Universidade
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JOSÉ RICARDO PIRES ADELINO

MACROECOLOGY OF INTRODUCED SPECIES:

PHYLOGENETIC AND CLIMATIC ASPECTS OF BIOLOGICAL INVASION

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Tese apresentada ao Programa de Pós-graduação em Ciências Biológicas da Universidade Estadual de Londrina - UEL, como requisito parcial para a obtenção do título de Doutor.

Orientador: Prof. Dr. Marcos Robalinho Lima

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RESUMO GERAL

A movimentação de espécies para além de seus limites de distribuição natural é uma das consequências das mudanças ambientais intensificadas pelas atividades humanas. Nas últimas décadas a intensidade de movimentação de espécies está aumentando em uma escala sem precedentes e não apresenta indícios de saturação. Contudo, apesar do grande número de mecanismos utilizados para explicar o sucesso no estabelecimento de uma espécie introduzida em um novo ambiente, a relevância de componentes abióticos e bióticos no estabelecimento de espécies introduzidas ainda é debatido. O nicho ecológico de uma espécie pode ser estimado a partir da adequação climática e ambiental que limitam o crescimento populacional de uma espécie (i.e., nicho de Grinnell) assim como a capacidade de explorar recursos disponíveis em conjunto com outras espécies (i.e., nicho de Elton). Desta forma, o estabelecimento de espécies introduzidas é o resultado de diferentes fatores que resultam na similaridade climática entre as regiões nativas e introduzidas assim como a interação interespecífica entre as espécies da comunidade não nativa em relação a espécie introduzida. Assim, devido a interação entre a história evolutiva das comunidades nativas com a história climática das regiões nativas e não nativas, entender padrões gerais do estabelecimento de espécies introduzidas requer abordar a ecologia da invasão em grandes escalas espaciais e temporais. A partir desta abordagem, o estudo da invasão biológica pode ser utilizado para conectar padrões e mecanismos com o objetivo de rastrear a relevância de processos ecológicos e evolutivos no estabelecimento de espécies introduzidas. Desta forma, esta tese tem por objetivo utilizar as similaridades e diferenças biológicas entre espécies nativas e introduzidas assim como similaridades e diferenças ambientais entre as regiões nativas e não-nativas para avaliar os padrões de ocorrências de espécies introduzidas em grandes escalas espaciais e biológicas. Para isso, alimentamos modelos computacionais para associar dados climáticos, de ocorrência de espécies introduzidas e de relações evolutivas para inferir sobre padrões gerais de introdução e estabelecimento das espécies em função das similaridades climáticas e biológicas com a região não-nativa e com a comunidade receptora, respectivamente. Encontramos que a similaridade climática e ambiental são fatores importantes que estão relacionados com a ocupação de áreas antropizadas distribuídas ao longo das regiões da costa do Brasil. Mais especificamente, encontramos que a ocupação de nicho similares a região nativa (i.e., niche unfilling) é o fator mais associado com a ocorrência das espécies introduzidas de vertebrados terrestres. Nossos resultados também mostram que as similaridades e diferenças entre as histórias evolutivas das comunidades das regiões não-nativas em relação as espécies introduzidas é importante e com contribuições distintas de diferentes mecanismos para regiões tropicais e temperadas. Mais especificamente, encontramos que em regiões tropicais, as chances de sucesso aumentam com o aumento da similaridade filogenética entre as espécies introduzidas em relação as espécies da comunidade nativa. Portanto, concluímos que fatores climáticos e evolutivos são importantes para a determinação do padrão observado de espécies não-nativas. Entretanto, que a magnitude da contribuição do clima e evolução devem ser examinados com mais detalhes em função de fatores locais, ambientais e biológicos para determinar o papel das similaridades e diferenças biológicas e ambientais como fatores complementares que contribuem diferentemente para o sucesso da introdução.

Palavras-chave: Ecologia da invasão; Biodiversidade; Rotas de introdução; Nicho ecológico; Nicho climático.

Adelino, José Ricardo Pires. **MACROECOLOGY OF INTRODUCED SPECIES: phylogenetic and climatic aspects of biological invasion**. 2022. (106) 200 pp. Thesis (Doctorate degree in Biological Sciences) – Universidade Estadual de Londrina, Londrina, ano de realização.

GENERAL ABSTRACT

The movement of species beyond their natural distribution limits is one of the consequences of environmental changes intensified by human activities. In recent decades, the intensity of species movement is increasing on an unprecedented scale and shows no signs of saturation. However, despite the large number of mechanisms used to explain the successful establishment of introduced species in new environments, the relevance of biotic and abiotic components in the establishment of introduced species is still debated. The ecological niche of a species can be estimated from climatic and environmental suitability that limit population growth of a species (i.e., Grinnell's niche) as well as the ability to exploit available resources in conjunction with other species (i.e., Elton's niche). Thus, the establishment of introduced species is the result of different factors that result in the climatic similarity between native and introduced regions, as well as the interspecific interaction between the species of the introduced community and introduced species. Thus, given the interaction between the evolutionary history of native communities and the climatic history of native and introduced regions, understanding general patterns of introduced species establishment requires addressing the ecology of invasion at large spatial and temporal scales. From this approach, the study of biological invasion can be used to connect patterns and mechanisms in order to track the relevance of ecological and evolutionary processes in the establishment of introduced species. Thus, this thesis aims to use the biological similarities and differences between native and introduced species as well as environmental similarities and differences between native and introduced regions to assess the occurrence patterns of introduced species at large spatial and biological scales. For this, we use computational models to integrate databases with climate information, introduced species and evolutionary relationships to infer the chances of establishment and introduction of species as a function of climatic and biological similarities. We found that the climatic and environmental similarity are both important factors related to the occupation of anthropic regions among the coastal region of Brazil. More specifically, we found that niche occupation was similar to the native region (i.e., niche unfilling) and the main factor explaining most of the occurrence of introduced terrestrial vertebrate species. Further, our results also show that the similarities and differences between the evolutionary histories of communities from non-native regions to introduced species are important and distinct in tropical and temperate regions. More specifically, we found that in tropical regions, the chances of success increased with increasing phylogenetic similarity between introduced species and the native community of the introduced region. Therefore, we conclude that climatic and evolutionary factors are important for determining the observed pattern of non-native species. However, the magnitude of the contribution of climate and evolution should be further investigated in function of spatial, environmental, and biological factors to determine the role of biological and environmental similarities and differences as complementary factors that contribute differently to the success of the introduction.

Keywords: Invasion ecology; Biodiversity; Introduction pathway; Ecological niche; Climatic niche

LIST OF FIGURES

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LISTA DE ABREVIATURAS E SIGLAS

ABNT	Associação Brasileira de Normas Técnicas
UEL	Universidade Estadual de Londrina

SUMMARY

Presentation

The citations and references format used in the general introduction of the thesis are set according to the Brazilian Association of Technical Standards (ABNT). Similarly, the citations and references used in chapters one and two are set accordingly to the journals, Ecology Letters and Biological Invasions, respectively. These are the candidate journals the chapters presented in the thesis will be submitted to.

Setting the scene: macroecology in the context of biological invasion

Macroecology beyond spatial scales

In the early millennium, the scientific community highlighted the necessity of thinking about terms of “big ecology” as a way to integrate several fields of research to investigate the interplay between biogeographical patterns and ecological processes (BROWN 1995, NEE 2002). The idea being that such an approach would bring new perspectives and potential solutions for the big questions in ecology and evolution, such as the global patterns of biodiversity (NEE 2002). The combination of biogeographical patterns and ecological processes resulted in the growth of a new field of research currently known as macroecology (BROWN 1995, FISHER 2002). Although in its origin the field of macroecology lacks a formal definition (BROWN 1995), the soaring progress in technological and computational advances and in the availability of biological data provided additional layers of information that allowed for a minimum definition of macroecological studies to fit in an independent research field (MCGILL 2019). This allowed macroecology to expand to new branches of investigation that integrated a large range of biological scales varying from species genomics, physiology, phylogeny, species richness to biomes (CRISP et al. 2009; LOVENGROVE 2010; LEIGH et al. 2021) for terrestrial and aquatic organisms (RABOSKY et al. 2018).

Currently, macroecology can be broadly defined as the field of research that focuses on searching for emergent patterns and processes at large scales (MCGILL 2019). However, this definition is far from being straightforward and some caveats concerning emergent and scale properties should be highlighted in the current proposed macroecology definition. Although it is quite common to correlate the word scale with geographical extent, the scales in macroecology do not necessarily reflect the geographical extent of biological sample units across the geographical space as a counterpart to the traditional local studies in ecology. As mentioned by SMITH; GITTLEMAN; BROWN (2014), the prefix *macro* in macroecology indicates the necessity in understanding the broader perspective of ecological components that should only be assessed through statistical analysis. Specifically, such ecological components are grounded in the origin and maintenance of species’ properties that allows the development of complex biotic organization and its rates of differences in time and space. Thus, these entangled components of macroecology converge to the notion of the pursuit in the generality of the properties of a system through spatial, temporal, and/or taxonomic scales (MCGILL 2019). Therefore, a macroecological approach requires that the study system should be on a moderate to large scale in at least one of three components (Figure 1).

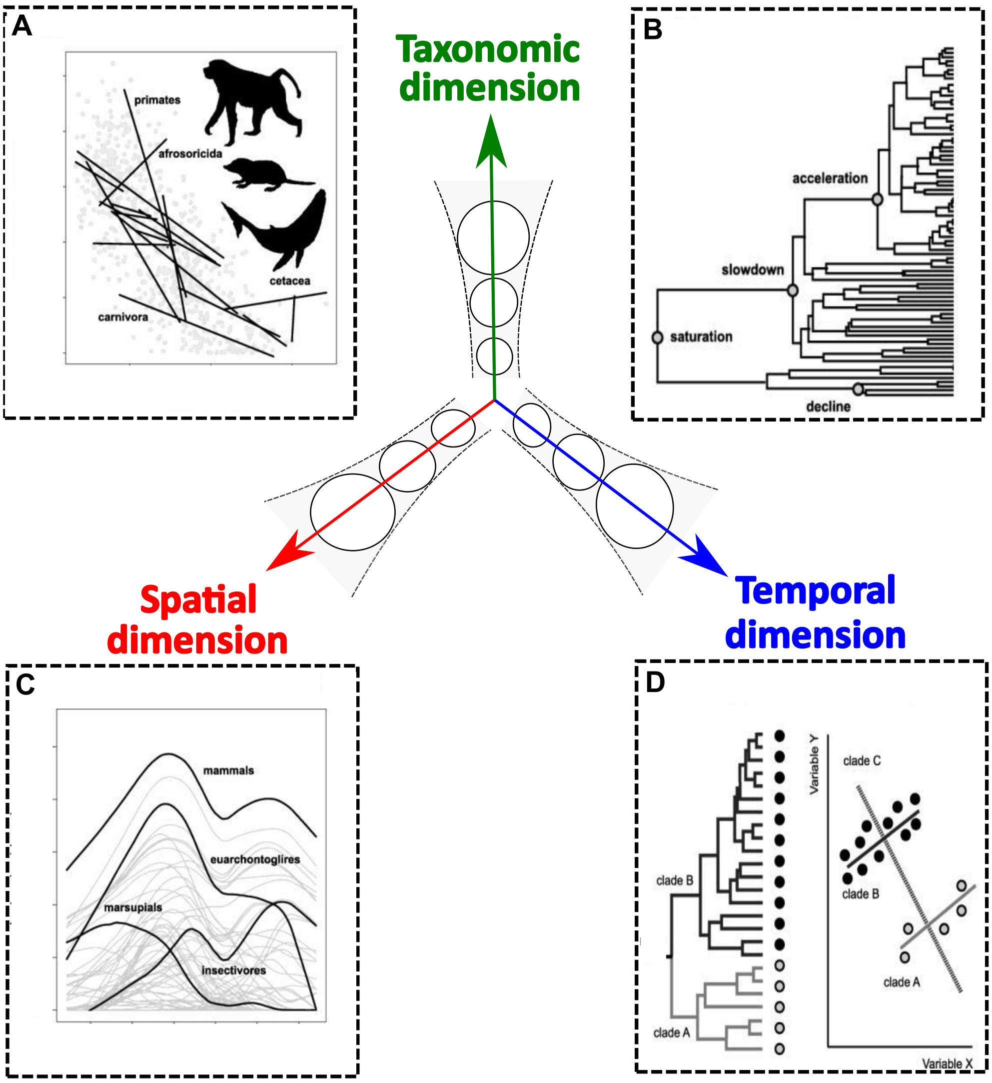

Figure I: Schematic representation of the main components in the study of macroecology. In the center of the image, the three-dimensional schematic representation of the macroecological space with each arrow indicating one of the three-dimensional components of macroecology. The red arrow refers to the spatial scales dimension that can be measured in continuous scales of geographical distance or by the boundaries of geographical delimited areas. The blue arrow indicates temporal scales and can be measured in evolutionary time scales or groups of lineages (i.e., phylogenetic relationship). The green arrow indicates the taxonomic scale that can be measure in species richness or in the number of biotic organization (i.e., population or communities). Each component can interplay with each other creating intermediate states of macroecological studies (see PIGOT et al. 2019). The arrow's dashed contour lines indicate the component expansion and circles indicates the cumulative magnitude of the scale in the axis. The four boxes around the three-dimensional schematic representation indicates examples of macroecological pattern and process. **A)** Abundance and body mass relationship. **B)** Diversification dynamics. **C)** Species richness and latitudinal gradient relationship. **D)** Statistical associations between clades and variables. The image was adapted from MCGILL (2019) and GRAHAM; STORCH; MACHAC (2018).

The emergent component is grounded on the mathematical field that studies the behavior of the complex mechanical system, and in macroecology it is analogous to considering biological entities (i.e., species) as particles that assemble in a complex and dynamic system. Consequently, the mechanics of a complex system impose theoretical and practical limitations regarding the scaling up patterns and processes from micro (i.e., local) to macro (i.e., regional, or global) system. Conceptually, it can be summarized by Jensen's inequality, which states that the average of a function is not the function of the average due to the non-linearity and heterogeneity of the variance in the particle-system relationship (*for more details see* MCGILL, 2019). Thus, the effect of ecological and evolutionary forces that act in the organism at small scale does not necessarily reflect the accumulative effect among large scales. Consequently, scaling up the organization level of ecological and biological entities across scales is not useful for capturing generalities of complex systems that include emergent properties. Therefore, the best solution might be using the properties of the objects of interest to build a macro system model rather than scaling up models. Finally, it is possible to conclude that macroecology is an approach in science that highlight the description and explanations of pattern and processes at divergent scales (SMITH; GITTLEMAN; BROWN, 2014)

Anthropocene: Humans as a natural force

We are witnessing a deep social, ecosystem, and ethical transformation in the earth that result from the leap of *Homo sapiens* as an ordinary species on the earth to the rise of humans as the new force of nature capable of changing the whole functioning of the earth system (ELLIS, 2018). In a paradoxical way, the source of these changes is grounded in the human capacity of learning in order to adapt to and control the functioning of a natural system, which is supported by the development of reasoning, a human trait that pushes scientific progress and at the same time causes its harmful effects in the earth environmental system. Since *H. sapiens* origin 300,000 years ago (Hublin et al. 2017), it is estimated that our activities modified three quarters of the earth surface accounting for the accumulated effects of land use changes by agriculture, forestry and human settlements and indirect physical consequences from atmospheric, environmental, and biotic changes (ELLIS, 2018). These human-induced transformations are changing the structure of societal organization of human lives, reshaping politics, economy, and technology. Therefore, it is currently accepted that the magnitude of human interference on the earth system compelled the earth to a new epoch, the Anthropocene (LEWIS; MASLIN 2015).

The starting point of the Anthropocene is tracked to the early Industrial revolution, in the year 1750 with the tipping point in the acceleration of the impact pressure imposed by human activities occurring in the middle of the 20st century, in the year of 1950 (STEFFEN et al. 2011, STEFFEN et al. 2015). Thus, Science reports a clear message, the velocity of change in the earth system due to human activities increased at an unprecedent rate in the history of humanity and in the history of planet Earth (ELLIS 2018). This is technically called "the great acceleration" and in terms of a complex system analogy, the accumulated human-driven pressures are changing the earth system functioning beyond the natural limits of variability and can lead the earth system to an unprecedented non-analog state of functioning (ELLIS 2018, STEFFEN et al. 2018). For instance, climate is one of the key elements in the earth system regulating biological and ecosystem processes. However, it is also one of the most affected by human pressures and might lead the earth's climate to a distant trajectory from those recorded during climate stability in the recent earth's history (STEFFEN et al. 2011b). These changes can lead to new climate regions as well as the disappearance of current climates (WILLIAMS; JACKSON; KUTZBACH, 2007, ORDONEZ; WILLIAMS; SVENNING, 2016). Therefore, the non-analog earth state highlights the unknown prospects of the earth system. Indeed, macroecological studies support the role of change in the climate regime with the shifting and redistribution of species (PECL et al. 2017), reshaping of biotic interactions (ALEXANDER; DIEZ; LEVINE, 2015), pushing adaptive evolution of species traits (RADCHUCK et al. 2019) and the rise of Anthropogenic Biomes (ELLIS; RAMANKUTTY, 2008). Therefore, human driven pressures are fully integrated in our perception of the ecology across scales and can be deliberated or indirectly used in a macroecological perspective.

Introduced species as human driven pressure

The movement of species through regions around the Earth can be considered under the perspective that species can actively, or passively expand its current distribution beyond a species' original distribution limits. A large number of these species' movement from one geographical region to another is documented with fossils and is referred to as biotic interchange (VERMEIJ 1991). This biogeographical understanding of the invasion process is considered as a natural event of biological invasion, where species expand their natural limits by overcoming the physical, environmental, and biological barriers to colonize one or more new geographical regions (VERMEIJ 2005). For example, the biogeography of horses (*Equus caballus*) show that the species originated in the Nearctic region (i.e. new world) and opportunistically spread to the Palearctic and Afrotropic regions (i.e., the old world) through the Bering bridge 11 million year ago (GARCÉS et al. 1997).

This perception of invasion events differs from contemporary ones in two main ways, the pathways of introductions and the magnitude (i.e., intensity and velocity) of the events. The former, refers to the condition of deliberate or unintentional introduction events of species with human assistance, which moves species through regions in a non-random pattern (BLACKBURN; DUNCAN, 2001) that matches with technological, cultural, and economic factors across the world (HULME 2009). The latter refers to the rate of human assisted introduction and the invasion process, which is faster today when compared with natural events of invasion. In the current perspective of biological invasions, advances provided by human technological development are permanently breaking down the geographical barriers that constraint species to its native region (HULME, 2009; CAPINHA et al. 2015; HULME, 2021), leading to a massive volume of trade and transport of species in a unprecedent rate through all regions of the world, including oceanic islands. The magnitude of the invasion pressure from human assisted activities predicts no signal of saturation in the number of non-native species introduction (SEEBENS et al. 2017), contributing to biodiversity loss (BELLARD; CASSEY; BLACKBURN, 2016), supporting the rise of global hotspots of invasive species (DAWSON et al. 2017) and impacting the global economy (ZENNI et al. 2021). In addition, other effects of human driven environmental change, such as biotic homogenization (Olden 2006) and forest fragmentation (TAUBERT et al. 2018) can trigger a cascade of events that result in unpredictable impacts beyond biodiversity and economic outcomes.

As an example of the unpredictable emergent outcome of invasive species, consider the magnitude of the impacts resulting from the global COVID-19 pandemic. On December 19th of 2019, the world witnessed the first 21st world pandemic outbreak that spread the non-native virus of SARS-CoV-2 lineages beyond its natural forested regions triggering the deepest global crisis in the 21st century so far (DOBSON et al. 2020; BUCK; WEINSTEIN, 2020; TOLEFFSON, 2020; NUÑEZ; PAUCHARD; RICCIARDI, 2020). Although non-usual food practices are reported as the pandemic tipping point, the magnitude of human-driven environmental changes are in the background of activities that promoted the leap of the virus from its host to humans. Human-driven deforestation and illegal animal traffic are in the center of the pandemic outbreak. Therefore, it is without question that biological invasion is fully integrated into the Anthropocene and have severe consequences. Also, it reinforces the urgency of macroecological study designs to provide insights that support the understanding of the causes, consequences, and potential solutions of the invasive species problem.

The challenges to study species introduction at large scales

The study of species introductions (i.e., non-native species) and its impacts (i.e., invasive species) as a field of research is recent (ELTON 1958). Although there have been fast advances in the understanding of how the process of non-native and invasive species occur and why it is relevant (LOCKWOOD; HOOPES; MARCHETTI, 2007; BLACKBURN; LOCKWOOD; CASSEY, 2009; HUI; RICHARDON, 2017; ENDERS et al. 2020), the knowledge about biological invasion is still growing (BOCK et al. 2015; CRYSTAL-ORNELLAS; LOCKWOOD, 2020). One of the main challenges in studying non-native and invasive organism lies in the availability of information, which is often biased at taxonomic, spatial, and temporal scales. In situations where non-native species are known and the species data is accessed through a systematic field survey among study sites, the available information is often biased to the local accessibility and species detectability. For instance, regardless of occasional observation of a dissonant species regarding its morphology and native distribution (LIMA; KAMADA, 2004), or previous knowledge of potential occurrences of non-native species in study sites, non-native species are not always known to be assessed by systematic field surveys. This is expressed in the perception that non-native and invasive species are uncontrolled natural experiments (SAX, 2001), which results in an underestimated perception of non-native species occurrence. Yet, even with the advances in technology for gathering and merging databases, at large scales, some geographical regions, and ecological groups tends to accumulate more information regarding non-native species (DYER; REDDING; BLACKBURN, 2017; CHONG et al. 2021). Thus, a key aspect in macroecology lies in the possibility of inferring patterns and processes from a biased pool of information is practical in the context of non-native and invasive species. In this sense, there are at least two ways of accounting for the macroecological approach that can be used. First, controlling the predictions for predictors in the native region of non-native species using correlative models that integrates species occurrences and environmental conditions to predict the suitability of non-native species in time and space. Second, controlling pattern and process predictions for the native species composition in the non-native region to measure the influence of assembly rules in the persistence of non-native species in the introduced region.

Ecological niche models and Environmental similarity

Formalized by HUTCHINSON (1957) the ecological niche is a seminal ecological concept used to describe and quantify the association of species with their environment. In the modern theory of ecological niches, abiotic and biotic conditions interplay to result in a realized, with abiotic conditions alone representing the fundamental component of the species niche. The fundamental niche consists in all the potential environments and conditions that support species population persistence in the absence of biotic interaction, and therefore is limited only by inherent species capacity to occupy an environment within a species' range of physiological tolerance (see Grinnelian niche in Figure 2A). Conversely, the realized niche consists in all the potential environments and conditions that support species persistence in the presence of biotic interaction (Figure 2B) and is limited by the species capacity to outcompete for the available resources. In addition, it is conventionally accepted that the realized niche is a subset of the fundamental niche where the species is a superior competitor and can persist. In the context of biological invasions, the interplay between the realized niche of a species in its native and non-native conditions can result in distinct niche scenarios in space and time, which reflect underlaying mechanisms that drive species persistence in a new condition given the similarities and differences between native and introduced environments (GUISAN et al. 2014, Figure 2C).

The fundamental niche is also the core concept in the Environmental niche model algorithms (Figure 2B). Environmental niche models consist in the use of several statistical tools to correlate the observed occurrences of a species with a set of climate or habitat information to predict the species occurrences under specific conditions or habitats (SILLERO; BARBOSA, 2021). However, in cases when species persistence is affected by species' dispersal capacity, Hutchinson's realized niche framework does not properly represent the species niche and to predict species occurrences using environmental predictors, a different framework has been developed. Such framework is part of the Biotic, Abiotic and Moving diagram (BAM) that explicitly declare that the occurrence of a species is limited by abiotic tolerance, biotic interactions, and species capacity of dispersion (SOBERÓN; PETERSON, 2005, see Figure 2B diagram). Assuming that species traits related to the BAM-framework are inherited and conserved through evolution, the environmental niche model assumes that well-calibrated models should result in modeled niches that implicitly include all these constraints and can be used to predict fundamental niches across space and time.

