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Prof. David Gatfield

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Summary

Human activities have resulted in profound changes on ecosystems worldwide, triggering a global decline in biodiversity. One key impact is species are expected to be exposed to novel climates outside of what they historically experienced. Two key causes of this are climate change, which for example is causing increases in average world temperatures, and species introductions, which is caused by human-mediated dispersal of species into new geographical areas where climatic conditions may differ. When species are observed to establish or persist in climates outside of what they historically experienced, this is referred to as a 'niche shift'. Niche shift studies aim to decipher how species respond to novel climates, whether induced by climate change or introductions to new areas, offering crucial insights for predicting and mitigating environmental impacts on global biodiversity. **Chapter 1** provides a thorough review of niche shifts in introduced species, revealing inherent subjectivity in the conclusions drawn, methodologies, and biases present across studies. The review highlights challenges arising from subjective interpretations of niche-shift metrics thereby impeding a cohesive understanding of niche-shift frequencies. This emphasises the imperative for standardised approaches in the study of niche shifts in introduced species. **Chapter 2** explores niche shifts among introduced ant species, revealing that invasive species (i.e. introduced species with large geographic spreads or documented negative impacts to ecology or economy) exhibit a decreased likelihood compared to non-invasive species to shift their niche. Larger expansions into new climates correlate with smaller dispersion and niche size in the native range, suggesting superior competitive abilities may not be the sole driver of niche shifts. **Chapter 3** broadens our knowledge of niche shifts in ants, emphasising the potential influence of microclimates, particularly soil-level data, on niche shifts and highlights the biological relevance of soil-level data for species primarily situated at ground levels. This underscores the promise of using microclimate datasets for predicting and explaining species distributions, thereby providing a novel dimension to the understanding of niche shifts. **Chapter 4** conducts the first meta-analysis of insect responses to climate change, revealing a complex mosaic of outcomes and underscoring the need for methodological refinements and clearer reporting. The chapter underscores the pivotal role of climatic data in predicting species distributions and advocates for clearer reporting of global circulation and emissions scenarios. Overall, this thesis has examined species responses to novel climates. We have explored the nuanced nature of niche shifts, particularly in relation to ant species, and have highlighted important factors that may impede studies in the field and offered future directions for the field.

Résumé

Les activités humaines ont entraîné de profonds changements dans les écosystèmes du monde entier, provoquant un déclin global de la biodiversité. Les études sur les changements de niche visent à comprendre la manière dont les espèces réagissent aux nouveaux climats, qu'ils soient induits par le changement climatique ou par l'introduction d'espèces dans de nouvelles régions. Elles offrent ainsi des informations cruciales pour prédire et atténuer les impacts environnementaux sur la biodiversité mondiale. Le chapitre 1 présente une revue approfondie des changements de niche chez les espèces introduites, révélant la subjectivité inhérente aux conclusions tirées, les variations méthodologiques et les biais présents dans les études. La revue met en évidence les problèmes posés par les interprétations subjectives des mesures de changement de niche et la tendance des études à se concentrer sur des espèces ou des groupes taxonomiques spécifiques, empêchant ainsi une compréhension cohérente de la fréquence des changements de niche. Ce chapitre souligne la nécessité d'adopter des approches standardisées dans l'étude des changements de niche chez les espèces introduites. Le chapitre 2 explore les changements de niche chez les espèces de fourmis introduites. Il montre, contrairement à ce qui pourrait être attendu, que les espèces envahissantes sont moins susceptibles de changer de niche que les espèces non envahissantes. Les grandes expansions vers de nouveaux climats corrèlent avec une dispersion et une taille de niche dans l'aire native plus faibles. Cela suggère que des capacités compétitives supérieures ne sont peut-être pas le seul moteur des changements de niche. Le chapitre 3 élargit nos connaissances sur les changements de niche chez les fourmis, soulignant l'influence potentielle des microclimats, en particulier des données au niveau du sol, sur les changements de niche. Il met en évidence la pertinence biologique des données au niveau du sol pour les espèces principalement terricoles. De plus, il souligne l'important potentiel de l’utilisation des données microclimatiques pour prédire et expliquer la répartition des espèces, apportant ainsi une nouvelle dimension à la compréhension des changements de niche. Le chapitre 4 présente la première méta-analyse des réponses des insectes au changement climatique, révélant une mosaïque complexe de résultats et soulignant la nécessité d'affiner les méthodes et de clarifier les rapports. Ce chapitre souligne le rôle essentiel des données climatiques dans la prédiction des répartitions d'espèces et plaide en faveur d'une communication plus claire des scénarios de circulation et d'émissions mondiales. Dans l'ensemble, cette thèse a examiné les réponses des espèces aux nouveaux climats, en se concentrant principalement sur les changements de niche des espèces introduites. Nous avons exploré la nature nuancée de ces changements, en particulier en ce qui concerne les espèces de fourmis, et avons mis en évidence les facteurs qui peuvent entraver les études de terrain. Finalement, nous avons proposé des directions futures pour ce domaine d'étude.

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Introduction

1 Species distributions and exposure to novel climates in the Anthropocene

Human activities have dramatically altered the earth. Recent years have witnessed heightened impacts of anthropogenic impacts, such as climatic changes, pesticide use, invasive species spread, urbanisation, deforestation, erosion, and climate change, resulting in widespread global declines in biodiversity (Baranov *et al.* 2020; Beaumelle *et al.* 2023; Hallmann *et al.* 2017; Newbold *et al.* 2016; Sánchez-Bayo & Wyckhuys 2019; Symes *et al.* 2018). Such significant impacts have led researchers to suggest that we are in a new geological epoch: the Anthropocene, defined by the profound influence of human activities on the earth's climate and ecosystems (Lewis & Maslin 2015).

One of the most critical influences of the Anthropocene is climate change. The global average land and ocean temperatures have risen by approximately 1.25°C since the early 20th century (Matthews & Wynes 2022). Climate variability has also intensified, marked by a rise in the frequency of extreme events like heat waves, cyclones, and floods (Coumou & Rahmstorf 2012; Field *et al.* 2012). Due to climate change, the survival and reproductive prospects of species are significantly altered as species are exposed to novel climatic conditions. For individual species, these changes imply potential shifts in the suitability of areas within their historical range, prompting the need to shift their geographical distributions, withstand novel conditions, or face local extinctions (Bellard *et al.* 2012; Moritz *et al.* 2008; Zhu *et al.* 2012).

A key question for researchers (and the central focus of this thesis) is how will species respond to novel climates? Species may remain within their historical distributions, tolerating novel conditions, for example, due to pre-adaptations, rapid adaptive evolution or acclimatisation to changing conditions (See Introduction section 2). Alternatively, a species may conserve its niche and track changes in climate, by shifting its distributional ranges into areas with climates resembling its historical climate niche (***niche conservatism***). If neither of the former responses is possible, it could mean local extinctions as conditions exceed the climatic limits the species can withstand. There are various strategies for coping with climatic changes, making it hard to predict what will happen in different species and regions. Unfortunately, observing climatic changes on real-time ecological scales is extremely difficult and requires long-term and intensive studies.

It is difficult to assess how frequently, and to which extent, species can establish in new environments. Fortunately, ***introduced species*** can serve as valuable model systems to investigate species responses to novel climates (Moran & Alexander 2014), creating a 'semi-natural experiment' to study species responses to novel climates and their implications for understanding climate change impacts (Moran & Alexander 2014). Increased global trade and travel have facilitated the unintentional transportation and introduction of thousands of species worldwide (Chapman *et al.* 2017; Early *et al.* 2016; Hulme 2009). This process can be compartmentalised into three separate phases; departure, transportation, and establishment (Blackburn *et al.* 2011; Gippet *et al.* 2019). The most common cause of such introductions is the accidental translocation of species as stowaways on traded commodities (Gippet *et al.* 2019; Meurisse *et al.* 2018). Some of these transported species can establish in new geographic regions and become introduced. However, not all transportation events lead to species introductions (Fenn-Moltu *et al.* 2023), as many factors can prevent a species from establishing self-sustaining populations in a new area, one of which is the area's climatic conditions. When a species establishes itself in a set of climatic conditions similar to that of its native range then this is referred to as '***niche conservatism***'. On the other hand, if a species can establish itself in novel climates then a '***niche shift***' is said to have occurred (See Glossary, Table 1). Biological invasions offer an opportunity to understand niche shifts and thus to better predict the potential consequences of climate change on global biodiversity patterns.

Furthermore, the uncertainty of predicting where species can establish is a major issue because introduced species themselves pose significant threats to global biodiversity (Bellard *et al.* 2021) and have detrimental impacts on ecosystems and ecosystem services (Enserink 1999; Van Kleunen *et al.* 2010; Vilà *et al.* 2010). When introduced species negatively impact native biodiversity, they are considered to be ***invasive*** (Simberloff *et al.* 2013; Vilà *et al.* 2010). The proliferation of introduced species, driven by trade globalisation, habitat loss, and land-use changes, underscores the urgency of understanding the underlying mechanisms of biological invasions (Bertelsmeier 2021; Gippet *et al.* 2019). In an unprecedented coordinated effort, the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) produced a report on introduced species (“Invasive Alien Species Report”) which estimated that a staggering

37,000 species have been introduced so far, with an economic cost of $423 billion (Roy *et al.* 2023). Furthermore, their numbers continue to rise, leading to economic losses and detrimental effects on ecosystems and services (Enserink 1999; Van Kleunen *et al.* 2010; Vilà *et al.* 2010). Therefore, to undertake immediate and evidence-based action, we need to better understand and predict the drivers of invasions.

While extensive research has addressed the environmental and anthropogenic drivers of biological invasions globally, the underlying processes are still not fully understood (Blackburn *et al.* 2011). Invasive species management programs frequently rely on species distribution models (SDMs) based on the assumption that native and historical niches encapsulate the full range of conditions a species can inhabit and that it is thus at equilibrium with its environment (Elith *et al.* 2010). These models project the realised niche onto maps of potential future or current climates but assume equilibrium between the current niche and the environment (Elith & Leathwick 2009; Soberon & Peterson 2005; Thuiller *et al.* 2005; but see recent work integrating physiological measurements to better represent species' niches; Barton *et al.* 2019; Kearney & Predavec 2000; Kirchhof *et al.* 2017). However, this conservatism assumption is not always valid leading to inaccuracies in projected distributions (Early & Sax 2014; Palaoro *et al.* 2013). If niche shifts are frequent and substantial, this assumption would be invalid, challenging the validity of biodiversity forecasts that use only correlative models (Randin *et al.* 2020; Thomas *et al.* 2004). Therefore, **understanding how often and to what extent species shift their niche when confronted with novel climatic conditions is a major challenge within ecology.** Addressing this question requires not only an understanding of individual species' responses but also an exploration of the frequencies of shifts between species, to understand what might cause some species to shift their niche more effectively than others.

2 Species' relationship to their environment

2.1 Fundamental vs realised niche

To understand how species respond to new climate conditions, be it through climate change or human-mediated dispersal, it is crucial to first define the climatic niche of the species (see Glossary, Table 1). Identifying the factors that define a species niche has been a longstanding pursuit in biogeography, ecology, and evolutionary biology (Hutchinson 1957).

Various environmental factors such as temperature, precipitation, solar radiation, wind speed, or snow cover exhibit variations across geographical space (Spence & Tingley 2020). If a species' range limits align with tolerance to extreme conditions, a species' range is influenced by its '***fundamental niche***' (see Glossary, Table 1). The fundamental niche represents the set of environmental conditions under which the species can survive and reproduce (Hutchinson 1957). This fundamental niche can be described within an 'n-dimensional space,' considering n variables to define the environmental space (Blonder *et al.* 2014) (Figure 1). Essentially it serves as a hypothetical set of abiotic conditions in which a species could exist in the absence of biotic interactions (herbivory, predation, competition etc) or geographical constraints and in the presence of unlimited resources (Hutchinson 1957).

However, it remains an open question to what extent range limits reflect fundamental niche limits. It is only rarely true that a species' range limits correspond perfectly to its fundamental niche limits (Gaston 2009; Sexton *et al.* 2009). For example, within a species historical (native) range, geographic barriers (Holt 2009; Keane & Crawley 2002) (including mountain ranges, bodies of water or highly heterogeneous habitats) that limit movement or biotic barriers (including competitors, predators, parasites (Holt 2009; Keane & Crawley 2002), or the absence of mutualistic species (Mondor & Addicott 2007; Prior *et al.* 2014)) may also limit species' ranges (Soberon & Peterson 2005). Consequently, the fundamental niche of a species is constrained, leading to the concept of the '***realised niche***,' (see Glossary, Table 1) where a species occupies only part of its fundamental niche hypervolume (Figure 1) (Gaston 2009; Sexton *et al.* 2009).

The realised niche is often the focus of research as it can be inferred from current distribution data (Araújo & Guisan 2006; Soberon & Peterson 2005), as compared to the fundamental niche which is extremely hard to measure (Jiménez *et al.* 2019; Jiménez & Soberón 2022). It is therefore the realised niche which is studied when we assess species responses to novel climates.

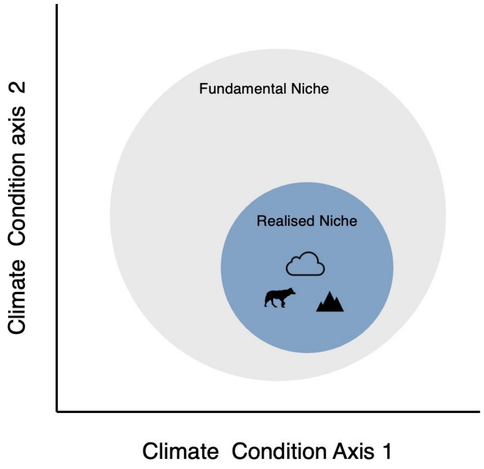

***Figure 1 Representation of fundamental and realised niche**. The fundamental niche represents the full set of climatic conditions that are suitable for a species survival and reproduction. In contrast, the realised niche lies within these fundamental limits as it is restricted by biotic and geographical barriers which prevent the species from filling the whole fundamental niche.*

2.2 Mechanisms of species responses to novel climates

A ***niche shift*** corresponds to the establishment (i.e. introductions) or persistence (i.e. changing climates) of a species under environmental conditions that are different from those in its current realised niche. Without knowing how much of its fundamental niche a species currently occupies, it is difficult to predict how it will fare under novel climatic conditions.

Transplant experiments with plants have shown that there are often large areas with potentially suitable environmental conditions that are not occupied by the species (Hargreaves *et al.* 2014). When a species is exposed to climate conditions outside of its current realised niche, several mechanisms can allow it to persist in such ways. The Biotic-Abiotic-Movement (BAM) model summarises the constraints on realised niches (Soberon & Peterson 2005), where species distributions are defined by biotic interactions (Biotic, B), ecophysiological adaptations that determine the range of abiotic conditions they can tolerate (Abiotic, A) and the ability of the species to disperse and move (Movement, M) across geographic barriers such as mountain ranges or oceans (Figure 2). The species ultimately resides in the area of conditions where all these three factors intersect (Soberon & Peterson 2005).

Species may respond to novel climatic conditions in several ways. Firstly, they may shift their spatial distribution to maintain equilibrium with suitable climatic conditions **(Movement, Figure**

2B). Species are shifting their distributions at an unprecedented rate in response to global change (Chen *et al.* 2011; MacLean & Beissinger 2017). This can occur as an increase in dispersal or movement to escape climate changes (which may in turn affect biotic niches allowing for realised niche expansion), at large scales by elevational or latitudinal range shifts (Urban 2018). Alternatively, species can move within their historical range, to exploit microclimatic refuges (Montejo-Kovacevich *et al.* 2020; Suggitt *et al.* 2011), for example, small-sized or mobile organisms may be able to utilise heterogeneity within habitats (i.e. microclimates, see glossary in Table 1) to buffer *macroclimatic* changes (Kearney *et al.* 2009; Ruiz-Aravena *et al.* 2014) as has been shown by the use of underground burrows by small mammals in the Mojave desert (Riddell *et al.* 2021). This phenomenon depends on the availability of different microclimatic conditions and is therefore expected to happen in heterogeneous environments offering a variety of habitats and microhabitats (Kearney *et al.* 2009; Ruiz-Aravena *et al.* 2014). Temporal heterogeneity in microenvironmental conditions is also a source of microclimatic refugial conditions and thus, changes in species' circadian activity can be one strategy to escape changing climatic conditions without range shift (Gippet *et al.* 2022; Rutt *et al.* 2023). The alteration of the movement niche can lead to realised climatic niche changes if changing conditions allow the species to disperse into novel climatic conditions. This change in 'movement' on the realised niche is an intrinsic characteristic of biological invasions, as species may colonise previously unreachable locations through human-mediated dispersal, and therefore access a new part of their climatic niche.

Secondly, a species may persist through changes in **biotic interactions (B)**. Species may have previously been restricted by 'biotic barriers' (Figure 2C), such as competitors, predators, parasites, or the absence of mutualistic species which have prevented the species from realising the full extent of its climatic niche (Holt 2009; Keane & Crawley 2002; Mondor & Addicott 2007; Prior *et al.* 2014. If these barriers are altered, the species may be able to access a different part of its environmental niche. This disruption to biotic interactions is particularly true for introduced species, who are translocated away from their native range and thus natural competitors and mutualists, meaning they will have a new suite of biotic interactions within their introduced range, which may enable or hinder their climatic niche (Herrmann *et al.* 2020; Keane & Crawley 2002).

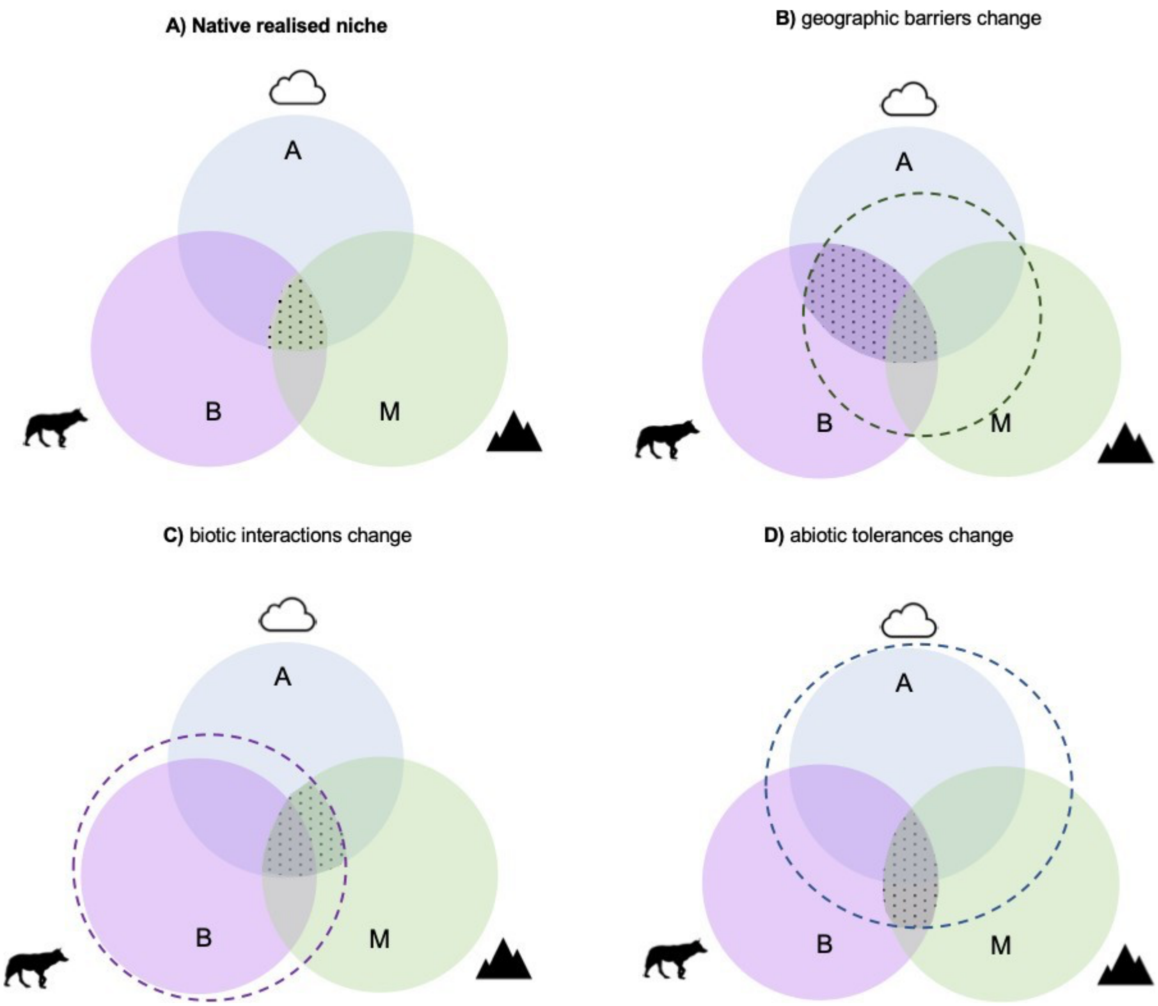

Figure 2: Biotic-Abiotic-Movement diagrams representing factors shaping the realised niche of a species. The three circles represent the biotic interactions (B), abiotic conditions (A) and areas reachable (M) by the species that define its native niche. The species will occur only in the area where biotic, abiotic and movement overlap (represented by a dotted area). (A) The realised niche of a species' native range. (B) A niche shift in which changes to the restrictions on a species' movement (green dashed circle) have allowed a larger section of biotic and abiotic niches to be realised (typically happening because of human-mediated dispersal). (C) A niche shift in which changes to the biotic restrictions on a species (purple dashed line) have allowed a larger section of the movement and abiotic niche to be realised. (D) A niche shift in which the abiotic limits of the species have changed (blue dashed line). From Bates and Bertelsmeier 2021.

Lastly, a species may be able to alter its abiotic niche (A, Figure 2D). A change in a previously unfilled abiotic niche (i.e. fundamental niche not filled by the realised niche- represented by the grey area in Figure 1) might occur due to acclimation/phenotypic plasticity (Bujan *et al.* 2021) (Lancaster *et al.* 2015). Acclimatisation is a reversible physiological change which enhances performance (Angilletta 2009). Unlike adaptation, acclimatisation is not heritable and phenotypic changes in adults caused by, for example, temperature are reversible. An example of acclimation is range-shifting damselflies (*Ischnura elegans*), which were shown to reduce their lower thermal limits along their northern range limits (Lancaster *et al.* 2015). Such changes cause a species to experience a '***realised niche shift***' (Keane & Crawley 2002; Shea & Chesson 2002). On the other hand, a species may be able to change its fundamental niche through adaptive evolution. Such changes due to the rapid evolution of tolerance to new climatic conditions would expand the absolute limits of the fundamental niche and thus be defined as a fundamental niche shift (Colautti & Lau 2015; Qiao *et al.* 2019). For example, rapid adaptation to climate has been shown to facilitate the introduction of the Purple loosestrife (*Lythrum salicaria*; Colautti & Barrett 2013), which has been thought to help it expand across different environmental gradients in its introduced range. However, the ability of species to evolve in response to climate change or during species introduction is debated, given the relatively short timescales of the species' exposure to new conditions (Hargreaves, Samis, and Eckert, 2014), and therefore such examples of fundamental niche shifts are rare (but for example see Santangelo *et al.* 2022) and would be expected to be less common than other mechanisms of species persistence (i.e over climate change) or establishment (i.e. over species introductions) in novel climates.

The distinction between realised and fundamental niches is crucial for understanding species' responses to novel climatic conditions. We are now confident that most biodiversity on Earth will be confronted with novel climatic conditions in the future, but whether species will be able to withstand such changes remains unclear (Bellard *et al.* 2012).

Table 1: Glossary of keywords used in this thesis

Keyword	*Definition*
False-positive niche shift	*Geographical expansions that are thought to represent niche shifts but are actually due to methodological issues or a lack of association between the tested macroclimates and the specific microclimates inhabited by the species that exist within the macroclimate.*
Fundamental niche	*The full set of environmental conditions under which a species can survive and reproduce (Hutchinson 1957).*
Introduced range	*The part of the geographic range of the species that is due to human-mediated dispersal*
Introduced species	*A species that has been introduced via human-mediated dispersal (accidental or intentional) to an area outside of its native range, where it has established a self-sustaining population.*
Invasive species	*An introduced species with detrimental impacts on native biodiversity, health, or the economy, following the definition by the Invasive Species Specialist Group (ISSG) of the IUCN.*
Macroclimate	*Broad-scaled climate data, derived from standardised meteorological stations located in open-air areas approximately two metres above ground level*
Microclimate	*Fine-scale climatic conditions that that differ from macroclimatic conditions due to heterogeneous environments*
Microclimatic buffering	*Climatic conditions experienced by a species that are different from macroclimatic conditions. This is typically the moderation of extreme conditions within areas of microclimatic refugia, and are therefore usually more stable to fluctuations in climatic conditions*
Native range	*The natural geographic distribution of a species without human intervention.*
Niche Coupling	*A correspondence between macroclimatic and microclimatic conditions, i.e. an increase in macroclimate correlates to a rise in microclimate conditions*
Niche expansion	*Establishment of a population in climatic conditions outside of the native realised niche of the species.*
Niche shift (climatic)	*When the niche of a new population (e.g. introduced) shifts its density of occurrence within its niche space or expands or retracts the limits of its niche*
Niche conservatism (climatic)	*When the niche of a new population (e.g. introduced) maintains ta species' fundamental niches niche space and stay within the same climatic limits of its historical niche.*
Occurrence point	*Georeferenced location where an organism has been observed*
Realised niche	*The climatic niche a species experiences. It is a subset of the fundamental niche of a species constrained by abiotic and biotic or geographical factors.*
SoilTemp	*A novel dataset of global temperature data derived from soil temperature loggers* (Lembrechts *et al.*, 2022)
WorldClim	*Classical climate dataset derived from weather station data (Fick & Hijmans 2017)*
Ordination – based methods	*The climatic conditions of occurrence points in the native and introduced ranges are compared directly using an ordination method to reduce the number of dimensions. Then, differences between native and introduced niches can be quantified in environmental principal components analysis space. The advantage of this approach is that it allows for the analysis of niche differences directly within environmental space. While it does not highlight the effect of observed shifts on spatial predictions, tools, such as the R package 'ecospat', can help to project ordination-quantified niches into geographic space*

Reciprocal SDM	*Separate models fitted based on occurrence data from either the native range or the introduced range only. Then, the spatial overlap of suitability maps based on these separate model predictions is estimated. A complete overlap of suitability maps would indicate niche conservatism.*
Hypervolume – based methods	*Allows for more direct comparisons in niche space within a n-dimensional hypervolume. Niches are projected into n-dimensional space allowing for direct comparisons in niche space without the need to overly reduce climate variables, unlike ordination methods. Two disadvantages of this method, however, are that it is computationally heavy and niche shifts may be overestimated due to the large number of axes used*

4 How do we predict species' responses to novel climates?

Studying historical trends in the relationship between species, climate and their geographic distribution can inform us about potential future changes, however they require data from many years of collection (Auld *et al.* 2022; Chen *et al.* 2011; Ramalho *et al.* 2023). To make accurate predictions of future species distributions, different computational models can be employed. These models are broadly based on the idea that information on the species' climate niches (i.e. the climatic conditions where they occur, or other environmental variables that are thought to be important for the species' biology), can be projected onto maps of either global climate or predicted future climate conditions (i.e. maps derived from global circulation models and predicted emission scenarios), will allow us to predict where and if these species can survive (Gallien *et al.* 2012; Jiménez-Valverde *et al.* 2011; Kramer *et al.* 2017).

Different approaches can be used to make predictions about species' geographical distributions under current or changing climate conditions. While most approaches use species occurrences in combination with climate data to model species' climate niches (Gallien *et al.* 2010; Guisan & Thuiller 2005; Mammola *et al.* 2021), the complexity of these models can range from simple correlational models to process-based mechanistic models. Unlike correlational models, mechanistic models can predict which regions will remain suitable under climate change by using ecophysiological data or vital rages, such as critical thermal limits (CTmax or CTmin), to model species-specific distributions. Sometimes such models even include life-stage specific growth and death rates in response to climatic variables (Kearney 2006; Kearney *et al.* 2009). The use of different models can have varying impacts on the geographic shifts of species under novel climatic conditions and determine if species may be able to expand or retract their ranges (explored in Chapter 4).

5 Testing species' responses to novel climates across species introductions

Although there are many ways in which we can predict future range changes, these predictions assume equilibrium between native/historical niches and those of the species in future climates/geographical locations, and thus do not integrate the species capacity to shift its niche. **Unsurprisingly, the extent of niche shifts in nature remains unclear, impairing predictions of future species ranges**.

Previous studies of niche shifts in introduced species have yielded contradictory results, some concluding that niche shifts are rare (Petitpierre *et al.* 2012; Strubbe *et al.* 2015), and others that they are common (Atwater *et al.* 2018; Hill *et al.* 2017). Two recent meta-analyses by Liu and colleagues, one using ordination (Liu *et al.* 2020a) and the other using reciprocal species-distribution models (Liu *et al.* 2020b), came to opposite conclusions (see glossary, Table 1, for method definitions). However, these reviews were based on small subsets of the current literature - flagging the need for broader and more in-depth critical reviews of what is already known. It therefore remains unclear whether niche shifts are a common response to **novel climatic conditions (see Chapter 1).**

Introduced species, due to the fact they are often exposed to novel climates during human-mediated dispersal make them an ideal model to test for niche shifts. Furthermore, it remains a major question why some species become invasive, becoming widely spread and ecologically dominant, while others do not (Van Kleunen *et al.* 2010). It has been hypothesised that the **ability to colonise novel climates may particularly facilitate establishment and spread into new environments, thereby increasing invasiveness**. However, **it remains unclear if invasive species are indeed better pioneers of novel climates than non-invasive introduced species (see Chapter 2).**

6 Methodological considerations: Scale

Invasion biologists have so far only examined niche shifts at a macroclimatic scale, overlooking the role of microclimates as potential refugia from macroclimatic fluctuations and changes. Microclimates are generated by environmental heterogeneity happening over short distances, for example, because of steep elevation changes (topography), differences in slope orientation (e.g., north versus south) or rugged terrains (effects of wind speed, exposition) (Graae *et al.* 2012; Lembrechts *et al.* 2019a). Factors like vegetation, canopy structure, and soil properties further contribute to the creation of diverse microclimates (De Frenne *et al.* 2019; Lenoir *et al.* 2017; Senior 2020; Suggitt *et al.* 2011). However, microclimatic variation across a species' range is not a problem to species distribution studies as long as the sign and amplitude of the deviation between micro- and macroclimate are constant (i.e. macro and microclimates are highly correlated) (Gril *et al.* 2023; Lenoir *et al.* 2017; Locosselli *et al.* 2016). For example, if a species consistently selects for microclimates 5°C cooler than macroclimatic air temperatures, and both temperatures rise at the same rate, the macroclimate suffices to characterise variations in the species niche. However, if a species selectively chooses varying degrees of cooler or warmer microclimates between different macroclimates to buffer against unfavourable conditions, microclimates become "uncoupled" from macroclimatic conditions (Scherrer & Körner 2011). If uncoupling (i.e. lack of coupling) occurs, we would be unable to predict the microclimatic conditions exploited by the species from macroclimatic measurements. This scenario can lead to a "false positive" niche shift where macroclimate conditions seem to show a niche shift that is, in fact, a case of niche conservatism when microclimate is considered (explored in **Chapter 3**).

Presently, there exists a trade-off between the coverage and resolution of climate data. The scale of interest when considering the impacts of microclimates can vary depending on the study system and taxon (Pincebourde & Woods 2020; Potter *et al.* 2013). Although testing for microclimatic selection with in situ or empirical measurements is extremely useful for understanding microclimatic processes on organisms, measuring the microclimate for many species at once and over broad geographic ranges remains impractical. Nevertheless, predicting the climate at species occurrences by enhancing data resolution to include information on, for example, below-canopy temperature, vegetation structures, and terrain features (Maclean *et al.* 2019; Mathewson *et al.* 2017; Zellweger *et al.* 2019), would improve the resolution of climate data compared to those derived from data from classical weather stations (e.g., WorldClim (Fick & Hijmans 2017). Indeed, downscaled microclimate data has already been shown to better predict distributions of native species (Ashcroft *et al.* 2008; Lembrechts *et al.* 2019b; Randin *et al.* 2009).

When predicting species ranges using climate data, increased resolution is beneficial up to the point where it no longer impacts the model performance (Bennie *et al.* 2014). For example, if the macroclimatic data accurately represents shifts in climatic conditions experienced by the species at the microclimatic scale, then data-heavy microclimatic data may not be required (Pincebourde & Suppo 2016). It is therefore important to identify a scale of climate data that consistently captures a species' niche across its range that can suffice for predicting its future spread.

7 Thesis outline

The main objective of this thesis was to understand and investigate species' capacities to respond to novel climates. In **Chapter 1**, we conducted a large-scale review of studies which have assessed niche shifts in introduced species, encompassing a meta-analysis review on the field of niche shifts, and then critically assessed the methodological and conceptual drawbacks that exist within the field.

Within **Chapters 2** and **3,** we pose the question: **How frequently do species shift their niche to novel climates globally?** We focus on ants (*Formicidae*) as a model taxon. Introduced ants have caused economic losses of 51.93 billion US dollars alone per year worldwide (Angulo *et al.* 2022), and are particularly interesting as they can be highly successful introduced species due to their advanced social organisation and variety of lifestyles and behaviours (Hölldobler, Bert 1990; Holway *et al.* 2002). As a result, there are more than 240 introduced ant species (Bertelsmeier *et al.* 2017) across terrestrial habitats, under a wide range of climatic conditions. Additionally, unlike more commonly studied taxa (e.g. plants), all ant introductions have occurred due to accidental human-mediated transport (Meurisse *et al.* 2018), with no deliberate human action for selecting hardy populations. Therefore, ants in particular are a highly suitable model to investigate the ability of introduced species to establish in novel climates.

We investigated niche shifts in ants (Insecta, Formicidae) to ask why some species shift their niche more than others (**Chapter 2**). We conducted a large-scale assessment of niche shifts on macroclimate scales across 82 introduced ant species. We investigated whether ants can enter novel climates and whether greater invasiveness stems from being able to colonise novel climates. We further explored if invasive species are indeed better pioneers of novel climates than non-invasive introduced species, and whether the size of the native niche can predict niche shifts.

We also investigated whether the methodological drawback of data resolution impacts niche shift studies (**Chapter 3**). When exposed to new macroclimates (the climate of a region measured above a $1\ km^2$ resolution), species may be able to maintain their native realised niche by selecting microclimates similar to their native range (Fig 2B). Microclimates can be observed horizontally (across a landscape) or vertically (e.g. below and above the canopy)[62]. Given that introduced ant species primarily inhabit the soil and forage on the ground, using data predicting soil-level temperatures is likely more pertinent than relying on air temperature measured by weather stations. We leverage a newly developed database (SoilTemp (Lembrechts *et al.* 2022)) to forecast soil-level temperatures, allowing us to compare niche shifts of invasive species with macroclimatic observations for 100 different introduced ant species.

Finally, we have reviewed the current state of knowledge on how we expect insect species to expand or retract their ranges with climate change (assuming niche shifts have not taken place) and investigated the impacts of different modelling techniques on predictions of range expansion (**Chapter 4**). This allowed us to compare the predicted responses of native vs introduced species to assess if introduced species were more likely to be predicted to increase their geographical range. Furthermore, despite being often discussed within the literature, a quantitative synthesis of predictions of insect species responses to climate change has not previously been done. We first present a meta-analysis of studies on the predicted range changes in insects under climate change, and then discuss models used in climate change predictions, correlational models, hybrid and semi-mechanistic models, and mechanistic models and the advantages and disadvantages of each approach. Finally, we discuss the use of different climatic data as model inputs, discussing how the choice of scale and type of climate data used can influence predicted distributions greatly. We discuss the benefits and drawbacks of different data types, sources and resolutions.

Throughout this thesis I have also explored further questions in collaboration with other researchers, such as the impact of acclimation on niche shifts of a novel introduced species (**Appendix 1**), the impact of climate on the flow and establishment of introduced insects (**Appendix 2** and **3**), and the extents of the predicted introduced spread of a pathogenic invasive mollusc species (**Appendix 4**).

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Contribution to Chapters

For Chapter 1, I was involved in study design, conducted the literature search and analysis myself, and took the lead in writing the manuscript. For Chapter 2, I conducted the niche shift analysis with help from Sebastian Ollier and took the lead in writing the manuscript and producing all figures and statistics. For Chapter 3, I took the lead in the design, analysis and writing. For chapter 4 I again took the lead in the study design, conducted the literature review by myself, produced all figures and took the lead in writing.

For Appendix 1, I conducted the niche shift computational analysis, providing Figures 1 and 2 of the paper, and contributed to the writing of the manuscript. For Appendix 2, I conducted the species distribution analysis, produced the map of climatic suitability, and contributed to the writing of the manuscript. For Appendix 3 and 4, I designed a between-country climatic similarity index, using Koppen-gieger maps (see methods sections).

Chapter 1

Climatic niche shifts in introduced species

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Review

Climatic niche shifts in introduced species

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SUMMARY

Predictions of future biological invasions often rely on the assumption that introduced species establish only under climatic conditions similar to those in their native range. To date, 135 studies have tested this assumption of ‘niche conservatism’, yielding contradictory results. Here we revisit this literature, consider the evidence for niche shifts, critically assess the methods used, and discuss the authors’ interpretations of niche shifts. We find that the true frequency of niche shifts remains unknown because of diverging interpretations of similar metrics, conceptual issues biasing conclusions towards niche conservatism, and the use of climatic data that may not be biologically meaningful. We argue that these issues could be largely addressed by focussing on trends or relative degrees of niche change instead of dichotomous classifications (shift versus no shift), consistently and transparently including non-analogous climates, and conducting experimental studies on mismatches between macroclimates and microclimates experienced by the study organism. Furthermore, an observed niche shift may result either from species filling a greater part of their fundamental niche during the invasion (a ‘realised niche shift’) or from rapid evolution of traits adapting species to novel climates in the introduced range (a ‘fundamental niche shift’). Currently, there is no conclusive evidence distinguishing between these potential mechanisms of niche shifts. We outline how these questions may be addressed by combining computational analyses and experimental evidence.

Introduction

All species on Earth have finite geographical ranges beyond which they do not occur. Since the emergence of ecology as a scientific discipline, researchers have been intrigued by the determinants of species’ range limits[1]. Interest in this topic has increased in recent years, as the effects of anthropogenic environmental changes have intensified[2] through accelerating climate change, deforestation, urbanization, land degradation, and pollution[3–7]. These changes, which define the rise of a new geological age termed the Anthropocene[8], are profound and affect all habitats on the planet[9]. Everywhere, species’ chances of survival and reproduction are altered. Areas that were previously part of a species’ range may become unfavourable and new areas may become suitable[10–12]. Therefore, species’ ranges are expected to move in response to global changes, reshuffling the planet’s biodiversity. Many species have already extended their ranges both latitudinally[13–15] and longitudinally[16,17]. Therefore, a better understanding of species’ range limits and dynamics is urgent.

A species’ distributional range is partly determined by its fundamental niche, that is, the set of environmental conditions under which the species can survive and reproduce (see Box 1 for a glossary of common terms used in this review). As this set of conditions may be defined using multiple variables (including rainfall, humidity, soil properties, temperature, snow cover, resource availability, etc.), G. Evelyn Hutchinson proposed in 1957 that a species’ fundamental niche should be described within an ‘n-dimensional space’[18], where n represents the number of different variables used to quantify the environmental space. A ‘niche hypervolume’ is the subset of this theoretical climate space experienced by the species: an n-dimensional geometric shape corresponding to the ecological requirements of the species[19,20]. This simple quantitative concept has been widely applied in ecology to try to predict a species’ potential future range[21–24].

However, linking a species’ range to the limits of its fundamental niche is not a straightforward matter. Species may not occupy all areas with suitable abiotic conditions. For example, geographic barriers[25,26] that limit movement or biotic barriers (including competitors, predators, parasites[25,26], or the absence of mutualistic species[27,28]) may limit species’ ranges[29]. As a result, species usually occupy only part of their fundamental niche hypervolume, which is referred to as their ‘realised niche’[18,26] (Box 1). Often, ecologists study a species’ climatic niche by recording environmental variables at locations where the species currently occurs[29,30]. Such data correspond to the species’ realised niche, which is often assumed to be representative of the species’ fundamental requirements. Recently, some studies have also measured physiological requirements under different climatic conditions to get a better estimate of the fundamental niche, yet such studies remain rare due to the large amount of data needed[31–35].

The discrepancy between the realised and the fundamental niche is one reason why it is difficult to forecast a species’ range under changing environmental conditions. For example, at a given location the temperature may increase up to a point where it falls outside of the current realised niche of a species. Yet, the climate at this location may still remain within the species’ fundamental niche. Thus, the species will be able to persist there despite changing conditions and is said to ‘shift’ its niche.

Box 1. Glossary.

Analogous climate: Climate conditions available to the species in its native range and present in its introduced range.
False-positive niche shift: Geographical expansions that are at first thought to represent niche shifts, but are found to arise due to methodological issues or a lack of association between the tested macroclimates and the specific microclimates inhabited by the species that exist within the macroclimate.
Fundamental niche: The full set of possible climatic conditions under which species can survive and reproduce in the absence of limiting factors that could constrain the species populations.
Fundamental niche shift: Niche shift caused by genetic changes within the introduced population that increase the population's fitness.
Introduced species: Species that have spread beyond their native range due to human-mediated transport.
Niche conservatism: When the niche of a new population (introduced) retains the niche space of the previous (native) population.
Niche shift: When the niche of a new population (introduced) shifts its density of occurrence within its niche space, or expands or retracts the limits of its niche.
Niche-shift methodologies: Methods used to quantify and distinguish the niche space of a species, including species distribution models, ordination, and high-dimensional multivariate methods approaches (Box 2).
Niche-shift metrics: Values used to quantify a change in niche.
Niche hypervolume: Multi-dimensional space consisting of all the conditions in which a species exists (typically more than three variables).
Niche unfilling: When a species range shift has occurred and part of the niche space present in the previous range is not filled in the future range[65].
Novel climate: Climate that is not experienced by the species in its native geographical range.
Non-analogous climate: Climate conditions not present or available to the species in its native range, but present in its introduced range.
Range shift: When the geographical limits within which a species survives and reproduces is altered.
Realised niche: The range of climatic conditions under which a species survives and reproduces within given geographical and biological constraints. It is a subset of the fundamental niche (above).
Realised niche shift: Caused by a species entering a new climate to which it was preadapted but did not inhabit in its native range. Occurs due to a release of biological, geographical, or climatic constraints that existed in the native niche[25] (Figure 2).

A niche shift corresponds to the establishment or persistence of a species under environmental conditions that are different from those in its current range. Niche shifts that occur when species fill a different part of their fundamental niche are referred to as 'realised niche shifts'. Sometimes realised niche shifts are enabled by developmental plasticity or acclimatisation to new climatic conditions[36,37]. Alternatively, the species' fundamental niche may evolve in response to changing conditions, thereby adapting the species to novel climates (Box 1). This is referred to as a 'fundamental niche shift'.

It is a great challenge for ecologists to understand how often and to what extent species may shift their niche when confronted with novel climatic conditions[38–40] (Figure 1; T1). Whatever the mechanism, niche shifts are problematic for correlative 'species distribution models', which are commonly used to predict future species ranges by projecting the realised niche onto maps of potential future climatic conditions[41,42] (but see recent work integrating physiological measurements to better represent species' niches[31–33,35,43]). A basic assumption of these models is that species are in equilibrium with their environment, that is, their current realised niche reflects the entire set of conditions under which the species may thrive[21,44–46]. However, if niche shifts are frequent and substantial, this would challenge the global forecasts of future biodiversity that often use such correlative models[12]. In species that have already displayed a niche shift, it has been recommended that researchers include points of occurrence within both the native and introduced range so as to make predictions of future ranges more representative of the entire set of conditions under which these species thrive[47,48]. However, species-distribution models cannot include such points of occurrence before a niche shift has occurred. Therefore, assessing the frequency of niche shifts is an unresolved issue of extreme importance for biodiversity forecasts.

A major obstacle to assessing niche shifts in response to ongoing global climate change is the timescale at which it operates. Paleo-ecological records of ancient pollen and fossils have been used in combination with reconstructed paleo-climates to estimate past realised niches[49–53] and how they changed over long timescales[51,52]. However, biodiversity is facing unprecedented rates of climate change at present[49,50], and it is difficult to infer from these paleontological records the extent to which species may be able to shift their niches in the near future. Recording current niche changes in response to climate change also has its limitations. It will likely take several decades to record any actual niche shifts of native species, making predictions of future responses to novel climates difficult. Therefore, it is particularly interesting to study species that are already experiencing novel conditions: several tens of thousands of species have been transported out of their native ranges as a result of ongoing globalization of human movements and trade[54–57]. Some of these species are able to establish and spread in their new environments. These introduced species provide a 'semi-natural experiment' in which they encounter novel environmental conditions[58], allowing researchers to study the frequency and amplitude of niche shifts. Here, we focus on niche shifts in introduced species — not only are these species useful models for the study

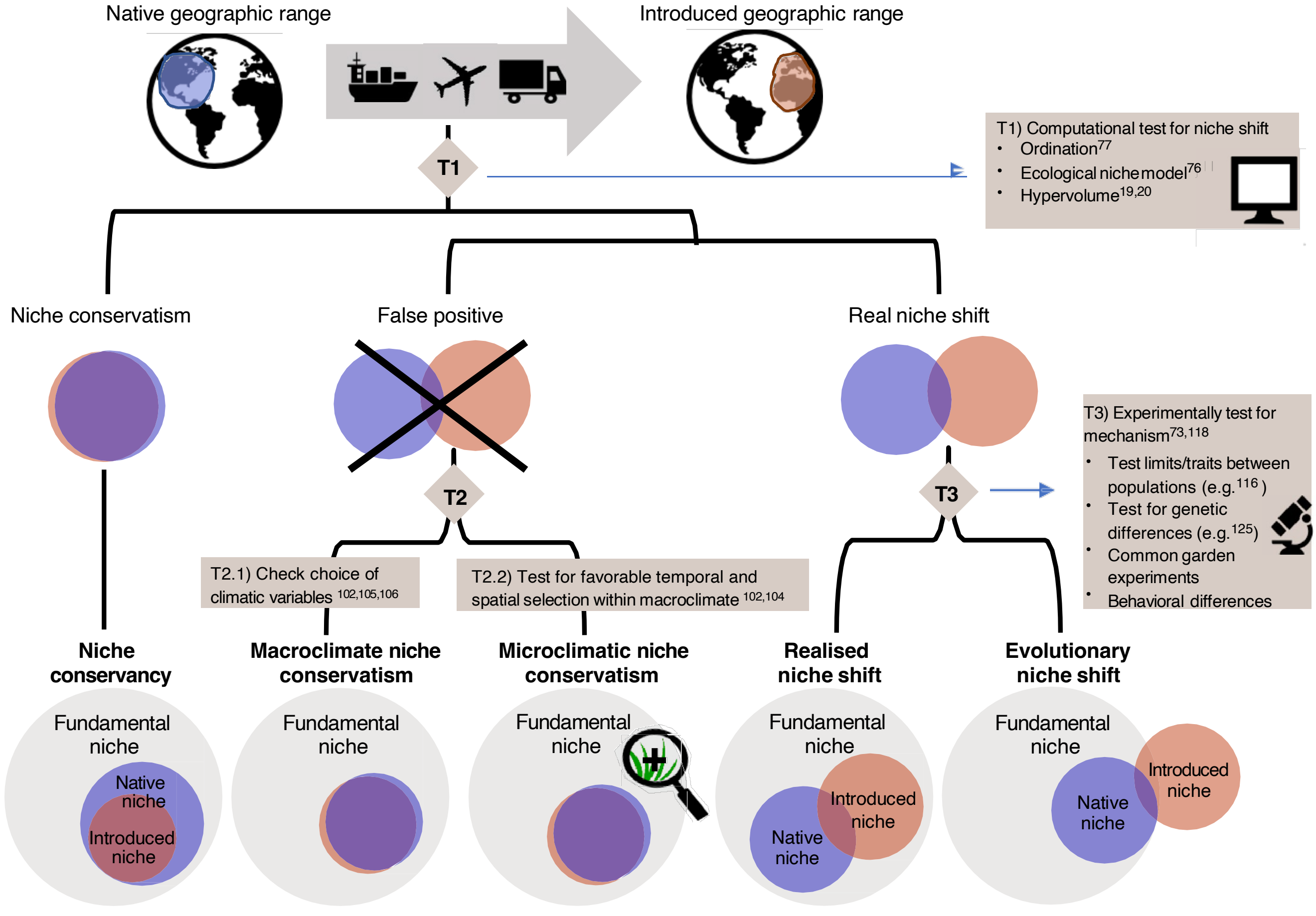

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Figure 1. Characterizing a niche shift.
Upon geographical expansion by a species, one should first determine whether the new niche is a case of niche conservatism or whether instead a niche shift has occurred using a variety of computational methods (T1). If it is determined that a niche shift has occurred, there is still a chance that the observed changes are not ecologically meaningful. These 'false positives' (T2) may occur because there has been no change in the climate experienced by the introduced population, either because the climate variables measured are not biologically meaningful (macroclimate niche conservatism) or the microclimate experienced by the species is consistent with its original niche (microclimate conservatism), despite climatic differences at the macro scale. False positives can be determined by experimental tests and expert knowledge. If an actual niche shift has taken place, the mechanism for this shift can be determined experimentally (T3). In some instances, the new niche will prove to be within the species' fundamental niche, in which case the shift is referred to as a 'realized niche shift'. However, in other cases evolutionary changes have occurred in the population that allow for the species' survival in the new niche (evolutionary niche shift).

of niche shifts, but also, they themselves are of significant ecological interest given that they pose enormous threats to local biodiversity[59], ecosystem services[60,61], agriculture[62], and human and animal health[63]. Because introduced species are notoriously difficult to eradicate once established[64], current mitigation efforts are centred on early detection and prediction of future invasions. Understanding how frequently invasive species may shift their niche is therefore crucial.

