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NATURALIZED PARROT (PSITTACIFORMES) DISTRIBUTION & LOCAL PROCESSES: AN INVESTIGATION OF ENVIRONMENTAL NICHES AND POPULATION GENETICS

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To all the non-natives doing their best in novel environments.

To do science is to search for repeated patterns, not simply to accumulate facts, and to do the science of geographical ecology is to search for patterns of plants and animal life that can be put on a map.

— Robert H. MacArthur, “Geographical ecology: patterns in the distribution of species”

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Abstract

The introduction of invasive species, along with climate change and habitat loss, are among the primary concerns for the conservation of biodiversity at a global scale. In this dissertation, I will assess the invasion process for Psittaciformes, more generally known as parrots, parakeets, cockatoos, and their kin. The introduction provides a review for the development of the field of invasion biology/ecology, as well as the relevance of parrots as species that have established non-native populations on all continents (except Antarctica). In Chapter 1, I review the available data on the presence and invasive status of all known non-native parrots at a global scale, to identify what species are the most widespread, determine the extent of their non-native distribution, and confirm what regions have the most non-native parrot species. In Chapter 2, I analyze the climatic and geographic determinants of non-native parrot distributions outside of their native range. Using species distribution models, the environmental space occupied by these species will be compared between their native and non-native range to determine whether they are subsets of one another or if there is divergence between the environmental niche spaces they occupy. These results are validated with the incorporation of null models trained using the same local environment data. In Chapter 3, I analyze the population genetics of the Monk Parakeet (*Myiopsitta monachus*), one of the most widespread non-native parrots, in order to confirm known patterns about the origin and genetic diversity of its non-native populations, including the previously unsampled populations of Chicago, Illinois and Aguada, Puerto Rico. This study also examines the demographic history of the different populations within the native range along with its only congeneric species, the Cliff Parakeet (*Myiopsitta luchsi*). Finally, I conclude the dissertation with a discussion on the results uncovered throughout the different chapters and the future projects I intend to investigate.

Introduction

Humans have been altering ecosystems by transporting non-native species across the world since the adoption of animal domestication and agricultural practices. The impacts of invasive species have steadily increased and now include causing species extinctions, altering ecosystems, impacting human agriculture and human health, and direct effects on basic economic activities. As such, the academic disciplines of invasion biology and invasion ecology have seen substantial growth including the development of many hypotheses and frameworks to identify and address the causes and effects of species invasions. My research focused on one of the lesser studied taxa within invasion research, i.e., parrots, parakeets, cockatoos, and the other members of the Order Psittaciformes. Through the study of non-native Psittaciformes, I had three main objectives to address in this dissertation. First, I quantify the extent to which Psittaciformes species have been introduced and have established non-native populations at a global scale. Secondly, I examine the differences in climate and terrain between the distributions of native and non-native populations of Psittaciformes. Third, I examine the evolution of these non-native populations at a genetic scale. Thus, in this dissertation I provide an in-depth examination of the local processes influencing the global distribution of non-native parrots, particularly comparing the environmental niches and population genetics between their native and non-native populations.

State of the Field: Invasion Biology and Ecology

Although human mediated biological invasions have had a long history, the concept of systematically studying biological invasions was first explored in the seminal works of Charles Elton (1958) on the disturbances caused by non-native species in the UK. Elton's focus was on animal community ecology, on how “invaders”, those species that were non-native to the region, negatively impacted the local native species and the importance in eradicating those non-native species (Simberloff, 2011). The modern field of invasion biology began to take shape around 1982 when the Scientific Committee on Problems of the Environment (SCOPE) endorsed the Scope Programme on the Ecology of Biological Invasions, a global project that sought to understand what factors are associated with successful invasive species, what properties make ecosystems resilient or vulnerable to invasions, and how management programs should be developed to handle invasive species (Simberloff, 2011). Since then, the field of invasion biology has experienced rapid growth and the development of multiple hypothesis and models to explain the process and factors associated with the successful establishment of non-native species.

Different facets of biology, ecology and genetics have been invoked to explain the differences in invasive success across species. Charles Elton’s development of the concept of the species niche as relating to its functional attributes within an ecosystem are the foundation for the hypothesis of limiting similarity, wherein successful invaders are those that are functionally different from species in the recipient community (Catford *et al.*, 2009). Another hypothesis concerns novel weapons, where the invader possesses biochemical substances that inhibit the growth or survival of native competitors, such as has been documented in several invasive allelopathic plant species (Chengzu *et al.*, 2011).

Many more hypotheses have been proposed as being relevant to invasive species success (see Catford *et al.*, 2009 and Jeschke, 2014 for reviews). The Catford *et al.* (2009) grouping of hypotheses is based on their focus: propagule pressure, abiotic factors, and biotic factors. The novel weapons and limiting similarity concepts are some of the hypotheses grouped under biotic factors, and it is important to note that both the invading species and the invaded community's traits as well as the interaction between them are the focus of interest. Invasion hypotheses regarding biotic interactions can revolve not only around the newly formed interactions between the invaders and the recipient community, but also between the absence of predators, mutualists, or parasites within the novel locations (Catford *et al.,* 2009). Hypotheses regarding abiotic factors are often concerned with resource availability, physiological tolerances to temperature, salinity, pH, and the effect of disturbances on colonization by invading species (Catford *et al.,* 2009).

Finally, hypotheses regarding propagule pressure are concerned with how invasion success is influenced by the number and frequency of propagules (be they individuals, seeds, spores, etc.) that arrive at a novel location, the pool of potential colonizers that can invade a location and the dynamics associated with small population sizes (allee effect, population bottleneck, sex ratio biases) (Catford *et al.,* 2009). A meta-analysis on the effect of propagule pressure found that propagule pressure was consistently and positively associated with invasion success (Cassey *et al.,* 2018). The significance of this finding is expected, as propagule pressure is by necessity a pre-requisite for biological invasions to occur (Catford *et al.,* 2009) and has been suggested as the null model with which to study biological invasions (Cassey *et al.*, 2018).

Another way scientists have approached the topic of biological invasions is through the development of frameworks that describe the invasion process and break it up into discrete units that can be studied independently (Williamson & Fitter, 1996; Richardson *et al.,* 2000; Blackburn *et al.,* 2011). These frameworks were developed independently from perspectives drawn from the study of plant and animal ecology, respectively, and have ultimately been unified into a singular framework for understanding biological invasions (Blackburn *et al.,* 2011). This framework explicitly designates the unit of interest within invasion sciences as the population, given that whether a species is native, non-native or invasive is a matter of relative and local perspective. Thus, populations can be classified based on the stage it occupies within the invasion process and the barriers to be overcome for a population to become more invasive (Blackburn *et al.,* 2011).

A full trajectory through the invasion process would involve: 1) a population is transported beyond the limits of its native range either into captivity, cultivation or directly into the wild; 2) the transported individuals are intentionally or accidentally released into the wild becoming an introduced population; 3) the introduced population must be able to survive the local conditions, reproduce, and become self-sustaining; 4) individuals from the naturalized population disperse beyond the initial site of introduction and begin surviving and reproducing at these novel locations; and 5) when these additional populations become self-sustaining and individuals continue to disperse into novel locations the populations become invasive (Blackburn *et al.,* 2011). This conception of the invasion process differentiates between the barriers that need to be overcome to progress through the invasion process and identifies distinct stages that populations can find themselves in, through which different traits and factors can impact a population's transition throughout this process. Furthermore, it clearly delimitates the time frame during which the previously mentioned invasion hypotheses would be operating within the invasion process.

Despite over six decades of history, interdisciplinary approaches and increasing global interest to mitigate the impacts of invasive species there are still facets of invasive species research that remain generally underexplored. For example, invasive species research on hybridization or in urban environments, at the individual and genetic level, is relatively scarce

(Crystal-Ornelas & Lockwood, 2020). Birds are an excellent taxon to attempt to explore these areas of concern. There is a wealth of observations collected by amateur birders that has been used to describe the timing of migration, distribution of species, changes in abundance, reporting survival of ringed individuals and surveys of diversity that span centuries (Greenwood, 2007). Furthermore, reduced cost of genetic library preparation and sequencing techniques allows for increased sampling of individuals to explore aspects of population genetics (Bayona-Vásquez, 2019).

Psittaciformes: a model taxon to understand invasion.

The Order Psittaciformes makes for an ideal group with which to address research questions regarding the effect of traversing the invasion process on genetic diversity and structure, the potential of adaptation to novel environments and the associations between non-native parrot populations, and the climates and environments in which they have become established. Non-native species of Psittaciformes have had varying success in traversing the invasion process, which provides an opportunity to examine the factors limiting their progression. Previous research on non-native Psittaciformes has validated the existence of different selective pressures occurring at the different stages of the invasion process (Cassey *et al.,* 2014). The movement of parrots through the invasion process is well known, as they are popular pets traded internationally (Cardador *et al.,* 2017; Mori *et al.,* 2017). As these pets escape into the wild, they can become introduced; with over 16% of species within Psittaciformes (N = 62 out of 355 species) having breeding populations outside of their breeding range (Menchetti & Mori, 2014). From the disparity between parrots in the pet trade and those that have begun breeding in the wild, certain traits that seem to be favored for becoming introduced have been identified. Cassey *et al.* (2014) demonstrates that Psittaciformes species that were considered pests had larger population sizes within the native range, had broader diets, or broader latitudinal extents were more likely to become introduced outside of their native range.

However, while much research has been done on non-native Psittaciformes, the focus of the research has been mostly unilateral, centering on a narrow set of species. As mentioned above, the majority of research on invasive species has been on quantifying their impact on native biota and human activity. In the case of Psittaciformes, this research has been mostly attributed to and centered on the two most widespread species: the Monk Parakeet (*Myiopsitta monachus*) and the Rose-ringed Parakeet (*Psittacula krameri*) (Menchetti & Mori, 2014). Additionally, efforts to understand how climate and human activity impact non-native parrot survival have also tended to focus exclusively on Monk Parakeet and Rose-ringed Parakeets (Strubbe & Matthysen, 2009).

Many species of Psittaciformes, beyond Monk Parakeets and Rose-ringed Parakeets are transported outside of their native range and have successfully established breeding populations. While it is possible that these species could be confronting a barrier to their progression along the invasion pathway, it is just as likely that, at some point, they might break past and become considered invasive species. In such a case, it is important to understand the factors that contribute to successful established populations across all species of Psittaciformes with non-native populations, not just Monk Parakeets and Rose-ringed Parakeets.

The next three chapters in this dissertation will each address a distinct aspect of invasion biology that requires updating or has been underexplored within the literature. In Chapter 1, I compiled published data on avian invasions, citizen science datasets and published articles on non-native distributions of Psittaciformes species to systematically account their occurrence on a global scale. My accounting reveals that within the 381 species of Psittaciformes: 170 have become introduced and 60 of these are also breeding or have become established outside of their native range. I also quantify the spatial extent of each species' occurrence outside of their native range to find that the Monk Parakeet is the most geographically widespread introduced species of Psittaciformes, even though the Rose-ringed Parakeet has been introduced into more countries.

In Chapter 2, I build upon my examination of which parrot species have become introduced and incorporate species distribution models to identify what climatic and landscape factors are the most significant in determining the distribution of non-native populations of Psittaciformes species. To accomplish this goal, occurrence data for the most widely distributed species within Psittaciformes were used to train MaxEnt distribution models (Phillips *et al.,* 2004) on occurrences from within the native and non-native range separately. The different models were then cross-referenced with the reciprocal range's occurrence points to determine whether one of these models could accurately predict the other's occurrences based on the underlying environmental variation. The results of these comparisons were validated using null models to statistically test for their significance. This analysis reveals that within the most widely distributed introduced parrots over 77% are found in environments that match the suitability of those described by their native range distribution. Another 11% of introduced parrots have non-native range distributions whose environmental breadth is broader than what is found within their native range. The remaining introduced parrots' distributions are explained either by their close association with human activity or a divergent environmental niche between their native and non-native populations.

Finally, in Chapter 3 I examine the population structure, genetic diversity and demographic history within 4 different non-native populations of Monk Parakeets, one of the most widespread species of non-native parrots. Reduced representation sequencing was used to identify allelic variants across the genome and I used ADMIXTURE methods to identify the most likely source populations within the native range. Comparing estimates of genetic diversity reveals that all non-native populations show reduced heterozygosity across the genome when compared to the different native range populations. The demographic history for this species, alongside its sister taxa the Cliff Parakeet (*Myiopsitta luchsi*), was estimated using a pairwise sequentially markovian coalescent (PSMC) model that determines the species' split around 4 Mya. This model also demonstrates that the Monk Parakeet has been experiencing population growth throughout all three of its populations and shows no signs of population bottlenecks.

Chapter 1

The Number and Distribution of Introduced and Naturalized Parrots

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Introduction

Parrots have been transported and traded by humans for at least the last 2,000 years and this trade continues today (Scheffers *et al.*, 2019). Cardador et al. (2021) summarized trade data available through the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; CITES, 2015) and documented that during the 20-year period 1975 to 2015, more than 19 million individual parrots of 336 species were legally traded among countries. This involved an average of more than half a million birds each year and parrot trade represented approximately 25% of all legal bird trade (Cardador *et al.*, 2021).

Inevitably, some individuals of introduced alien species, usually imported for the pet trade, either escape captivity and/or are accidentally or purposefully released and may begin breeding in the wild in the novel area (Carrete & Tella, 2008; Vall-llosera & Cassey, 2017). Parrots are no exception and released or escaped parrots are often quite successful at surviving in the wild in new areas. Over time, if a successful breeding population is established, the species would be considered to be a naturalized species in that area. In some cases, the new populations can expand rapidly and grow exponentially in size (van Bael & Pruett-Jones, 1996; Hobson *et al.*, 2017; Postigo *et al.*, 2017, 2019; Jackson, 2021). If the species expands its naturalized range and establishes additional populations, it may become invasive.

Naturalized and invasive species are increasing worldwide, and parrots represent an increasingly large proportion of the naturalized bird species (Cardador *et al.*, 2017; Pruett-Jones, 2021). Although the invasive nature of established foreign parrot species is debated (Menchetti & Mori, 2014; Brightsmith & Kiacz, 2021; Mori & Menchetti, 2021), naturalized parrot populations are increasing in distribution and size and their interactions with humans are also increasing and becoming more complex and involves both positive and negative aspects (Senar *et al.*, 2016; Crowley *et al.*, 2017, 2019; Crowley, 2021; Kiacz & Brightsmith, 2021). This interaction with humans also includes control of some populations. In many cities around the world two common introduced parrots, the Rose-ringed Parakeet (*Psittacula krameri*) and Monk Parakeet (*Myiopsitta monachus*) are being controlled due to real or perceived problems with human activity. This is also true for some species in their native distribution (Bucher, 2021).

The wildlife trade that ultimately gives rise to naturalized populations of parrots can also directly and negatively impact populations of species in their native ranges (Tella & Hiraldo, 2014). In many cases, this trade is causing species to be endangered in their native area, while at the same time inadvertently creating the possible situation where a population may establish itself in a novel and foreign area. Also, the established populations can have impacts on local and native species (Menchetti & Mori, 2014). It seems critical, therefore, to know exactly how many parrot species have established breeding populations in novel areas outside of their natural distribution. Such information is critical for monitoring introduced populations, informing management priorities, and understanding how introduced population may relate to the conservation of endangered populations in the native range of species (Kiacz & Brightsmith, 2021). That is the purpose of this review. We summarize available databases and attempt to arrive at an estimate for the number of parrot species both introduced and naturalized in the world. Our effort includes providing a database combining information from separate sources for use by other researchers.