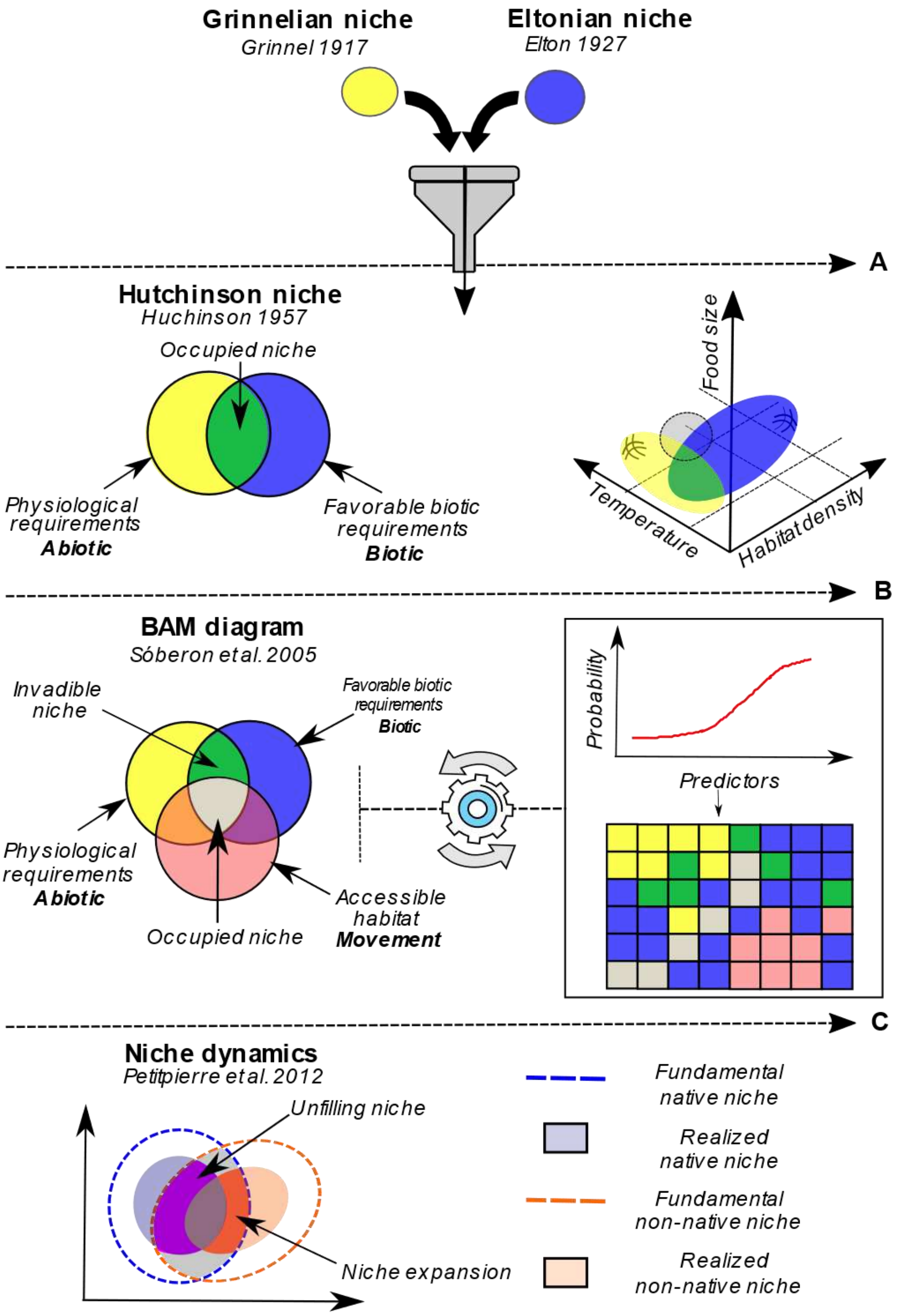

Figure II: Overview of niche concept and its uses as a tool to investigate non-native patterns and processes at large scales. Dashed arrows delimit the step forward progression in the use of ecological niches. The blue circle and yellow circle indicate Grinnell's (GRINNEL 1917) and Elton's (ELTON 1927) niches, which were mixed to compose the Hutchinson's (HUTCHINSON 1957) niche. **A) Hutchinson's niche:** In the left, a heuristic representation of Hutchinson's niche. Yellow and blue circles indicate the abiotic and biotic fundamental niche, respectively. Green area indicates the realized niche (i.e., the set of environments within which a species is found that derive from suitable abiotic and biotic conditions). In the right, a cartesian representation of Hutchinson's niche. Axes delimit the multidimensional nature of Hutchinson's niche and ellipses indicate the niches' volume within the multidimension niche space. This is the core of vacant niche hypothesis where hollow spaces (represented as dashed lines) within the niche volume should be available to be filled by a colonizing species (i.e., non-native species). **B) Modeling niche framework:** In the left, heuristic representation of environmental niche model components that represents Hutchinson's niche diagram in the presence of species movement constraint (red circle). In this framework the realized niche is referred as occupied niche and is the intersection of the biotic, abiotic and accessibility of species. The potential niches outside species occupied niche that match with the portion of Hutchinson's realized niche. These information are processed by environmental niche model algorithms to predict the suitability of a locality using a set of environmental conditions (*modeling procedure*), and then spatializing the estimation on geographical space to classify areas suitable for species presence (*lattice grid*). **C) Niche dynamics framework:** This framework decomposes the Hutchinson's niche into at least three set of niches: Niche filling, niche unfilling, and niche stasis, which are used to infer ecological and evolutionary processes underlying the non-native species persistence (for more details see GUISAN et al. 2014).

As a consequence, environmental niche models are widely used to investigate a large number of questions in theoretical and applied ecology. Such environmental niche models can be used to support the design and decision for conservation priorities and biodiversity assessment (GUISAN et al. 2013), predict zones of climate stability among time (CARNAVAL; MORITZ, 2008), and predict the risk assessment of biological invasions (ADELINO et al. 2017; SALES et al. 2017; DASILVA et al. 2018; PEREIRA et al. 2019).

Phylogenies and species differences

The filtering framework is the main process used to study ecological communities and has been widely explored in the context of non-native and invasive species (GALLIEN; CARBONI, 2017). In the filtering framework, the focal question is investigating if abiotic constraints or biotic interaction leads to the observed patterns of species and traits structure in the community. Thus, two major approaches are used to quantify species ecological (dis)similarities, based on species ecological function (i.e., trait-based approach), and the evolutionary divergence (i.e., phylogenetic approach). In the former, the morphological trait diversity is used to access trait variation within the community to describe the relevant characteristics of species performance in the community under the assumption that these traits can link species interaction and environmental conditions. The latter use species evolutionary relationship to describe community structure based on species evolutionary history under the assumption that species differences increase with increasing evolutionary time. Together, the combination of species traits and phylogenies compose the field of ecophylogenetics that consists in integrating the background niche information contained in the phylogenetic structure with the ecological function contained in species morphological traits (CADOTTE; DAVIES, 2016). In ecophylogenetics it is assumed that species niches evolve in low evolutionary rates and closely related species tends to share similar niches (i.e., phylogenetic niche conservatism; Figure 3B) and, consequently, morphological traits. Thus, communities structured by closely related species are assembled by abiotic conditions that act as a filter that select species adapted to the local conditions. Conversely, communities structured by less closely related species are assembled by biotic interaction and assume that other ecological filters (i.e., competition) should influence the community structure (Figure 3C). However, it is possible that phylogenetic niche conservatism does not occur (Figure 3B), leading to the same inferred mechanism (Figure 3D) from distinct community pattern (CAVENDER-BARES, 2009; MAYFILD; LEVINE, 2010, GERHOLD et al. 2015, CADOTTE; TUCKER, 2017; Davies, 2021).

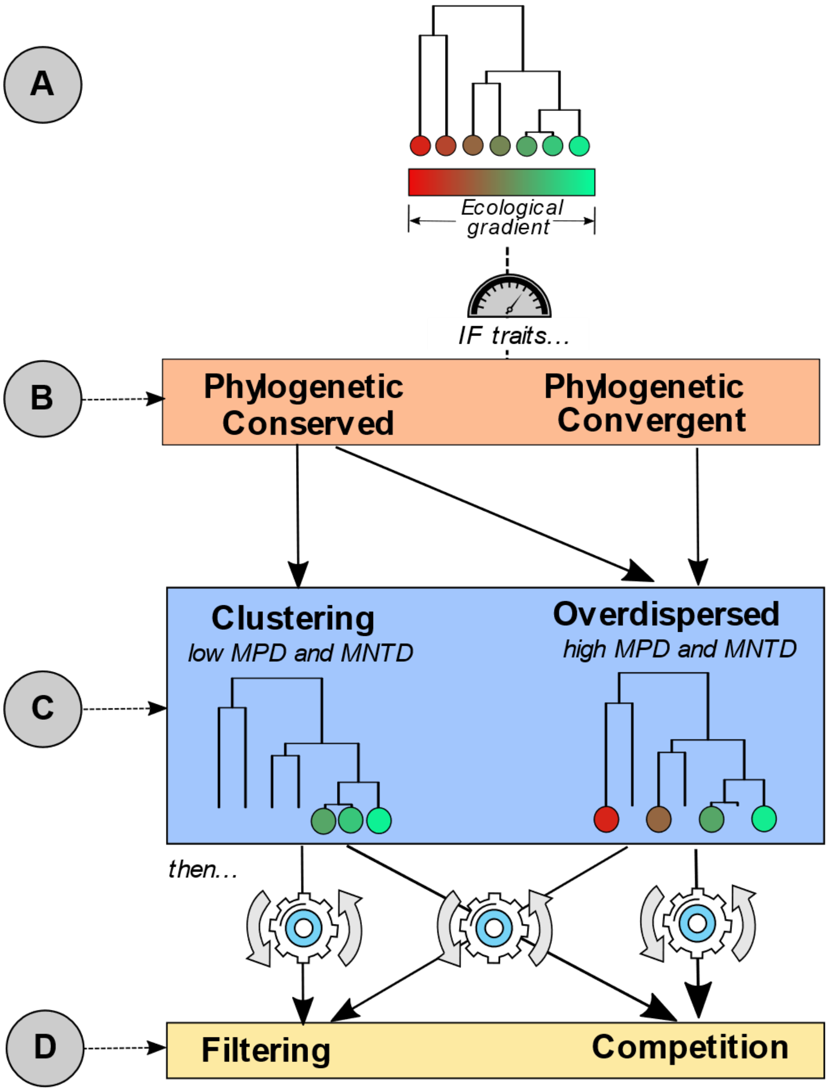

Figure III: Pathway map for phylogenetic mechanism inferences in four steps. **A)** Indicates the species pool within a geographical extent. Color indicates environmental gradient, and the dial button refers to the degree of phylogenetic conservatism or convergence in species traits. **B)** Trade-off between phylogenetic conserved and phylogenetic convergent assumption. **C)** Local community pattern derived from the filtering procedure of species pool phylogeny. **D)** Inferring process that structure local communities from the observe community patterns. Arrows indicates the potential trajectories that can result in similar outcomes.

The use of ecophylogenetics has proved useful in investigating the mechanisms related to invasive species. The method has been used to investigate the invasiveness potential of non-native species (LOSOSOVÁ et al. 2015) and the invasibility of native communities (GERHOLD et al. 2011).

The aim of this thesis

The general aim of this thesis is to investigate general patterns and processes regarding non-native species in order to understand how non-native species can enter and persist in introduced regions within a large-scale perspective. We propose that with a macroecological perspective it is possible to provide insightful information about the general properties of the ecological and evolutionary processes involved in biological invasions in a human-altered world. To achieve this, I evaluated non-native species occurrence records from several biological, geographical, and phylogenetic open-source databases at the species level to investigate the community level and climatic properties of non-native species at large geographical gradients.

In the first part of the thesis, I used phylogenetic species relatedness to investigate potential similarities between the global patterns of non-native bird species and evolutionary biodiversity patterns for the native species pool in the introduced regions. Specifically, I considered the native species composition in the recipient community to examine how the phylogenetic distance of non-native bird species to the native species of the recipient community varies between biogeographical regions, as well as between tropical and temperate regions. Additionally, I used the biogeographical realms as discrete geographical categories to investigate the influence of the phylogenetic distance from non-native to native species in the pattern of success and failure of non-native bird species.

In the second chapter of the thesis, we used non-native species occurrences and climate models to investigate the spatial pattern and potential niche processes associated with the observed introduced vertebrate species in Brazil, one of the most biodiverse countries in the world. Specifically, we investigated the degree of environmental similarity observed in Brazil with the native distribution of non-native vertebrates, and how much a species' environmental occupancy is influenced by the species' native niche similarity (i.e., niche filling) or the occupancy of new environments (i.e., niche expansion).

I hope that this Ph.D. thesis could be used to motivate theoretical insights and practical designs that support ecological, conservation, and management practices for Brazil.

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Chapter 1 – Global mainland bird introductions reveal higher phylogenetic similarity of introduced birds to native bird communities in tropical regions

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Abstract

The investigation of the causes and consequences of species introduction is central to the understanding of current patterns and processes that drive the current distribution of introduced species. One way is to investigate the general properties of ecological and evolutionary drivers of non-native species at large scales. Here, we combined several non-native and native species database information with phylogenetic approaches to investigate macroecological and macroevolutionary patterns of non-native bird species at the global scale. We found a clear latitudinal gradient of phylogenetic similarity between non-native and native species. Our results suggests that phylogenetic imbalance of the recipient community and phylogenetic diversification differ in explaining the current patterns of phylogenetic similarity from non-native to native species. However, it allows to acknowledge underlying ecological and evolutionary mechanisms of species introductions. We conclude that both ecology and evolution matter and should interplay towards general explanation of successful of introduced species.

Introduction

The increase in international trade and faster means of transportation of goods is responsible for the breakdown of geographical barriers leading to the unprecedented increase in the worldwide distribution of non-native species (Capinha et al. 2015, Seebens et al. 2017). This reshuffling of the earth's biota has enormous negative impact on biodiversity and can culminate with the emergence of new ecosystems (Olden 2006, Ellis & Ramankutty 2008, Pecl et al. 2017, Pyšek et al. 2020). Current developments in the field of invasive ecology recognize the relevance of non-native and invasive species in the loss of biodiversity (Bellard et al. 2016), in the modification of ecosystem functions and services (Ricciardi et al. 2013, Crystal-Ornelas & Lockowood 2020) and in causing severe economic damage and health problems around the world (Diagne et al. 2021, Zenni et al. 2021). In addition, there is no expectation of saturation on the accumulation of non-native species, resulting in advancing the threat of invasive species across the globe in the near future (Seebens et al. 2017, Essl et al. 2020, Seebens et al. 2021). Thus, due to the urgent necessity of understanding the global drivers and impacts of biological invasion in a changing world, the large-scale investigation of patterns and processes (i.e., macroecology approach) that shaped the current non-native species distribution is essential to the comprehension of the potential causes and consequences of species introductions (Reeding et al. 2019, Essl et al. 2020). For instance, macroecological studies highlight the tendency of non-native species to retain their native climatic characteristic even in the presence of anthropogenic environmental changes (Petitpierre et al. 2012, Broeniman et al. 2012, Dawson et al. 2017, Reeding et al.

2019, Liu et al. 2020). In this sense, most studies at a broad scale usually use climatic models to link non-native species and environmental conditions (Sales et al. 2017, da Silva et al. 2018, Liu et al. 2020, Broennimann et al. 2021), while general questions regarding macroecological patterns and processes of non-native species remains open (Blackburn et al. 2019). For instance, some studies have looked at macroecological patterns of non-native species, such as the latitudinal gradient of species richness (Sax 2001) and Bergmann's rule (Blackburn et al. 2018), but other patterns particularly on species distribution is lacking. Thus, the macroecology of non-native species has the potential to address questions regarding the underlying causes of the distribution of non-native species in a faster environmental-changing world.

The study of biodiversity patterns (i.e., Bergman's rule, latitudinal gradient in species richness) is well established in biogeography and has resulted in important theoretical frameworks for understanding species distribution patterns (Wiens & Donoghue 2004). The same theoretical principles can be applied to non-native and invasive species (e.g., niche conservatism), allowing a better understanding of the ecological and evolutionary drivers associated with the distribution of non-native and invasive species (Wiens & Graham 2005, Wiens et al. 2010). Similarly, macroecological approaches have contributed to the investigation of hidden drivers of non-native and invasive species as well as in forecasting the trajectories of invasive impacts in an accelerating changing world (Seebens et al. 2017, Essl et al. 2020, Seebens et al. 2021, MacLachlan et al. 2021). For instance, macroecology has been crucial to the understanding of the movement of non-native species by tracking the changes in the historical and contemporary routes, and its effects in the tree of life (Reino et al. 2017, Scheffers et al. 2019), reinforcing that anthropogenic driver alone, such as the economy and the species trade, does not fully explain the patterns of introduced species (Moser et al. 2018). In this sense, macroecological parameters such as the range size of the native distribution of the non-native species and the geographical distance of the native region to non-native regions could influence in the distribution patterns of non-native species. Consequently, the relevance of species-area relationship, latitudinal gradient of species richness (Guo et al. 2019, Guo et al. 2020) as well as non-native and invasive knowledge shortfalls (Pyšek et al. 2008, Chong et al. 2021) can be accessed through macroecology. Therefore, it is now possible to integrate several fields of ecology and evolution to scrutinize theoretical hypothesis of biological invasion at large scales, giving insights to the mechanisms associated with the causes and consequences of the introduction and establishment of non-native species.

A widely studied mechanism in ecology and evolution is the role of species differences in shaping community composition (HilleRisLambers et al. 2012). Community ecologists have used species ecological traits and its evolutionary relationship (i.e., functional and phylogenetic approach, respectively) to infer if species coexistence is derived from abiotic (i.e., environmental filter) or biotic (i.e., competitive exclusion) processes (Cavender-Bares 2009). To date, the filter perception has been successfully integrated in the non-native and invasive species context, which are used to address fundamental questions regarding ecological interactions, environmental gradients, and co-occurrence processes in recipient community (Gallien & Carboni 2017). For instance, the changes in species richness imposed by the introduction of non-native species can severely change the functional structure of recipient native communities leading to a pervasive impact on local biodiversity and ecosystem functioning (Toussanint et al. 2018). This is related to the non-native species capacity to invade a new community (i.e., invasiveness), as well as the degree to which recipient communities are opened to new species or lineages (i.e., invasibility) given the interplay of ecological and evolutionary effects of non-native and native species differences (Gerhold et al. 2011, Lossovà et al. 2015, Cadotte et al. 2018). For instance, the unresolved Darwin conundrum predicts that non-native species that have low phylogenetic relatedness to the recipient community can co-existence due to the differences of niche-based mechanisms than non-native species with high phylogenetic relatedness to the recipient community (Cadotte et al. 2018). Non-native species closely related to species in the recipient community can coexist due to shared pre-adaptations for specific conditions or habitats. This can be currently interpreted as the relevance of environmental filtering in supporting the establishment of closely related non-native species. Conversely, non-native species that are less phylogenetically related to the species in the recipient community can also coexist due to the advantages of niche differences (Cavender-Bares 2009). This is currently interpreted as the result of the weak effect of the environment in selecting the non-native species, which is consistent with species assembly being structured by interspecific competition processes (Cavender-Bares 2009). However, few studies based on non-native and invasive species look at broad macroecological patterns considering the phylogenetic relationship of non-native and native species. For instance, a key question that can be addressed is the potential occurrence of a latitudinal gradient regarding phylogenetic structure of non-native species.

The latitudinal pattern in species diversity is potentially the most recognized biological pattern in ecology and evolution. Although there are a few exceptions to the increase in species diversity towards low latitudes (Rabosky et al. 2018), the latitudinal gradient of diversity is remarkable for its consistency at different geographic scales and taxonomic groups (Mittelbach et al. 2007, Kinlock et al. 2018). While no consensus exists in explaining the disparity of species across a tropical to non-tropical gradient (Mittelbach et al. 2007, Brown et al. 2014, Pontarp et al. 2019), at large scales, biogeographical, evolutionary, and climatic mechanisms often vary with the latitudinal gradient (Hawkins 2003, Wiens & Donoghue 2004, Pigot et al. 2016). However, few studies have addressed latitudinal gradient questions in the field of biological invasion (Sax et al. 2001, Guo et al. 2012, Blackburn et al. 2018, Kirk et al. 2021) and the manner in which non-native species interplay with native species in an evolutionary context across latitudinal gradients remains open. In addition, the latitudinal gradient of non-native species can inform the role of ecological and evolutionary processes influencing non-native species establishment. Indeed, the relevance of evolutionary history and contemporary factors (i.e., ecological, and human-induced environmental changes) in influencing the establishment of non-native species were previously stated (Sax 2001). However, the contribution of non-native to native species phylogenetic relatedness (i.e., lineage legacy *sensu* Sax 2001) in shaping non-native species latitudinal gradient and its implications are still elusive. Therefore, at large scales, phylogenetic relatedness between non-native and native species has the potential to scrutinize classical (i.e., biotic resistance hypothesis) and contemporary (i.e., invasive meltdown) theoretical assumptions regarding the drivers of non-native species establishment (Enders et al. 2020).

In this study we examine the phylogenetic relatedness of non-native bird species to the native species of the recipient community along a latitudinal gradient. We explicitly considered the native species composition in the recipient community to examine how the phylogenetic distance of non-native bird species to the native species of the recipient community varied between biogeographical regions, as well as across a latitudinal gradient. Specifically, we used the introduced status of non-native species to investigate the influence of phylogenetic relatedness on the success of establishment. In addition we applied phylogenetic methods to investigate the relevance of tree topology (i.e., lineage dependencies) and the phylogenetic diversification process of the species in the recipient community in supporting non-native species across the latitudinal gradient.

Methods

Non-native species list and assembly definition

The list of non-native species was collected from the GAVIA database (Dyer et al. 2017). GAVIA is currently the world's most up-to-date collection for non-native birds that is based on peer-reviewed and unpublished studies, encompassing data from atlases, country-level species lists and, expert repositories (Dyer et al. 2017). In addition to the taxonomic information at the species level, the database provides information on introduced biogeographical regions, five classes of introduction status, and sources for the localities where each non-native species was observed, including mainland and island regions. Therefore, the GAVIA database is currently the most comprehensive evidence-based collection for non-native bird species list. Despite the notable impacts of introduced species in the ecology and biodiversity of oceanic islands (Spatz et al. 2017), as well as the influence of human activities in transport and trading of non-native species to continental regions (Hulme 2009, Reino et al. 2017, Hulme 2021), general patterns regarding mainland non-native species are still lacking. Thus, we considered only non-native species observations from mainland regions.

We used the available references of the localities for each species classified as successfully established and unsuccessful established in the GAVIA database to define the assembly locality. In this study, the assembly locality refers to the composition of native bird species occupying the same locality of non-native bird species. To collect the geographical coordinates of each assembly in the database, we used the worldwide global maps of administrative areas database (GADM, available at www.gadm.com) considering the resolution that best fitted each non-native observation (see below). GADM is an open-source database that organize spatial data information in digital maps with at least four distinct resolution levels that varies following: Country level boundary (GADM_0 in study dataset), province level boundary (GADM_1 in study dataset), city level boundary (GADM_2 in study dataset) and neighborhood level boundary (GADM_3 in study dataset). Thus, the GADM database was used to collect the geographical coordinates for each non-native species occurrence by matching GAVIA's and GADM localities considering the most precise resolution level for each observation. Because of the variation among GADM resolution levels, we set the following importance levels to prioritize retaining high resolution administrative layers: GADM_3 > GADM_2 > GADM_1 > GADM_0. Then, the geographical coordinate of each locality was obtained by extracting the center of the selected spatial polygon for the selected level used.