Much progress has been made in the development of computational methods comparing realised niches across ranges of introduced species (Box 2). These methods quantify environmental conditions at points of occurrence within each range. To do this, one needs to first select a set of climatic (or other environmental) variables that are thought to be important for the species' biology. Important variables can be identified through literature reviews of previous field or experimental work, or from expert knowledge. Based on these variables, many studies differentiate three aspects of niche shifts: the overlap between the old and the new realised niches, the amount of expansion into novel environments, and the degree of 'niche unfilling' (Box 1) that occurs when the species abandons environmental conditions that were present in its historical range. Together, these different assessments are thought to provide an objective quantification of niche shifts[65]. However, despite these methodological advances, the extent of niche shifts in nature remains disputed, impairing predictions of future species' ranges.

Do introduced species establish under novel climates?

So far, the frequency of niche shifts in introduced species remains unknown because previous studies have yielded contradictory results, some concluding that niche shifts are rare[66,67]

Box 2. Three methodologies to quantify niche shifts.

The three most common methods to test for niche shifts are species distribution models, ordination-based approaches, and high-dimensional multivariate approaches.

Reciprocal species-distribution models: Separate models fitted based on occurrence data from either the native range or the introduced range only. Then, the spatial overlap of suitability maps based on these separate model predictions is estimated. A complete overlap of suitability maps would indicate niche conservatism. A disadvantage of this approach is that it uses projections in geographic space, which may distort the niche comparisons, for example, if large geographic areas have similar climatic conditions[77]. Furthermore, niche truncation effects caused by marginal climates can lead to the overestimation of niche shifts [136,137]. However, species-distribution models are particularly useful to directly test the effect of climatic niche shifts on species-distribution-model predictions, allowing direct comparisons in spatial predictions as they can weigh the likelihood of a species inhabiting various climates based on their current geographic distribution. Species-distribution models are useful to directly test if invasive niches are conserved by using them to predict the native range of the species.

Ordination-based methods: The climatic conditions of occurrence points in the native and introduced ranges are compared directly, using an ordination method to reduce the number of dimensions. Then, differences between native and introduced niches can be quantified in environmental principal components analysis space. The advantage of this approach is that it allows for the analysis of niche differences directly within environmental space. Although it does not give us an idea of the effect of observed shifts on spatial predictions, tools such as the R package ‘ecospat’ can help to project ordination-quantified niches into geographic space[138].

High-dimensional multivariate methods[19,120,139–141] allow for more direct comparisons in niche space within a n-dimensional hypervolume. Niches are projected into n-dimensional space allowing for direct comparisons in niche space without the need to overly reduce climate variables, unlike the ordination methods. Two disadvantages of this method, however, are that it is computationally heavy and niche shifts may be overestimated due to the large number of axes used[101].

and others that they are common[68,69]. Two recent meta-analyses by Liu and colleagues, one using ordination[70] and the other using reciprocal species-distribution models[71], came to opposite conclusions. However, these reviews were based on small subsets of the current literature. Here, we conducted the first comprehensive review of studies on niche shifts in introduced species, critically evaluating the current evidence for niche shifts and their potential mechanisms. In the first part of this review, we assess the available evidence for climatic niche shifts. We argue that the available evidence regarding climatic niche shifts is inconclusive, due in part to three factors: divergent interpretations of the same niche-shift methodologies and metrics; the exclusion of non-analogous climates (that is, climates not available in the native area) from the niche-shift analysis, which biases conclusions towards niche conservatism; and the use of climatic data that are not biologically meaningful, which can lead to ‘false positives’ in niche-shift analyses (Figure 1, T2).

But even carefully conducted computational analyses cannot determine the underlying mechanism of a niche shift: a realised niche shift by filling the fundamental niche or a fundamental niche shift through an evolutionary adaptation to novel conditions (Figure 2). A fundamental niche shift may occur through adaptive evolution of traits enabling the colonization of novel climates[72–74]. Although adaptive evolution is an attractive hypothesis, we argue in the second part of this review that no study has yet presented conclusive evidence distinguishing between realised and fundamental niche shifts (Figure 1, T3). We outline experimental evidence that would be needed to demonstrate adaptive evolution and argue that in the absence of such evidence the null hypothesis should be a realised niche shift (or a ‘false positive’; Figure 1, T2).

Overall, we highlight the clear need for interdisciplinary work to understand the frequency, mechanisms, and biological relevance of niche shifts. We highlight surprising knowledge gaps within this field and hope to stimulate future work investigating how species may respond to novel climates.

Current evidence for climatic niche shifts

In September 2020, we conducted a literature search on Web of Science using the key words ‘niche shifts’ OR ‘niche conserv*’ OR ‘niche modelling’ AND ‘invas*’. Results were filtered for papers in the field of biology and ecology, resulting in 4,218 studies. These were then manually filtered to include only papers that have investigated climatic niche shifts between native and introduced ranges (Table S1).

In total, 135 studies reported niche-shift analyses in introduced species: the majority concentrated on plants (Figure S1) and 68.1% of studies focused on a single species. The majority of studies (63.7%) reported the presence of niche shifts (Figure 3A) and among the 639 species studied, 53.5% were found to shift their niche (Figure 3B). However, this high frequency of niche shifts may not be representative because of potential publication biases against studies reporting niche conservatism[75]. Moreover, calculating such frequencies across all studies may not be meaningful due to the variety of methodologies employed to quantify niche shifts, most commonly including reciprocal species-distribution models[76], ordination-based methods[77], and high-dimensional multivariate methods[19] (Box 2). For that reason, the use of a single framework has been recommended[65] and a recent meta-analysis assessed just 30 studies that used only this framework to determine the frequency of niche shifts[70]. Despite the inherent differences between approaches, however, we found that species-distribution models and ordination were equally likely to detect niche shifts across studies (Pearson’s chi-squared test, $X^2 = 1.32$, df = 4, p = 0.86; Figure S2). Therefore, the plurality of methods may not be a major obstacle to progress in the field. Future research may compare the three approaches directly by using the same

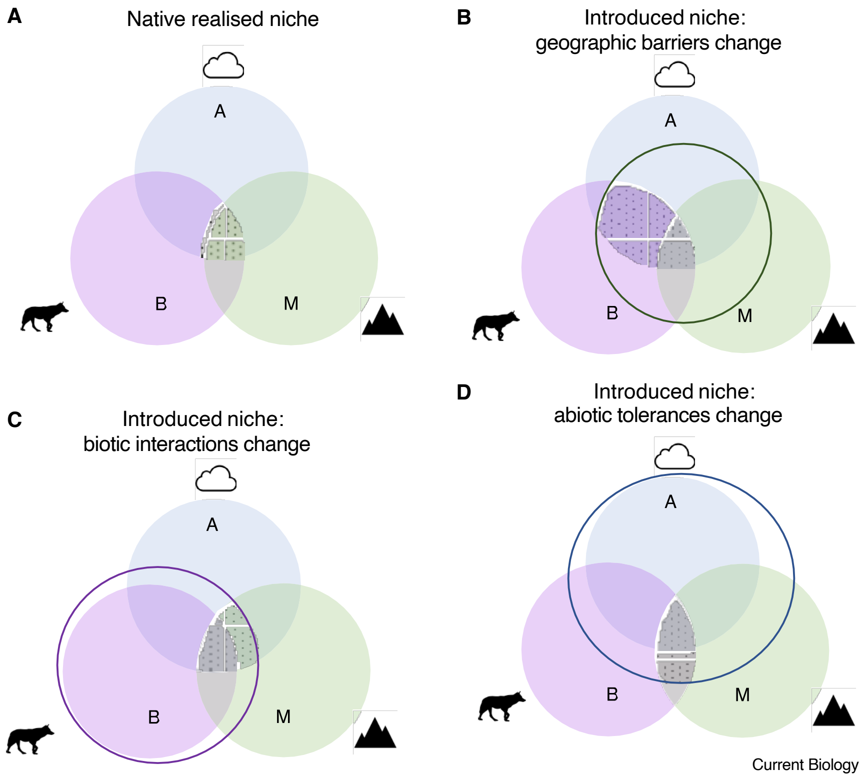

Figure 2. Mechanisms of a realized niche change.

Biotic-Abiotic-Movement diagrams representing factors restricting the realised niche of a species[29]. The three circles represent the biotic interactions (B), abiotic conditions (A) and areas reachable (M) by the species that define its native niche. Only in the area where biotic, abiotic and movement overlap will the species be able to thrive (represented by dotted area). (A) The realised niche of a species' native range. (B) A niche shift in which changes to the restrictions on a species' movement (green dashed circle) have allowed a larger section of biotic and abiotic niche to be realised. (C) A niche shift in which changes to the biotic restrictions on a species (purple dashed line) have allowed a larger section of the movement and abiotic niche to be realised. (D) A niche shift in which the abiotic limits of the species have changed (blue dashed line).

species pool to assess different likelihoods of detecting niche shifts. But we argue that using several methods simultaneously may allow us to better understand the extent and direction of niche shifts, as each has its advantages (Box 2). First, using multiple different approaches may increase confidence in study conclusions. If all methods agree and detect a large niche shift, we may attribute a higher likelihood that a niche shift has indeed occurred. Using multiple different approaches is already common practice in species-distribution modelling (also called 'ensemble modelling')[78,79], where a higher likelihood of presence is assigned to areas predicted as suitable by multiple methods. In addition to increasing confidence in the interpretation of niche shifts, different approaches are useful to address different questions. To quantify the difference between climates in the native and the introduced range, ordination and high-dimensional multivariate (hypervolume) methods are most appropriate as they allow the researcher to directly test for niche shifts in environmental space. This is informative if one is interested in 'biological' questions, for example investigating which species have experienced the greatest climatic differences between their native and introduced range and if these differences are linked to their ecological traits. However, to assess the consequences of potential niche shifts for predictions of potential future species ranges, it is best to use reciprocal species-distribution models. For example, ordination-based methods may detect a small niche shift, whereas a reciprocal species-distribution model might predict a large one. This would imply that the species expanded little in environmental space, but this small change has a big impact on the potentially suitable area predicted using a species-distribution model. This can happen if large geographic areas worldwide have the precise new climatic conditions under which the species has established in its introduced range, and therefore even a small shift in environmental space can lead to a large increase in the predicted potential range of the species. On the other hand, a large shift in ordination-space and a small shift in a species-distribution-model approach would indicate that the species was able to thrive under climates that are extremely different from those in its native range, but this has minimal impact on the size of the predicted range of the species. This will be interesting to a researcher studying species' capacity to face novel climates but not to a modeler interested in predicting the size and location of future species distributions.

Divergent interpretations of niche-metric results

A much greater issue than the use of different approaches to compare niches is the lack of standards to interpret niche-shift-metric results. Metrics are descriptive statistics used to quantify niche shifts and are subject to author interpretation. For example, the commonly used metrics 'Schroeder's D' and 'Hellinger's I' measure the degree of overlap in occurrence densities within the environmental space, comparing the native and introduced ranges[80]. Both metrics vary between 0 and 1, with lower values indicating a larger niche shift[77,80], but there is no general limit when one should conclude niche conservatism versus a niche shift. Some studies do not attempt to find a threshold at all and among those that did, we strikingly found no difference in species' Schroeder's D overlap between reports of niche conservatism and niche shifts (Figure 4A; Kruskal-Wallis rank sum test, $X^2 = 4.80$, df = 2, p = 0.18). For example, one study[81] concluded a niche shift due to a 'low' Schroeder's D overlap value of 0.49, whereas different authors estimated that a Schroeder's D overlap of 0.18 was 'high', concluding niche conservatism[82]. Similarly, no standards exist concerning another commonly used metric, 'niche expansion' (Box 1; Guisan *et al.*[65]), which determines the degree of 'new' niche in the introduced range[77]. Some authors[40] concluded that a niche shift has occurred only if expansion was above a threshold of 50%,

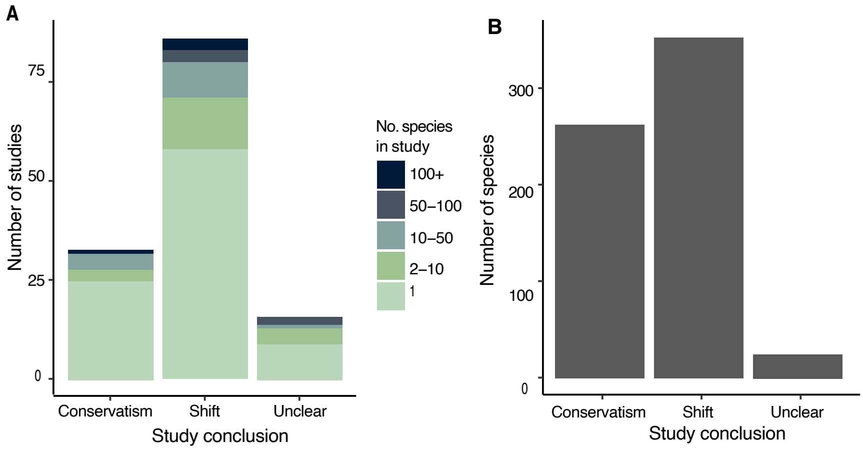

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Figure 3. Overview of 135 studies that conducted niche-shift analysis.

Conclusions indicating niche shifts or niche conservatism from 135 studies investigating niche shifts between native and introduced ranges are presented. (A) The overall conclusion from each study as to whether a niche shift or niche conservatism occurred. In some studies, there was an unclear decision between the two. Colours represent the number of species that each of the studies used to make their overall conclusions. (B) Individual assessments for all species examined by studies (for which data were available). Conclusions as to whether the species has shifted or been conserved or if no conclusion was made are presented.

whereas others[83] speak about niche shifts based on 10% expansion.

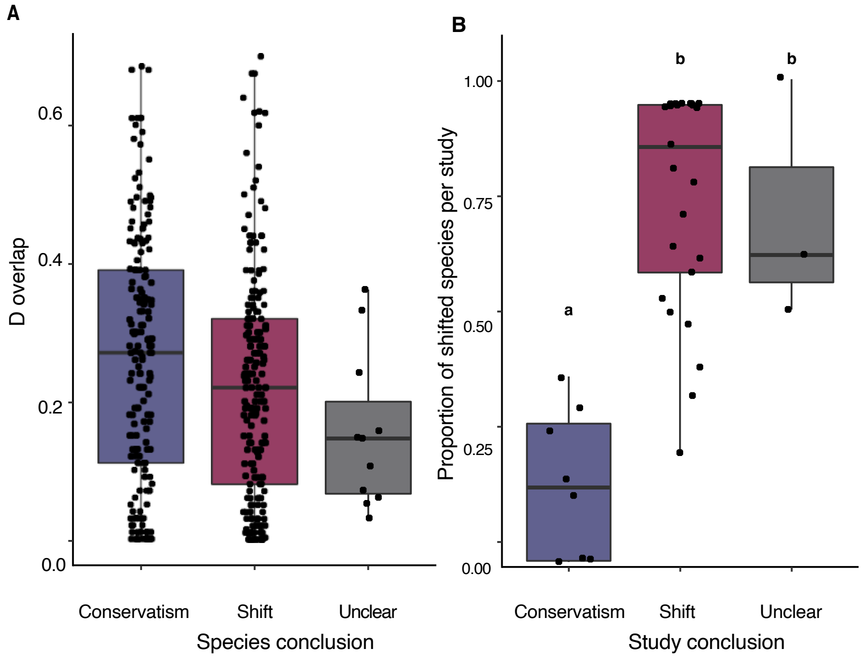
Although thresholds of Schroeder's D overlap are not intuitive, niche similarity and niche equivalency tests determine whether niche overlap values are significantly different from random[77]. Niche similarity tests compare the niche in the native range to random selection of the 'background' climate in the introduced range[77,80]. They are therefore influenced by the way in which background climate is defined[84], and a significant result may not be reliable. For example, in the literature, 81 species that appeared to have conserved their niche according to a similarity test were instead found to have shifted their niche based on evidence from other approaches (for example, reciprocal species-distribution modelling) or metrics (for example, niche expansion) (Figure S3). The second statistical test for Schroeder's D overlap is the niche-equivalency test, which assesses whether the niches occupied in the native and introduced ranges are significantly different from each other, using a random permutation of points. However, this test will reject the null hypothesis of 'equivalent niches' if there are only slight differences in the frequency distribution of the climates occupied by the species. This can happen without any expansion or unfilling of the niche. Because the chances are low that the species' niche will have the exact same frequency distribution of climates in both ranges, the test will almost always be significant. Indeed, among 334 species for which equivalency tests were conducted, only 2 species had 'equivalent' niches (Figure S3). Furthermore, for 120 of 334 species with non-equivalent niches, the authors concluded that the species had conserved their niche based on opposing evidence from other metrics and tests. It is clear then that neither approach to testing of the null hypothesis provides solid evidence for a niche shift. Furthermore, statistical tests to determine if an expansion value is 'significant' are completely lacking. This is problematic as the expansion metric is perhaps the most interesting measure of a niche shift, as it quantifies the degree to which a species occupies novel climates, expressed as the percentage of the invasive niche that was not occupied in the native range.

In addition to the issues of when or how to conclude that a niche shift has occurred for a given species, multi-species studies lack objective standards when concluding that niche shifts are common or rare. For example, studies claiming that niche shifts are 'common' have based this conclusion on a proportion of 'shifting' species being anywhere between 25 and 100% — a staggering variation. Overall, as expected, the proportion of species showing niche shifts was higher in studies reporting niche shifts to be common (range = 0.25–1) compared to studies that reported niche shifts to be rare (range = 0–0.4) (Figure 4B; Kruskal-Wallis sum rank test, $X^2 = 92.78$, df = 2, $p < 0.001$). Yet, there was no clear cut-off point indicating when niche shifts should be considered common or rare. For example, one study argued that because 11 out of 30 species had shifted their niche, niche shifts are a problem for future models that assume niche conservatism[85]. In contrast, another study with 10 out of 25 species shifting niches concluded that there is 'good evidence' for niche conservatism between native and introduced ranges[86].

These striking variations in the interpretations of metrics and the proportions of shifting species may reflect the author's beliefs, which is a concerning issue that has been neglected so far within the field. In order to make progress, the vast variation in interpretations of the same metrics needs to be addressed. We note, however, that not all authors attempt to find a threshold or conclude definitively whether their study species have shifted their niches, and such approaches can be useful within comparative frameworks[68,87–89]. As arbitrary dichotomous conclusions do little to contribute to our understanding of niche shifts, it is more useful to identify trends and indicators of different degrees of niche shifts. For example, larger niche shifts have been linked to degree of invasiveness[88], length of introduction history[40,67,90], native niche and range sizes[40,68,88,90,91], and particular continents of origin[40,90–92]. Such information may indicate which species are more likely to shift their niche in the future. Broader, multi-taxa studies might identify characteristics of species displaying a greater propensity for niche shifts, and thus help to predict which species are likely to shift their niche in the future. Until then, current studies should be treated with caution due to the possible interpretation biases outlined above.

Methodological issues: exclusion of non-analogous climates

To quantify niche shifts in the introduced range of a species, some authors exclude 'non-analogous' climates from their analysis. A non-analogous climate refers to novel climate space that



Current Biology

Figure 4. Reports of niche conservatism, niche shifts, or unclear results in the literature.

(A) Measured Schroeder's D overlaps for each species examined throughout the 135 studies we assessed, and the conclusion of whether the species had exhibited niche conservatism or niche shifts, or whether the results were unclear. (B) The proportion of species reported to shift their niche in the conclusions of each multi-species studies, and the overall conclusion of the study as to whether there has overall been common niche conservatism, niche shifts, or if the results were unclear and inconclusive. Different letters denote significant differences among groups. Boxplots show the median (center horizontal line), upper and lower quartiles (box limits), and the 1.5x interquartile range (whiskers).

was not available to a species in its native range. Consequently, if the species establishes in a non-analogous climate in the introduced range, this can be qualified as a 'niche shift'. However, authors have argued that such niche shifts into non-analogous climates must be disregarded because it is impossible to determine if they represent a 'real' niche shift[65,93]. This term lacks a clear definition, but it is used in way that it implies a meaningful change in the species' biology linked to the niche shift (for example, a change in the fundamental niche; Figure 2D) as opposed to simple expansion of the range of climatic conditions under which the species thrives (for example, a change in the realised niche; Figure 2A–D). Excluding non-analogous climates to ensure the detection of 'real' niche shifts assumes that it is possible to determine the cause of a niche shift into analogous climates: if a species occupies novel climates in its introduced space that had been available in its native range, this change is supposed to stem from a 'real' niche change[65]. However, this argument is flawed, as all kinds of niche shifts (biologically meaningful or not) can also occur in analogous space[94,95]. For example, when species are moved outside of their native ranges they are frequently released from constraints limiting their native distributions, such as natural enemies (biotic changes) or dispersal barriers (movement changes), and may spread and establish in new analogous climates in the absence of changes to the fundamental niche requirements through adaptive evolution[25,96,97] (Figure 2). Therefore, excluding non-analogous climates from niche-shift studies does not help distinguish between realised and 'real' fundamental niche shifts. To do that, experimental evidence is needed.

Overall, failure to consider niche shifts into previously 'unavailable' climates does not help to ensure that a computationally determined niche shift has biological meaning, as the removal of non-analogous climates excludes large parts of climate space newly colonized by introduced species. Furthermore, the absence of niche shifts when non-analogous climates have been removed does not demonstrate niche conservatism, as the most relevant part of the data (that is, the area where niche expansion has occurred) has been removed. As a consequence, studies considering only shifts into analogous climates (following Broennimann *et al.*[77]) are more likely to report niche conservatism (Figure 5A; Pearson's Chi-squared test, $X^2 = 3.87$, df = 1, $p = 0.05$). This bias may be a reason that a recent meta-analysis, which was based on only 30 niche-shift studies excluding non-analogous climates, found that niche conservatism was common[70]. We recommend that niche-shift analyses should either include both non-analogous and analogous climates, or at least conduct analysis with and without non-analogous climates and present these separately in a clear and transparent way[69].

Methodological issues: Climate data that are not biologically meaningful

In addition to the issues leading to the failure to detect niche shifts, there is also a danger of detecting 'false positives' due to the use of biologically irrelevant climate data (Figure 1). For example, the type and number of climate variables included can influence the size of the estimated niche[98–100], with a high number of variables increasing the likelihood of finding a niche shift in at least one of the dimensions of the climatic niche hypervolume, a problem particularly apparent in the high-dimensional multivariate approach[101]. This can result in misleading conclusions if the species has conserved its niche for the most relevant climate variables that actually limit its distribution[102]. It has been suggested that researchers should just consider fewer environmental variables[98]. But this approach would not solve the issue of identifying biologically relevant variables. Most species will experience niche changes on some environmental axes but not others; however, such changes may be irrelevant to the species[102]. For example, air surface temperature is unimportant for subterranean species and detecting a 'niche shift' based on that variable will not have any biological meaning for the species[103,104]. To avoid detecting false-positive niche shifts, climate variables should be selected with consideration of the species' biology where possible[105,106]. Selecting relevant climate variables requires expert knowledge and careful consideration of the scales that are most relevant for the focal species.

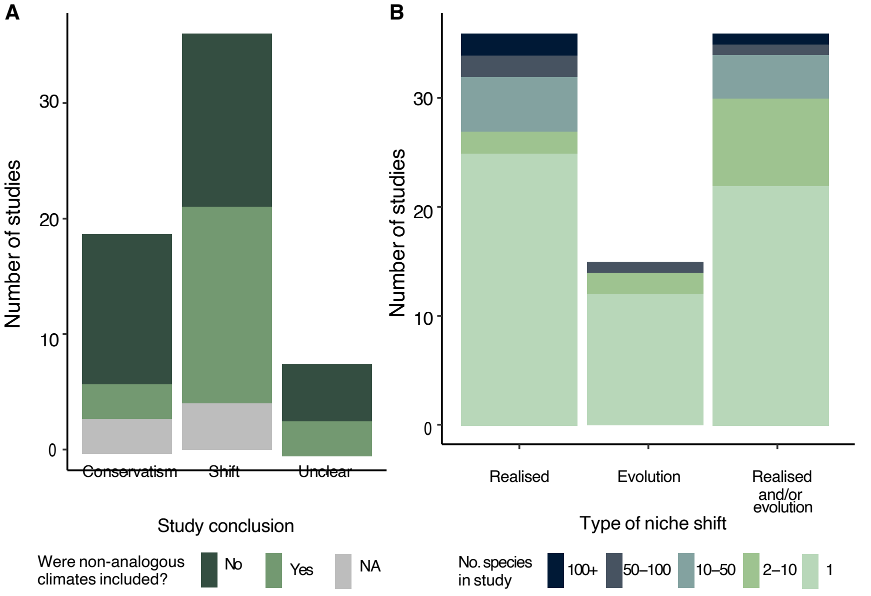


Figure 5. Study conclusions based on consideration of different factors.

(A) The effect of excluding non-analogous climates on studies reporting niche conservatism or niche shifts. Of the studies that used the most common method of niche determination, those that concluded niche conservatism were more likely to have only considered analogous climates (restricting niche-shift analysis to only consider climates available to the species in their native range). The category ‘NA’ includes studies where the inclusion or exclusion of non-analogous climates was not specified. (B) For studies finding a niche shift, the graph shows both the mechanisms identified and the number of species examined. The proportion of studies that leaned strongly towards a realised niche shift (a release from native constraints on niche; Figure 2), an evolutionary niche shift (adaptive evolution caused the species to change), or gave a balanced argument for either mechanism.

Current Biology

So far, all studies investigating niche shifts in introduced species have examined the species’ niche on a macroclimatic scale, which may not adequately represent the microclimatic conditions experienced by the species[103,107] (Figure 1). Macroclimates are the broad-scale climate conditions usually recorded by meteorological stations; by only considering these, the smaller-scaled microclimates caused by heterogeneous habitats within the macroclimate are neglected, despite potentially being very different from the macroclimate[108]. These can differ substantially[109], especially in forests where shade buffers microclimates[108,110]. However, differences between macro- and microclimates are not necessarily problematic if they are correlated across the species’ range. For example, if a species always selects microclimates that are 5ºC cooler than the temperatures measured at the macroclimatic scale, then the macroclimate can still be used to characterize the species’ niche. However, if a species selects cooler or warmer microclimates to buffer against unfavourable macroclimatic conditions in the introduced range, macroclimates become ‘uncoupled’ from microclimates[107]. Species may change their daily activity patterns (for example, foraging[111]) or spatial location[112] (for example, nesting sites) to maintain optimal microclimate conditions[35,111,113]. In that case, a macroclimatic ‘niche shift’ could hide a microclimatic niche conservatism, revealing a scale issue. For example, macroclimatic data suggest that the red imported fire ant *Solenopsis invicta* has shifted to areas with extremely low precipitation in its introduced range, but at a local scale it is evident that these areas benefit from human irrigation[102]. Although the choice of relevant spatial scales has been discussed in the species-distribution-model literature[102,114], this issue has been neglected in studies on niche shifts. To our knowledge, no study has yet examined whether a macroclimatic ‘niche shift’ could in reality correspond to microclimatic niche conservatism. We hope that future research will address this question by combining computational niche-shift analyses and experimental approaches. With new microclimate datasets emerging, such studies become more feasible[115]. In particular, it would be exciting to test the degree of microclimate-to-macroclimate decoupling taking place between native and introduced ranges and between different species by measuring differences in observed niche shifts. Such approaches would include using different resolutions of macroclimate data, comparing macroclimates (from weather stations) and field-recorded climate data (from data loggers), and recording activity or nesting patterns of species in order to evaluate precisely the microclimates that they are selecting.

Mechanisms behind niche shifts

An attractive explanation for niche shifts is the adaptive evolution of species’ traits, which in turn alter climatic tolerances[116] — that is, a change in the species’ fundamental niche (Box 1). It has been suggested that rapid genetic adaptation may be important for invasive species faced with rapidly changing environmental conditions, possibly favoured by admixture of different source populations in the introduced range or genetic bottlenecks during the transport process[72–74,117]. However, to demonstrate this, experimental evidence is required showing that the spread of a population has been enabled by genetic changes adapting the species to new climates[73,118]. Because only a few studies have supplied such evidence (but see a carefully conducted field experiment in *Lythrum salicaria*[119]), it still remains a big question in invasion biology as to whether rapid adaptation of invasive populations is a frequent occurrence[73,118]. Without such evidence, the alternative and more parsimonious hypothesis is that a realised niche shift has occurred (Figures 1 and 2). Realised niche shifts happen when a species enters a new climate in its introduced range to which it had been preadapted, therefore filling a greater part of its fundamental niche[25,65,120]. This should be the null hypothesis for explaining niche shifts in introduced species, given that they are often transported by humans over long distances and are likely to encounter abiotic conditions different from their native range while being released from their dispersal constraints and other biotic limitations. Computational niche-shift analyses[65,66] do not address the drivers behind

Table 1. Studies concluding that niche shifts in introduced species took place due to evolutionary mechanisms.

Species	Evidence required to demonstrate that an evolutionary niche shift has taken place				Alternative explanation given	Reference
	Identify source population?	Trait changes observed between native and introduced populations	Genetic basis of trait difference between native and introduced populations	Fitness advantage of introduced populations		
Lactuca serriola	Yes (microsatellite)	Yes — flowering phenology	Yes — common garden	No	No — but mentions that genetic admixture is possible and acknowledges that there is no direct evidence that the observed change in flowering phenology is linked to the shift in climate niche	122
Ambrosia artemisiifolia	No	Yes — phenotypic traits	Yes — common garden	No	No — argue for the high likelihood of rapid adaptive evolution	127
Anolis cristatellus	Source population previously defined	Yes — thermal tolerance	No	No	Yes — discuss that realised niche shifts are possible and were likely in some introduced populations, and acknowledge that observed changes may have arisen from genetic drift or plasticity within the population	123
Argiope bruennichi	No	Yes — thermal tolerance	Yes — GWAS	No	No — but discuss how the genetic changes observed in the population could be due to population admixture, but are likely due to rapid evolution of particular regions	124
Gracilaria vermiculophylla	Yes	Yes — thermal tolerance	Yes — common garden	No	Partially — mention that observed trait differences could be due to plasticity within the species; however, go on to stress the greater likelihood of evolution	116
Ambrosia artemisiifolia	Yes — invasion history	Yes — life history traits	Yes — common garden	No	Yes — mention that in general niche shifts can be caused by both realised and evolutionary shifts, but suggests that evolution of the introduced population is likely in this case	125
Coffee species (3)	No	Yes — flowering phenology	Yes — GWAS	No	No — potential for hybridization between the three coffee species might lead to further niche shifts	131
Phragmites australis	Yes	No	No	No	No — argue that realised nice shifts are unlikely due to the high degree of unfilling. Trait differences have been observed in previous studies (common garden experiment) and another study has shown genetic divergence of introduced population compared to source population observed	132
Schinus terebinthifolius	Yes	No	No	No	Yes — discuss the possibility of realised niche shift	133

(*Continued on next page*)

Table 1. *Continued*

Species	Evidence required to demonstrate that an evolutionary niche shift has taken place				Alternative explanation given	Reference
Aedes albopictus	No	No	No	No	Yes — discuss that realised niche shifts are also possible but unlikely due to previous evidence of highly competitive behavior in the species (meaning biological restriction is unlikely)	76
Aves (92)	No	No	No	No	Yes — discuss that realised niche shifts are also possible, but because their species did not seem restricted in their native ranges (few island endemics), infers evolutionary shifts are more likely	134
Plantae (10)	No	No	No	No	No — Discuss how the niche shifts observed may have been promoted by niche evolution. Also discuss human activity and climate change as factors that promote adaptation to new climates. No mention of realised niche shifts is made	135

expansion into novel climates. Despite that, among the 86 studies reporting niche shifts, 41.4% indicated realised niche shifts as the favoured explanation and 17.2% suggested adaptive evolution as the cause. A discussion of the equal possibility of either scenario was present in 41.4% of studies (Figure 5B). So far, no study has provided conclusive evidence for adaptive evolution as the driver of a niche shift, and only a few studies have provided partial evidence. Below we discuss the evidence supplied so far, as well as what is needed to conclusively determine adaptive evolution.

Evidence needed

To determine whether adaptive evolution of traits has occurred, several steps are necessary, without which an evolutionary niche shift should not be concluded[73,118], as outlined by Bertelsmeier and Keller[118]. First, the precise source population must be identified to quantify potential trait changes between this source and the introduced population[121]. This is important to exclude the possibility that an observed trait change is not simply a local adaptation in a certain native population, pre-adapting it for colonization of the invaded area[73]. In total, five studies have identified trait changes between the source population and the introduced population (Table 1) that may have driven a niche shift. These include changes such as flowering phenology[122], thermal tolerance[116,123,124], and life-history traits[125]. However, such trait changes can arise from natural plasticity or acclimatisation ability within the species[36,37] and may accompany a realised niche shift. Therefore, the second step is to show that trait changes in the introduced population have a genetic basis. This can be achieved using, for example, a 'common garden' experiment[73], where traits expressed by individuals from the source and the introduced population are measured under constant conditions. Such experiments were conducted in only four studies[116,125–127] (Table 1).

Thirdly, the observed trait change must be linked to an increase in fitness within the introduced population, enabling it to colonize a novel climate[118]. To test if the trait change increases fitness, reciprocal transplant experiments are needed to test if the introduced population has a greater fitness under the environmental conditions in the introduced range compared to the native population[118]. This evidence was not supplied in any of the studies on niche shifts (Table 1). We acknowledge, however, that logistical and ethical constraints involved in such experiments make this impossible for many invasive species. For example, placing introduced species in transplant experiments may contribute to their spread or impacts. When reciprocal transplant experiments are impossible, assessment of fitness traits (such as reproductive capacity, survival, growth rates) in a common garden or controlled laboratory environment could indicate a genetic basis of a trait difference potentially enabling an observed niche shift in the introduced population. This would indicate evolution of the introduced population, but not establish the link with fitness differences in the local environmental conditions in the introduced range and therefore the niche shift.

We acknowledge that it is labour intensive to combine a computational niche-shift study with these experimental approaches in order to determine the underlying mechanism of an observed niche shift. However, in the absence of such evidence, the null hypothesis should be that the species has extended its realised niche without adaptive evolution[128].

Perspectives and conclusion

Given that the numbers of introduced species worldwide are steadily rising and that many of these species threaten native biodiversity and human livelihood, it is urgent to better understand and predict the global spread and establishment of these species. Furthermore, introduced species can be extraordinarily useful models to test the degree of niche change of which a species is capable and inform predictions about how all species will respond to continued climate change. Over the last few years, an increasing number of studies have reported computational analyses of niche shifts using newly developed, sophisticated statistical tools[19,77,129]. Despite enormous progress in methodological developments and data availability, the likelihood and frequency of niche shifts across species remain unclear. Major reasons for this are subjective interpretations of niche-shift metrics, the exclusion of non-analogous climates by some studies, and the use of only macroclimatic data, which is not meaningful for many small-sized species. We argue that the three issues we have outlined here need to be addressed before we can objectively compare niche-shift results among studies. Furthermore, future research should also investigate the mechanisms of niche shifts, requiring the use of direct experimental approaches to ultimately inform modelling studies that hope to predict future niche shifts.

Questions that can be addressed with current approaches

Despite the problems and open issues that we have highlighted, researchers studying niche dynamics have developed a multitude of useful tools and investigated many interesting questions. Given the issues within the field, it is currently difficult to answer the dichotomous question of whether a species has shifted or conserved its niche, or to estimate the overall proportion of introduced species that have shifted their niche compared to those that have not. Although methodological issues and a lack of consensus about interpretation make comparisons between studies difficult, comparative studies are still useful to investigate why some species shift their niche more than others. Such studies can help predict the degree to which a species may enter novel climates in the future, considering its biological characteristics. Furthermore, as it is known that niches do not remain stable over time, elucidating whether larger niche shifts occur early in their introduction history[90], or later[67,87,130], may also inform us as to how quickly we should expect niches to change in the future.

Overall, to make progress in the field, we advocate for improving the integration of modelling and experimental work so as to better link patterns to processes and ultimately help to improve species distribution models. This will include computational analyses (identifying niche shifts), population genetics (discovering source populations of introduced species) and experiments (testing fitness advantages of trait changes in novel climates). Without such interdisciplinary work, which is currently lacking, the field of niche-shift studies cannot provide mechanistic explanations for its findings. We hope that our findings and suggestions will stimulate such research. Better understanding the capacity of species to establish under novel climates and to evolve in response to these conditions is crucial, not only for informing predictions of future invasions, but also to forecast species responses to climate change.

SUPPLEMENTAL INFORMATION

Supplemental information includes supplemental results, three figures and one table and can be found with this article online at https://doi.org/10.1016/j.cub.2021.08.035.

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DECLARATION OF INTERESTS

The authors declare no competing interests.

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Chapter 2

Smaller climatic niche shifts in invasive than non-invasive alien ant species

Olivia K Bates, Sébastien Ollier and Cleo Bertelsmeier

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Smaller climatic niche shifts in invasive than non-invasive alien ant species

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The globalization of trade and human movement has resulted in the accidental dispersal of thousands of alien species worldwide at an unprecedented scale. Some of these species are considered invasive because of their extensive spatial spread or negative impacts on native biodiversity. Explaining which alien species become invasive is a major challenge of invasion biology, and it is often assumed that invasiveness is linked to a greater ability to establish in novel climates. To test whether invasive species have expanded more into novel climates than non-invasive alien species, we quantified niche shifts of 82 ant species. Surprisingly, invasive species showed smaller niche shifts than non-invasive alien species. Independent of their invasiveness, the species with the smallest native niches and range sizes, experienced the greatest niche shifts. Overall, our results challenge the assumption that invasive species are particularly good pioneers of novel climates.

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Ever-increasing trade and travel have facilitated unprecedented globalization and the dispersal of an increasing number of species outside of their native ranges[1,2]. This has resulted in over sixteen-thousand 'alien' species globally[3]. Some of these species are considered 'invasive' as they cause significant detrimental impacts on ecosystems, human health, and economies worldwide[4,5] (See Table 1). A major challenge is to understand why only some and not all alien species become invasive[6]. The identification of ecological characteristics distinguishing non-invasive alien and invasive species, which would allow predictions of future invasions, is still considered as the holy grail of invasion biology[6,7]. It has been hypothesized that traits conferring high plasticity and adaptability to new conditions may favor establishment and spread in new environments, thereby increasing invasiveness[8–10]. For example, previous research has suggested that invasive species show higher plasticity under new environmental conditions[11], a greater ability to maintain dense monocultures[12], and higher levels of allelopathy[13]. Such traits could be particularly important when a species is introduced to areas where the climate is different from its native range. Yet, it is still unknown whether the ability to colonize novel climates contributes to the success of invasive species[14].

Although many studies have compared realized climatic niches within native and non-native ranges, the majority focus on such "niche shifts" in a single invasive species, with few including multiple species (but see e.g., refs. [15,16]). Importantly, no study has evaluated whether climatic niche shifts of invasive species are in fact larger than those of non-invasive alien species, a key prediction of plasticity-based hypotheses of invasiveness. To test this prediction, we focused on ants (*Formicidae*), a taxon which includes particularly prominent alien and invasive species[17]. Ants are highly successful due to their complex social structure and variety of lifestyles, behaviors, diet requirements and nest constructions[17,18]. Importantly, ants have been dispersed accidentally[19] and there has been no human selection for 'hardy' traits, such as increased tolerance to climatic conditions, as in other taxa such as plants. Moreover, they are present across all major terrestrial habitats and thrive under a wide range of climatic conditions[20] and previous work on *Solenopsis invicta* has suggested that ants may be able to colonize novel climates not present in their native range[21]. There are currently more than 200 known alien ant species, with 19 classified as 'invasive' by the IUCN due to their impacts on biodiversity, ecosystem functioning, agriculture, infrastructure and human or animal health, causing important economic losses[17,22].

Here, we quantified the frequency and extent of niche shifts in 82 ant species. We show that invasive species displayed smaller niche shifts than non-invasive alien species. Instead, native range and niche size impacted the extent of niche shifts. Our results challenge the hypothesis that invasive species are better at colonizing novel climates, and has implications for predictive species distribution modeling.

Results and discussion

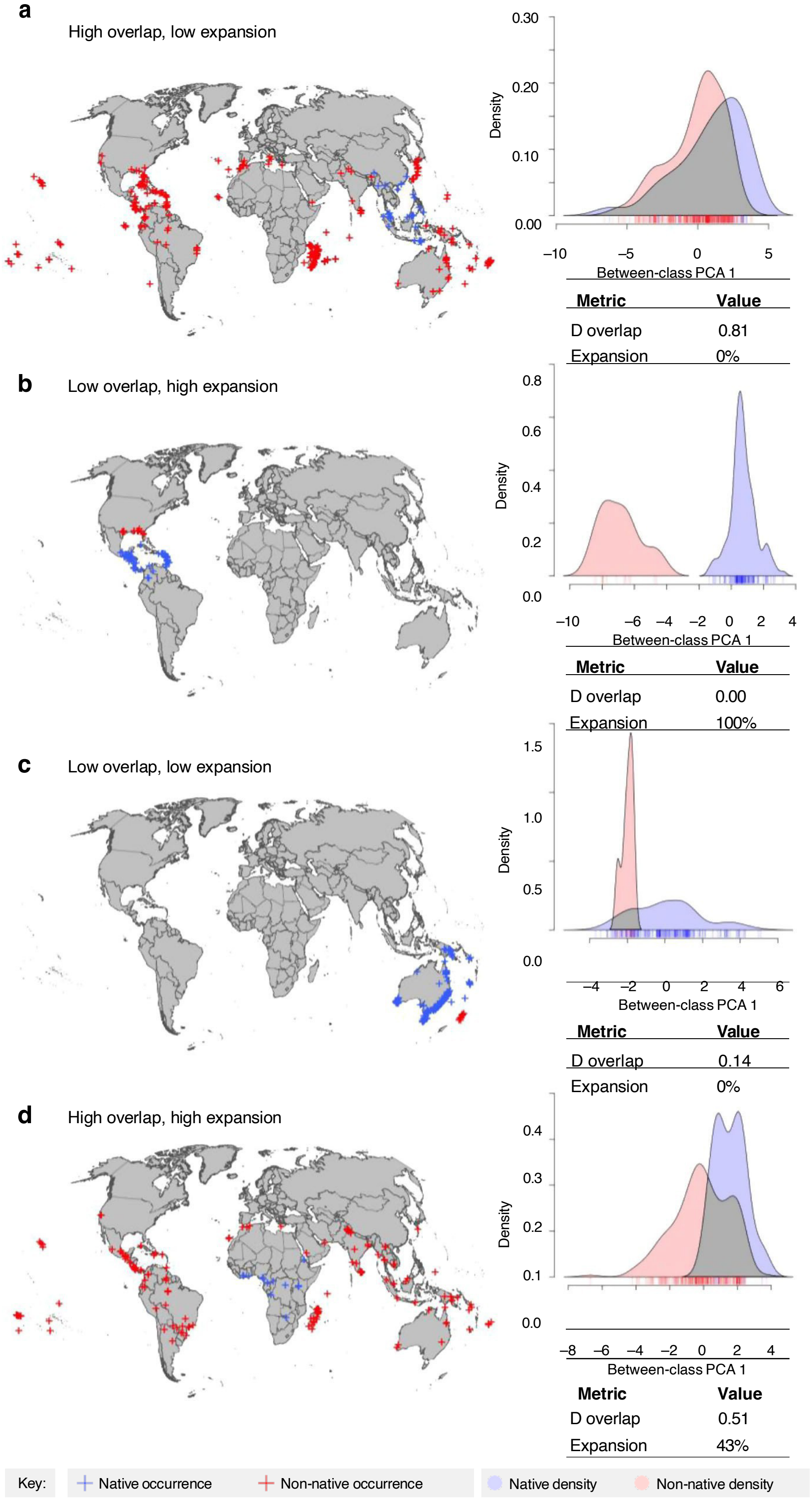
We assessed niche shifts of all 82 alien and invasive ant species for which at least 10 occurrence points in both their native and non-native ranges were available (median number of occurrence points per species: 209, range: 27–3531. Importantly, the number of occurrences per species had no effect on the results (See "Methods" section). We quantified different aspects of niche shifts between native and non-native niches (Table 1) by calculating niche overlap (Schoener's D; shift in niche centroid, range: 0–0.81) and expansion into novel climates (percent of non-native niche extending beyond native niche, range: 0–100%). We also performed niche equivalency tests (probability of observed niche shift due to chance) which revealed that all but two of the 82 species, *Nylanderia bourbonica* ($p = 0.08$) and *Tetramorium bicarinatum* ($p = 0.07$), had significantly divergent niches between the native and non-native range, compared to random ($p < 0.05$) (see Supplementary Data 1). Some species had high niche overlap and low expansion between their native and non-native range (Fig. 1a), whereas others showed no niche overlap and high expansion (Fig. 1b), indicating near complete niche shifts. However, low niche overlap does not necessarily equate to high expansion. For example, some species had low niche overlap and low expansion (Fig. 1c), with limited non-native niches largely encompassed by the native niches. Other species had high niche overlap and high expansion (Fig. 1d), representing non-native niches that largely include the native niche, but also extend beyond it.

Surprisingly, invasive species had on average higher niche overlap with their native range than non-invasive alien species

Table 1 A glossary of key terms used in the study, split between definitions of keywords and concepts used, and metrics used in measurements of niche change.

Term	Definition

Keywords	
Alien species	A species that has been introduced via human-mediated dispersal (accidental or intentional) to an area outside of its native range, where it has established a self-sustaining population.
Invasive Species	An alien species with detrimental impacts on native biodiversity, health or the economy, following the definition by the invasive species specialist group (ISSG) of the IUCN.
Native range	The natural geographic distribution of a species without human intervention.
Niche shift (climatic)	The newly established outdoors range of an alien species.
Niche expansion (climatic)	Establishment of a population in climatic conditions outside of the native realized niche of the species.
Fundamental niche	The full set of environmental conditions under which a species could thrive in the absence of competition or dispersal constraints.
Realized niche	The environmental conditions under which a species lives as a result of limiting factors (typically a subset of the fundamental niche).
Niche metrics	
D overlap (Schoener's *D*)	A measure of niche overlap. The overlap of the density of occurrences between two populations in niche space, ranging from 0 (no overlap) to 1 (complete overlap)[60].
Equivalency test	A permutation test where all occurrences are pooled and randomly split, to simulate a random distribution of *D* overlap values. If 95% of the simulated overlap is higher than the observed D value, the assumption of niche equivalency can be rejected[60].
Expansion	The percentage of the non-native niche that is not present in the native niche[16].



Metric	Value
D overlap	0.81
Expansion	0%

Metric	Value
D overlap	0.00
Expansion	100%

Metric	Value
D overlap	0.14
Expansion	0%

Metric	Value
D overlap	0.51
Expansion	43%

Fig. 1 Shifts in climatic niche and geographic distribution between native and non-native ranges. Species demonstrated are: (a) *Tetramorium bicarinatum*, (b) *Strumigenys margaritae*, (c) *Amblyopone australis*, and (d) *Monomorium pharaonis*.

(Kruskal–Wallis sum rank test, $X^2 = 4.19$, df = 1, $p = 0.04$), and the amount of niche expansion did not differ between non-invasive alien and invasive species (Pearson's chi-squared test, $X^2 = 1.50$, df = 1, $p = 0.22$) (Fig. 2b). That is, while the average expansion into novel climates was not different between invasive and alien species, invasive species tended to have less divergent niche centroids between their native and non-native niches. These results demonstrate that invasiveness in ants, defined by the severity of ecological impacts, does not rely on a greater propensity for climatic niche shifts. Indeed, invasive species

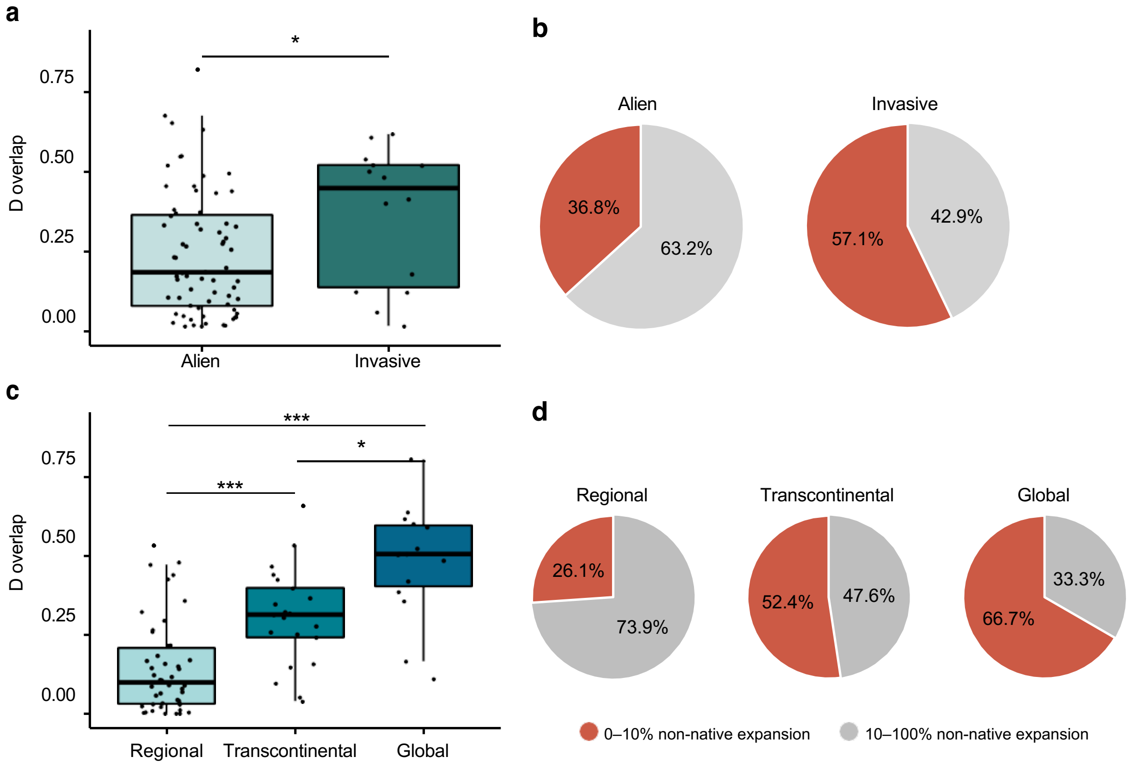


Fig. 2 Comparison of niche similarity between the native and non-native ranges of different ant species using different definitions of invasiveness. a Compared to non-invasive alien species (n = 68 species), IUCN-classified invasive species (n = 14 species) have a larger D-overlap (Kruskal–Wallis sum rank test, $p = 0.04$) and (b) the similar percentages of species that have expanded above 10% (Pearson's chi-squared test). c Between species distributed at regional ($n = 46$ species), transcontinental ($n = 21$ species), and global ($n = 15$ species) levels, with increasing levels of global dispersion quantifying higher invasiveness, there are increasing amounts of D-overlap (Post-hoc Dunn test with Benjamini-Hochberg correction, regional-transcontinental, $p < 0.001$; transcontinental-global, $p = 0.02$; regional-transcontinental, $p < 0.001$), and (d) decreasing percentage of species with expansion above 10%, as levels of geographical dispersion increase (regional to transcontinental to global, Pearson's chi-squared test). Boxplots elements show; center line, median; box limits, upper and lower quartiles; whiskers, 1.5× interquartile range.

showed overall smaller niche shifts compared to non-invasive alien species.