Efforts to estimate the number of naturalized parrots have been made for almost two decades, and a comparison of the results highlights that the number and distribution of naturalized parrots is increasing. In one of the first efforts at counting naturalized parrots, Lever (2005; see also Royle & Donner, 2021) reported that 34 species of parrots have established populations outside their native range. Two years later Runde et al. (2007) reported that there were 39 naturalized parrot species. Subsequently, Menchetti & Mori (2014) reported that about 60 parrot species were breeding outside their native distribution, and Avery & Shiels (2018) reported that 54 species have been introduced into foreign areas and that 38 of these have become established. And, most recently, Royle & Donner (2021) examined records in the Global Avian Invasion Atlas (GAVIA) database (Dyer *et al.*, 2017) from 1993-2012 and documented records of 129 species of parrots observed in 106 countries. From these records, Royle & Donner concluded that there were at least 47 species of parrots in 21 genera that are naturalized in at least one country outside their native range. Lastly, a recent estimate of the geographical range of naturalized parrots is that of Mori & Menchetti (2021) in which they conclude that species are found in 47 countries and all continents except Antarctica (Ancillotto *et al.,* 2015; Menchetti *et al.,* 2016; iNaturalist Alien Parrots Observatory, 2019). The variation in recent estimates is due in part to the sources of the information reviewed, and the time frame considered. Although our study is also subject to the same limitations, our review represents the first attempt to estimate the number of naturalized species based on a combination of the available data sets that have previously been analyzed separately.

Methods

Our examination of world parrot species follows the taxonomy of the International Ornithological Congress (Gill & Donsker, 2019). According to that taxonomy, there are 398 recognized species of parrots, including 17 taxa now extinct, and 381 extant species.

Terminology

There are a wealth of terms now used in the literature on introduced and naturalized alien species (Richardson *et al.*, 2011). We use the terminology of Blackburn *et al.* (2009; 2011) and Richardson *et al.* (2011) as follows: a) Introduced species – a non-native/alien species that has been transported outside of its native range by human means and for which individuals have been observed in the wild in the new and novel area; b) Breeding - non-native/alien species for which there is evidence of breeding activity in the wild; c) Naturalized - non-native/alien species that has established a self-sustaining population; d) Invasive – non-native/alien species that has established a self-sustaining populations at multiple sites across a range of habitats.

Databases

We were focused on identifying populations of species of Psittaciformes that occur in areas outside of their natural ranges. Thus, records of sub-species were subsumed under their corresponding species. To assess the status of each species, we summarized all records in the Global Avian Invasions Atlas (GAVIA) database (Dyer *et al.*, 2017). GAVIA is a spatial and temporal database that summarizes published literature on naturalized birds and classifies the occurrence of species into various categories based on published findings. The GAVIA database consists of 27,723 records of observations and/or data on alien birds, representing 971 species and spanning the period 6000 BCE – 2014 CE. Each record details an introduced species' status within a country, as referenced by a particular publication. For our analysis, the GAVIA dataset was filtered to only include records of Psittaciformes. Furthermore, 76 records of introductions (corresponding to 22 species) for conservation purposes or reintroductions back into a species' native range (known or presumed) were excluded. The final GAVIA dataset that we examined consisted of 3,422 records of 127 species introduced into 109 different countries and administrative regions. Of these 127 species, 101 were also present in the eBird database (see below), whereas 26 were unique to the GAVIA database.

In the GAVIA database, the status of species is classified into one of six categories: Breeding = a species that is known to be breeding or to have bred in the area of introduction, but for which the population is not self-sustaining; Established = a species that has formed self-sustaining populations in the area of introduction; Unsuccessful = an introduced species that has been seen in the wild but has not been able to establish a breeding population; Died Out = a species that was once established in the area of introduction, but has become extinct (by non-human means); Extirpated = a species that was once established in an area, but has subsequently been exterminated by humans; and lastly Unknown = a species that is observed in the wild in the area of introduction but whose status is unknown relative to the other categories (Dyer *et al.*, 2017).

We sorted these records by species and country and collapsed the six categories to four: Introduced (Unsuccessful or Unknown status in GAVIA), Breeding, Naturalized (Established status in GAVIA), and Historic (Extirpated or Died Out status in GAVIA). We complimented the above data from GAVIA with citizen science records from eBird (eBird, 2020) and the Alien Parrots Observatory project in iNaturalist (iNaturalist Alien Parrots Observatory, 2020). These are spatial and temporal databases of species' observations as reported by citizen scientists. All eBird records (whether from checklists or individual observations) between 1960-2017 were downloaded and filtered to include only extant species of Psittaciformes (N = 2,342,926). We then mapped these observations onto a high-resolution world map (from the R packages rworldmaps and rworldxtra (South, 2012; Brunsdon & Chen, 2014; R Core Team, 2018)) to identify the country/territory where the observation was made. Observations of a given species were excluded if they were made within that species' native range, as based on distribution maps available from BirdLife International (BirdLife International and Handbook of the Birds of the World, 2019). Furthermore, observations within 100 km of the native range were also excluded under the assumption that these observations likely represent extralimital sightings rather than observations of introduced birds. If there were at least three observations of individuals that occurred on different days and were more than 100 km outside of their native range, we considered those observations to represent an introduced population.

The final data set of eBird observations comprised 225,531 records of 139 species. Observations in iNaturalist were handled similarly to those from eBird, and the resulting data comprised 12,760 observations of 34 species from 1960-2017. All 34 species present in the iNaturalist data set were also in the eBird database.

Although the records from GAVIA provide information on the status of introduced parrots (breeding, etc.) the records from eBird and iNaturalist generally do not, at least in terms of the occurrence data that we summarized. In our data set (Table A1, A2, A3), we scored a species as 'Observed' if the records came from eBird or iNaturalist. The category Observed is thus the same as Introduced (from GAVIA) but these are listed separately in the database to indicate where those data came from. In cases where the GAVIA database indicated a status of 'Historic' for a species, but there were also records in eBird and iNaturalist, the status was listed as 'Historic/Observed'.

Lastly, using the eBird and iNaturalist records, we determined each species' Area of Occupancy (AOO) using the R package redlistr (Lee & Murray, 2019) to quantify the area (in km^2) occupied by each species outside its native distribution. The AOO analysis examines a species distribution based on 2 x 2 km grids, and the total AOO for a given species is the sum of the area for the total number of grids in which that species has been recorded. For the six species of introduced parrots with the largest values for AOO, we also map their worldwide distribution, using the R packages rworldmaps and rworldxtra (South, 2012; Brunsdon & Chen, 2014; R Core Team, 2018).

Separate from examining the records in the above databases, we examine in detail the parrot species present in the United Sates. Several recent, and in-depth analyses of introduced parrots in the United States (Falcón & Tremblay, 2018; Uehling *et al.*, 2019, 2021; VanderWerf & Kalodimos, 2021), permit comparisons between various data sets.

Political Designations

The GAVIA database, and records on eBird and iNaturalist, are only as geographically widespread as the publications or actual observations themselves. Thus, there are not records or observations for every country or geographical area. In our summary, we designated the country of observation as that location on the observation or reference publication.

Many countries administer political territories. When there were data for territories these were combined but designated as occurring separately from the country itself, as follows. Observations from Norfolk Island and Christmas Island were combined and listed as Australian Territories. Observations from Hong Kong and Macao were combined and listed as Chinese Special Administrative Region. Observations from French Polynesia, Guadeloupe, Martinique, Mayotte, and Reunion were combined and listed as French Territories. Observations from Aruba, Curacao, Sint Maarten and Netherlands Antilles were combined and listed as Netherlands Territories. Observations from Bermuda, British Indian Ocean Territory, Isle of Man, British Virgin Islands and Cayman Islands were combined and listed as U.K. Territories. Lastly, observations from Puerto Rico and U.S. Virgin Islands were combined and listed as U.S. Territories. In our analyses, we counted each territory separately, but for presentation (Table A1, A2), the territories of a country are grouped together, e.g., Puerto Rico and the US Virgin Islands are combined to be 'US Territories').

Results

Based on the GAVIA, eBird, and iNaturalist databases (hereafter referred to as the combined database), there are records of 170 species of Psittaciformes having been introduced (seen in the wild) in 126 countries or territories outside of the native range (Figure 1.1; Table A1, A2). These species comprise approximately 45% (170 of 381) of all known species of Psittaciformes. Of these 170 species, 60 species have been recorded or are now known to be naturalized and an

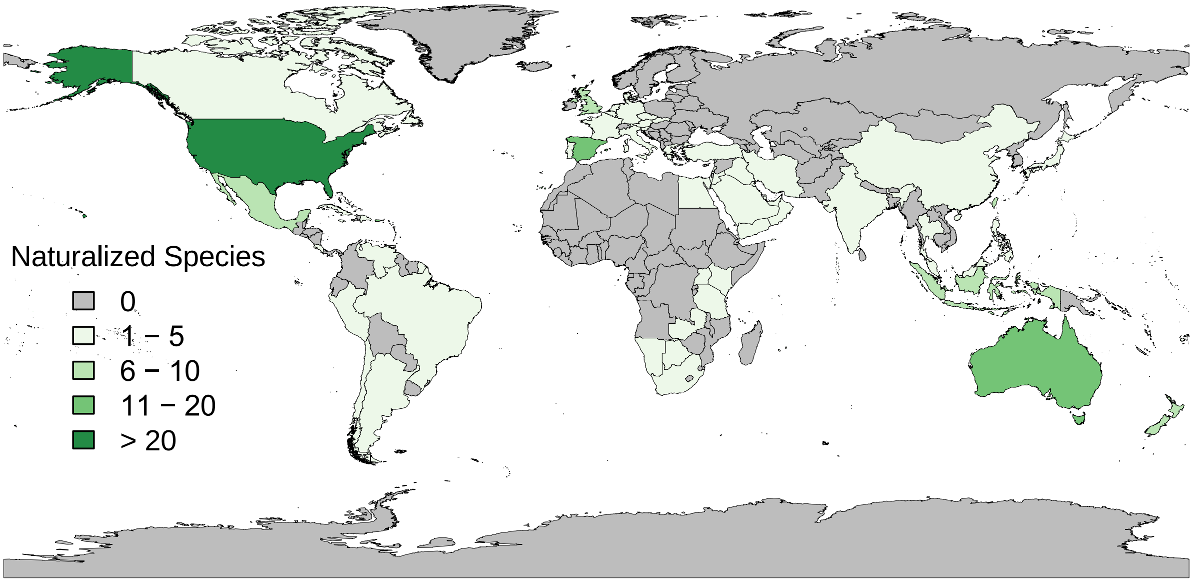


Figure 1.1 Distribution of naturalized and breeding species of parrots (Psittaciformes) per country, according to the GAVIA (Dyer et al., 2017) dataset.

additional 11 species are breeding in at least one country outside of their native range, being present in a total 86 countries or territories.

For the 71 species either breeding or naturalized, the mean number of countries (or territories) in which these species occur is 3.8 with a wide range of 1-51 (Figure 1.2). Almost half (30) of these species are recorded as either breeding or having a naturalized population in just one country. The six most widely distributed naturalized parrots, in terms of countries occupied are: Rose-ringed Parakeet, naturalized in 47 countries or territories; Monk Parakeet, naturalized in 26 countries or territories; Budgerigar (*Melopsittacus undulatus*), naturalized in 12 countries or territories; Alexandrine Parakeet (*Psittacula eupatria*) naturalized in 12 countries or territories; Brown-throated Parakeet (*Eupsittula pertinax*), naturalized in eight countries or

Figure 1.2

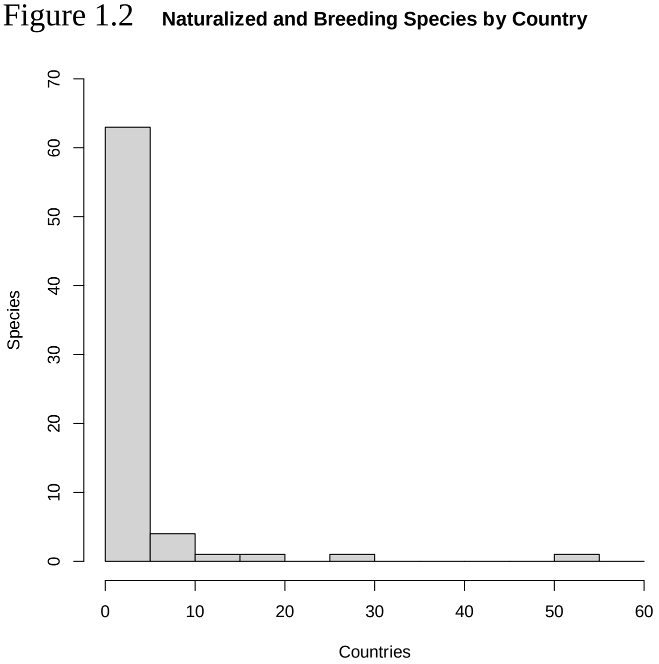
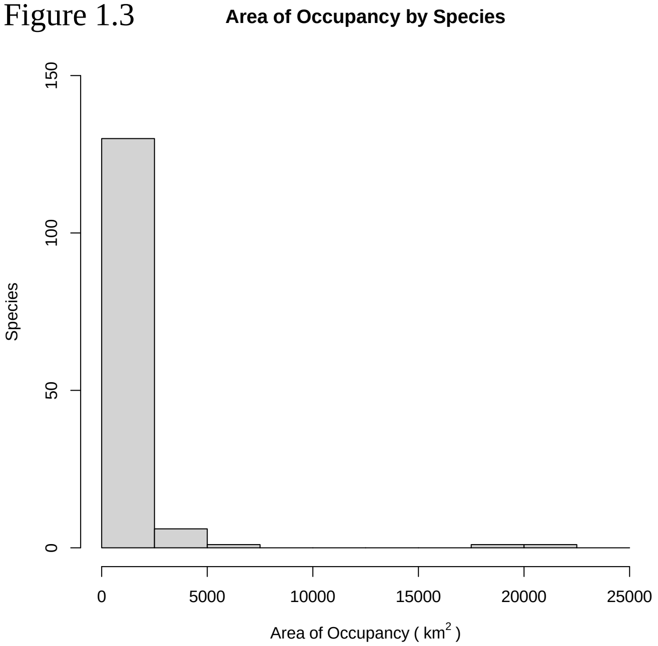


Figure 1.3



Figures 1.2-1.3. The frequency distribution of introduced and naturalized or breeding species of parrots (Psittaciformes) Fig. 1.2) across countries and Fig. 1.3) by Area of Occupancy (AOO). The AOO only refers to the introduced populations.

territories; and Grey-headed Lovebird (*Agapornis canus*), naturalized in six countries or territories (Table A1).

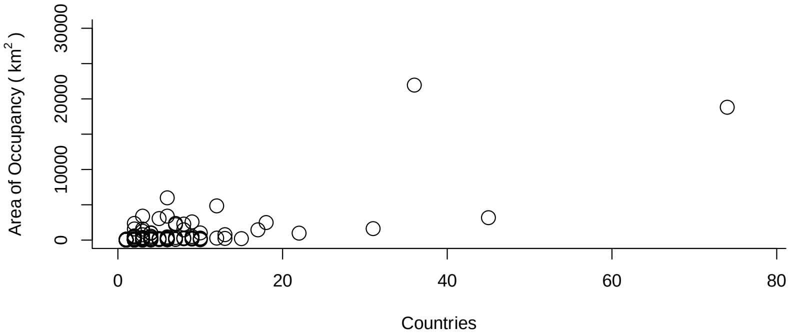


Figure 1.4. Relationship between Area of Occupancy and the number of countries that introduced parrots have been seen in the wild or are naturalized or breeding.