Native species list and assembly composition

The list of native species for each assembly was obtained from the BirdLife International database (hereafter BirdLife; data available on www.birdlige.org). BirdLife is a global partnership focused on conserving birds' habitat, biodiversity, and natural resources. Consequently, BirdLife owns the most currently comprehensive database of worldwide birds that includes digital maps, conservation status, and species lists validated by experts. However, for the purpose of this study, we selected only mainland species (N = 1103), which are set as terrestrial species according to the BirdLife database. Therefore, our native species list is formed by the subset of species that represent only mainland birds without intercontinental migratory behavior or range distribution over the sea surface (i.e., frigates). We used the BirdLife spatial polygons to obtain the occurrence of native species for each non-native species locality. We did this by extracting the native species that had its range distribution overlayed with each non-native geographical locality.

Phylogenetic data

We used 1000 phylogenic trees from the complete Jetz et al. (2012) backbone phylogeny (data available on www.birdtree.com) and the maximum clade credibility method (Schliep 2011) to obtain the consensus tree used in further analysis. Additionally, because of potential mismatches of species identity between the databases, due to the update in species taxonomy since Jetz et al. (2012), we controlled our species list to match the species in the phylogeny. We did this by manually crossing the species identities from both BirdLife and Jetz et al. (2012) phylogeny against the Handbook of the Birds of the World (Billerman et al. 2020).

Phylogenetic tree measures of native species

We used the Colless index (Heard 1992, Coronado et al. 2020) standardized by Yule process to measure the degree of phylogenetic imbalance (Mooers & Heard 1997) of the native species pool over the latitudinal gradient. Phylogenetic imbalance is informative regarding the underlying evolutionary processes (i.e., speciation and extinction) involved in the shaping of the topology of the phylogenetic tree. Therefore, phylogenetic imbalance measures the dispersal of the clades accounting for taxa variability among different clades in the phylogeny. While several indexes (Agapow & Purvis 2002) have been proposed to quantify the phylogenetic imbalance, the Colless index (hereafter Ic) is pointed out as a powerful strategy to investigate underlying processes in clade diversification using phylogenetic trees (Kirkpatric & Slatckin 1993; Agapow &

Purvis 2002). The Ic index inspects the tree internal nodes by partitioning the species that descend from the same internal node (i.e., clade ancestor) in the phylogenetic tree. It then computes the degree of evenness of the distribution of clades over the phylogenetic tree. Greater values of Ic indicates that some clades have more descendent species than others, which leads to an increase in tree imbalance. Conversely, low values of Ic indicates an even distribution of clades along the tree, which leads to a decrease in tree imbalance. Colless index were estimated using the pruned tree for the native pool of species in each geographical locality.

In addition, we used the phylogenetic tree to investigate the influence of the phylogenetic diversification processes in shaping the phylogenetic similarity of non-native species with native species. The diversification process was measured using individual level analysis that accounts for the path from the root of the tree for each individual species using the equal splits measure (Redding & Moorers 2008). The equal splits measure evenly divides the phylogenetic distance among its daughter edges, where species with fewer close relatives are weighted. The reduced phylogenetic proximity (i.e., the reduced number of nodes) indicates a shorter path between the tip and the root of the phylogenetic tree and reflects the magnitude of the dissimilarity with other species. Thus, equal split, is a measure that accounts for the whole phylogenetic tree to measure the degree of species rarity. We then used the inverse of the equal split measure, as implemented by Jetz et al. (2012), to infer the phylogenetic diversification rate. The inverse of equal splits (hereafter iES) can be used to estimate the splitting rate of the path to a tip, where rapid diversifying clades will have short edges length shared among the species. Thus, low values of iES indicates recent lineage diversification events and high values of iES indicates no evidence of recent diversification rates.

Phylogenetic distance of native and non-native birds

Phylogenetic distance of non-native species to the closest native in the recipient bird community was determined using the minimum nearest trait distance (Cadotte and Davies 2016, hereafter MNTD). Because large phylogenetic distances indicate the accumulation of evolutionary changes among species (Webb et al. 2002), the MNTD provides a conservative measure of the minimum degree of species similarity between non-native to native species in the recipient bird assembly. The MNTD value is calculated using the cophenetic distance obtained from the branch length in the phylogenetic tree to estimate the evolutionary distances between the pair of species. Thus, low values of MNTD (i.e., values toward zero) indicate a high degree of similarity between the species and high values of MNTD (i.e., values away from zero) indicate a low degree of similarity between the species. To investigate the spatial variation of MNTD, we grouped all assembly localities in regular intervals of one degree of latitude and used the average MNTD values of the latitudinal intervals as a response variable against latitude. To inspect the robustness of the MNTD values with latitude, we investigated the magnitude of the observed MNTD values against the MNTD values obtained from a null distribution. The null distribution was determined by calculating the expected MNTD values for all non-native established species (n = 256) and its closest native species relative for each bird recipient community in one-degree latitudinal intervals. We then calculated the effect size of observed MNTD against null expectation (Cadotte and Davies 2016). Effect sizes were estimated by the difference between the observed MNTD values and mean MNTD values obtained from the null distribution divided by the standard deviation of MNTD for the null distribution. Lower negative values of effect sizes indicate that the magnitude of the observed MNTD tends to be phylogenetically more similar to the native bird assembly. Conversely, positive values of effect sizes indicate that the non-native species tends to be phylogenetically less similar than the native bird community than expected by chance.

Finally, we estimate the influence of phylogenetic similarity from non-native to native species in the proportion of successful introduced species between tropical and temperate latitudes. The proportion were estimated using the total number of successful introductions over the sum of success and non-success introductions by latitudinal band. Them, we used 30 degrees latitude north and south as threshold to distinct temperate from tropical bands and used additive models to inferring the proportion of successful species as a function of MNTD values for tropical and temperate regions independently.

Statistical analysis

To model the MNTD values across latitude, we used generalized additive models (hereafter GAM; Wood 2017). The gain in using additive models is the capacity to simultaneously capture linear and non-linear effects of predictors. For the latter, GAM use smooth function parameters to express nonlinear specification of the predictor and response covariates in a flexible way (Wood 2017). Smooth functions are piece-wise polynomials functions (*usually splines*) that interpolate smooth curves among the sum of K fixed basis function (*knots*). The number of K basis functions influence the complexity of the smooth curve leading to the wiggly curves when it is modeled in the presence of an excessive number of basis function (i.e., model overfit). Model overfit is counteracted by internal penalty parameters, we used effective degrees of freedom and k-index statistical tests to properly inspect the relevance in the number of used base functions. In GAM, the complexity of basis function is measured by the effective degrees of freedom (EDF) that range from 1 in a linear relationship to K-1 in smooth relationship. We inspected the number of basis function using the k-index. The k-index estimates if the dimension of the basis function is adequate by computing an estimate of the residual variance based on differencing residuals that are near neighbors according to the covariates of the smooth (*for details see* Wood 2017). K-index values below 1 indicates missing smooth patterns left in the residuals. The GAM models were fitted using the mgcv package (Wood 2011) and model assumptions were inspected using the mgcViz package (Fasiolo et al. 2020). To evaluate if species richness affected MNTD values, we fitted GLM considering the module of latitude (MNTD ~ latitude + richness) and compared with a nested modeled (MNTD ~ latitude) using a maximum likelihood ratio test.

In addition, we used a linear model to inspect if the phylogenetic imbalance of native species (*see phylogenetic imbalance of native species section*) predicted the phylogenetic similarity of non-native to native species using MNTD (*see Non-native to native relationship section*) as response variable. For statistical analysis we used the R version 4.0.3 (RCore team 2020).

Results

Overall, our dataset covered the six zoogeographical regions of the world (Figure 1.1).

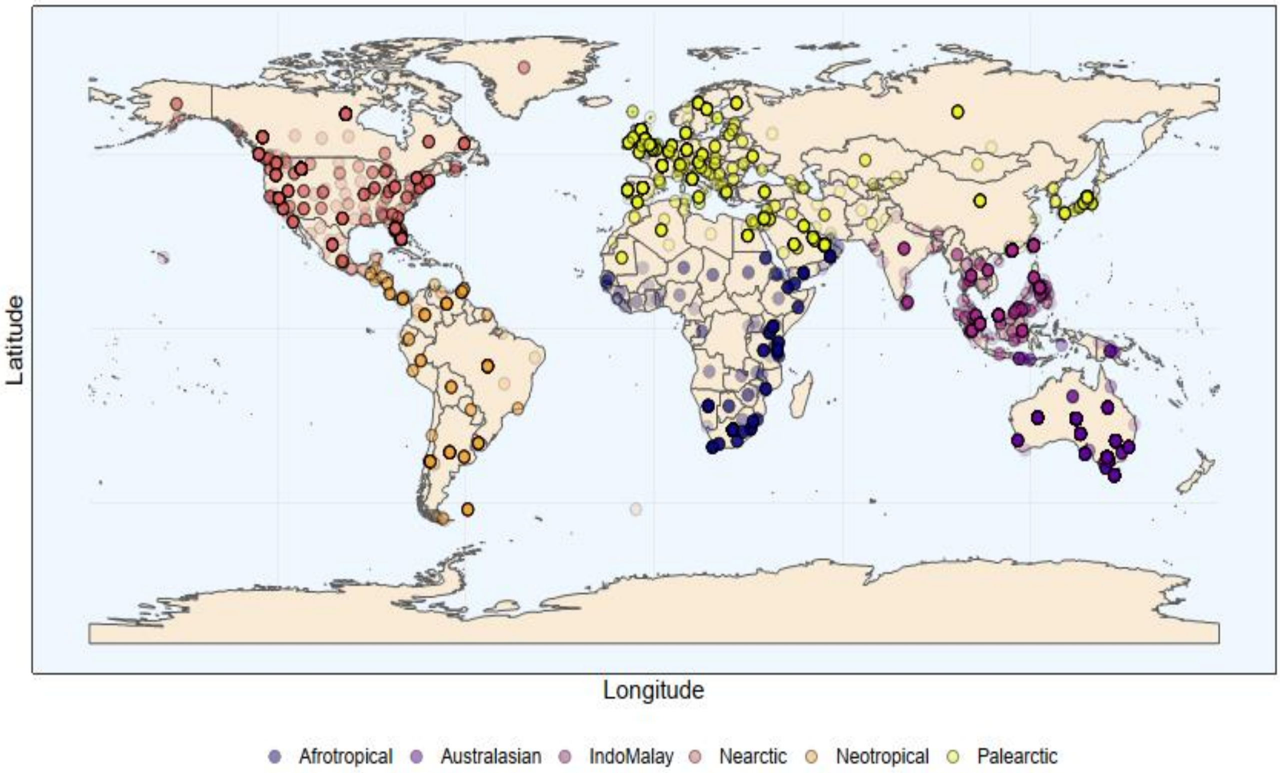

Figure 1.1: Map showing the 573 local bird assemblages grouped by biogeographical regions. Circles indicate the local recipient assembly locality obtained from matching Dyer et al. (2017) local description and the global administrative boundaries (GADM) data base (see Non-native species list and assembly definition). Lighter to opaque shades of transparency indicates the degree of overlap among recipient assembly localities for each biogeographical realm. Colors indicates biogeographical realm. **Orange:** Neotropical, **Red:** Nearctic, **Yellow:** Palearctic, **Dark blue:** Afrotropical, **Purple:** Indomalay and **Dark purple:** Australasia.

We collected data for 573 mainland bird assemblages that had the presence of non-native bird species. A total of 436 non-native bird species belonging to 73 bird families were distributed among the 573 bird assemblages evaluated. Our data report a clear disparity between successful and unsuccess establishment of non-native birds. The former comprises of 85% of the available information (N = 6617) and is unevenly distributed over the globe, particularly along North America, Europe, Indonesia, and Australia (Figure 1.2). Unsuccessful established non-native bird species comprised of 14.8 % of the available information (N = 1157) and are restricted to North America, Europe, and South of Australia (Figure 1.3).

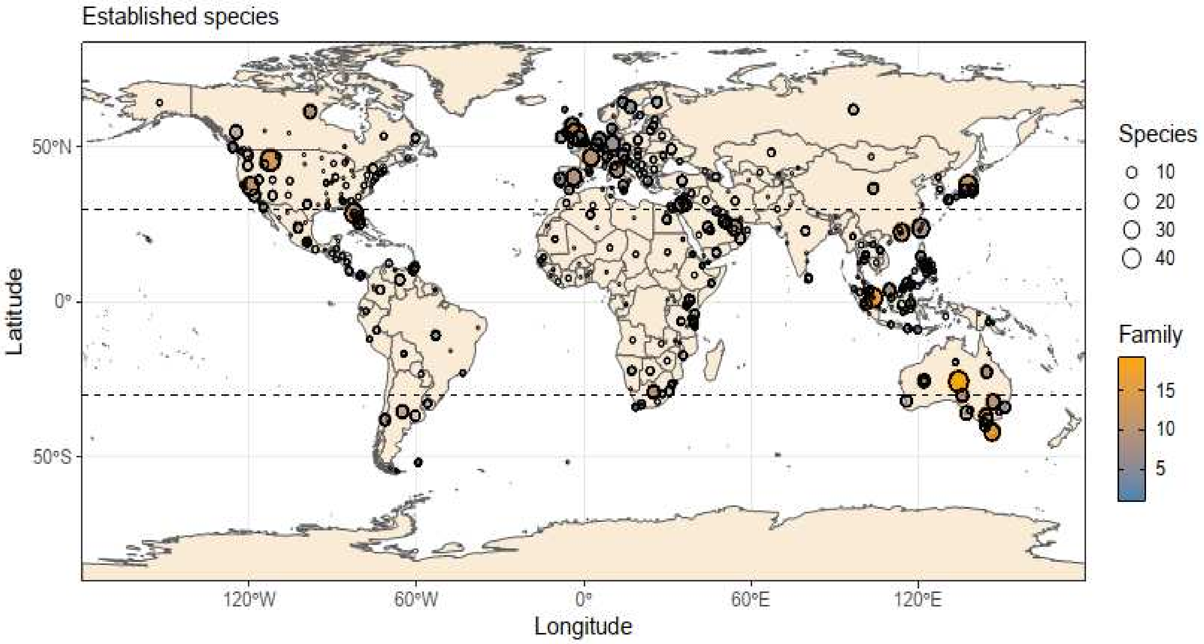

Figure 1.2: Map showing the local bird assemblages where non-native birds were successfully established according to Dyer et al. (2017). Horizontal dashed lines delimit the reference latitudes of 30 degrees north and south used to group the dataset in temperate and tropical regions. Bubble size indicates non-native species richness. Blue to orange color gradient indicates the number of bird families represented by non-native species.

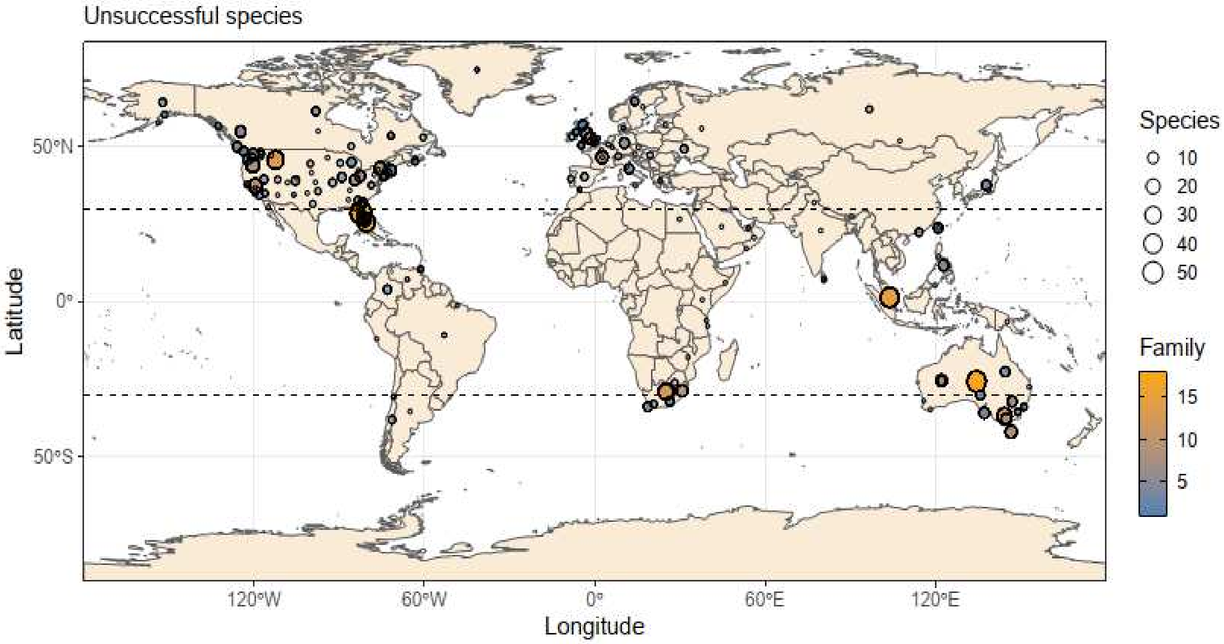

Figure 1.3: Map showing the local bird assemblages where non-native birds were unsuccessfully established according to Dyer et al. (2017). Horizontal dashed lines delimit the reference latitudes of 30 degrees north and south used to group the dataset in temperate and tropical regions. Bubble size indicates non-native species richness. Blue to orange color gradient indicates the number of bird families represented by non-native species.

The phylogenetic tree of the non-native species is formed by 427 non-native birds from 19 orders, from which five orders (Passeriformes, Psittaciformes, Galliformes, Anseriformes, Columbiformes; N = 363) represent 85% of the phylogeny. Passeriformes (N = 161) and Psittaciformes (N = 75) together represent 55% of the phylogeny and are the main groups of non-native bird species. We did not find any patterns of successful and unsuccessful introduced bird species among the phylogeny (Figure 1.4).

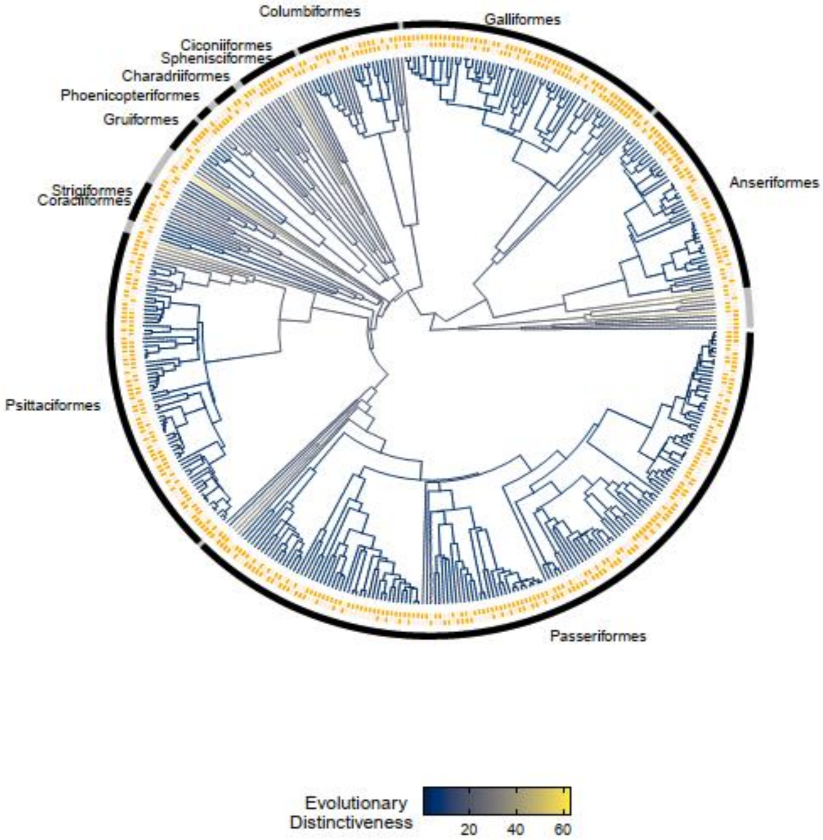

Figure 1.4: Phylogenetic relationship for 427 non-native bird species (successful and unsuccessful establishment). Branch color indicates the evolutionary distinctiveness (ED) of each non-native species from the full phylogenetic tree obtained in Jetz et al. (2012) containing 9993 bird species. Evolutionary distinctiveness uses the number of the nodes of species to the root to measure the degree of uniqueness of each species within the phylogeny, where greater ED values indicate the more unique the species is. Dark and light orange in the inner circle indicate the presence and absence of information for successfully introduced species, respectively. Dark and light orange in outer circle indicates the presence and absence of information for unsuccessfully introduced species, respectively. Black bars indicate species order. Grey bars indicate groups with less representative order in the non-native bird phylogeny. Blue to yellow color gradient indicates the degree of evolutionary distinctiveness.

Phylogenetic similarity of successfully established non-native bird species followed an inverse latitudinal pattern (Figure 1.5), with phylogenetically similarity increasing towards lower latitudes (R^2 =0.50, $p < 0.000$; see Table 1.1). The maximum likelihood ratio test indicates no effect of species richness in the latitudinal pattern (F = 0.02, df = 1 p = 0.865).

Table 1.1: Generalized Additive Model (GAM) of the average phylogenetic similarity (measured using the minimum nearest trait distance – MNTD) of successfully established non-native bird species with introduced bird assemblages against latitude. GAM was fitted with cubic splines smooth parameter and 10 basis function (k = 10). **Fixed Effects:** Indicates non-smooth parameters; **Coefficient:** Coefficient value; **SE:** Standard error; **95% CI:** Confidence interval; **t (94.44):** t- test; **p:** p-value; **R²:** Model accuracy. **Smooth Terms:** Indicates non-linear parameters; **F:** Hypothesis test (H0 = smooth term equal Zero); **df:** Degrees of freedom; **df_error:** error of degrees of freedom; **p:** p-value, **K':** the upper limit (K-1) on the number of used knots for the smooth base function; **edf:** effective degrees of freedom; **k – index:** index of the smooth base functions; **pk-value:** test of smooth base function parameter adequacy which p > 0.05 indicating adequate number of k used parameter.