Because invasiveness can also be defined in terms of total spatial spread instead of impacts, with higher spatial spread relating to higher invasiveness, we tested if more widespread species have a greater propensity for climatic niche shifts. To do this, we separated the 82 species into three groups of similar levels of geographic dispersion (following[23]). For each species, we determined the number of political entities within which it had established (spatial richness, see "Methods" section) and estimated the Rao spatial diversity of its entire range, taking into account the pairwise distances between the centroids of these regions[23]. Using a cluster analysis within this richness-diversity space, species were classified as members of a regional, transcontinental, or global dispersion group (see "Methods" section,[23]). Species in the regional dispersion group mostly occur across multiple countries within the same continent. Transcontinental species have spread across multiple continents but only to a few countries within each. Global species have successfully dispersed across continents and spread throughout the countries within each continent. Species that were classified as invasive by the IUCN based on their impacts occurred in all three dispersion groups (global = 9, transcontinental = 2, regional = 3). Interestingly, species with a broader total geographical distribution exhibited a higher D overlap (Kruskal–Wallis test, $X^2 = 31.04$, df = 2, $p < 0.001$) (Fig. 2c). Moreover, niche expansion decreased with increasing total geographical range (Pearson's chi-squared test, $X^2 = 10.80$, df = 2, $p < 0.001$) (Fig. 2d). This demonstrates that invasiveness, defined as greater spatial spread, is also associated with smaller climatic niche shifts.

We acknowledge that some non-invasive alien species may still be in the early stages of their invasion process and will become invasive in the future[24], due to time lags between initial introduction and subsequent spread or impacts of the species[25,26]. However, this is likely to concern only a few species, given that most alien ant species have been moved by humans around the planet for a long time. The vast majority of currently alien ant species has indeed started colonizing new areas even before World War II[23]. Therefore, most species currently recorded as "alien" have likely had sufficient time to become invasive.

It is counterintuitive that for both definitions of invasiveness, species with greater invasiveness exhibit smaller climatic niche shifts. This may be because the colonization of novel climates has nothing to do with a species' propensity to spread or cause impacts on native ecosystems. Species distributions are known to be the result of several limiting factors, as summarized by the BAM (Biotic, Abiotic, Movement) model[27]. This conceptual scheme, which has been widely used in invasion ecology, displays areas with the necessary biotic interactions (B), the areas with necessary abiotic conditions (A) and areas that can be reached by the species via movements in space (M). A species is able to thrive in places where all three conditions are met. Our results suggest that there is greater overlap between the B, A, and M areas for invasive than non-invasive species. For alien species, there might be large areas which meet the abiotic conditions for its survival (i.e., the species fundamental niche), but cannot be colonized by

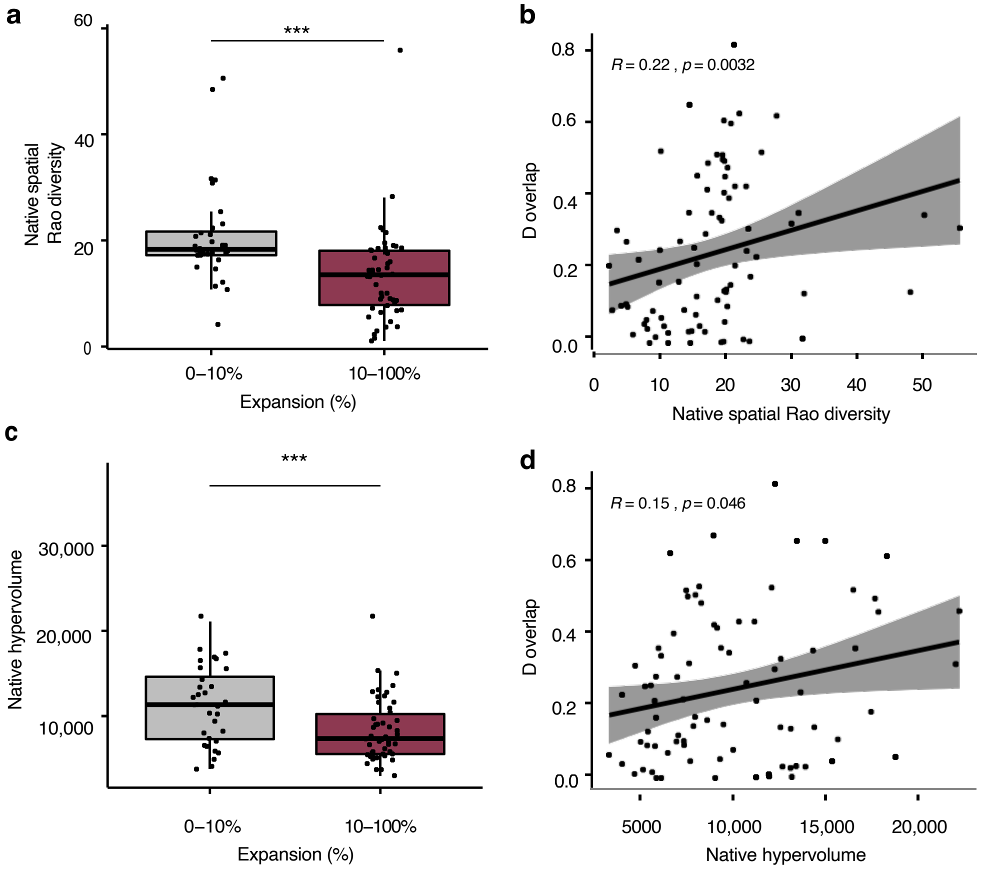


Fig. 3 Effects of native range characteristics on the level of expansion and *D* overlap between native and non-native ranges on different ant species. a Species with low expansion (0–10%) ($n = 32$ species) had a higher native spatial Rao diversity than species that expanded above 10% ($n = 50$ species), and (b) increasing native spatial Rao diversity also led to higher *D* overlap ($n = 82$ species) (Kendall's Tau rank correlation coefficient test, $p < 0.001$). c There was a higher Native Hypervolume size for the low expansion group, and (d) with increasing Native Hypervolume size, *D* overlap also increased (Kendall's Tau rank correlation coefficient test, $p < 0.001$). Kendall Rank Coefficient regression lines are observed with 95% confidence intervals. Boxplots elements show; center line, median; box limits, upper and lower quartiles; whiskers, 1.5× interquartile range.

the species due to biotic interactions or dispersal barriers[28,29]. Establishment outside of their native range would therefore more frequently result in observed "niche shifts", when these species are released from B and M constraints (e.g. refs. [30,31]).

To test whether niche shifts are more frequent in species with a smaller native range, we calculated Rao spatial diversity for the native range (as a measure of native geographic dispersion) for each species. We found that species which showed minimal niche expansion (<10%)[16,32], were more widely dispersed in their native range (Rao spatial diversity, Kruskal–Wallis test, $X^2 = 22.86$, df = 2, $p < 0.001$) (Fig. 3a). Higher Rao spatial diversity also correlated to higher *D* overlap (Kendall Rank Coefficient, $r\tau = 0.22$, $p = 0.003$) (Fig. 3b). Because the extent of spatial spread does not always represent the diversity of climatic conditions within that range, we also assessed the size of the species' climatic niche within its native range. To do that, we calculated the n-dimensional niche hypervolume of the species' native range[33], using multidimensional kernel-estimation in PCA space (see "Methods" section). Species that showed little expansion also had significantly larger niche hypervolume in their native range (Kruskal–Wallis test, chi-squared = 12.17, df = 2, $p < 0.001$) (Fig. 3c), furthermore, species with higher *D* overlap had larger native niche hypervolumes (Kendall Rank Coefficient, $r\tau = 0.15$, $p = 0.05$) (Fig. 3d).

Native range size and niche hypervolume were independent of impact-based invasiveness (native Rao spatial diversity: Kruskal–Wallis test, $X^2 = 0.22$, df = 1, $p = 0.64$, native hypervolume: Kruskal–Wallis test, $X^2 = 0.32$, df = 1, $p = 0.57$). However, native range size was linked to dispersion-based invasiveness (Kruskal–Wallis test, $X^2 = 8.32$, df = 2, $p = 0.02$), indicating that species that are widespread within their native range also realized the largest global distributions. Despite this, the native niche hypervolume was also independent of dispersion-based invasiveness (Kruskal–Wallis test, $X^2 = 1.61$, df = 2, $p = 0.45$). Therefore, the size of the native niche volume conditions the extent of niche shifts independently of the species' invasiveness. Species with smaller niche shifts may have had less constrained realized niches in the native range. On the contrary, species with a low natural dispersal capacity and small niche size in their native range may benefit more from human-mediated dispersal, allowing them access novel climatic conditions within their fundamental niche[34].

The negative relationship between the size of the native niche hypervolume or geographic range, and the extent of niche shifts suggests that it is generally the realized niche rather than the fundamental niche which has shifted. For example, the observed niche shifts could be explained by increases in thermal plasticity in the invaded range, given that critical thermal limits may change with season[35] and diet[36] in ants. Realized niche shifts can occur because of relaxed ecological constraints, and do so in the absence of adaptive evolution in the non-native population[37–39].

However ruling out that evolution, either through founder effects[40], novel genetic combinations[41] or adaptive evolution[42], has altered climatic tolerance during the invasion process of individual species would require experimental evidence[42–44]. Given the high frequency of niche shifts found in our study, we hope that future research will disentangle potential mechanisms explaining these shifts by combining computational and experimental approaches. To better understand the dynamics of niche shifts, it would also be interesting to quantify the expansion of the non-native niche over time for species with documented invasion histories. This would allow testing if species start by colonizing climatically similar areas before shifting their niche, or, if on the contrary they tend to colonize novel climates first before filling their niche when they arrive in their introduced range. Previous research found that the highly ant species *Solenopsis invicta* tended to first invade areas more similar to the native range[21], but it is not yet known if alien species in general follow such dynamics.

Our findings have implications for predictive species distribution models (SDMs). These models make the strong assumption of niche conservancy between native and non-native ranges. Many studies have used SDMs to predict potentially suitable areas for invasive species[45]. However, if niche shifts occur during invasion, be they realized or fundamental niche shifts, these SDM predictions will not be reliable[46]. But for invasion biologists, it is encouraging that the most invasive species showed the smallest niche shifts, indicating that SDM predictions or climate-matching risk assessments for species which pose the greatest environmental risks may be the most reliable. However, many non-invasive alien ant species were capable of colonizing novel climates not present in the native range. This suggests that studies assuming niche conservancy cannot predict accurately the future threat of these species, particularly those with small native niche sizes. More generally, this is not just a problem for modeling potentially suitable areas of alien species, as SDMs are a major tool used to predict the effects of climate change for endemic and threatened species[47], which typically have much smaller geographical ranges than non-invasive alien and invasive species. In order to predict a species' capacity to expand its climatic niche, experimental evidence is needed. Incorporating experimental data on changes in physiology, phenology or species interactions in response to environmental changes into more mechanistic models may capture a more realistic view of the climates that can be tolerated (e.g., refs. [48–50]).

Overall, our findings reveal that, contrary to expectations, invasiveness is not linked to a species' ability to shift its niche. This challenges the assumption that invasive species are particularly good pioneers of novel climates. Instead, we found that the characteristics of a species' native range were linked to the ability to colonize novel climates. Species with small ranges and niches in their native range showed larger niche shifts. These findings caution against using SDMs to predict future invasions of species with small geographic distributions in their native range since they may be constrained by other ecological factors and therefore not be representative of the full range of conditions under which the species can thrive.

Methods

Distribution data. We compiled distribution data for all 241 ant species known to have expanded beyond their native range, using the authoritative database AntMaps[51,52]. Native and non-native ranges were distinguished in AntMaps based on the published literature. We cleaned all occurrence records by removing any dubious or indoor occurrences from the analysis. To account for sampling bias, we used the nearest neighbor distance (NND) method to thin the data, where occurrence points that were ≤0.02 units away from each other were removed (roughly 2 km) to avoid errors due to spatial autocorrelation[53]. As the resolution of the climate maps was larger than this distance, duplicate records in the same climate grid cells were removed. In addition, species that had fewer than 10 occurrence points in their native or non-native range were also removed from the analysis. Therefore, in total 82 ant species were used for the analysis. Invasive species were defined according to the categorization of the Invasive Specialist Group (ISSG) of the IUCN[54]. All other species with non-native ranges were classified as non-invasive alien species.

Using the AntMaps classification, the world map was sectioned into polygons covering all landmasses. For larger countries, such as the US, these polygons were on a provincial/state level, while for smaller countries they were on a country level[51]. Niche shift levels were compared between species grouped into 'regional', 'transcontinental', and 'global' dispersion categories. Species were assigned to these dispersion groups according to the number of polygons occupied and the geographical distance between occupied polygons, using the methods of Bertelsmeier et al.[23]. Polygons were used to account for the varying sizes of politically-defined countries.

Climate data. Current global climate data was sourced from the WorldClim Global Climate Database at a resolution of 2.5 arc-minutes[55]. For each occurrence point of all 82 species, climate data was extracted using 17 of the 19 available bioclimatic variables. We excluded BIO2 and BIO7 in our analysis because these values are derived from a combination of other bioclimatic variables.

Niche shift analysis. For each species, the climatic variables for each occurrence point in both the native and non-native ranges were reduced using PCA with ade4 package[56]. We performed a between-class analysis using the 10 axes of the resulting PCA using 'native' and 'non-native' as a priori classes to identify the axis separating these two ranges the most for each species[15]. For all three niche shift metrics, we used this axis to define the climatic niche. Using the methods of Broennimann et al.[57], this axis was rescaled into 100 × 100 grid cells and converted into densities of occurrences using the R package 'ecospat'[58]. The occurrences for each range were then smoothed using kernel density smoothers, to control for errors in sampling efforts. This allowed us to directly compare the niches in the native and non-native ranges in environmental space, while considering all available climates.

We determined the intersection of the occurrence densities in environmental space using Schoener's D (D)[59,60]. This measure of niche overlap between the native and non-native ranges produces a value between 0 (no overlap) and 1 (complete overlap).

We defined niche expansion as the percentage of the non-native range that is not present in the native range. For this study, expansion was categorized into non-significant (<10%) and significant expansion (>10%)—as this threshold has previously been used for classification in a significant proportion of studies[16,32]

Finally, we also performed niche equivalency tests[57,60]. All occurrences were pooled (N–E_{pool}) and randomly split into two datasets, at the same observed ratio of native to non-native occurrences for each species, then the *D* overlap was calculated. This process was repeated 1000 times. The distribution of the simulated overlaps was then compared with that of the observed *D* value. If the *D* value was lower than 95% of the simulated values, the hypothesis of niche equivalency was rejected. We adjusted the *p*-values for multiple statistical comparisons using Benjamini–Hochberg correction[61].

Native range and niche size. Geographic dispersal within the native range was calculated by determining the pairwise geographical distance between the centroids of the occupied polygons of each species' native range, from which a dissimilarity matrix was constructed. Then, Rao's quadratic entropy was calculated for each species' native dispersal, to provide a 'Rao spatial diversity' value[23]. Native niche size was calculated from the volume of the native range n-dimensional niche using the R package 'hypervolume'[33]. This method allows high-dimensional estimation of the niche using multidimensional kernel density estimation to calculate the density distribution of species records. This was calculated from PCA-space of all climates on earth derived from the 17 bioclimatic variables, which allowed comparable estimations of niche volumes between different species. For each species, the native occurrences were projected into hypervolume space using the gaussian method with a chunk size of 500. Bandwidths were fixed for every species, calculated as the maximum bandwidth when hypervolumes were calculated preliminarily using the maximum bandwidth for each axis derived from the 'free_bandwidth' option within the R package 'hypervolume'[33].

Statistical tests. The differences in the *D* overlap between the non-invasive alien and invasive groups were compared using a Kruskal–Wallis test. The differences in the level of expansion (<10% vs. >10% expansion) between the non-invasive alien and invasive groups, was compared using chi-squared tests. We also tested if species with different levels of dispersion differed in *D* overlap using a Kruskal–Wallis test, and observed pairwise differences using a post-hoc Dunn test with Benjamini–Hochberg correction for multiple comparisons. Between dispersion groups, the levels of expansion were compared using chi-squared tests. To compare the level of expansion to native range dispersion and niche size, the different levels of expansion were compared for both native hypervolume size and native Rao diversity using a Kruskal–Wallis test. Correlations between *D* overlap and both native hypervolume size and native Rao diversity were tested with Kendall's Tau rank correlation coefficient test.

We tested if the number of occurrence points had an effect on the results. To do this, we tested if the test metrics *D* overlap and Expansion changed with the number of native occurrence points (after thinning- see "Methods" section). We found no correlation between *D* overlap and the number of native occurrence points (Kendall's rank correlation tau, $R\tau = -0.04$, $p = 0.63$). There was also no difference in the number of occurrence points among species belonging to different expansion groups (10–100%), (Kruskal–Wallis test, $X^2 = 2.65$, p-value = 0.10).

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All data used in this study can be downloaded from Github (https://github.com/OliviaKBates/AlienInvasiveNicheShift/blob/master/data_invasiveants.RData)[62]. Worldclim Global Climate Database (https://www.worldclim.org) and the AntMaps database (https://antmaps.org) can both be accessed through their respective websites.

Code availability

All analyses were done in R version 3.6.0[63] and a script is supplied to generate all figures using the R workspace which contains all data used is available on Github (https://github.com/OliviaKBates/AlienInvasiveNicheShift)[62].

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Author contributions

O.K.B., S.O., and C.B. designed the research. O.K.B. performed the research, and O.K.B. and S.O. analyzed the data. O.K.B., S.O., and C.B. all contributed to the writing of the paper.

Competing interests

The authors declare no competing interests.

Additional information

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Chapter 3

Do soil and air temperatures predict similar niche shifts in introduced ants?

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This work is currently unpublished.

Do soil and air temperatures predict similar niche shifts in introduced ants?

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ABSTRACT

Increases in global trade and human movement over the past century have led to the spread of thousands of species worldwide. It is crucial to predict where introduced species can establish based on their climatic niche. However, it has been suggested that introduced species may frequently establish in climates outside of their realised climatic niche in their native range, experiencing 'niche shifts'. Yet, research on niche shifts is typically conducted on macroclimatic scales, and observed niche shifts may be an artefact of climate data that does not accurately characterise the species' microclimatic niche. Using 95 introduced ant species (Formicidae), we used two maps of predicted global temperatures (based on soil and air temperature respectively) to investigate the effect of local-level soil temperature (SoilTemp) on the frequency of niche shifts in introduced ant species compared to macroclimatic air temperature (WorldClim). We quantified niche shifts using two methods: ordination of environmental variables and a high-dimensional multivariate approach (n-dimensional hypervolume). There was some correlation (coupling) between the air and soil temperature conditions experienced by each species - however, this varied between species and bioclimatic variable considered, with the highest correlations relating to ‘annual mean temperature’ and the lowest temperature ‘isothermality’. Niche shifts experienced by each species also seemed to be coupled (correlated) to some degree, with a near 1:1 relationship for the most commonly used metric for niche shift studies (D overlap), however, this coupling was only true for one metric.

Furthermore, we found that for most metrics used the majority of species (68-96.8%) experienced less niche niche when using soil-level datasets. In summary, our study highlights the importance of considering new microclimatic datasets, at more biologically relevant scales, for soil-dwelling species. This may have the potential to improve predictive models related to the distribution of introduced ants, which is essential for the management and conservation of ecosystems.

INTRODUCTION

A hallmark of the Anthropocene is the global spread of many species outside of their historical range, at an ever-accelerating pace (Bonnamour et al., 2021; Seebens et al., 2015). Introduced species, i.e., species with self-sustaining populations outside of their native range (Gippet et al., 2019), can have wide-ranging impacts on ecosystems, health, and agriculture (Bradshaw et al., 2016; Doherty et al., 2016; Young et al., 2017). Therefore, it is vital to understand and be able to predict their spread to new geographical areas. One way to achieve this is to use the native (historical) niche (Glossary, Table 1) of the species to geographically project areas that are similar in climatic conditions under which the species might establish (Elith & Leathwick, 2009; Peterson

& Soberón, 2012; Thuiller et al., 2005). However, these species are often subjected to climates different from those in their native range, prompting the question: will species be able to establish and survive in these novel climates? (Bates & Bertelsmeier, 2021).

A niche shift corresponds to the establishment (i.e. introduction) of a species under environmental conditions that are different from those in its current niche (Glossary, Table 1). Drivers of niche shifts fall into two categories: methodological factors, such as an inadequate original estimation of native niche, or biological drivers, such as a release in constraints to the realised niche (geographical or biotic release, phenotypic plasticity (Bujan et al., 2020, 2021), or rapid adaptations (Colautti & Lau, 2015)). Many studies aim to predict future distributions of introduced species (Hoffmann et al., 2023; Olivera et al., 2020; Peterson & Soberón, 2012; Thuiller et al., 2005), however, the presence of niche shifts complicate such predictions. If niche shifts are prevalent and substantial, the assumption that native niches alone can be used to predict the future niche of a species would be invalid. Frequent niche shifts then would highlight the potential unreliability of biodiversity forecasts using correlative models (Bellard et al., 2012). Therefore, understanding whether introduced species can shift their niche, and the extent of such shifts between species, is crucial to understanding introduced species distributions and remains a major challenge in ecology. There have been several multi-species studies that have assessed niche shifts in recent years (Atwater et al., 2018; Bates et al., 2020; Tingley et al., 2014). However, the prevalence of niche shifts is still hotly debated, with arguments for both the commonality and rarity present within the literature and cross-study comparisons difficult due to non-comparable methodologies and biases within the literature (Bates & Bertelsmeier, 2021). However, to date, researchers have only examined niche shifts using the most widely available macroclimatic datasets (see Glossary, Table 1), ignoring the potential influence of microclimates (see Glossary, Table 1) as refuges from broader climatic variations (Bates & Bertelsmeier, 2021), which are particularly relevant for small organisms (Pincebourde & Woods, 2020).

Macroclimate data - derived from standardised meteorological stations located in open-air areas approximately two metres above ground level - obscure microclimatic variation over short distances, especially in regions with diverse topography or rugged landscapes (Geiger 1950). Other factors, such as vegetation, canopy structures, and soil properties, further contribute to the diversity of microclimates (De Frenne et al., 2019; Lenoir et al., 2017; Senior, 2020; Suggitt et al., 2011), which can act as a buffer for macroclimatic conditions and provide refuge to extreme temperatures (see Glossary, Table 1 and Figure 1A). For example, within a 1 square kilometre area in northern Europe, the annual average microclimate air temperature can vary spatially by as much as 6 °C (Lenoir et al., 2013).

Regardless of the degree of buffering, however, if microclimatic buffering is correlated to macroclimatic conditions, then the microclimate could be predicted from the macroclimatic conditions, and the two are considered ‘coupled’ (Figure 1C). Such coupling (i.e., correlation) can be assessed by measuring the slope of correlation between the two variables, with a slope value of 1 meaning complete coupling, 0 indicating complete uncoupling, and numbers in between presenting a continuum between the two (Gril et al., 2023; Lenoir et al., 2017; Locosselli et al., 2016). If a species consistently experiences constant microclimate buffering corresponding to macroclimatic conditions in direction and extent (see Glossary, Table 1), then macroclimate proxies can effectively capture the realised niche of the species throughout its range, even if actual climates encountered by the species deviate from these macroclimatic patterns (Pincebourde & Suppo, 2016). However, it is important to note that such coupling may represent one point in time, and coupling may change when climatic conditions shift, such as due to with climate change (Caillon et al., 2014; Raven & Wagner, 2021). In contrast, a species may actively select relatively cooler or warmer microclimates across its range depending on the macroclimates (Figure 1D). In this case, the slope correlation would be lower or greater than 1, meaning that the microclimatic buffering may be affecting the relationship between the climates (Gril et al., 2023). Furthermore, if the variance of microclimatic conditions compared to macroclimates is high, the microclimate can be considered "uncoupled" from the macroclimate (Scherrer & Körner, 2011). The influence of buffering on species occurrences has created the possibility of ‘false positive’ or ‘false negative’ niche shifts in introduced species (see Glossary, Table 1). Uncoupling between macro- and microclimates could lead to a "false positive" niche shift in introduced species, where large-scale climatic conditions suggest a change, but the species itself does not experience significantly different microclimates from those in its native range because it selects relatively cooler or warmer microclimates (Bates & Bertelsmeier, 2021) (Figure 1F). For example, at the warm range margin, it may select cooler and shadier microclimates, and at the cold range margin, it could select warmer and sunnier microclimates.

To assess the degree of false-positive to false-negative niche shifts between different species, the idea of coupling and uncoupling can also be applied (Figure 1E and F) - and thus we can ask if niche shifts on the macroclimatic scale between species relate to shifts in the microclimatic scale. This process is then referred to throughout this manuscript as ‘*niche-shift-coupling*’, referring to whether niche shifts experienced by each species are correlated, and ‘*niche-shift-uncoupling*’, referring to when niche shifts experienced by each species are uncorrelated to each other. If the difference between macro- and microclimatic niche shifts is correlated between species, this would highlight niche shift coupling for a particular taxa (Figure 1E), and deviations from this indicate varying degrees of uncoupling between the different levels of climate data for the niche shifts experienced by species (Figure 1F). The question remains, therefore: how will the use of microclimatic data affect predictions of niche shifts (i.e., how does the temperature difference displayed in Figure 1A affect that of Figure 1B)? This question is of particular importance for small-bodied organisms due to their size. For climate data to apply to the conditions these species experience, a much finer scale than that provided by existing macroclimatic datasets (Pincebourde & Woods, 2020) used in previous studies of introduced insect niche shifts is required (Bates et al., 2020; Hill et al., 2017).

In this study, we focussed on ants (Formicidae) as a model taxon as they are ectothermic species, making them highly sensitive to temperature, particularly as ant foraging ability and resource acquisition are directly governed by their thermal tolerance (Cerdá et al., 1998; Roeder et al., 2021). With over 240 species that have spread and established outside of their native range globally, ants are among the most widespread and well-known introduced insect species (Angulo et al., 2022; Rabitsch, 2011), and thus provide an ideal group to identify characteristics of species displaying a greater propensity for niche shifts among species (Bates et al., 2020). Furthermore, given many species' primary micro-habitat is soil, predicting soil-level temperatures is more relevant than air temperature data from weather stations situated at least two metres above the ground. This may be particularly relevant for ground-nesting species, compared to canopy and leaf-litter ants which may be less able to make use of soil-level climate buffering and thus more exposed to macroclimatic air temperatures (Parr & Bishop, 2022). It may then be expected that soil-nesting species may have higher amounts of niche conservatism due to this soil-level buffering, as they may select nest site locations in soil-level climates most similar to their native range. If the hypothesis that macroclimatic niche shift studies are hiding niche conservatism at the soil-level, we would then expect higher niche conservatism in soil-nesting species, but little impact on species that nest also in the canopy.

Therefore, we have leveraged a newly developed soil-level temperature database called ‘SoilTemp’ (Lembrechts et al., 2020, 2022) that measures soil temperatures just below the soil level (0-5 cm below). The vertical resolution (e.g., whether the climate data is concentrated at soil level, above the canopy air, or below the canopy) (Lembrechts & Lenoir, 2020) is greatly increased as it uses temperature logger data to interpolate global climate estimates (Lembrechts et al., 2020). Consequently, it is thought that this dataset more accurately represents microclimatic conditions compared to classical macroclimate conditions (Lembrechts et al., 2022). We, therefore, use the term ‘microclimate’ to describe this soil-level database.

In this study, we compared the niche shifts of 95 introduced ant species using SoilTemp data to those using the widely-cited macroclimatic WorldClim dataset (Fick & Hijmans, 2017). First, we tested for differences in species' climatic conditions between macro- and microclimatic conditions between the datasets for each species, assessing the degree of correlation between the datasets, and how that relates to the correlation of occupied niches across each species range. Second, we assessed the different impacts of using macro- and microclimate data to assess niche shifts between native and introduced ranges. We tested for niche-shift-coupling between species, and whether the SoilTemp data indicated smaller or larger niche shifts compared to WorldClim data. Lastly, we assessed whether the differences in niche shifts between the datasets were related to factors previously shown to impact niche shift results (sample size, year of first introduction, and extent of geographical dispersion) (Hill et al., 2017; Strubbe & Matthysen, 2014) along with predictors for ant ecology that might indicate a higher use of soil-level refugia, i.e., species nesting type (Soil vs canopy nesting) and colony size.

METHODS

Data

We compiled occurrence point data for 95 ant species, for which we had over 20 occurrence points in both the native and introduced ranges, using the databases AntMaps (Guénard et al., 2017; Janicki et al., 2016), Antweb (www.antweb.org), and global biodiversity information facility (GBIF; https://www.gbif.org). Native and introduced ranges were distinguished from the native and introduced maps produced by antmaps.org, which is linked to the GABI database, which uses published literature to define the regional-level extent of species distributions (Guénard et al., 2017; Janicki et al., 2016). We cleaned all occurrence records by removing any 'dubious' (Erroneous records published in the past but later identified as misidentifications) or indoor occurrences from the analysis (classified as such on the Antmaps database (Guénard et al., 2017; Janicki et al., 2016). Occurrence points were then cleaned using GADM maps (Global Administrative Areas (2012); (version 2.0. [online], URL: www.gadm.org.) GADM is a database of administrative areas (i.e. countries, states, geographic boundries)), and was used to to remove all occurrences falling in seas or oceans. The R package 'CoordinateCleaner' was used to remove invalid (i.e. latitudes and longitudes that do not exist), duplicated, zero, and fossil record occurrences (Zizka et al., 2019). To account for sampling bias from the overrepresentation of niches in locations that are heavily sampled, leading to spatial autocorrelation, we used the nearest neighbour distance (NND) method to thin the data, removing occurrence points that were less than 1 km away from each other (Pearson et al., 2007) using the R package 'spThin' (Aiello-Lammens et al., 2015). After this, to account for species where there is a low sample size, species that had fewer than 20 occurrence points in either their native or introduced range were removed from the analysis. In total, 95 ant species were used for the analysis.

Macroclimate data at a 30 arcseconds resolution (~1 km) from the WorldClim Global Climate Database (Fick & Hijmans, 2017) contains interpolated data regarding yearly temperature-based bioclimatic variables (BIO 1 to 11). These variables are all temperature-derived (BIO1 = Annual Mean Temperature, BIO2 = Mean Diurnal Range, BIO3 = Isothermality, BIO4 = Temperature Seasonality, BIO5 = Max Temperature of Warmest Month, BIO6 = Min Temperature of Coldest Month, BIO7 = Temperature Annual Range, BIO8 = Mean Temperature of Wettest Quarter, BIO9 = Mean Temperature of Driest Quarter, BIO10 = Mean Temperature of Warmest Quarter, and BIO11 = Mean Temperature of Coldest Quarter). Soil-level climate data was downloaded at a 30 arcseconds resolution (~1 km) from the 'SoilTemps' database (0-15 cm below the soil) (Lembrechts et al., 2020, 2022). The same variables as those from the WorldClim database were available (SBIO 1 to 11).

Quantifying the effect of niche coupling between datasets

To test the amount of coupling between the WorldClim and SoilTemp datasets, the bioclimatic variables for each occurrence point were extracted for each species from both datasets. For each species and each bioclimatic variable, we calculated the correlation of climatic conditions at occurrence points using the WorldClim and SoilTemp dataset using Kendall's rank correlation Tau (Kendall, 1938). This correlation coefficient ranges between -1 and 1, with values close to 0 indicating a high degree of uncoupling between the datasets. Distributions of the per-species correlations could then be calculated for each bioclimatic variable. These distributions were compared to randomly generated occurrence points. We generated 1,000 occurrence points using the function st_sample from the package 'sf' using the 'rworldmap' map so that only occurrence points on land were sampled from, to produce a correlation between the two datasets for each axis. This randomised process was then repeated 1,000 times to obtain a distribution of random correlations, which was compared to observations from the ant species dataset.

Niche shift assessments

Ordination approach

The ordination-based approach we used quantifies differences between native and introduced niches using environmental principal component analysis spaces (Di Cola et al., 2017). First, for each species seperaratly, the 11 bioclimatic values for each occurrence point were reduced to 5 using a principal components analysis (PCA) by utilising the 'dudi.pca' function in 'ade4' (Dray & Dufour, 2007). A between-pca, using the function 'bca' also in the 'ade4' package, was then conducted using the two ranges as *a priori* groups to identify the axis that separated these two ranges to the greatest extent for each species (Bates et al., 2020; Gallagher et al., 2010). Using the methods of Broennimann et al. (2012), this axis was rescaled into 100×100 grid cells and converted into densities of occurrences using the R package 'ecospat' (Broennimann et al., 2012; Di Cola et al., 2017). A kernel function was applied to smooth the distribution of the densities, to account for errors due to sampling efforts. The extent of niche shifts within this ordination space was then assessed for each species using two different metrics.

Two commonly used metrics were calculated for each species to determine the difference in niche between native and introduced ranges - Schoener's D (D) overlap (Schoener, 1968; Warren et al., 2008) and niche expansion (Guisan et al., 2014; Petitpierre et al., 2012). D overlap measures the degree of overlap in occurrence densities within the environmental space, comparing the native and introduced ranges(Warren et al., 2008). D overlap varies between 0 (low similarity) and 1 (high similarity). On the other hand, expansion is a measure of new niche space occupied in the introduced range and is the percentage of the introduced niche not present in the native range. It is calculated as the percentage of the introduced range not present in the native range and varies between 0 and 100%, with 100% representing complete expansion of the niche and thus no niche space occupied by the introduced niche should be present in the native range. The expansion can be further categorised into 'non-significant' and 'significant' niche expansion for results below and above the classically used 10% threshold, with 0-10% defined as 'negligible' expansion, and 10-100% defined as significant expansion occurring (Petitpierre et al., 2012; Torres et al., 2018).

Hypervolume approach

A high-dimensional method enables more direct comparisons within a standardised n-dimensional hypervolume (i.e. all ranges and species are compared on the exact same axis), although this method may encounter issues related to over-dimensionality (Blonder et al., 2014). We conducted the hypervolume approach using the R package 'hypervolume' (Blonder et al., 2014). This method allows for high-dimensional estimation of niches using multidimensional kernel density estimation to calculate the density distribution of species records. Comparing differences between hypervolumes is only possible within the same niche space, i.e., if axes are standardised and the same. Therefore, unlike the ordination-based approach, the PCA-step was done for the dataset as a whole before niche shifts were compared within it. A PCA axis was used to reduce the number of axes assessed for the hypervolume approach and account for collinearity between the climate variables. To assess niche shifts using the WorldClim dataset, all 11 global variables were reduced to 5 variables via principal components analysis (PCA) using the 'rasterPCA' function in R (Leutner et al., 2017). The first 5 axes explained 97.1% of the variance. As only one hypervolume for each species can be projected at a time , occurrences from the native and introduced ranges were projected separately into hypervolume space. These algorithms infer the shape and volume of high-dimensional objects via a thresholded kernel density estimate (Blonder et al., 2014). We used a Gaussian kernel density estimator method with the standard ‘chunk_size’ of 500 (Blonder et al., 2014). Bandwidths, a parameter which determines the size of the smoothing kernel used, were fixed for all species, This parameter was calculated as the maximum bandwidth for each axis when hypervolumes were estimated using the Silverman estimator derived from the ‘free_bandwidth’ option within the R package ‘hypervolume’ (Blonder et al., 2014). Then, for each species, niche shifts between the native and introduced range were assessed in hypervolume space. To do this, three different metrics were calculated to encompass different approaches of comparing hypervolumes: centroid distance (Blonder, 2018), Jaccard similarity (Blonder, 2018), and Bhattacharyya distance (Lu et al., 2021). Centroid distance measures the Euclidean distance between the centroids of each niche hypervolume (i.e. between the native and introduced) within hypervolume space, whereas Jaccard similarity is a similarity index based on the volume ratio, which ranges from 0 (both input hypervolumes are fully disjunct) to 1 (both input hypervolumes are identical). These two metrics have been shown to complement each other when measuring niche dynamics (Mammola, 2019; Mammola & Cardoso, 2020). Bhattacharyya distance can be calculated using the ‘MVNH’ package in R (Lu et al., 2021). It provides parametric measures of the size and dissimilarity of niche hypervolumes. The Bhattacharyya distance (BD; a function of the geometric mean of two probability distributions) between two hypervolumes is a measure of niche dissimilarity. The BD partitions total dissimilarity into the components of Mahalanobis distance (standardised Euclidean distance with correlated variables) between hypervolume centroids and the determinant ratio (the ratio between hypervolume size differences) (Lu et al., 2021).

This process was then repeated for the SoilTemp dataset, again all 11 global variables were reduced to 5 variables using principal components (PCA) (Figure S1B), which standardized it to the WorldClim data but also explained 99.2% of the variance in the SoilTemp climatic variables, created using the same ‘rasterPCA’ function from the ‘RSToolbox’ package in R (Leutner et al., 2017)

Statistical analysis

Comparisons between SoilTemp and WorldClim datasets

First, to assess for between-species-coupling between the two datasets (i.e. if the degree of differences in niche shift results between datasets were consistent between species), correlations between the SoilTemp and WorldClim datasets were compared for each metric using Kendall's rank correlation Tau. Differences between bioclimatic variables were tested using pairwise Wilcoxon tests with Benjamin-Hochberg corrections for multiple p-value comparisons.

Comparisons between Niche shifts using SoilTemp and WorldClim datasets

For each metric, we then compared the niche shifts result for each species between the SoilTemp and WorldClim datasets (Ordination-based: D overlap and expansion; Hypervolume-based: centroid distance, Jaccard similarity, and Bhattacharyya distance). Along with visual inspection of the data, Shapiro-Wilk normality tests revealed the niche shift metrics to be non-normal, and thus nonparametric statistics were used throughout. First, to assess for niche-shift-coupling between the two datasets, correlations between the SoilTemp and WorldClim datasets were compared for each metric using Kendall's rank correlation Tau.

Second, to test if SoilTemp predicted higher or lower niche shifts, pairwise Wilcoxon tests were conducted for each of the four continuous niche shift metrics (D overlap, centroid distance, Jaccard similarity, and Bhattacharyya distance) to compare the differences regarding the results for each species. Differences in the niche expansion results (categorised into 10-100% (significant expansion and 0-10 % expansion (negligible expansion)) were assessed using a Chi-squared test. Furthermore, to test for direct differences between the methods, raw differences were calculated by subtracting the results of the SoilTemp dataset from those of the WorldClim dataset for each species.

All analysis was conducted using R version 4.2.2

Factors influencing niche shift differences between datasets

We tested if the difference in sample size, year of first introduction, extent of geographical dispersion, species nesting type, and colony size were linked to the raw differences between the two datasets for each metric. Sample size, year of first introduction, extent of geographical dispersion have all been previously seen to affect niche shift results in insect species (Bates et al., 2020; Hill et al., 2017). Species nesting type and colony size were tested to get a representation of the microhabitat each species exists within. The sample size was the number of occurrence points used for analysis after spatial thinning. Geographical dispersion was calculated by determining the pairwise geographical distance between the centroids of the occupied polygons of each species' native range, from which a dissimilarity matrix was constructed. Then, Rao's quadratic entropy was used as a measure of native geographic dispersion for each species. This provided us with a 'Rao spatial diversity' value (Bertelsmeier et al., 2017), with high values representing species with large and dispersed geographic ranges, and low values representing species with small and spatially clustered ranges. The year of introduction (the first year the species was reported to be established outside of its range), species nesting type (where the species is found nesting according to AntWeb, categorised into whether the species is found nesting exclusively in the soil ('soil' group) or in both the soil and canopy ('soil and canopy')), and colony size (an estimation of the average number of workers found in species nests based on AntWeb data) were determined from the literature (See Supplementary Material, Table 1).

Separate Gaussian Generalised Linear Models (GLMs), with interactive terms between each correlative variable, were run separately for each metric result using the package ‘DHARMa’ (Hartig & Hartig, 2017) packages in R.

Accounting for geographic bias

As SoilTemp was released in 2022 (Lembrechts et al., 2022), with the original call for temperature logger data being in 2020 (Lembrechts & Lenoir, 2020), the current number of temperature logger data points are overrepresented in Europe and North America. Therefore, to test if differences in the results are due to differences in geographic dispersion, we restricted the analysis to these two regions and repeated all analyses.

RESULTS

Were ant species occurrences coupled between WorldClim and SoilTemp?

To evaluate the potential coupling between the WorldClim and SoilTemps datasets (Figure 1C vs Figure 1D), we initially quantified the correlation between macro- and microclimatic conditions for the occurrence points of each species (Figure 2). These observed correlations were compared to a set of randomly selected data points. The correlation coefficients ranged from -0.31 to 0.91, with substantial variability among species and climatic variables. For each bioclimatic variable, observed correlations showed higher variability than the randomised ones (Figure 2). This difference between random and occurrence point data may suggest there is a biological process occurring, where some ant species are occurring at microclimatic conditions that are either less or more coupled to the macroclimate than would be predicted from random - with the degree of coupling varying with bioclimatic variables and species.

We observed distinct patterns in the distributions of macro- to microclimate correlations between the different bioclimatic variables (Figure 2). Specifically, correlations approaching either 1 or -1 indicated a stronger coupling between the two datasets. Annual mean temperature (Bio1; median = 0.76), temperature seasonality (Bio4; median = 0.74), minimum temperature of the coldest month (Bio6; median = 0.78), mean temperature of the wettest quarter (Bio8; median = 0.71), mean temperature of the driest quarter (Bio9; median =0.73), mean temperature of the warmest quarter (Bio10; median = 0.67), and mean temperature of the coldest quarter (Bio11; median = 0.81) consistently exhibited high levels of coupling (Figure 2). However, for isothermality (Bio3; median = 0.1), temperature seasonality (Bio4; median = 0.52), max temperature of the warmest month (Bio5; median = 0.52), and temperature annual range (Bio7; median = 0.63) we observed a much lower correlation and thus more uncoupling. Additionally, some of these bioclimatic variables had very large ranges and inter-species variability, such as Bio3 (range = -0.3-0.65), Bio4 (range = 0.08-0.90), and Bio5 (range = 0.04-0.75) (Figure 2).

Did we observe niche-shift-coupling between WorldClim and SoilTemp datasets?

To investigate the impact of the varying amounts of niche-shift-coupling between the datasets (Figure 1E and F), we tested both per-variable niche shifts and overall niche shifts within ordination space. Per-axis niche shifts revealed varying results relative to the bioclimatic variable considered (Figure 3). Interestingly, the bioclimatic variables that displayed high variability in niche shifts between the datasets were often the same as those that exhibited a broad range of correlations when considering correlations alone (Figure 3A). For example, the correlations in the D overlap between WorldClim and Soiltemp were lowest for isothermality (Bio3), mean diurnal range (Bio2), max temperature of the warmest month (Bio5), and temperature annual range (Bio7) (all below 0.6, Figure 3A). However, it is worth noting that although some of the per-axis niche shifts exhibited niche-shift uncoupling for the D overlap (Figure 3A), this did not impact the D overlap results when the entire climate space was used due to the presence of high niche-shift-coupling (Figure 3B). The impact on the expansion was much less pronounced, with weak coupling between all of the bioclimatic variables (Figure 3C and D).

When all bioclimatic variables were considered in a single analysis, the WorldClim and SoilTemp datasets had significant correlations for all niche shift metrics except for the centroid distance (Figures 3 and 4). The D overlap metric had the strongest correlation between the niche shift results of the WorldClim and SoilTemp datasets (Tau = 0.77, Figure 3B). However, this level of coupling was not evident for the other metrics. Jaccard similarity exhibited relatively weaker correlations (Figure 4). Bhattacharyya and expansion metrics displayed stronger correlations, albeit with a higher degree of variability (Figure 4). Therefore, while correlations were statistically significant for all metrics aside from the D overlap, it's crucial to acknowledge the substantial variation and low correlation slope (Figure 3B, 3D, and 4). Consequently, a one-to-one relationship between the results obtained from the WorldClim and SoilTemp datasets is not present, signifying that they are largely uncoupled from each other for all metrics except for the D overlap.

Did soil temperature data predict more or fewer niche shifts?

The SoilTemp dataset consistently predicted smaller niche shifts for most species across all metrics, except for the D overlap metric. For example, expansion, Jaccard, and centroid metrics all exhibited smaller niche shifts for the SoilTemp dataset (Green region, Figure 3 and 4). Furthermore, for all metrics, pairwise Wilcoxon tests showed significant differences between the datasets, with SoilTemp predicting lower niche shifts than WorldClim (Figure 5A-D). The D overlap, Jaccard, and centroid distance exhibited significantly higher niche conservatism for the

SoilTemp dataset compared to the WorldClim dataset (Paired Wilcoxon tests, Figure 5A-C). For the Jaccard similarity, just four species had higher niche shifts when the SoilTemp dataset was used, while the centroid distance prompted six species to have higher niche shifts (4.2% and 6.4% respectively, Figure 6). This trend was less obvious for the Bhattacharyya distance, which was much more similar between the two datasets; however, there was still a significantly higher Bhattacharyya distance for the WorldClim dataset than the SoilTemp dataset (Figure 3D). The relative differences between the two datasets were small for the Bhattacharyya distance, with some large outliers (Figure 6D). When the expansion metric was considered, the SoilTemp dataset resulted in a significantly smaller number of niche shifts compared to the WorldClim dataset (Figure 5E, Chi-squared test, $\mathcal{X}^2$ = 4.14, df = 1, p = 0.04). However, when assessing direct differences in expansion per species, a large percentage (75.8%) of species maintained an above-10% expansion between the two datasets, with 20% going from a significant niche shift to a non-significant niche shift, and only 4.2% of species switching from a non-significant niche shift to a significant niche shift (Figure 5F).

What factors predict the difference between SoilTemp and WorldClim databases?

Raw differences in niche shift metrics D overlap, Expansion-conclusion (0-10% vs 10-100% expansion) , Jaccard similarity, centroid distance, and Bhattacharrya distance between WorldClim and SoilTemp were not correlated with any of the correlative factors (Generalised linear models, $p > 0.05$). We however did observe an overrepresentation of soil-dwelling species where the result switched from a significant (> 10 %) to a non-significant (< 10%) expansion between the WorldClim and SoilTemp datasets (compared to species nest in both the soil and canopy) (Chi-squared test, $\mathcal{X}^2$ = 12.02, df = 3, p = 0.001) (Figure 7).

DISCUSSION

Our multi-method niche shift analysis enabled a comparison of two global datasets, one estimating air temperature and the other soil temperature, regarding the frequency of niche shifts between the introduced and native ranges of introduced ant species. Firstly, there were intra-species differences in the degrees of coupling between macro- and microclimatic conditions, more variability between species and lower average correlations than would be predicted at random. Within the niche shift analysis, we found there was often niche-shift-uncoupling between the two datasets (Figure 1F) (except when the D overlap metric was used), with SoilTemp consistently predicting lower niche shifts for most species across all metrics.

The D overlap metric, the most widely utilised in the literature on niche shifts (Bates & Bertelsmeier, 2021), exhibited the highest correlation between the two datasets, indicating an almost 1:1 relationship. This suggests that if this commonly used metric continues to be employed, studies that investigate niche shifts in soil-dwelling organisms, such as ants, will not need to consider the differences between these two datasets, as the increase in vertical resolution will have limited impact on niche shift predictions (Pradervand et al., 2014). It is, however, interesting to note that the bioclimatic variables that exhibited the least amount of coupling between the datasets were those relating to temperature ranges within an area (isothermality (Bio3), temperature seasonality (Bio4), max temperature of the warmest month (Bio5), and temperature annual range (Bio7)). This would suggest that species are selecting their nest site locations in climates that are different to macroclimates. However, as there are varying extents between species, making generalistic conclusions on the impact of microclimate conditions on taxon distributions would be invalid. This is particularly worrying as temperature extremes, such as maximum temperatures during hot summers, are important predictors for species distributions (Moore et al., 2023; Zimmermann et al., 2009) and are thought to be the biggest stressors on insect species (Harvey et al., 2020), and thus may be key determinants of ant geographic distributions. Furthermore, although niche coupling may appear to be present at one point in time, it is possible that climate change and changing land use may lead to changes in the coupling between macro and microclimatic conditions (Caillon et al., 2014; Raven & Wagner, 2021), and it is therefore still important to consider the most biologically relevant climate data even if they may appear to be coupled with more macroclimatic conditions at one point in time

Furthermore, the high niche-shift-coupling between datasets with the D overlap metric was not observed for the other metrics. Notably, the centroid distance and Jaccard similarity showed almost complete decoupling, with very low correlations between the two ranges for each of these metrics. Bhattacharyya and expansion metrics demonstrated slightly stronger correlations, albeit with high variance (Figure 1). This implies that not all metrics possess equivalent discriminative power in assessing the extent of niche shifts between the two datasets (Mammola, 2019). Dissimilarities seen between the different metrics may have arisen from the fact that assess varying aspects of niche differences, from overlap (D overlap and Jaccard similarity), amount of novel climate the species is experiencing (expansion), the average distance between niches (Centroid distance), and a combination of changes in niche size and differences in centroid distance (Bhattacharyya distance) (Lu et al., 2021). Species are able to shift their niche in just one aspect of these measured factors and stay constant in the other, highlighting the power of using multiple metrics together to assess niche shifts.