Countries vary enormously in size, and the Area of Occupancy (AOO) is a more objective measure of the geographical distribution of introduced species than number of countries. For introduced parrots (species observed in the wild outside their native range), the AOO varied widely. The mean AOO was 756.6 km^2 (n = 139; range = 4 – 21,944 km^2; SD = 2571.4; Figure 1.3). Above, the six most widely distributed parrots are listed in terms of countries occupied. This list changes when considering AOO. The six species with the largest AOO are: Monk Parakeet (21,944 km^2), Rose-ringed Parakeet (18,812 km^2), Eastern Rosella (*Platycercus eximus*, 5,976 km^2), Nanday Parakeet (*Aratinga nenday*, 4,840 km^2), Red-crowned Amazon (*Amazona viridigenalis*, 3,376 km^2), and the Budgerigar (*Melopsittacus undulatus*, 3,172 km^2). Only the Budgerigar, Monk Parakeet and Rose-ringed Parakeets overlap in these two ranked lists. Figures S1-S6 illustrate the global distributions of the sightings of these six species outside their native ranges. Despite the difference between countries as an indicator of geographical spread and AOO, there was a significant correlation between the number of countries a species was introduced in and the AOO (Figure 1.4; Spearman $R_s = 0.724$, $P < 0.001$).

In terms of countries supporting naturalized parrots, and based on the combined database, the six countries or territories with the largest number of naturalized or breeding species are:

United States (40 species), Australia, Spain, and the US Territories each with 14 species, Taiwan (9 species), and Singapore (8 species). This order is different if we consider records for all introduced species combined. That list is: United States (87 species), Brazil (53 species), Spain (52 species), US Territories (36 species), Australia (35 species), and Mexico (20 species) (Table A1).

The records for Australia of 13 naturalized species (Table A1) illustrate the complexity of the parrot trade and the current distribution of introduced species. In Australia, all naturalized parrots except one (Rose-ringed Parakeet) are species native to Australia but introduced in areas outside of their native range on the continent (Rogers & Kark, 2021). Thus, these species fall within the definition of transported, introduced, and naturalized used by authors, but the species' novel distributions are still within their native country Australia.

For the continental United States, there are records of 82 species of parrots introduced, breeding, or naturalized (Table A1, A2). At least two of these records are suspected to be in error or are inaccurate (that of Kuhl's Lorikeet *Vini kuhlii* and Kakapo *Strigops habroptila*), leaving 80 species. In comparison, the work by Uehling et al. (2019, 2021), focusing on the continental United States and during the 15-year period 2002-2016, documents records of 56 species of parrots either introduced or naturalized. These two lists (the combined database [Table A1] and Uehling et al. (2019, 2021)) overlap considerably when just considering naturalized species, but less so when considering all species. Thus, of the 25 naturalized species listed in (Uehling *et al.*, 2019), all but one is listed as naturalized in the combined database. Similarly, of the 22 species listed as naturalized in the combined database, 17 species are also listed as naturalized by Uehling *et al.* (2019). There is even greater overlap for the data in Hawaii and Puerto Rico. Of the five species of parrots listed by VanderWerf & Kalodimos (2021) as naturalized in Hawaii, each of those species is listed as either breeding or naturalized in the combined database (Table A3). For Puerto Rico, of the 12 naturalized species identified by Falcón & Tremblay (2018), all but one is also listed as introduced or naturalized in the combined database (Table A3). Despite this considerable overlap when considering currently known naturalized species, the combined database (Table A1) also contains records of many species that have not been recently confirmed or verified. Thus, for the continental US, the combined database contains records of 27 introduced and six breeding species not confirmed by Uehling *et al.* (2019, 2021).

Combining the lists of the recent studies (Falcón & Tremblay, 2018; Uehling *et al.*, 2019, 2021; VanderWerf & Kalodimos, 2021), 28 species of Psittaciformes are naturalized in either the continental US, Hawaii, or Puerto Rico, and an additional 16 species are breeding there (44 species total). If we ask the same question of the combined database, there are records of 24 species as naturalized in either the continental US, Hawaii, or Puerto Rico, and an additional 15 species are breeding there (39 species total).

Discussion

Parrots are one of the most endangered groups of birds in the world, and in part this is because of the global trade driven primarily by the pet trade. As a result of this international trade, parrots as introduced and naturalized species are also among the most widely distributed groups of birds in the world, although much of this distribution is in novel areas outside of species' native ranges. It was our goal in this review to attempt to estimate the number of naturalized species of parrots in the world. This effort updates past estimates (Lever, 2005; Runde *et al.*, 2007; Menchetti & Mori, 2014; Avery & Shiels, 2018), and also provides a combined database of parrot specific records from GAVIA, eBird, and iNaturalist available for use by other researchers. While previous efforts have utilized separate data sets, by combining data sets our goal was to a reliable, current estimate for introduced parrots around the world.

Of the 381 extant species of Psittaciformes, the majority of these (336) have been transported around the world through the global pet trade (Cardador *et al.*, 2021). Our review indicates that more than half of these species (216 of 336, 56.6%) have escaped captivity or been released in the novel area and observed in the wild in no less than 138 countries or territories. Not surprisingly, introduction in a new area does not guarantee establishment success, but nevertheless at least 71 species are known to have established breeding or naturalized populations in 86 different countries or territories. Considering past estimates of the number of naturalized species (Lever, 2005; Runde *et al.*, 2007; Menchetti & Mori, 2014; Avery & Shiels, 2018) it is obvious that the number of naturalized parrots has increased over time. Part of this increase is related to a general increase in parrot trade around the globe (Cardador *et al.*, 2021), although this trade has changed drastically in some countries due to bans on trade that been imposed by some countries, e.g., the United States and the European Union (Carrete & Tella, 2008; Cardador *et al.*, 2017; Cardador *et al.*, 2021; Uehling *et al.*, 2021). Some of the increase in naturalized parrots is likely also related to increased numbers of escapes or releases of individuals already present in a locality as the result of past trade activity.

There are necessary qualifications to the data that we summarized as well as our methods of analysis. Citizen science data are increasingly used to examine distributional patterns of species worldwide including introduced parrots (Bonter *et al.*, 2010; Dickinson *et al.*, 2010; Minor *et al.,* 2012; Uehling *et al.*, 2019; Royle & Donner, 2021). Nevertheless, issues concerning species identification and spatial and temporal biases in sampling must be considered in analysis and interpretation (Dickinson *et al.*, 2010; Ratnieks *et al.*, 2016; Robinson *et al.*, 2018). Our combined database (Table A1) is subject to these considerations, and our conclusions about the numbers of introduced and naturalized species should be viewed as our best attempt to conservatively review the combined database. We acknowledge, however, for any geographical area, combining citizen science records with detailed field observations by knowledgeable researchers will ultimately yield the most accurate and reliable records for distribution of introduced parrots, as exemplified by (VanderWerf & Kalodimos, 2021). We hope that by providing the combined database (Table A1) other researchers can use these data as the starting point for such field observations.

Our comparison of the combined database with recent publications on parrots in the United States illustrates one method of checking for consistency and accuracy. This comparison showed general but not exact agreement for species either breeding or naturalized, but less so for all introduced species. Considerable overlap was expected given that both Uehling *et al.* (2019) and this study made use of eBird data. However, Uehling *et al.* (2019) reported species for which there was at least one observation recorded in eBird, whereas we used a minimum of three observations. Clearly, any conclusion we or other researchers reach is dependent on the exact data set summarized. Although not summarized specifically here, comparison of the combined database with recent surveys of introduced parrots in England (Butler, 2021), Europe (Braun, 2021), Spain and Portugal (Carrete *et al.*, 2021), and South Africa (Symes *et al.*, 2021) also show general agreement with respect to naturalized and breeding species.

Similarly, our use of a 100 km distance as a filter for observations from eBird affects our conclusion about the number of introduced species. Without such a filter, every extralimital observation from eBird would have been included but, in our opinion, would not necessarily improved our understanding of the number or distribution of naturalized parrots. If a new, extralimital population establishes itself on a new island or in a far-distant country it is clearly a novel naturalized population. However, if an extralimital population establishes itself close to the native population, it can simply be a matter of judgement whether that population is considered naturalized or just an example of a range expansion. This is particularly true in some countries, e.g., Australia, where the majority of naturalized parrot species are also species native to Australia.

Calculation of the Area of Occupancy (AOO) for introduced species allows for a more objective analysis of a species' spread than just comparing the number of countries a species is recorded in. The number of countries a species has colonized as a naturalized species is important, but we expect that any examination of life-history correlates of success would be more likely to identify significant factors if such analyses focused on AOO. A comparison of the data for the two most common introduced species, the Rose-ringed Parakeet and Monk Parakeet, highlight the value of examining both measures of success. The Rose-ringed Parakeet is now introduced in a total of 47 countries, whereas introduced Monk Parakeets are found in 26 countries. In contrast, the AOO of Monk Parakeets is ~20% larger than that of Rose-ringed Parakeets (22,656 km^2 compared to 18,996 km^2; Table A1). One possible explanation for this difference is that the Rose-ringed Parakeet is more widely traded worldwide in the pet trade than is the Monk Parakeet, leading to Rose-rings establishing themselves in more countries. In contrast, Monk Parakeets are highly adaptable and successful in areas where they establish themselves (Calzada Preston *et al.*, 2021), leading to population increases and range expansions that would be observed through calculation of the AOO. We encourage consideration of both the AOO and countries occupied in future studies of the spread and success of introduced parrots.

Naturalized parrots are increasingly common in some areas and can present a host of both positive and negative interactions with humans. As Kiacz & Brightsmith (2021) review, naturalized parrots offer timely and significant opportunities for conservation, research, and human society. The potential negative impacts of naturalized parrots, thoroughly reviewed by Mori & Menchetti (2021) and Brightsmith & Kiacz (2021) can be significant in some situations, as with damage to electrical infrastructure by Monk Parakeets or localized agriculture by some species. Nevertheless, overall, Brightsmith & Kiacz (2021) conclude that these impacts are minor and do not in general justify the widespread and indiscriminate control of naturalized parrot species.

Given that populations of naturalized parrots are expanding, becoming urbanized in many cities, and generally representing larger fractions of local avifauna, a greater understanding of their population biology, behavior, and interactions with humans is needed. We encourage regular local and regional surveys for species presence and abundance as well as large scale reviews of global patterns. Accurate data on the species richness and diversity of naturalized parrots will be critical for understanding the role of parrots as introduced and possibly invasive species, conservation efforts of threatened or endangered species, any management efforts when needed, and increasing the public knowledge and understanding of this important group of birds.

Chapter 2

Species Distribution Models of Naturalized Parrots: Environmental and Species-specific Factors Contributing to Success

Introduction

Among the approximately 381 species of parrots and their allies (Order Psittaciformes; Gill & Donsker, 2020) 166 are known to have been introduced outside of their native range (Calzada Preston & Pruett-Jones, 2021). Non-native parrot species have been sighted within at least 106 territories or countries around the world (Royle & Donner, 2021), primarily due to entering these locations through the pet trade (both legal and illegal) and then escaping or being released into the wild (Blackburn *et al.*, 2011).

According to the framework for biological invasions proposed by Blackburn *et al.* (2011), the invasion process for a species can be divided into sequential stages and barriers that impede a species from becoming an invasive species. The main stages that this framework references are Transport, Introduction, Establishment and Spread. For a species to move along this framework, it must first overcome the geographic barriers that separate its native range from the novel location, corresponding to the transport stage, and then be released from captivity or brought directly into the novel location's environment, thus entering the introduction stage. Afterwards, in the establishment stage the individuals must survive and reproduce in the novel location, being considered established or naturalized if successful. Finally, the species is considered invasive in the spread stage, where it is capable of dispersing from its location of introduction and successfully become established and causes harm to native fauna and/or flora. This multi-stage framework helps to organize the mechanisms affecting potentially invasive species during different stages of the process, as well as helping to untangle the factors leading a particular non-native species to becoming invasive (Blackburn *et al.* 2011).

Currently, captive pet escapees are the main source of avian introductions of exotic species (Carrete & Tella, 2008) and the popularity of parrots in the pet trade is often attributed to their wide array of colorful plumages, high intelligence and mimicry. Variation in size among species and abundance within their native range has been associated with reduced prices, further driving commerce of non-native parrots in the international pet trade (Vall-llosera & Cassey, 2017). The reaction to introduced parrots around the globe has been mixed and many governments and local institutions have implemented strategies for eradicating invasive parrot species (see Senar *et al.*, 2021). However, it has been known for decades that the most effective management strategy for all invasive species involves the prevention of a species entering a region in the first place, as the cost and effort for eradicating or managing invasive populations continues to increase with time after invasion (Simberloff *et al.*, 2013). In the case of parrots however, the international pet trade is a well-established global market with active cultivation of captive birds outside breeding ranges. Another strategy has been monitoring locations that are high risk for species introduction and establishment, particularly using species distribution models (also known as environmental niche models) to predict locations that are favorable for a particular species to thrive (Falcón & Tremblay, 2018; Ørsted & Ørsted, 2019). These models use various algorithms to compute the association between a species' occurrence with the underlying environmental and/or spatial variation in native ranges (Elith & Leatherwick, 2009). The software MaxEnt has become a popular tool with which to carry out such predictions, as it does not require information on a species' absence within the region of interest, instead calculating the association using presence only data and the surrounding environmental landscape (Elith *et al.*, 2011).

In this study, I make use of the wide availability of occurrence records for Psittaciformes species around the world via the eBird Basic Dataset (EBD) and investigate whether a species' response to environmental variation changes when introduced outside of their native range. I make use of Reciprocal Distribution Models (RDMs; NA *et al.*, 2022), a modeling technique where Species Distribution Models (SDMs) are trained using a species' occurrence records within the native range and a reciprocal model is trained using species occurrence records outside of its native range. The RDMs characterize the species' response to the environmental variation in native and non-native locations, respectively, and then evaluate the occurrences in the contrasting locations to determine if there are differences in how each species responds to the non-native climates and terrain in which they have been introduced. I make use of the 19 WorldClim Bioclimatic and Elevation variables to create a composite representative of climate across the world, which is supplemented terrain classifications from the International Geosphere Biosphere Programme Land Cover Classification and a human impact metric constructed from the Global Human Settlement Urban Centre Database (GHS-Urban Centre Database, 2015). Climate and terrain are typically understood to be important for determining a species niche within the environment, but human activity plays another important role for introduced parrots. Introduced parrots are often the result of escaping from captivity, intentionally and unintentionally, and often end up depending on humans for food (Hyman & Pruett-Jones, 1995). Given the potential significance of human activity to the introduction and persistence of non-native parrots, I include the distance from urban centers as a proxy for these species' dependence on human activity, independent of whether the terrain is considered urbanized. These multiple variables compose the “environment” that species occurrences are associated with and that this study will attempt to untangle, to understand whether climatic forces, terrain type or relationships with human modified areas drive the occurrence of non-native parrots outside their native range.

Methods

To study the relationship between species occurrence in native and non-native locations, I used MaxEnt, a maximum-entropy approach modeling software (Stephens *et al.*, 2004) capable of using presence-only data and information on the environmental background being modeled to generate response curves of each environmental variable in relation to the species’ occurrence, in so modeling the species relation to the local environment. The resulting model can be tested using a different subset of occurrence data from the same local environment (e.g. native range) to confirm that the model is accurate in recognizing the associations that the species has with its local environment. Furthermore, the same method can be used to test whether data from differing environments (e.g. the non-native range) conforms to the pattern of associations observed in the initial environment (in this case, the native range).

Occurrence data for all available species of Psittaciformes (N = 353 species) were downloaded from the eBird Basic Dataset (EBD) (eBird, 2023) for the years 2000-2020. The eBird Basic Dataset consists of occurrence records from around the world submitted by citizen scientist users to the eBird data platform. The EBD is updated monthly and, as of 2023, species’ occurrence records are vetted and assigned an exotic species code if found to occur outside of the species’ native range (eBird Help Center, 2023). The three categories an exotic species can be assigned depend on its breeding and establishment status at a particular location and time; naturalized (N) refers to self-sustaining populations that have persisted at the location for several years by breeding in the wild, provisional (P) refers to populations that are established in the wild at the location for several years but have not been declared naturalized by the local ornithological authority for whatever reason, and escapee (X) which includes birds that have escaped or been released from captivity and are not known to be breeding or have an established population at the location (eBird Help Center, 2023). Species with <100 native occurrence records or <100 non-native occurrence records were excluded from analysis. The resulting, restricted, dataset consisted of 27 species. Using the species occurrence records, bias files were made in order to restrict background sampling to grid cells within a 100 km buffer surrounding the native range and non-native range occurrences of each species, respectively. In this way, the environmental background of native and non-native ranges could be accounted for without including environmental grid cells too far away from the occurrence records of each species. Finally, it is often claimed that occurrence data originating from citizen science databases contains inherent biases regarding sampling locations and efforts that can impact the resulting conclusions garnered from their analysis. To reduce the impact of such potential spatial bias, as well as to comply with Maxent's default settings (Stephens *et al.*, 2004), occurrence records were thinned to 1 per grid cell for each species.