<table>
<tr><td colspan="7">Fixed effects</td></tr>
<tr><th>Parameter</th><th>Coefficient</th><th>SE</th><th>95% CI</th><th>t (94.44)</th><th>p</th><th>R²</th></tr>
<tr><td>Intercept</td><td>4.10</td><td>0.04</td><td>[4.03, 4.18]</td><td>103.16</td><td>< .001</td><td>0.50</td></tr>
</table>

<table>
<tr><td colspan="9">Smooth Terms</td></tr>
<tr><th>Parameter</th><th>F</th><th>df</th><th>df_error</th><th>p</th><th>K'</th><th>edf</th><th>k-index</th><th>p_k-value</th></tr>
<tr><td>s(Latitude)</td><td>15.90</td><td>4.56</td><td>94.44</td><td>< .001</td><td>9.00</td><td>4.56</td><td>1.52</td><td>0.56</td></tr>
</table>

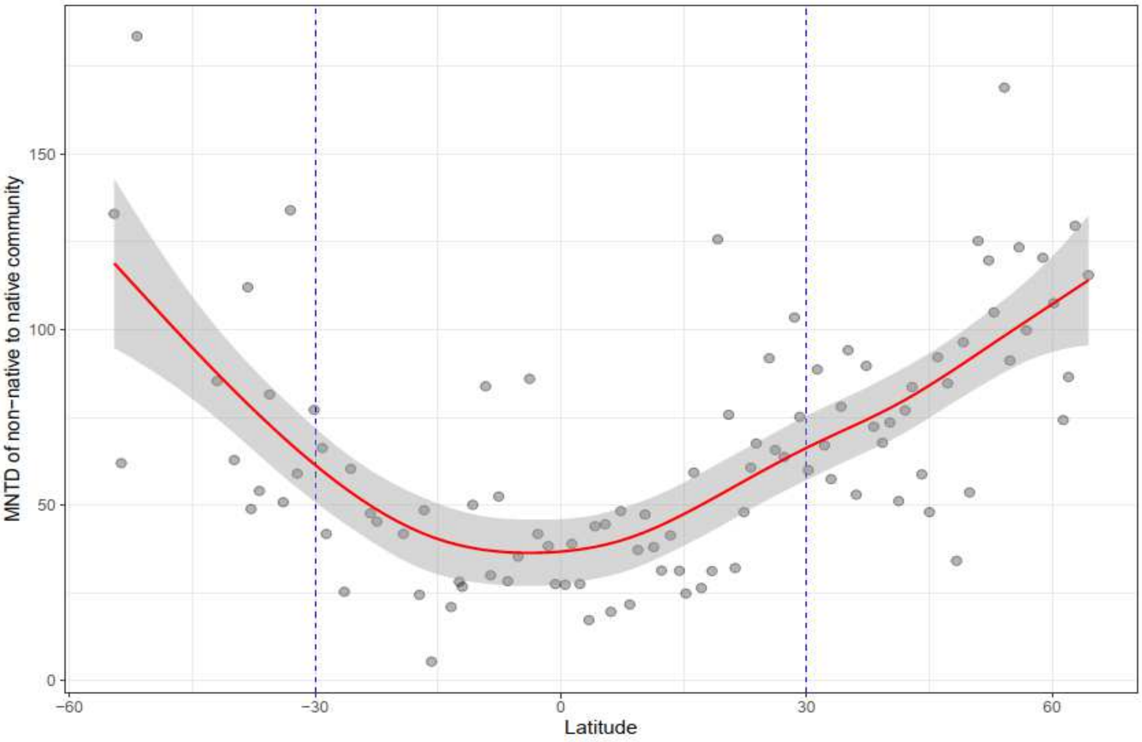

Figure 1.5: Generalized Additive Model (GAM) of the average phylogenetic similarity (measured using the minimum nearest trait distance – MNTD) of successfully established non-native bird species with native bird assemblages against latitude. GAM was fitted with cubic spline smooth parameter and 10 basis function (k = 10). Blue vertical dashed lines delimit the reference latitude of 30 degrees north and south used to group the dataset in temperate and tropical regions. Red line indicates GAM model fit and gray filling the 95% confidence interval.

Conversely, phylogenetic similarity of unsuccessfully established non-native bird species had no association with latitude (Figure 1.7; R^2 =0.005, p = 0.22; see Table 1.2).

Table 1.2: Generalized Additive Model (GAM) of the average phylogenetic similarity (measured using the minimum nearest trait distance – MNTD) of unsuccessfully established non-native bird species with introduced bird assemblages against latitude. GAM was fitted with cubic splines smooth parameter and 10 basis function (k = 10). **Fixed Effects:** Indicates non-smooth parameters; **Coefficient:** Coefficient value; **SE:** Standard error; 95% **CI:** Confidence interval; **t (68.00):** t- test; **p:** p-value; **R^2:** Model accuracy. **Smooth Terms:** Indicates non-linear parameters; **F:** Hypothesis test (H0 = smooth term equal Zero); **df:** Degrees of freedom; **df_error:** error of degrees of freedom; **p:** p-value, **K':** the upper limit (K-1) on the number of used knots for the smooth base function; **edf:** effective degrees of freedom; **k – index:** index of the smooth base functions; **pk-value:** test of smooth base function parameter adequacy which p > 0.05 indicates adequate number of k used parameter.

<table>
<tr><td colspan="9">Fixed effects</td></tr>
<tr><th colspan="2">Parameter</th><th>Coefficient</th><th>SE</th><th>95% CI</th><th>t(68.00)</th><th colspan="2">p</th><th>R^2</th></tr>
<tr><td colspan="2">Intercept</td><td>4.40</td><td>0.07</td><td>[4.27, 4.53]</td><td>67.55</td><td colspan="2">< .001</td><td>0.0005</td></tr>
<tr><td colspan="9">Smooth Terms</td></tr>
<tr><th>Parameter</th><th>F</th><th>df</th><th>df_error</th><th>p</th><th>K'</th><th>edf</th><th>k-index</th><th>p_k-value</th></tr>
<tr><td>s(Latitude)</td><td>1.52</td><td>1.00</td><td>68.00</td><td>0.221</td><td>9</td><td>1</td><td>0.95</td><td>0.4</td></tr>
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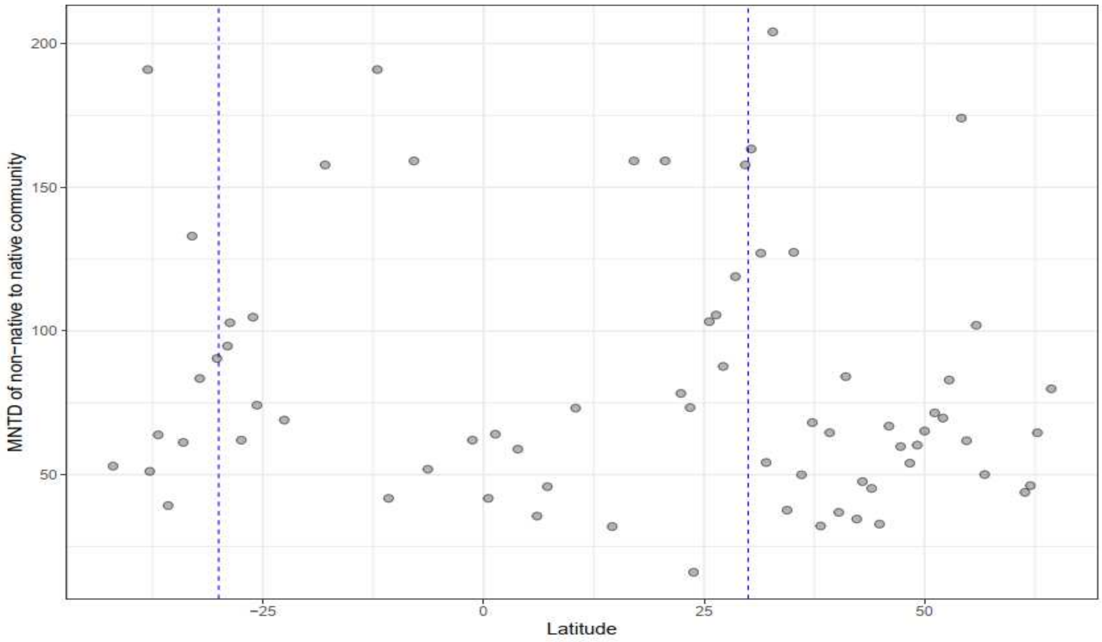

Figure 1.6: Generalized Additive Model (GAM) of the average phylogenetic similarity (measured using the minimum nearest trait distance – MNTD) of unsuccessfully established non-native bird species with native bird assemblages against latitude. GAM was fitted with cubic spline smooth parameter and 10 basis function (k = 10). Blue vertical dashed lines delimit the reference latitude of 30 degrees north and south used to group the dataset in temperate and tropical regions.

Effect sizes of the phylogenetic similarity of established non-native bird species with native bird assemblages decrease towards lower latitudes (Figure 1.7), which indicates that non-native bird species were phylogenetic more similar to native bird assemblages in tropical latitudes.

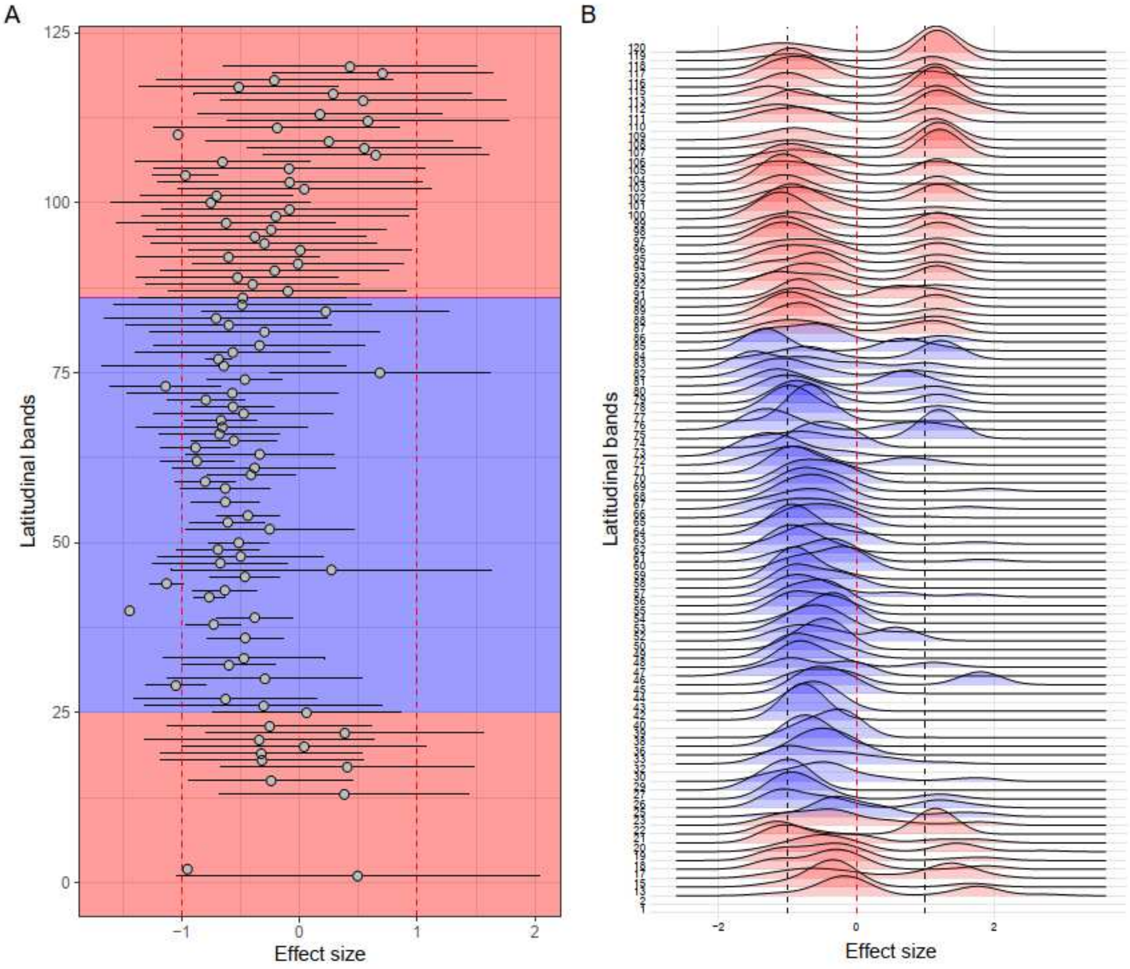

Figure 1.7: Effect sizes of the phylogenetic similarity (measured using the minimum nearest trait distance – MNTD) of successfully established non-native bird species with native bird assemblages across one-degree latitudinal bands. **A)** Mean effect size and standard deviation respectively. **B)** Density distribution of effect sizes for all non-native bird species across latitude. Vertical dashed lines indicate the threshold of one unity of effect size. Horizontal axis indicates effect size. Vertical axis indicates latitudinal bands from one in south to 120 in north ranges respectively.

Finally, the proportion of non-native species establishment reached high values with increasing phylogenetic similarity of non-native bird species to recipient bird assemblages in tropical latitudes ($R^2 = 0.50$; $p < 0.000$). Conversely, the proportion of non-native species establishment reached high values with reduced phylogenetic similarity of non-native bird species to recipient bird assemblages in temperate regions (Figure 1.8; see Table 1.3) ($R^2 = 0.34$; $p < 0.000$).

Table 1.3: Generalized Additive Model (GAM) of the proportion of non-native bird species establishing in native bird assemblages in tropical and temperate latitudes. Response variable was obtained by calculating the proportion of successful and unsuccessful non-native bird species by latitudinal band. Predictor indicates the average phylogenetic similarity (measured using the minimum nearest trait distance – MNTD) of successfully established non-native bird species with bird assemblages across one-degree latitudinal bands. GAMs were fitted with the cubic spline smooth

parameter and 10 basis function (k = 10). **A)** GAM for temperate regions, **B)** GAM for tropical region. **Fixed Effects:** Indicates non-smooth parameters; **Coefficient:** Coefficient value; **SE:** Standard error; **95% CI:** Confidence interval; **t:** t-test; **p:** p-value; **R^2:** Model accuracy. **Smooth Terms:** Indicates non-linear parameters; **F:** Hypothesis test (H0 = smooth term equal Zero); **df**: Degrees of freedom; **df_error:** error of degrees of freedom; **p:** p-value, **K':** the upper limit (K-1) on the number of used knots for the smooth base function; **edf:** effective degrees of freedom; **k – index:** index of the smooth base functions; **pk-value:** test of smooth base function parameter adequacy which p > 0.05 indicates adequate number of k used parameter.

A)

Fixed effects

Parameter	**Coefficient**	**SE**	**95% CI**	**t(36.88)**	**p**	**R^2**
Intercept	-0.36	0.02	[-0.40, -0.31]	-14.57	< .001	0.30

Smooth Terms

Parameter	**F**	**df**	**df_error**	**p**	**K'**	**edf**	**k-index**	**p_k-value**
s(MNTD)	6.91	2.12	36.88	0.002	9.0	2.12	1.08	0.64

B)

Fixed effects

Parameter	**Coefficient**	**SE**	**95% CI**	**t(25.75)**	**p**	**R^2**
Intercept	-0.28	0.04	[-0.36, -0.20]	-6.99	< .001	0.37

Smooth Terms

Parameter	**F**	**df**	**df_error**	**p**	**K'**	**edf**	**k-index**	**p_k-value**
s(MNTD)	12.71	1.25	25.75	0.001	9.0	1.25	1.04	0.49

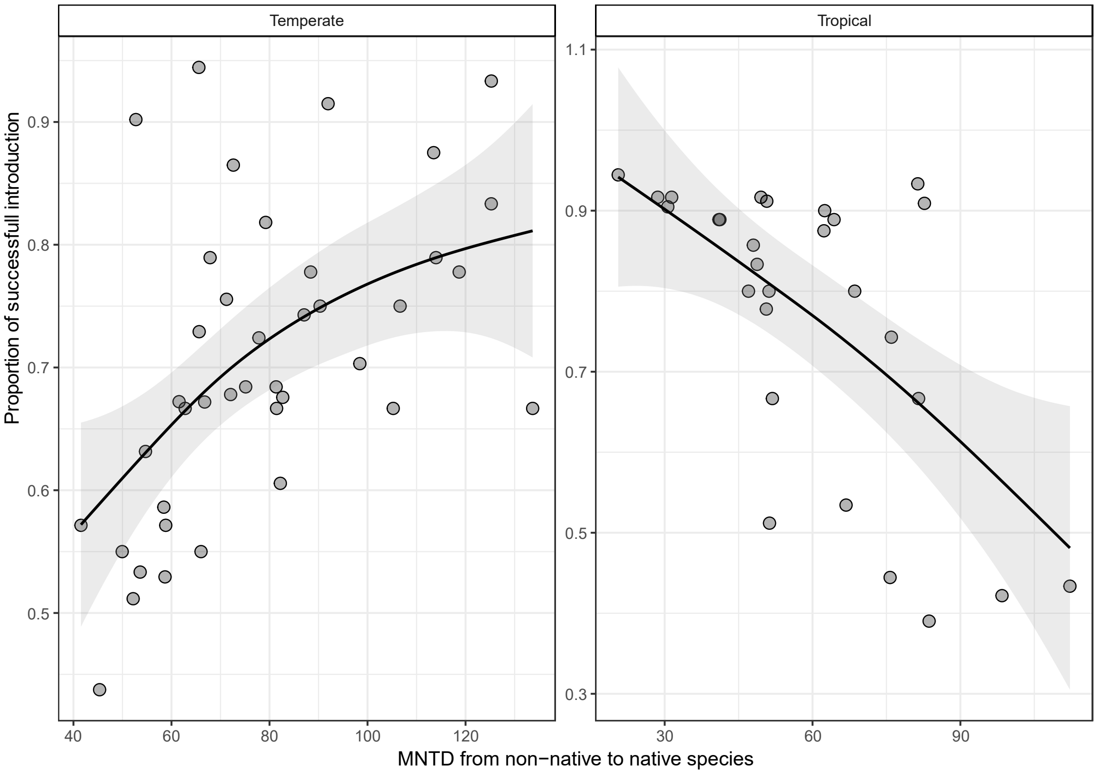

Figure 1.8: Generalized Additive Model (GAM) of the proportion of non-native bird species establishing in native bird assemblages in tropical and temperate latitudes. Response variable was obtained from the proportion of the number of successful non-native species by latitudinal band. Predictor indicates the average phylogenetic similarity (measured

using the minimum nearest trait distance – MNTD) of successfully established non-native bird species with bird assemblages across one-degree latitudinal bands.

The phylogenetic imbalance of the native bird assemblages increased towards lower latitudes ($R^2 = 0.57$, $p < 0.000$; see Table 1.4 and Figure 1.9) and is negatively associated with phylogenetic distance of non-native bird species with native bird assemblages ($R^2 = 0.10$; $t_{model} = -3.331$; $p_{model} = 0.001$; $W_{residue} = 0.979$; $p_{residual} = 0.125$) (Figure 1.10 and Table 1.5). The iES (i.e., diversification rate of the native bird assemblages) was not statistically significant with the phylogenetic distance of non-native bird species with native bird assemblages ($R^2 = 0.010$, $p = 0.153$; see Table 1.6 and Figure 1.11).

Table 1.4: Generalized Additive Model (GAM) of the phylogenetic imbalance (measured using Colless index) of native bird assemblages in function of latitude. GAM was fitted with the cubic spline smooth parameter and 10 basis function (k = 10). **Fixed Effects:** Indicates non-smooth parameters; **Coefficient:** Coefficient value; **SE:** Standard error; **95% CI:** Confidence interval; **t (91.25):** t- test; **p:** p-value; **R^2:** Model accuracy. **Smooth Terms:** Indicates non-linear parameters; **F:** Hypothesis test (H0 = smooth term equal Zero); **df:** Degrees of freedom; **df_error:** error of degrees of freedom; **p:** p-value, **K':** the upper limit (K-1) on the number of used knots for the smooth base function; **edf:** effective degrees of freedom; **k – index:** index of the smooth base functions; **pk-value:** test of smooth base function parameter adequacy which p > 0.05 indicates adequate number of k used parameter.

Fixed effects

Parameter	**Coefficient**	**SE**	**95% CI**	**t(91.25)**	**p**	**R^2**
Intercept	1.79	0.02	[1.75, 1.82]	104.97	< .001	0.57

Smooth Terms

Parameter	**F**	**df**	**df_error**	**p**	**K'**	**edf**	**k-index**	**p_k-value**
s(Latitude)	35.08	7.75	91.25	< .001	9.00	7.75	0.96	0.35

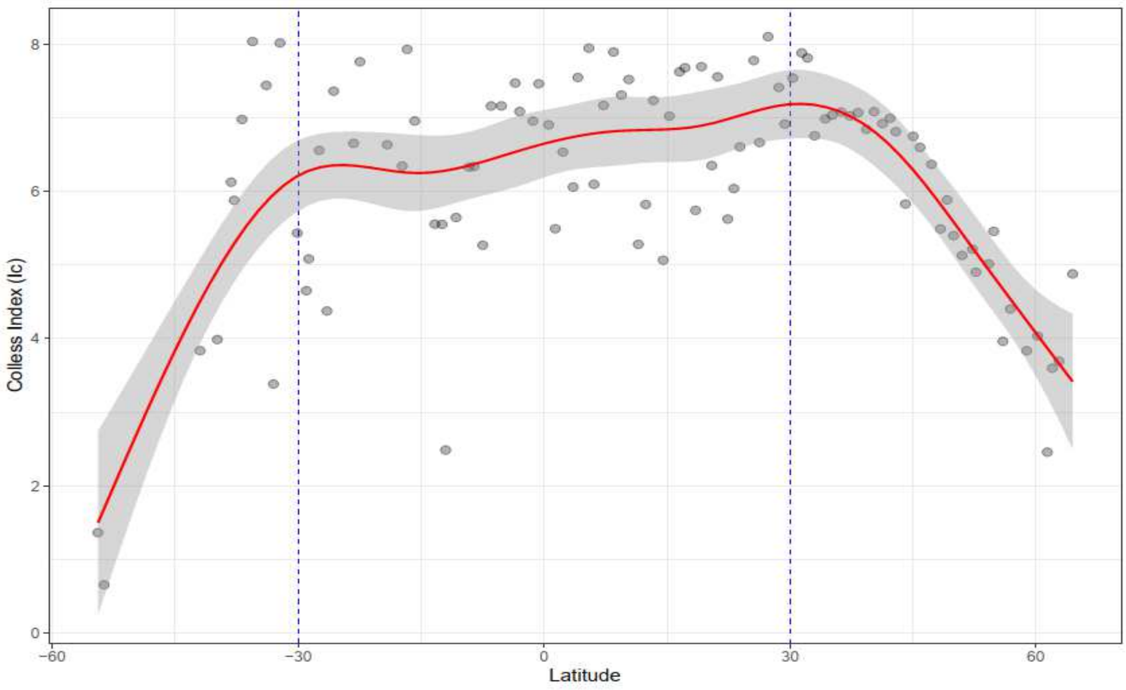

Figure 1.9: Generalized Additive Model (GAM) of the phylogenetic imbalance (measured using Colless index) of native bird assemblages in function of latitude. Blue vertical dashed lines delimit the reference latitude of 30 degrees north and south used to group the dataset in temperate and tropical regions. Red line indicates GAM model fit and gray filling the 95% confidence interval.

Table 1.5: Linear model of the average phylogenetic similarity (measured using the minimum nearest trait distance – MNTD) of successfully established non-native bird species with native bird assemblages in function of phylogenetic imbalance of native species (measured using Colless index).