As the results were highly variable according to the species, we tested whether raw differences (WorldClim - SoilTemp) in the overlap metrics between datasets could relate to factors previously shown to impact niche shift results. We found that only the nesting type impacted the results, suggesting that soil-nesting species may undergo substantial niche expansion when soil temperatures are considered, which aligns more closely with the relevant vertical microclimate for such species. However, it's important to highlight that this finding is based on a small sample size and was not corroborated by the other metrics.

Enhancing the data resolution to encompass information on additional factors — for example, below-canopy temperature, vegetation structures, and terrain features — enhances the precision of climate data compared to data derived from traditional weather stations (e.g., WorldClim (Fick & Hijmans, 2017)). As global-level fine-scale (below 1 km resolution) microclimate data is currently hard to obtain for species with an introduced range spread over multiple continents, data that have coarse grid cells but better represent the microhabitat type (i.e., soil temperature) are a useful compromise to predict and explain species distributions. Additionally, the SoilTemp dataset provides a more biologically relevant representation of the climates experienced by ants, as many species either forage and/or nest in the soil (Lucky et al., 2013), and may be a preferred dataset for estimating the niches of ant species and other soil-dwellers. However, one drawback is that the SoilTemp dataset, derived from temperature logger data on a global scale, does not currently have uniform coverage in logger data points, with the majority of its data points concentrated in Europe and North America (Lembrechts *et al.* 2022). Consequently, a major criticism arises as observed differences between species may be attributed to the uneven distribution of data points utilised in constructing each dataset. To address this concern, we repeated our analysis with species and occurrence points only present in Europe and North America. While slight differences emerged, the overarching conclusions remained consistent despite the smaller sample size (See supplementary material).

Recent years have witnessed a surge in research within the field of microclimates, which have predominantly maintained a landscape-level focus to enhance our comprehension of the drivers behind disparities between microclimate and macroclimate temperatures (Zellweger et al., 2019), as well as the prediction and mapping of microclimate temperatures across spatial and temporal scales (Greiser et al., 2018; Kearney et al., 2020). The relevance of microclimates in ecological research has also been shown in recent biogeographical investigations and applications (Hylander et al., 2022; Lembrechts et al., 2019; Zellweger et al., 2020). The appropriate scale for considering the impacts of microclimates can vary depending on the specific study system and taxon (Pincebourde & Woods, 2020; Potter et al., 2013). Despite the stark contrast in vertical resolution between the two datasets used in this study, both databases still face challenges in aligning with the fine-scale nature of insect species (Pincebourde & Woods, 2020; Potter et al., 2013). For most climatologists, horizontal microclimates typically correspond to horizontal distances of 0.001-100 m, with macroclimates corresponding to distances above 200 km (Bramer et al., 2018; Pincebourde & Woods, 2020). However, microclimates can exist on a multitude of scales depending on the study system addressed (Lembrechts et al., 2019). Hence, it has been suggested that ratios between body scales and distances are much more relevant when deciding micro-scales (Pincebourde & Woods, 2020; Potter et al., 2013). Therefore, it is plausible that neither WorldClim nor the soil-level climate data adequately represent the climates experienced by these ant species, potentially explaining why some species exhibit larger, smaller, or opposing directional disparities between the datasets. Even the 'micro-scaled' climate data employed here operates at resolutions of 1 km, addressing only vertical resolutions. However, fine-scale horizontal data is also imperative to such studies.

Such resolutions are not currently possible on any large-scale climate database. The best publicly available data is represented by the 25x25 m ForestClim dataset, centred on the

European subcontinent (Haesen, Lembrechts, et al., 2023), and the 'microclima' package which focuses on downscaling climate data to as fine as 1 m resolution at regional scales (Maclean et al., 2019). These microclimatic mapping approaches have demonstrated enhanced accuracy in species distribution models (Haesen, Lenoir, et al., 2023), confirming previously proposed theories (Lembrechts et al., 2019) and emphasising the substantial potential of microclimate datasets in ecological studies of species distribution and niches. Presently, global microclimate datasets are unavailable due to limitations in further downscaling existing datasets on such expansive scales (Maclean, 2020). However, this is currently among the highest-resolution data for predicting ant climate niches on a global scale, and this study provides evidence for the clear need to use more fine-scale data within the field of ecology to make better predictions (Körner & Hiltbrunner, 2018). There is, therefore, a need to produce global fine-scale microclimate datasets.

However, the need for empirical work is also important for a comprehensive assessment of whether climates truly differ between native and invasive ranges, or if observed disparities are artefacts stemming from the resolution of the climate data employed. Datasets based on occurrence points can only go so far to predict the niches that species are experiencing. Empirical solutions could allow studies to further understand the thermoregulatory behaviour of ant species, e.g., fine scale microclimate selection during foraging, nest selection, and their ability to adapt their microclimate via nest architecture or other behavioural solutions (Duffy et al., 2015). Such fine-scale climatic information may reveal further microclimatic niche conservatism in introduced species. This would not only increase our understanding of the basic biology of such ecologically important species but also help us build better models to predict how introduced ant species are distributed.

CONCLUSION

In conclusion, our findings underscore the metric dependency in assessing niche shifts, emphasising the necessity of employing multiple metrics for a comprehensive evaluation. Although the high inter-species correlation between macro- and microclimate data for the D overlap metric might suggest that microclimates have a limited impact on global scale niche shifts of ants, it is imperative to recognise that this was not the case with the other metrics. Furthermore, the SoilTemp data predicted fewer niche shifts between species using all methods and metrics. While macroclimate datasets remain a valuable tool for certain approaches, the soil-level SoilTemp dataset offers a more conservative estimate and possesses greater biological relevance for species predominantly situated at the soil level. Nevertheless, further micro-scale and experimental investigations are necessary to draw definitive conclusions. This study highlights the ongoing need for a nuanced understanding of the intricate interplay between micro- and macroclimates in shaping the ecological dynamics of ant species.

Contributions

OB and CB designed the research. SO conducted data formatting and collation. OB conducted the analysis. OB and CB wrote the manuscript.

Acknowledgements

We thank Jerome Gippet for feedback during the data analysis stages, and Alexander Bates for graphical design feedback. We also thank Eddie Perechon for collating the data needed for the colony size and nesting type.

Tables:

Table 1: List of definitions

Keyword	*Definition*
Microclimatic buffering	*Climatic conditions experienced by a species that are different from macroclimatic conditions. This is typically the moderation of extreme conditions within areas of microclimatic refugia, and are therefore usually more stable to fluctuations in climatic conditions*
False-positive niche shift	*Geographical expansions that are at first thought to represent niche shifts, but are found to arise due to methodological issues or a lack of association between the tested macroclimates and the specific microclimates inhabited by the species that exist within the macroclimate*
Niche Coupling	*Correspondence between the macroclimatic niche and microclimatic niche of a species occurrences or between species i.e., a rise in macroclimate correlates to a rise in microclimate conditions*
Macroclimate	*Broad-scale climate data derived from standardised meteorological stations located in open-air areas approximately two metres above ground level*
Microclimate	*Fine-scale climatic conditions that differ from macroclimatic conditions due to heterogeneous environments*
SoilTemp	*A novel dataset derived from soil temperature loggers (Lembrechts et al., 2020)*
WorldClim	*A classical climate dataset derived from weather station data (Fick & Hijmans, 2017)*
Niche Shift (climatic)	*When the niche of a new (introduced) population shifts its occurrence density within its niche space or expands or retracts the limits of its niche*
Niche expansion	*Establishment of a population in climatic conditions outside of the native realised niche of the species*
Introduced species	*A species that has been introduced via human-mediated dispersal (accidental or intentional) to an area outside of its native range where it has established a self-sustaining*

	population. Can often also be referred to as ‘invasive’ or ‘non-native’ species
Native range	*The natural geographic distribution of a species without human intervention*
Introduced range	*The range of a species due to human-mediated dispersal*
Hypervolume Method	*Allows for more direct comparisons in niche space within a n-dimensional hypervolume. Niches are projected into n-dimensional space allowing for direct comparisons in niche space without the need to overly reduce climate variables, unlike ordination methods. Two disadvantages of this method, however, are that it is computationally heavy and niche shifts may be overestimated due to the large number of axes used*
Ordination-based methods	*The climatic conditions of occurrence points in the native and introduced ranges are compared directly using an ordination method to reduce the number of dimensions. Then, differences between native and introduced niches can be quantified in environmental principal components analysis space. The advantage of this approach is that it allows for the analysis of niche differences directly within environmental space. While it does not highlight the effect of observed shifts on spatial predictions, tools, such as the R package ‘ecospat’, can help to project ordination-quantified niches into geographic space*

Figures:

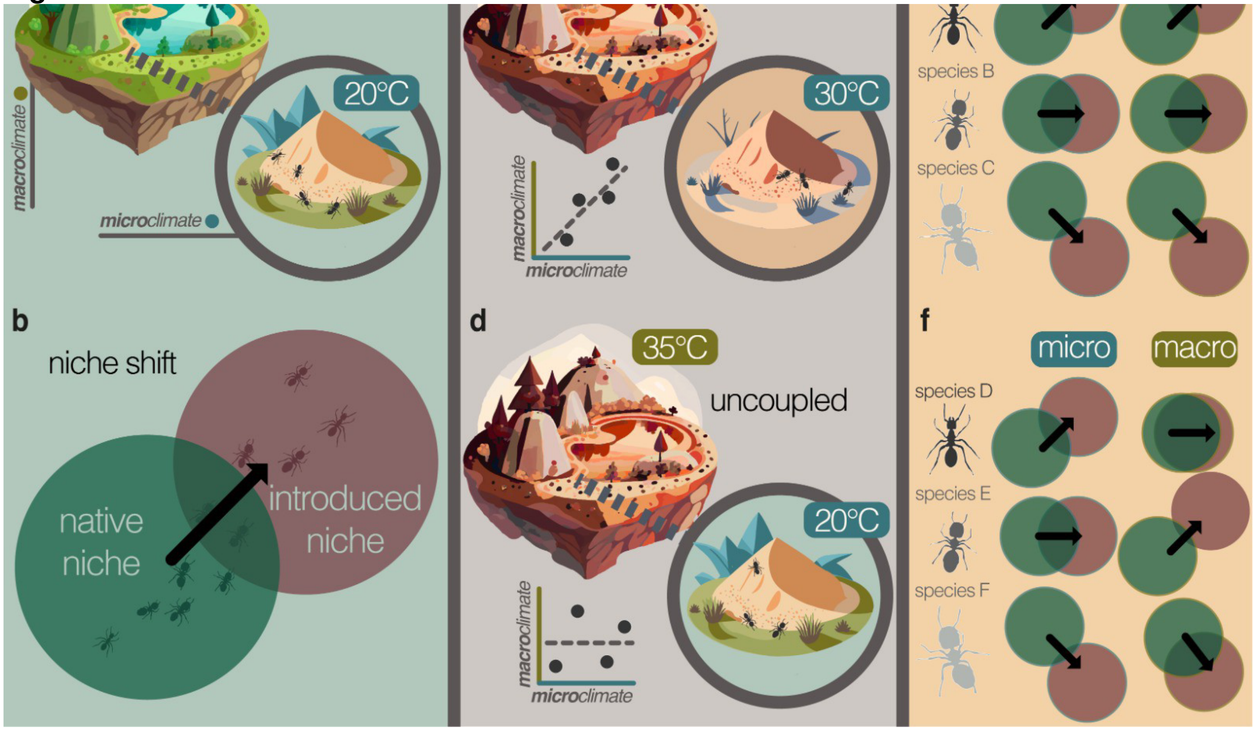

Figure 1: The effect of microclimate buffering, coupling, and uncoupling on niche shift analysis. The first panel represents temperature difference questions asked in this study, the second the effect of such buffering across landscapes of a species occurrence leading to coupling or uncoupling between macro- and microclimates, and the third the impact of coupling and uncoupling on niche shift analyses. a) The buffering between macroclimatic (air temperature) and microclimate (soil-level temperature) conditions, where the temperatures at these different locations are different due to factors including vegetation, landscape, and wind. b) A niche shift representing a change in the climatic niche between the native and introduced range of a species. c) Coupling in the occurrence points of a species between macro- and microclimatic conditions. d) Uncoupling in the occurrence points of a species between macro- and microclimatic conditions. e) Coupling in niche shifts between macro- and microclimatic conditions as species here have the same level of niche shifts in both the macro- and microclimatic conditions. f) Uncoupling in niche shifts between macro- and microclimatic conditions as species here have a varying amount of niche shifts (sometimes bigger, sometimes smaller) when the macro- and microclimatic resolutions are considered.

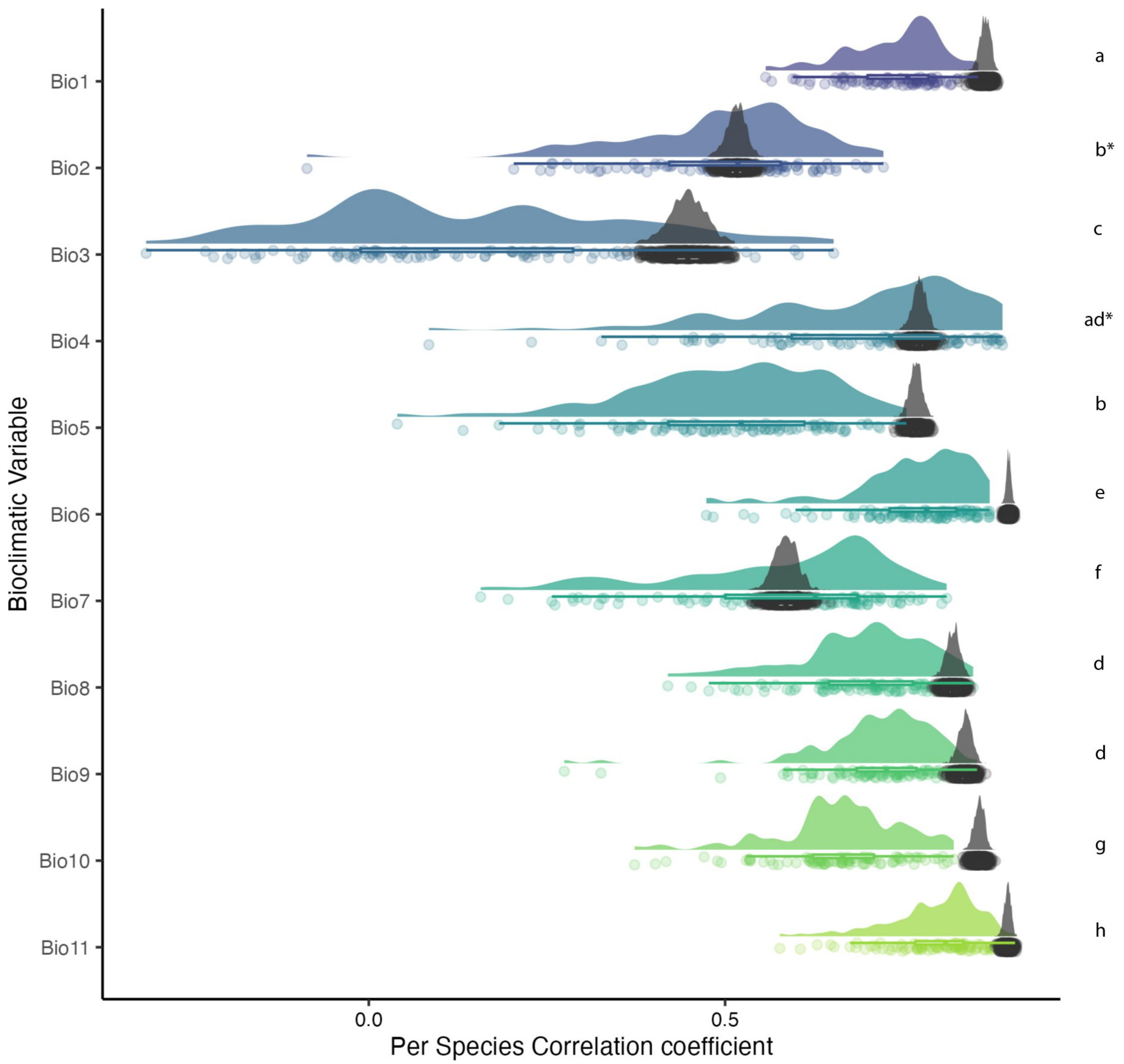

Figure 2: Kendall's correlation coefficient for each bioclimatic variable between 95 ant species occurrences between WorldClim and SoilTemp datasets. Density distributions of correlations for species (colour, n = 95) and random (grey). Boxplot elements show: centre line, median; box limits, upper and lower quartiles; and whiskers, 1.5× interquartile range. Each bioclimatic variable dot represents the correlation coefficient between air (WorldClim) and soil (SoilTemp) temperature at the species occurrence points, for each species. Bioclimatic variables represent a range of temperature variables (BIO1 = Annual Mean Temperature, BIO2 = Mean Diurnal

Range, BIO3 = Isothermality, BIO4 = Temperature Seasonality, BIO5 = Max Temperature of Warmest Month, BIO6 = Min Temperature of Coldest Month, BIO7 = Temperature Annual Range, BIO8 = Mean Temperature of Wettest Quarter, BIO9 = Mean Temperature of Driest Quarter, BIO10 = Mean Temperature of Warmest Quarter, and BIO11 = Mean Temperature of Coldest Quarter). Letters represent significant differences between species distributions for each bioclimatic variable (pairwise Wilcoxon tests), and stars indicate where the distribution of species is different from random distribution of that variable (Kruskal-wallis test).

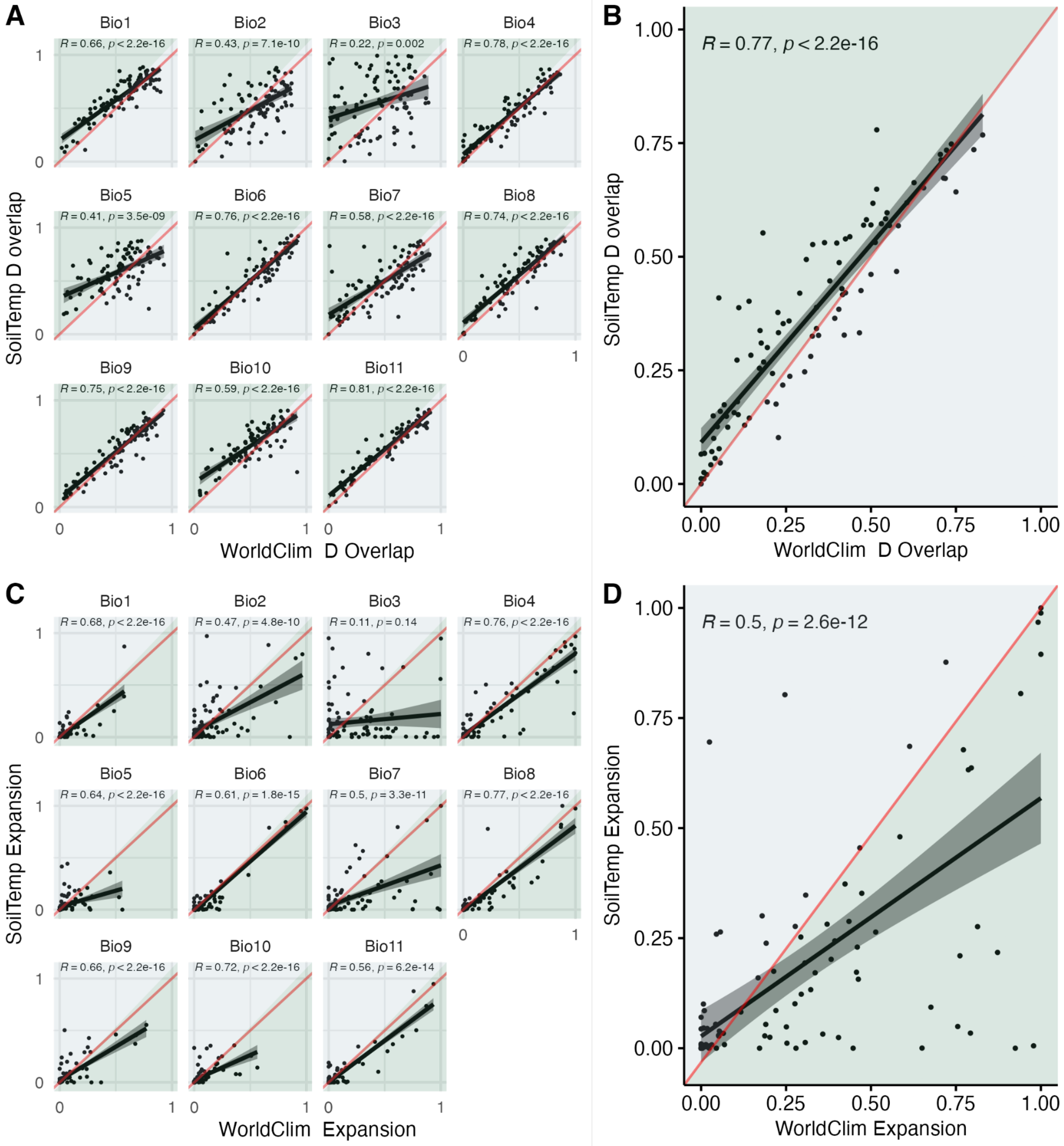

Figure 3: Correlations in niche shift results between WorldClim and SoilTemp datasets for each species (n = 95). A) D overlap metric per bioclimatic variable (Bio1-Bio11), B) D overlap in between-pca space (using all bioclimatic variables), C) expansion per bioclimatic variable (Bio1-Bio11), D) expansion in between-pca space (using all bioclimatic variables). For all plots the red line depicts an exact 1:1 match between the datasets. Green shading represents the area

where the SoilTemp dataset predicts a higher niche overlap, and blue represents where the WorldClim dataset predicts a higher niche overlap. Correlation lines show Kendall's correlation Tau. R depicts the Tau correlation coefficient and p represents the p-value significance of the relationship.

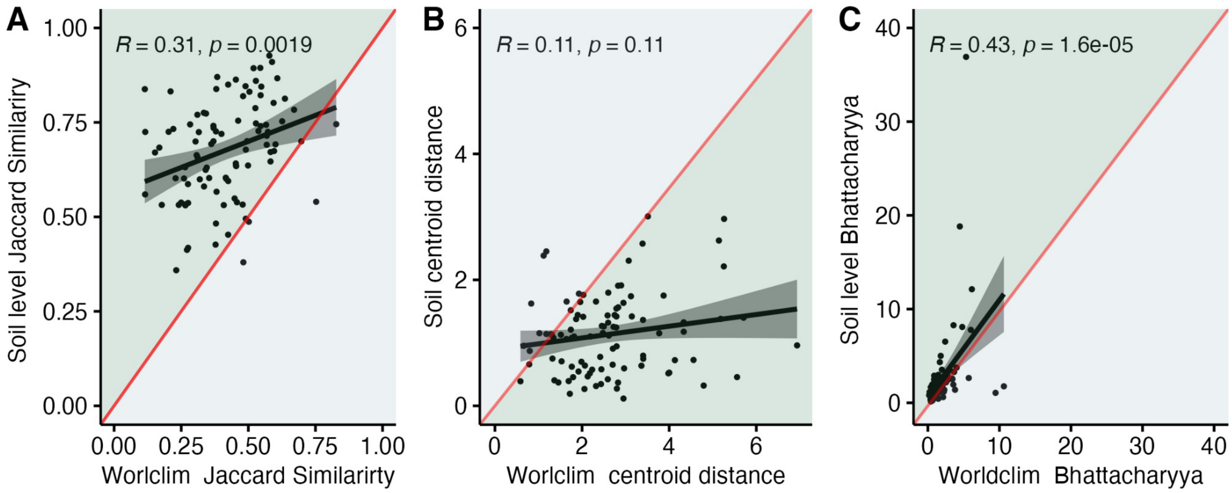

Figure 4: Correlations in niche shift results between WorldClim and SoilTemp datasets for each species (n = 95). Red line depicts an exact 1:1 match between the datasets. Green shading represents the area where the SoilTemp dataset predicts a higher niche overlap, and blue represents where the WorldClim dataset predicts a higher niche overlap. Correlation lines show Kendall's correlation Tau. R depicts the Tau correlation coefficient and p represents the p-value significance of the relationship. A) Jaccard similarity, B) Centroid distance, C) Bhattacharyya distance.

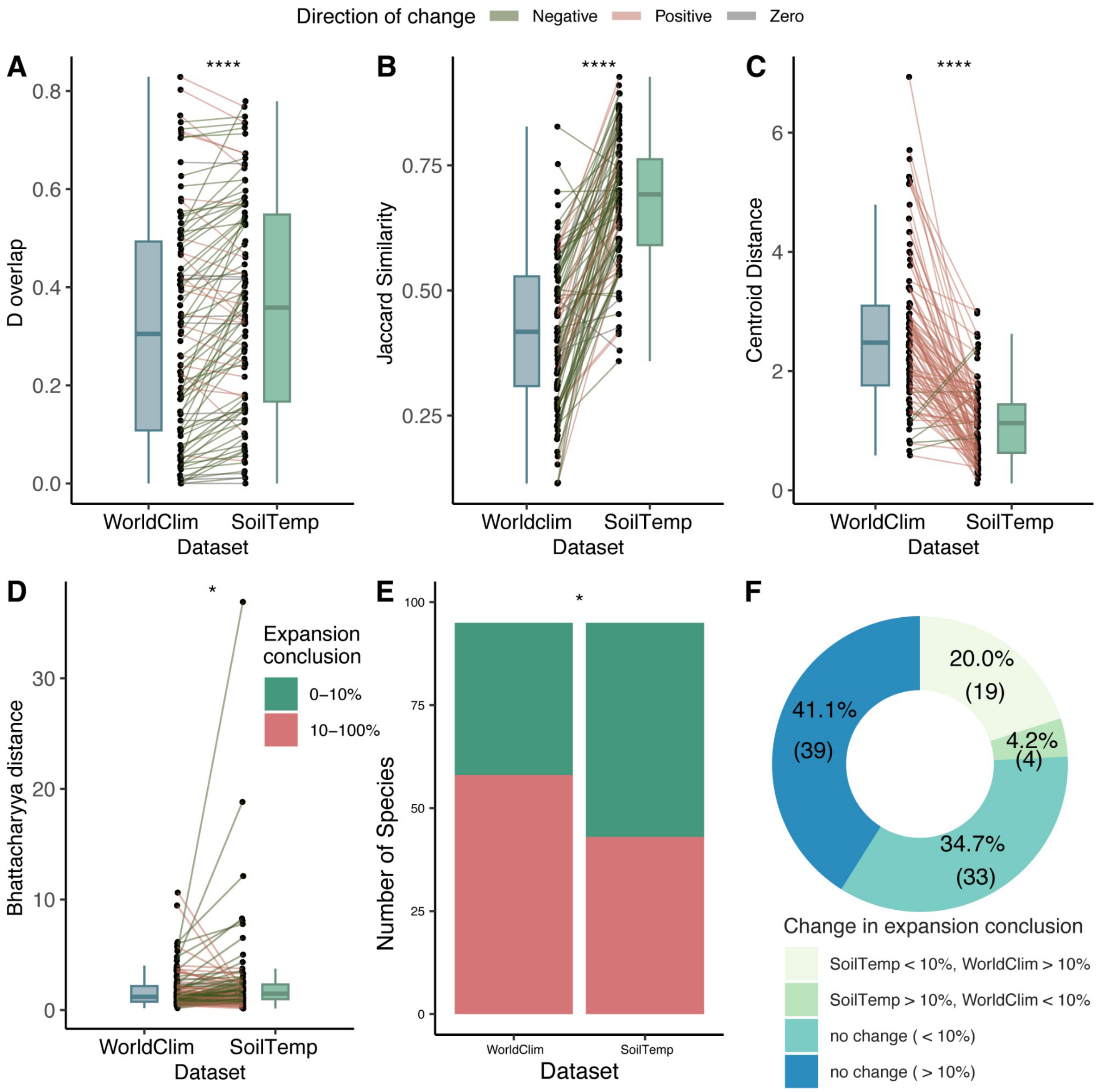

Figure 5: Differences in niche overlap statistics between the WorldClim and SoilTemp datasets for each species (n = 95). A) D overlap (higher values represent higher niche similarity), B) Jaccard similarity (higher values represent higher niche similarity), C) centroid distance (lower values represent higher niche similarity), D) Bhattacharya distance (lower values represent higher niche similarity). Statistical tests depict pairwise Wilcox tests. Results for each species are presented as dots, with line in between boxplots representing the same species, to display the pairwise difference between the two datasets. Boxplot elements show: centre line, median; box limits, upper and lower quartiles; and whiskers, 1.5× interquartile range. E) *Frequency changes in the number of species predicted to have a negligible (0-10%) and significant (10-*

100%) expansion between the WorldClim and SoilTemp dataset. Chi-squared test, $X^2 = 4.14$, df = 1, p = 0.04*. F) Difference in niche expansion result per species between the WorldClim and SoilTemp datasets.*

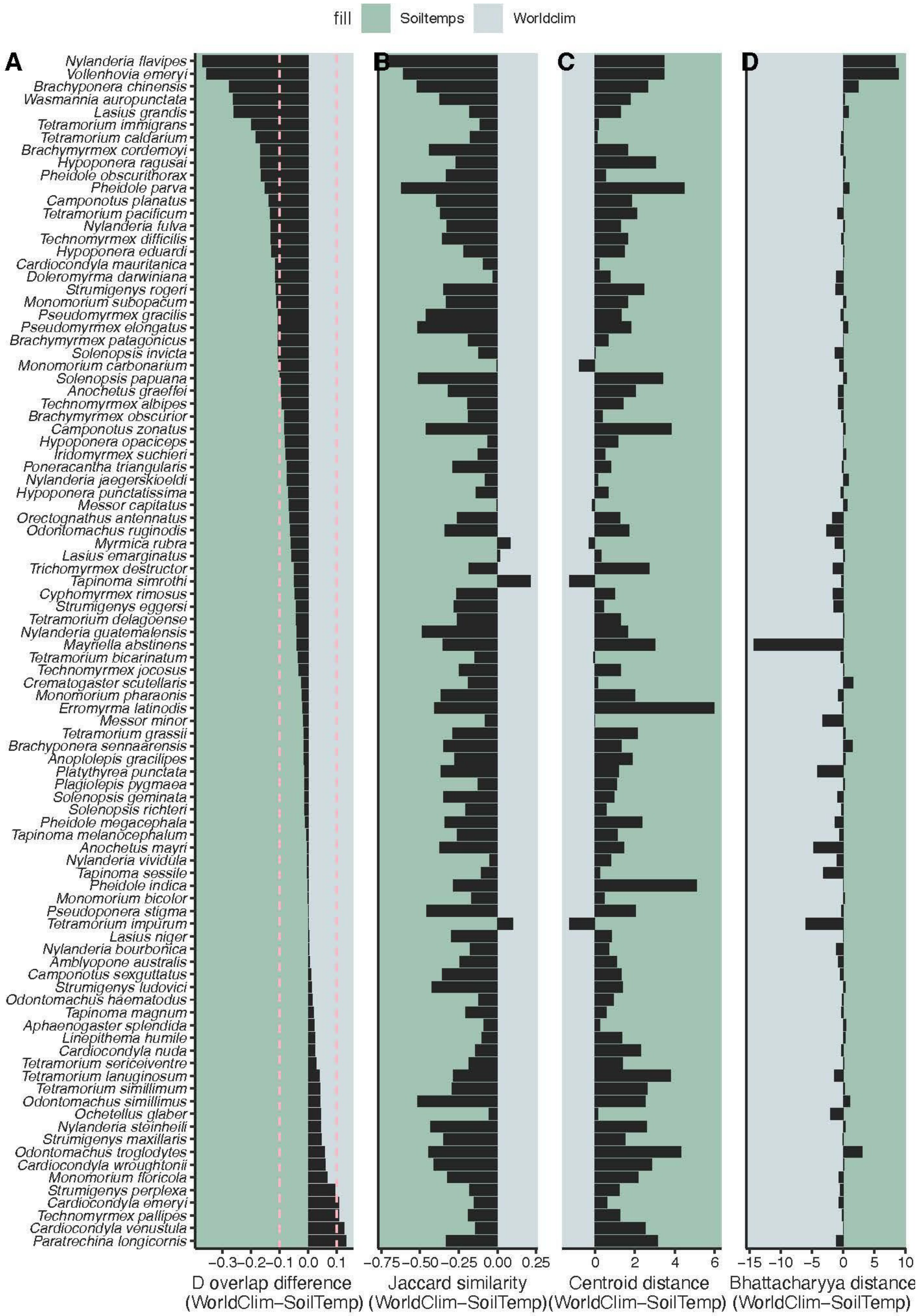
fill
Soiltemps
Worldclim
A
B
C
D
Nylanderia flavipes
Vollenhovia emeryi
Brachyponera chinensis
Wasmannia auropunctata
Lasius grandis
Tetramorium immigrans
Tetramorium caldarium
Brachymyrmex cordemoyi
Hypoponera ragusai
Pheidole obscurithorax
Pheidole parva
Camponotus planatus
Tetramorium pacificum
Nylanderia fulva
Technomyrmex difficilis
Hypoponera eduardi
Cardiocondyla mauritanica
Doleromyrma darwiniana
Strumigenys rogeri
Monomorium subopacum
Pseudomyrmex gracilis
Pseudomyrmex elongatus
Brachymyrmex patagonicus
Solenopsis invicta
Monomorium carbonarium
Solenopsis papuana
Anochetus graeffei
Technomyrmex albipes
Brachymyrmex obscurior
Camponotus zonatus
Hypoponera opaciceps
Iridomyrmex suchieri
Poneracantha triangularis
Nylanderia jaegerskioeldi
Hypoponera punctatissima
Messor capitatus
Orectognathus antennatus
Odontomachus ruginodis
Myrmica rubra
Lasius emarginatus
Trichomyrmex destructor
Tapinoma simrothi
Cyphomyrmex rimosus
Strumigenys eggersi
Tetramorium delagoense
Nylanderia guatemalensis
Mayriella abstinens
Tetramorium bicarinatum
Technomyrmex jocosus
Crematogaster scutellaris
Monomorium pharaonis
Erromyrma latinodis
Messor minor
Tetramorium grassii
Brachyponera sennaarensis
Anoplolepis gracilipes
Platythyrea punctata
Plagiolepis pygmaea
Solenopsis geminata
Solenopsis richteri
Pheidole megacephala
Tapinoma melanocephalum
Anochetus mayri
Nylanderia vividula
Tapinoma sessile
Pheidole indica
Monomorium bicolor
Pseudoponera stigma
Tetramorium impurum
Lasius niger
Nylanderia bourbonica
Amblyopone australis
Camponotus sexguttatus
Strumigenys ludovici
Odontomachus haematodus
Tapinoma magnum
Aphaenogaster splendida
Linepithema humile
Cardiocondyla nuda
Tetramorium sericeiventre
Tetramorium lanuginosum
Tetramorium simillimum
Odontomachus simillimus
Ochetellus glaber
Nylanderia steinheili
Strumigenys maxillaris
Odontomachus troglodytes
Cardiocondyla wroughtonii
Monomorium floricola
Strumigenys perplexa
Cardiocondyla emeryi
Technomyrmex pallipes
Cardiocondyla venustula
Paratrechina longicornis
−0.3
−0.2
−0.1
0.0
0.1
D overlap difference
(WorldClim−SoilTemp)
−0.75
−0.50
−0.25
0.00
0.25
Jaccard similarity
(WorldClim−SoilTemp)
0
2
4
6
Centroid distance
(WorldClim−SoilTemp)
−15
−10
−5
0
5
10
Bhattacharyya distance
(WorldClim−SoilTemp)

Figure 6: Raw differences in the niche shift results for each ant species (WorldClim-SoilTemp). Bars represent species niche shift differences between the datasets. A) D overlap, B) Jaccard similarity, C) Centroid distance, D) Bhattacharya distance. Species are ordered according to the D overlap results. Colours represent whether the SoilTemp dataset (green) or WorldClim dataset (blue) has predicted higher niche conservatism.

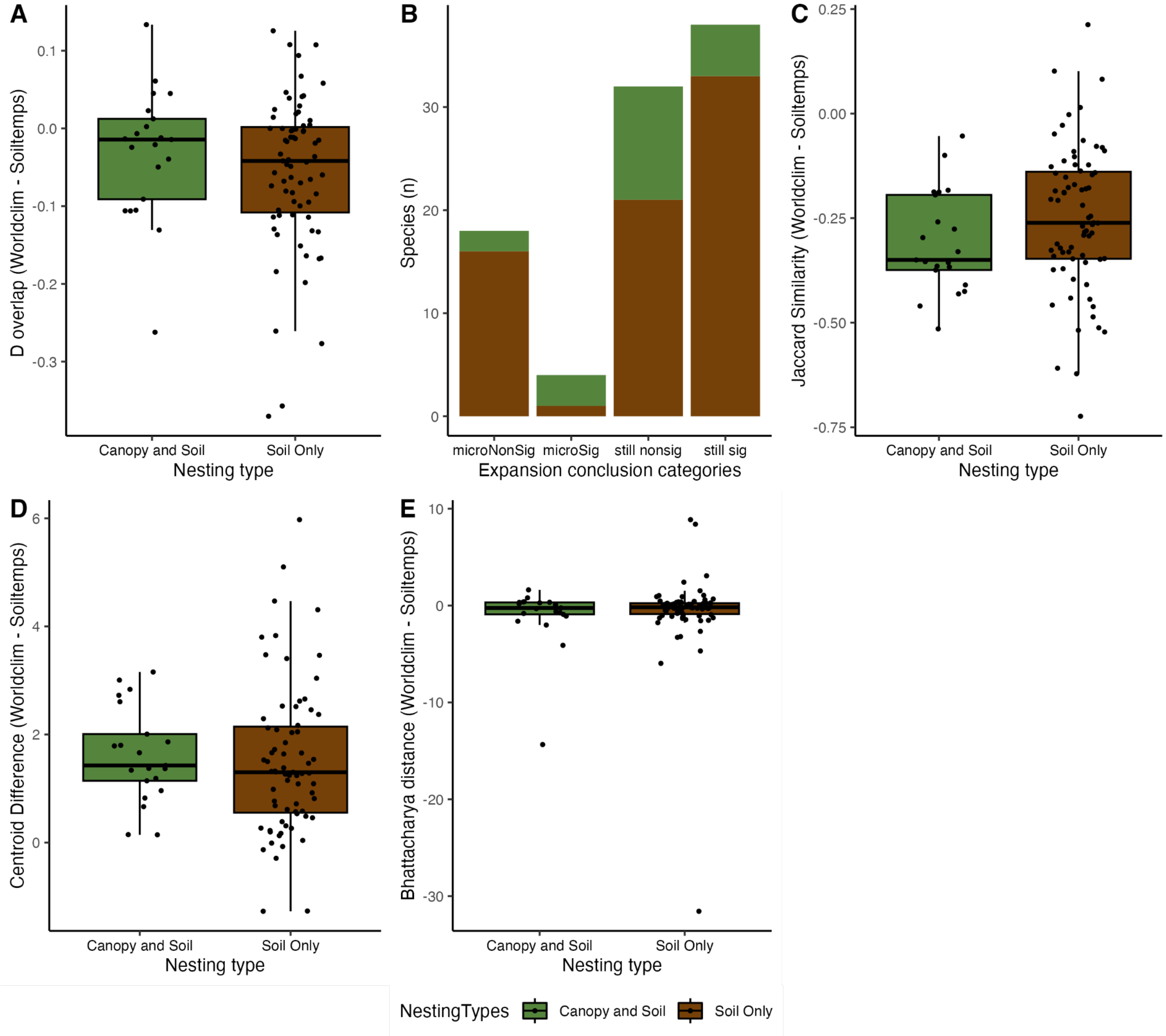

Figure 7: Niche metric differences between the WorldClim and SoilTemp datasets for each nesting type. A) D overlap (WorldClim - SoilTemp), B) Difference in expansion conclusions for each study MicroNonSig (Worldclim expansion > 10%, Soiltemp expansion < 10%), Microsig (Worldclim expansion < 10 %, soiltemp expansion > 10%), still nonsig (Worldclim and Soiltemp expansion < 10%) and stillsig (WorldClim and Soiltemp expansion > 10 %). C), Centroid distance (WorldClim - SoilTemp), D) Jaccard similarity (WorldClim - SoilTemp), E) Bhattacharya distance (WorldClim - SoilTemp). Boxplot elements show; centre line, median; box limits, upper and lower quartiles; and whiskers, 1.5× interquartile range.

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Supplementary material

1 Principle components analysis of the world

The temperature-related bioclimatic variables were derived from monthly temperature). These 11 variables were then reduced to axes 5 by conducting a principal components analysis (PCA) on the world maps using the function 'PCAraster' to account for co-linerality between the different variables (Fig. S1, S2).

2 Results from restricted analysis

All analyses (see main manuscript, methods section) were repeated when all occurrences except those occurring in north america and europe were removed. This was to see if there was an impact of data coverage within the climatic maps which have a western-centric nature.

2. 1 Were niche shifts results coupled between WorldClim and SoilTemp datasets?

When all bioclimatic variables were considered in a single analysis, the WorldClim and SoilTemp datasets had significant correlations for all niche shift metrics, with again D overlap showing the highest correlation (D overlap; kendall's correlation Tau, R=0.78, $p < 0.001$). The other metrics had much lower correlations: Expansion had a lower correlation than the global dataset (kendall's correlation Tau, R=0.45, $p < 0.001$). Like with the global-dataset, the centroid distance metric was not significantly correlated (R = -0.03, p = 0.8). Jaccard similarity (R = 0.40, p= 0.02) and Bhattacharya (0.62, $p < 0.01$) had higher correlations than the world-dataset. Despite these differences however, we can still conclude that there is not a one-to-one relationship between the results obtained from the WorldClim and SoilTemp datasets, signifying that they are largely uncoupled from each other for all metrics except for the D overlap metric.

2.2 Did soil temperature data predict more or fewer niche shifts?

The SoilTemp consistently predicted lower niche shifts for most species. This was true for the D overlap (Pairwise Wilcoxon test, $p < 0.01$), Jaccard Similarity (Pairwise Wilcoxon test, $p < 0.01$), Centroid distance (Pairwise Wilcoxon test, $p < 0.01$), and Bhattacharya distance (Pairwise Wilcoxon test, $p < 0.01$). This was however not the case for the expansion-conclusion (below of above 10% expansion) metric (Chi-squared test, $\mathcal{X}^2 = 2.3063$, df = 1, p = 0.1288).

However, when assessing direct differences in conclusion per species, a large percentage (71.9%) of species maintained the conclusion of niche shift between the two datasets, with 25% going from a niche shift to a non-niche shift (more than for the global analysis), and only 3.1% of species switching from a non-significant niche shift to a significant niche shift (Figure 5F).

2.3 What factors predict the difference between SoilTemp and WorldClim databases?

Raw differences in niche shift results between WorldClim and SoilTemp were not correlated with any of the correlative factors (Table S2). Expansion-conclusion result could not be analysed as only one species shifted from non-significant to significant expansion with the SoilTemp dataset.

Chapter 4

Predictions of future insect distributions of insects under climate change

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This work is currently unpublished.

Predictions of future insect distributions of insects under climate change

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Abstract

Climate change has severe consequences for insects worldwide, many of which play key ecological roles. However, a quantitative synthesis of predictions of insect responses to climate change is still lacking. Here, we conducted a meta-analysis of 289 studies on insect range size predictions under climate change. We found 46.5% of species were predicted to face range size reductions, and only 30.5% increased. While invasive species showed a more frequent range increase than native species, both increases and decreases were observed in both groups highlighting species-specific changes. Differences could be driven by factors such as species' physiology and geographic distribution, however we argue that large amounts of uncertainty remain due to differences in methodologies and data sources. We discuss how these methodological choices (from correlational to mechanistic models) can impact conclusions about whether a species is predicted to alter its geographic range in different ways. In particular, we discuss the impact of choice of climate data used, as many studies do not report the specific global circulation and emissions scenarios used. We critically review current methods to predict insect distributions and outline future research directions.

1. Introduction

Anthropogenic global changes such as the use of pesticides, the spread of invasive species, urbanisation and climate change have led to widespread declines in insect biodiversity worldwide (Baranov *et al.* 2020; Hallmann *et al.* 2017). Aquatic macroinvertebrate species have already declined by up to 82% (Baranov *et al.* 2020), and flying insects by 75% over 30 years (Hallmann *et al.* 2017). It has been suggested that around 5 to 10% of the the estimated 5.5 million insect species worldwide (Stork 2018), have undergone extinction since the industrial era (Cardoso *et al.* 2020; Régnier *et al.* 2015). Since insects play key ecological roles, their decline will severely impair ecosystem functioning (Thomas 2010). The so-called "insect apocalypse" has caused widespread concern. Although many stressors may affect insects (Cardoso *et al.* 2020; Dirzo *et al.* 2014), climate change stands out because it affects insect communities worldwide even in remote or protected areas (Wagner *et al.* 2021), and it has already contributed to large scale insect declines (Soroye *et al.* 2020). Although many studies have observed declines in both abundance and range sizes (Wagner *et al.* 2021), predictions of what may happen in the future are crucial. Most research forecasting species responses to climate change has focussed on predicting range size changes.

As the global climate becomes both warmer and more variable (Urban 2015), insect species will expand ('winners') or contract ('losers') their ranges (Rubenstein *et al.* 2020; Thomas 2010; Thomas *et al.* 2004). It is particularly worrying that many of the climate change winners are expected to be invasive species (defined here as species that have been introduced and established outside of their native ranges via human-mediated transport) (Hellmann *et al.* 2008). Some of these introduced species may also act as a vector for disease (hereafter "vector species", defined as being recorded as an insect which can carry a disease/pathogen and transmit it to another non-infected organism that is of a different species). These species are expected to spread and disperse at accelerated rates, exacerbating the impact of climate change on already declining native insect populations (Buckley & Csergo 2017; Sangle *et al.* 2020).

In this review, we focus on changes in range size in response to climate change, i.e. the geographic extent of the physical distribution of species. This is because this is an extremely active domain of research, and the aim of a large part of predictive studies on climate change impacts on biodiversity. These forecasts are primed to play an important role in alerting scientists and policymakers to potential future risks, bolstering both action and discussions about how to mitigate the negative effects of a changing world (Pereira *et al.* 2010). To predict range shifts, researchers use data on species' current distributions, sometimes in combination with information on their physiology and/or behaviour, along with climate scenarios to predict the presence and extent of future geographic ranges (Guisan & Thuiller 2005; Mammola *et al.* 2021).

Surprisingly, despite being often discussed within the literature, a quantitative synthesis of predictions of insect species responses to climate change has not been done before. Here, we first present synthesis of studies on predicted range changes in insects under climate change (Section 1), revealing large numbers of species range increases as well as decreases, with higher amounts of increases for invasive/vector species. Due to the large variety in approaches between each of the studies, it is not possible to do a formal meta-analysis for this work, we therefore discuss the broad variety in approaches between different prediction studies which likely have a large impact on study results. We discuss models used in climate change predictions; correlational models (section 2.1), hybrid and semi-mechanistic models (section 2.2), and mechanistic models (section 2.3) and the advantages and disadvantages of each approach. Finally, we discuss the choices of different climatic data used as input for all models, choices which can have large impacts on study results, and the benefits and drawbacks of different data types, sources, and resolutions (section 3).

2. Methods

For our meta-analysis, we performed a Web of science search for papers that predict insect future distributions in response to climate change. The keyword search string used was Topic Search = (insect* OR protura* OR collembola* OR diplura* OR microcoryphia* OR thysanura* OR ephemeroptera* OR odonata* OR orthoptera* OR phasmotodea* OR grylloblattodea* OR mantophasmatodea* OR dermaptera* OR plecoptera* OR embiidina* OR zoraptera* or isoptera* OR mantodea* OR blattodea* OR hemiptera* OR thysanoptera* OR psocoptera* OR phthiraptera* OR coleoptera* OR neuroptera* OR hymenoptera* OR trichoptera* OR lepidoptera* OR siphonaptera* OR mecoptera* OR strepsiptera* OR diptera*) AND TS= ((climate OR weather) and change*) AND TS= (range shift*OR migration* OR distribution*) AND TS= (prediction OR model*). This search was conducted in English in January 2023, and yielded 971 papers within the field of ecology, these papers were further filtered to retain only papers that predict future insect distributions under climate change in English, resulting in 289 papers.

For each study, we recorded the species studied, time horizon, climate data and scenarios used, and whether the overall study conclusion for each species was an increase, decrease, or no change in range, or if the predictions were ‘uncertain’ meaning both increases and decreases were predicted within the same study.