Bioclimatic variables (19 in all) as well as elevation were downloaded from WorldClim (Fick & Hijmans, 2017) at 2.5 minutes resolution (about 4.5 km^2 at the equator; all data used in this analysis was adjusted to match this resolution). Using the WORLDCLIM climate and elevation data, values associated with all occurrence records were extracted and used to calculate the principal components to reduce the dimensionality of the environmental data. The resulting first five principal components accounted for 89% of the variance in the environmental data and were used to create a raster file of the scores of these first five principal components. The loadings for the principal components (Table B1) can be interpreted to better understand the environmental data being modeled. The first principal component, which accounts for 41.1% of the variance in the climate data, is most strongly associated with the Minimum Temperature of the Coldest Month, the Mean Temperature of the Coldest Quarter and the Annual Mean Temperature (bio1, bio6, and bio11; positively correlated) indicating that PC1 mostly explains the variance within the climate data by distinguishing between regions given the coldest temperatures experienced. Therefore, any associations between species presence and PC1 may indicate a strong adherence of the species to remain in or avoid regions that experience colder temperatures. PC2 (24.0% of the variance in the climate data) is most strongly associated with Max Temperature of the Warmest Month (bio5; positively correlated), Precipitation of the Driest Month (bio14; negatively correlated), and Precipitation of the Driest Quarter (bio17; negatively correlated), which may be considered as a measure of aridity. PC3 (9.1% of the variance) is most strongly associated with Temperature Seasionality (bio4; positively correlated), Temperature Annual Range (bio7; positively correlated), and Isothermality (bio3; negatively correlated). PC4 (8.0% of the variance) is most strongly associated with Elevation (elev; negative correlation). PC5 (6.8% of the variance) is most strongly associated with Mean Diurnal Range (bio2; positive correlation).

The International Geosphere Biosphere Programme Land Cover Classification raster layer (Loveland *et al.*, 1997) was downloaded at 1km resolution to determine whether the role of the terrain plays a limiting factor within the process of species introductions, or if climate is the sole, most important factor. Lastly, the Global Human Settlement Urban Centre Database (GHS-Urban Centre Database, 2015) was downloaded to create a raster of distance from the nearest urban center. The GHS Urban Centre Database defines urban centers as: “the spatiallygeneralized high-density clusters of contiguous grid cells of 1 km^2 with a density of at least 1,500 inhabitants per km^2 of land surface or at least 50% built-up surface share per km^2 of land surface, and a minimum population of 50,000" (GHS-Urban Centre Database, 2015, p. 13). Areas with high levels of urbanization frequently feature reduced species richness (McKinney, 2008) which can signify reduced levels of competition for resources such as food and shelter. Urban areas also tend to feature a higher density of non-native plant species, which can serve as food sources and nesting sites, and have been reported as being positively associated with non-native bird densities (Mills *et al.*, 1989). Furthermore, this metric takes into account the geographic distance from urban centers rather than the terrain type at the location, whereby it is able to distinguish whether the important factor for a particular species is how far away it can disperse from its location of introduction or the actual terrain that it inhabits, be it urban or otherwise. I calculated the distance in meters from each grid cell to the nearest urban center as a measure of human activity and as a proxy for distance from likely locations of introduction from captivity into the wild.

Raster files for the WorldClim environmental data (PC1, PC2, PC3, PC4, PC5), and the IGBP Land Cover (Land_Use) were used to train the MaxEnt models for each species using occurrence records from the native range. Of the native range occurrence records, 80% were used to train the models and 20% were used for evaluating the models by calculating the "Area Under the receiver operating characteristics Curve" (AUC), as a measure of the model's performance that ranges from 0 (100% of the model predictions are incorrect) to 1 (perfect prediction by the model). The non-native occurrence records were then used to evaluate whether species occurrences in the non-native range conform to the relationship exhibited by the models trained using records from the native range. The 'evaluate' function of the "dismo R package" calculates the AUC using the true positive and true negative prediction rates from the confusion matrices to visualize the performance of the model trained on native range occurrences in accurately predicting occurrences outside the native range. Finally, these models were compared to identical evaluations of null models that were trained with the same number of data points, but by randomly sampling presences from grid cells within the species native range.

In the null models, presence records were created by randomly sampling grid cells from the native range bias file, thus restricting the background environment to grid cells that lie within or just beyond the species native range. By creating 500 such null models, the effect size for the model's performance metric, in this case native and non-native range AUC, could be calculated (as a Z-score computed as the $\frac{(real\ model's\ performance - mean\ of\ 500\ null\ model's\ performance)}{standard\ deviation\ of\ the\ 500\ null\ models}$; Bohl *et al.* 2019) to ask whether the model performs better than models trained on a random subset of grid cells from within the species' native range. I computed a one-sided P value one-sided Z-tests, as I was only interested in models that performed significantly better than the null models. The Z-Score of the AUC is representative of how well the model performs relative to the null models in characterizing the species environmental niche. A Holm-Bonferroni correction was applied across the p-values calculated for the effect size of model performance in both native and naturalized AUC evaluations. The Z-score of the AUC for each species was used to look for correlations (using parametric tests when possible; non-parametric if data was not able to be transformed to normality) that may arise due to data biases: the number of occurrence records available per species in the native and non-native locations to train the models, as well as biogeographical factors including: the size of the native range, body size, and Hand-Wing Index (an index equivalent to Kipp's index, but scaled to the wing's size; as in Claramunt, 2021). Larger native range sizes may provide non-native species with an evolutionary background that has already exposed them to environments similar to those they will experience in the non-native range. The Hand-wing Index is often used as a measure of dispersal capacity within birds, an aspect that could prove useful in searching for ideal environmental conditions in novel locations. Body size may also play a role within the dynamics of biological invasions as larger parrots may be better suited to outcompete local species for food and nesting sites, while also being better suited for thermoregulation in temperate climates due to a reduced surface area to volume ratio. Data were downloaded from AVONET, a comprehensive dataset of functional trait data for all bird species (Tobias *et al.*, 2022). I confirmed whether these variables, as well as the model AUC values, were normally distributed, transformed the data for normality when possible, and carried out Pearson/Spearman correlation tests to detect any correlations that might indicate patterns for why some species models performed better than others.

If there were any species where the SDMs could not predict the non-native occurrences, Reciprocal Distribution Models were used to train models with the non-native occurrences and then used to evaluate the native range occurrences. The resulting AUC values were compared with AUC values from null models trained by randomly sampling the non-native range, as previously described. Similarly, the resulting Z-scores of the AUC values were tested for correlations relating to species traits as described previously for the native range models. Finally, in cases where the Reciprocal Distribution Models could not predict native range occurrence, the species were re-evaluated while including the distance from urban centers raster layer, in addition to the land cover and environmental data mentioned previously. These models were evaluated with newly generated null models to determine if the distance from urban centers could explain the differences between models trained using native range and non-native range occurrences.

Results

The model's performance for each species reflects the ability of occurrences from the native range to predict the non-native range occurrences, and if those models were unsuccessful, the reciprocal model's ability to predict the native range using the non-native range occurrences (Table 2.1). For the models evaluated with occurrence records from the species' native range, I expected that the effect size of the species distribution model's performance would be significantly better than the null models at predicting species occurrence. For the 27 species evaluated, all MaxEnt models were significantly better than the null models at predicting species presence within the native range (Holm-Bonferroni correction of Z-Scores; N = 27: $p < 0.00001$). The species with the lowest evaluation AUC was the Blue-and-Yellow Macaw (*Ara ararauna*) with $AUC_{Test} = 0.\ 0.6642189$, but when this result is used to calculate the Z Score, $Z = 3.740241$, indicating a significant deviation from the null models randomly sampling the environmental background. In fact, the species with the lowest Z Score was the White-winged Parakeet (*Brotogeris versicolurus*) with $AUC_{Test} = 0.7972422$ and $Z = 2.683585$, which as stated previously is still significantly better than the null models performance. When evaluating non-native occurrences with the MaxEnt models, the models for 21 species were statistically significantly better than the null models at predicting species occurrences within the non-native range (Holm-Bonferroni corrections of Z-Scores; N = 21: $p < 0.0001$; N = 6: $p > 0.05$; see Figure 1 for suitability map example). This implies that for 21 species in our dataset the occurrence records from the non-native range conform to the pattern observed within the native range and can be accurately predicted using the models trained using the native range occurrences.

Table 2.1. Differences in model performance (AUC) for Reciprocal Distribution Models. Native abbreviated to NA and Non-native abbreviated to NN.

Species	Number of Occurrence Records		AUC of Native Model evaluation		Native Model's Z-test p-value		AUC of Non-Native Model evaluation		Non-native Model's Z-test p-value	
	NA	NN	NA	NN	NA	NN	NA	NN	NA	NN
Agapornis fischeri	102	139	0.807	0.654	$2x10^{-263}$	$2x10^{-32}$				
A. roseicollis	107	582	0.761	0.606	$6x10^{-151}$	$2x10^{-21}$				
Amazona aestiva	1075	101	0.705	0.780	0.0	$8x10^{-25}$				
A. albifrons	1879	117	0.780	0.600	0.0	$2x10^{-17}$				
A. amazonica	1505	213	0.675	0.889	0.0	$1x10^{-23}$				
A. autumnalis	1864	299	0.821	0.621	0.0	$4x10^{-29}$				
Ara ararauna	1203	227	0.664	0.741	0.0	$1x10^{-208}$				
Aratinga nenday	206	800	0.777	0.848	$5x10^{-183}$	$1x10^{-43}$				
Brotogeris chiriri	1604	471	0.747	0.853	0.0	$5x10^{-90}$				
B. versicolurus	297	374	0.797	0.630	$3x10^{-130}$	$2x10^{-11}$				
Cacatua galerita	6783	273	0.849	0.563	0.0	1.0	0.462	0.838	0.99	0.0
C. tenuirostris	1227	1099	0.851	0.558	0.0	0.1	0.755	0.892	$4x10^{-282}$	$1x10^{-267}$
Eclectus polychloros	203	164	0.769	0.714	0.0	$2x10^{-6}$				
Forpus coelestis	457	154	0.839	0.863	$6x10^{-261}$	$2x10^{-11}$				
F. passerinus	553	119	0.762	0.202	$6x10^{-253}$	1.0	0.493	0.674	1.0	$5x10^{-75}$
Melopsittacus undulatus	1186	1531	0.681	0.577	0.0	$3x10^{-46}$				
Myiopsitta monachus	3683	4195	0.784	0.684	0.0	$6x10^{-216}$				
Nymphicus hollandicus	1393	907	0.737	0.566	0.0	$3x10^{-7}$				
Platycercus eximius	4215	1829	0.787	0.634	0.0	$5x10^{-13}$				
Psittacara erythrogenys	210	387	0.841	0.857	0.0	$2x10^{-40}$				
P. holochlorus	218	261	0.787	0.662	0.0	0.0	0.527	0.934	0.0	$2x10^{-48}$
P. mitratus	378	422	0.787	0.426	0.0	1.0	0.593	0.933	$8x10^{-4}$	$1x10^{-52}$
Psittacula eupatria	1463	415	0.749	0.731	0.0	$1x10^{-120}$				
P. krameri	6911	4841	0.768	0.781	0.0	0.0				
Psittacus erithacus	194	136	0.754	0.482	0.0	1.0	0.560	0.831	$3x10^{-48}$	$1x10^{-238}$
Thectocercus acuticaudatus	688	333	0.696	0.727	0.0	$6x10^{-58}$				
Trichoglossus moluccanus	4763	198	0.870	0.661	0.0	$1x10^{-5}$				

Regarding the relative contribution of the environmental predictors to overall model performance (Figure 2.1), there was no single environmental predictor that was most informative across all 27 species. However, when looking at the frequency distribution of the variable contributions to the models, PC2, PC1 and Land_Use were consistently the most important predictors. When looking at the model responses to the different environmental predictors (Figures S1a-f), there are distinct intraspecific probabilities of occurrence/preferences across the range of environments in each species native range. These species response curves indicate the species' probability of occurrence at a certain environmental value when the other environmental variables are set at the median (or mode for categorical). The resulting curve intends to demonstrate the environmental values at which the species is most likely to occur, given a uniform environmental background. The overlap across many species environments is to be expected, with parrots being a mostly tropical clade, but even within the overlapping regions, there are peaks in distinct regions of environmental variation, suggesting that within their native range parrots occupy distinct environmental niches and do not have a universal response to their local environment.

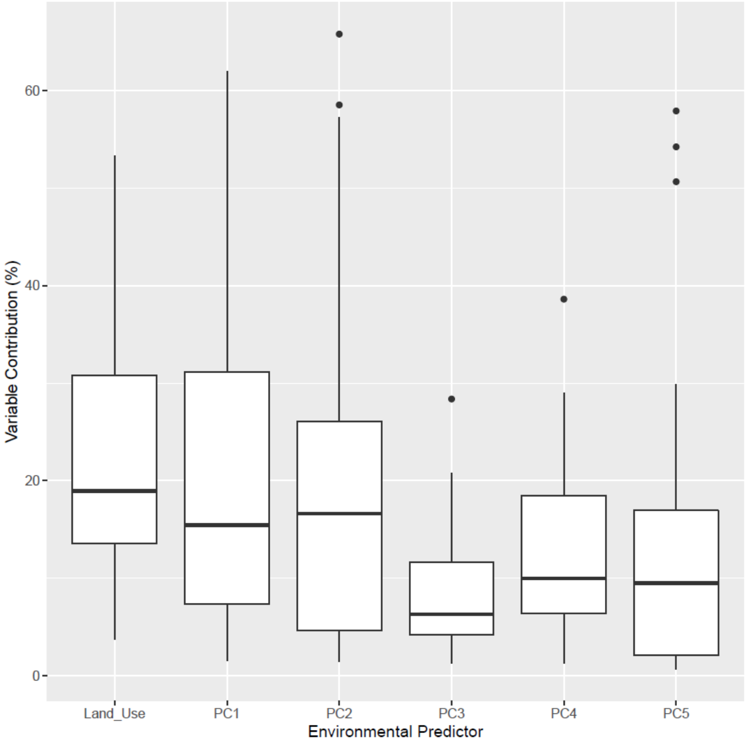


Figure 2.1 Variable contributions to the species distribution models of 27 species trained using native range occurrences.

Using the resulting performance metrics for each species' model, correlation tests were run between the performance metric (Z score of AUC) and species traits (mass (g), Hand-Wing Index, and native range size (km^2)), as well as with the number of native and non-native occurrence records (Table 2.2). There was one significant correlation detected between the performance metric for the native range models in predicting native range occurrences (the model validation metric) with the number of native range occurrences (Native Length) and remained significant after applying the Holm-Bonferroni correction. This correlation was negative, indicating that models trained with fewer data points were more likely to have a higher model validation metric.

Table 2.2. Results of correlation tests between native range model performance metrics and species-specific variables (N = 27). Significant results are bolded.