Fixed effects						
Parameter	**Coefficient**	**SE**	**95% CI**	**t(94.44)**	**p**	**R²**
Intercept	106.51	13.21	[80.29, 132.73]	8.06	< .001	0.10
Coless index (Ic)	-6.91	2.09	[-11.05, -2.77]	-3.31	0.001	

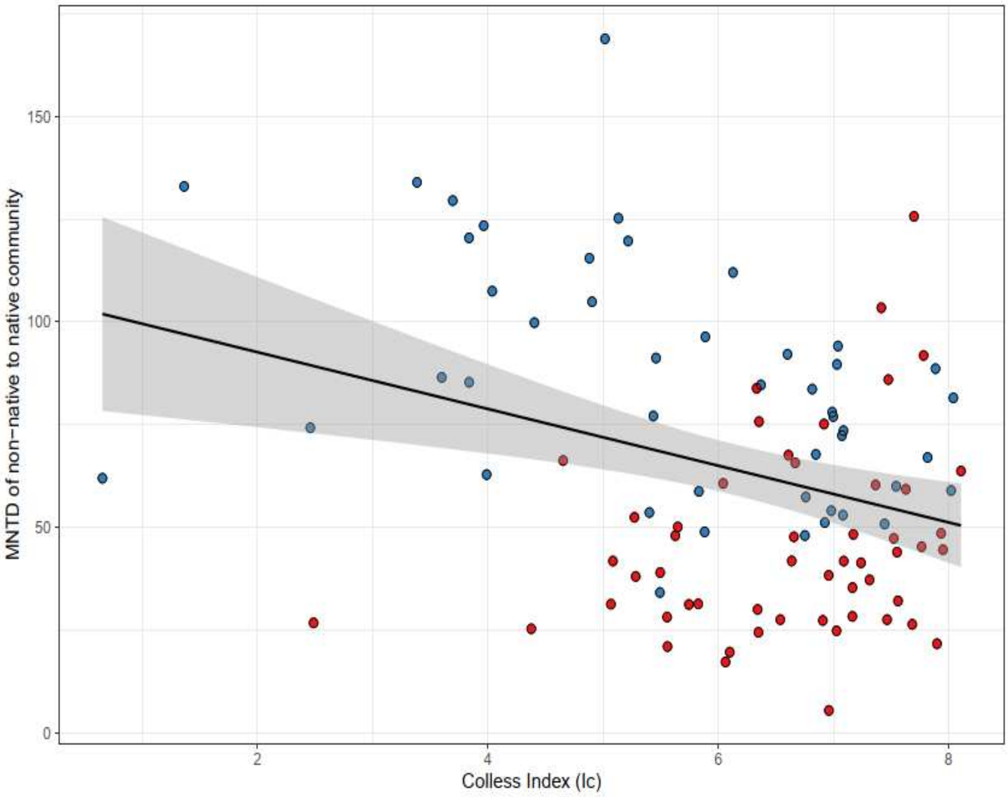

Figure 1.10: Linear model of the average phylogenetic similarity (measured using the minimum nearest trait distance – MNTD) of successfully established non-native bird species with native bird assemblages in function of phylogenetic imbalance of native species (measured using Colless index). Blue and red circles represent temperate and tropical latitudes respectively.

Table 1.6: Linear model of the average phylogenetic similarity (measured using the minimum nearest trait distance – MNTD) of successfully established non-native bird species with native bird assemblages in function of diversification rate of native species (measured using the inverse of equal splits).

Fixed effects					
Parameter	**Coefficient**	**SE**	**t**	**p**	**R²**
Intercept	34.70	21.65	1.603	0.112	0.010
Diversification rate (iES)	130.19	90.40	1.440	0.153	

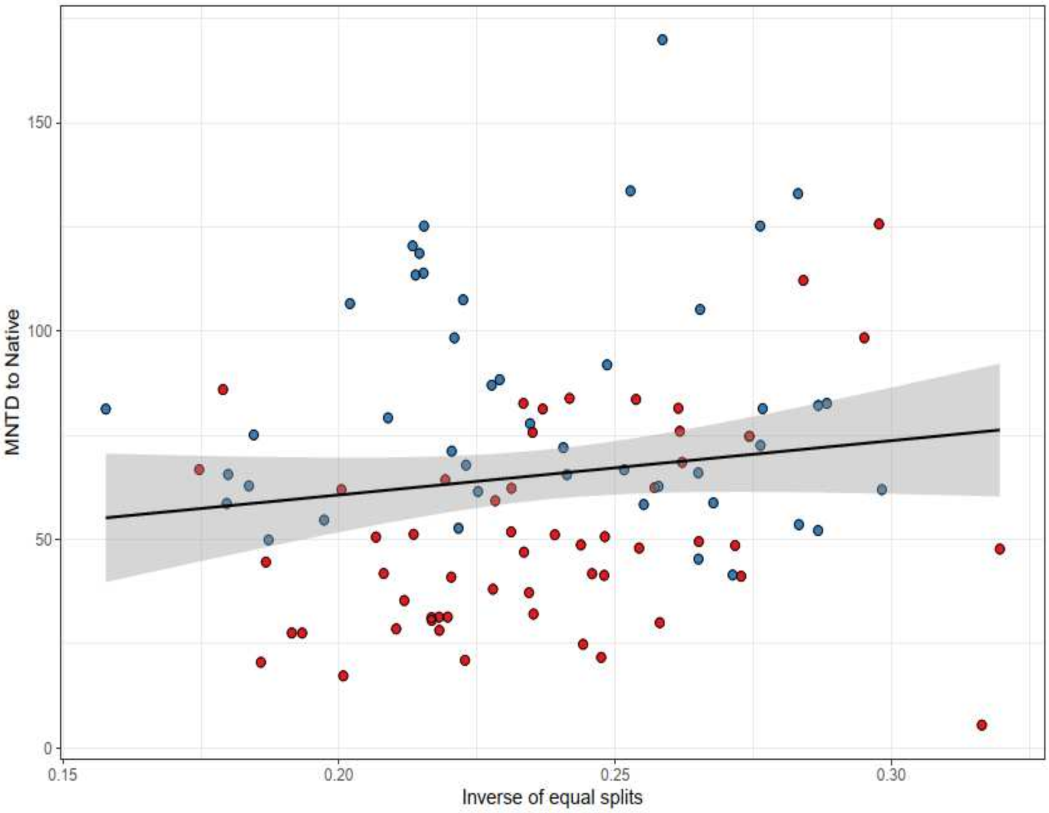

Figure 1. 11: Linear model of the average of the phylogenetic similarity (measured using the minimum nearest taxon distance – MNTD) of successfully established non-native bird species with native bird assemblages in function of diversification rate of native species (measured using the inverse of equal splits). Blue and red circles represent temperate and tropical latitudes respectively.

Discussion

Previous studies have shown that the use of phylogenies has an important contribution in understanding the co-occurrence of non-native and native species (Gerhold et al. 2011, Li et al. 2015, Li et al. 2015b, Cadotte et al. 2018). However, the standard approach of inferring ecological and evolutionary mechanisms from the observed pattern of species co-occurrences (the inductive approach sense Gerhold et al. 2015) fails to identify broad perspectives in which eco-evolutionary situations could be used to investigate the causes of observed patterns (Gerhold et al. 2015, Gerhold et al. 2018). Following Gerhold et al. (2015) perspective, our study has the aim of providing insights in the investigation of both the potential causes (i.e., phylogenies as a result) and the potential mechanisms (i.e., phylogenies as an ecological proxy) in the understanding of large-scale patterns of non-native and native bird species across the world. Remarkably, our results show a clear latitudinal gradient of phylogenetic similarity of non-native species to native bird assemblages and phylogenetic imbalance for species in the recipient community. This suggests that the evolutionary history of non-native and native species in recipient communities is a relevant factor with potential influence in the outcome of the introduction of non-native species. Therefore, we propose that our results might be scrutinized under a conceptual framework of ecology and evolution with the aim of debating theoretical and practical pathways for the understanding of invasive ecology across latitudinal gradients.

Phylogenies as a proxy of ecology

Phylogenetically similar species are expected do have similar ecological niches (Webb et al. 2002, Wiens & Graham 2005, Li et al. 2015). Our findings suggest that in tropical latitudes, the phylogenetic similarity of non-native bird species to the recipient bird community is compatible with the occurrence of non-native bird species. Although this could indicate that the introduction process in tropical latitudes is occurring with species competition, it is more likely that non-native bird species have the necessary pre-adaptation to establish a successful population (Fig. 1.12 A). Pre-adaptation can be associated with the shared similarity in the evolutionary history between the non-native species and the native species that compose the local community in the introduced regions. This is supported by the possibility that different pools of species can share similar clade positions in the phylogenetic relationship (see figure 2 in Cavender-Bares et al. 2009), which can reflect in trait similarities such as physiological tolerances. Also, it is likely that these phylogenetic similarities could support ecological interactions, because non-native species might have the ecological attributes that allow them to interact with the species that the native bird species interacting with in the community (Traveset & Richardson 2014). Therefore, historical processes of non-native bird species in their native region might have been similar to those in the recipient bird community, resulting in the evolutionary convergence of ecological traits (Webb et al. 2002, Gerhold et al. 2015). In addition, the phylogenetic similarity of the non-native species with the recipient bird assemblage decreased for bird assemblages that were more phylogenetically imbalanced, with tropical regions having high tree imbalance (Fig 1.11), indicating that the evolutionary equilibrium and the differences between the subclades can influence the invasion process. This can occur because the Imbalance is a measure of the disparity of clades among the tree-topology accounting for the species richness within and between. However, we did not identify to which clade the non-native bird species was phylogenetically closer. Therefore, two possibilities are plausible, that non-native birds are phylogenetically similar to clades with high speciation rate or to clades with low speciation rate. The former might be less likely because species radiation might have resulted in niche saturation in the recipient bird community preventing the introduction of the non-native bird species (i.e., biotic resistance hypothesis), while the latter is more likely specially if the non-native bird species presents niche divergence (even if small) that allows it to fill a potential empty niche (Fig. 1.12 A and D).

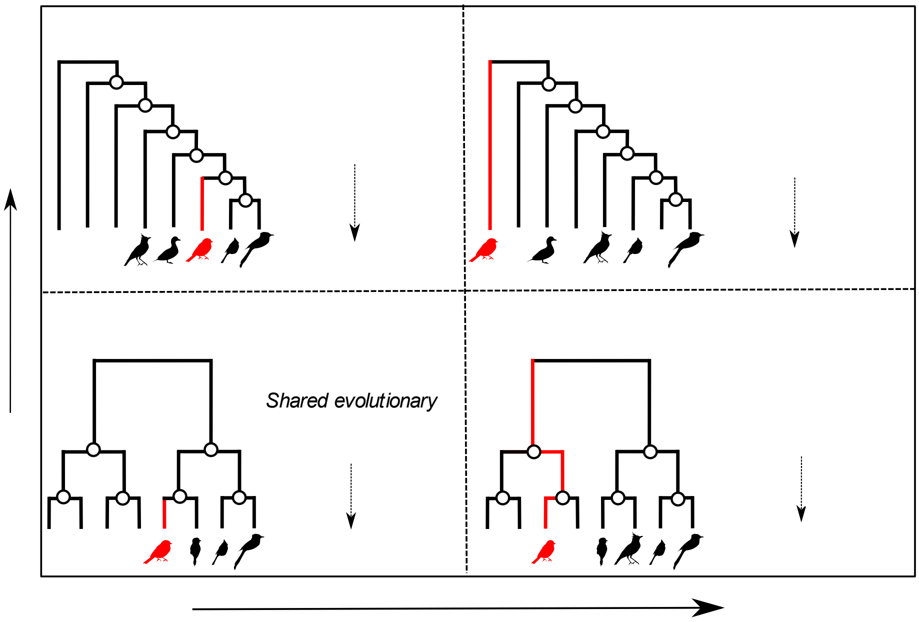

Figure 1.12: Schematic ecological and evolutionary scenarios accounting for non-native and native species phylogenetic relatedness. Horizontal arrow indicates the phylogenetic similarity of the non-native species to the native species assembly, while the vertical arrow indicates the phylogenetic structure of the native bird community. Balanced phylogenies (i.e., evenly distribution of species lineages in phylogenetic tree) indicates phylogenetic tree with low speciation rate. Imbalanced phylogenies (i.e., unevenly distribution of species lineages in phylogenetic tree) phylogenetic tree with high speciation rate. Pairwise blocks indicate the hypothesis associated with each non-native and native combination and the potential mechanisms associated with the hypothesis. Bird silhouettes indicate the species that are present in the community, with black silhouettes for native birds and red silhouettes for non-native birds.

Surprisingly, we found no effect of the net rate of diversification in the phylogenetic similarity between native and non-native species (Figure 1.11), suggesting that the diversification processes of native species do not contribute with the observed phylogenetic pattern of non-native to native species. This can be addressed with the poor resolution in native species community and the differences in the drivers for diversification rates in temperate and tropical regions. Because macroevolutionary outcomes requires long time to be detected, the reduced signal of diversification in temperate region is consistent with the recent evolutionary events of diversification. Conversely, the climate stability and expected stronger effects of competition in tropical regions can lead to more relevant signals of diversification processes in these regions. Thus, our results suggests that, in general, diversification processes are not influencing the pattern of non-native to native phylogenetic similarity. However, it can distinctly influence the non-native species distribution in tropical and temperate regions. Therefore, reinforcing the role of regionality in shaping the current pattern of non-native species.

Our findings point to a divergent result for higher latitudes, where lower phylogenetic similarity (e.g., greater phylogenetic distance) of non-native species to the recipient bird communities facilitated the occurrence of non-native bird species. If phylogenies are proxies for species traits, the lower phylogenetic similarity could indicate that non-native species have different ecological functions (i.e., low redundancy) to the ones present in the recipient bird assemblage. In this case, non-native species in more temperate regions could be filling potential empty niches (Fig. 1.12 D). The empty niche hypothesis predicts that in non-saturated regions, the association between species traits and environmental conditions should result in niche spaces to be filled by non-native species, which should result in an increase in functional disparity. However, factors that allow non-native species to occupy these empty niches are still unknow but should be associated with both the functional traits of non-native species and the structure (i.e., resources, conditions, and environment) of the empty niches to be filled (MacDougall et al. 2009, Gauzere et al. 2020). For example, the size and the number of empty niche spaces will influence in the likelihood of non-native species to successfully invade new regions. Because we found that the phylogenetic distance of the non-native species to the recipient bird community increased with latitude, it is possible that there is a potential gradient on the availability of empty niche spaces to be filled (Gauzere et al. 2020). Also, larger phylogenetic distances can reflect in the lack of natural enemies such as competitors and pathogens (i.e., enemy release hypothesis) and should influence in the capacity of non-native species to occupy empty niches that are unavailable in the native range of the species. However, the capacity that a non-native bird species has of persisting in the filled niche space could be linked with its functional traits. In situation where non-native species introduce multiple traits in the recipient community, it can result in an increase in the likelihood of functional redundancy in regions with high functional disparity (Cooke et al. 2019). For example, the introduction of non-native species can also increase local (i.e., alpha) species richness, which could result in an increase of niche overlap and a reduction in functional disparity (Toussaint et al. 2018). In this case, despite non-native species being phylogenetically distant to the recipient bird community, phylogenetic convergence of traits could also be a possibility (Fig. 1.12 B). In addition, rapid evolution due to an adaptive response could also influence the trajectory of invasion. In this case, non-native species phylogenetically closer to the recipient bird community can increase its niche differences and, phylogenetic divergence of traits could also be a possibility influencing species establishment (Gerhold et al. 2015)

According to the specialization hypothesis (i.e., one of several proposed hypotheses used to explain the latitudinal gradient of diversity), in tropical latitudes, ecological niches are saturated and high species richness and diversity can be explained by the increase in species specialization that reduces the ecological niche overlap, resulting in lower population density and occupancy of functional trait space (Pigot et al. 2016). This packing of ecological niches reduces the likelihood of available functional trait spaces to be filled by non-native species without leading to competitive exclusion. In addition, it is expected that ecological traits are conserved throughout the lineages and niche traits can be inherited from species that share the same clade by the process of phylogenetic niche conservatism (Peterson et al. 1999, Wiens et al. 2010). Because phylogenetic niche conservatism is grounded in past evolutionary events across space and time, it can be used to bring an evolutionary perspective to the observed phylogenetic similarity of non-native bird species to the recipient bird community. Therefore, if non-native species are phylogenetically similar to the recipient bird community, this should be reflected in species morphology because non-native bird species will have the necessary adaptation (i.e., inherited pre-adaptations) that maximize the resources consumptions in the invaded region, which increases the likelihood of non-native species in outcompeting in a narrow and specialized niche space due to its niche similarities with the resident community. Considering that non-native bird species will enter human modified habitats (González-Lagos et al. 2021), it is possible that human disturbance in tropical regions is opening potential niches to be filled, or at least reducing population sizes of native bird species allowing non-native species to enter the system.

In contrast, communities in ecosystems with high abiotic range regimes, such as those in more temperate latitudes, are less likely to be ecologically saturated and resources remain underexplored (Melbourne et al. 2007). In this situation non-native species could face reduced resistance in the occupation of unused niches (Gauzere et al. 2020), just as long as they are capable of surviving sharp changes in environmental conditions. Our results match with this expectation given that non-native bird families introduced in temperate latitudes are overrepresented by bird families expected to have innovative and adaptative behavior related to learning and memory traits (Lefebvre et al. 2004, Sayol et al. 2016, Fristoe et al. 2017). Thus, evolutionary processes that shape non-native species idiosyncrasies could enhance the rise of novel ecological functions that emerge from the interplay between environmental conditions and non-native species traits (Sol 2007, Willman 2014). This in turn could allow the reshaping of niche breadth limits and change the adaptative capacity of resource consumption given the species resource requirement and local resources availability.

Phylogenies as result

It is a long-standing debate regarding the understanding of the drivers that causes the observed latitudinal gradient of diversity (Pontarp et al. 2019). Empirical data support water-energy (Hawkings et al. 2003), metabolic theory (Gillooly & Allen 2007), abundance hypothesis (Storch et al. 2018), high phylogenetic diversity (Voskamp et al. 2017), old species lineages (Jablonski et al. 2006), and high levels of functional redundancy (Cooke et al. 2019) in tropical latitudes. Under this scenario, it is likely that the high diversity of lineages in tropical regions increase the likelihood of non-native species being phylogenetic similar to the recipient bird community when compared to temperate regions. Therefore, it is suitable to recognize that in tropical latitudes our result would simply be due to the sampling effect (i.e., more species increases the likelihood of non-native to native similarities) that indicates the role of species richness, and not ecological or evolutionary reasons shaping non-native species pattern. However, after controlling the phylogenetic similarities by the effects of species richness, we found that the sampling effect is not influencing the observed phylogenetic latitudinal gradient (see result section). Therefore, both the ecological and evolutionary processes associated with species richness could not be considered in influencing the pattern of non-native species suggesting the relevance of other factors in driving the latitudinal gradient of phylogenetic similarity between non-native to native species.

In addition, we found distinct patterns in effect sizes (i.e., the density distribution) along the latitudinal gradient. On average, the mean effect sizes are shifted to left and right in tropical and temperate regions respectively (Figure 1.10A). Remarkably, the density distribution showed the presence of an additional peak skewed to the left (i.e., towards phylogenetic similarity) in temperate latitudes suggesting the role of underlying processes in disrupting the density distribution in two peaks. However, we do not have strong empirical evidence to link the underlying processes of non-native species establishment with patterns in effect size distributions. Thus, we hypothesize situations that could be shaping the observed divergent distributions. One candidate explanation lies in the number of introduction events in recipient communities (i.e., geographical localities). For instance, in the same latitudinal band, different recipient communities (i.e., geographical localities) can accumulate more introduction events than others as a response of the past and contemporary invasive events. This is expressed by the association of species introduction with historical and contemporary economic development (Hulme 2009, McNeely 2012, Essl et al. 2018). Indeed, temperate regions are the cradle of modern civilization (Reba et al. 2016) where humans have been translocating species for a long-time within a broad extent of landmasses through commercial routes and colonization processes (i.e., roman empire expansion and silk route commerce, see McNeill 2012 for more details). This historical human assisted species dispersal has been scrutinized with the support of molecular tools (i.e., phylogeographic perspective) that allows one to correlate the geographical origin and non-native propagule pressure with human history (McNeill 2012, Sherpa et al. 2019). Thus, now it is possible to use molecular tools to disentangle the long-term contribution of human activities in disrupting the natural species composition, which in the long run could result in the homogenization of local biota (Olden 2004). This allows one to scrutinize the contrast between past and current human mechanisms (i.e., globalization, economy and war) associated with human assisted species movement (Hulme 2021, Bonnamour et al. 2021). Similarly, current economic development seems to be concentrated at high latitudes leading to the preference for certain locations for the transport and introduction of species for different purposes during past periods (Reino et al. 2017).

In addition, it is important to highlight that in our results it was not possible to assume that the recipient communities belong to pristine or highly natural conserved areas. Thus, the uneven colonization pressures in anthropogenic environments together with the lack of information about the recipient community before events of non-native species disturbance, reinforce the limit in inferring the mechanisms associated with the non-native species permanence. Thus, it is suitable to consider that recipient communities are not naïve regarding previous human disturbances, which includes previous events of non-native and invasive species. In this sense, anthropogenic activities can progressively accumulate modifications in recipient community promoting further invasive events (i.e., invasive meltdown hypothesis) (Simberloff & Von Holle 1999). Indeed, facilitation due to previous invasive events can reshape the recipient community assembly leading to non-native to native species turnover or coexistence (Godoy 2019). Thus, it is possible that the level of exposure to past invasive events in more temperate regions can progressively reduce the phylogenetic differences between non-native to native species in the recipient community, which in turn could lead to the rise of new peaks toward phylogenetic similarity in temperate regions. However, to scrutinize the mechanisms associated with the bimodal distribution it might be necessary to investigate the role of ecological functions of non-native species in the structuring of the recipient community (Latombe et al. 2021). We argue that ecological function could be properly used to correlate evolutionary and ecological mechanisms with the distinct peaks in the bimodal distribution by linking community ecology and invasive processes through global gradients of climate and human pressures.

Temperature is one of the main abiotic factors limiting species distribution, which explains why species adaptation to climate is usually highly conserved in the phylogeny (Araújo et al. 2013). Temperature profiles are very different for tropical and temperate regions, which could explain the latitudinal phylogenetic pattern found in our study. Although tropical regions tend to have more stable temperatures (i.e., less variation) than temperate regions, species need to be physiologically adapted to high temperatures. In addition, non-native species are usually associated with human dominated landscapes, which in turn tend to have higher temperatures (e.g., heat island effects and changes in albedo in agricultural areas). Therefore, non-native species need to be physiologically adapted to deal with high temperatures, which could explain why in tropical regions they were phylogenetically more similar to the recipient bird community. Thus, anthropogenic environmental changes could act as an intensifying factor for non-native species. For example, the exploitation of tropical forests through deforestation and land use changes (Lewis et al.2015, Taubert et al. 2018) are dramatically impacting the thermal characteristics of these regions, which can result in a shift towards higher temperature and an expansion of warm climates (Staten et al. 2018). In tropical regions, thermal range shifts could be larger than the maximum limit supported by endotherm species and native species can become locally extinct (Staten et al. 2018, Román-Palacios & Wiens 2020) allowing non-native species or lineages exhibiting labile thermal traits to occupy the space. Similarly, temperate regions will have a seasonal temperature profile and regions in higher latitudes will have extreme winter. In this sense, human activities at the regional and local level might increase winter temperatures or at least provide shelter for species, which could explain why non-native species at higher latitudes were phylogenetically distant to the recipient bird community. Gradual increases in temperature in environments with severe lower temperatures can increase the likelihood of species or lineages to overcome the climatic conditions. Therefore, the latitudinal gradient of phylogenetic similarity can be a result of thermal transition states derived from anthropogenic environmental change.

However, it is also plausible that other anthropogenic traits rather than physiological thermal traits can be enhanced by the environmental and landscape changes imposed by human activities, which in turn increases the likelihood of niche occupancy by non-native species in human altered landscape. For instance, at least for birds, it is recognized that non-native species usually fail to occupy the core area of a tropical forest, although it can successfully occur in forest edges. In South America, consider as an example, the house sparrow (*Passer domesticus*), which is certainly a ubiquitous non-native bird. This bird species has a very low temperature limit of -30ºC (Kendeigh 1969) and yet it fails to occupy dense forests in the tropics (Smith 1973, Smith 1980, Silva & Orin 1990). However, its occurrence across rural to urban gradients is undeniable with occurrence in cities of the Amazon region of Brazil. Therefore, even at a large spatial scale, the presence of non-native species is associated with anthropogenic environments. Indeed, a growing body of evidence supports the influence of anthropogenic environment in expanding species niche of non-native species (Pagani-Núñez et al. 2019) and its influence in the ecology of non-native species (Strubbe et al. 2015, Seebens et al. 2015, Jackson et al. 2015, Cardador & Blackburn 2018). Taken together, these results indicate that the several mechanisms acting in tropical and temperate regions can be unified through environmental change processes. Since non-native species have a proximal association with anthropogenic environments that should reflect their ecological and environmental capacity to adapt to these environments, in the presence of these characteristics it is expected that niche expansion should be the response of species to anthropogenic environmental change. Therefore, niche expansion could be one of the main processes driving the non-native species occurrence.