For each species reported in each study, an ‘native’, ‘invasive’ or ‘vector’ label was given. Species were categorised by how the paper defined the species itself (i.e. if they mentioned that it was an invasive/vector species or not), or for invasive species if they were present in the GRIIS database (Pagad *et al.* 2022) – or in the absence of such information due to a literature searches on the species using google scholar. If the species was defined as being invasive or a vector species in any area of the world it was defined as such in our study. Species were further categorised into ‘terrestrial’, ‘aquatic’ or ‘both’ (with the both category depicting species found in both terrestrial and aquatic environments for example in different life stages). These were categorised either by what was defined by the paper itself, or in the absence of such information for literature searches on the species using google scholar. For species assignments see table S1.

For studies where exact range change predictions were reported, we recorded the predicted range change (in %) for each species in each study. Studies which did not report exact numbers were removed from this part of the analysis, resulting in 112 studies for which we could extract data. Due to the large number of studies assessed, and as the number of predictions varies substantially between studies, with some studies reporting many scenarios (based on different climate data and future time horizons) and others just one, we extracted from the subset of studies both the most pessimistic (most severe predicted range decline for a specific species within a study) and optimistic (least severe range decline for a species within a study) change for each species to analyse the full range of potential change that is predicted for each species within each study. All analysis was conducted in R version 4.2.2.

3. Current predictions of species range changes

Throughout the literature, there is a clear bias towards certain groups of species. For example, most studies (87%) investigated predicted impacts on terrestrial species (Fig 2A), despite the fact that there are over estimates of aquatic insect diversity number greater than 200,000, (Dijkstra *et al.* 2014). Furthermore, only 14 out of 31 insect orders have been studied, covering 899 species. Lepidoptera (moths and butterflies) have been the most studied, with 267 species. Yet, this represents just 0.14% of the total number of known Lepidoptera species (estimated ~157,000 (Stork 2018)). Furthermore, studies are heavily biased towards introduced species representing almost half of species assessed (Fig. 1AB). While there are more than 7,700 recorded introduced insect species worldwide, they represent less than 1% of known insect species (Mammola *et al.* 2021; Zhao *et al.* 2022). Moreover, most studies (87%) concern terrestrial species. There is therefore a vast knowledge gap when it comes to species and taxonomic coverage of insect range shift predictions.

In total, an extremely large number of species (46.5%) are predicted to decrease in range size, adding to the general concern that most species will suffer from climate change (Wagner *et al.* 2021). However, a significant number of species (30.5%) were also predicted to increase their ranges, which seems to suggest that there also will be some 'climate change winners'. However, these estimates do not take account changes in abundance or biotic interactions with resident communities, which may oppose resistance to the establishment of the range shifting species. The proportion of climate change winners and losers is similar across most insect orders (Fig. 2A), with the exception of Coleoptera, which had a significantly greater proportion of range increases (Chi-squared test, $X^2 = 150.1$, df = 48, $p < 0.001$). This s surprising, as for example, Lepidoptera have been shown to suffer more under historical climate changes than other insect orders (Warren *et al.* 2021) (although not always), but were not predicted to show larger range size decreases in the future compare to other Orders (Figure 2A). For 21.6% of species, the conclusions were recorded as "unclear," as both increases and decreases were predicted by the same study, for example due to multiple methods or data sources used.

While a wide range of species have been studied, only 35% of studies examined more than one species and only 18% examined more than two. This makes direct comparison of predictions extremely difficult given the vast array of different methodologies among papers (see section 2). Future research could make progress using a comparative cross- species approach, taking into account phylogeny. Phylogenetic niche conservatism in niches is often expected in relation to species past or current distributions, with closely related species expected to have more similar niches. This raises the question if closely related insect species are also expected to experience similar range shifts as a result of changing climates. If this is the case, conservation efforts and strategies for species which are understudied could be built by using the niche of their closest studied relatives as a proxy (Buckley & Kingsolver 2012).

In contrast with climate change impacts on native biodiversity, introduced species are often thought to benefit from climate change allowing them to expand their ranges (Hellmann *et al.* 2008). Our meta-analysis supports this expectation with 54.7% of invasive and vector species that were predicted to increase in range size, compared to just 23.9% of native species (Chi-squared test, $X^2 = 97.555$, df = 3, $p < 0.001$). Significant differences in average amount of changes in range size (in % relative to the historical range size) were also observed between native vs. invasive/vector species and optimistic vs. pessimistic scenarios (Kruskal-Wallis test, $X^2 = 152.8$, df = 3, p-value < 0.001). Post-hoc Dunn tests revealed that overall, native species had significantly higher range losses under pessimistic scenarios compared to optimistic scenarios ($p < 0.001$). Strikingly, mean range changes for invasive/vector species were positive (i.e. increases) in both pessimistic and optimistic scenarios (Fig. 2B). Increases for invasive/vector species were significantly greater for optimistic scenarios than pessimistic ($p < 0.001$). Overall, invasive/vector species had higher increases in range size than native species under both pessimistic ($p < 0.001$) and optimistic scenarios ($p < 0.001$). Therefore, native species had generally stronger declines in range size and introduced/vector species greater increases. This shows that the vast majority of species expected to benefit from climate change are damaging and likely to exacerbate the negative impacts of climate change on biodiversity. However, there were climate change winners and losers among native and invasive species (Fig. 2B). These interspecific differences could be biologically meaningful (for example differences in traits rendering species more or less vulnerable to climate change (Halsch *et al.* 2021; Kellermann & van Heerwaarden 2019)) or may be simply due to methodological differences between studies i.e. data choices (see section 5), or methodological choices (see Section 4), that can impact extents of predicted increases or decreases.

Although much published work looks at either native or invasive/ vector species, we found no study that compared both. Future research might do that using phylogenetically independent contrasts (e.g. pairs of native and invasive sister species) to provide insight into why and how similar species can respond differently to the same environmental challenge. One reason why only few species have been assessed so far is the lack of spatial distribution data needed as input for most predictive models (Lobo 2016). As a result, many studies focus on a limited number of "flagship" or well-known species, with a disproportionate number of studies on invasive and vector species (Fig. 1).

Although reported results of range size change (i.e. increases vs decreases) (Fig. 2) suggest overall trend in “winners” or “losers” of climate change, it is important to note that methodological choices can affect these conclusions. A number of key steps that need to be taken in order to predict insect responses to climate change. Firstly, there is the nature of the species studied, i.e. the order, and whether the species is and invasive or vector species. However, it is also important to note that other life-history factors may influence species along with geographical factors such as latitude**.** Secondly, there is the choice of model type (section

2), as model choice can largely affect predictions within even the same species, with for example broad modelling types having variable abilities to integrate for example physiological and life history information, which may lead to more or less accurate depending on the species and approach used (discussed in section 2). Furthermore, the choice of climatic data used is a vital and often overlooked factor which can largely influence the predicted future distribution of a species (i.e. number of circulation models, number of climate scenarios and resolution of climate data, discussed in section 3) (see Fig. 3, as a simplified diagram of steps involved). Within each of these steps however there are many factors which can change the predictions and thus overall outcomes of the study, which we will discuss in section 2 and 3.

4. The effect of model usage

Differing methodologies to predict future species ranges can yield drastically divergent results – impacting the study conclusions seen in section 1. For example, correlational models are a useful tool, however do not incorporate key information on biological processes that impact insect distributions. On the other hand, more complex models may provide better performance, such as hybrid or mechanistic models, by directly simulating the dispersal of species based on their biology and their relationships to climatic factors. However, they require more data and are computationally intensive and are therefore less common within the literature. Below we describe the benefits and drawbacks of three broad model types, highlighting the impact of these models on future predictions in the variations possible within each model type.

4.1. Correlational models

Species distribution models (SDMs), also known as ecological niche models (ENMs), have been used in 169 of the 289 studies predicting future distributions of insects in response to climate change, and have become increasingly popular over the past 27 years (Fig. 4). One of the greatest advantages of SDMs is that they require only species occurrence data by using algorithms to describe the relationship between these points and climatic data, meaning they can be used for many species (Evans *et al.* 2015; Hill & Thomson 2015). Although No 'gold standard' in algorithm choice currently exists (Carvalho *et al.* 2017), it has been shown that the majority of SDM insect studies have used a single algorithm despite the fact different algorithms can yield remarkably variable predictions and we are lacking studies which compare algorithm performances (Mammola *et al.* 2021). The most popular SDM algorithm is 'Maxent' (Phillips *et al.* 2006), which was used in 55.6% of the SDM studies. Often, multiple model types present an apparently good predictive performance (e.g. based on True Skill Statistics (TSS) or area under the curve (AUC) scores) - and the choice between such models may significantly affect predictions of future range sizes. One solution is to combine different algorithm results to create 'ensemble' models (Araújo *et al.* 2005), which were used in 32.5% (55) studies which employed SDMs in their analysis. However, there are many different methods to average multiple models, and selection criteria/thresholds to select models for the final ensemble model, which may significantly impact result predictions– however these choices are not always even reported, as a 'lack of unambiguous information' regarding ensemble approaches has been noted on a previous review focussing on ensemble modelling (Hao *et al.* 2019) . Therefore, even between studies which 'just' employed SDMs, there is an enormous variability to what is predicted based on algorithm choice or ensemble methodology.

Furthermore, due to their simplicity and broad nature, correlational models make several key assumptions (Hill & Thomson 2015; Maino *et al.* 2016). SDMs assume that the climate conditions currently experienced by the species represent the climatic niche the species will occupy in the future – ignoring the possibility of niche shifts (Elith *et al.* 2010; Gallien *et al.* 2010; Soberon & Peterson 2005). However climatic niche shifts are frequent in insect species during invasion (Bates *et al.* 2020; Hill *et al.* 2017). Therefore, it might be expected that some species will show niche shifts with upcoming climate change. Therefore, assuming static niches can be considered as ecologically unrealistic (Dormann 2007).

Despite their limitations, SDMs are still useful to approximate future insect distributions, especially for species for which we have minimal data (Dormann 2007; Evans *et al.* 2015; Hill & Thomson 2015) – however the large amounts of variation in approach between models of this type makes direct comparisons in conclusions of range changes extremely difficult and thus differences in choices between studies which used SDMs may have had a large impact on the results we discussed in Section 1.

4.2. Hybrid/Semi-mechanistic models

Another popular model type is hybrid or niche-population models. These models focus on the responses of individual populations at specific study sites to predict changes in species distributions (Aragón *et al.* 2010; Holloway *et al.* 2016; Zurell *et al.* 2016). For example, hybrid models can explicitly incorporate dispersal, which is particularly useful for migratory or flying species (compared to dispersal-limited insects) (Holloway *et al.* 2016; Zhang & Kubota 2021). Many studies have included flight distance or speed information (Kim *et al.* 2020), from either the literature (e.g.(Buse & Griebeler 2011)), expert knowledge (e.g. (Fischer *et al.* 2011; Liang & Fei 2014)), or calculations based on collected data (Arribas *et al.* 2012; Della Rocca & Milanesi 2020) such as mark-recapture experiments (Walters *et al.* 2006). For example, a recent study on the invasive pine processionary moth (*Thaumetopoea pityocampa*) used range movement distances in previous years to predict range dynamics with climate change (Godefroid *et al.* 2016), by including estimations of dispersal into their analysis via kernel distributions (Zhang & Kubota 2021). However, natal dispersal distance is often difficult to estimate (Thuiller *et al.* 2013), therefore the majority of studies on insects either assumes unlimited or no dispersal (Mammola *et al.* 2021; Martínez-López *et al.* 2021; Xing *et al.* 2019).

Some models have also included population dynamics alongside dispersal (Nenzén *et al.* 2012). However, these methodologies are much easier to apply to sessile taxa and so far, there are no studies on insects using such methods to our knowledge. Other methods involve integrating physiological traits into correlative models include spatial Bayesian process-based derived dynamic range models (DRMs) and physiological niche models (Brewer *et al.* 2016). These approaches explicitly model population dynamics together with range dispersal to predict abundance and range dynamics (Pagel & Schurr 2012). These more process-based Bayesian models perform better than simpler models without taking up too much computational power (Feng *et al.* 2020; Mammola *et al.* 2021). Unfortunately, models that account for meta-population level responses and dispersal ability were not common in the literature. Using such models on larger spatial scales and for more species is an exciting avenue for future research regarding species range changes.

A key example of spatial Bayesian species distribution models is the extremely popular semi-mechanistic modelling tool 'CLIMEX' (Kriticos *et al.* 2015), used in 13% of insect studies we reviewed. CLIMEX quantifies the habitat suitability of a specific species in different locations by creating an 'ecoclimatic index' (EI) (Kriticos *et al.* 2015). Unlike DRM models, input data includes lab-derived measured variables, such as the range of optimal and upper limits of both temperature and moisture, as well as responses to heat, cold, and water stress. It can also include phenological factors, which allow the incorporation of periodic seasonal events. We found that the use of CLIMEX models was relatively common in the reviewed literature, comprising all the categorised 'hybrid' models (Fig. 4).

Overall, hybrid models have the potential to improve model accuracy, but they require more input data and biological knowledge than correlative models (Zurell *et al.* 2016).

4. 3. Mechanistic Models

Mechanistic models, also known as process-based, or process-explicit models, estimate species fitness in different environments, therefore providing an estimation of the species' fundamental (rather than realised) niche. Mechanistic models may use data on biological interactions, functional or life-history traits, and the relationship between species and their environment (Kearney & Porter 2009). They are less common in the literature, making up 16% of studies predicting insect distributions with climate change, but their usage has been consistent since 2014 (Fig. 4). Over the last decades the increases in computational methods and capabilities have greatly increased the speed of calculations, allowing the deployment of increasingly complex models (Evans *et al.* 2015; Maino *et al.* 2016).

Eco-physiological traits are often incorporated into mechanistic models (Aragón *et al.* 2010; Régnière *et al.* 2012). For example, physiologically-based demographic models (PBDM) have been used to predict future insect distributions (Gilioli *et al.* 2014; Gutierrez *et al.* 2018; Gutierrez & Ponti 2014). Mechanistic models can vary in complexity. Generally, models based solely on eco-physiology are prone to over-predicting potential species distributions as they do not consider biotic and dispersal constraints (Soberon & Peterson 2005). Additionally, limits based on laboratory conditions may not accurately represent the limits of a species due either to condition-dependent plasticity in responses, the wrong abiotic factors assessed, or lack of standardisation in the ways in which climate limits are measured (Leong *et al.* 2022; Roeder *et al.* 2021).

Despite these difficulties, mechanistic models are a promising development, especially for insects. Many insects undergo multiple life stages, and each stage can have very different thermal sensitivities, inhabit different climate conditions, and employ different mechanisms to cope with novel climate conditions (Kingsolver *et al.* 2011). For instance, the brood and larval stages of insects are known to have different climate sensitivities compared to adult stages (Kingsolver & Buckley 2020). To account for this, degree-day models, or phenological models, base predictions on the temperatures required for development as determined by physiological experiments. Degree-day models have been shown to outperform SDMs and other more complex mechanistic models in some cases (Buckley *et al.* 2011; Buffo *et al.* 2007). Degree-day models can also include dynamic energy budget (DEB) models, which describe the rate at which an organism metabolises energy for maintenance, growth, and reproduction in relation to its physiological tolerances and its environment (Llandres *et al.* 2015; Maino *et al.* 2016). However, DEB models have not yet been used to predict future range changes in the context of climate change impacts on insects, making them a potentially valuable area of future research.

Mechanistic models are rare among studies on future insect distributions. Additionally, a very small number assess multiple species at once, as they require a large amount of data and have only been used in 4 multi-species studies found in our literature search (Aparício *et al.* 2018; Estay *et al.* 2009; Morimoto *et al.* 1998; Ziter *et al.* 2012). It is necessary to collect more data for a wider number of species to do cross-species comparisons. It is however important to note that there is a trade-off between complexity and generality, and that more complex models require extensive data. Therefore, a more complex model may not necessarily be better, as correlational models can be just as effective as mechanistic models for certain species (Fordham *et al.* 2018; Kearney *et al.* 2010). Thus, careful consideration needs to be made when applying different models, considering both the available datasets and the performance of each model for their subject species.

5. The impact of input climate data for modelling

There are several climate data inputs that can significantly affect future range prediction outcomes. One is that predicting species distributions under climate change requires scenarios of expected environmental changes (Beaumont *et al.* 2008). To predict future climates, greenhouse gas emission scenarios are combined with global circulation models (GCMs). GCMs can be limited by computer memory and time limitations, and the input physical processes and climate data. Emission scenarios depend on predictions of human population size, technological advancements, and socio-economics variables. The choice of emission scenarios and global circulation models is difficult and fairly subjective, and so can lead to widely differing projections (Berzitis *et al.* 2014). For example, predictions for the future distribution of the bean leaf beetle (*Cerotoma trifurcata*) varied from an increase of 45% to a decrease of 82% of its range based on different combinations of three global circulation models (GCMs) and two carbon emission scenarios (Berzitis *et al.* 2014). To deal with these sources of variation, we argue that it is necessary to compare predictions based on multiple combinations of GCMs and emission scenarios.

Emission scenarios typically fall into three categories: business-as-usual, accelerated growth and mitigation strategies. When dealing with of s of future climates, there is no ‘right answer’ as to which data source or prediction to use - all are in theory possible, but can be widely different based on the ways in which they are produced - making it vital to consider a variety of emission scenarios and GCMs to encompass the full variation of future possibilities.

The most used GCMs included those from the Hadley centre (e.g. HADGCM, HADCM) used in 39 studies, and the Community Climate System Model (e.g. CCSM4) used in 26. For some studies, it was impossible to extract the number of GCMs used as they were not reported in the study (22%, Fig. 5A), highlighting a worrying lack of reproducibility. Among those that did report the GCMs used, studies on average used three GCMs (range = 1-34) to create a high-likelihood scenario (Fig. 5A). However, 55.6% (94) of studies used only one GCM (Fig. 5A), with only 22 studies using more than five GCMs. Furthermore, 36 studies used just one GCM and one emission scenario – even though individual GCMs or emission scenarios can greatly impact results. Therefore, results based on just one GCM or emission scenario should be treated cautiously as they do not consider a range of future possibilities (Baker *et al.* 2017). We also stress that there needs to be more transparency as to the exact GCM and emission scenarios used in each study to understand and interpret results. In addition, we advocate for using multiple GCM and emissions scenarios and to do a sensitivity analysis to estimate the robustness of the study's conclusions. To do this, a new R package 'GCM compareR' has been developed to allow comparing outputs based on different GCMs and climate change scenarios in a way that can be fully reproducible (Fajardo *et al.* 2020).

Variations due to different GCM projections are amplified as they are projected further into the future, which is problematic as many studies aim to predict insect distributions at least 20 years into the future, with the majority focusing on 2050 (33%) and some even predicting until 2100 (Fig. 5B). The choice of which time horizon to use can also significantly influence results, with different conclusions based on the years chosen and even completely reverse the sign of the prediction (loss or gain of potential habitat) (Bertelsmeier *et al.* 2013).

To accurately predict the potential future distribution of a species under climate change, high-resolution climate data is essential - which is lacking for current predictive modelling. Climate resolution in the studies reviewed here ranges between 0.01-340 km (mean = 49.3, median = 5) (Fig. 6). However, these resolutions do not represent microclimates experienced by small species such as insects, which can significantly influence a species' response to climate change (Potter *et al.* 2013). The resolution of the climate data should be carefully chosen based on the size, behaviour, and dispersal ability of the species in question, as microclimatic conditions can vary greatly even within a small area (Pincebourde & Casas 2019; Potter *et al.* 2013). This may mean resolutions varying between regional levels of around 1 km down to the millimetre within a single leaf (Pincebourde & Casas 2019), which can vary by up to 10°C within a single day (Bernard *et al.* 2022).

However, it is not enough to simply use ever more precise maps of climatic conditions. One also needs to understand how organisms interact with heterogeneous microclimatic conditions. For example, behavioural selection of optimal microclimates may buffer species against unfavourable macroclimatic conditions. In this way species may appear to survive outside of their physiological or preferential limits. Such behavioural buffering has already been used to predict future distributions of desert mammals (Riddell *et al.* 2021), but not in insects so far. While the impact of microclimates on insects is beginning to be explored (Bladon *et al.* 2020; Duffy *et al.* 2015), more research is needed to understand how insects may utilize microclimatic variations to respond to climate change (Woods *et al.* 2015). In the future, incorporating microclimates and behavioural data could improve SDMs and provide a more complete understanding of the impact of climate change on a variety of species.

Another important issue is the type of environmental variables used as model input. Different insects may be more limited by different factors such as winter or summer temperatures, or extreme weather events (McDermott Long *et al.* 2017; Román-Palacios & Wiens 2020). While temperature and precipitation are commonly used in models, other abiotic factors such as soil or water chemical characteristics (Beaumelle *et al.* 2021), land use data, or water quality and availability (Chown *et al.* 2011) may also be important in predicting the distribution of insects. Currently, most models, especially the mechanistic ones, have focused on terrestrial species (Maino *et al.* 2016) but aquatic and terrestrial species may have differential responses to climate change (Jourdan *et al.* 2019; Shah *et al.* 2020). Modelling distributions of aquatic insects will require different variables relating to water quality and chemistry. Moreover, in addition to climate change, other global change drivers will impact insect species distributions during the Anthropocene, such as changes in human activities, population density, trade, or travel.

6. ***Conclusion***

Our meta-analysis has revealed a worrying decline in range size for species belonging to most insect orders. However, the majority of invasive/vector species were predicted to increase in range size. Differences among species are probably partially due to different physiologies, life histories and geographic distributions. However, it is unknown to what extent these differences among species are due to the specific set of methodologies and data used to model the species' distribution, given that individual studies vary greatly in regard to the methodologies and data used to make predictions, calling for comparative studies in the future. The literature is also limited in taxonomic and geographical scope (Halsch *et al.* 2021) and it is unclear to what extent the studied species are representative of all insect biodiversity.

To improve predictive models, the integration of correlative methods with mechanistic models that use functional traits has recently been advocated, to begin bridging macroecology and functional ecology (Benito Garzón *et al.* 2019; Mammola *et al.* 2021). Additionally, more experimental data is needed as input for hybrid and mechanistic models. In particular, there is a clear need for more information on the physiological and behavioural responses of insects to different climates, such as behavioural data related to microclimates. It is also crucial to better understand the physiological limits of different insect species at different life stages, and how species ranges are limited by biotic interactions or geographic constraints for a larger number of insect species. Furthermore, it appears that choice of climatic data used to make future projections has a large impact on results, and thus the continuation of studies which employ multiple scenarios and models, at relevant resolutions and scales, to get a full range of predictions is vital. Overall, this will help understanding species responses to novel climates, and predicting niche shifts and range size changes.

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Supplementary Data

Table S1: Excel file describing all of the studies used in this review

Table S2: Excel file all of the individual results for each species within each study used in this review

Figures

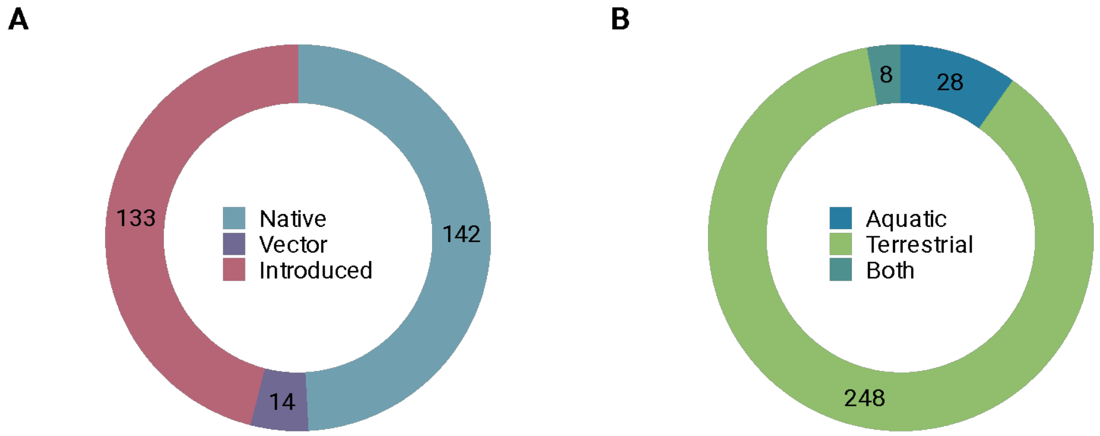

Fig. 1: Studies which predicted the future distribution of insect species. *A) Studies split by whether native, introduced or vector species were the focus of the studies. B) Studies split into whether the species studied were terrestrial, aquatic or a mix of both. Categories were defined based on author definitions between studies, or through literature searches.*

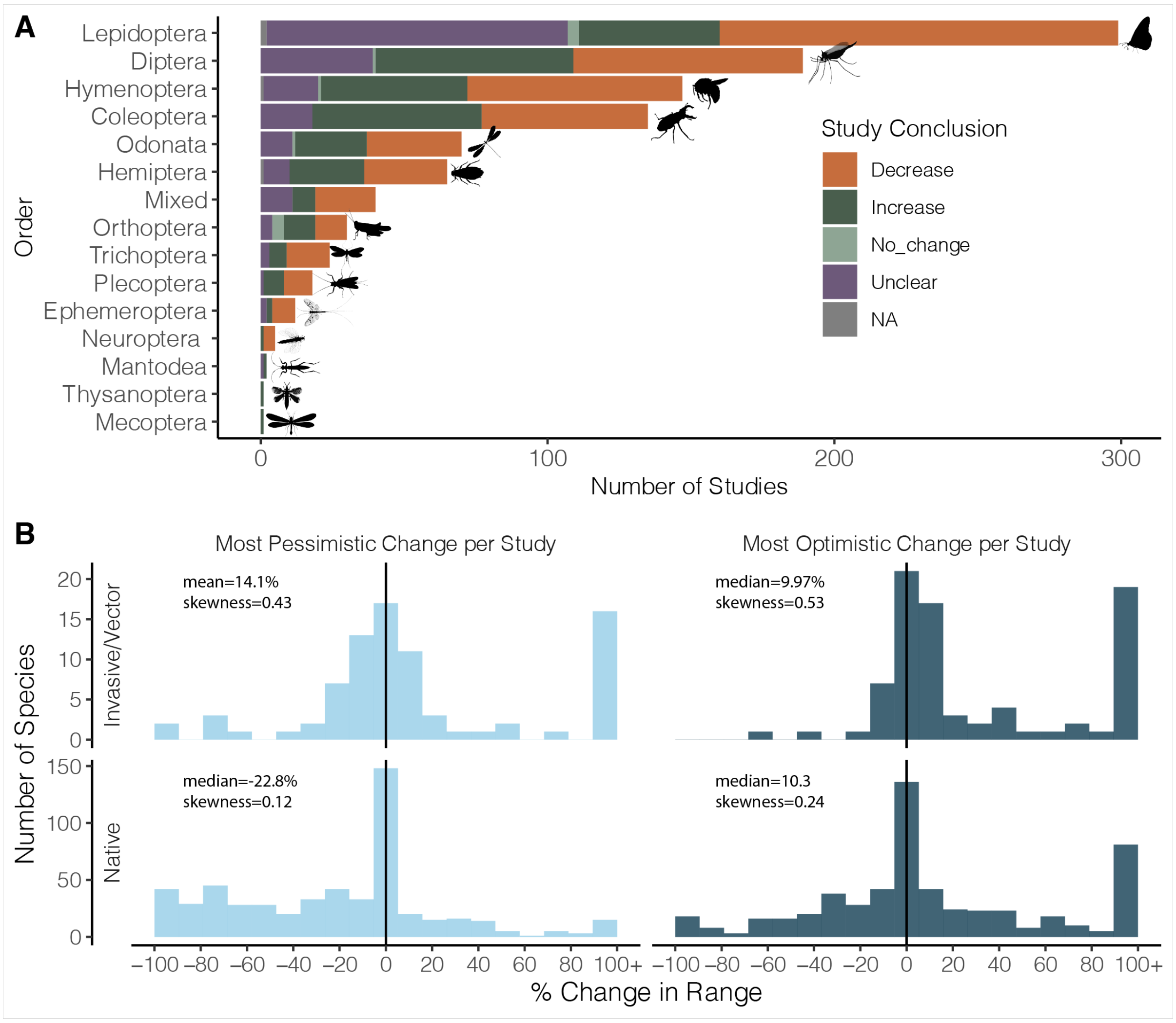

***Fig. 2: Predicted range dynamics per insect species studied.** A) Predicted range changes per order. The unclear group depicts species where due to variations in methodologies, datasets or predicted year used within studies, both increases or decreases were predicted. B) For 112 studies, quantitative estimates of changes in range size were available. Here, we present the distribution of percentage range changes. Presented is the ‘most pessimistic change per study’, which represents the most severe predicted range decline for a specific species within a study, and the ‘most optimistic change per study’, representing the least severe range decline for a species within a study. This allows a representation of full range of potential change that is predicted for each species within each study. Predictions of range increases above 100% of the current range were grouped together for visual representation.*

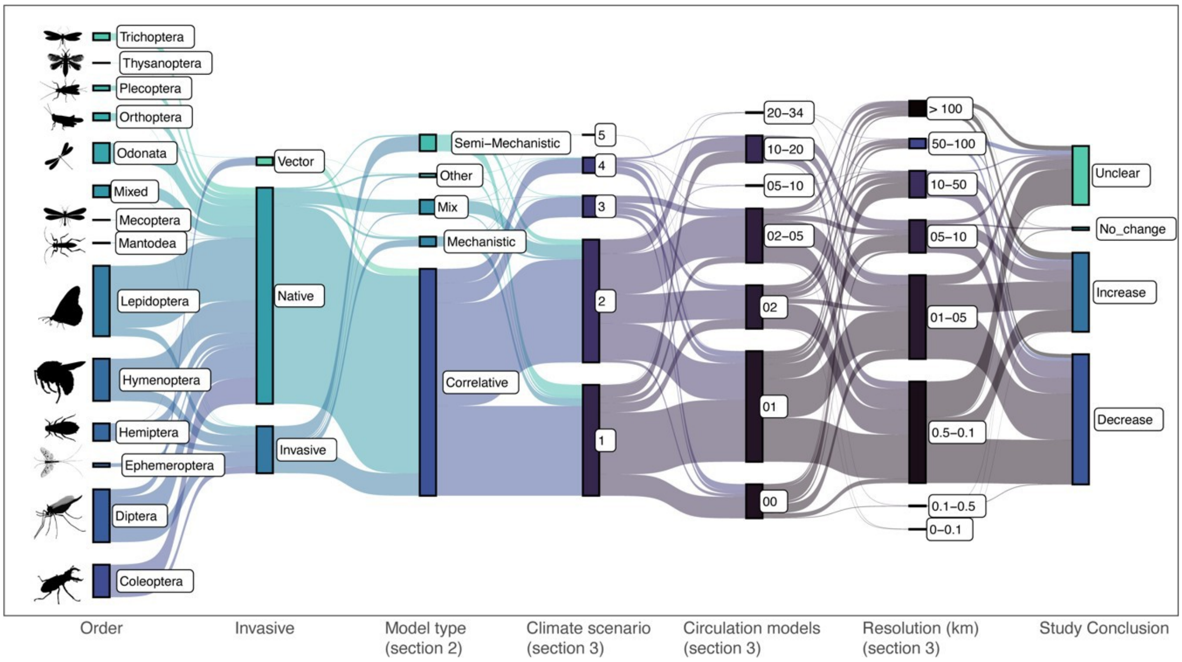

Fig. 3: A simplified diagram showing the different steps involved in the modelling process. This illustrates the multiplicity of factors including methodological and taxonomic differences influencing the overall conclusion of a given study. *All nodes displayed can influence whether ranges predicted by a species under future climate scenarios is expected to increase, decrease or remain unchanged. Only studies where information was present for all 7 steps were included. The first node represents species orders, the second whether the species is invasive, vector or native species. Next, the broad model type (simplified into just four main categories) is displayed (discussed further in section 2). The fourth, fifth and sixth nodes represent - the number of climate scenarios used, then the number of circulation models used grouped into categories for simplification, then the resolution of the climate data used in kilometres – all of which are discussed further in section 3. The last node represents the overall study conclusion for each species within the studies.*

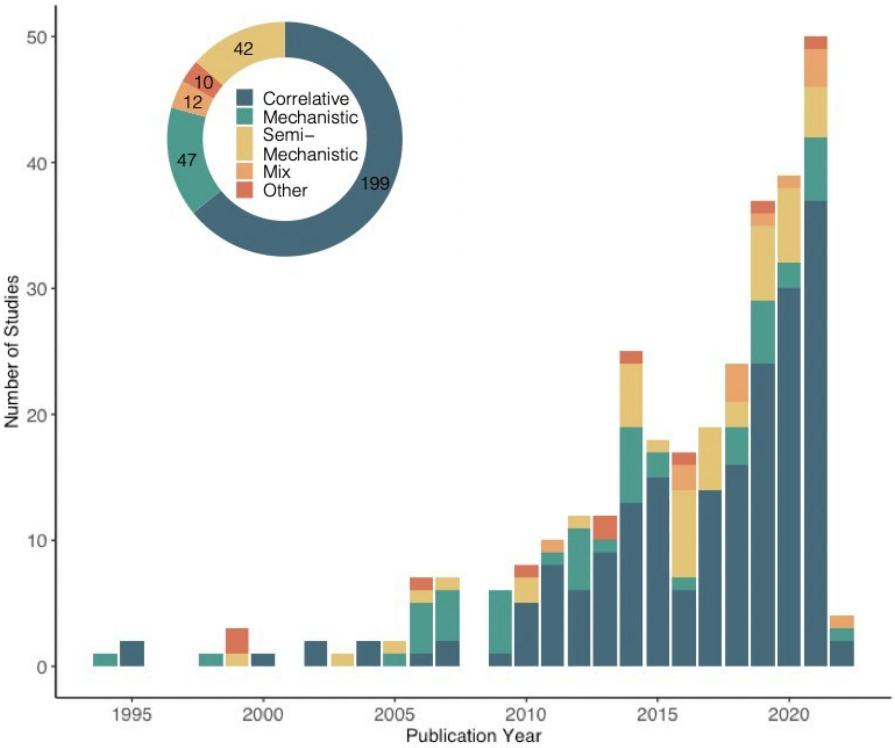

Fig. 4: Proportion of broad model types used for predicting the future distribution of insects from a search conducted in early 2022. Representation includes a doughnut plot representing the overall proportion for all studies and a time series bar chart representing the change in publication proportions over time.

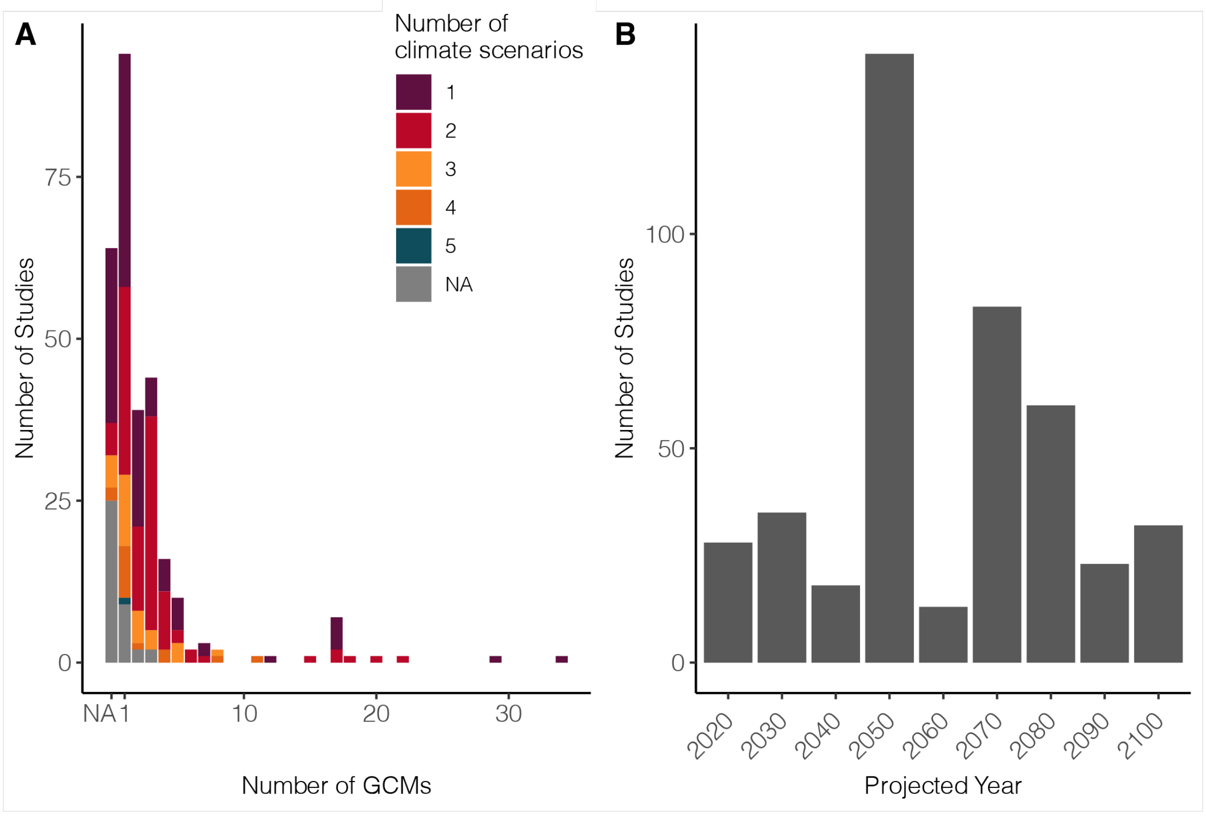

Fig. 5: The number of studies which predicted the future distribution of insect species with climate change. *A) Study counts split by the and which number of general circulation models (GCMs) were used. Bar charts are coloured by the number of emission (climate) scenarios used in each study. NA's represent when the specific GCM or climate scenario is not reported. B) The years projected into the future for each study. For some studies multiple years were projected, resulting in them appearing multiple times in this graph*

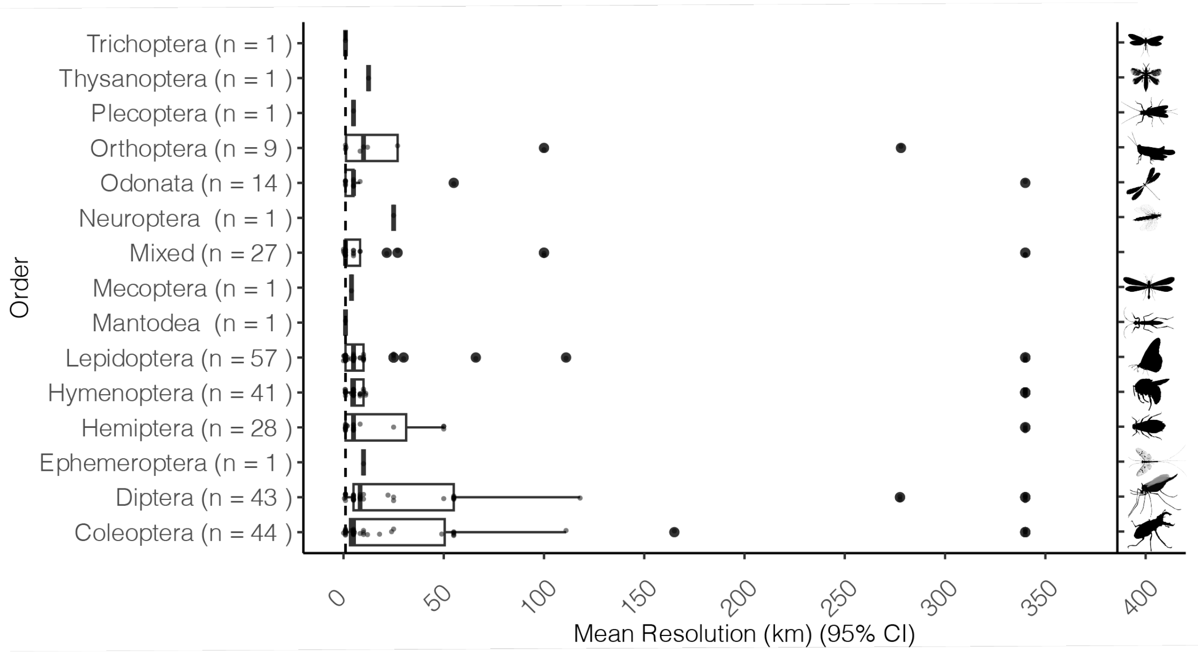

Fig. 6: Climate Resolution of studies that predicted the future distributions of insect species under climate change*. Resolution of climate data in each study for each taxonomic order studied. Boxplot* elements show; center line, median; box limits, upper and lower quartiles; whiskers, 1.5× interquartile range.

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Summary of results

Chapter 1

A critical review was conducted of the current state of research on niche shifts in introduced species. Despite a general observation that there is a higher prevalence of niche shifts compared to niche conservatism for introduced species (**Chapter 1**, Figure 2), we highlighted the subjective nature of the conclusions drawn from studies on niche shifts, variations in methodologies, and inherent biases among studies. Moreover, many studies focused on just a single species or a single taxonomic group, further complicating our overall understanding of the frequencies of niche shifts among introduced species. We discussed the substantial disparities between studies and methodological challenges within the field including subjective interpretations of niche-shift metrics, the exclusion of non-analogous climates by some studies, and the reliance on macroclimatic data, which may lack relevance for many small-sized species. We concluded that, despite significant strides in methodological advancements and increased data availability, the likelihood and frequency of niche shifts across species remain unclear.

Chapter 2

We investigated niche shifts among invasive species, employing ants as a model organism, which demonstrated that invasive species were less likely than non-invasive introduced species to expand into novel environmental conditions. This held true for both an impacts-led definition and a global dispersion-based definition of invasiveness. Additionally, results indicated that larger expansions into novel climates were associated with smaller dispersion and niche size in the native range. This suggested that the ability to shift one's niche may not necessarily result from superior competitive ability but could involve the filling of vacant niches, as evidenced by our observation that species with smaller native niches exhibited the most pronounced niche shifts, suggesting a more constrained realized niche in their native range.

Chapter 3

To comprehensively understand how species respond and adapt to changing environmental conditions, recent research has highlighted the significance of incorporating microclimatic data into species distribution analysis. However, using microclimates to assess niche shifts has not previously been performed. We assessed if the extent of niche shift among species was consistent between macroclimate and the best global-level proxy obtainable for microclimate data (SoilTemps). While the widely used D overlap metric might imply a limited impact of microclimates on global-scale niche shifts for ants, with a high amount of inter-species correlation between the macro- and microclimatic datasets, all metrics used had higher niche conservatism when the soil-level microclimate dataset was used. Furthermore, the soil-level dataset holds greater biological relevance for species predominantly situated at the soil level. Overall, this highlights the potential of using this dataset to make predictions and to explain species distributions.

Chapter 4

While numerous studies have investigated changes in range size and insect decline, often within specific species or limited geographic regions, there is a lack of comprehensive synthesis of these results for insect species as a whole; this Chapter contributes the first meta-analysis in this respect. Results highlight the complexity of the issue, with a mix of winners (expected range increase) and losers (expected range decrease) observed among insect species. Indeed, the uncertainties surrounding the predicted responses of insect populations arise due to methodological and data differences. Discussed are key methodological differences in modelling that could influence the outcomes of these studies. We examine correlational, hybrid and semi-mechanistic, and mechanistic models, and critically assess the role of climatic data in predicting species distributions. Emphasis is placed on the importance of clearly reporting global circulation and emissions scenarios used to make predictions concerning range sizes. By providing a comprehensive synthesis of current knowledge of how climate change impacts insect distributions, and the methodological drawbacks and considerations of such studies, our paper serves as a valuable resource for researchers seeking to address this critical issue.

General Discussion

The main objective of this thesis was to understand and investigate the capacity of species to respond to novel climates. Asking this question using introduced species, or considering all species on Earth that will be impacted by climate change, constitutes a monumental task. To begin to address this, I have posed specific questions, as outlined in this thesis, however, there are many directions that this research could have taken, some of which are discussed below.

The taxonomic scope of niche shifts in introduced species

Chapter 1 highlighted both a limited taxonomic scope and a lack of multi-species studies that would enable us to discern the frequencies of niche shifts between different species and taxa. Efforts to bridge this knowledge gap have predominantly focused on reanalysing limited segments of the literature, such as studies that have only assessed niche shifts using species distribution modelling (Liu et al., 2022). However, the field requires large-scale studies employing standardised methodologies to compare species and taxa under a common framework, enabling inter-species differences to be systematically assessed. Such studies on specific taxonomic groups have aimed to identify trends or signals for niche shifts in general (Hill et al., 2017; Strubbe et al., 2013; M. W. Tingley et al., 2009), including our own (**Chapters 2** and **3**); however, comparing estimations of the extent and frequencies of niche shifts across taxonomic groups will also be required. Remarkably, a large multi-taxon assessment has not yet been undertaken. Therefore, a future direction in the field could involve conducting such an analysis, employing multiple standardised methods. This would help build confidence in our attribution of differences between species and taxa to biological drivers rather than methodological discrepancies. Increased understanding here is important, as indications of greater niche conservatism in some species or taxa can indicate more vulnerability to climate change, while a higher frequency of niche shifts can indicate taxa that may spread or establish further than expected by just their historical niche. Knowledge concerning niche shifts for invasive species is essential for predictions and prevention of spread, and for eradication of species deemed problematic (Jiménez-Valverde et al., 2011; Kramer et al., 2017).

Ants as a model system

This thesis mainly used ant species as a model system, which offers a rich source of potential inquiries within the realm of invasion biology. Ants, like other insect groups, have ecological ubiquity, diverse ecological roles, and notable adaptability, and therefore serve as invaluable subjects for investigating climatic niche shifts. Furthermore, ant colonies' social structure and foraging behaviour make them sensitive indicators of environmental change (Tiede et al., 2017), allowing researchers to observe how these insects respond to novel climates (Andrew et al., 2013; Bujan et al., 2020; Parr & Bishop, 2022). Ants' ability to thrive across a wide range of ecosystems, from tropical rainforests to arid deserts, provides a diverse set of conditions for studying climatic niche shifts. Additionally, as ants remain within the most invasive groups worldwide, the advent of invasive ant species in various parts of the world makes them particularly relevant for examining how these organisms adapt to and exploit new environments (Bertelsmeier et al., 2017). Indeed, many pioneering studies have utilised ants as a model system to unravel the complexities of invasion biology, shedding light on the mechanisms underlying introduction processes (Bertelsmeier et al., 2017; Gippet & Bertelsmeier, 2021; Ollier & Bertelsmeier, 2022; Suarez et al., 2005, 2009; Wong et al., 2023) and offering insights applicable to broader ecological and conservation contexts (Hoffmann et al., 2009; Huang et al., 2020; Siddiqui et al., 2021; Tillberg et al., 2007). Moreover, the fact that ant species make colonies, which are often less mobile, but have highly mobile foragers on a local level, adds to making them a very interesting study system (Parr & Bishop, 2022). Lastly, ants are hugely abundant, both in terms of species and biomass (Schultheiss et al., 2022), on every continent except Antarctica. Indeed, they are essential for ecological networks and processes, for example playing key roles in soil turnover (Whitford & Eldridge, 2013), decomposition (Eubanks et al., 2019) and as a food source (Redford & Dorea, 1984), underscoring their significance in ecological research and the study of climatic niche shifts.

The extent of niche shifts within insect populations is still largely unknown. Ants often exhibit complex social structures and cooperative behaviours, which can complicate the isolation of individual responses to climate shifts, with individual occurrence points representing colonies, or groups of colonies, rather than individuals or populations of individuals. The reliance on ant species as a model system only may overlook the unique adaptations of other taxa, potentially leading to an incomplete understanding of broader questions as to how introduced species respond to novel climates. For example, flying insects have very different dynamics. Flying insects typically have larger foraging areas, and interaction with climatic variables (Robinet et al., 2019) - with air temperatures having much more relevance for such species (Kenna et al., 2021). Furthermore, as ant species create colony structures which may be able to help buffer species from climatic changes, for example, through nest architecture (Sankovitz & Purcell, 2021), they are particularly able to change their climate, which may influence niche shift observations. Thus, comparing niche shifts to other colony nesting and solitary insects, or those that live within plant or other material, may be extremely complex as niche shift patterns may differ to to varying degrees of microclimatic buffering. Hence future steps in the field could be to compare the responses of ants to novel climates to that of other insect species, and then to include ants in multi-taxon cross-order assessments.

Directions and further questions for niche shift studies in ants

In Chapter 2, we suggested that the ability to shift one's niche may result from the filling of vacant niches (Dlugosch & Parker, 2008), evidenced by our observation that species with smaller native niches exhibited the most pronounced niche shifts, suggesting a more constrained realised niche in their native range. Furthermore, our results of smaller niche shifts in invasive species compared to non-invasive introduced species have since been corroborated by other studies of taxonomic groups, such as beetles (Montgomery et al., 2022), further contributing to the evidence that ecological limits on native niche breadth could be linked to constraints in the realised native niche. Particularly important, is the ability to predict the future ranges of the most dangerous species, due to their damaging nature to ecosystems and humans (Barbet-Massin et al., 2018; Jiménez-Valverde et al., 2011). Our study asserts that our predictive capabilities remain robust when utilising the native range of widely spread invasive species for forecasting. The implications of our findings extend to various facets of invasive species management, risk assessment, and predictions linked to climate change. This underscores the pivotal role of considering niche shifts in the development of effective conservation strategies.