			Z Score of Naturalized AUC		Z Score of Native AUC	
Variable	**Data Transformation**	**Correlation Test**	**r statistic and p-value**	**Post-Bonferroni p-value**	**r statistic and p-value**	**Post-Bonferroni p-value**
Native length	Log-transformed	Pearson (Parametric)	r = 0.232; 0.245	1	r = -0.596; **0.001**	**0.02972937**
Naturalized length	Reciprocal transformed	Pearson (Parametric)	r = -0.349; 0.074	1	NA	NA
Mass	Log-transformed	Pearson (Parametric)	r = 0.077; 0.701	1	r = -0.379; 0.051	1
Range Size	Log-transformed	Pearson (Parametric)	r = 0.275; 0.165	1	r = -0.339; 0.083	1
Hand-Wing Index	NA	Pearson (Parametric)	r = 0.092; 0.649	1	r = 0.045; 0.822	1

For the six species where the SDMs could not accurately predict the non-native range occurrences, I trained reciprocal distribution models (RDM) using the non-native range occurrences as the training data, to observe the difference in patterns described by the models between the native and non-native locations (Table 2.1). For these six species, all RDMs were statistically significantly better (Holm-Bonferroni correction; N = 6: $p < 0.00001$) at predicting species presence within the non-native range, and the model with the lowest evaluation AUC and the lowest Z-Score was for the Green-rumped Parrotlet (*Forpus passerinus*) with $AUC_{Test} = 0.6741966$ and Z = 2.081413. However, when evaluating the native range occurrences with these RDMs, three were statistically significantly better at predicting species occurrences within the native range (Holm-Bonferroni correction; N = 3: $p < 0.005$; N = 3: $p > 0.05$; see Figure 4 for example), while three models were no better at predicting species occurrences within the native range than the null models. Following data transformation, parametric correlation tests were conducted using the same methods as above for the six models trained using naturalized occurrences (Table 2.3). There was one significant correlation detected between the Z-Score of the non-native model's performance metric for predicting non-native range occurrences (the model validation metric) with mass and it remained significant after applying the Holm-Bonferroni correction. This association was positively correlated with the model validation metric, indicating that the models for species with greater mass were better at outperforming the null models in quantifying the non-native environmental niche. As for the relative variable

Table 2.3. Results of correlation tests between non-native range model performance metrics and species-specific variables (N = 6). Significant results are bolded.

			Z Score of Naturalized AUC		Z Score of Native AUC	
Variable	**Data Transformation**	**Correlation Test**	**r statistic and p-value**	**Post-Bonferroni p-value**	**r statistic and p-value**	**Post-Bonferroni p-value**
Native length	Log-transformed	Pearson (Parametric)	NA	NA	r = -0.036; 0.945	1
Naturalized length	Log-transformed	Pearson (Parametric)	r = 0.612; 0.197	0.98385133	r = 0.770; 0.073	0.51414399
Mass	NA	Pearson (Parametric)	r = 0.951; **0.004**	**0.03160528**	r = 0.360; 0.483	1
Range Size	NA	Pearson (Parametric)	r = 0.423; 0.404	1	r = -0.364; 0.478	1
Hand-Wing Index	NA	Spearman (Non-parametric)	rho = 0.086; 0.919	1	rho = 0.657; 0.175	1

contributions to the non-native models (Figure 3), PC4 ranked as a higher contributor in most models, indicating the predictive importance of elevation in non-native populations. The next most important variable contributors to the models were Land_Use and PC2, reflecting their importance in the native range models.

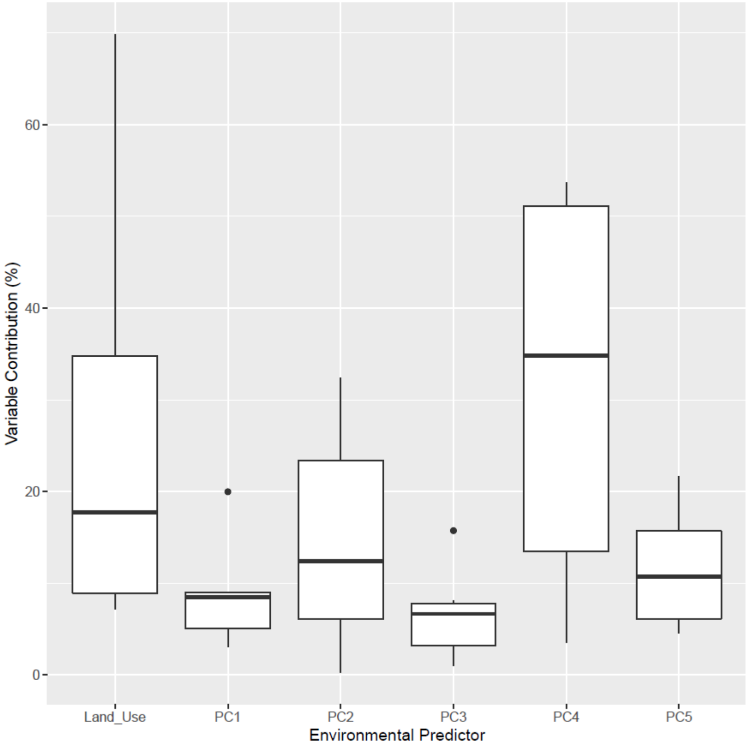


Figure 2.2 Variable contributions to the species distribution models of 6 species trained using non-native range occurrences.

For three species, (*Cacatua galerita*, *Forpus passerinus*, *Psittacara holochlorus*) the SDM and RDMs could not predict these species occurrences outside of the region where the models were trained. When comparing the contributions of the different variables to the SDM and RDM it is possible to see the drivers of occurrence in the native and non-native locations. The importance of the PC4 variable increased in these three species in the models trained using non-native species occurrences, becoming the most important model contributor in each species' model. There were no other patterns of change in environmental variable importance across all three species.

The models for these three species were updated by including the environmental layer of Distance from Urban Centers, with null models being re-run to compare the results of models trained with occurrence records from the native range and non-native range, as was done

Table 2.4. Differences in model performance (AUC) for Reciprocal Distribution Models that include Distance from urban centers (Urban_Dist).

Species	Number of Occurrence Records		AUC of Native Model evaluation		Native Model's Z-test p-value		AUC of Non-Native Model evaluation		Non-native Model's Z-test p-value	
	NA	NN	NA	NN	NA	NN	NA	NN	NA	NN
Cacatua galerita	6783	273	0.871	0.575	0	1	0.445	0.887	1	9x10^{-252}
Forpus passerinus	553	119	0.855	0.421	8x10^{-116}	1	0.510	0.736	1	2x10^{-61}
Psittacara holochlorus	218	261	0.801	0.859	0	3x10^{-20}	0.584	0.942	8x10^{-84}	3x10^{-178}

previously. With the inclusion of Distance from Urban Centers (Urban_Dist), the models trained with occurrences from the native range had Urban_Dist as the most important variable contributor for *C. galerita* and *F. passerinus,* while it became the second most important contributor for *P. holochlorus,* with PC1 being the most important for this species. For the models trained using non-native range occurrences, Urban_Dist was the most important contributor to the models of *F. passerinus* and *P. holochlorus*, with PC4 being the second most important. Meanwhile, *C. galerita* had PC4 as the most important contributor with Urban_Dist being the second most important contributor. In these cases (Table 2.4), all models were able to predict occurrences from which the training data was drawn (native to native or non-native to non-native). However, only the Green Parakeet (*Psittacara holochlorus*) was able to predict non-native range occurrences from the model trained with native range occurrences ($AUC_{Non\text{-}native}$ = 0.8594648; p = 2.886x10^{-20}). In this case, the non-native range model was also capable of reciprocally predicting species occurrences from the native range (AUC_{Native} = 0.584; p = 7.691x10^{-84}). Regarding *C. galerita* and *F. passerinus*, the reciprocal distribution models, regardless of whether Urban_Dist is included as an environmental predictor, model different environmental niches. When looking at *C. galerita* in particular, the distribution of the occurrences for PC2 extend into more negative values than in the native range with a peak in predicted value within this negative range of PC2 that strongly contrasts with the predicted value response curve from the native range (Figure S3b). Meanwhile, for *F. passerinus*, the distribution of values for PC4 overlap significantly and have a similar peak in the positive values near 0, but the native range model has an occurrence in the far negative values that is found to be unsuitable for the species (Figure S3d). Similarly, when looking at Urban_Dist for *F. passerinus* (Figure S3f), the non-native range model has a peak of high predicted value at 120,000 km of distance from an urban center, due to occurrences on the island of Tobago, particularly Little Tobago.

Discussion

An important issue regarding this study is that, when included, models found that Distance from Urban Centers (km) was consistently among the highest contributors for predicting species occurrences within the native and non-native range (Figure 5). While it is expected that distance from urban centers plays an important role in the distribution of non-native species outside of their native range, due to the importance of human activity to this process, within the native range it is unclear why this predictor would have such an importance. As I mentioned previously, there is a possibility that the distribution models might be detecting inherent biases in the data due to clustered sampling locations and efforts in locations more accessible to the public and signifying the conditions at those locations as relevant for predicting occurrences. However, I took measures to reduce spatial clustering for each species individually and only include species with occurrence records above a threshold of 100 in both the non-native and native range to ensure that the species has been observed in a non-trivial number of locations. It is also likely that the species pool under study, particularly species of Psittaciformes that have established non-native populations, are already species that are accustomed/adapted to human activity already within their native range, as has already been shown for some of the species in our analysis (Daoud-Opit & Jones, 2016; Álvarez-Castillo *et al.*, 2022; Lera *et al.*, 2023).

Another issue that must be addressed is that when the environmental conditions between the native and non-native range differ greatly, the distribution models are forced to extrapolate predictions to environmental values that they were not trained with. While these issues are addressed with our reciprocal distribution models, which respectively use training data from each region allowing comparisons across predicted regions, the issue of handling extrapolation is persistent in distribution modeling. MaxEnt's default settings clamp the response curves so that values more extreme than those found in the training and background data are treated as if they were the most extreme values in the data set, effectively clamping the extrapolation to the most extreme value encountered in the training dataset.

According to the MaxEnt models, 21 of the 27 parrot species analyzed (77%) showed a strong relationship between their non-native occurrences and the characteristic composition of their native environment. Based on MaxEnt models for these 21 species trained using data from the native range, occurrences from the naturalized range were in environments that matched the suitability of those from its native range. This indicates a trend in which naturalized parrot species thrive in similar environmental conditions to those they inhabit within their native range. Whether this is due to introduction into already favorable locations or spreading from less favorable locations is not an aspect that this study can address. However, there were six species for which these models indicated that the non-native occurrences were locations considered unsuitable according to the species' environmental niche from the native range. When interpreting the results of the reciprocal distribution models for these six species, trained using data from the non-native range and compared with null models that randomly sample the non-native range, the occurrences from the native range were found to be within suitable environments for three species, indicating that these species (*Cacatua tenuirostris*, *Psittacara mitratus*, and *Psittacus erithacus*) are capable of surviving in environmental contexts outside those of their native ranges. This also suggests that within their native range the species may be limited by habitat availability or biotic factors, such as competition, predation, or poaching. Although the results from these MaxEnt models are likely affected by extrapolating to information from environments outside the region where the training data originates, it seems that for these three species, the species' environmental niches in the native range do not encompass the entire breadth of potential niches. Given that these species are being introduced across locations globally, these models suggest that these species are constrained within their native range and distribution models that focus solely on the environmental conditions that the species currently inhabit will be missing out on the full potential of suitable conditions in geographic and environmental niche space.

Take for example the Long-billed Corella (*Cacatua tenuirostris*), one of these three species whose non-native model predicts the native range distribution significantly better than the null models. When looking at the variable response curves of this species towards the PC1 environmental variable (Figures S1a and S2a), the peak response in the native range trends towards the extreme negative values, indicating a preference for cooler climates, while the non-native range model overlaps the values present in the native range and extends beyond to indicate the opposite trend, a peak towards the positive values of PC1, implying a greater suitability within warmer climates.

For three species (*Cacatua galerita*, *Forpus passerinus, Psittacara holochlorus*), the reciprocal distribution models trained using non-native occurrences indicated that occurrences from the native range were found in unsuitable locations according to the environmental niche in the non-native range. This incompatibility between the characterization of the native and non-native populations, as indicated by these species' reciprocal distribution models, implies that the species are occupying locations that are significantly distinct in environmental space. When the environmental layer of Distance from Urban Centers is included the model for *P. holochlorus* is then capable of predicting the occurrences outside of the respective training data region. This means that in both the native and non-native range, the species is found in locations within 100 km of an urban center (Figure S3g). This is supported by recent work which concludes that alien bird richness is driven primarily by propagule pressure and secondarily by environmental factors, with native and alien bird richness being strongly positively correlated (Dyer *et al.*, 2017).

However, there remains the two species that were found to have native and non-native ranges incompatible with each other. The Sulphur-crested Cockatoo (*Cacatua galerita*) is a lowland forest parrot broadly distributed across the east and northern continent of Oceania and across the island of New Guinea, whereas the Green-rumped Parrotlet (*Forpus passerinus*) is a forest and grassland species native to the northeastern coast of South America. In terms of the differences between the native range and non-native range models, both species had an increased contribution of the PC4 variable in the non-native range with increasing predictive value towards positive values of PC4, locations at generally lower elevations (Figure S1d and Figure S2d). When the Urban_Dist variable is included, the native range models place Urban_Dist as the most important variable contributor to their models, while in the non-native range Urban_Dist is the most important variable contributor for *F. passerinus* but PC4 (elevation) remains the most important variable contributor for *C. galerita*. For *C. galerita*, Land_Use was consistently determined to have an importance ranging between 8% - 13%, with occurrences in open shrublands, woody savannas and urban/built-up terrain types being the most suitable in both native and non-native locations. Therefore, the difference in environmental niches between native and non-native locations seems to stem from climatic differences with the species tolerating cooler and more seasonal climates within the native range and becoming established within less arid climates in the non-native range. On the other hand, *F. passerinus* preferred terrain types according to the models are open shrublands (to a lesser degree), water bodies and urban/built-up within the native range and croplands and urban/built-up in the non-native range. However, the non-native range model that incorporates Urban_Dist found urban/built-up terrain to be the least likely of terrain types to be considered suitable in the non-native range. This would seem to indicate that *F. passerinus* indeed does occupy distinct environmental niches, as in its native range it is highly associated with water bodies, and in its non-native range the association with water bodies is not persistent, though this might be due to the non-native range being oceanic islands that have more access to water bodies/coasts.

Regarding comparative intrinsic factors, the correlations between the native range model performance metrics and the species traits showed that there was a negative correlation between the native range model's validation metric with the amount of native training occurrences. This implies that species with more training points, though not with larger range sizes, are less likely to have a high model validation metric. The association between the number of data points used and the AUC metric is likely a product of spatial autocorrelation of the environmental data, given that species with restricted ranges (and therefore fewer occurrence records) are less likely to experience strong environmental shifts or turnover in the geographic space they encompass. On the other hand, species with large distributions are more likely to be found across environments that differ from whatever ideal environment is predicted by the model. Meanwhile, the non-native range model's correlations with species traits only detected a positive correlation between the non-native model validation metric with species mass. This association might result from larger species generally being more mobile and capable of traversing their local environment to arrive at more optimal locations. However, the analysis by Blackbird *et al.* (2019) suggests that body size in non-native birds follows Bergmann's Rule (a positive correlation between body size and latitude) and that this relationship is largely explained by patterns of human introduction rather than selection on body size.

A recent study (NA *et al.*, 2022) addressing niche shifts by incorporating reciprocal distribution models, lends support to the results I found in this paper. NA *et al.* (2022) analyzed 33 species of plant and animal including one parrot, the Rose-ringed Parakeet, *Psittacula krameri.* In their analysis, *P. krameri* appears to have a marginal, non-significant shift in the niche occupied within the native range and non-native range. In our study, the MaxEnt model trained using the native range data for *P. krameri* predicted the species' occurrences within the native and non-native range at a level significantly better than the null models. This indicates that the non-native populations of *P. krameri* have become established in locations that, while they may be generally cooler, are still classified as suitable according to the model trained on the environmental conditions the species experiences across its native range. In the study by NA *et al.* (2022), 90% of species showed no significant niche shifts between the native and non-native locations. I found that a majority (≈77%) of the analyzed species' non-native occurrences were found in environments that would be considered suitable according to the models trained using the native range occurrences. Furthermore, the reciprocal distribution models showed that for three of the six species analyzed, the non-native range encompassed environments found both within and outside of the native range. I suggest a focus on these particular species through a time series analysis to determine if they were initially introduced to locations more similar to the native range and then expanded into locations that differed, as was proposed to be the case for the fire ant (*Solenopsis invicta*) in Fitzpatrick *et al.* (2007), or whether introductions can be traced to dissimilar locations from those found in their native range.