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Chapter 2 – Niche filling drive the establishment of introduced non-native vertebrates in Brazil

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Abstract

Biological invasions are one of the several consequences of human environmental changes. The investigation of the causes and consequences of introduced species is crucial to the understanding and management of the detrimental effects of invasive species. Although several hypotheses are proposed to explain the mechanism associated with species colonization in non-native regions, climate is the best candidate mechanism to support species colonization at large scales. Climate matching predicts that in the absence of evolutionary events, the colonization of new regions should satisfy the range of non-naïve species abiotic tolerance by the mechanism of niche conservatism. Correlative models such as niche dynamic and habitat suitability models are widely used to investigate the similarities and differences between the species' environmental conditions in native and non-native regions supporting the investigation of pattern and processes of introduced species. Using species occurrence together with climatic and anthropogenic data, we found that climate is a relevant condition associated with non-native species distribution in the non-native region due to the occupancy of regions with similar climatic niches with the native regions and the considerable range of the coastal regions of Brazil are suited for vertebrate introductions. Our results reinforce that at least for vertebrates, niche shifts are rare in biological invasions, however, the role of different taxonomic groups should be investigated. Taken together, our results highlight the relevance of correlative models in improve the understanding of the biological invasion phenomena.

Introduction

The investigation of the ecology and evolution of species in novel habitats is central to understanding the causes and consequences of the introduction and invasion of species in new environments. While the current understanding in invasion biology highlights invasion as a multistage process (Blackburn et al. 2011), the interplay of several ecological and evolutionary responses (e.g., abiotic tolerance and population persistence) are needed for an introduced species to overcome the barriers associated with each stage of the invasion process (Rius & Darling 2014). For instance, niche evolution and adaptation through genetic admixture are relevant factors that contribute with the likelihood of species in overcoming the stages of the invasion process and colonization of novel environments (Alexander & Edwards 2011). Similarly, propagule pressure, life history traits and interspecific interactions are pointed out as relevant factor that influence the occupancy and maintenance of population in novel environments (Lockwood et al. 2009, Blackburn et al. 2015). However, general properties regarding the ecological and evolutionary processes within and among the invasive stages are not clear, resulting in a substantial number of ecological and evolutionary hypotheses (i.e., at least 32 hypotheses) proposed to explain the success of introduced species (Enders et al. 2020). In addition, these hypotheses do not clearly discriminate the effects of biotic and abiotic process as well as the influence of biological and geographical scales (Enders et al. 2020). For instance, at large scales, climate factors strongly influence the geography and distribution of species (Peterson et al. 2011), and its effects in shaping the current distribution of species in non-native region is a reliable assumption (Holt et al. 2005). Thus, since the climate affect species' life history traits (Duncan et al. 2001), climate conditions could support the start of the population processes necessary for the persistence of the species in the non-native region and can be considered a relevant factor to the understanding of the causes that precede the processes of non-native species permanence at the population and community level (Reeding et al. 2019). Therefore, the similarity with species native region should be informative at predicting the potential zones suitable for the persistence of introduced species (Blackburn et al. 2009, Redding et al. 2019).

At large spatial scales, species' ecological responses vary in response to population and demographic dynamics (i.e., internal factors) and environmental conditions (i.e., external factors), which challenges inferences of general mechanisms that drive the successful introduction of non-native species in novel environments (Sol et al. 2012). However, because of species tendency to retain its ancestral characteristic through niche conservatism, abiotic conditions (i.e., climate or environmental factors) can be used to track the degree of shift in abiotic conditions in space or time (Peterson 2003, Tingley et al. 2009). Consequently, correlative models are widely used to fit abiotic and environmental conditions with a pool of observational information of non-native species (Kozak et al, 2008, Guisan et al, 2014). Although the use of correlative models in biological invasion are criticized due to the lack of control in spatial prediction (Qiao et al. 2019), correlative models can be used to gain crucial information regarding general patterns of non-native species distribution (Sales et al. 2017, da Silva et al. 2018). The advantage of correlative models lies in the capacity of fitting different models for different purposes in the absence of controlled conditions for supporting the improvement in the understanding of the causes and consequences of biological invasion (Guillera-Arroita et al. 2015). For instance, correlative models can improve predictive outcomes in an invasive context supporting decision-making designs that consider the faster pace of climate and environmental changes (Gallardo et al. 2017, Bellard et al. 2018, Pereira et al. 2020). Similarly, correlative models can be used to identifying focal areas for management plans to prevent the invasion (Mantovano et al. 2021) and investigate the role of climate in driving species niche shift in the non-native region (Liu et al. 2020). In addition, due to the multiplicity of factors that influence the success of the introduction, several theoretical frameworks are addressed through correlative models to understand biological invasions regarding the specific context in which they occur (Reeding et al. 2019, Enders et al.2020). Therefore, the use of correlative models is crucial to improve the understanding of the biological invasion phenomena.

Climate matching (Holt et al. 2005) is potentially one of the most relevant abiotic mechanisms in explaining the establishment of non-native species (Redding et al. 2019). Climate matching can be defined as the extent of climatically suitable environment or habitat (e.g., temperature and precipitation) in the introduced range of the non-native species (Blackburn et al. 2009). Because species tolerate a certain range of abiotic conditions, a species' range will be limited to geographical areas that have the appropriate abiotic conditions that allows the perpetuation of a population without recurrent immigration (Holt et al. 2005; Tingley et al. 2009), and species that tolerate greater environmental variation should have large non-native ranges. Therefore, climate similarity between the native and non-native regions is an important condition for the establishment and persistence of introduced populations in non-native geographical regions (Holt et al. 2005). According to the climate matching hypothesis, if the climatic conditions of the native region of an introduced species is met at a given non-native region, then population establishment can occur, since environmental fit is a necessity for positive population growth (Holt et al. 2005). This is predicted by niche conservatism (Wiens et al. 2010), where fundamental aspects of species' niches are stable and not easily altered. In addition, niche conservatism is the basis of correlative models (Peterson, 2003; Guisan et al. 2017), which have been broadly applied to predict suitable environments for non-native species at large spatial scales (Strubbe et al. 2015). Yet, although niche conservatism requires that niches are maintained through time and space, it is possible for niche shifts to occur in the introduced range through adaptation or plasticity (Broennman et al. 2007).

However, niche shifts are rare in biological invasions (Petitpierre et al. 2012, Strubbe et al. 2015, Liu et al. 2020) supporting the use of correlative models in invasion biology (Strubbe et al. 2015). Because correlative models use environmental predictors to estimate the habitat requirements for species occurrence in a region, its suitability outputs represent a quantitative measure of climate or environmental matching (Guisan et al. 2017). Therefore, it is expected that suitability values reflect the evolutionary history of the species with its native environment and, therefore, shape the adjustment of the species within the new environment (Taylor & Keller 2007; Alexander & Edwards 2010) through species' ecological niche characteristics such as physiological tolerance. Thus, niche conservatism is a necessary assumption in the understanding of biological invasion.

Currently, it has been shown that correlative model approaches are a robust technique with reliable performance in applied and theoretical ecology that goes beyond predicting suitable geographical regions for non-native and invasive species with the potential for inferring mechanism of non-native species occurrences (Petitpierre et al. 2012, Guisan et al. 2014; Guisan et al. 2017). For instance, it is possible that the current non-native species occurrences were driven by processes of niche expansion (i.e., the occupancy of new niches in the introduced region), or niche unfilling (i.e., the occupancy of niches that are similar but non-available in the native range). The niche expansion implies that species persistence can be explained by the differences between non-native and native regions under the mechanisms of niche evolution. Conversely, niche filling implies that species persistence is related with the occupancy of niches similar to the niches in the species native region through the process of niche conservatism. Therefore, this approach allows the use of empirical evidence to synthesize the dynamics of how climatic niche changes between native and non-native regions. In addition, it represents an opportunity to study if non-native species track their ancestral niches and how it responds to human environmental changes. Thus, in this study we used niche modeling approach to investigate the patterns and processes that drive the distribution of non-native vertebrates in Brazil. Specifically, we investigated the role of niche similarity in the distribution of non-native terrestrial vertebrate species in Brazil. Investigating the influence of human landscape changes among the non-native species occurrences, we detect that the regions which non-native occurrence is available reflects high level of anthropogenic disturbance and a relevant degree of abiotic similarity with the native regions of the non-native species. In addition, we show that niche expansion rarely occurs in recent vertebrate introduction, highlighting that environmental similarity between native and non-native regions are relevant for the current pattern of non-native species distribution, reinforcing that the combination of modeling approach is informative in understanding general patterns of introduced species.

Methods

List of non-native terrestrial vertebrates, occurrence data, and data cleaning

We compiled a list of non-native terrestrial vertebrates for Brazil that was consistent with the definition in Richardson (2011) “Those whose presence in a region is attributable to human actions that enable them to overcome fundamental biogeographical barriers (i.e., human-mediated extra-range dispersal)”. We choose this criterion to satisfy the condition that introduced species were clearly human-mediated introductions. Specifically, we considered as non-native species those in which its native range occur outside the boundaries of the Brazilian territory. For instance, species such as *Callithrix penicillate* and *Callithrix jacchus* which were widely translocated to regions beyond its native region within Brazil were not considered in this study. Similarly, non-native species with relevant level of domestication process (i.e., dogs, cats, and horses) were also not considered. For Brazil, a list of non-native birds (Fontoura et al. 2013) and mammals (da Rosa et al. 2017) species have already been published. We evaluated which species on those lists fitted the definition being used in this study and expanded the list of non-native vertebrate species using the scientific literature and the I3N Brazilian invasive species database (https://institutohorus.org.br). The I3N species database belongs to the Inter American Biodiversity Information Network (IABIN) and provides information on non-native and invasive species that are currently present in Brazil. For the full list of non-native terrestrial species published in Brazil see Table 2.1. For each species, we searched the literature for the potential first records of occurrences. This approach allowed us to obtain the potential year of introduction and the geographical coordinate of the introduction site. When the locality of the first documented observation or geographical coordinate was not available, we used the geographical coordinate of the city in which the species was observed for the first time (see appendix I). We did this by manually crossing the available description of city or neighbourhood level of species occurrence with the geographical coordinates for the cities obtained from digital maps available at the “Instituto Brasileiro de Geografia e Estatística” (IBGE). Additionally, occurrence records for each species were obtained from the Global

Information Facility Database (www.gbif.com). We complemented the non-native occurrences in the introduced region by adding occurrences records available in the Vertnet (http://vertnet.org) and species link (http://www.splink.org.br/) databases. The latter is an open-access database of the Brazilian biodiversity and therefore represents regional assessment for Brazilian occurrences.

We used IUCN range maps to determine the native boundaries (i.e., native geographical distribution) of each species, and used all species occurrence records within these boundaries to calibrate the species habitat models (see below). Because datasets on occurrence records usually present geographical sampling bias and different levels of variation in the coordinate's precision (Naimi et al. 2011), it is not possible to assume that the occurrence points are accurate (Radosavljevic & Anderson 2014, Guisan et al. 2017). However, because at larger spatial scales coarser resolutions do not necessarily affect model accuracy (Guisan et al. 2017), it is possible to overcome potential sampling bias by building habitat suitability models using coarser resolutions of the environmental variables. Therefore, to maximize the sample size and remove as many points as possible, we excluded all unnecessary coordinate points within the same grid cell using a 10 arc-min cell resolution (hereafter rarefied data). This procedure allows the retention of one-occurrence point per grid cell.

The introduced range occurrences data were used to: 1) model niche dynamics between native and non-native regions (see *Framework for quantifying species niche*), 2) investigate the distribution of the anthropogenic pressures among the localities where non-native species are distributed in the non-native region (see *Environmental Layers and Variable selection*), and 3) evaluate environmental niche model prediction (see *Habitat suitability Model)*.

Introduction history of non-native vertebrates

Using the scientific literature, we reviewed the introduction history of non-native species. First, we used IUCN species' digital maps for the native regions to map the geographical origin of each non-native species introduced in Brazil. The overall geographical origin of non-native species was identified using the overlap of the native range of non-native species. This approach was chosen because it represents a visualization of the contribution of the geographical region as the native source of the non-native species. We then reviewed the literature to determine the pathway in which each species was introduced. This approach allowed us to group non-native species into seven classes of introduction pathway: 1. Biocontrol, 2. Colonization, 3. Conservation and Science, 4. Environmental enhancement, 5. Food and game, 6. Range expansion and 7. Unknow (See table 2.2 for introduction pathway descriptions).

Table 2.1: Non-native vertebrate species occurring in Brazil. * Indicate species in the non-native species pool that were not used in niche models due to the low sample size (N < 5). Remaining species (N = 32) were used in environmental niche models and † indicate species (N = 27) with adequate mode fit. ⊕ indicate species with available occurrence information in the introduced region (N = 27) from which 17 were used in niche dynamic model fit based on the

minimum of five occurrences in different cells on non-native range. **Species:** scientific species name. **Common name:** vernacular name of species. **Order:** order of species. **Class:** species class. **Nº occurrences:** The number of occurrences in the native range of non-native species used to calibrate habitat models after rarefaction procedure.

Species	Common name	Order	Class	Nº occurrences
*Agapornis personatus**⊕	Yellow-collared Lovebird	Psittaciformes	Bird	NA
Agapornis roseicollis⊕	Rosy-faced Lovebird	Psittaciformes	Bird	8
Alopochen aegyptiacus†⊕	Egyptian goose	Anseriformes	Bird	641
Anas platyrhynchos†⊕	Mallard	Anseriformes	Bird	77642
Anolis porcatus†⊕	Cuban anole	Squamata	Reptile	6
Axis axis⊕	Chital	Cetartiodactyla	Mammal	37
*Bubalus arnee**	Wild Water Buffalo	Cetartiodactyla	Mammal	NA
Cacatua galerita†	Sulphur-crested Cockatoo	Psittaciformes	Bird	5857
*Callipepla californica**	California Quail	Galliformes	Bird	NA
Capra aegagrus⊕	Wild goat	Cetartiodactyla	Mammal	37
Carduelis carduelis†⊕	European Goldfinch	Passeriformes	Bird	18465
*Chloris chloris**	European Greenfinch	Passeriformes	Bird	NA
Columba livia†⊕	Rock dove	Columbiformes	Bird	6140
Corvus albus†⊕	Pied crow	Passeriformes	Bird	3080
Eleutherodactylus johnstonei⊕	Lesser Antillean Whistling Frog	Anura	Amphibia	26
Estrilda astrild†⊕	Common waxbill	Passeriformes	Bird	2394
Geopelia cuneata	Diamond dove	Columbiformes	Bird	1610
Lepus europaeus†⊕	European hare	Lagomorpha	Mammal	3855
Lithobates catesbeianus†⊕	Bullfrog	Anura	Amphibia	1079
Lonchura oryzivora	Java sparrow	Passeriformes	Bird	17
Melopsittacus undulatus⊕	Budgerigar	Psittaciformes	Bird	1962
Mus musculus†⊕	House mouse	Rodentia	Mammal	3262
Mustela putorius†	Western polecat	Carnivora	Mammal	5199
Numida meleagris†⊕	Helmeted Guineafowl	Galliformes	Bird	2656
Nymphicus hollandicus†⊕	Cockatiel	Psittaciformes	Bird	2551
*Oryctolagus cuniculus**	European rabbit	Lagomorpha	Mammal	NA
Passer domesticus†⊕	House sparrow	Passeriformes	Bird	25411
Psittacus Erithacus	Grey parrot	Psittaciformes	Bird	156
Pycnonotus jocosus	Red-whiskered Bulbul	Passeriformes	Bird	1536
Rattus novergicus†⊕	Brown rat	Rodentia	Mammal	5145
Rattus rattus†⊕	House rat	Rodentia	Mammal	20
Rusa unicolor⊕	Sambar	Cetartiodactyla	Mammal	17
Serinus canaria⊕	Island Canary	Passeriformes	Bird	134
Streptopelia decaocto†⊕	Eurasian Collared dove	Columbiformes	Bird	16411
Sturnus vulgaris†⊕	European starling	Passeriformes	Bird	23765
Sus scrofa†⊕	Wild boar	Cetartiodactyla	Mammal	7037
Xenopus laevis†⊕	African Clawed Frog	Anura	Amphibia	8

Table 2. 2: Seven potential introduction pathway for non-native vertebrate species in Brazil. Introduction purposes were classified similar to Lockwood et al. (2007), with the exception of the classes "Colonization" and "Unknow", which were created according to the available information on the introduction process of non-native species for Brazil.

Introduction purposes	**Variable descriptor**
Biological control	Deliberate introduction of species with the objective of controlling, reducing, or eliminating populations of other species. This is the case of *Passer domesticus* introduction in Brazil. Sick (1997) highlight that the house sparrow's introduction occurred in 1906 in the city of Rio Janeiro due to phytosanitary control of vector- borne disease.
Colonization	Unintentional/Intentional introduction of species during the early stages of the European colonization (i.e., century XVI, XVII). Despite the paucity of historical documents, it is suggested that some species were introduced and widely spread during European colonization due to the increase in navigations (Long et al. 2003; da Rosa et al. 2017). For instance, it is presumed the rats (i.e., *Rattus* spp.) were likely transported inside ships over centuries.
Conservation and Science	Deliberate introduction of species with the goal of supporting conservation actions (Schlaepfer et al. 2011) and scientific development. This is the case of *Xenopus laevis*, which is broadly used as a model organism in laboratory research (Harland & Grainger 2011, Horb et al. 2019).
Environmental enhancement	Deliberate introduction of species with the objective of improving or enhancing the aesthetic value of human environment or improving human well-being. These species are often suited with aesthetic traits that benefit human well-being (Blackmore et al. 2009). This is the case of *Estrilda astrild*, an aesthetic bird from Africa and still used as caged bird in Brazil (Sick et al. 1997).
Food and game	Deliberate introduction of species with the objective of supporting food production or providing mechanic traction for food production. Despite the paucity of historical documents, it is well known that some bird families were introduced due to hunting purposes, while other species such as goats were introduced for food provision (Long et al. 2003, Balckburn et al. 2009)
Range expansion	The range expansion of non-native species that were human introduced in neighboring countries of Brazil but arrived in Brazil due to their dispersal capacity. For instance, Silva et al. (2017) highlights the great dispersal capacity of *Sturnus vulgaris*, which was broadly introduced in Brazil's neighboring countries. Similarly, Dias (2000) and Bencke et al. (2010) detected the occurrence of *Carduelis carduelis* and *Chloris chloris*, respectively, in the southern border of Brazil.

Unknow	No information available

Environmental Layers and Variable selection

The 19 bioclimate variables were obtained from the WorldClim database version 2.0 (Fick & Hijmans 2017) with WGS84 projection and grid cell resolution of 10 arc minutes. To reduce model over-fitting, we tested for each species the collinearity among predictors using variation inflation factor analysis (Guisan et al. 2017). The procedure was applied to each species region independently, using only climatic information from grid cells that had occurrence points. We only included predictors that had a variance inflation factor lower than 10, and we also used a correlation threshold of 0.75 (Guisan et al, 2017). Further, because human activities are an important component in biological invasions (Hulme, 2009), we chose to analyse non-native species using an up-to-date version of the Human Influence Index (HII) (Sanderson et al. 2002; Venter et al. 2016a). HII synthesize eight detrimental factors of human activities on the landscape (1. Built environments, 2. Human population density, 3. Night-time lights, 4. Croplands, 5. Pasture, 6. Roads, 7. Railways, 8. Navigable waterways) to measure the direct and indirect human pressures on the environment (for details of each factor see Venter et al. 2016a). Using the Venter et al. (2016b) approach, we classified the HII in the following five classes of human pressure: 1. no pressure, 2. low pressure, 3. moderate pressure, 4. high pressure and 5. very high pressure. We then evaluated the intensity of human pressure in the localities where non-native species occurred in Brazil.

Framework for quantifying magnitude and orientation of niche changes

Species niches were measured using the Centroid, Overlap, Unfilling, Expansion framework (hereafter COUE; for details see Guisan et al. 2014). COUE uses principal component analysis (PCA) at all sites that constitute the native and invaded areas to estimate species environmental space and quantify the magnitude and orientation of niche changes (Broennimann et al. 2012, Guisan et al. 2017). Niche change metrics uses species' PCA scores projected onto a 100 by 100 grid of cells and a smoothed density of occurrence in each cell to measure the overlapped proportions between native and non-native environments (Broennimann et al., 2012). Niche orientation lies in inferring if niche changes are related to process of niche expansion or unfilling (Petitpierre et al. 2012). The latter estimates the proportion of species occurrence densities in the native distribution that have similar conditions to the ones available in the introduced range but are not currently filled by the non-native species. Similarly, the former, estimates the proportion of densities in the non-native distribution located in conditions other than the native distribution and is interpreted as an expansion into environments new to the species but not filled in the native range. To calculate the overall fit between niches over the full environmental space, we used the Schoener's D metric. Schoener's D metric varies from 0 (no overlap) to 1 (complete overlap) and allows one to test if we can infer the characteristics of the non-native niche from the native niche using niche similarity randomization tests as proposed by Broennimann et al. (2012). The rejection of the null hypothesis indicates that the niches of native and non-native species are more similar than expected by random.

Habitat suitability Model

Habitat models were calibrated using only the rarefied occurrence data from the native range of the introduced vertebrate species (Table 2.1). Thus, each species was modelled considering the rarefied occurrences in the geographic domain that belongs to the species native distribution range and projected into Brazil. We used the maximum entropy approach implemented in the Maxent software version 3.4.0 (Phillips et al. 2017) to model species environmental suitability. The maximum entropy algorithm belongs to the class of machine learning algorithms, which allows modelling species environmental conditions without absence data and with low number of occurrences (Galante et al. 2018). Because machine learning methods lies in increasing the predictive capacity of unknown information (i.e., validation data) based on known information (i.e., calibration data), it is necessary to control the calibration of training models to obtain the most adequate parameter that maximise the predictions (James et al. 2013). In order to obtain the most adequate calibration model, machine learning algorithms control the over fit (i.e., excessive complex models) by penalizing models with unnecessary parameters and smoothing the shape of the model (regularization parameter in Maxent) (James et al. 2013). In Maxent the control for model over fit is done using internal functions (hereafter model parameters) that can be adjusted in order to smooth the shape of the relationship between occurrences and environmental data and prevent model over fit. Therefore, it is possible to calibrate the models according to the function that the species best respond to (i.e., model tuning), which increases model quality (Phillips & Dudík 2008). In the Maxent environment, two main model parameters (regularization and features) can be adjusted. Tuning of these parameters is important because they can affect the accuracy and precision of model predictions (Radosavljevic & Anderson 2014).

The features parameter are functions used to estimate the relationship between the environmental data and occurrence data. In the default setting, Maxent can perform individual and six different combinations of features (see Model Selection and Model Evaluation), which will not necessarily lead to the best model predictions. The regularization parameter is important to maximize the differences between the well-fitted model and the excessively complex models (Phillips & Dudík 2008). In Maxent, the regularization parameter is a positive continuous value that controls the level of penalties (i.e., constraints) imposed to each environmental variable, where high values of the regularization parameter imply stronger penalties (Anderson & Gonzales 2011). Therefore, in order to obtain the most adequate model, it is important to find the regularization parameter that protects against model over fit considering all model parameters.