Niche shifts in introduced species can be used to test further questions, which may explain why some species shift their niche more than others, for example, other studies have correlated the prevalence of niche shifts with human disturbance (Hill et al., 2017) or influenced by the time of invasion history (Strubbe et al., 2013, 2015; Strubbe & Matthysen, 2014). Expanding the knowledge of introduced ant species would help to discern and explain trends and patterns between ant species. For instance, it is currently unclear how invasive niches are affected by how long the species has been introduced. Previous studies have linked the time from the first introduction to current niche shifts, yet there is disagreement on the direction of this impact. Some studies suggest that niche shifts are less likely (Strubbe et al., 2013, 2015; Strubbe & Matthysen, 2014), while others propose that they are more likely (Li et al., 2014), for species that have earlier introductions. Meanwhile, some studies find no significant impact of time since introduction (Early & Sax, 2014). Time series information could help answer crucial questions, such as whether species immediately establish in novel climates or initially thrive in similar climates to their native niche before expanding. For example, it has been shown that the highly invasive fire ant (Solenopsis invicta) and Drosophila species have a pattern where they first invade climates similar to their native range and subsequently expand into novel climates (Fitzpatrick et al., 2007; Fraimout & Monnet, 2018). However, it is unclear whether such trends are seen on a broad multi-taxon scale. Utilising occurrence records, often dated at the time of collection, and employing analyses as demonstrated throughout this thesis, could facilitate further exploration of questions related to the time scale of niche shifts into novel climates.

The promise of microclimatic studies

Currently, research using microclimatic conditions to predict or explain species distributions is limited by the unavailability of high-resolution global climate maps with a resolution finer than 1 km, attributable to the complexity of, and high computational demands inherent in, generating such maps (Hannah et al., 2014; Potter et al., 2013). For example, a combination of *in situ* measurements and range modelling has shown that microclimatic data better predicts the distributions of potato moth species in the Andes (Rebaudo et al., 2016). An increasing number of studies have benefited from the inclusion of microclimatic data in their species distribution modelling analysis (for review see Lembrechts et al., 2019). However, studies such as these require climatic data to be recorded with loggers *in situ* and are limited in geographical scope, which is problematic when applying to globally distributed introduced species.

The implementation of large, fine-scaled maps has the potential to enhance predictions of the climates in which small organisms, such as ants, thrive. Notably, spatial heterogeneity in temperature, derived from local measurements, has been demonstrated to be nearly twice as extensive as that computed from globally interpolated temperatures (Lenoir et al., 2013). In recent years, several easily accessible microclimate modelling packages have emerged in R to forecast fine-scale climates (Kearney & Porter, 2017; Maclean et al., 2019). While these models show great promise, they necessitate a multitude of background variables, including coastal tidal variations, air pressure, and digital elevation models (Maclean et al., 2019), making them computationally intensive to produce on large geographical scales. Nevertheless, we expect global-scaled datasets through the application of such methodologies to become available in the near future. Thus, future studies could assess if increases in horizontal resolution impact the frequencies of niche shifts between native and introduced ranges.

Although the presence of global microclimate maps will allow a better view of landscape heterogeneity, this alone will not explain fine-scale microclimatic processes, such as the influence of behaviour. This is particularly important for small-scaled organisms such as ants, where empirical studies have demonstrated the utilisation of microclimatic refugia. For instance, two woodland floor foraging ant species (dominant meat ant (*Iridomyrmex purpureus*) and the large bull ant (*Myrmecia brevinoda))*, have been observed through temperature comparisons of their habitat vs their body temperature, to employ behavioural traits to regulate body temperature (Hemmings & Andrew, 2017). Additionally, research has indicated that ants of varying body sizes utilise distinct microclimates in tropical regions (Kaspari, 1993). This adds to the extreme example of desert ants, which may encounter extreme variations in summer surface temperatures (ranging from 25 to even above 50 degrees Celsius) with different ant species active at different temperatures (Kaspari, 1993; Schultheiss & Nooten, 2013). Behavioural selection of foraging activity may also play a role as shade patterns, created by human buildings, or experimentally enforced, have been shown to affect the foraging patterns of native and invasive ant species (J. M. W. Gippet et al., 2022; Wittman et al., 2010). It is therefore plausible to conclude that ant species can thermally buffer their nests and foraging activity at the soil level to avoid temperature extremes.

Unfortunately, the role of insects' behavioural thermoregulation in choosing more favourable microclimates to mitigate the impacts of temperature extremes is rare (Kearney et al., 2009). However, examples of this in insects offer a very promising approach and show that refugia can buffer against climatic changes. For example, it has been shown that the simple behaviour of butterflies of changing the angle of their wings can drastically cool their body temperature by varying degrees between different species (Bladon et al., 2020). These behavioural responses, however, can be highly species or taxa specific and there is a need to expand such work to assess how microclimatic processes, from behaviour to heterogeneity in the environment can help insect species to tolerate or enter novel climates. For example, leaf borer insects can use climate variations on leaf surfaces to escape unfavourable conditions (Pincebourde & Woods, 2012), thoracic vibrations of bumblebees can warm their body temperatures (Heinrich, 1993), and ants can shift their location and nest structure in response to climates (Sankovitz & Purcell, 2021). Unfortunately, thus far, the link between such behaviours and the distributions of species is not commonly linked. One example is to integrate behaviour into models in species distribution, which have been can represent a species use of microclimatic refugia (i.e. shade) from fluctuations and changes in climates (Bladon et al., 2020; Dowd et al., 2015; Riddell et al., 2021; Zellweger et al., 2020). This is a very promising future avenue and would be highly beneficial to the field if such information could be routinely incorporated to observe species responses and distribution in current and novel climates. For example, the R package 'nichemapR', provides a mechanistic modelling technique which applies heat, water, energy and mass exchange between any kind of ectothermic organism and its environment (M. R. Kearney & Porter, 2020). It can be used to predict core body temperature and evaporative water loss as a function of microclimatic conditions and behavioural thermoregulation, and thus explain and predict species distributions by integrating these factors ('Dynamic energy budget models', discussed in Chapter 4). However, thus far these models have only been used on larger ectotherms such as reptiles (Jiang et al., 2023; Mi et al., 2022). Applying these methodologies to answer questions, such as those addressed in this thesis, may determine the extent to which niche shifts influence insect populations when microclimatic behaviour is incorporated.

However, it is crucial to note that microclimates are not stable, the impacts of anthropogenic changes, such as land use change, may lead to less heterogenous environments exacerbating the risks of local extinction associated with climate change (Raven & Wagner, 2021). Furthermore, refugia may not always be sufficient to escape the effect of warming (Caillon et al., 2014; Ma et al., 2021), and we cannot rely on microclimatic availability alone to account for species experiences of novel conditions - thus making it important to discover in what cases, and to what extent, species use microclimates as refugia from macroclimatic changes.

Can mechanistic models solve problems caused by niche shifts?

Climatic niche shift studies usually focus on the presence of the shifts based on occurrence data (Broennimann et al., 2007; Li et al., 2014; Orsted & Orsted, 2019), while the underlying mechanisms behind niche shifts are rarely tested (Hill et al., 2013; Krehenwinkel et al., 2015; Kumar et al., 2015), and the causes of variation in frequencies and extent of niche shifts between species are not fully understood. One way in which we can begin to understand these processes is to use more modern approaches to niche and distribution analyses. Mechanistic modelling can allow researchers to predict distributions by inputting various factors into modelling processes- for example, differences in life stages, and dispersal abilities. As was discussed in **Chapter 4**, mechanistic models may use data on biological interactions, functional or life-history traits, and the relationship between species and their environment (Kearney et al., 2009). Currently, mechanistic models have largely been performed for species experiencing climate change. However, they can also be used to explain introduced species spread, see for example, Coulin et al., 2019 report on mechanistically integrated critical thermal limits to explain the distribution of the fire ant, *Wasmannia auropunctata*. At the global scale, the critical thermal minimum alone, with the bioclimatic variable minimum temperature of the coldest month, explained the southernmost limit of the species' native distribution and its physiological capacity to expand in the Mediterranean region. This prediction has since been proven true as the species has recently been found in Sicily (Menchetti et al., 2023). Thus, eco-physiological approaches may help explain the current distribution of species that have shifted their niche, and predict the potential spread of populations to novel conditions. It may therefore be promising to use such techniques to answer questions about how species respond to novel climates and see to what extent physiological limits can explain species niche shifts. Taking advantage of such techniques may allow us to further disentangle species introductions and species responses to novel climates.

Physiological experiments, such as critical thermal limits, on climatic tolerances can play a crucial role in complementing niche shift studies by offering insights into why certain species exhibit more pronounced niche shifts than others (Diamond et al., 2013). In collaboration with Bujan *at al.,* (refer to Appendix 1), we conducted experiments to test observed shifts in the thermal niche of an invasive ant species, *Tapinoma magnum*, and revealed a thermal niche shift within the invaded range of Tapinoma magnum; specifically, a shift towards colder climates was correlated with a heightened acclimation ability to colder temperatures within the introduced range of the species, potentially facilitating its expansion into northern territories in Europe (Bujan et al., 2021). If this pattern holds true across many species, and if many species possess a robust acclimation capacity enabling climatic niche shifts, predictions of future distributions based solely on occurrence data may lack the accuracy that mechanistic modelling may provide - as they use both occurrence points and physiological information to make their predictions (Cornelissen et al., 2019; Strubbe et al., 2023). Therefore, there is a pressing need for more studies that use mechanistic modelling to see if physiologically-derived niche estimates can help unravel the processes involved in species expansion into novel climates (Chapman et al., 2017). This interdisciplinary approach can provide a more comprehensive understanding of how physiological traits, such as thermal optima or critical thermal limits, contribute to observed niche shifts, contributing valuable insights for predictive modelling and conservation planning.

Predictions of species under climate change

Throughout the thesis, we have used invasive species as a model system for climate change. Introduced species can often exhibit rapid and observable responses to environmental changes, providing researchers with valuable insights into how organisms might react to shifting climates (Moran & Alexander, 2014). This can offer a practical and efficient way to study the impacts of climate change on ecosystems in real-time. Additionally, invasive species are frequently well-documented, making it easier to gather comprehensive data on their distribution. However, there are notable drawbacks to relying on invasive species for climate change research. Species which have not been established in new geographical areas due to human-mediated dispersal may be due to their inability to establish under novel conditions. Therefore, the focus on invasive species might overlook the unique traits and sensitivities of local biodiversity. Findings derived from invasive species may not be easily extrapolated to other regions or ecosystems, leading to misleading conclusions about broader ecological responses to climate change.

Furthermore, the interaction of introduced species and climate must also be considered. Many invasive species are themselves ecosystem engineers, which adds to their damaging impacts. These species may be able to alter environmental, and potentially climate conditions, to suit their needs. For example, invasive ants themselves are agents of environmental change (Lester & Gruber, 2016), and can significantly impact soil structure, nutrient cycling, and even microclimate through their foraging and nesting behaviours. These alterations in environmental and climate conditions can create a feedback loop, further influencing the success of the invasive species and potentially exacerbating the challenges faced by native organisms.

Importance of climate in predictions of introduced species

Using the climatic niche of a species to make predictions about future distributions is challenging for species that have undergone a niche shift (such as non-invasive introduced species). However, for invasive species that have established broad introduced ranges, the recommendation is to incorporate native and introduced niches to anticipate and prevent future spread (Gallien et al., 2012; Petitpierre et al., 2016). In Appendix 2, we employed ensemble species distribution modelling to predict the spread of the highly invasive giant land snail (*Lissachatina fulica*). This study, conducted by Gippet et al., 2023, assesses disease transmission risk and the overall threat posed by this species, considering both pathogenic risk and its quantified involvement in the pet trade. Our application of ensemble species distribution modelling reveals that, despite its potential risks, the giant land snail is currently hindered from establishing in temperate regions due to climatic factors. Additionally, we identify regions where the species has not been introduced yet and has the potential to do so based on climate similarity. This approach provides valuable insights into the current limitations and potential future spread of the giant land snail, taking into account both climate conditions and various factors contributing to its invasive potential.

In this thesis, the primary focus has been on examining the capacity of species to thrive in new climates, aiming to enhance predictions related to the spread of invasive species. Nevertheless, the process of an introduced species becoming established involves several stages (Blackburn et al., 2011). Firstly, there is the initial dispersal event, during which individuals become associated with a transport vector, or are intentionally captured for transportation. Subsequently, transport occurs, wherein species are relocated beyond their native range via various vectors (e.g. cars, trains, boats, or aeroplanes). Upon reaching their destination, surviving individuals are introduced to a new area, either by detaching from the commodities or transport vectors they were initially associated with, escaping captivity, or being deliberately released. Those who encounter suitable conditions in the introduced range may then establish a self-sustaining population (Blackburn et al., 2011; Gippet et al., 2019). Climate may have an impact in all of these stages, however, the biggest barrier will be establishment in new regions, as the species will need to be able to survive the bioclimatic conditions within their new range, be able to acquire critical resources under the conditions and survive long enough to reproduce and establish a population (Hellmann et al., 2008).

Predictions regarding the movement of invasive species extend beyond climatic considerations, with several studies employing trade and travel as explanatory factors for species invasions (Bertelsmeier et al., 2017; Bonnamour et al., 2021; Fenn-Moltu, Ollier, Caton, et al., 2023; J. M. W. Gippet & Bertelsmeier, 2021). Indeed Fenn-Moltu *et al.* used biosecurity interception data from country borders to investigate introduced species 'flows' (i.e. movement of introduced species via transportation networks) and concluded that trade intensity and biogeographic origin significantly influenced the flow of introduced species (Fenn-Moltu et al., 2023, Appendix 3). The influence on climate however had no impact on the transport stage of the invasion process, which is unsurprising as the species are often inside of transport vectors, where climate may even be controlled.

However, despite the prevalence of niche shifts in introduced species, the establishment of species has still been shown to be impacted by the climatic distance between native and introduced ranges (Tingley et al., 2018). Using a broad, conservative measure of climatic distance between geographic regions (**See Appendix 4**), Mwebaze *et al.,* found that climatic similarity combined with cumulative imports during the 20 years before a species discovery is an important predictor of species establishment (Mwebaze et al., 2023). This study shows that trade and climate can interact with each other to explain species invasion establishment. This confirms previous studies which have shown the impact of environmental similarity on establishment success, for example, in fruit flies (Trombik et al., 2023), reptiles and amphibians (Bomford et al., 2009; Capinha et al., 2017, p. 201), and mammals (Broennimann et al., 2021). Similarly, for insects, analogous climates have been used to identify potential sources of non-native species (Peacock & Worner, 2006; Worner & Gevrey, 2006).

One further step that could be made is to investigate how predictions of future invasion pathways and distributions are explicitly linked to niche shifts - for example, for species that shift their niches more than others, other correlative factors may be more important (for example, in the form of trade intensity or trade flow patterns) in explaining species' geographic spread to new regions. Combining the work focussed on the impacts of trade and travel on species invasions with that of species' ability to enter novel climates, may mean we can make predictions when one or both of these factors are important in explaining species introductions, and thus offers a powerful solution to explaining species introductions worldwide.

Conclusion

This thesis has delved into the complex realm of species responses to novel climates, with a primary focus on niche shifts among introduced species. Firstly, I examined the extent to which species can alter their niches, especially in the context of invasive species (Chapter 1). Despite the prevalent observation of niche shifts in introduced species, the nuanced nature of these shifts, variations in methodologies, and the inherent biases among studies all contribute to the uncertainty surrounding the frequency and likelihood of niche shifts across species. The research further narrowed its focus to niche shifts among invasive ant species (Chapter 2), revealing surprising trends. Contrary to the common assumption that invasive species are highly adaptable and exhibit broad niche shifts, results described in Chapter 2 indicate that invasive species were less likely than non-invasive introduced species to expand into novel environmental conditions. An important highlight of this thesis is the recognition of the significance of microclimates in understanding niche shifts. While macroclimatic data provide valuable insights, the inclusion of microclimatic data for niche shift analyses, particularly at the soil level, offers a more conservative estimate and greater biological relevance for species predominantly situated at ground level (Chapter 3). Finally, we also reviewed the ongoing debates in the scientific community on how climate change is predicted to affect insect species distributions, observing that invasive species show greater increases than native ones. We highlight methodological differences in modelling and emphasise the need for clear reporting (Chapter 4).

Future directions in the field of niche shift studies are proposed, including the exploration of correlative factors such as human disturbance, time scales since introduction, and the integration of physiological experiments to understand the underlying mechanisms of niche shifts. The role of climatic similarity and trade intensity in species establishment is discussed, highlighting the need for a comprehensive approach that combines the transportation stage of introduction with the ability of species to adapt to novel climates. This interdisciplinary perspective is essential for developing effective conservation strategies, predictive modelling, and addressing the challenges posed by invasive species in the context of climate change. This thesis contributes valuable insights and sets the stage for further exploration and understanding of species dynamics in response to environmental changes

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Appendix 1

Increased acclimation ability accompanies a thermal niche shift of a recent invasion

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Increased acclimation ability accompanies a thermal niche shift of a recent invasion

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Abstract

1. Globalization is removing dispersal barriers for the establishment of invasive species and enabling their spread to novel climates. New thermal environments in the invaded range will be particularly challenging for ectotherms, as their metabolism directly depends on environmental temperature. However, we know little about the role climatic niche shifts play in the invasion process, and the underlining physiological mechanisms.
2. We tested if a thermal niche shift accompanies an invasion, and if native and introduced populations differ in their ability to acclimate thermal limits.
3. We used an alien ant species—*Tapinoma magnum*—which recently started to spread across Europe. Using occurrence data and accompanying climatic variables, we measured the amount of overlap between thermal niches in the native and invaded range. We then experimentally tested the acclimation ability in native and introduced populations by incubating *T. magnum* at 18, 25 and 30°C. We measured upper and lower critical thermal limits after 7 and 21 days.
4. We found that *T. magnum* occupies a distinct thermal niche in its introduced range, which is on average 3.5°C colder than its native range. Critical thermal minimum did not differ between populations from the two ranges when colonies were maintained at 25 or 30°C, but did differ after colony acclimation at a lower temperature. We found twofold greater acclimation ability of introduced populations to lower temperatures, after prolonged incubation at 18°C.
5. Increased acclimation ability of lower thermal limits could explain the expansion of the realized thermal niche in the invaded range, and likely contributed to the spread of this species to cooler climates. Such thermal plasticity could be an important, yet so far understudied, factor underlying the expansion of invasive insects into novel climates.

KEYWORDS
acclimation, alien, climatic niche shift, ecophysiology, phenotypic plasticity, range expansion

1 | INTRODUCTION

Invasive species reduce biodiversity and disrupt ecosystem functioning (Bongaarts, 2019; Mack et al., 2000; Simberloff et al., 2013). The spread of invasive species has been facilitated by globalization of trade and transport which introduce species beyond their native range (Chapman et al., 2017). Once introduced to a new habitat, a species needs to survive and reproduce before starting to spread

(Blackburn et al., 2011). Sometimes, new habitats present climatic conditions that are different from those in the species' native range (Hill et al., 2017; Kumar et al., 2015; Ørsted & Ørsted, 2019).

Yet, established invasive species are thought to conserve their niche in general, although studies assessing these climatic niche shifts have predominantly focused on plants (Guisan et al., 2014; Liu et al., 2020a; Petitpierre et al., 2012). Terrestrial ectotherms may have a higher capacity for colonization of new climates compared to endotherms (Liu et al., 2020a). Additionally, climatic niche shifts have been considered common in invasive insects (Bates et al., 2020; Hill et al., 2017), but studies report niche conservatism in key invasive insect species (Cunze et al., 2018; Roura-Pascual et al., 2006). Thus, it is unknown to what extent invasive insects succeed to establish under novel climates (Renault et al., 2018), that is, if they show a climatic niche shift between their native and invaded range. Also, the quantitative methods used to assess the climatic niche shifts do not reveal physiological differences of invasive populations.

A thermal niche shift could be particularly challenging for ectotherms, whose body temperature, and consequently metabolism and fitness, directly depends on the environmental temperature (Angilletta, 2009). Ectotherms, such as arthropods, can also locally adapt to novel climates to which they expand (Krehenwinkel et al., 2015; Lancaster et al., 2015). Local adaptation includes the evolution of a phenotype that increases performance and ultimately fitness in a set of local conditions (Kawecki & Ebert, 2004). But, a more rapid way to adjust to the environmental temperature changes would be thermal acclimation—a reversible physiological change which enhances performance (Angilletta, 2009). Unlike adaptation, acclimation is not heritable and phenotypic changes in adult workers, caused by temperature, are reversible. Here, we combine niche modelling with experimental approach to test if thermal plasticity underlies a climatic niche shift of an invasive insect.

We chose an invasive ant as a model system because ants are successful invaders with over 240 species established outside their native range (Bertelsmeier et al., 2017). There are several traits which facilitate their establishment like omnivory, polygyny and supercoloniality (Bertelsmeier et al., 2017; Holway et al., 2002). Most invasive ants are native to tropical and subtropical areas (Bertelsmeier et al., 2015), and as such are considered to be thermal specialists (Diamond & Chick, 2018). Because ant foraging ability and resource acquisition are directly governed by their thermal tolerance (Cerdá et al., 1998; Roeder et al., 2018), new thermal conditions are a key barrier ants need to overcome to establish in climatically distinct habitats.

To test if introduced populations can shift the thermal niche, and if this can be explained by differences in acclimation ability, we focused on *Tapinoma magnum*. This ant species had recently been introduced from its native range in North Africa to Europe (Seifert et al., 2017). Specifically, we asked three questions: (a) Does a thermal niche shift occur in the invaded range? (b) Do native and introduced populations differ in their critical thermal limits? (c) Do native and invasive populations differ in their acclimation ability? We predicted a niche shift between native and introduced ranges to be accompanied by a greater ability to acclimate to lower temperatures in the introduced range, as cold tolerance is likely limiting the spread of this ant species to higher latitudes.

2 | MATERIALS AND METHODS

2.1 | Climatic and thermal niche analyses

To assess the difference in the climatic niche space between native and introduced populations, we used occurrence data points from our 17 sampling locations, combined with occurrence points from Seifert et al. (2017), which provides coordinates for 90 *T. magnum* colonies. We collected colonies at 17 sampling locations across native and introduced range (Figure 1) and brought them to the laboratory for acclimation experiments (see details below). To avoid errors due to spatial autocorrelation, nearest neighbour distance (NND) method was used to thin the data and occurrence points that were <0.05 units away from each other were removed (~5 km). After thinning, we had 18 occurrence points in the native and 62 in the invaded range (Figure 1). For each location, we extracted the 19 BIOCLIM variables from the WorldClim Global Climate Database at 2.5 arc minutes (~5 km) (Hijmans et al., 2005). These variables are frequently used in studies on climatic niches of species because they are biologically meaningful and publicly available (Peterson, 2011). They are derived from monthly temperature and rainfall values and represent annual trends (e.g. mean annual temperature, annual

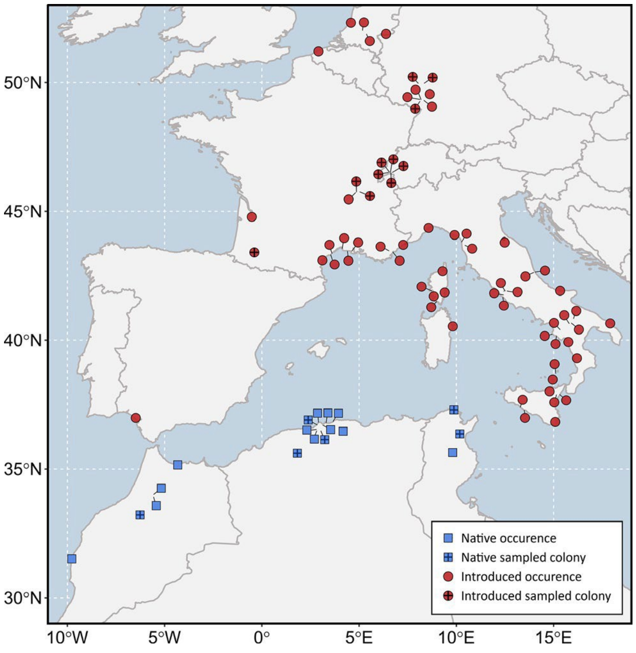

FIGURE 1 Distribution of the sampled *Tapinoma magnum* colonies across their native range in North Africa (blue squares) and introduced range in Europe (red circles). Six colonies were sampled in the native range: Morocco (*N* = 1), Tunisia (*N* = 2), Algeria (*N* = 3), and 11 in the introduced range: France (*N* = 3), Switzerland (*N* = 5), Germany (*N* = 3)

precipitation), seasonality (e.g. annual range in temperature and precipitation) and extreme or limiting climatic factors (e.g. temperature of the coldest and warmest months, and precipitations of the wet and dry quarters). Both analogous and non-analogous climates were considered in our analyses.

First, we tested for an overall climatic niche shift using all 19 BIOCLIM variables. We then analysed the thermal niche shift, using only temperature variables (BIO1–BIO11), as temperature variables are predicted to be more strongly correlated with ant thermal limits. We reduced these climate variables using a between-class analysis (BCA) with 'range' (invaded or native) as explanatory variable. BCA is a special case of a principal component analysis in which there is only one instrumental variable (Thioulouse et al., 2018). This analysis was done using the ade4 package (Dray & Dufour, 2007). The resulting BCA axis was rescaled into 100 × 100 grid cells and converted into occurrence densities using the ecospat package (Broennimann et al., 2012). To control for potential bias in the occurrence data, we calculated occurrence densities using kernel density smoothers, which smoothed potential gaps in the niche-space within a grid cell resulting in even density of occurrences for each grid cell (Broennimann et al., 2012). This allowed us to directly compare the environmental niche space in the native and invaded ranges.

2.2 | Niche comparisons

To determine the overlap of occurrence densities in the defined climatic niche space, we used Schoener's *D* (*D*) overlap (Schoener & Schoener, 1968; Warren et al., 2008). Schoener's *D* measures the overall match in occupied niche between the native and invaded range, spanning between 0 (no overlap) and 1 (complete overlap). To test whether the climatic niches in the native and invaded range are equivalent, we performed a niche equivalency test (Broennimann et al., 2012; Warren et al., 2008). We first pooled all occurrence points and randomly split them into two groups and calculated *D* overlap. We then repeated this 1,000 times to compare the distribution of simulated *D* overlaps to the observed *D* overlap. A *D* overlap below 95% of the simulated *D* overlap means the null hypothesis of niche equivalency is rejected. To examine the direction of niche shift, we calculated niche expansion, which is the percentage of the introduced niche that is not present in the native range. We also calculated unfilling—the percentage of native niche not present in the introduced range—and stability—the percentage of introduced niche shared with the native niche (Guisan et al., 2014).

2.3 | Acclimation experiments

We collected colonies from 17 different localities to test the acclimation ability of *Tapinoma magnum*. Six of our localities were from the native range in North Africa, and 11 colonies were collected across their invaded range in Europe (Figure 1). Across the whole range, *T. magnum* consistently chooses to nest in disturbed areas close to buildings, roads, parking lots and in flower beds. However, North African colonies are small, monogynous and less abundant than European colonies (C. Lebas, field obs.). Even colonies in Mediterranean France and Italy have a strictly invasive phenotype where they dominate the landscape by creating polygynous and polydomous super colonies (C. Lebas, field obs.). We were conservative in our assignment of the native range to North Africa only, based on the behavioural differences observed between the continents, and the suggestion made by Seifert et al. (2017). *Tapinoma magnum* belongs to the *T. nigerrimum* complex that consists of four species. Three of those species have a supercolonial behaviour (workers from different nests are not mutually aggressive), and among them *T. magnum* shows the strongest invasive potential (Seifert et al., 2017). We assigned colonies to species based on worker morphology (Seifert et al., 2017). We confirmed identifications by typing three workers per colony at 11 diagnostic microsatellite markers: *Ant1368, Ant2794, Ant3648, Ant4155, Ant5035, Ant7249, Ant8424* and *Ant9218* (Butler et al., 2014), and *TM_3, TM_10* and *TM_16* (Zima et al., 2016). As reference samples, we used workers from all four species in the *T. nigerrimum* complex (*T. darioi, T. ibericum, T. nigerrium* and *T. magnum*) that were previously identified by B. Seifert. The four species were detected as four different groups in STRUCTURE analyses (Pritchard et al., 2000), which allowed us to distinguish *T. magnum* from other species in the complex (Darras et al. in prep.). All colonies used in the experiments had pure *T. magnum* ancestry.

After collection, we kept our source colonies in the laboratory for at least 100 days at 25°C, 60% relative humidity (RH) and 12L:12D hr photoperiod (*M* ± *SE*: 141 ± 7 days). These source colonies were used to create experimental colonies which were acclimated at 18°C or 30°C, 60% RH and 12L: 12D photoperiod for 21 days. Experimental colonies consisted of 100 workers placed in a plastic box (22 × 18 × 8 cm) lined with Fluon to prevent ants from escaping. We provided ants with an artificial nest consisting of a glass test tube (2 × 20 cm), half filled with water and sealed with cotton. We fed experimental colonies every 4 days with flies (*Calliphora vicina*), honey water and an agarose gel supplement containing vitamins, egg and honey (Bhatkar & Whitcomb, 1970). From each source colony, we created an experimental colony for each acclimation temperature. Exceptions were four colonies represented with two replicates for each acclimation temperature: one colony from Morocco and Switzerland, and two from France and Germany. In total, we incubated 23 experimental colonies at 18°C and 23 at 30°C, 7 from the native and 16 from the invaded range.

2.4 | Measuring critical thermal limits

Critical thermal limits (CTs) are temperatures at which animals lose muscle control (Lutterschmidt & Hutchison, 1997). To measure CTs, we used chilling/heating dry bath (Torrey Pines Scientific EchoTherm™

IC50; advertised accuracy ±0.2°C) and a standardized protocol for recording ant thermal limits (Bujan, Roeder, Beurs, et al., 2020). In this dynamic protocol, five workers per colony are individually tested. Each worker is placed in a 1.5-ml microcentrifuge tube whose cap has been filled with cotton, to prevent the ants from hiding in the cap outside the heating block. Measuring critical thermal maximum (CT_{max}) trials starts at 36°C and temperature is increased by 2°C every 10 min. Before the temperature increase, each tube was inspected and rotated to determine whether ant lost muscle control, that is, loss of a righting response. We used the same procedure to measure CT_{min} but the trials started at 20°C and the temperature was lowered at 10-min intervals. We measured CTs for each colony at the beginning of the experiment, when all colonies were acclimated to 25°C, and after 7 and 21 days of experimental acclimation at 18 or 30°C. In total, we tested CT_{max} and CT_{min} of 1,088 workers. Ants are known to acclimate their critical thermal limits during a 7-day incubation (Chown et al., 2009; Clusella-Trullas et al., 2010; Jumbam et al., 2008). We used an additional 21-day incubation, as this period is sufficient for acclimation of ant traits related to thermal tolerance and desiccation resistance (Menzel et al., 2018).

2.5 | Analysing differences in critical thermal limits

We analysed the effects of acclimation temperature, incubation time and distribution range on CT_{max} and CT_{min} with generalized linear mixed-effect models (GLMMs). We used *lmer* function in the lmerTest package (Kuznetsova et al., 2017) and included colony identity as a random factor. We performed the analyses separately for CT_{max} and CT_{min} at 18 and 30°C. We examined the country-level differences in CT_{min} at 18°C, as this treatment showed the strongest acclimation effect. To choose the optimal model, we compared Akaike Information Criterion (AIC) of GLMMs with a different number of fixed factors. In all cases, the optimal model was the complete model (Table S1). We tested the significance of model terms via pairwise comparisons using the package emmeans (Lenth et al., 2018). Because we observed a high mortality in colonies incubated at 18°C, we counted the number of live workers remaining after 21 days and compared the mortality rates observed in colonies originating from native and introduced ranges. All analyses were performed in r version 3.6.2 (R Core Team, 2019).

3 | RESULTS

3.1 | Climatic niche shifts

In the introduced range, *T. magnum* experiences a 3.5°C lower mean annual temperature compared to its native range (Native: $M \pm SE$ = 17.1 ± 1.3°C, Invaded: 13.6 ± 2.7°C). Minimum mean annual temperature is 4.2°C lower in the invaded range; however, maximum mean annual temperature is the same across both ranges (Native: 13.3–18.2°C, Invaded: 9.1–18.2°C). There was little overlap between the native and introduced thermal niches (D = 0.33), and niche equivalency was rejected (p < 0.001). The divergence between the two thermal niches was related to high expansion (52%), and relatively low unfilling (17%), while the stability between the two niches was 48% (Figure 2). When all climatic variables were considered, we observed equally low overlap among ranges (D = 0.29), and also rejected niche equivalency (p < 0.001; Figure S1).

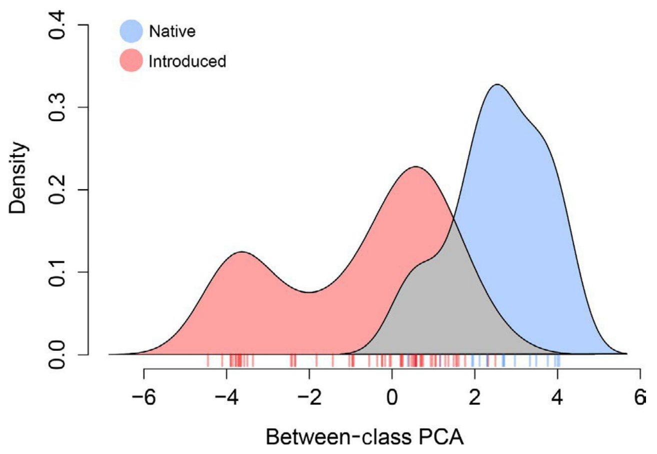

FIGURE 2 Density plot of observed occurrences between native and introduced range of *Tapinoma magnum* in between-class PCA space, reduced from 11 climate temperature variables

3.2 | Thermal limits of the source colonies

After spending a minimum of 3 months in the laboratory acclimated at 25°C, critical thermal minimum of the source colonies did not differ between the native and invaded range (Figure 3; GLMM: β = 0.62, SE = 0.49, z (90), p = 0.23). Critical thermal maximum was slightly higher in native populations (GLMM: β = 0.60, SE = 0.23, z (90), p = 0.024), but this difference was only 0.5°C. The effect of colony, as a random factor, was significantly contributing to the CT_{min} optimal model (p = 0.0007), but not CT_{max} (p = 0.67).

3.3 | Acclimation of CT_{min}

After a 7-day incubation at 18°C, colonies from both native and invaded range lowered their CT_{min} (Figure 4; Table S1). This trend did not continue in native colonies while the introduced colonies tolerated on average −1.4 ± 0.1°C ($M \pm SE$) after 21 days of incubation. This temperature was 2.9°C lower than at the beginning of the experiment and two times lower than the decrease recorded in native colonies after 21 days. Significant CT_{min} decrease with prolonged incubation was consistent across colonies from all countries within the invaded range (Table S2; Figure S2). In native colonies, 71% of the workers died after 21 days of incubation at 18°C which was 2.4 times higher mortality than in colonies from the invaded range (χ^2 = 8.8, df = 2, p < 0.002). Incubation at 30°C did not alter CT_{min}

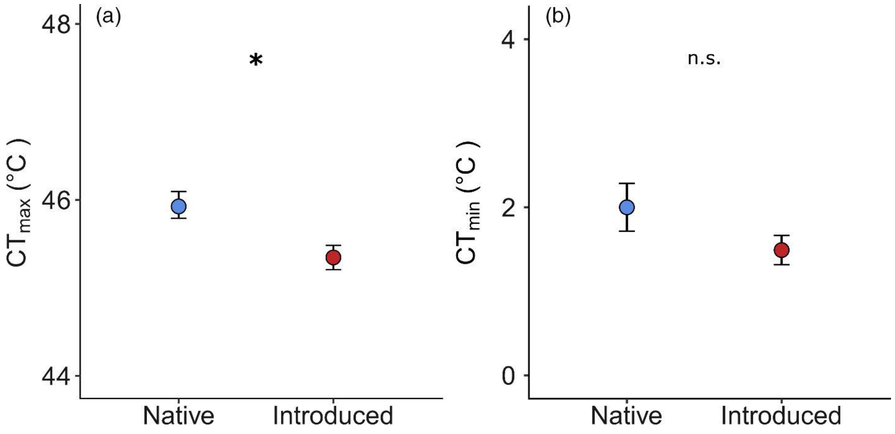

FIGURE 3 Critical thermal limits of native and introduced colonies after spending a minimum of 3 months in the laboratory at 25°C: (a) mean critical thermal maximum (CT$_{\text{max}}$) and (b) mean critical thermal minimum (CT$_{\text{min}}$). The error bars are showing ±*SE*

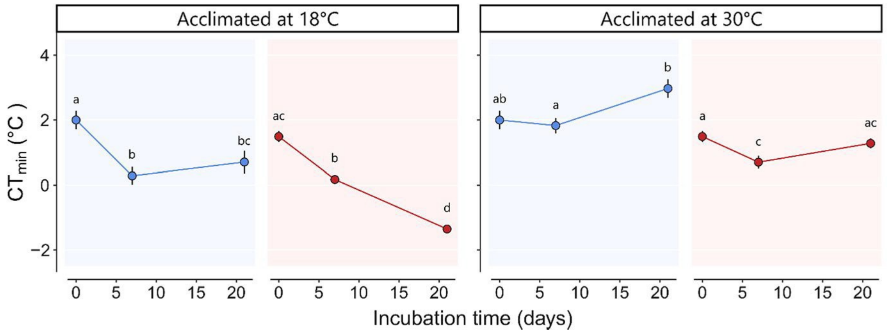

FIGURE 4 Mean critical thermal minimum (CT$_{\text{min}}$) after incubation time of 7 and 21 days at 18°C, and 30°C. Colonies from the native range are shown in blue, and introduced range in red panels. The error bars are showing ±*SE*

of introduced colonies while native colonies show a slight increase in CT$_{\text{min}}$ after 21 days (Figure 4; Table S1).

3.4 | Acclimation of CT$_{\text{max}}$

There was no marked change in CT$_{\text{max}}$ at 18°C across the native and introduced populations throughout the 21-day incubation period (Figure S3a; Table S1). At 30°C, ants from both native and introduced populations had a significantly higher CT$_{\text{max}}$ after 7 days (Figure S3b). During this time, CT$_{\text{max}}$ of native populations increased for 1.4°C, and we observed a similar increase of 1.0°C in introduced populations. After 21 days, introduced populations maintained this elevated CT$_{\text{max}}$ while native populations decreased their CT$_{\text{max}}$ (Figure S3b; Table S1).

4 | DISCUSSION

Using a combination of niche shift analysis and acclimation experiments, we found that a recent introduction into colder climates resulted in a realized thermal niche shift, accompanied by higher acclimation ability of CT$_{\text{min}}$. Such thermal plasticity was recorded in some invasive populations of amphibians (Winwood-Smith et al., 2015), and insects (Nyamukondiwa et al., 2010), including ants (Coulin et al., 2019). But here we show that higher acclimation ability accompanies a climatic niche shift in the invaded range, using a quantitative analysis of niche equivalency, expansion and unfilling. We found that prolonged exposure to low temperatures results in higher acclimation ability of CT$_{\text{min}}$ and higher survival in introduced populations. Considering the ability of introduced populations of *T. magnum* to decrease CT$_{\text{min}}$ without high mortality costs, the acclimation capacity of introduced populations is likely contributing to their invasive success due to greater fitness in colder climates.

Our findings that a cooler climate promotes acclimation ability of CT$_{\text{min}}$ offers one of the mechanisms for ectotherm expansion to novel climates. Climatic niche shift studies usually focus on the presence of the shifts based on occurrence data (Broennimann et al., 2007; Hill et al., 2017; Li et al., 2014; Ørsted & Ørsted, 2019) while the mechanisms behind niche shifts are rarely tested (Hill et al., 2013; Krehenwinkel et al., 2015; Li et al., 2014). For example, a realized niche shift was observed in another invasive ant—*Nylanderia fulva*—but the mechanism behind it was not examined (Kumar et al., 2015). Realized niche shifts can occur after removing biotic or dispersal constraints present in the native range by human-mediated movement to the invaded range (Bolnick et al., 2010; Brooks et al., 2012; Keane & Crawley, 2002). In that case, the species is filling its fundamental niche, which was constrained in its native range. But the expansion of the realized niche can also be enabled by adaptive thermal plasticity (Kolbe et al., 2012; Lancaster et al., 2015). While adaptation of thermal tolerance can occur after species establishment under novel climatic conditions (Krehenwinkel et al., 2015; Sotka et al., 2018), we find this an unlikely scenario for *T. magnum*. We did not find differences in critical thermal minimum across the ranges, after an extended period in the laboratory (>3 months, Figure 3). This suggests that introduced populations maintained the thermal adaptations from the native range and are not locally pre-adapted to the novel climatic conditions.

We found low acclimation ability of CT_{max} across native and invaded range, in both acclimation treatments. This is in accordance with other studies showing that upper thermal limits of insects are less variable than lower thermal limits (Addo-Bediako et al., 2000; Hoffmann et al., 2013), including in ants (Bishop et al., 2017; Bujan, Roeder, Beurs, et al., 2020). Moreover, acclimation of CT_{min} is common in insects (Gaston & Chown, 1999; Hu & Appel, 2004; Klok & Chown, 2003; Terblanche et al., 2006). Acclimation ability of CT_{min} was not a unique feature of our introduced populations. We found that across all native populations, a short-term exposure to 18°C resulted in lower CT_{min} (Figure S4). This might suggest an innate ability of *T. magnum* to acclimate to low temperatures and expand its realized niche. But longer exposures to lower temperatures resulted in high mortality in native colonies. As CT_{min} of native populations was the same after 7-day and 21-day incubation at 18°C it is unlikely that high mortality in native colonies selected for workers with a higher acclimation potential. Additionally, in both ranges, maximum mean annual temperature is 18°C, so this acclimation temperature was not expected to be detrimental.

Tapinoma magnum was introduced from a hot and dry Mediterranean climate to, on average, 3.5°C cooler habitats in Europe, so there is a greater selective pressure on CT_{min}. Thus, acclimation to cooler temperatures would be beneficial in the invaded range allowing for an earlier onset of foraging and food acquisition. Higher acclimation ability in CT_{min} observed in the invaded range could be an adaptation of the founder populations, or developmental and acquired in-situ in cooler climates of the invaded range. To test these hypotheses, a common garden experiment would be necessary, ideally over multiple generations (Bertelsmeier & Keller, 2018; Colautti & Lau, 2015).

Our results show that the ability to withstand lower temperatures corresponds to the climatic and thermal niche shifts, likely facilitating the spread of *T. magnum* to novel climates. Because invasive ants have a strong negative impact on native animal and plant communities, and ecosystem processes (Lach & Hooper-Bùi, 2009; Ness & Bronstein, 2004; Porter & Savignano, 1990), the extent of acclimation ability in other invasive ants is important. Particularly for 19 ant species which are listed among the 360 most invasive animals (www.iucngisd.org) by the International Union for Conservation of Nature (IUCN), because of their negative impact on biodiversity, human health and economy. We know that at least three of those 19 ant species show some ability to acclimate (Bujan, Roeder, Yanoviak, et al., 2020; Coulin et al., 2019; Jumbam et al., 2008).

Species distribution models predict future species spread based on current species distributions while assuming climatic niche conservatism (Bertelsmeier et al., 2015). However, models, which are calibrated using data from the native range only, have been shown to be poor predictors of the species' introduced range (Capinha et al., 2018). This model transferability is particularly limited in terrestrial ectotherms (Liu et al., 2020b). Additionally, if many species hold a strong acclimation capacity, which allows for a climatic niche shift, then predictions of future distributions solely based on occurrence data will not be accurate. This is of particular importance for newly invasive species such as *T. magnum*, which are likely to continue their northern spread, and have significant impacts on native communities (Seifert et al., 2017). The data on acclimation ability of invasive species can help us better predict the likelihood of their establishment and define areas most vulnerable to invasion. Complementing computational analyses of climatic niche shifts with experimental studies could help us elucidate the drivers of invasions in a changing climate.

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AUTHORS' CONTRIBUTIONS

J.B., C.B., O.K.B. and J.G. conceived the ideas and designed methodology; J.G. and C.L. conducted the field collecting; E.C. and J.B. performed the acclimation experiments and collected the data on thermal limits; J.B. and O.K.B. analysed the data; H.D. performed the microsatellite sequencing and molecular ant identification; J.B., O.K.B. and C.B. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at https://doi.org/10.6084/m9.figshare.12847151 Bujan, Charavel et al (2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Appendix 2

The global risk of infectious disease emergence from giant land snail invasion and pet trade

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Parasites & Vectors

BRIEF REPORT

Open Access

The global risk of infectious disease emergence from giant land snail invasion and pet trade

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Abstract

Background Pathogen outbreaks mostly originate from animals, but some species are more likely to trigger epidemics. The giant land snail (*Lissachatina fulica*) is a widespread invader, a popular exotic pet, and a notorious vector of the rat lungworm, causing eosinophilic meningitis in humans. However, a comprehensive assessment of the risks of disease outbreak associated with this species is lacking.

Methods We assessed and mapped the risk of disease transmission associated with the invasion and pet trade of *L. fulica*. First, we conducted a review of the scientific literature to list all known *L. fulica* parasites and pathogens and query host–pathogen databases to identify their potential mammalian hosts. Then, to assess the potential for *L. fulica* to spread globally, we modelled its suitable climatic conditions and tested whether, within climatically suitable areas, the species tended to occur near humans or not. Finally, we used social media data to map *L. fulica* possession as an exotic pet and to identify human behaviours associated with increased risk of disease transmission.

Results *Lissachatina fulica* can carry at least 36 pathogen species, including two-thirds that can infect humans. The global invasion of *L. fulica* is climatically limited to tropical areas, but the species is strongly associated with densely populated areas where snails are more likely to enter in contact with humans. In temperate countries, however, climatic conditions should prevent *L. fulica*'s spread. However, we show that in Europe, giant snails are popular exotic pets and are often handled with direct skin contact, likely increasing the risk of pathogen transmission to their owners.

Conclusions It is urgent to raise public awareness of the health risks associated with *L. fulica* in both tropical countries and Europe and to regulate its trade and ownership internationally. Our results highlight the importance of accounting for multiple types of human-wildlife interactions when assessing risks of infectious disease emergence. Furthermore, by targeting the species most likely to spread pathogens, we show that it is possible to rapidly identify emerging disease risks on a global scale, thus guiding timely and appropriate responses.

Keywords Biological invasions, Emerging disease, Exotic pets, Instagram, *Lissachatina fulica*, Social media, Zoonoses

Background

Emerging infectious diseases are a major and growing threat to biodiversity and human societies worldwide. The emergence and spread of novel pathogens have already wiped out entire species, led to the death of millions of farmed animals and profoundly impacted humans throughout history [1–3]. Wild animals are the most frequent origin of such outbreaks [4]. However,

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some species are more likely to be the source of epidemics than others for three key reasons. First, species that are reservoirs for many or particularly virulent pathogens have a higher probability of spreading harmful diseases [5, 6]. Second, introduced species can spread new pathogens globally or propagate known diseases as they are abundant and widespread, especially in densely populated areas. This increases chances of spill-over to other animals and humans [7, 8]. Finally, species that are directly ingested by humans (as food or ingredients for traditional medicine) or kept as non-traditional pets are more likely to cause outbreaks due to frequent and close contact with humans [6]. It is therefore essential to assess public health risks associated with species that meet one or more of these criteria as they are the most likely sources of future epidemic events.

The giant land snail *Lissachatina fulica*, the largest terrestrial gastropod, meets all of these criteria: (i) the species is a vector of the rat lungworm, a parasitic nematode that can cause severe health impairments in humans [9]; (ii) it originates from East Africa and is currently spreading to other parts of the world with self-sustaining populations outside of its native range [10] (cabidigitallibrary.org); (iii) it can be easily purchased in physical and online stores as an exotic pet [11, 12]. Surprisingly, however, a comprehensive global assessment of the risk of zoonotic disease emergence associated with the giant land snail's global invasion and pet trade is still lacking. Here, we assessed and mapped the risk of transmission of pathogens and parasites (hereafter 'pathogens') from giant land snails to humans and other mammals (wild and domestic) globally.

Methods

Pathogens carried by giant land snails and their potential mammalian hosts

To list all known parasites and pathogens that are carried by *L. fulica*, we performed a literature review on Web of Science (on October 4, 2022) with the query: ("lissachatina fulica" OR "achatina fulica") AND (parasit* OR pathogen* OR zoonos* OR virus* OR bacteria* OR worm* OR helminth* OR fung*). We then reviewed the 192 papers found, excluded irrelevant papers based on title and abstract, and listed parasite and pathogen species associated with *L. fulica* by reading the abstract or the entire text of relevant papers (*n* = 73; see Supplementary information for details). Papers were only included if they reported a direct observation of an association between *L. fulica* and one or more parasite or pathogen species. This screening step was performed twice (by JMWG and JM, independently) to ensure that no host-pathogen interaction was omitted. We then determined which species can be infected by these pathogens by searching for host-parasite interactions in four extensive databases: the global biotic interactions database (GloBI) [13], London Natural History Museum's host-parasite database (LNHM host-parasite database) [14], enhanced infectious disease database (EID2) [15] and global mammal parasite database version 2.0 (GMPD2) [16]. The GloBI and LNHM host-parasite databases were accessed on October 10, 2022, using their respective R packages [14, 17]. The EID2 and GMPD2 were accessed through the October 2020 release of the CLOVER database [18]. Host names were then checked for validity and synonymity and harmonized using the R package taxize [19]. Alluvial plots were used to visualize the host-pathogen interactions (Fig. 1C, D) with the geom_*alluvium* function of the ggalluvial R package [20].

Environmental suitability for giant land snails

Global climatic suitability for *L. fulica* was computed using bioclimatic variables derived from monthly temperature and rainfall values [21] and represent annual trends (e.g. mean annual temperature, annual precipitation), seasonality (e.g. annual range in temperature and precipitation) and extreme or limiting environmental factors (e.g. temperatures of the coldest and warmest month, and precipitation of the wet and dry quarters). We used a spatial resolution of 2.5 arcmin (~ 5 km). These 19 variables were then reduced to 5 by conducting a principal components analysis (PCA) on the world maps using the function 'PCAraster' [22] in R to account for collinearity between the different variables (Additional file 1: Figs. S1, S2).