I found three species where the reciprocal distribution models show that the native and non-native range environments are significantly distinct from each other. However, after incorporating the Distance from Urban Centers metric, the models for one of these species (*Psittacara holochlorus*) were then capable of predicting occurrences from outside their training region, indicating that the distance from urban centers, or environmental variables correlated with it, make up an important aspect of this species' environmental niche. However, there remain two species with incompatible niches, with potentially distinct reasons for this incompatibility. There are strong climatic differences between the native and non-native populations of *C. galerita* and it seems that there may be biotic interactions in its native range that prevent it from becoming established in the locations the non-native models indicate as being suitable (Figure 6). Similarly, the models predict that environments in the non-native range for *F. passerinus* are not concordant with their environmental responses within the native range, which might be due to the species' introduction to islands resulting in release from predators or competitors enabling it to survive in distinct environments. Furthermore, there may be an issue of scale, with the non-native occurrences being exclusively on islands, where the limited availability of sampling pseudoabsences could introduce biases when fitting the non-native range models. However, in both cases the variable response curves predict high occurrences close to urban centers as is to be expected in non-native species whose introduction is closely linked with human activity. It is estimated that a minimum of 19 million parrots were transported internationally between 1975 and 2015. This represents approximately 25% of the volume for the international legal bird trade (Cardador *et al.*, 2021). The close association these two species (*C. galerita* and *F. passerinus*) have to urban environments is attributable to them being the introduction localities for these species, but a time series perspective may elucidate if their close association is due to being an early stage in the process of naturalization or due to ecological constraints outside of urban areas.

Chapter 3

Demographic history, structure, and genetic diversity within introduced populations of Monk Parakeets (*Myiopsitta monachus*)

Introduction

The introduction of non-native species has often led to species extinctions, altered community dynamics, reduced native genetic diversity due to hybridization, the spread of novel diseases, and impacts on human economic and agricultural systems (Mooney & Cleland, 2001; Pejchar & Mooney, 2009). Such non-native species that have established successful populations and spread beyond the initial introduction location are classified as invasive species (Blackburn *et al.*, 2011), although sometimes a harmful effect on the local ecosystem is a requirement to be considered invasive (Beck *et al.*, 2008). As a result, the field of invasion biology has frequently focused on quantifying the negative impacts invasive species have on their environments while ignoring any potential positive effects (Vimercati *et al.*, 2020). To avoid this confusion, I will refer to invasive species as non-native species, which are not inherently harmful to the ecosystems into which they are introduced. In fact, non-native species can fill ecosystem niches left empty due to species extinctions, provide ecosystemic services and serve as catalysts for the recovery of native species (Schlaepfer *et al.*, 2011).

For a non-native species to become established, individuals or propagules of the species need to be transported outside of their native range, released into the wild in the novel environment, and survive and reproduce successfully within the new environment (Blackburn *et al.*, 2011). Successful establishment for a non-native species depends on how many individuals are introduced into the initial population, i.e. the propagule pressure, which is positively associated with establishment success (Cassey *et al.*, 2018). Most invasive species' introductions begin with small population sizes, as they are a subset of individuals from their native range, which can subject the introduced population to a reduction in genetic diversity through founder effects, subsequent inbreeding and genetic drift. Furthermore, selection can act throughout the invasion process as early as the introduction stage, as Mueller *et al.* (2017) detected changes in the allelic frequencies of 2 SNPs within a gene known for the species to be linked to behavioral activity in response to novelty between individuals in the native range and individuals sampled in captivity (Mueller *et al.*, 2017). Understanding the genetic mechanisms underlying the successful establishment and spread of non-native species is crucial for effective management and mitigation strategies.

Multiple introductions of a particular non-native species to different places can be considered replicate experiments of the invasion process and can occur across distinct climates and environments, subjecting these new populations to different selective pressures. By analyzing the patterns of genetic diversity, population structure, and adaptation, population genetic studies offer insights into the origins, spread mechanisms, and potentials for evolutionary change in invasive populations. These insights are fundamental for predicting invasion trajectories, assessing risks to native biodiversity, and designing targeted management interventions.

This paper focuses on the population genetics of the Monk Parakeet (*Myiopsitta monachus*), a species transported internationally as a pet that has become one of the most widely distributed non-native parrot species across the world (Calzada Preston & Pruett-Jones, 2021). Monk parakeets are native to a broad area in the southern portion of South America. Where they have been introduced, they have garnered attention due to their rapid population growth and disruptive effects on agricultural and electrical utilities (Van Bael & Pruett-Jones, 1996; Senar *et al.*, 2016; Calzada Preston *et al.*, 2021), making this species an ideal model to explore the genetic underpinnings of invasion success. By integrating genetic data with ecological and climatic information, this study aims to address key questions regarding the origins, genetic diversity, and demographic history of non-native Monk Parakeet populations.

Given its prominence as one of the most widely distributed non-native parrots globally, several aspects of Monk Parakeet population genetics have already been explored, both in their native and parts of their non-native ranges. There are three sub-species of Monk Parakeet described across their native range distribution: the *M. m. cotorra*, *M. m. calita*, and *M. m. monachus* whose distributions border each other. It should be mentioned that the allopatric Cliff Parakeet (*Myiopsitta luchsi*) found in Bolivia used to be recognized as a subspecies of Monk Parakeet. An analysis of the mitochondrial DNA across sub-species in the native range found that *M. m. luchsi* is distinct and deserved elevation to allospecies status (Russello *et al.*, 2008). That same study found no support for genetic differentiation among the other three subspecies, and one mitochondrial haplotype was shared across all three sub-species (Russello *et al.*, 2008). Additionally, (Figure 3.1) analysis of nuclear microsatellites show that genetic diversity is highest in the

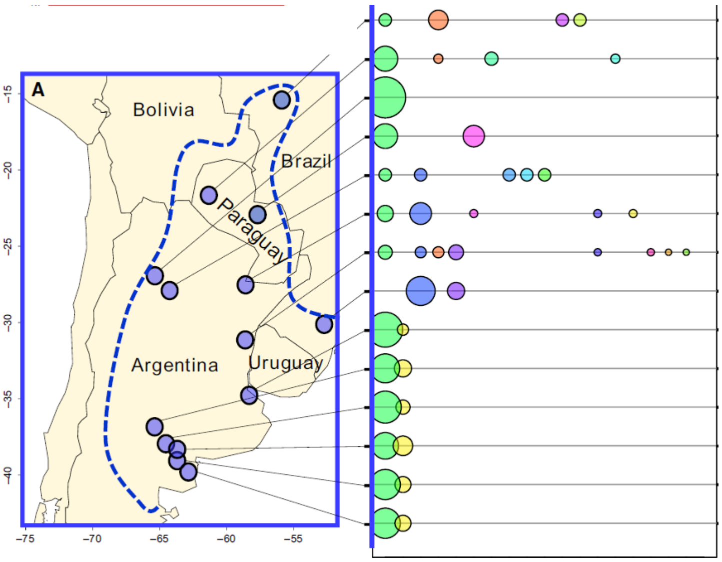


Figure 3.1. Map of mitochondrial haplotype diversity and distribution across the Monk Parakeet native range. Adapted from “Shared genetic diversity across the global invasive range of the monk parakeet suggests a common restricted geographic origin and the possibility of convergent selection” by Edelaar, P. *et al.*, 2015, *Molecular Ecology*, 24, p. 2168.

northern parts of the native range distribution, and it decreases gradually towards the most southern populations (Edelaar *et al.*, 2015). However, it should be noted that there were no samples collected from within Uruguay in this nuclear microsatellite analysis, even though Monk Parakeets exported for commercial trade come almost exclusively from Argentina and Uruguay (Edelaar *et al.*, 2015).

The communal breeding behavior within native populations of Monk Parakeets is associated with a high genetic relatedness between the breeding pair as well as with adult helpers, implying inbreeding, as quantified with microsatellite markers (Bucher *et al.*, 2016). A population of Monk Parakeets established in Barcelona, Spain have a higher reproductive output than observed for the species within the native range (Senar *et al.*, 2019) and Spanish populations of monk parakeets have become successfully established and begun spreading from their sites of introduction, with population size across the country estimated to be around 20,000 (Postigo *et al.*, 2019). These populations comprise about 84% of the total number of Monk Parakeets in Europe and their rapid growth and expansion within the last four decades has led to the species' consideration as an agricultural pest and an invasive species (Postigo *et al.*, 2019; Senar *et al.*, 2016; Muñoz & Real, 2006). Such rapid population growth following a bottleneck event can lead to an imbalance in allele size variance and heterozygosity given that the population is not at equilibrium (Kimmel *et al.*, 1998), which should be considered when filtering for loci that may be under selection.

Studies of Monk Parakeet population genetics across their non-native range have all found evidence of genetic bottlenecks relative to native populations and decreased genetic variation found in non-native populations established at greater latitudes (Russello *et al.*, 2021). Within their study, Edelaar *et al.* (2015) found a positive correlation between lower average winter temperatures and reduced genetic diversity across the non-native populations they examined, though more independent populations would be needed to test the relationship. Strubbe & Matthysen (2009) demonstrate that the establishment success of monk parakeets is influenced by the number of frost days and the density of the local human population, lending credence to the importance of the climate-matching hypothesis in this species' invasion process (Strubbe & Matthysen, 2009). Colder climates might impose a stronger population bottleneck which would lead to reduced genetic diversity, although strong selection on behavioral or physiological cold tolerance might also result in such reduced genetic diversity. Regarding the origin of non-native populations, individuals collected from introduced populations in North America and Spain seem to be sourced from a restricted region of the native range, between Argentina and Uruguay, respectively (Edelaar *et al.*, 2015).

My research brings genomic data to the study of these patterns of genetic diversity and population structure in non-native Monk Parakeet populations (Barcelona, Spain and Florida). I gathered RAD markers from across the Monk Parakeet genome and collected data from previously unexamined populations (Puerto Rico and Chicago, IL). These non-native populations were contrasted with historic whole genome samples collected across the Monk Parakeet's native distribution. The tissue samples available from the native range were toepads from bird skins in museum collections, some of which were collected more than 100 years ago. DNA extracted from historic or ancient specimens tends to have shorter fragment sizes, due to degradation (Settlecowski *et al.*, 2023). To ensure that I sequenced the genomic regions recovered from the more affordable 3RAD methods, I carried out whole genome sequencing (WGS) on all the toepad samples acquired for this study. Additionally, I used a Pairwise Sequentially Markovian

Coalescent (PSMC) model to examine the species' demographic history in conjunction with the Cliff Parakeet.

Methods

Sample Collection and DNA Extraction:

Blood samples were collected from a colony of Monk Parakeets in Puerto Rico (N =18), while tissue samples preserved in 95% ethanol of birds from Illinois (Field Museum of Natural History, FMNH), Florida (Florida Museum of Natural History, FLMNH) and Barcelona, Spain (Museu de Ciències Naturals de Barcelona, MCNB) were obtained from museum collections (see sampling list in Appendix C: Tables C1 and C2). DNA of blood and tissues were extracted using a Qiagen DNeasy Blood & Tissue Kit. DNA concentration and fragment sizes were assessed using an Invitrogen Qubit 2.0 Fluorometer and 2% agarose gel electrophoresis.

Library Preparation and 3RAD Sequencing:

For the 3RAD library preparation, genomic DNA (500 ng) from each individual was digested with the EcoRI, XbaI, and NheI restriction enzymes and ligated to unique barcoded adapters according to the 3RAD protocol (Bayona-Vásquez *et al.*, 2019). DNA libraries were size-selected using Sage Science Inc. BluePippin agarose gel electrophoresis to enrich for fragments between 480-600 bp. Following library preparation, barcoded libraries with low concentrations were excluded and the rest were pooled equimolarly and sent for paired-end sequencing on a NovaSeq X platform (Illumina, Inc.) at the University of Chicago's Genomics Core Facility.

Toepad DNA Extraction, Library Preparation and Sequencing

Toepads of museum specimens from populations throughout the Monk Parakeet's native range were obtained from the FMNH's Bird Collection (N = 14) along with toepads from one bird collected in Illinois and two collected in Florida which had no tissue samples available (N = 3).

The DNA extraction and library preparation for these samples was carried out in a PCR-free clean lab at the FMNH. DNA was extracted from the toepads using a silica column extraction with a swinging bucket centrifuge, as detailed in McDonough *et al.* 2018, and then the extracted DNA was treated with New England Biolabs' PreCR DNA Repair Mix following the kit's standard protocol. Whole genome sequencing (WGS) library preparation was carried out following KAPA HyperPlus kit (KAPA Biosystems) protocol. Sequencing for these libraries was done on a NovaSeq X platform (Ilumina, Inc.) at the University of Chicago's Genomics Core Facility.

Data Processing and Bioinformatics Analysis:

Raw sequencing reads were processed to remove adapter sequences and low-quality bases using Stacks (Catchen *et al.*, 2013) for the 3RAD libraries and Trimmomatic-0.39 (Bolger *et al.*, 2014) for the WGS libraries. Processed 3RAD reads were demultiplexed based on barcodes, and individual-specific sequences were identified and extracted using the Stacks command process_radtags. Individuals with a mean coverage below 5X were excluded from subsequent analysis. Following de-multiplexing, reads were aligned to a chromosomal-assembly reference genome for the Monk Parakeet (Genbank Accession Number: GCA_017639245.1). WGS library reads were filtered for contaminant DNA by using the Kraken2 Standard-8gb database to classify and exclude reads from common contamination sources (Wood *et al.*, 2019). The resulting FASTA read files were then aligned to the same reference genome using the Burrows-Heeler Aligner algorithm implemented in BWA-MEM (Li, 2013). Variant calling was performed using bcftools (Danecek *et al.*, 2021) to generate a catalog of single nucleotide polymorphisms (SNPs) and genotypes across the native and non-native populations filtering for only those variant sites with a quality score greater than 20 '-i "(QUAL>20)"'. The resulting VCF file was processed using vcftools following the filtering scheme in Prost *et al.* (2022) to filter for SNPs found in 25% of individuals, with a minimum coverage depth of three and a maximum coverage per site of 120x.

Additionally, the SRA sequence data for three outgroup species (*Brotogeris chrysoptera* - SRR23336496; *Brotogeris tirica* - SRR25665017; *Myiopsitta luchsi* - SRR23998349) was downloaded from the National Center for Biotechnology Research (NCBI) using the SRA Toolkit 3.1.1. These reads were aligned to the Monk Parakeet reference genome, cleaned, and processed as described above for the rest of the WGS sequence data. After processing, I created a FASTA file by selecting the most common base at each locus across the three outgroup species using ANGSD -doFasta 2 option. The resulting FASTA file represents the ancestral states for each locus across the Monk Parakeet genome.

Population Structure

The aligned sequence reads for the native range individuals were filtered to remove sites that were not in Hardy-Weinberg Equilibrium and sites that were in linkage disequilibrium were pruned as well. The resulting SNP dataset was input into NGSadmix, a tool for estimating individual admixture proportions (Skotte *et al.*, 2013) and used to estimate the likelihood that there are K genetic clusters or populations within the native range (Evanno *et al.*, 2005). Each K, from 2 to 10, was estimated 10 times and used to calculate delta K using the methods of Evanno *et al.* (2005). These methods of determining the optimal K value overcome the issue of the likelihoods of K, as well as the variance of the likelihoods, continually increasing as the admixture programs estimate larger values of K by calculating delta K, the second order rate of change of the likelihood of K with respect to K (see Evanno *et al.*, (2015) for more information). The K value also was estimated through an independent principal component analysis implemented within pcangsd (Meisner & Albrechtsen, 2018), which estimates the covariance matrix of the filtered native range genetic data. The principal components of the covariance matrix were then graphically inspected to visually identify the number of clusters within the native range.