Further, the partitioning method (i.e., technique to generate the calibration and the evaluation dataset) is also an important strategy to increase the accuracy of the model, and specific partitioning methods should be used for different biological situations (Muscarela et al. 2014; Radosavljevic & Anderson 2014; Galante et al. 2018). Maxent performs four partitioning methods (for more details see Phillips & Dudík 2008), with the default setting using the K-bin approach. K-bin randomly splits the dataset in user-required number of bins (K) that have approximately the same sample size. It then uses K-1 bins to calibrate the model and the remaining bin (K = 1) to evaluate the model. However, in situations that require predictions among different geographical space (i.e., spatial transferability), it is recommended to partition the data using K geographical bins (Radosavljevic & Anderson 2014). K geographical bins differ from the default K-bins settings in Maxent because it uses the geographical extent instead of random sampling to split the dataset into the calibration and evaluation data. This data partitioning strategy allows an increase in the accuracy of model predictions when spatial transferability is involved (Radosavljevic & Anderson 2014), which is the usual scenario for invasive and introduced species. We used K geographical bins in our models.

Model Selection and Model Evaluation

To determine the best environmental suitability model for each species, we calibrated the Maxent algorithm using six different maxent features (L, H, LQ, LHP, LQH, LQHP; for more details about the acronym see supplementary file) and 20 different regularization parameters (values range from 0.5 to 10.0 with regular interval of 0.5). This resulted in 120 different models per species. For each species, we used Akaike Information Criteria (AIC) to access the best model among the candidate models as proposed by Warren & Seifert (2011) and implemented in ENMeval package (Muscarela et al 2014) for the R software (R Core team 2019). We chose only the best model ($_{\Delta}$AIC = 0) among the 120 candidate models. However, because ENMeval uses all the occurrence points and the number of model parameters (i.e., parameters used to fit the curve; lambdas in the Maxent) to estimate the goodness of fit and $_{\Delta}$AIC by each model, $_{\Delta}$AIC does not measure the accuracy in model predictions. Therefore, we use the Area Under the Curve of the evaluation data (AUC_{TEST}) to access model accuracy. The AUC is a threshold independent measure widely used to evaluate the capacity of the models to correctly predict the evaluation data (see K geographical bins in Habitat suitability Model section). The AUC uses the sensitivity (i.e., the degree of absence in omission error, or false negative) against 1-specificity (i.e., the degree of absence in commission, error or false positive) values to measure the accuracy of the model to discriminate the observed occurrence from the background occurrences (Peterson et al. 2011). Here, models with area under the curve values for evaluation data (hereafter AUC_{TEST}) equal or higher than 0.75 were considered properly capable of differentiating occurrences from background information and were used to predict species distribution into the Brazilian geographical extent.

To estimate the potential distribution of the habitat suitability in the predicted region we combined all species models that presented $AUC_{TEST} \geq 0.75$ into a single non-native suitability grid. This was done by calculating the mean suitability of each grid cell, where each grid cell represents the average habitat suitability of introduced vertebrate species in Brazil. In this sense, it is an indicative measure of environmental matching between native and non-native regions. Additionally, to evaluate the potential species geographical distribution, we used the maximum sensitivity plus specificity threshold from the best candidate model (ΔAIC = 0) to classify the prediction of each grid cell into presence and absence classes. We chose the maximum sensitivity plus specificity threshold because of its consistency in classify presence and absence grid cell across several distinct model parameter (Liu et al. 2013, Liu et al. 2016). Grid cells with values equal or greater than the threshold was classified as a presence and grid cells with values lower than the threshold values were classified as absence. The values of threshold were estimated by species independently and then the sum of classified distribution were used to measure the overall species distribution.

Results

Species composition, occurrence, and introduction history

We identified 37 introduced terrestrial vertebrate species in Brazil, out of which 59.4% were birds (N=22), 29.7% were mammals (N=11) and 10.8% were reptiles and amphibians (N=4). Our map of the geographical origin for non-native terrestrial vertebrates shows that the palearctic region of the world is potentially the main source of terrestrial vertebrate species introduced in Brazil (Figure 2.1).

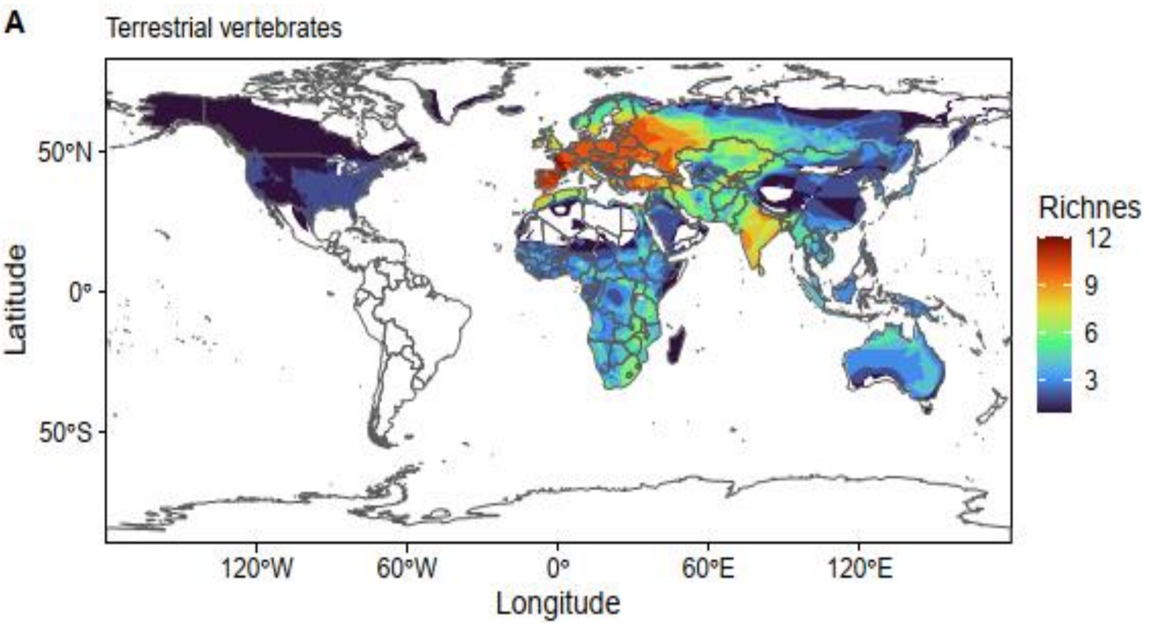

Figure 2.1: Geographical origins of the non-native vertebrate species listed for Brazil. Maps indicate the prevalent geographical region considering all non-native vertebrate species (N = 37) **(A)**. Color gradient indicates the sum of the number of species with overlapping ranges in their native region (scale at 0.5-degree cells), where warm colors indicate regions that have a high number of non-native species that were introduced to Brazil.

We found that the main introduction pathway was environmental enhancement, which represented 43.2% of the introduced vertebrate species (N = 16) containing 8 non-native orders. These orders are mainly formed by birds, with six species belonging to the order of Psittaciformes (i.e., parrots and macaws) followed by four Passeriformes (i.e., perch birds and songbirds) species, three Columbiformes (i.e., doves and pigeons) species and one species from the Anseriformes order (Figure 2.2).

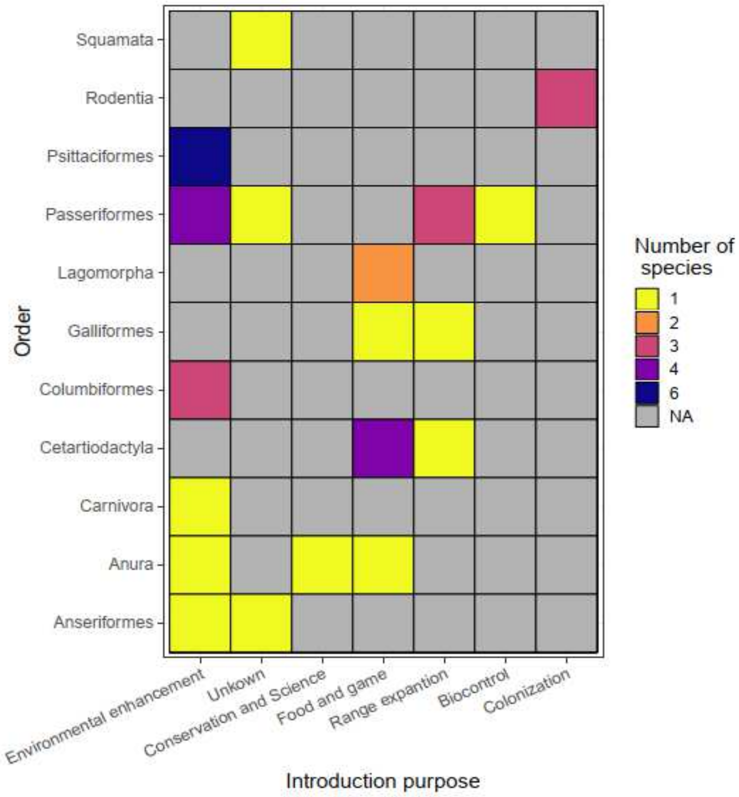

Figure 2. 2: Heat map showing the number of non-native vertebrate species associated with its respective order and introduction pathways. Each row of the heatmap corresponds to the biological order and each column of the heat map corresponds to the introduction pathways. Gray blocks are not available associations.

The remaining orders were represented by only one species from the order Anura and Carnivora. The second main introduction pathway was Food and Game, which represent 21.6% of the species (N = 8) belonging to 4 orders. These orders are formed by mammals with four species belonging to the order Cetartiodactyla (i.e., deers and goats), two species belonging to the order Lagomorpha (i.e., rabbits and hares) and one species belonging to the order Anura (i.e., frogs) and to the order Galliformes (i.e., chickens) (Figure 2.2). Range expansion was the third main introduction pathway of non-native species, which corresponded to 13.5% (N=5) of introduced species, with three species belonging to the order Passeriformes, one species belonging to the order Galliformes and the order Cetartiodactyla. Unknow introductions contributed with 8.10% (N=3) of non-native species, with one species belonging to the Passeriformes order, Squamata (i.e., lizards) order, and Anseriformes (i.e., ducks and gooses) order. The introduction pathway of Conservation and Science, Biocontrol and Colonization were represented by one order each. The latter is formed by three species belonging to the order Rodentia (i.e., rats and mouses), while Conservation and Science, and Biocontrol were respectively formed by the order Anura and Passeriformes.

Density of occurrences of non-native vertebrate species and human pressure

The density of occurrences was higher in the southeast and southern region of the country in localities that surround port locations (Figure 2.3).

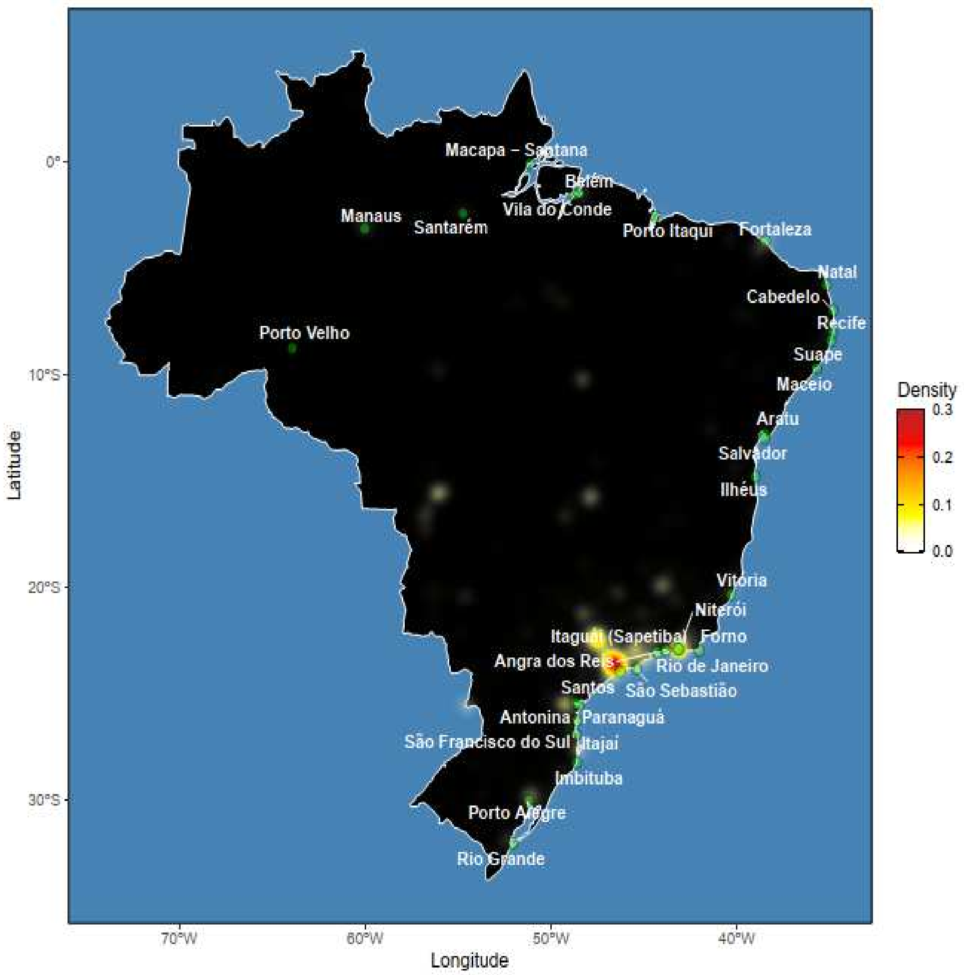

Figure 2.3: Density of occurrences of non-native vertebrate species of Brazil. White to red color gradient indicate low and high density of non-native species occurrences, respectively. Light green circles show Brazilian ports

We also found that non-native vertebrate species were observed in regions of high and very high human pressure (Fig. 2.4).

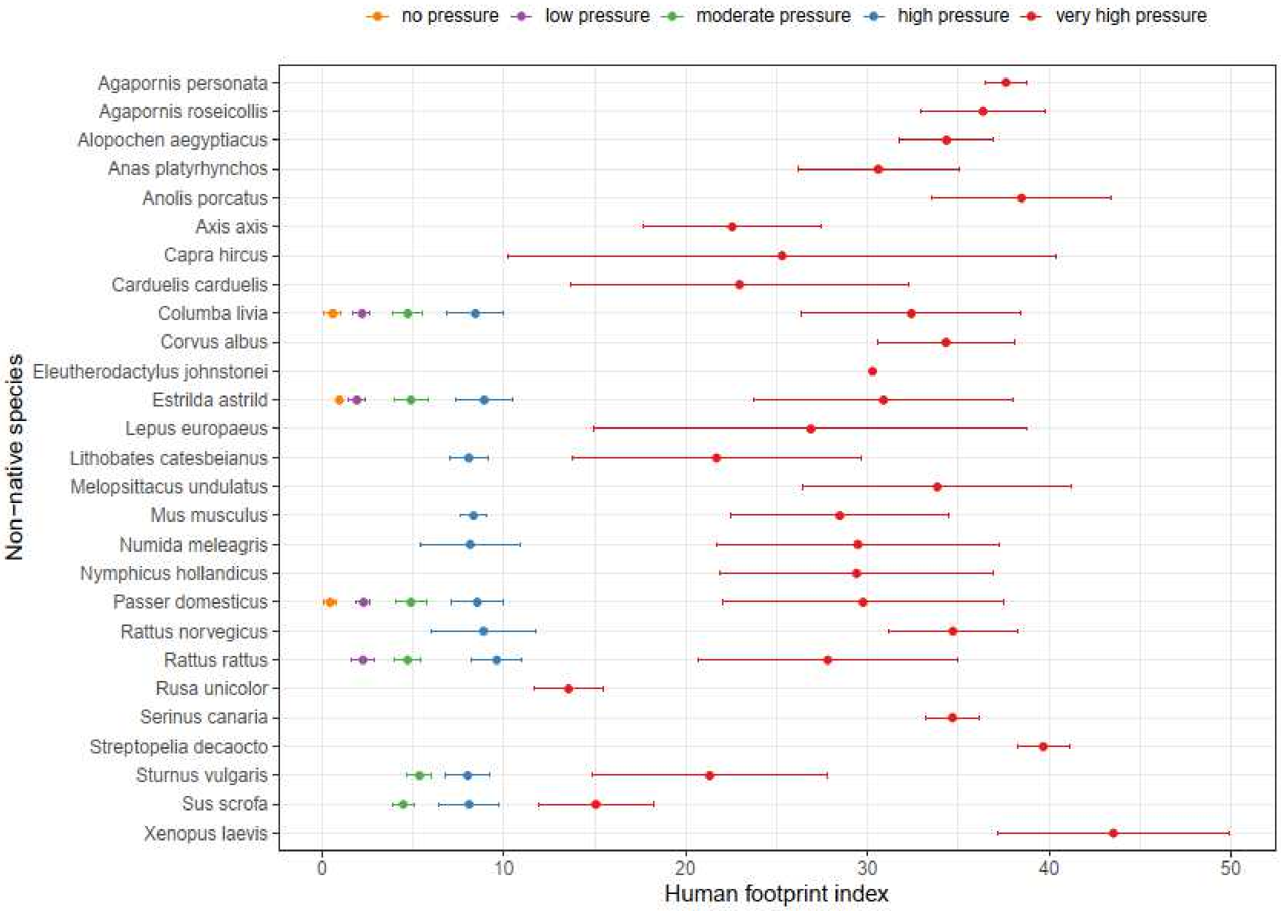

Figure 2.4: Human pressure index of the localities where non-native vertebrate species were observed in Brazil. Human footprint index was grouped into five classes that indicate the degree of human influence in the landscape. Circles and bars indicate the mean values and standard deviation of human pressure index, respectively, for all occurrences available for the 27 non-native vertebrate species in Brazil.

Environmental niche models, niche changes and entry regions

A total of 32 species had the minimum of five occurrences records and were eligible for the modeling procedures (Figure 2.5). However, only 21 species had well-adjusted (i.e., AUCTEST ≥ 0.75) models to be used in the next steps of the modeling procedures (Table 2.3). Model predictions highlight that the environmental matching between native and non-native environments is higher in areas closer to the coast, which indicate that on average these areas can be considered environmentally suited for the majority of non-native vertebrate species used in habitat models (Fig 2.6). We found that niche unfilling was the main process associated with the permanence of non-native vertebrates in Brazil ($t = -2.6232$, $df = 31.262$, $p\text{-value} = 0.006$) (Fig. 2.7 and Table 2.4).

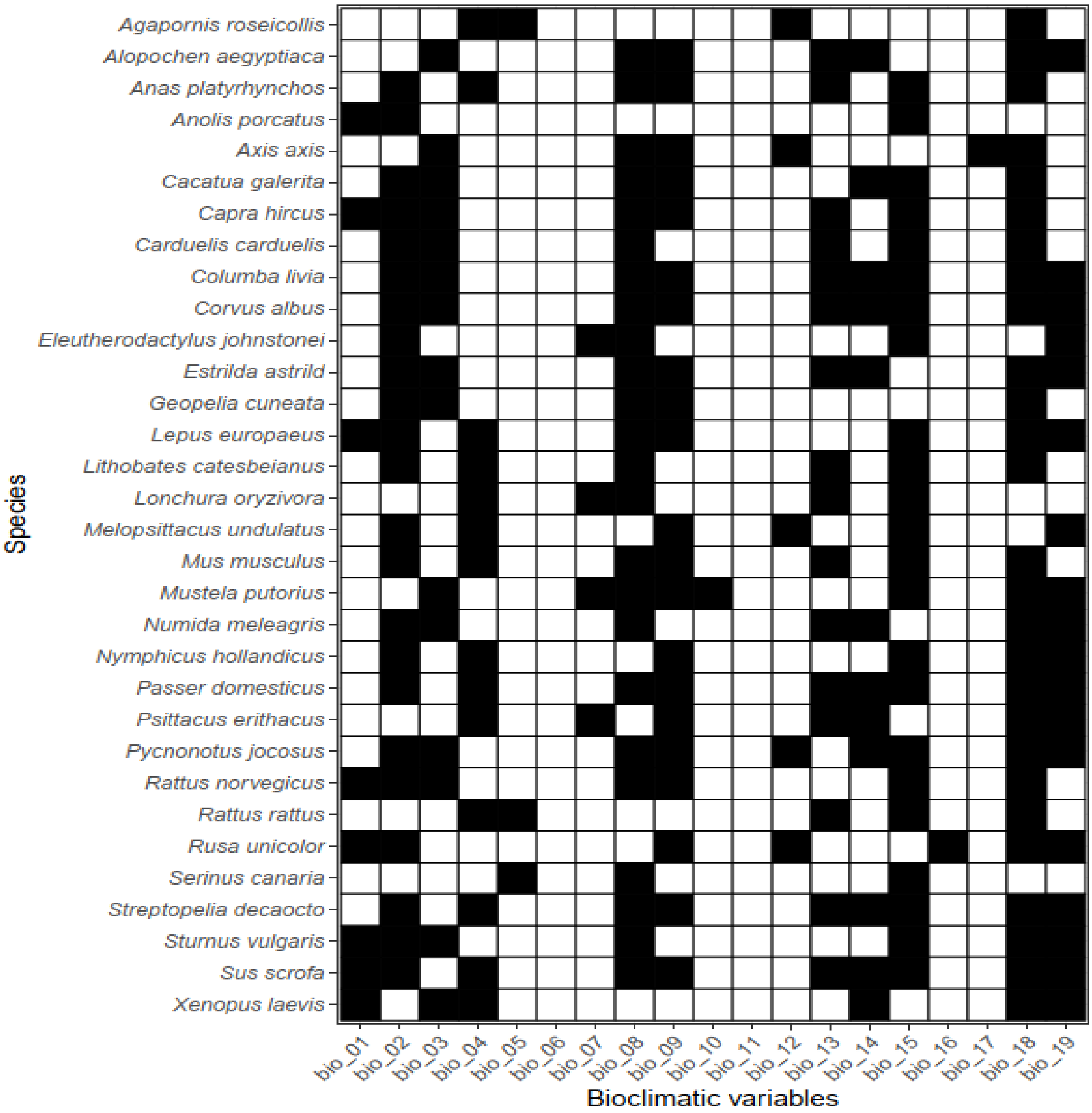

Figure 2.5: Tile plot showing the selected variable for all 32 non-native vertebrate species of Brazil. Columns indicates the 19 WorldClim bioclimatic variables (www.worldclim.org). Rows indicates species with the minimum of five occurrence records for variable selection. Black squares indicate selected variable per species. White squares indicate excluded variables per species. Variable selection procedure was executed using variable inflation factor (VIF) of variables within models as indicated by Guisan et al. (2017).

Table 2.3: Maxent niche model output of the best models (AIC = 0). **Species:** Species name. **Class:** biological class of species. **Settings:** Indicate the combination of feature functions used in the selected model. **Regularization:** Indicate the regularization values used in the selected model. **AUCTRAIN:** Indicate the AUC value calculated with the full dataset for each species. **AUCTEST:** Indicates the mean AUC values with ± Standard Deviation. **AUCDIFF:** Indicates the mean difference between the AUC values of the training and the test data ± Standard deviation. **Threshold:** Sensitivity equal specificity values to estimate species presence and absence regions from suitability values. Grid cells greater or equal than threshold values were reclassified as presence. Grid cells with lower threshold values were reclassified as absence. **Parameters**: Indicate the number of parameters used in the model. **Boyce**: Indicates the model performance when niche models are tested using independent dataset in the non-native region. Negative to positive values indicate the low-to-high model performance.