To calibrate and validate our models, we obtained > 11,000 native and invasive occurrences of *L. fulica* from GBIF (gbif.org; Fig. 2B). For background points (pseudo-absences), we used the > 3,000,000 occurrences of terrestrial gastropods (Stylommatophora) from GBIF [23]. All occurrences were then cleaned by excluding records with imprecise (i.e. > 1 km inaccuracy), invalid (i.e. equal latitude and longitude, coordinates equal to zero, coordinates outside land masses) or dubious coordinates (i.e. duplicated coordinates, coordinates corresponding to country centroid or capitals) using the CoordinateCleaner R package [24]. For each species, occurrences were thinned so that remaining occurrences were at least 5 km apart from each other using the R package 'SpThin' [25]. This was done to limit spatial autocorrelation biases that may arise if some locations are heavily sampled and that can affect the results of species distribution models [26]. The resulting data have 1541 occurrences for *L. fulica* and 115,162 background occurrences. We randomly subsampled 1541 background occurrences to ensure equal weighting of presence and background occurrences in our models.

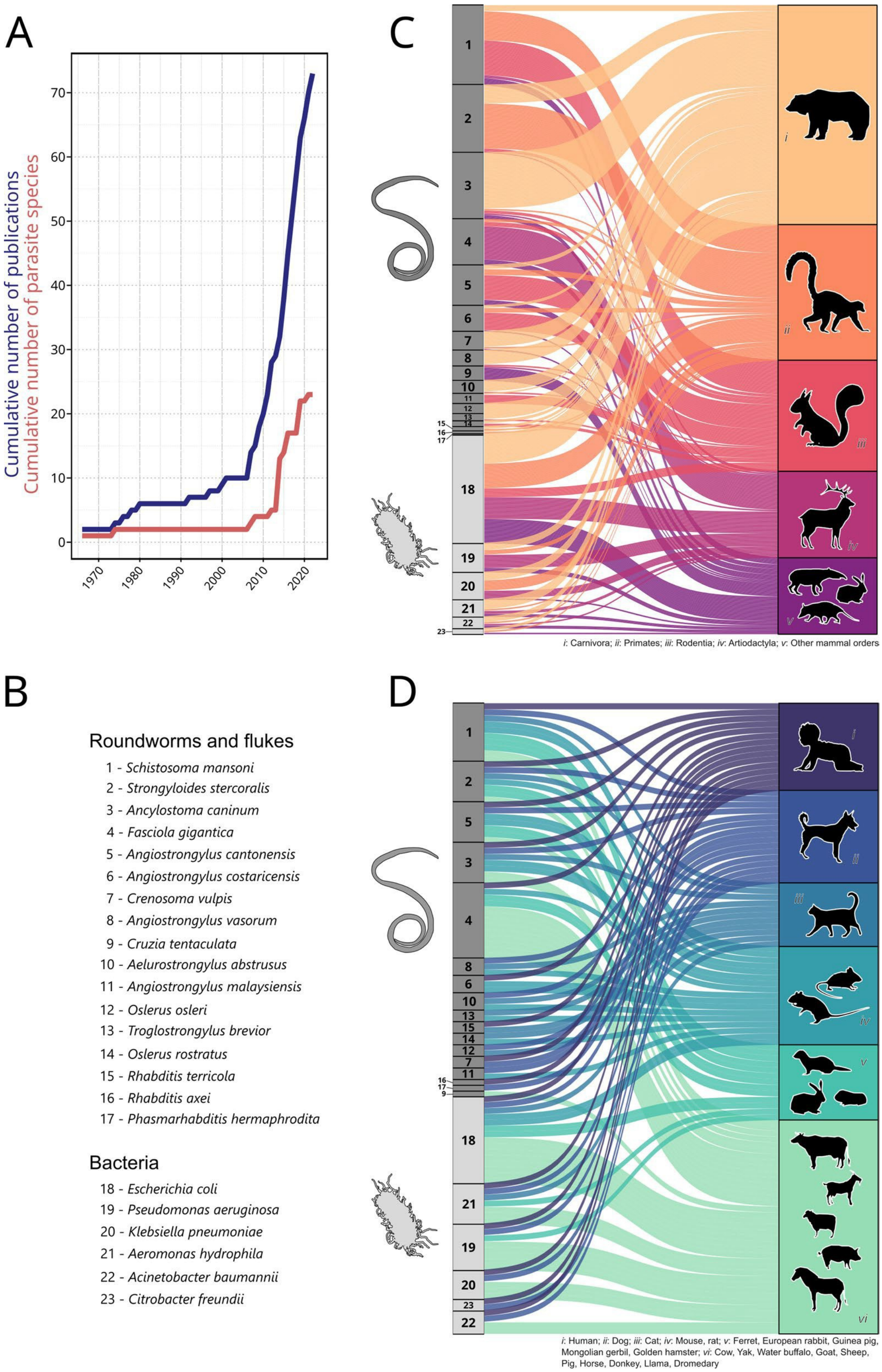

Fig. 1 Pathogens carried by the giant land snail, *Lissachatina fulica*. **A** Cumulative number of scientific publications documenting pathogens in *L. fulica* and cumulative number of pathogen species (identified to the species level) documented in these publications. **B** List of the 17 helminths and six bacteria species identified with **C** their potential hosts among all mammals (*n* = 248 species) and **D** among humans and domesticated mammals (*n* = 19). Each curve in the alluvial plots represents a documented association between a pathogen and a host

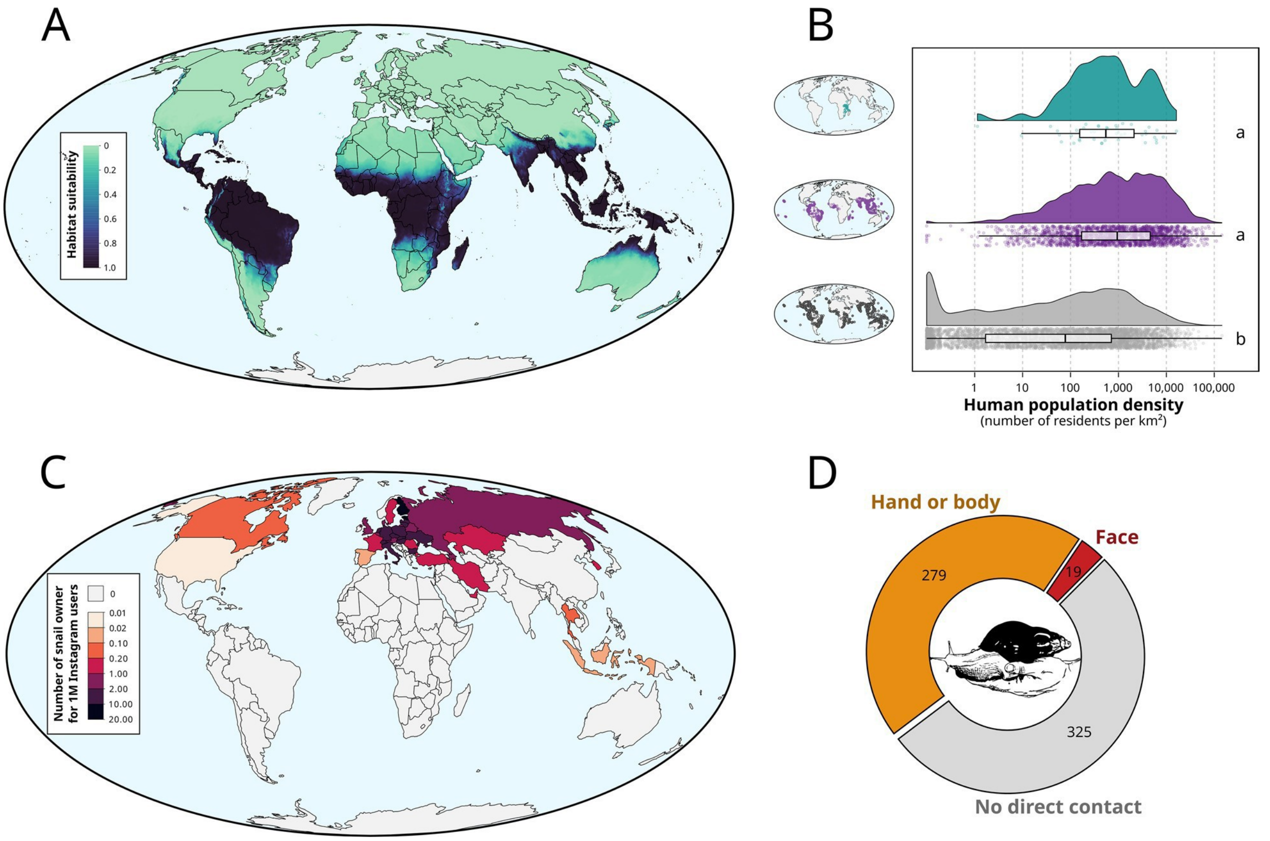

Fig. 2 Geographical patterns of invasion risk **A**, **B** and pet trade **C**, **D** in giant land snail, *Lissachatina fulica*. **A** Forecast of global climatic suitability for *L. fulica* based on an ensemble of seven algorithms using 19 climatic variables reduced to five axes using a principal component analysis. Model's performance was high (TSS = 0.87). **B** Human population density where *L. fulica* occurs (native and invasive range) compared to background occurrences (i.e. records of other terrestrial gastropods inside the climatically suitable area for *L. fulica*). Small maps depict the location of occurrences for each group (*L. fulica* native = 61, *L. fulica* invasive = 1480, background = 115,162). **C** Distribution of Instagram users posting about their pet giant land snails. **D** Proportion of Instagram users displaying direct skin contact with their pet snails

We produced 10 sets of subsampled background occurrences which were run separately for each model used (Additional file 1: Fig. S3).

To assess environmental suitability for *L. fulica* at global scale, we used an ensemble model by creating an ensemble prediction from the predictions of seven ecological niche models in the Biomod2 package [27]: (i) generalized linear model (GLM), (ii) generalized boosting model (GBM), (iii) classification tree analysis (CTA), (iv) artificial neural networks (ANN), (v) multiple adaptive regression splines (MARS), (vi) random forest (RF) and (vii) maximum entropy (MAXENT). The models were calibrated with 70% of the data selected at random and the predictive performance of each model was evaluated on the remaining 30% [28] using the true skill statistic (TSS) [29]. This process was repeated 10 times (tenfold cross-validation), for each of the 10 background occurrence datasets, resulting in 700 models. An ensemble model was created using only models with TSS scores > 0.7 (Additional file 1: Fig. S4). This was then projected onto the whole world to assess suitability with the weighted mean method.

Human density maps for 2020 were downloaded at 30 arc seconds from the Center for International Earth Science Information Network [30]. Human density was then extracted for each occurrence of the native and invasive range of *L. fulica* and for the background occurrences. Only background occurrences that were within the area suitable for *L. fulica* were considered (based on the prediction of our ensemble model; Fig. 2A, B). As the data were non-normally distributed, human density differences between groups were determined using a Kruskal-Wallis test followed by a post hoc Dunn test for pairwise significance comparisons with Benjamini-Hochberg *p*-value adjustments [31].

Global distribution of pet snails and pet owners' behaviour

To assess the ownership of *L. fulica* as an exotic pet worldwide, we searched Instagram for posts referencing *L. fulica*. Instagram is a popular social media platform for sharing pictures and text about exotic pets, regroups over 1.4 billion active users worldwide (as of 2022; statista.com) and is reliable for monitoring emerging pet trades [32]. We collected all Instagram posts containing the hashtag *#achatinafulica*. We chose this keyword because it is among the most frequently used hashtags for referencing *L. fulica* on Instagram (based on a preliminary manual search), it is specific (contrarily to #achatina), and it is Latin and thus independent from the user' language and geographical origin (contrarily to, for example, *#giantafricanlandsnails*). Our data mining campaign was carefully designed to not overload Instagram servers (i.e. several seconds separated each request). Only public data were retrieved, and all collected posts were anonymized [33, 34]. On November 2, 2022, we retrieved the text content (comments and responses) and geolocation (when available) of 30,039 unique posts (published since 2015) from 6640 unique Instagram users. Instagram users with no or more than one geolocation information were discarded and, among the 1667 remaining users, those using combinations of multiple non-specific and highly popular hashtags (e.g. *#love*, *#photography*, *#nature*, *#animals*, *#snail*, *#aquarium*) were removed (526 additional users removed). Most of these Instagram users corresponded to artificially grown accounts that use generic pictures and hashtags to build a follower base, probably with the objective to sell the account for targeted advertisement or to create revenue with sponsored content [35]. Then, we visited at least one random post from each of the 1141 remaining users and visually screened the picture(s) and comments to assess whether the user was really posting about *L. fulica*, whether the snail was depicted as a pet, an invasive species or a food resource, and whether there was a direct contact between the snail(s) and people skin (hand/body or face). Finally, to be able to compare the number of pet snail owners among countries, we divided the number of Instagram pet snail owners per country by the total number of Instagram users per country (obtained from napoleoncat.com).

Results and discussion

Pathogens carried by giant land snails and their potential mammalian hosts

We found that, over the last 60 years, 36 pathogen species have been documented to infect *L. fulica* (based on 73 scientific publications). However, the majority of these pathogens (80%) were found in *L. fulica* during the last 10 years, when the number of publications on pathogens of this species started to grow exponentially (Fig. 1A). It is therefore likely that many pathogens associated with giant land snails are yet to be discovered. Pathogen species found currently include 22 helminths, 7 bacteria and 7 protozoa. Among these 36 pathogens, 23 were identified to the species level (Fig. 1B). Most publications focused on a few pathogen species: the rat lungworm *Angiostrongylus cantonensis* (53/73 papers), the cat lungworm *Aelurostrongylus abstrusus* (7/73), *Angiostrongylus costaricensis* (4/53) and the French heartworm *Angiostrongylus vasorum* (4/53). All other pathogens were cited by just one or two papers (Table S2). The pathogen identified by our literature search had a wide variety of mammal hosts and could infect most domesticated mammal species, including household pets and livestock (Fig. 1C, D). Moreover, 15 of the pathogens recorded can infect humans (Fig. 1D). As most zoonotic pathogens carried by *L. fulica* can also infect domesticated mammals, popular household pets such as dogs and cats could serve as sentinel hosts for detecting pathogens transmitted by giant land snail and allow early detection of potential disease outbreaks [9, 36].

The rat lungworm, *A. cantonensis*, was the most frequently documented pathogen of *L. fulica*. This parasitic nematode causes eosinophilic meningitis in humans, a condition associated with severe neurological impairments in adults and death in young children [9, 37]. The rat lungworm is particularly concerning as, in countries invaded by *L. fulica*, it often infects > 20% of snails [9]. This parasitic nematode probably originates from Southeast Asia but it was reported all over the globe in the last century [9]. As a frequent intermediate host, *L. fulica* might facilitate the global spread of *A. cantonensis*, and other pathogens, at regional to global scale [8].

Environmental suitability for giant land snails

Ensemble modelling based on bioclimatic data revealed high climatic suitability for *L. fulica* throughout all tropical regions. This suggests that the potential range of *L. fulica* is even larger than what is currently observed and that regions such as Northern Australia and Southern Japan could be invaded if the snail were accidentally or deliberately introduced (Fig. S3, Fig. 2A). Models' performance was high with TSS between 0.88 and 0.99 for individual models (Additional file 1: Fig. S4) and equal to 0.87 for the final model. Explanative importance varied greatly among the five PCA axes used for modelling *L. fulica*'s climatic suitability, with PCA first axis being the most important (PCA axis: mean ± SD variable importance; PCA1: 0.9 ± 0.13; PCA2: 0.09 ± 0.06; PCA3: 0.06 ± 0.06; PCA4: 0.03 ± 0.02; PCA5: 0.1 ± 0.07).

Furthermore, inside the climatically suitable area for *L. fulica*, human population density differed between background occurrences and native and invasive *L. fulica* occurrences (Fig. 2B, Kruskal-Wallis test, χ^2 = 1150.9, df = 2, P < 0.001). Pairwise comparisons using Dunn's test indicated that current invaded locations had the same human density as native occurrences ($P > 0.05$) and both the invasive ($P < 0.001$) and native ($P < 0.001$) occurrences were observed at higher human densities than background occurrences, indicating that giant land snails thrive in densely populated areas (Fig. 2B). This is likely to increase the opportunities for pathogen transmission to humans by multiplying direct contacts and the contamination of foodstuffs [38]. The risk of infection is especially high for young children that are more likely to put contaminated fingers, soil, objects or snails into their mouths [37]. Pathogen transmission from giant snails to humans can also occur by the direct consumption of undercooked snails [9]. Giant land snails are a culinary ingredient in many tropical regions and their presence near human settlements might encourage their consumption as an abundant and cheap food resource [9].

Global distribution of pet snails and pet owners' behaviour

In addition to being an edible invader in tropical regions, our social media survey revealed that giant land snails are popular exotic pets in Europe (Fig. 2C). We retrieved a total of 30,039 unique posts from 6640 unique Instagram users. These numbers are similar to the number of posts and Instagram users retrieved for the global pet trade in ants [32], suggesting that *L. fulica* alone is as popular as an entire emerging pet taxa. Among the 1141 users with geolocation information that we manually checked, 750 were really posting about *L. fulica*, including 623 depicting them as pets (Fig. 2C, Additional file 1: Fig.S5), 114 as invasive species and 13 as a food resource (including 10 from Nigeria) (Additional file 1: Fig. S6). As temperate climates are unsuitable for *L. fulica*, the pet trade poses a low risk of further spread and establishment of populations at outdoor locations in Europe (Fig. 2A); however, pathogen transmission from individual pets is still an important risk. Our social media survey showed that pet snail keepers commonly hold their snails in their hands and occasionally on their face (Fig. 1D), a behaviour likely to greatly favour pathogen transmission between snails and humans. This suggests that pet owners are not aware of the health risks associated with giant land snails. These risks seem to have been overlooked so far, given that we identified only a single study that screened pathogens of pet snails [39], detecting four different nematode species in 60 *L. fulica* individuals from three private collections in Italy (but not the rat lungworm). Our findings highlight the usefulness of social media data for investigating potential threats associated with exotic pets. However, a more comprehensive sampling design that included additional search terms, languages or social media platforms would allow a more exhaustive risk assessment. For example, we may have missed some countries where Instagram is unpopular or unavailable (typically China) and some age groups, as > 60% of Instagram users are aged between 18 and 34 (statista.com), which may not represent the full spectrum of exotic pet owners or the average risk behaviour of pet owners.

Conclusions

Biological invasions and emerging pet trades will continue to grow in the coming decades [40, 41]. Unavoidably, this will create more opportunities for the introduction and spread of harmful pathogens to humans and other animals [8, 42]. Our results highlight the importance of accounting for multiple types of human-wildlife interactions when assessing risks of infectious disease emergence. Furthermore, by targeting the species most likely to spread pathogens, we show that it is possible to rapidly identify emerging disease risks on a global scale, thus guiding timely and appropriate responses.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13071-023-06000-y.

Additional file 1: Fig. S1. First five axes of the principal component analysis (PCA) computed with the 19 bioclimatic variables. **Fig. S2.** Standardized scores of the 19 bioclimatic variables on the five PCA axes used to model global climatic suitability for *Lissachatina fulica*. **Fig. S3.** Occurrence points used to calibrate and validate species distribution models. **A** Native (green) and invasive (purple) GBIF occurrences of *Lissachatina fulica* (after cleaning and spatial thinning). **B** Background dataset containing 115,162 GBIF occurrences (after cleaning and spatial thinning) of 3848 terrestrial gastropod species in the order Stylommatophora. Only a random subset of 10,000 occurrences is displayed here. **Fig. S4.** True skill statistics (TSS) scores for each algorithm used in the ensemble model of *Lissachatina fulica* climatic suitability: generalized linear model (GLM), generalized boosting model (GBM), classification tree analysis (CTA), artificial neural networks (ANN), multiple adaptive regression splines (MARS), random forest (RF) and maximum entropy (MAXENT). **Fig. S5.** Number of Instagram users referencing *Lissachatina fulica* as a pet per country (countries with only one user were not displayed). **Fig. S6.** Number of Instagram users referencing *Lissachatina fulica* as an invasive species (yellow bars) or as a food resource (orange bar) per country (countries with only one user were not displayed). **Dataset S1** (separate file). List of articles reviewed for evaluating the number and identity of pathogens carried by the giant land snail *Lissachatina fulica*. **Dataset S2** (separate file). List of pathogens carried by carried by the giant land snail *Lissachatina fulica*. **Dataset S3** (separate file). Host-pathogen associations for the 25 pathogens of *Lissachatina fulica* identified at the species level. **Dataset S4** (separate file). R files allowing replication of the ensemble model performed to predict environmental suitability for *Lissachatina fulica*. This .Rdata object contains the cleaned and thinned GBIF occurrences for *L. fulica* presence and background (i.e. occurrences of Stylommatophora mollusks); the R script necessary to prepare data and run models; the R script necessary to prepare data and test differences in human density between *L. fulica* occurrences (native and invasive) and background occurrences. **Dataset S5** (separate file). Number of Instagram users referencing *Lissachatina fulica* as pets per country and total number of Instagram users per country (source: napoleoncat.com).

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Author contributions

JMWG, JM and CB designed the study. JMWG and OKB collected, processed and analysed the data. JMWG and OKB performed data visualisation. JMWG and JM drafted the first version of the manuscript. All authors participated in revising the manuscript and read and approved the final version.

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Availability of data and materials

The complete data file and methods are publicly available in the public GitHub repository: https://github.com/JGippet/Gippet2023_GiantLandSnails

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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Publisher's Note

Appendix 3

Global flows of insect transport and establishment: The role of biogeography, trade and regulations

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RESEARCH ARTICLE

Global flows of insect transport and establishment: The role of biogeography, trade and regulations

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Abstract

Aim: Non-native species are part of almost every biological community worldwide, yet numbers of species establishments have an uneven global distribution. Asymmetrical exchanges of species between regions are likely influenced by a range of mechanisms, including propagule pressure, native species pools, environmental conditions and biosecurity. While the importance of different mechanisms is likely to vary among invasion stages, those occurring prior to establishment (transport and introduction) are difficult to account for. We used records of unintentional insect introductions to test (1) whether insects from some biogeographic regions are more likely to be successful invaders, (2) whether the intensity of trade flows between regions determines how many species are intercepted and how many successfully establish, and (3) whether the variables driving successful transport and successful establishment differ.

Location: Canada, mainland USA, Hawaii, Japan, Australia, New Zealand, Great Britain, South Korea, South Africa.

Methods: To disentangle processes occurring during the transport and establishment stages, we analysed border interceptions of 8199 insect species as a proxy for transported species flows, and lists of 2076 established non-native insect species in eight areas. We investigated the influence of biogeographic variables, socio-economic variables and biosecurity regulations on the size of species flows between regions.

Results: During transport, the largest species flows generally originated from the Nearctic, Panamanian and Neotropical regions. Insects native to 8 of 12 biogeographic regions were able to establish, with the largest flows of established species on average coming from the Western Palearctic, Neotropical and Australasian/Oceanian regions. Both the biogeographic region of origin and trade intensity significantly influenced the size of species flows between regions during transport and establishment. The transported species richness increased with Gross National Income in the source country, and decreased with geographic distance. More species were able to establish when introduced within their native biogeographic region.

Main Conclusions: Our results suggest that accounting for processes occurring prior to establishment is crucial for understanding invasion asymmetry in insects, and for quantifying regional biosecurity risks.

KEYWORDS
establishment, globalization, human-mediated dispersal, insects, interceptions, invasion asymmetry, invasion stages

1 | INTRODUCTION

The globalization of trade and travel has led to an unprecedented acceleration of species introductions (Bonnamour et al., 2021; Seebens et al., 2017), which is increasingly impacting native ecosystems and human societies (Pagad et al., 2015). Mapping non-native species diversity and exchanges between world regions is therefore key to understanding large-scale drivers of invasions and identifying regionally specific biosecurity risks. Extensive and spatially explicit databases (e.g. CABI Invasive Species Compendium (CABI, 2022); DAISIE (Delivering Alien Invasive Species Inventories for Europe; Roy et al., 2020)) are increasingly available to document non-native species distributions, and there have been considerable advances in describing regional invasion patterns (e.g. Capinha et al., 2017; Casado et al., 2018; van Kleunen et al., 2015). Other studies have focused on the characteristics of trade and travel network topologies driving human-mediated dispersal (Banks et al., 2015; Tatem, 2009), or have identified socio-economic and biogeographic variables that are linked to non-native species richness (Baiocchi & Dalmazzone, 2000; Capinha et al., 2017; Dawson et al., 2017; Lantschner et al., 2020). Yet while non-native species have been recorded in almost every biological community around the world (Convention on Biological Diversity, 2001), species establishments outside of their native range are not evenly distributed geographically. The imbalance in species exchanges, with some regions over- or under-represented as donors and recipients, is referred to as 'invasion asymmetry' (Torchin et al., 2021). For example, many non-native plants in the Southern hemisphere have originated in the Northern hemisphere, while the opposite trend is not observed (van Kleunen et al., 2015).

Different mechanisms have been proposed to explain invasion asymmetry (Figure 1), often focussing on environmental factors and biotic acceptance or resistance during establishment (Jeschke & Genovesi, 2011). However, biological invasions are composed of a series of sequential stages: transport, introduction, establishment and subsequent spread (Blackburn et al., 2011; Gippet et al., 2019; Figure 1). Each stage constitutes a barrier that must be overcome for a species or population to successfully establish and proliferate. The overall invasion success of a species is accordingly determined

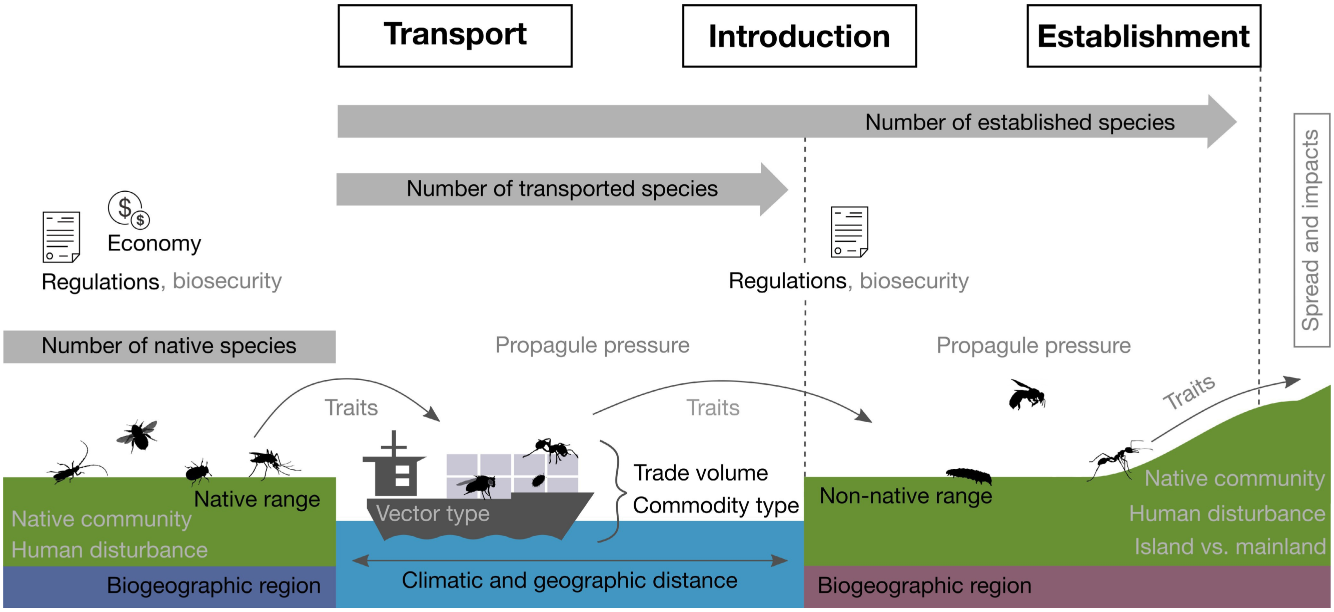

FIGURE 1 The invasion process for unintentional species introductions. The stages of transport, introduction and establishment are shown, along with key mechanisms affecting success/failure at each stage. Transport includes both maritime, aerial and overland introduction pathways. We have not included secondary, bridgehead introductions. Mechanisms and stages not explicitly included in our analyses are shown in grey. The dotted lines indicate the two points we analysed data from; border interceptions after transport, and lists of established insects. Adapted from Schulz et al. (2019).

by the extent to which its individuals or propagules can overcome these barriers (Blackburn et al., 2011). The number of individuals introduced or the number of introduction events (hereafter propagule pressure; Lockwood et al., 2005; Williamson, 1996) is a key element in species invasion success or failure. However, previous work has often not considered that the mechanisms responsible for differential invasion success, often linked to species traits, are likely to vary considerably throughout the invasion process (Blackburn et al., 2011; Gippet et al., 2019). While it has been possible to control for the introduction stage in rare cases where release attempts are well recorded (birds: Blackburn et al., 2008; Chiron et al., 2009; mammals: Jeschke & Genovesi, 2011), in most previous analyses of invasion patterns it has not been possible to isolate the factors responsible for invasion success at each stage (Puth & Post, 2005). Consequently, our understanding of species richness introduced from a source region to a destination region, hereafter referred to as species flows, is largely based on the distribution of already established non-natives (e.g. Capinha et al., 2015; Dawson et al., 2017; van Kleunen et al., 2015), hindering our ability to separate ecological factors from the influence of introduction pressure.

In this study, we address key mechanisms determining the number of non-native species exchanged between regions at the transport stage, and after establishment. Firstly, regions differ in the size of the native species pool potentially available for transport (Liebhold et al., 2017; Seebens et al., 2018). The pool of species in an area thereby sets an upper limit for the number of non-natives that area can supply. Furthermore, the environmental conditions species are adapted to also vary regionally, and likely play a role in establishment success outside their native range (Bomford et al., 2009; Cunze et al., 2018). Secondly, invasion asymmetry can arise from differences in propagule pressure, or the number of species introduced (colonization pressure; Blackburn et al., 2020; Lockwood et al., 2009). Propagule- and colonization pressure have been identified as key drivers of invasion success for several taxa (Blackburn et al., 2020; Lockwood et al., 2005), and are tightly linked to human activities (Pyšek et al., 2010). As most introductions occur via human-mediated dispersal (Hulme et al., 2008), the spatial and temporal heterogeneity of global trade and transport networks is likely a key contributor to invasion asymmetry (Banks et al., 2015; De Benedictis & Tajoli, 2011). Lastly, many countries put significant efforts into preventing invasions (Black & Bartlett, 2020; Saccaggi et al., 2016). Biosecurity measures that exclude new species introductions are generally considered more efficient than managing already established populations (Leung et al., 2002), and are coordinated through national policies and international conventions. Nonetheless, resources to regulate non-native species are also unevenly distributed, potentially exacerbating invasion asymmetry (Bacon et al., 2012; Early et al., 2016; McGeoch et al., 2010).

To disentangle the processes occurring during transport and establishment, we analysed insect border interception records (transport stage) and country-level lists of established non-native insects (establishment stage). Border interceptions generally represent live insects that have been successfully transported, and as such can be considered as a proxy for introductions. Insects are among the most widespread and damaging non-native species in terrestrial habitats, costing at least 70 billion US $ annually (Bradshaw et al., 2016; Lovett et al., 2016). Due to their small size, they are easily transported accidentally through human activities (Meurisse et al., 2019). While the introduction pathways of established species remain poorly known (National Research Council, 2002), insects are the focus of considerable biosecurity efforts globally (Lance et al., 2014; Leung et al., 2002; Nahrung et al., 2022). In addition to growing inventories of established non-native species, many countries record insect species detected during inspections of trade goods, mail and personal baggage at ports of entry (i.e. land borders, air- and sea ports and transitional facilities) as part of national biosecurity programmes (Black & Bartlett, 2020; Saccaggi et al., 2016). These border interceptions offer insight into the largely unobserved processes occurring prior to unintentional introductions (Turner, Brockerhoff, et al., 2021).

We quantified flows of transported species based on interceptions of 8199 insect species arriving in Canada, mainland USA, Hawaii, Japan, New Zealand, Great Britain and South Africa, from 227 countries around the world. Lists of 2076 established non-native insects, along with records of their native biogeographic region, allowed us to quantify flows of established species to the same destinations, plus Australia and South Korea. We modelled the effects of biogeography, trade intensity and biosecurity efforts on flows of insect species among regions, allowing us to test (1) whether insects from some biogeographic regions are more likely to be successful invaders, (2) whether the intensity of trade flows between regions determines how many insect species are intercepted and how many successfully establish, and (3) whether the variables driving successful transport and successful establishment differ.

2 | METHODS

2.1 | Flows of transported species

We analysed border interception records from Canada, mainland USA, Hawaii, Japan, New Zealand, Great Britain and South Africa to quantify the flows of insect species arriving from countries worldwide. See Table S1 for a description of the interception records available from each destination. The data consist of records of insect species detected during inspections of international cargo, mail, vessels and passenger baggage at air, land and maritime ports of entry. These border interceptions represent a fraction of the total insects being transported. While interceptions can be considered a proxy for species' undetected arrival, they do not directly represent introductions (Turner, Brockerhoff, et al., 2021). Furthermore, different types of organisms differ in the probability that they will be detected and recorded during inspection. We only include records with information on the source country and the associated commodity, and where the intercepted insect was identified to the species level (56%). We counted any genera with no members identified to species level as representing one additional species. We standardized insect taxonomic names across years and recording regions according to the Global Biodiversity Information Facility (GBIF) backbone taxonomy (GBIF Secretariat, 2019) using the 'taxize' (Chamberlain & Szöcs, 2013) and 'rgbif' R packages (Chamberlain et al., 2021). This process was largely automated, but a small proportion of synonyms may still be present. We analysed interceptions between 1960 and 2019, depending on their availability per country (see Table S1). We carried out all analyses at a decadal scale to capture changing trade patterns while limiting the influence of random yearly fluctuations.

2.2 | Flows of established species

We used comprehensive lists of established non-native insect species in Australia, New Zealand, Great Britain, Japan, North America (continental USA and Canada), Hawaiian Islands, South Korea and South Africa. The native biogeographic region was recorded for each species using Holt's system (see below). The species lists and main source references are available from Turner, Blake, and Liebhold (2021). We did not include species that were intentionally introduced in our analyses. Furthermore, non-native populations often become the source of secondary introductions through a process termed the 'bridgehead effect' (Bertelsmeier & Ollier, 2021; Lombaert et al., 2010). To increase the likelihood that species arrived directly from their native region rather than via already invaded areas elsewhere, we excluded any species established in, or native to more than one biogeographic region. We restricted our analyses to first records of species establishment from 1960 onwards when detailed import values are available by commodity.

2.3 | Socio-economic factors

There is ample evidence linking biological invasions to trade, and broad metrics of economic activity such as Gross Domestic Product (GDP) have been used to predict invasion success in several previous studies (e.g. Baiocchi & Dalmazzone, 2000; Dawson et al., 2017; Sharma et al., 2010). However, Gross National Income (GNI) represents total income, whether earned within a country's borders or derived from foreign investments, and may provide a better measure of countries' economic condition (Maverick, 2022). Measures of GDP (constant 2015 USD) and GNI (constant 2015 USD) from World Bank and OECD National Accounts data were highly correlated, so we used yearly GNI per capita (The World Bank Group, 2022), summed per decade to quantify the economic status of each source country.

We standardized commodity descriptions in the interception records using the international Harmonized Commodity Description and Coding Systems (HS) for classifying traded goods (World Customs Organization, 2021), and subsequently grouped commodities into broad classes based on the type of product (see Table S2). To provide a precise measure of relevant trade flows, we used the 'tradestatistics' R package (Vargas, 2022) to access historical import values per commodity based on UN Comtrade data (United Nations, 2022). Additional import records for Hawaii were obtained from the US Census Bureau as imports to the district of Honolulu (United States Census Bureau, 2022). We summed yearly import values in US dollars for each combination of commodity class, source country and destination, per decade. The dollar value of imports was corrected for inflation using the ots_gdp_deflator_adjustment() function in the 'tradestatistics' package with 2018 as the reference year.

While we know the exact year when species were intercepted, there is commonly a lag time between a species' establishment and its detection (Kowarick, 1995; Sakai et al., 2001). Such discovery lags for plant invasions sometimes exceed 50 years (Aikio et al., 2010; Kowarick, 1995; Larkin, 2012), but may be shorter for animals (Aagaard & Lockwood, 2014; Essl et al., 2011). In Japan, non-native insects generally have a lag time of 4–10 years before detection (Kiritani & Yamamura, 2003). Consequently, we used import values in the same decade as establishment to predict variation in species richness.

2.4 | Biogeographic regions

To describe insect invasion asymmetry between regions, we assigned all source countries and destinations to biogeographic regions. The regions were classified as per Holt et al. (2013), with the large Palearctic region divided into the Eastern and the Western Palearctic (Figure S1). Due to the low sample size, we excluded flows from the Antarctic and Madagascan biogeographic regions and combined the Australasian and Oceanian regions in our analyses.

2.5 | Climatic and geographic distance

While environmental similarity between the source and destination may be of limited importance during the early stages of the invasion process, it is likely to have a strong impact on establishment success (Bomford et al., 2009; Cunze et al., 2018). We quantified the climatic similarity between countries using the 19 bioclimatic variables from the WorldClim Global Climate Database at a resolution of 5 arc-minutes (Hijmans et al., 2005). The bioclimatic variables were reduced to eight axes using Principal Components Analysis (PCA) using the dudi.pca() function from the 'ade4' package (Dray & Dufour, 2007), then grouped based on the 32 Köppen-Geiger climate categories (Kottek et al., 2006). For each Köppen-Geiger climate, the eight PCA axes representing bioclimatic conditions were projected into hypervolume space using the Gaussian method, with a chunk size of 500 in the 'hypervolume' package (Blonder et al., 2014). We calculated the Euclidean distance between the centroids of each climate in hypervolume space using the dis_centroid() function (Blonder et al., 2014). We then used a double PCA to create a dissimilarity matrix of how frequently each Köppen-Geiger climate occurs per country based on these distances. The values were normalized so that 0 represents no dissimilarity between regions, and 1 represents complete dissimilarity.

In addition to climatic distance, the geographic distance transported may have an impact on introduction success if species more easily survive transport across short distances (Chapman et al., 2017; Seebens et al., 2013). We used a vector map of country boundaries from the 'rworldmap' package with the WGS 84 coordinate reference system (South, 2011), and calculated the geographic distance transported as the distance in kilometres between country centroids. We calculated country centroids using the gCentroid() function in the 'rgeos' package (Bivand & Rundel, 2021) and the great circle distances between them using the st_distance() function in the 'sf' package (Pebesma, 2018).

2.6 | Native insect richness

Species that are transported from an area are necessarily a subset of the pool of species present there. While regional variation in species richness and diversity is therefore likely important for invasion asymmetry, insect biodiversity remains poorly quantified in many parts of the world. Stork et al. (2015) estimate that there are 5.5 million insect species globally. The distribution of Formicidae is well documented compared to most other insect taxa, so to estimate the species pool potentially available for transport in each source country, we divided 5.5 million by the proportion of native ant species present in that country using data from Global Ant Biodiversity Informatics database (Guénard, 2017). This follows the method used by Stork (2018) to estimate the number of insect species per biogeographic region. The number of native vascular plants per country based on the World Checklist of Vascular Plants (Govaerts et al., 2021) was highly correlated with our estimates of insect species richness (Pearson's $r = .84$), so we used the latter to quantify the size of the native species pools available for transport.

2.7 | Biosecurity regulations

National biosecurity programmes direct considerable efforts towards preventing insect invasions through extensive pre-border measures (Sequeira & Griffin, 2014). As a proxy for biosecurity efforts, we used the number of international treaties, regulations and legislation (referred to as regulations from here on) relevant to invasive species that a country is a member of. The number of regulations was based on the ECOLEX database, as per Turbelin et al. (2017). ECOLEX consolidates information on global environmental law, including international treaties, national legislation and technical guidance documents (FAO, IUCN, UNEP, 2016).

3 | STATISTICAL MODELLING

3.1 | Flows of transported species

A 'flow' here represents the species richness associated with a specific source country and destination pair, the commodity class insects arrived with, and the decade when insects were intercepted. Because interception data only record positive detections (they do not record absences), these data are inherently zero-truncated. Therefore, insect flows during transport were modelled using a generalized linear mixed model (glmm) with a zero-truncated negative binomial distribution from the 'glmmTMB' package (Brooks et al., 2017). We also considered a zero-truncated Poisson model to represent the counts of species but based on model AIC the zero-truncated negative binomial model provided a better fit. The model included the variables in Table 1, as well as an interaction term between the import value and commodity class, as the effect of trade intensity may differ between commodities. We included the decade of interception as a random effect to account for variation over time. There are differences in inspection methods, targets and efforts, as well as in trade patterns depending on the partners involved, so we also included the source country, the destination, and the source-destination pair as random effects.

3.2 | Flows of established species

A 'flow' here represents the number of species from a specific biogeographic region of origin that have established in a specific destination, per decade. We do not have information on the exact introduction pathway for most established species, but as plant products are the main commodities associated with insect movements through trade (Fenn-Moltu et al., 2022; Liebhold et al., 2012; Meurisse et al., 2019) we used the US dollar value of plant products imported to represent trade intensity. We assessed other trade metrics including total commodity import values, imports of agricultural commodities and imports of plant and wood products, as well as these values for the preceding decade, but plant product imports in the same decade was the best fit based on model AIC. We again used a glmm with a zero-truncated negative binomial distribution to predict the species richness per flow (Table 2). We included the decade in which a species established, and the area in which it established as random effects to account for variation in detectability and establishments over time and between destinations. We used the Anova() function in the 'car' package (Fox & Weisberg, 2018) to compute analysis-of-variance tables using type II Wald chi square tests for both models. All analyses were conducted in R (R Core Team, 2017).

4 | RESULTS

Overall, 8199 insect species were intercepted from 227 countries across all biogeographic regions (Figure 2). Insects were intercepted arriving with 14 different commodity classes. During transport, the

TABLE 1 The variables included in the model of species flows during transport, along with their description and the type of variable they represent.

Variable	Description	Type
Species richness	Number of insect species intercepted per flow (unique combination of source country/ destination * commodity class * decade)	Response
Import value	Log value imported per flow in US dollars	Explanatory
Commodity class	Identity of 14 broad commodity classes that insects were intercepted with (e.g. plant products, machinery or stone/glass)	Explanatory
Biogeographic region	Biogeographic region the insects arrived from	Explanatory
Source species pool	Estimated number of native insect species in the source country	Explanatory
Regulations per source country	Number of regulations relating to invasive species the source country is a member of, ranging from 0 to 30	Explanatory
Regulations per destination country	Number of regulations relating to invasive species the destination country is a member of, ranging from 12 to 21	Explanatory
Gross National Income (GNI)	Log GNI per capita for the source country in constant 2015 US dollars	Explanatory
Geographic distance	Distance in km between the source and destination country centroids	Explanatory
Climatic dissimilarity	Climatic dissimilarity between the source and destination country, ranging from 0 (no dissimilarity) to 1 (complete dissimilarity)	Explanatory
Within or between regions	Whether species are transported within the same biogeographic region (intra) or not (inter)	Explanatory
Source	Which country intercepted species arrived from	Random
Destination	Area where species were intercepted; either Australia, New Zealand, Great Britain, mainland USA, Hawaii, Japan or South Africa	Random
Source and destination area	Specific combination of source and destination areas the insects are transported between	Random
Decade	Decade of port interception	Random

TABLE 2 The variables included in the model of established species flows, along with their description and the type of variable they represent.

Variable	Description	Type
Species richness	Number of established insect species per flow (unique combination of native region * destination * decade)	Response
Import value	Log value of plant products imported per flow in US dollars	Explanatory
Biogeographic region	Biogeographic region the established insects are native to	Explanatory
Regulations per destination	Number of regulations relating to invasive species the destination country is a member of, ranging from 12 to 24	Explanatory
Within or between regions	Whether species have established within their native biogeographic region (intra) or not (inter)	Explanatory
Destination area	Area where insects have established; either Australia, Great Britain, Hawaii, Japan, New Zealand, North America (continental USA and Canada) or South Korea	Random
Decade	Decade of establishment first record	Random

species richness per flow ranged from 1 to 967 species, with a median of three. The full output of the model predicting flow size during transport is in Table S4. A total of 3994 species had established in the eight destinations we considered, encompassing insects native to the Afrotropical, Eastern and Western Palearctic, Sino-Japanese, Neotropical, Nearctic, Oceanian and Australasian regions (Figure 2). The decade when establishment was first recorded was available for 2076 of these species. The species richness per flow of established insects ranged from 1 to 107 species, with a median of three. The full output of the model predicting flow size of established species is in Table S5.

4.1 | Are insects from some biogeographic regions more likely to be successful invaders?

Interception records from the seven destinations analysed in this study documented the transport of a total of 2490 insect species

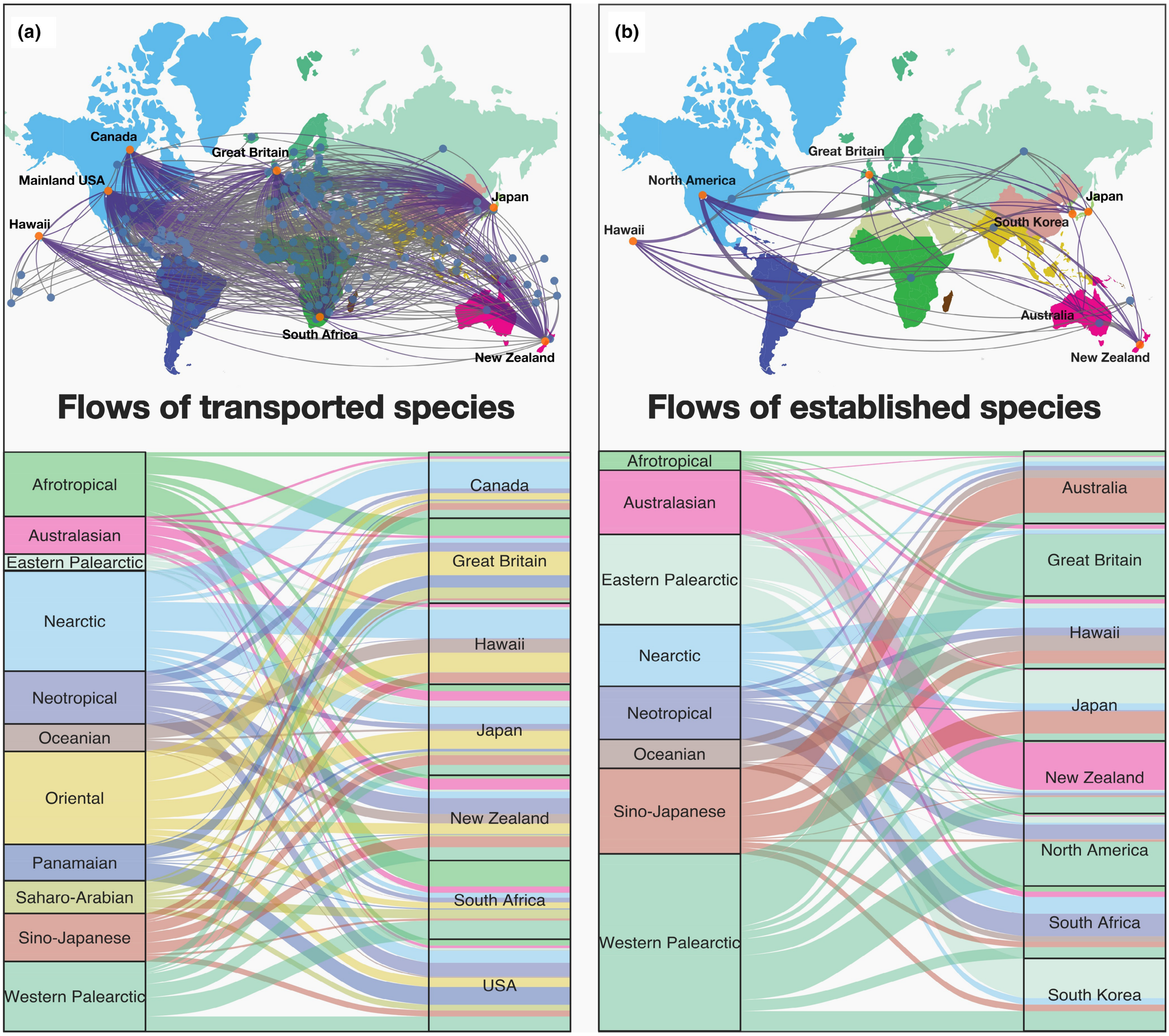

FIGURE 2 Flows of (a) transported and (b) established insect species. The maps show the geographical location of the flows analysed, and the links are proportional to the size of the flows. The alluvial plots show the percentage of species arriving in each destination from each biogeographic region of origin. In the alluvial chart (a) small flows from the Madagascan and Antarctic regions are not labelled.

from the Panamanian region, 2376 from the Nearctic, 2283 from the Western Palearctic, 2104 from the Neotropical, 1691 from the Oriental, 1090 from the Afrotropical, 1069 from the Sino-Japanese, 894 from the Saharo-Arabian, 668 from the Australasian, 464 from the Eastern Palearctic, 330 from the Oceanian, 31 from the Madagascan region and 1 species from the Antarctic region. On average, the greatest species richness per flow originated from the Nearctic (mean of 31.1 species, SD = 114), Panamanian (mean 21.8, SD 75.9) and Neotropical regions (mean 15.5, SD 60.8) at the transport stage. In the eight destinations where we had lists of non-native insects, 1482 Western Palearctic species had established, along with 561 Australasian, 512 Neotropical, 394 Nearctic, 365 Sino-Japanese, 298 Eastern Palearctic, 263 Oceanian species and 119 Afrotropical species. The mean species richness per flow was greatest from the Western Palearctic (mean of 18.4 species, SD 20.3), Neotropical (mean 11.4, SD 20.4) and Australasian plus Oceanian region (mean 8.5, SD 12.3).