The most likely K value identified within the native range was then used to create a reference panel, an estimate of each population K's allele frequencies, based on the samples from the native range. This reference panel was then used to estimate the admixture proportions for each non-native individual to determine whether admixture between individuals from different native range populations has occurred within introduced populations.

Pairwise Sequentially Markovian Coalescent (PSMC)

To estimate the species' demographic history and infer changes in the size of each population, I used a Pairwise Sequentially Markovian Coalescent (PSMC) model (Cahill *et al.*, 2016). This model estimates the distribution of the time to the most recent common ancestor between alleles at each locus across the genome. As alleles are expected to coalesce rapidly when population sizes are small, changes in the coalescent rate across time indicate changes in the effective population size. From the native range WGS libraries, I selected one sample with a relatively high mean coverage (> 8x), though lower than the ideal coverage (see Nadachowska-Brzyska *et al.*, 2016), from each genetic cluster (K) estimated previously within the native range, as well as the sequence data for the Cliff Parakeet (*Myiopsitta luchsi*). To scale the time to the most recent common ancestor, I used the generation times for the two species, which were 6 and 5.2 years respectively, based on the estimates provided by IUCN Red List (BirdLife International, 2018 & 2020). The neutral mutation rate was estimated by Taylor Hains (Hains, T. personal communication, 2024) following Zhao *et al.* (2013) as:

$$\mu = \frac{sequence\ divergence\ (\%)\ \ x\ generation\ time\ (years)}{2\ x\ divergence\ time\ between\ both\ species\ (years)},$$

using the genomes of the Zebra Finch (*Taeniopygia castanotis*) and the Sun Conure (*Aratinga solstitialis*) and the divergence time between Psittaciformes and Passeriformes estimated from a Ultraconserved Elements (UCE) tree (Gelabert *et al.*, 2020). This method estimated the neutral mutation rate to be 1.0 x 10^{-8} mutations per site per year. The three samples from the native range provide a glimpse at the effective size of populations within the native range prior to non-native populations being introduced outside of the native range. The inclusion of the Cliff Parakeet provides an estimate of how far back in time the two species have been untangled from each other's demographic history.

Genetic Diversity

To obtain estimates of heterozygosity within the native range, I split the native range samples based on their admixture proportions to the K clusters and used the angsd program to calculate the allele frequency at each site for each individual and then obtained the maximum likelihood for the site frequency spectrum (SFS). I follow the recommendations outlined by Schmidt *et al.* (2021) by reporting the heterozygosity rate across all sites, both fixed and variant. This provides a more accurate estimate of genome-wide heterozygosity that can be comparable with reduced representation sequencing approaches. The sum of the observed heterozygous sites over the total number of sites gives an individual's estimate of the observed rate of heterozygosity, which was then averaged across the other individuals within the native range clusters. This same approach was done for each non-native population, incorporating both 3RAD and WGS libraries. Heterozygosity calculated over all sequenced sites provides an estimate of the proportion of heterozygosity across the genome, or across fragments of the genome in the case of 3RAD libraries, which were then averaged across the individuals from each non-native population, regardless of library type. I also used the Stacks program ‘Populations’ to calculate the mean heterozygosity and nucleotide diversity (π) across the RAD marker loci to quantify genetic diversity within and across each non-native population.

Results

Sequencing and data quality

The 3RAD libraries successfully sequenced reads from all individuals with average coverage per sample varying between 1.1X and 117.1X. Given that 3RAD libraries are a type of reduced-representation sequencing, coverage in this regard refers to the average number of reads sequenced for each RAD marker loci recovered across an individual. Twenty individuals with average coverage < 5X were removed from the subsequent analysis (Table C2). The toepad libraries successfully sequenced reads from all individuals with average coverage varying between 7.1X to 11.0X and no individuals were removed from analysis. This resulted in 98 individuals from the non-native range (Captive = 2; Florida = 18; Illinois = 9; Puerto Rico = 16; Spain = 53) and 14 from the native range. Toepad library raw reads filtered through Kraken2 revealed that less than 2% of the total reads were classified as bacterial, viral or human DNA and were removed from downstream analysis.

Population Structure

All sites were found to be in Hardy-Weinberg Equilibrium and sites were pruned due to being in linkage disequilibrium resulting in a dataset consisting of 3,092 SNPs. After running

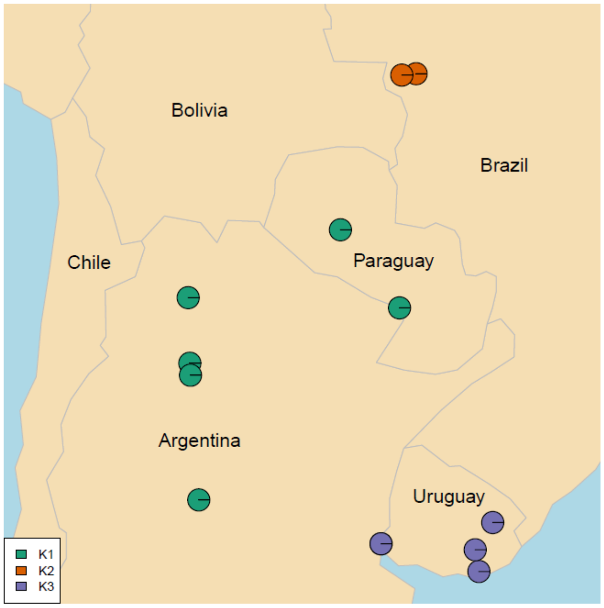


Figure 3.2 Map of South America depicting the collection sites and admixture proportions of native range individuals.

admixture models, the K value with the greatest likelihood for describing the genetic clusters within the native range was K=3 (Figure C.1). The reference panel based on the native range individuals was used to determine the admixture proportions for those same samples in the native range, in order to visualize population structure across the native range. Plotting the admixture proportions geographically (Figure 3.2) shows that population structure seems to be based on geographic distance described by a Northern cluster (K2), a South-Eastern cluster (K3), and a Central-Western cluster (K1).

The principal component analysis for the native range genetic diversity revealed that samples cluster in the same three groups as

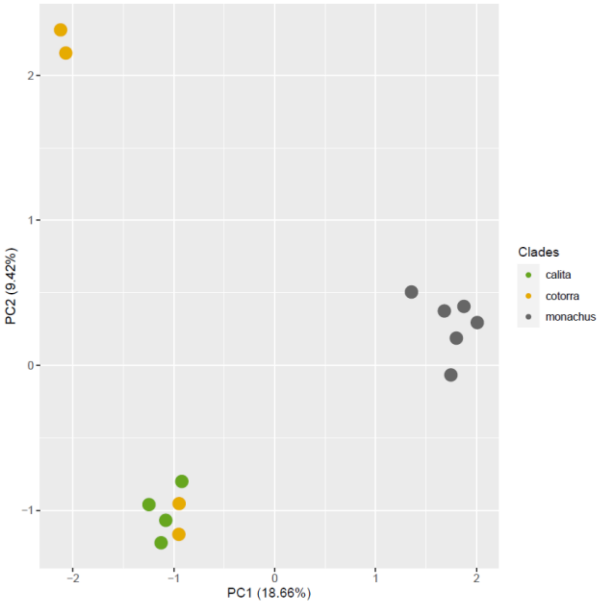


Figure 3.3 Principal component analysis of genetic variation from native range samples. Note that color corresponds to the subspecies each specimen was classified by the museum collection, while clustering patterns indicate genetic similarity.

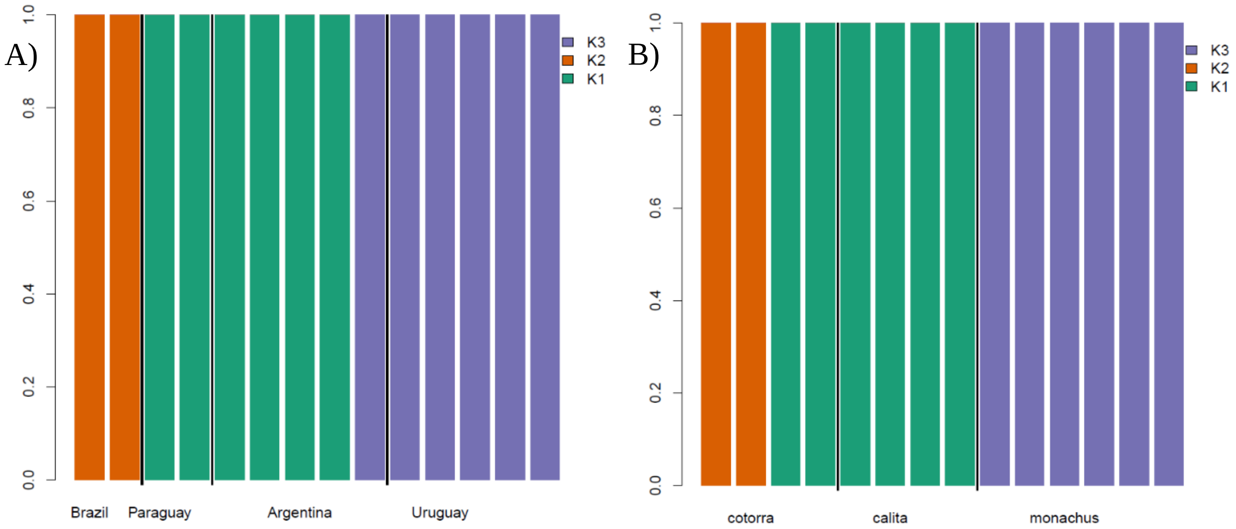


Figure 3.4. Admixture proportions for native range samples based on the native range reference panel as described by K = 3. Native range individuals are grouped by the country the specimen was collected and B) the subspecies its was classified under. Individual bars represent the same individuals in both figures. Note the mis-match in clustering by subspecies and K cluster in B).

estimated using admixture proportions (Figure 3.3). The K3 cluster corresponds to the nominate subspecies *monachus*, but the K1 and K2 clusters do not clearly correspond to the distributions of the other two subspecies, *cotorra* and *calita* (Figure 3.4). Particularly, the two individuals from Paraguay were archived as belonging to the *cotorra* subspecies, but PCA (Figure 3.3) and admixture models (Figure 3.4A) show that they are genetically more similar to the *calita* subspecies found in Argentina.

When the reference panel was used to estimate the admixture proportions of the non-native population individuals from the K=3 clusters in the native range, most individuals seem to be descendants of Monk Parakeets from clusters K1 and K3 (Figure 3.5). Overall, 97% of the individuals from the non-native populations have the greatest proportion of admixture attributed to K3.

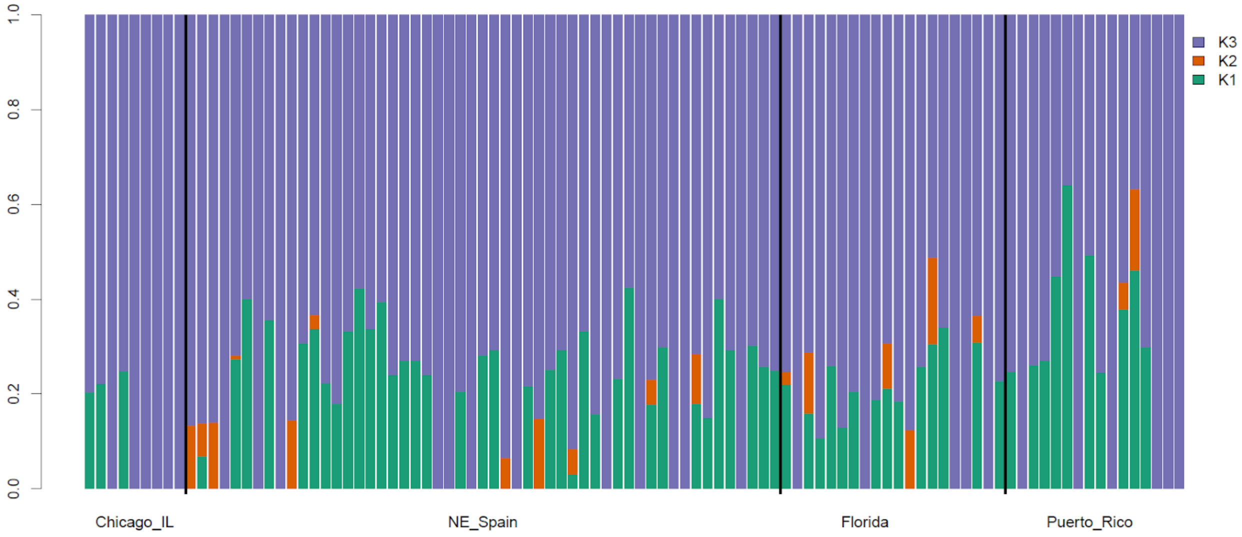


Figure 3.5. Admixture proportions for non-native range individuals based on the native range reference panel as described by K = 3. Samples are grouped by the region they were collected.

Pairwise Sequentially Markovian Coalescent (PSMC)

The PSMC model for native range Monk Parakeets and the Cliff Parakeet suggests that the Cliff Parakeet and the Monk Parakeet have been separate for at least 2 Mya (Figure 3.6). Furthermore, it suggests that Monk Parakeets experienced a peak in population size around 400 and 500 kya and have since decreased by an order of magnitude following the interglacial periods that have occurred during the last 2 million years.

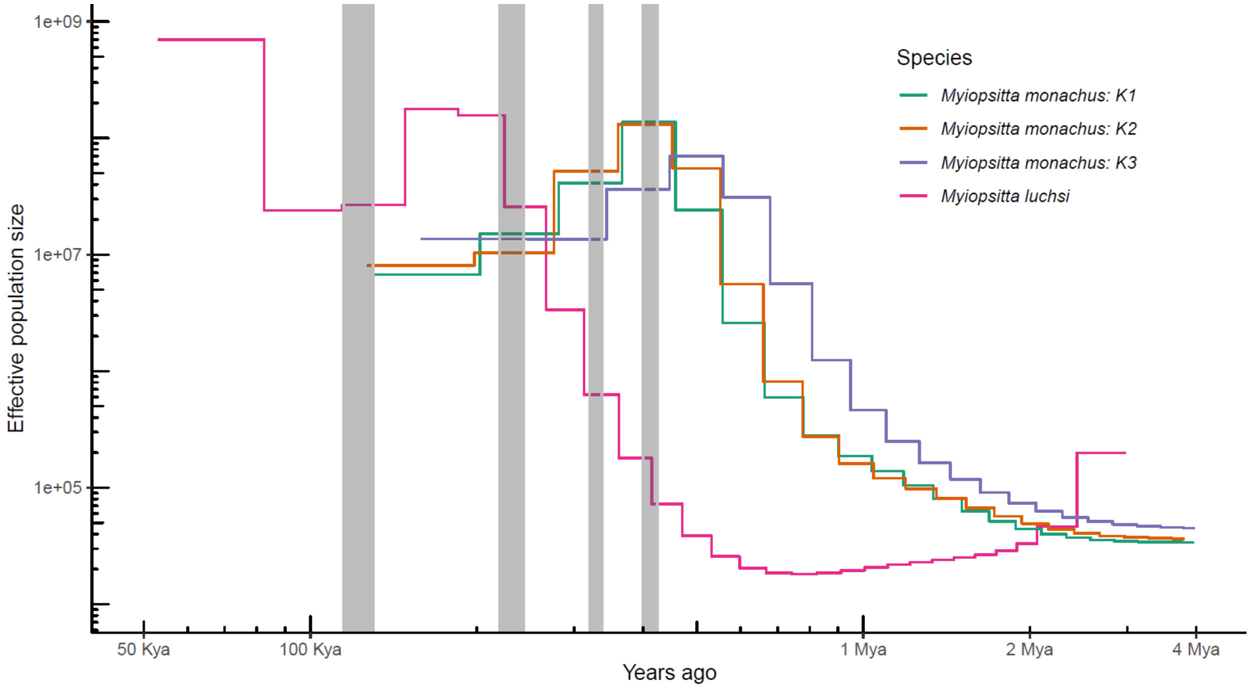


Figure 3.6. Pairwise sequentially Markovian Coalescent (PSMC) step-wise plot of effective population size through time. Individuals from each cluster K follow the coloration scheme used above, while including the Cliff Parakeet (*Myiopsitta luchsi*). Time and effective population size are displayed on a logarithmic scale and are based on a genome mutation rate of 1.0 x 10^{-8} per site per year and a generation time of 6 years for the Monk Parakeet and 5.2 years for the Cliff Parakeet.