Species	Class	Settings	Regularization	AUC_{TRAIN}	AUC_{TEST}	AUC_{DIFF}	Threshold	Parameters	Boyce
Alopochen aegyptiacus	Bird	LQHP	1.6	0.9193	0.869 ± 0.022	0.064 ± 0.018	0.212	76	0.536
Anas platyrhynchos	Bird	LQHP	0.4	0.8856	0.789 ± 0.000	0.084 ± 0.007	0.258	227	0.618
Anolis porcatus	Reptile	LQ	1.4	0.8978	0.774 ± 0.101	0.058 ± 0.015	0.430	1	0.264
Cacatua galerita	Bird	LQHP	0.2	0.8856	0.762 ± 0.076	0.150 ± 0.084	0.354	229	1
Carduelis carduelis	Bird	LQHP	0.4	0.8993	0.861 ± 0.011	0.061 ± 0.004	0.257	186	0.033
Columba livia	Bird	LQHP	1.8	0.9061	0.823 ± 0.017	0.094 ± 0.010	0.198	168	0.924
Corvus albus	Bird	LQHP	2.4	0.8666	0.760 ± 0.079	0.146 ± 0.069	0.379	90	0.7
Estrilda astrild	Bird	LQHP	0.8	0.9204	0.872 ± 0.014	0.068 ± 0.008	0.203	134	0.189
Lepus europaeus	Mammal	LQHP	0.2	0.9192	0.793 ± 0.019	0.127 ± 0.016	0.213	340	1
Lithobates catesbeianus	Amphibia	LQHP	2.2	0.7997	0.784 ± 0.002	0.014 ± 0.000	0.436	93	0.82
Mus musculus	Mammal	LQHP	0.2	0.941	0.868 ± 0.011	0.063 ± 0.008	0.166	255	0.139
Mustela putorius	Mammal	LHQP	0.2	0.8501	0.758 ± 0.053	0.106 ± 0.053	0.377	300	NA
Numida meleagris	Mammal	LQHP	0.4	0.8963	0.823 ± 0.056	0.118 ± 0.042	0.255	156	0.067
Nymphicus hollandicus	Bird	LQHP	0.8	0.8051	0.753 ± 0.104	0.114 ± 0.099	0.451	129	0.786
Passer domesticus	Bird	LQHP	0.4	0.9231	0.894 ± 0.016	0.036 ± 0.007	0.206	222	0.28

Rattus novergicus	Mammal	LQHP	0.2	0.9078	0.803 ± 0.045	0.110 ± 0.034	0.217	274	0.648
Rattus rattus	Mammal	LQ	0.4	0.878	0.848 ± 0.031	0.068 ± 0.041	0.481	7	0.371
Streptopelia decaocto	Bird	LQHP	0.4	0.9397	0.898 ± 0.025	0.044 ± 0.013	0.178	188	0.49
Sturnus vulgaris	Bird	LQHP	0.4	0.9361	0.920 ± 0.002	0.021 ± 0.002	0.155	187	0.858
Sus scrofa	Mammal	LQH	0.2	0.9823	0.816 ± 0.152	0.0317 ± 0.003	0.116	237	0.569
Xenopus laevis	Amphibia	L	0.4	0.8847	0.844 ± 0.140	0.127 ± 0.145	0.504	3	0.279

Table 2.4: Niche dynamic output considering species with a minimum of five occurrences available in the non-native regions. **Species:** Species name. **Class:** biological class of species. **Expansion:** measure the degree of niche expansion. **Stability:** measure the degree of niche stability. **Unfilling:** measure the degree of niche unfilling. **Schoener's D:** measure the degree of niche overlap between native and introduced range. **Schoener's DPVALUE:** p value for randomization test. **Boyce:** Indicates the model performance when niche models are tested using independent dataset in the non-native region, where negative indicate low model performance and positive values high model performance. *Indicates p values less than 0.05.

Species	Class	Expansion	Stability	Unfilling	Schoener's D	Schoener's D_{PVALUE}	Boyce
Alopochen aegyptiacus	Bird	0.000	1.000	0.951	0.001	0.242	0.536
Anas platyrhynchos	Bird	0.000	1.000	0.931	0.032	0.042*	0.618
Carduelis carduelis	Bird	0.000	1.000	0.958	0.008	0.068	0.033
Columba livia	Bird	0.000	1.000	0.258	0.200	0.004*	0.924
Corvus albus	Bird	0.000	1.000	0.997	0.003	0.021*	0.700
Estrilda astrild	Bird	0.109	0.890	0.112	0.191	0.027*	0.189
Lithobates catesbeianus	Amphibia	0.673	0.326	0.442	0.096	0.113	0.82
Mus musculus	Mammal	0.999	0.000	0.786	0.005	0.347	0.139
Numida meleagris	Mammal	0.000	1.000	0.641	0.083	0.137	0.067
Passer domesticus	Bird	0.036	0.963	0.122	0.279	0.000*	0.280
Rattus novergicus	Mammal	0.541	0.458	0.438	0.018	0.089	0.648
Rattus rattus	Mammal	0.529	0.470	0.000	0.151	0.046*	0.371
Sturnus vulgaris	Bird	0.000	1.000	0.884	0.011	0.056	0.858
Sus scrofa	Mammal	0.473	0.526	0.058	0.184	0.031*	0.569
Xenopus laevis	Amphibia	0.000	1.000	0.681	0.207	0.022*	-0.279

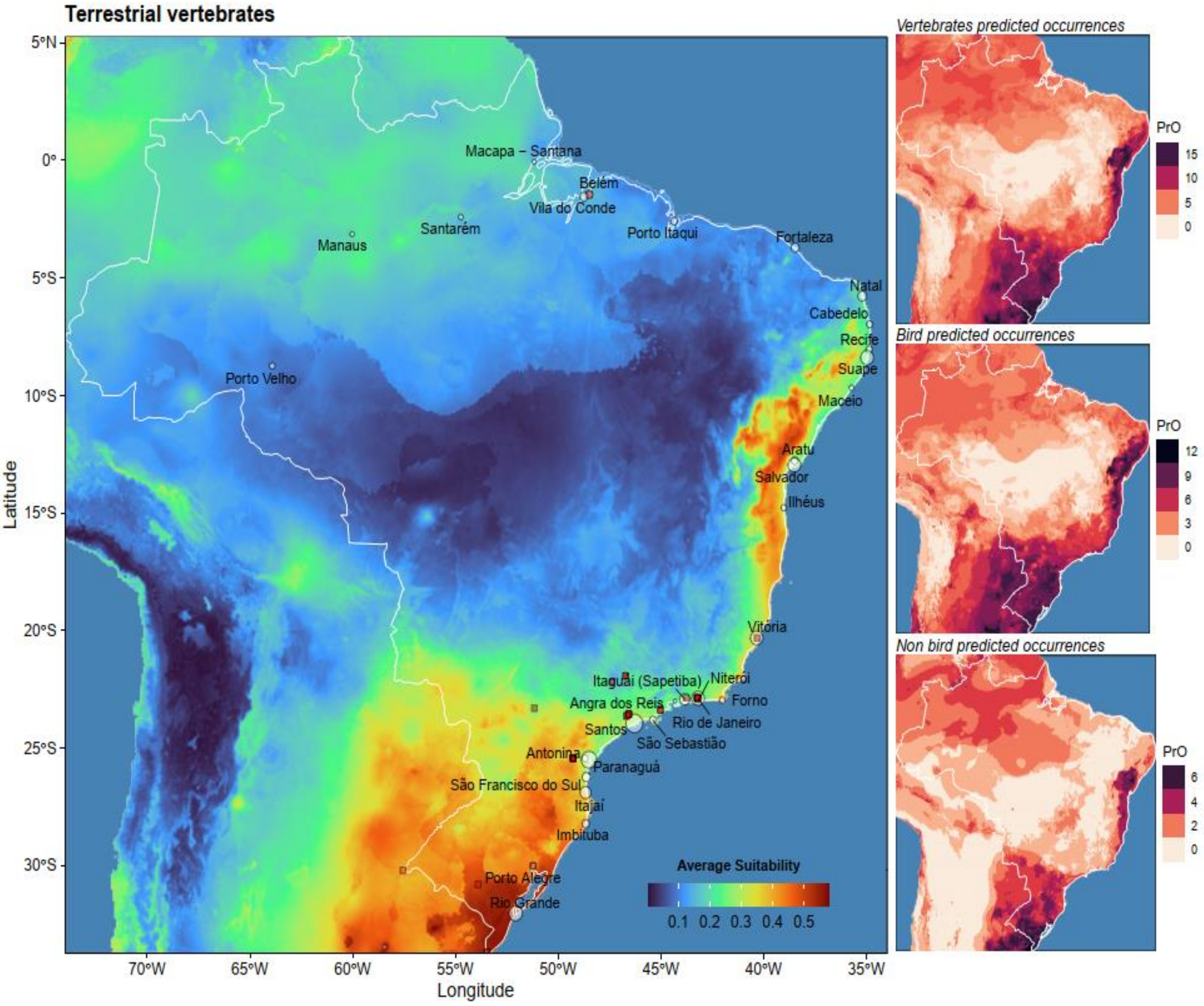

Figure 2.6: Environmental niche modeling prediction for 21 non-native vertebrate species of Brazil. The main picture shows the average suitability values considering all species with AUCTEST ≥ .75. Cold to warm color gradient indicates regions with low and high environmental matching between native and non-native regions. White circles indicate Brazilian port localities and circle size indicates the number of international ships docked in each port. Red squares show the first documented observation of each non-native species, which is potentially the first successful introduction event, or close to the where the first successful introduction event took place. The light to dark red gradient indicates the low and high intensity of historical occurrence in the potential introduction locations, respectively. The smaller maps summarize the expected number of non-native species (see colored squares), which was obtained by summing the output grids of each species using the maximum sensitivity equal specificity threshold. The upper map indicates all non-native vertebrates (N = 21 models), the middle map indicates non-native bird species (N = 11 models), and the lower map indicates non-native species that are not birds (N = 9 models).

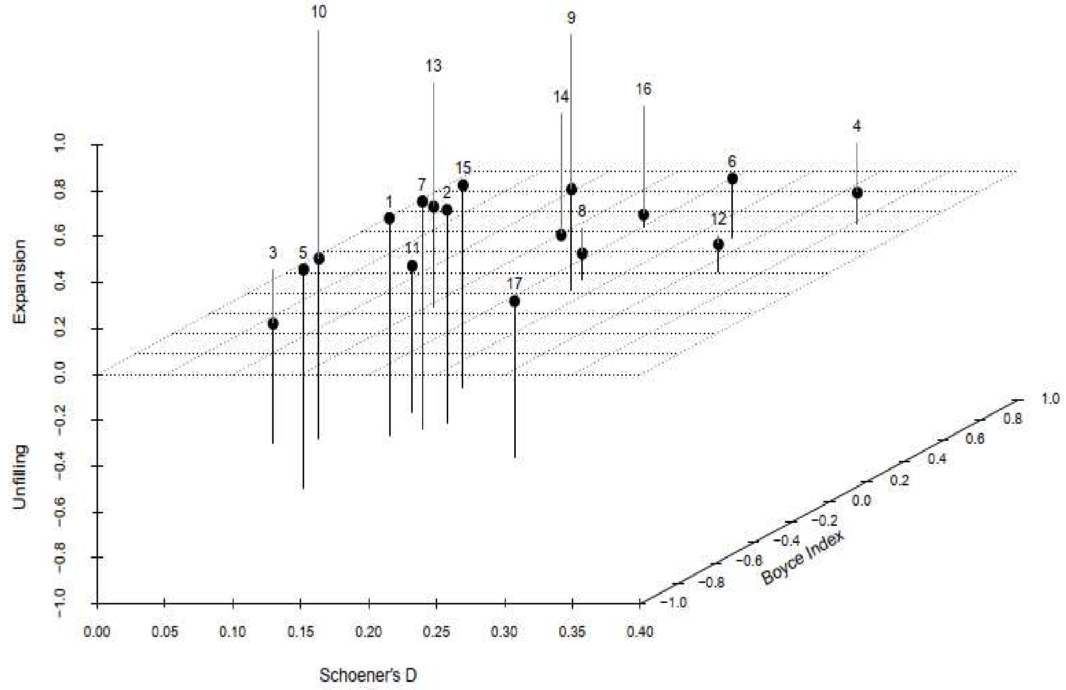

Figure 2.7: Niche dynamic plot. Niche changes and niche overlap between native and non-native ranges of 17 non-native vertebrate species introduced in Brazil. The reduction from 21 to 17 is species is because four species did not have the minimum of 5 occurrences available in the non-native regions. Vertical plane and bars respectively measure the orientation and the magnitude of niche changes. Grey (above the zero plane) and black (bellow the zero place) indicate, respectively, niche expansion and niche unfilling. Horizontal plane measures the niche overlap (Schoener's D metric), and the Boyce index evaluates how well are native niche models projection onto analogue climates in the introduced region. Boyce index ranges from -1 (poor predictions) to 1 (perfect predictions). Intersection with the zero plane is shown with black dots. Numbers above bars indicates the following species index: 1. *Alopochen aegyptiacus*, 2. *Anas platyrhynchos*, 3. *Axis axis*, 4. *Capra aegagrus*, 5. *Carduelis carduelis*, 6. *Columba livia*, 7. *Corvus albus*, 8. *Estrilda astrild*, 9. *Lithobates catesbeianus*, 10. *Mus musculus*, 11. *Numida meleagris*, 12. *Passer domesticus*, 13. *Rattus novergicus*, 14. *Rattus rattus*, 15. *Sturnus vulgaris*, 16. *Sus scrofa*, 17. *Xenopus laevis*.

Discussion

Biological invasion is a complex process, which is why so many hypotheses have been proposed to explain the success of non-native species in their non-native regions (Enders et al. 2020). However, it is becoming clear that the invasion process is a combination of several ecological processes that act on different scales, at different magnitudes, and at different stages of the invasion process (Redding et al. 2019). Our results corroborate this perception by showing that candidate mechanisms such as niche conservatism and climate similarity contribute to non-native species occurrences in the introduced region. Testing several mechanisms associated with the establishment of non-native species is challenging due to the difficulty of obtaining data on unsuccessful introductions. However, our results point to the importance of the environmental characteristics of introduction localities in explaining the observed occurrence of non-native vertebrate species in Brazil, allowing us to have an overview of the species' introduction pattern. We found that only four of the 37 non-native vertebrates' species had its occurrence associated with species dispersing from neighboring countries of Brazil, reinforcing that the introduction of non-native vertebrate species is assisted by anthropogenic structures. Therefore, if regions have similar environmental conditions to the native region and high human pressure, then non-native species will be more likely to establish (Venter et al. 2016, Souza et al. 2020).

One of the challenges in inferring population processes associated with species establishment using satellite and GIS data lies in disentangling the interplay between local and large-scale processes. At the local scale, propagule pressure is one of several population processes that is consistently pointed out as the main determinant in the successful establishment of introduced species (Simberlof 2009; Lockwood et al. 2009; Blackburn et al. 2015). However, introduced species should only manage to establish a viable population in a new region if the species' niche requirements are met (Holt et al. 2005). Corroborating this perception, we found that introduced localities with high similarity to the native region are distributed over the coastal regions of the country, which can result in in high rates of new propagules, due to the potential interplay between habitat suitability, propagule pressure and human infrastructure (i.e., ports).

Similarly, we detected that niche unfilling was greater than niche expansion in the introduced regions (Figure 2.8), which is expected due to the short time span for evolutionary processes to act on non-native species (Petitpierre et al. 2012, Strubbe et al., 2013). Indeed, species that were introduced more recently were those that had high niche filling index (Figure 2.9 and Table 2.4), such as *Corvus albus*. The time needed for evolutionary processes to act on introduced species highlights the necessity of introduced regions having abiotic conditions that fulfill niche requirements (i.e., niche conservatism) in the early stages of the introduction process (Holt 2005, Strubbe et al. 2013). However, evolutionary processes could be stronger depending on the introduction history of a species, for example, if the introduction process leads do the admixture of genetically distinct populations (Dlugosch & Parker 2008). For instance, species with expressive expansion index (see *Lithobates catesbeianus, Rattus norvergicus, Rattus rattus, Mus musculus* and *Sus scrofa* in Figure 2.9 and Table 2.4) seem to be adapted to explore a variety of habitats, which in turn could allow them to occupy new environments with considerable levels of dissimilarity from their native ones. However, it is expected that even in the presence of favorable ecological traits, evolutionary events that support niche expansion requires a long time to be realized (Alexander & Edwards 2010). This supports our findings that species with expressive expansion index are those that were probably introduced during the colonization of Brazil (e.g., *Mus musculus*, *Rattus novergicus, Rattus rattus*) in the sixteen-century giving them time to accumulate ecological differences that lead to niche expansion. Therefore, climate similarity can be a proximal cause and a potential first selective filter that increases the chances of positive population growth and, consequently, increases the likelihood of propagules overcoming the negative effects of environmental stochasticity.

Although our species pool is based only on available records of non-native observations it was still possible to infer important biological patterns. The species distribution models clearly show that the coastal region of the country has higher habitat suitability values (Figure 2.9) indicating a large portion of the country being more susceptible to the occurrence of non-native vertebrate species. Not surprisingly, these are the major economic regions of the country emphasizing the relevance of anthropogenic activities in the observed occurrences of non-native vertebrate species. Indeed, we found that the occurrences of introduced species are concentrated in regions with high and very high anthropogenic pressure (Figure 2.6). This agrees with previous studies that have already shown that urbanization supports more introduced species than natural regions as well as facilitating their permanency (McKinney 2006, Hui et al. 2017), reinforcing the importance of measuring the association of introduced species with human activities, such as economic and technological advances (Hulme, 2009, Hulme 2021) and, urban infrastructure and development (Cunningham et al. 2016, Cardador & Blackburn 2018). Therefore, anthropogenic variables should be able to capture several human components (e.g., social, cultural, and technological) associated with the permanence of introduced species.

This result was expected for vertebrates with small body size that can be unintentionally introduced (e.g., rats and geckos). In the case of species with larger body size, most of which were birds and mammals, several of them also have a large brain size (e.g., parrots, crows), a trait that is correlated with species cognitive ability indicating the potential for behavioural complexity and innovation capacity (Lefebvre et al. 2004). Higher cognitive ability can increase the chances of species survival during long distant travels on ships, while also allowing the exploration of new ecological opportunities in novel environments (Fristoe et al. 2017). In addition, in the context of contemporary species movements (Seebens et al. 2017) the improvement of technological advances (Hulme 2021) can increase the chances of multiple events of introduction in the same or neighbouring region, which in turn will increases propagule pressure and genetic diversity of introduced populations (Rius & Darling 2014; Dusglosh et al. 2015). These multiple introductions could increase genetic diversity of the introduced population due to the genetic admixture process if the propagules are from genetically dissimilar populations in its native region (Alexander & Edwards 2010; Uller & Leimu, 2011).

Finally, the taxonomical groups used in our study were limited to terrestrial vertebrates and for different classes of organisms such as plants and freshwater fish, distinct geographical distributions patterns could be found. For example, plants can easily be transported in small packages over large distances and, consequently, different distribution zones could be more relevant for plants. In this sense, an integrative approach that investigates the role of different vector sources, such as airports, freshwater ports, and the vulnerability of the landscape towards the introduction of non-native species, should be explored for different taxonomical groups. We believe that by integrating invasion ecology with data on the transportation of goods and people is an important step for the understanding of the pattern and processes involved in the spreading and colonization of non-native species as well as to the development of evidence-based designs to prevent and manage non-native and invasive species. Therefore, modelling the available information of non-native species should support the integration of theory with applied requirements of invasion biology.

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Appendix I

References used to collect the list of vertebrate species in Brazil.

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Conclusion

Although there has been notable progress in the knowledge of biological invasion in the last decade, a clear understanding of pattern and process that drive the establishment of non-native species in introduced environments remains unclear. This is reflected by the large number of invasive hypotheses that remains without empirical investigation (Enders et al. 2020). The challenges in investigating mechanisms associated with non-native species introduction lie in the urgency of using evidence-based solutions to mitigate impacts imposed by non-native and invasive species, as well as by the limitation of inferring ecological and evolutionary processes using correlative models. The former indicates the awareness of using the available information to design prevention strategies and understand candidate solutions in biological invasions. However, an effective solution also requires a clear understanding of the underlying processes that drive the establishment and impact of non-native and invasive species. In this sense, we argue that macroecological approach has the potential to move the knowledge of invasive science to beyond the native and non-native biotic and abiotic factors, leading to predictions of novel ecological and evolutionary opportunities (i.e., emergent properties) that support non-native establishment. This can be used to examinate the role of multiple factors that structure biotic, abiotic, and anthropogenic components of biological invasion allowing to investigate hypothesis and mechanisms that interplay of biodiversity, urbanization, climate change and biological invasions. Therefore, the use of macroecological modeling is underestimated in the field of biological invasion and should be further explored as a relevant tool to scrutinize general mechanisms regarding the biotic, abiotic, and anthropogenic factors in non-native and invasive species establishment.

In this thesis, I focused on investigating the role of these (phylogenetic, climatic, and anthropogenic) factors in the current distribution of non-native and invasive species independently. However, I was not able to scrutinize inherent mechanism associated in each factor, which reinforces the relevance of high-quality data derived from local sampling design for invasion ecology. For example, although merging databases allows to measure the phylogenetic similarity between non-native to native species to depict species differences, it was not possible to measure the magnitude of biotic interactions (i.e., species competition) and niche processes (i.e., sense Elton). Similarly, although climatic similarity between native and non-native regions should reflect environmental preferences for population performance (i.e., fitness), the available information to measure the contribution of population process in the observed species pattern is limited. In addition, we argue for the necessity of investigating how anthropogenic mechanisms interplay with biotic and abiotic factors in the context of non-native and invasive species. For instance, how social or economic status can correlate with commodities demand, propagule pressure and environmental requirements of non-native species establishment across taxa. Further, the role of environmental changes in community structure and its effect of invasiveness and invasibility is crucial for theoretical and applied ecology of non-native and invasive species.

Another relevant point lies in the support of computer processes and digital data accessibility to progress the field of biological invasion. Currently available databases of non-native and invasive species do provide useful information to improve the understanding of biological invasions. However, although its benefits, the databases also limit the inferring of ecological and evolutionary mechanisms involved in biological invasions. This can be associated with the lack of accuracy regarding the quality in morphological and molecular data required to estimate the drivers of non-native and invasive species establishment. These data are widely used to measure functional and evolutionary responses and is rarely assessed at large scales. Even with the growing number of non-native and invasive species data, the integration across databases do not correct for potential geographical and morphological bias, which in turn can limit tracking pattern and processes across scales. For instance, information of life history traits differs from temperate to tropical regions (SCHOLER; STRIMASMACKEY; JANKOWSKI, 2020) and close relative species can be dissimilar for the same life history trait between tropical and temperate latitudes (BOYCE.; MARTIN, 2017). Consequently, the use of traits present in species databases, could does not match with life history traits information obtained from field sampling. Thus, it is possible that the same non-native species could differ in their traits resulting in distinct responses to the demographic and selective pressures associated with the latitude and its anthropogenic disturbance levels across introduced localities. Further, tropical, and temperate discrepancies in biological invasions were previously highlighted (Pyšek et al. 2008, Chong et al. 2021) indicating potential idiosyncrasies regarding geographical and economic aspects. This certainly influences the overall perception of the biological invasion processes and patterns.

Finally, I conclude that biological invasion is a complex issue that lacks the generalities in explaining the mechanisms associated with the invasive processes. Taken together, the results of this thesis reinforce the relevance of historical biogeography and evolutionary processes of native and non-native abiotic (i.e., climate) and biotic (i.e., species composition) factors involved in the shaping of the current pattern of non-native species. In general, I conclude that both climate and evolutionary aspects interplay across geographical scales that can result in idiosyncratic processes of species establishment. Consequently, the biotic, climatic, geographical, and anthropogenic factors matter in biological invasion indicating the dependency of the context in species establishment. Specifically, I conclude that the macroecological approach can properly capture patterns and processes of biological invasion and is a powerful tool to scrutinize distinct mechanisms across different contexts of the invasive process.

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