During the transport stage (assessed using interceptions), the species richness per flow varied significantly depending on the biogeographic region of origin ($\chi^2 = 29.32$, $p < .001$) (Figure 3), and decreased significantly with geographic distance ($\chi^2 = 10.43$, $p = .001$). The number of established species also varied significantly depending on their native biogeographic region ($\chi^2 = 410.10$, $p < .001$).

Larger pools of native species in the source country led to a marginally significant increase in species richness per flow during transport ($\chi^2 = 3.48$, $p = .06$). We lack the precise information on species' native ranges needed to test the effect of species pools on flows of established insects, but neither species richness per flow nor the

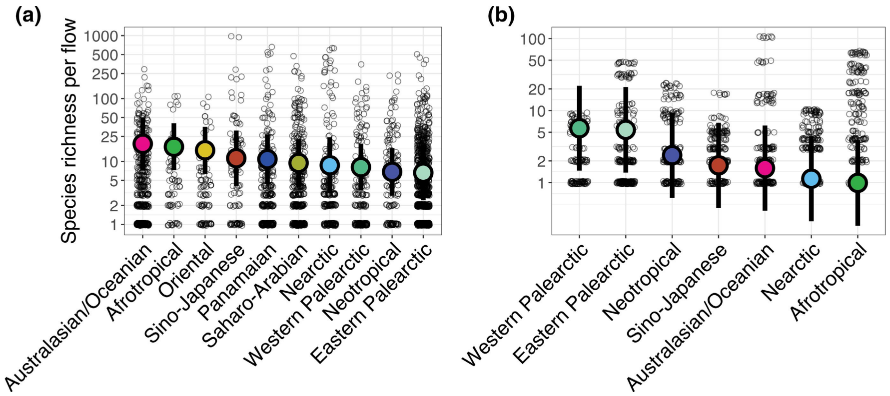

FIGURE 3 The species richness per flow depends on the biogeographic region of origin for (a) intercepted species and (b) established insect species. The grey circles represent individual flows (unique combinations of source/destination * commodity class * decade intercepted), and the coloured circles show model predictions using the ggpredict() function from the 'ggeffects' package (Lüdecke, 2018). The error bars are 95% confidence intervals. The *x*-axis has been log transformed for readability.

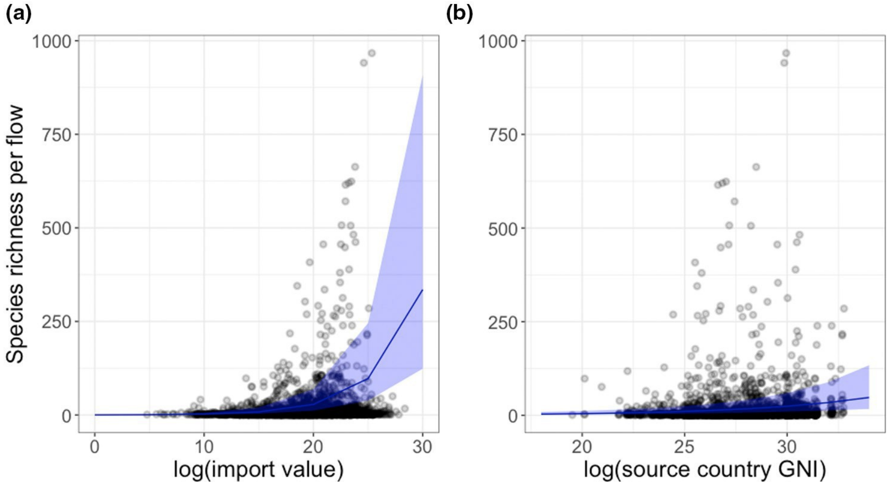

FIGURE 4 Species richness per flow during transport (estimated by interceptions) as a function of (a) the log transformed import value in US dollars (b) the log transformed Gross National Income (GNI) in the source country in US dollars. The grey circles represent individual flows (unique combinations of source and destination area * commodity class * decade intercepted), and the blue line shows model predictions using the ggpredict() function from the 'ggeffects' package (Lüdecke, 2018). The shaded blue areas represent 95% confidence intervals.

total number of established species were correlated with species richness in the native region (Table S3). For example, the greatest number of established species originated from the two Palearctic regions, which together only comprise the fifth-largest pool of native insect species.

4.2 | Does the intensity of trade flows between regions determine how many insect species are intercepted and how many successfully establish?

Greater import values were associated with significantly more species intercepted during transport (χ^2 = 137.48, $p < .001$), as was a higher GNI in the source country ($\chi^2 = 19.04$, $p < .001$; Figure 4). As expected, based on previous studies (e.g. Fenn-Moltu et al., 2022; Kenis et al., 2007; Liebhold et al., 2012; Ollier & Bertelsmeier, 2022; Suhr et al., 2019), the species richness intercepted also depended on the commodity class (χ^2 = 2391.74, $p < .001$). Greater plant product import values were associated with more established species per flow ($\chi^2 = 246.26$, $p < .001$).

4.3 | Do the variables driving successful transport and successful establishment differ?

Due to the lack of fine-scale spatial information on species' native ranges in our data, we could not directly compare many variables between transport and establishment (i.e. climatic distance, geographic distance, GNI of the source country, native species pool size or regulatory efforts in the source country). The species richness transported did not decrease significantly with either the number of regulations in the destination ($\chi^2 = 1.74$, $p = .187$), or the source

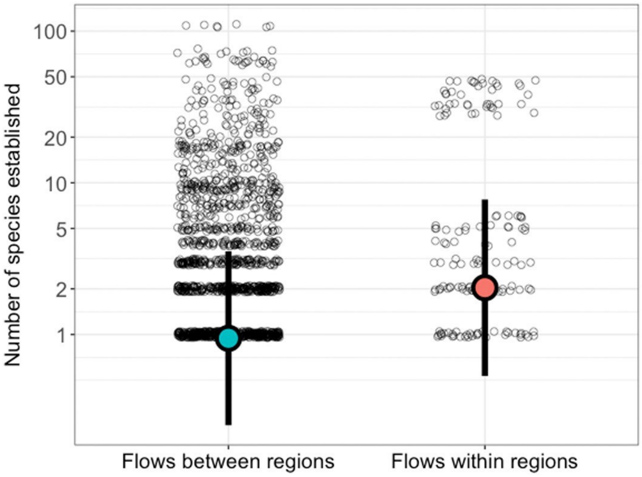

FIGURE 5 Species richness per flow of established insect species, when introduced between biogeographic regions (blue) or within their native biogeographic region (red). The grey circles represent individual flows (unique combinations of native biogeographic region * destination * decade established), and the coloured circles show model predictions using the ggpredict() function from the 'ggeffects' package (Lüdecke, 2018). Error bars are 95% confidence intervals. The *x*-axis has been log transformed for readability.

country ($\chi^2 = 0.07$, $p = .789$). We could only test the effect of regulations in the destination country for established species flows, but there was no significant effect at this stage either ($\chi^2 = .21$, $p = .643$).

Whether species were transported within the same biogeographic region or not had a significant effect on the number of species establishing ($\chi^2 = 51.32$, $p < .001$) (Figure 5), but not on the number of species being transported ($\chi^2 = .12$, $p = .734$). Climatic distance did not have a significant impact on transported species richness either ($\chi^2 = 0.05$, $p = .822$).

5 | DISCUSSION

We analysed border interception records and lists of established non-native insects to assess the factors driving invasion asymmetry during transport and establishment. Both trade intensity and species' biogeographic origins influenced the size of species flows throughout the invasion process, while the relevance of environmental matching differed pre- and post-introduction.

We found that species from some biogeographic regions were more likely to be transported and established successfully, but the key donor regions varied between the two stages. During transport, the largest species flows generally arrived from the Nearctic, Panamanian and Neotropical regions. Yet flows of established species were on average greatest for flows originating from the Western Palearctic, Neotropical and Australasian and Oceanian regions. Similarly, Isitt et al. (2023) found that Europe (i.e. the Western Palearctic) was the dominant source of established non-native insects between North America, Europe and Australasia. It is possible that the difference in dominant donor regions between stages is due to the specific data we analysed, but it may also be that species which are particularly successful at entering introduction pathways, and at successfully establishing once introduced, arrive from different regions. We currently lack sufficient information to explore this further, but it would be an interesting focus for future studies on insect introductions. Due to the limited number of areas with data available for both invasion stages, the ranking of donor regions we observed may not be the same for insect exchanges globally. Furthermore, important introduction pathways such as mail and airline baggage may not be sufficiently captured by our model variables, and would require further study using representative data. The observed asymmetry in flows during transport may also be biased by the varying breadth and focus of inspections between destination countries, alongside differences in import volume, production practices, trade partners and biosecurity measures (Saccaggi et al., 2016; Turner, Brockerhoff, et al., 2021). Inspections often focus on introduction pathways that are considered particularly high-risk, and targeted inspections could thus generate more species detections with goods from certain regions (Eschen et al., 2015). We have also only considered records identified to species level, which may not be representative of less easily identifiable taxa. Randomized, statistically sound inspection systems, such as the USDA Agricultural Quarantine Inspection Monitoring system (USDA, 2011), would provide greater power to assess pathway risks and understand patterns in insect introductions.

We found that species richness increased significantly with import value during both stages, and that more species were transported from countries with a higher GNI. This likely reflects the dominant effect of trade on propagule- and colonization pressure (Levine & D'Antonio, 2003). The socio-economic and development status of a country likely influences their environmental standards and capacity to implement biosecurity measures (Brenton-Rule et al., 2016). While the effect of broad socio-economic variables like GDP or GNI on establishment success is debated (Brenton-Rule et al., 2016; Sharma et al., 2010; Westphal et al., 2008), more precise measures, such as the value of relevant commodity imports, appear to be better predictors of invasion risk for unintentionally introduced taxa (Ollier & Bertelsmeier, 2022). Isitt et al. (2023) conclude that plant introductions driven by European colonization is the most compelling explanation for the invasion asymmetry they observed, while native species pool sizes and total import values have little effect. The contrasting influence of trade value in our study may be due to using import values for plant products, a key insect introduction pathway (Fenn-Moltu et al., 2022; Kiritani & Yamamura, 2003; Liebhold et al., 2012; Meurisse et al., 2019), rather than total import values to predict establishments and using trade value per commodity type at the transport stage. As well as increasing opportunities for introduction, greater trade intensity could improve the chances of species establishing through repeated introductions (Lockwood et al., 2005). Isitt et al. (2023) further found no evidence for the hypothesis that a larger pool of native species leads to proportionally more species being exported. However, the history of European colonization in North America, and Australia and New Zealand may have obscured the impact of native species pool size.

We did not detect a significant effect of relevant treaties, regulations and legislation on non-native species richness at either stage, suggesting that regulatory efforts have a limited impact on insect introductions. This is in contrast with previous work, where a wider set of development and governance indicators indicated a greater risk of non-native species arriving from 'poorly regulated' countries (Brenton-Rule et al., 2016). The regulatory efforts we considered were not specific to insect invasions however, and it is possible that analysing more targeted regulations would be a better predictor of insect species movements. Turbelin et al. (2017) state that while much of regulation is focused on introductions, control and management of current invasive species, fewer measures are in place to prevent species being exported. They suggest that while countries are often concerned with non-native species within their borders, less attention is given to preventing species from leaving unless there are known public health impacts. Additionally, there is geographical bias in the information available on regulatory efforts, representing either a lack of data or a genuine lack of policy (Turbelin et al., 2017). If the latter applies, developing biosecurity efforts in these areas could help limit new introductions and reduce the spread and impact of existing non-native species (Early et al., 2016; Sikes et al., 2018).

While biogeography and trade intensity were important for insect flows throughout the invasion process, the influence of environmental matching (exchanges within or between regions, climatic distance) differed pre- and post-introduction. We found that more species were able to establish when introduced within their native biogeographic region, but, along with climatic distance, this did not influence species flows during transport. The impact of environmental similarity on establishment success has been shown in previous studies, for example, in fruit flies (Trombik et al., 2022), reptiles and amphibians (Bomford et al., 2009; Capinha et al., 2017), and mammals (Broennimann et al., 2021). Similarly, for insects, analogous climates have been used to identify potential sources of non-native species (Peacock & Worner, 2006; Worner & Gevrey, 2006), and insect invasions have further been linked to climate change (Renault et al., 2018; Ward & Masters, 2007). Environmental similarity after introduction could potentially affect spread rates as well as establishment success (Abellán et al., 2017). Furthermore, we found that the number of transported species decreased with geographic distance, similar to Suhr et al. (2019). This could potentially be due to lower survival rates over longer journeys, but we would need additional information on survival and detectability to verify this.

Our results support previous research highlighting globalization as a key driver of invasion patterns, and reinforces the importance of including processes occurring prior to establishment in analyses of invasion risk (Bonnamour et al., 2021; Chapman et al., 2017; Essl et al., 2020; Hulme, 2009). Using border interceptions to quantify flows of insects during transport allows us to assess the factors influencing this largely unobserved stage of the invasion process. Moving forward, thorough records of introductions, establishments and native species from a wider range of areas, including developing countries, would provide a more comprehensive picture of the invasion risk presented by trade between different biogeographic regions. More precise information on the native ranges of established species could further improve our understanding of the link between climatic conditions and establishment success. Ultimately, biosecurity resources are limited both nationally and internationally, and any information that enables more efficiently targeted measures is of considerable value for limiting insect invasions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in Dryad at 10.5061/dryad.dv41ns243.

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BIOSKETCH

Our research interests lie in understanding large-scale anthropogenic changes to ecosystems and patterns of biodiversity. Our current research focuses on the impacts of globalization on biological invasions, using the human-mediated dispersal of insects to study the mechanisms driving unintentional species introductions.

Author Contributions: GFM curated and analysed the data, with support from SO and CB. GFM and CB conceived the original idea. AML, HFN, DSP and TY curated and provided access to the interception records. OKB calculated climatic distance measures. All authors contributed to the design, discussed the results and contributed to the writing of the manuscript.

SUPPORTING INFORMATION

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

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Appendix 4

The role of climatic similarity and bridgehead effects in two centuries of trade-driven global ant invasions

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ARTICLE

The role of climatic similarity andbridgehead effects in two centuries of trade-driven global ant invasions

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Abstract
International trade continues to drive biological invasions. We investigate the drivers of global nonnative ant establishments over the last two centuries using a Cox proportional hazards model. We use country-level discovery records for 36 of the most widespread nonnative ant species worldwide from 1827 to 2012. We find that climatic similarity combined with cumulative imports during the 20 years before a species discovery in any given year is an important predictor of establishment. Accounting for invasions from both the native and previously invaded "bridgehead" regions substantially improves the model's fit, highlighting the role of spatial spillovers. These results are valuable for targeting biosecurity efforts.

KEYWORDS
bridgeheads, climatic similarity, invasion, trade

JEL CLASSIFICATION
Q57: Ecological Economics: Ecosystem Services, Biodiversity Conservation, Q56: Environment and Development. Environment and Trade, Sustainability

1 | INTRODUCTION

Nonnative insect species outnumber all other alien animal species, with nearly 500 nonnative insect species established in Japan, over 1500 in Europe and nearly 4000 in North America (Yamanaka et al., 2015). Insects also include some of the most notorious damaging invaders, with ant species noted among the most widespread and costly nonnative insects (Angulo et al., 2022; Holway et al., 2002; Rabitsch, 2011). Five ant species are ranked among the 100 of the world's worst invaders by the International Union for Conservation of Nature (IUCN), including the Argentine ant, *Linepithema humile*, and the Red Imported Fire Ant, *Solenopsis invicta* (Global Invasive Species Database, 2020). Within introduced regions, nonnative ants can cause declines in native biodiversity, alter ecosystem processes and trigger declines in ecosystem services such as agricultural production and human health. Nonnative ants can lead to substantial economic costs (Angulo et al., 2022). In the United States alone, the total costs associated with *S. invicta* have been estimated at $6.7 billion per year (Lard et al., 2006). In Australia, the total losses incurred from *S. invicta* in rural industries is estimated to be $5.1 billion over 30 years (ISSG, 2014).

Most invasions of insects are unintended consequences of globalization manifested in trade and travel. Many types of insects are inadvertently transported in cargo or accidentally introduced directly with people and their belongings via tourism, migration and during wars (Brockerhoff et al., 2006; Liebhold et al., 2006, 2012). While individual countries and international conventions have made considerable progress implementing quarantine measures to limit the movement of insects (MacLeod et al., 2010), increases in trade and travel continue to drive insect movement worldwide (Liebhold et al., 2016). Garnas et al. (2016) and Roques et al. (2016) provide evidence to show that invasive insect species are spreading much faster now than in the past likely due to rapid changes in the pathways. To develop more effective strategies for minimizing future invasions and their impacts, it is necessary to understand both the biogeographic and socioeconomic drivers of invasions as well as their interactions. Even though there has been good progress in identifying specific invasion pathways that are responsible for transporting insects in trade (Gippet et al., 2019; Meurisse et al., 2019), the connection between imports and insect invasions remains murky.

To address these issues, we analyze historical patterns of ant invasions globally and over many decades to elucidate the individual roles of—and interplay between—biogeographic and socioeconomic drivers. Biological drivers in the form of species attributes have been emphasized in the ecological literature as key drivers of invasion patterns for insects and other taxa (Allen et al., 2017; Capellini et al., 2015; Hill et al., 2016; Jeschke & Strayer, 2006; Lester, 2005; Sol et al., 2012). Specifically for ants, several studies have identified ecological traits often associated with invasive species (Fournier et al., 2019; Lester, 2005; Lloret et al., 2005; Wittenborn & Jeschke, 2011). While these studies make clear the important role of biology, they have typically done so in isolation from socioeconomic drivers. Two exceptions within the ecological literature highlight the important role of trade as a key driver, including Westphal et al. (2008) who found it was the most important explanatory variable in a global study of invasions across all taxa and Liebhold et al. (2016) who showed it was more strongly linked to global insect invasions than was the life history of the species involved.

The economics and environmental management literature has focused on imports as a key driver, highlighting that this risk varies among trading partners (Costello et al., 2007; Dalmazzone & Giaccaria, 2014; Hlasny & Livingston, 2008; Hulme, 2021). Using historical trade data, both Costello et al. (2007) and Essl et al. (2011) showed the importance of prior economic variables (trade and GDP) on current discoveries of biological invasions (in San Francisco, United States and European countries, respectively). Overall, these studies found that imports contribute significantly to biological invasions, however, they mostly focussed on trade and ignored biological drivers such as species characteristics and climatic similarity. However, as we show, these drivers do not operate independently but rather interact with one other.

An important feature of global invasions that was, until recently, absent from economic and ecological analyses of historical invasions is the so-called "bridgehead effect," where previously invaded regions serve as the source of additional invasions elsewhere through secondary introductions (Bertelsmeier & Keller, 2018; Lombaert et al., 2010). Bridgeheads are a form of "spatial" spillover in trade-facilitated invasions, where invasion of a new region creates a spillover risk for their trading partners (Barbier & Shogren, 2004; Zipp et al., 2019). Yet, most analyses ignore the extent of these spatial spillover effects (e.g., Perrings et al., 2000). In the context of marine invasions, Keller et al. (2011) was an early example of research highlighting the role of stepping-stone invasion processes. More recently, Bertelsmeier et al. (2018) showed that bridgehead effects play a major role in ant invasions in the United States and New Zealand. While these studies illustrate the pivotal role of bridgeheads in shaping insect invasions globally, the relative importance of bridgehead effects within the broader set of biogeographic and socioeconomic drivers still remain uncertain and thus important for study (Ricciardi et al., 2021).

A final key environmental driver—and one that modulates the role of imports and the network of potential bridgeheads—is the habitat suitability of the receiving environment. A proxy for this suitability is the climatic similarity (CS) between a species' native range and a new environment, which has been found to be a major determinant of the probability of species establishment (Duncan, 2016; Pauchard et al., 2004; Roura-Pascual et al., 2011; Thuiller et al., 2005). Three economic studies have either implicitly or explicitly accounted for this factor. Costello et al. (2007) allow for the "infectiousness" of imports to vary by exporting partner, but only at the aggregated scale of seven global regions. The regional distinctions thus coarsely account for a host of factors (CS and others like shipping technology and policy) specific to each region, which are not disentangled. While Springborn et al. (2011) is the first paper from the economics literature that explicitly introduces a metric for climate similarity in a study examining the risk of introductions of invasive species with trade, they ignore import volumes. Dalmazzone and Giaccaria (2014) incorporate CS between trading partners within a model that links the establishment of invasive species to import volumes disaggregated by the country and region of origin. They showed that accounting for the geographic structure of trade flows and CS between origin and destination countries significantly improves our understanding of the drivers of biological invasions. A limitation of this study is that they model aggregate numbers of invasive species, and do not account for individual species traits.

With a few exceptions (e.g., Costello et al., 2007; Hlasny & Livingston, 2008), the studies summarized above equated species discoveries with species introductions and restricted analyses to short periods. This is problematic because there are typically long lags on the order of decades between introduction and discovery. Many previous studies also suffer from the difficulty of using a flow variable such as imports measured for a specific year to explain the variation in a stock variable, such as the cumulative number of invasive species up to a certain date (Dalmazzone & Giaccaria, 2014; Perrings, 2007; Perrings et al., 2000). We address these issues by using a long-run multidecadal data set for both imports and nonnative ant discovery records and account for lags between species establishment and discovery by relating historical species discoveries to historical trade-flows and dates during periods that well precede the time of discovery.

Just as multidecadal invasion dynamics require a long run temporal scale, the global nature of trade and the complexities of bridgeheads motivate a global scale of analysis. Prior studies of invasion drivers have been conducted at various scales, from national (Areal et al., 2008; Levine & D'Antonio, 2003; Liebhold et al., 2013; Lin et al., 2007; Ward et al., 2020) to regional (Hulme, 2007; Pyšek et al., 2010; Vilà & Pujadas, 2001) and global (Bellard et al., 2016; Dalmazzone & Giaccaria, 2014; Liebhold et al., 2016, 2018; Lin et al., 2011; Westphal et al., 2008). Despite the broad spatial coverage of some of these analyses, several are confined to a few species and countries (except Bellard et al., 2016; Dalmazzone & Giaccaria, 2014; Fournier et al., 2019; Liebhold et al., 2018) and examine pathways and species traits in isolation (except Liebhold et al., 2016). To date, most of these drivers are considered separately, with little examination of the interactions between the level of imports and other variables that can also influence biological invasions (Hulme, 2021).

We address the limitations surveyed above by estimating a model of ant invasions that incorporates both species traits and trade as well as modulating factors of CS and bridgeheads in a multidecadal and global analysis. We use a Cox proportional hazards model (Cleves et al., 2016), to estimate the relative role of these drivers in contributing to the "hazard" or likelihood of a nonnative species establishing. We model the accumulation of nonnative ant species as a hazard function of historical trade-flows while accounting for biogeographic factors such as source native regions, CS, and species-specific attributes. The model incorporates imports from both native regions and invaded (or bridgehead) countries over a period spanning 185 years. Our study addresses the following questions: (1) How much do imports increase the risk of the introduction of nonnative ant species globally? (2) How does invasion risk change over time and vary by different trading regions? (3) How significant are imports, species attributes and CS as drivers of ant species invasions? (4) Is the bridgehead effect important in explaining historical ant invasions?

Our study offers four contributions relative to the existing literature. First, it unifies two strands of models which are more narrowly focused on establishment risk from either: (A) species attributes and CS, or (B) trade. Our approach integrates these static and dynamic factors and allows assessment of the significance of each to forecast invasion risk. Second, it expands the scope and scale of analysis by utilizing global bilateral imports data spanning 185 years (1827–2012) and using individual species-level establishment records (rather than simple cumulative counts). Third, the model accounts for invasions from both the native range and from previously invaded regions (i.e., bridgehead regions). Fourth, we incorporate CS between source country and recipient country. No previous studies of species invasions have integrated data on species attributes, CS and dynamic propagule pressure (trade) at a global scale. We show that CS interacted with cumulative imports during the 20 years before a species discovery in any given year is an important predictor of establishment, consistent with a delay between initial species establishment and discovery. Ultimately, our results can be used to target biosecurity efforts to prevent new ant establishments, while the methods are easily generalizable to other taxa that hitchhike through international trade pathways.

2 | METHODS

2.1 | Econometric model

We used a Cox proportional hazards model (Cox, 1972), which includes time-dependent and time-independent predictors (Cleves et al., 2016), to estimate the relative drivers of invasion risk. We combined two groups of predictors. First, we considered the intensity of the import pathway, specifically the value of region-specific imports recently received (leading up to any given year), as potentially modulated by the CS between source and receiving region. Second, we considered a set of species attributes, that is, morphological and life-history traits potentially associated with invasiveness (Bertelsmeier et al., 2017). Given the panel structure of the data and to control for spatial variation between regions that is constant over time, we included fixed effects for (1) species native regions and (2) importer regions. While survival analyses have been used to estimate invasion risk as a hazard function for individual invasive insect species such as the emerald ash borer in the United States (Ward et al., 2020), these studies do not fully integrate invasion risk from pathway volumes with species attributes.

The invasion status for each species in each receiving country in the data set is a binary variable set to "uninvaded" annually until the discovery of invasion occurs, triggering a status of "invaded" thereafter. In our Cox proportional hazards model framework, the probability of discovering species k, in receiving country i, in year t is given by:

$$d_{tik} = h_0(t)\exp(f(\overset{\square}{M}_{tik}, C\underline{S}_{ik}|\alpha) + \beta Z_k + \varphi_l + \varphi_j), \tag{1}$$

where $h_0(t)$ is the baseline hazard, Z_k is a vector of species attributes, l is region in which receiving country i is located, j is the source region of the imports, and φ_l and φ_j are importing region and exporting region fixed effects, respectively. In this case, the effects of all regions are treated as fixed and we can □account for them by including indicator variable□s identifying regions in the model. The function $f(\bar{M}_{tik}, \overline{CS}_{ik}|\alpha)$ specifies the way in which imports ($\bar{M}_{tik}$) and climate similarity ($\overline{CS}_{ik}$) enter the model. In addition to fixed effects, the coefficients to be estimated include the vectors α and β. Next, we describe our approach to characterizing relevant imports and CS before specifying possible forms for their combination in the imports-CS function, *f*.

The import summary variables were constructed as a vector of aggregate lags, $M_{tijk}^{u,v} \equiv \sum_{s=u}^{v} m_{sijk}$, where *m* is annual imports from year *u* through *v*. Specifically, we considered imports from *j* to *i* over the most recent decade ($M_{tijk}^{t-9,t}$), the decade before that ($M_{tijk}^{t-19,t-10}$) and, alternatively, over the most recent 20 years ($M_{tijk}^{t-19,t}$). Thus, the import measure may either be a scalar, for example, $M_{tijk}^{t-9,t}$, or a vector, $M_{tijk} = [M_{tijk}^{t-9,t}, M_{tijk}^{t-19,t-10}]$. We included these aggregate (over time) lags since we expect that the likelihood of discovering a species in year *t* depends on the likelihood it was introduced via imports in a year leading up to *t*. These import summary variables are the time-varying measures of interest in the model, which are the main potential drivers of dynamic estimates of invasion risk (along with the expansion of newly invaded bridgehead regions).[1]

We define J_{tk} as the set of countries in which species *k* is present by year *t*. Recall that M_{tijk} summarizes cumulative imports to country *i* from country *j* which has species *k* over a fixed number of years leading up to year *t*. We aggregated over the n_{tk} relevant countries in J_{tk} for species *k* and take the natural log: $\tilde{M}_{tik} = \log(\sum_{j \in J_{tk}} M_{tijk}) \cdot CS_{ij}$ is an index of climatic similarity between source and receiving countries. The average *CS* across the n_{tk} relevant countries is given by $\overline{CS}_{tik} = (1/n_{tk}) \sum_{j \in J_{tk}} CS_{ij}$.[2] Our "full" specification is given by direct and interacted import and climate similarity terms in the imports-CS function:

$$f_{\tilde{M}}(\tilde{M}_{tik}, \overline{CS}_{i} | \alpha) = \alpha_0 \tilde{M}_{tik} + \alpha_1 \overline{CS}_{ik} + \alpha_2 \overline{CS}_{ik} \tilde{M}_{tik}. \tag{2}$$

We considered models with each term in this function on its own as well as all three together (as indicated in Equation 2) to identify a preferred specification. While these specifications allow us to test for whether CS is a significant contributing variable in general, they constrain the impact of CS to a linear form.

To assess whether the effect of varying CS depends on the level of CS, we also considered a heterogenous CS effects model using a dummy variable for each block of CS values *I* in the set of blocks, *L*, where *I* denotes CS percentiles. In this case, the imports-CS function is given by:

$$f(\tilde{M}_{tik}, CS_{ik} | \alpha) = \sum_{I \in L} \alpha_I \cdot 1(CS_{ik} \in CS_I) \cdot \tilde{M}_{tik}. \tag{3}$$

We evaluated two approaches to specifying J_{tk}. In the first, $J_{tk} = J_k$ does not vary over time and is limited to countries in which species *k* is *native*. In the second "bridgehead" specification, newly invaded regions may themselves become source regions for further invasion, thus we allowed for J_{tk} to grow over time, adding countries in which species *k* is newly discovered. We used robust standard errors clustered at the importing country-species level and Cox-Snell residuals to evaluate model fit (Cox & Snell, 1968).

We estimated multiple versions of the Cox model, which differ in three ways. First, we considered two approaches to the scope of imports to include: imports from countries within the native range of each species only versus combined imports from native range *plus* bridgehead (previously invaded) countries. Second, we allowed for CS to enter as a standalone variable and/or

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[1] We also estimated models including the three import summary variables separately and jointly in the same model. However, there were strong collinearity problems in the latter model, which was subsequently dropped. The current analysis estimated separate models for the three import summary variables.

[2] Instead of a simple average of CS values, another logical way to specify CS is by computing a trade-weighted CS index. We compared results from such a model to the specification in the main text and found that results were very similar. We do not report these additional results for brevity purpose.

interacting with imports, or not included at all.[3] Third, we allowed for the length of recent import history driving discovery likelihood each year to be either the past 10 years or 20 years (including the current year). We included a set of dummy variables for each native region and each importing biogeographic region in the model. The omitted reference region (for both native and importing region) was selected to be Asia. These fixed effects capture nontime varying factors such as the underlying invasibility of the destination region, and properties associated with the invasiveness of species from different source regions. This would include the persistent effect of export or import commodity mix, shipping technology, and policy-related variables including implementation of sanitary and phytosanitary standards (SPS) that are specific to either native or destination regions (Lichtenberg & Olson, 2018).

2.2 | Data

For estimation, we merged the economic and ecological data listed in Table 1. Information on the year that each established nonnative ant species was first discovered in each country represents the core outcome data. These were compiled by Bertelsmeier et al. (2017) from different sources including public online databases, scientific publications, books and personal collections. The data set contains historical first records for the 36 most widespread alien ant species across the world (1793–2012) for which dates of first observation at the country level were available from the literature (Bertelsmeier et al., 2017). For each ant species included, the data set specifies native regions as well as each country outside of its native region where it has been discovered and the year it was first reported there. We also compiled two key life-history traits for each species that have previously been associated with invasiveness (Bertelsmeier et al., 2017): (i) Gyny, indicating whether the species typically has single or multiple queens (0,1; 0 = monogynous, 1 = polygynous), and (ii) Habitat generalism, indicating the number of different habitat types in which the species occurs (integers, 1:8).[4] This data set was compiled by Bertelsmeier et al. (2013) using the Antprofiler database, which leveraged expert opinion from professional ecologists. We combined ecological data with global bilateral import value data obtained from the TRADHIST database (Fouquin & Hugot, 2017).[5] The data set contains nominal trade flows for 197 countries from 1827 to 2014, converted to real values (2019 US$).

Many studies have shown that CS between a species' native range and a new environment is a major determinant of the probability of species establishment (Pauchard et al., 2004; Roura-Pascual et al., 2011; Thuiller et al., 2005). We calculated CS for each country pair as follows. First, we quantified the land area of each of the 32 Köppen–Geiger Climatic subgroups in each country (Kottek et al., 2006). Then, we specified a distance measure between each Köppen–Geiger climate using 19 bioclimatic variables sourced from the WorldClim Global Climate Database at a resolution of 5 arc-minutes globally (Hijmans et al., 2005). Finally, we took the proportion of land area falling in each Köppen–Geiger subgroup land area for each country pair and weighted it by the distance measure between each subgroup category. After normalizing values to the unit interval and subtracting from 1 we arrived at a CS index spanning from 0 (no similarity) and 1 (identical) (see Supporting Information: Appendix). In Supporting Information: Figure A1, we show the distribution of CS index levels for the full set of country pairs. The CS index is relatively low for country pairs that are distant in terms of climatic conditions (e.g., Canada–Brazil, $CS_{ij} = 0.36$) and relatively high for climatically similar countries (e.g., Canada–United States, $CS_{ij} = 0.78$).

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[3] As a robustness check we considered additional specifications for CS, which are discussed in the Supporting Information: Appendix.

[4] Habitats include: tropical rain forest, tropical dry forest, temperate forest, boreal forest (taiga), tundra, grasslands, scrubland, riparian zones, desert, coastland, urban areas and agricultural areas.

[5] Available at: http://www.cepii.fr/CEPII/en/welcome.asp

TABLE 1 List of variables and data sources.

Variable	Description	Years	Source
Discovery years	Year of discovery for each species and invaded country (years)	1793–2012	Bertelsmeier et al. (2017)
Value of imports	Bilateral trade ($billions/year)	1827–2014	TRADHIST (Fouquin & Hugot, 2017)
Species attributes	Morphological and life history traits	static	Bertelsmeier et al. (2017)
Climatic similarity	Climatic similarity between origin and importing countries	static	Derived from Kottek Koppen–Geiger climate subgroups (Kottek et al., 2006)

3 | RESULTS AND DISCUSSION

3.1 | Descriptive statistics

Figure 1 shows the temporal distribution of the year a species was discovered in each country, pooled across importing countries. From 1793 to 2012, a total of 1485 discoveries were reported across all countries, giving an average of approximately seven discoveries per year. Recorded invasions increased in the second half of the 19th-century corresponding to the first wave of globalization (Baldwin & Martin, 1999) while the second increase in invasions corresponds to the post-World War II second globalization (Bertelsmeier et al., 2017). Thus, ant invasions have been increasing over time, although with fluctuations due to changes in trade. This is consistent with a more general finding from Bonnamour et al. (2021) that insect and plant invasion rates surged following the two globalization waves. The average number of countries invaded by each of the 36 species is approximately 53. Supporting Information: Appendix A2 shows an example of the geographical distribution of the year of discovery for one selected species, the red imported fire ant, *Solepnosis invicta*.

In Table 2 we present descriptive statistics of key variables used in the final regressions. The overall data set spans 197 countries, 36 ant species and about two centuries. In Supporting Information: Appendix A3, we show annual imports for seven regions over the last several decades, during which time imports to North America, Asia and Europe have sharply increased. To bridge the slight mismatch between the spans of datasets covering ant discovery (1793–2012) and imports (1827–2014) we truncate to 1827–2012. At the start of the data set, this means that the two species discovered before 1827 (both in 1793) are treated as being discovered in 1827. We also tested the effect of dropping the two earlier discoveries and found that it had no impact on the model estimates. Figure 1 illustrates that the vast majority of species discoveries occur from 1850 onward.

3.2 | Cox hazard regression model results

We now turn to the results of the hazard model estimation. The full estimation results are shown in Supporting Information: Tables A4–A7. Our preferred model (3B in Supporting Information: Table A1, based on Akaike and Bayesian information criteria) features a cumulative import over the last 20 years (vs. 10) and imports interacted with CS (vs. uninteracted). In Table 3, we present the full set of hazard ratio estimates for this preferred model (3B). For any country in any year, we estimate that an increase in CS-interacted cumulative imports from the previous 20 years leads to a significant increase in the likelihood of discovering a new species invasion in that year. With respect to the combined impact of CS and imports, these results align with those of Hlasny and Livingston (2008);

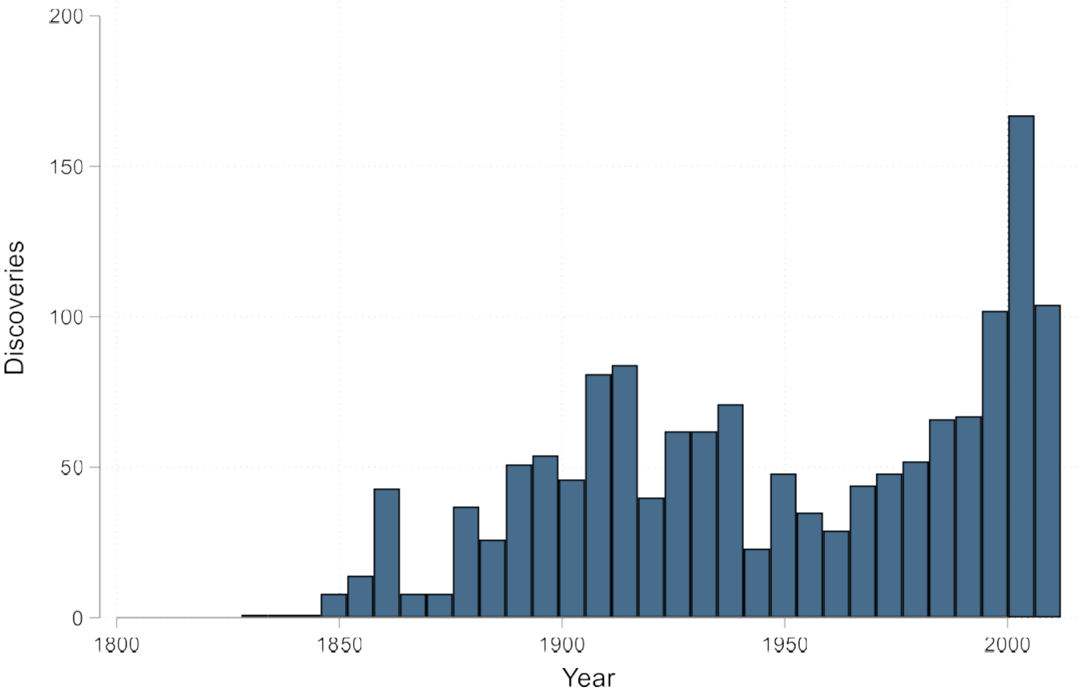

FIGURE 1 Worldwide nonnative ant species discoveries (new species-country combinations) during the period 1793–2012.

TABLE 2 Summary statistics for regression variables.

Variable	Obs.	Mean	SD	Min.	Max.
Dependent variable					
Year of discovery (by species and country)	1485	-	-	1793	2012
Trade partner variables (bilateral)					
Value of imports (US$2019, billions)	1,129,259	0.13	2.03	0.00	365.9
Climatic similarity index	17,952	0.63	0.10	0.00	1.00
Species attributes					
Gyny (queen number)	36	1.33	0.48	1.00	2.00
Habitat generalism	36	4.42	2.06	1	8

Costello et al. (2007); Westphal et al. (2008); and Dalmazzone and Giaccaria (2014) showing imports to be the major determinant of invasions.

We also confirmed findings in the literature that species attributes are significant predictors of invasion risk for individual ant species (Table 3, first column). Our results show that species that have a wide habitat range (habitat generalism) present a higher relative risk of invasion. Thus, a unit increase in the habitat range is associated with an 11% increase in the hazard rate. This can be explained by the fact that habitat generalists can exploit many different habitats spanning many countries (Bertelsmeier et al., 2017). The effect of multiple queens per colony (polygyny) was also statistically significant. Polygynous ant species present a 20% higher hazard compared to

TABLE 3 Full Cox regression model hazard ratio results for the preferred model specification, model 3B, where imports are from native and bridgehead regions over the past 20 years and are CS-weighted.

Variable	Preferred model (3B)	Trade-focused model	Species-focused model
Log imports		1.04 (2.50)*	-
CS			1.39 (1.05)
CS*Log imports	1.04 (3.70)**		
Species attributes			
Monogynous	0.80 (−2.60)***	-	0.81 (−2.44)*
Habitat generalism	1.12 (5.11)**	-	1.12 (5.33)**
Native region			
Africa	0.80 (−2.27)*	0.71 (−3.74)**	0.84 (−1.85)
Central and South America	0.65 (−3.71)**	0.77 (−2.45)*	0.67 (−3.61)**
Indo-Pacific	0.78 (−2.51)*	0.75 (−3.02)***	0.80 (−2.31)*
Other	0.84 (−1.63)	0.84 (−1.65)	0.85 (−1.44)
Importer region			
Central and South America	1.03 (0.25)	1.03 (0.27)	
Europe	0.68 (−3.44)**	0.67 (−3.68)**	
Middle East & North Africa	1.13 (1.02)	1.12 (0.93)	
North America	1.38 (1.74)	1.17 (0.91)	
Oceania	1.15 (1.01)	1.18 (1.20)	
Sub Saharan Africa	0.91 (−0.75)	0.94 (−0.46)	
Model statistics			
χ^2	80.3	42.6	57.3
LL	−4958.5	−4978.8	−4974.5
AIC	9942.9	9979.6	9963.0
BIC	10,063.7	10,081.8	10,028.0
Obs.	79,997	79,997	79,997

Note: Alternative limited models (trade- and species-focused) are also presented in the final two columns. Figures in parentheses are *t* values; significance levels: omitted category for native and importer regions is Asia.

Abbreviation: LL, log pseudolikelihood.

$^{*}p < 0.05$; $^{**}p < 0.001$; $^{***}p < 0.01$.

monogynous species. Our results for these attributes agree with those of Bertelsmeier et al. (2017) who showed that species traits are important for ant establishment. We advance the analysis of Bertelsmeier et al. by considering multiple variables in the regressions simultaneously in a probabilistic fashion. More generally, these results are consistent with existing findings that such species traits are significant predictors of invasion risk for many taxa (Allen et al., 2017; Sol et al., 2012).

As anticipated, the relative risk of invasion varies across native/source regions as well as across importing/receiving regions (Table 3). The omitted region in both groups is Asia, which thus carries an implicit hazard ratio of 1. Compared to Asia, we found that ant species from Africa, Central, and

South America, and Indo-Pacific regions have decreased risk. For example, ant species from Africa present a 20% lower hazard than species from Asia. Similarly, ant species from Central and South America and Indo-Pacific convey a 36% and 22% lower hazard, respectively, compared to species from Asia. This finding is consistent with several studies which suggest that invasion risks from certain regions are higher—although these studies are not for individual species and part of the elevated invasion risk identified in these studies may arise because there may simply be more species, that is, a larger species pool (Hui et al., 2016; Liebhold et al., 2017). Bellard et al. (2016) reported that most of the invasion of invertebrates and plants into Europe and Central America originated from species native to Asia, especially India, China, and Indonesian islands. Dalmazzone and Giaccaria (2014) reported that countries in Asia are the riskiest trading partners for invasive species. The higher invasion risk that we identified for individual species native to Asia may reflect the inherent greater invasiveness of these species, though it remains unclear what species characteristics may drive such a difference. This result suggests that exports from Asia—and from countries in which Asian species have established bridgehead populations—present a higher-risk source region for ants and should be considered for biosecurity focus.

Turning to importing regions, our results indicate that Europe faces a significantly lower hazard compared to Asia (Table 3). Countries in Europe face only 68% of the risk of invasion faced by Asia. North America and Oceania have hazard ratios greater than one but are not significant. No other regions were significant at a 5% level compared to Asia. This may reflect differences in the inherent invasibility of these regions but the reasons for these differences also are not disentangled here. One possible hypothesis is that policy variables such as investment in invasive species prevention and control could also play a role. It has been shown that inspection efforts can reduce invasibility (Hill et al., 2016; Surkov et al., 2008). Another explanation is the fact that low-income countries tend to have less effective regulations thereby increasing the risk of invasions (Perrings, 2007). A related factor is the heterogeneity in the level of biosecurity expenditures globally, with Australia, New Zealand, the United States and the United Kingdom as the countries with the largest investment in prevention policies (0.076%–0.001% of GDP) (Convention on Biological Diversity [CBD], 2012).

Our preferred model in Table 3 integrates two strands of existing models, which are more narrowly either (1) a "trade-focused" model without species attributes (e.g., Costello et al., 2007; Dalmazzone & Giaccaria, 2014; Hlasny & Livingston, 2008), or (2) a "species-focused" model with only species attributes and CS as an independent variable but without an indicator of propagule pressure like imports (e.g., Allen et al., 2017; Sol et al., 2012). In Table 3 we show estimates from implementing both of these typical, more narrow approaches. In the trade-focused model, we use total imports from all countries instead of imports from only native and bridgehead countries (for each species) to be more comprehensively naïve on the species dimension. One caveat here is that the species-focused model presented here indirectly and partially accounts for imports via the region dummy variables, which will loosely account for regional differences on average imports.

Surprisingly, we do not find that either narrower model leads to substantial bias in hazard ratio estimates for terms shared with the comprehensive (preferred) model. In addition, for the trade-focused model, cumulative imports have the expected positive impact on species discoveries. In the species-focused model, the hazard ratios on species attributes remain statistically significant and in the expected direction of impact as in the previous models. Thus, while both "incomplete" models miss important drivers, in our case the estimates they do provide are not misleading. As before, we evaluated the overall fit of the alternative models using Cox–Snell residuals. In Supporting Information: Figure A6, we observe a lack of fit for both of the limited models (trade-focused and species-focused). Note that the first subplot is the same as the first subplot in Supporting Information: Figure A4 (i.e., the preferred model). The comprehensive model shows the best overall fit, indicating that both the biological and economic factors should be incorporated for accurate prediction of invasions.

We further explore the role of CS using the full specification of the imports-CS function (model 4B) in Equation (2). Supporting Information: Appendix 4 provides a detailed analysis and results of varying the level of CS on establishment risk. These results have several important implications. First, they demonstrate that accurate estimates of the impacts of trade on establishments require information on both trade and CS. Models that include only trade provide a good estimate of the hazard of trade for countries with average CS. But trade-only models will overestimate the hazard for countries that are climatically dissimilar and underestimate the hazard for more similar country pairs. Second, these results imply that it may be desirable to vary the intensity of biosecurity effort focused on imports from different countries. Trade between countries that have more similar climates presents a higher hazard. The results indicate that risk of ant invasions is lowest between country pairs with the lowest 15% of CS values and that above this threshold CS has a strong impact on risk.

Finally, we estimated the fitted hazard function, which shows that the hazard rate is increasing over time and varies across exporter regions (Supporting Information: Figure A7). We also conducted several robustness checks to test and evaluate the model fit (Supporting Information: Appendix 6–8). Overall, we fail to find evidence of problems with the assumption of proportional hazards (see Supporting Information: Appendix 6).

4 | CONCLUSIONS

In this study, we assessed the socioeconomic and ecological drivers of ant invasions globally by fitting a Cox proportional hazard model. Our key results highlight the importance of bridgehead imports in explaining invasion risk. This indicates that such spatial spillover effects are important temporal and dynamic drivers of biological invasions. We also find that expanding the historical horizon over which cumulative imports are considered from one decade to two decades improves explanatory power. Our preferred model incorporates CS as an interaction of imports (the likely pathway of species introduction) rather than as a standalone factor. We find that a model including only trade (and excluding species-specific factors) can still provide a reasonable estimate of the hazard of trade for countries with average CS. But trade-only models will over-estimate the hazard for countries that are climatically dissimilar and vice versa.

When we compare estimates of individual effects of key variables from our comprehensive model to those obtained from a less-complete (trade- or species-focused model) surprisingly we find little bias in these less-complete model effect estimates. However, when we turn our attention from individual drivers to prediction of risk, the comprehensive model shows a much better fit overall. As expected, we found that the relative risk of establishment also varies by species attributes, native regions of a species, and by importing region.

There are also limitations to this study. As previously stated, the data on trade flows is highly aggregated and does not allow us to identify how establishment risk may differ by product type or time of year. A limitation to our study of the role of CS is that this measure was calculated at the country scale to match the scale of the establishment and import data. We would expect CS to show even greater explanatory power should future resolution of data make it possible to pinpoint the subnational location of species establishment, allowing for tighter connections between that localized climate and the source region climate. While we accounted for regional fixed effects as well as establishments, trade and CS at the country level, there may be other important sources of within-region heterogeneity that are not represented. Finally, while international trade is likely responsible for the increased spread of ant invasions, it is not the only factor here at stake and knowledge of ant taxonomy and biogeography, ease of identifications, and increased sampling efforts in particular habitats and regions are important cofactors. While this approach in this paper is novel in its integration of both trade flows over time and species attributes, additional integration in further research would be fruitful. Specifically, recent studies have identified climate change, and land-use change as important factors in biological invasions (Epanchin-Niell et al., 2021; Robinson et al., 2020; Roura-Pascual et al., 2021).

These results provide useful information for informing biosecurity policies that facilitate international trade while minimizing future invasions. Our results provide support to allocating substantial resources for mitigating invasive species at the introduction stage through policy instruments such as trade inspections. Several economic studies have shown that allocating resources for the prevention of introductions of invasive species can be more cost-effective than control and eradication (Born et al., 2005; Leung et al., 2002, 2005). Our results show that global ant invasions are driven by international trade and suggest that essentially all countries should be implementing one or more of the trade policy instruments available to address invasive species—targeted inspections (Surkov et al., 2008), tariffs (Lichtenberg & Olson, 2020; Margolis et al., 2005; Perrings et al., 2005) and tradable risk permits (Horan & Lupi, 2005)—to address this market failure. There is also potential to use insights from our analysis to improve surveillance and early warning systems for the management of biological invasions. Our findings on the importance of bridgeheads emphasize the importance of countries with deep experience and expertise in preventing trade-driven invasion risk working to disseminate that knowledge to other countries. In addition, our model can be applied to other taxa for which accidental transport through trade is the primary pathway and where there is data on the year individual nonnative species were discovered to have invaded individual countries or regions, for example, bark beetles, termites, and other insects.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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

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