Genetic Diversity

Estimates of genetic diversity show reduced diversity across the non-native populations when compared to the native range (Table 3.1). Native range birds had similar levels of genetic diversity, which were around six times greater that most non-native populations. Within non-native populations, observed heterozygosity and nucleotide diversity (π), for fixed and variant sites, was highest for the Captive population and lowest for the Puerto Rico population. Expected heterozygosity was highest in the Florida population and lowest in the Puerto Rico population.

Table 3.1. Genetic diversity estimates for native and non-native range populations of Monk Parakeet. Birds from the native range have been grouped according to the admixture model clusters. N refers to the number of samples in each population; Obs. Het. is the average observed heterozygosity; π refers to the average pairwise nucleotide diversity; and F$_{IS}$ refers to the average inbreeding coefficient of an individual relative to its own population.

Population ID	Estimation Method	N	Private alleles	Sites	Variant Sites	Polymorphic Loci (%)	Obs. Het.	π	Fis
Native_K1	ANGSD-SFS	6	-	8.2x10^{8}			0.007		
Native K2	ANGSD-SFS	2	-	8.3x10^{8}			0.00669		
Native K3	ANGSD-SFS	6	-	8.4x10^{8}			0.00699		
Spain	ANGSD-SFS	53	-	1.0x10^{7}			0.00346		
	Stacks-Populations	53	18808	1.0x10^{7}	88355	0.7649	0.00121	0.00127	0.00037
Puerto Rico	ANGSD-SFS	16	-	8.7x10^{6}			0.00252		
	Stacks-Populations	16	1694	9.5x10^{6}	27877	0.13773	0.0002	0.00021	0.00004
Florida	ANGSD-SFS	18	-	1.0x10^{8}			0.00293		
	Stacks-Populations	16	8313	9.6x10^{6}	81592	0.63403	0.00119	0.00129	0.0004
Illinois	ANGSD-SFS	9	-	1.0x10^{8}			0.00268		
	Stacks-Populations	8	2073	9.2x10^{6}	82310	0.40114	0.00116	0.00118	0.00006
Captive	ANGSD-SFS	2	-	1.2x10^{7}			0.00235		
	Stacks-Populations	2	1188	1.1x10^{7}	98210	0.28602	0.00144	0.00157	0.00019

Discussion

This analysis confirms the standing views regarding the putative source populations for Monk Parakeets being found between Uruguay and its border with Argentina (Edelaar *et al.*, 2015 and Russello *et al.*, 2008). The sampling in this analysis suggests that most non-native individuals are descendants of the *monachus* subspecies that dominates within the Uruguayan-Argentinian border. However, there is evidence for admixture from all populations found within individuals in the non-native range. The samples analyzed from the native range conform to a broad sampling of the overall distribution, but at a coarse resolution. Increased samples sizes for native range populations can clarify whether the admixture observed in non-native populations is a result of individuals from different populations being brought together outside of their native range or if it is the result of migration between populations in the native range which is then sampled when birds are captured in the regions adjacent to the Argentina-Uruguay border. Furthermore, the population structure observed within the native range suggests that geographic distance might best explain the differentiation between the three identified genetic clusters. Additionally, the Río Paraná, Río Paraguay, and Río Uruguay river systems might constitute the edges between the three different clusters identified in this analysis (see Figure C.2). Similar patterns of population structure associated with South American river systems have been documented in passerines (Fernandes *et al.*, 2014), parrots (Ribas *et al.*, 2005), and other avian taxa (Ribas *et al.*, 2012 and Lutz *et al.*, 2013) though these are all related to the Amazon and its tributaries.

The PSMC analysis of native range Monk Parakeets indicates that the species split from the Cliff Parakeet about 2 Mya, supporting the validity of their treatment as distinct species. The different populations of the Monk Parakeet seem to share the same demographic history and reached a maximum population size between 400 and 500 Kya. Within recent timescales, the Monk Parakeet has further expanded its range within its native distribution by more than 300,000 km^2 in the last 150 years (Bucher & Aramburú, 2014) and shows no population size declines within its native range despite hundreds of thousands of Monk Parakeets being captured for export in the pet trade (BirdLife International, 2022).

Finally, genetic diversity is clearly reduced in the non-native range with respect to the native range populations, with the lowest levels of genetic diversity observed within individuals from Puerto Rico. The birds collected in Puerto Rico were from a single colony that I believe to have been established within the last decade (Personal communication with residents near sampling locality). Given the reduced levels of genetic diversity, the birds sampled from Puerto Rico might more accurately be representing genetic diversity at the local colony level, particularly given that inbreeding is believed to be common for the species at local scales (Bucher *et al.*, 2016). Collecting samples from additional colonies throughout the island will help clarify whether genetic diversity is reduced throughout the island's populations. Additionally, it is striking that birds in captivity have increased levels of genetic diversity, when compared to the other non-native populations. Further sampling of captive individuals will reveal whether the reduction in genetic diversity seen in non-native populations occurs due to selective capture in the wild, from differential survival after introduction in non-native locations, or a combination of both. If we exclude the birds from Puerto Rico from the analysis, this dataset complements the results of Edelaar *et al.* (2015) that populations in colder climates have reduced genetic diversity, as seen with individuals from Chicago, IL having reduced genetic diversity, when compared to the warmer introduction sites of Florida and Barcelona, Spain.

Ethical Considerations

All sampling procedures were conducted following relevant guidelines and regulations, and appropriate permits from IACUC and state agencies were obtained for fieldwork. Institutional ethics approval was obtained for the collection and use of animal samples.

Chapter 4

Conclusion

Throughout this research, I compiled the known number and distributions of Psittaciformes outside of their native range from available published literature, citizen science data, and the GAVIA dataset dedicated to describing known avian invasions (Chapter 1). Building upon the understanding of which species have established populations outside of their native range, I investigated how the relationship between species occurrence and local climate, topography, and human activity differs between native and non-native range occurrences of the most widespread non-native Psittaciformes (Chapter 2). Lastly, I examined the genetic differences between populations of the most widely distributed non-native parrot (Monk Parakeet; *Myiopsitta monachus*) and explored the potential influence of climate on patterns of genetic diversity across its non-native distribution (Chapter 3). As a whole, these chapters comprise an inter-disciplinary/multi-faceted approach/analysis of the ecological and evolutionary factors governing the distributions of non-native Psittaciformes that points towards future areas of research regarding the invasion ecology, distribution, and adaptation of this and other potentially invasive taxa.

Broader Conclusions & Future Directions

Psittaciformes are a popular taxon within the international pet market, with close to 88% of extant species (336 out of 381 Psittaciformes) having been traded to some degree through the global pet trade (Cardador *et al.*, 2021). This, in turn, has led to their introduction and proliferation outside of their native range. My examination of GAVIA, eBird, and iNaturalist databases revealed that of the 336 species previously found to be traded internationally, more than half are known to have been introduced outside of their native range, and more than 20% are now breeding in the wild. When contrasted with previous known information on parrot introductions, it becomes clear that parrot introductions worldwide are ongoing, and the number of naturalized parrots has increased accordingly. The increased introductions on a global scale have been associated with national bans on bird imports, which in turn shifts the parrot pet market towards a different part of the world (Cardador *et al.*, 2017). Recent assessments and frameworks of wildlife trade have made strides in unveiling the drivers of wildlife trade that can predict the movement of wildlife internationally (Symes *et al.*, 2018; Gippet & Bertelsmeier, 2021; Hughes *et al.*, 2023). However, to the extent that trade bans are being enforced domestically and not globally, the wild-caught bird trade will continue to transport internationally into untapped markets, likely in developing countries (Cardador *et al.*, 2019).

Invasion risk has been assessed by modeling the environmental niche within a species' native range distribution and finding the matching environments outside of their native range which the species could become introduced. The conclusions from these studies are informative, but they may not be entirely accurate at predicting species distributions, as discussed in Chapter 2. Species distributions are indeed shaped by the physiological constraints and behavioral preferences that individuals have with their associated habitats. However, the current distributions may also be the result of competitive exclusion by other species, fragmentation of adjacent favorable habitats due to recent land use changes, or aspects of species history, such as stochastic or disturbance related extinctions.

Within Chapter 2, I found that across naturalized Psittaciformes the distribution of a species within its native range can predict their known occurrences outside of the native range. However, I also found evidence of the opposite, that some species occur in locations that extend beyond the environmental conditions predicted to be favorable within the native range. Environmental niche modeling that relies on native range occurrences to evaluate areas at risk for invasion must be wary to not underestimate the environmental tolerances for the species under examination. Developments in the understanding of physiological tolerances of vertebrates to climate can help to fine-tune environmental niche models (Boardman *et al.*, 2022) to accurately delimit the conditions at which survival becomes unlikely.

A rich avenue of inquiry for future projects would be in examining whether nesting or social behaviors differ by climate and across the timeline of establishment. Species in Psittaciformes have great cognitive abilities, associated with their social behavior. In cases of adaptation to novel environments, these cognitive abilities can help overcome some of the detrimental factors experienced in non-native locations which they might not find within their native distributions (e.g. snowfall). In particular, Monk Parakeets are the only parrot that builds stick nests, rather than nesting in cavities. They are known to selectively incorporate materials into their nests, which is believed to provide insulation for thermoregulation and even bactericidal properties (Viana *et al.*, 2016). They are also known to build nests on electrical utility transformers (Reed *et al.*, 2014), which some have argued may be due to the transformer's flat top being a useful substrate, though there may also be a thermal advantage, as these transformers are known to generate heat. Additionally, Monk Parakeets in Chicago are recently known to be nesting underneath bridges which might shield them from snowfall in the winter.

The process of species invasion involves many barriers and stages that each present unique challenges and possibilities for failure. In Chapter 3, I analyzed the genetic structure and diversity between native range samples and four distinct non-native populations. My study confirms that non-native populations of Monk Parakeets show reduced levels of genetic diversity with respect to native range populations and that the putative source population where birds have been harvested for export lies between the Uruguay-Argentina border. Even with the reduced levels of genetic diversity found in non-native populations, these populations are growing and continually expanding their non-native range.

An important aspect of study, which was not discussed in this dissertation, but which could be the focus of a future project, is the role of captivity on genetic diversity and how captive populations might differ from both native and non-native populations. Within captivity, it is common practice to breed birds for distinctive and unique color combinations, like albinism, melanism or in the case of Monk Parakeets, blue morphs. Even if individuals that escape captivity are not color morphs, pervasive selective breeding within captivity could significantly alter patterns of genetic diversity at this stage. Furthermore, captivity provides a safe environment within which admixture of birds from geographically distinct populations can come together before being introduced into the wild. I believe that the Monk Parakeet represents a unique model system with which to study the effects of captivity and captive breeding on populations transitioning from native to non-native locations.

Appendix A: Chapter 1 Data Tables and Supplementary Figures

Following is a collection of three data tables and six supplementary figures referred to in Chapter 1.

Table A1. Status of all species of Psittaciformes in a country outside of their native range.

Country	**Naturalized**	**Breeding**	**Introduced**	**Historic**	**Total Species**
Afghanistan	0	0	1	0	1
Albania	0	0	1	0	1
Algeria	0	0	1	0	1
Antigua and Barbuda	1	0	0	0	1
Argentina	1	0	13	0	14
Australia	13	1	23	0	37
Australian Territories	1	0	1	0	2
Austria	2	0	2	0	4
Azerbaijan	0	0	1	0	1
Bahamas	0	0	2	0	2
Bahrain	2	0	4	0	6
Barbados	1	3	4	0	8
Belgium	3	0	1	1	5
Belize	0	0	2	0	2
Bhutan	0	0	1	0	1
Bolivia	0	0	7	0	7
Botswana	1	0	1	0	2
Brazil	1	0	43	0	44
Canada	1	0	1	0	2
Cape Verde	0	1	0	0	1
Chile	1	0	1	0	2
China	4	0	0	0	4
Chinese Special Administrative Region	4	0	14	0	18
Colombia	0	0	23	0	23
Comoros	1	0	1	0	2
Cook Islands	0	0	1	0	1
Costa Rica	1	0	3	0	4
Côte d'Ivoire	0	0	1	0	1
Croatia	0	0	1	0	1
Cuba	1	0	0	0	1
Czech Republic	1	0	4	0	5
Denmark	1	0	0	0	1
Dominica	1	0	0	0	1
Dominican Republic	2	1	3	0	6
Ecuador	0	0	7	0	7
Egypt	1	0	0	0	1
El Salvador	0	0	1	0	1
Equatorial Guinea	0	0	1	0	1
Fiji	1	0	3	0	4
France	4	0	7	0	11
French Territories	6	0	2	1	9

Table A1. Status of all species of Psittaciformes in a country outside of their native range, continued.

Country	**Naturalized**	**Breeding**	**Introduced**	**Historic**	**Total Species**
Germany	3	0	7	3	13
Ghana	0	0	3	0	3
Greece	2	0	1	0	3
Grenada	0	0	1	0	1
Guatemala	0	0	2	0	2
Guyana	0	0	1	0	1
Honduras	0	0	4	0	4
India	1	0	5	0	6
Indonesia	6	0	9	0	15
Iran	1	0	1	0	2
Iraq	1	0	0	0	1
Ireland	0	0	1	0	1
Israel	4	0	1	0	5
Italy	4	0	9	0	13
Jamaica	2	0	1	0	3
Japan	5	0	0	0	5
Jordan	2	0	0	0	2
Kenya	5	0	1	0	6
Kiribati	1	0	0	0	1
Kuwait	1	0	2	0	3
Lebanon	1	0	0	0	1
Liberia	0	0	1	0	1
Lithuania	0	0	1	0	1
Malaysia	2	0	1	0	3
Maldives	1	0	0	0	1
Malta	1	0	1	0	2
Mauritius	2	0	13	0	15
Mexico	7	0	15	0	22
Moldova	0	0	1	0	1
Morocco	0	0	1	0	1
Mozambique	0	0	1	0	1
Namibia	1	1	1	0	3
Netherlands	2	0	6	0	8
Netherlands Territories	3	1	3	0	7
New Zealand	6	0	8	2	16
Nicaragua	0	0	3	0	3
Nigeria	0	0	2	0	2
Oman	2	1	2	0	5
Pakistan	0	0	1	0	1
Palau	2	0	0	0	2
Palestine	1	0	1	0	2
Panama	0	0	5	0	5
Papua New Guinea	0	0	5	0	5
Paraguay	0	0	5	0	5
Peru	1	0	14	0	15
Philippines	1	0	7	0	8
Poland	0	0	1	0	1
Portugal	2	0	6	0	8
Qatar	1	1	2	0	4
Romania	0	0	1	0	1
Russia	0	0	1	0	1

Table A1. Status of all species of Psittaciformes in a country outside of their native range, continued.

Country	**Naturalized**	**Breeding**	**Introduced**	**Historic**	**Total Species**
Saint Kitts and Nevis	0	0	1	0	1
Sao Tome and Principe	1	0	0	0	1
Saudi Arabia	1	0	4	0	5
Serbia	0	0	2	0	2
Seychelles	1	0	2	0	3
Sierra Leone	0	0	1	0	1
Singapore	7	1	12	0	20
Slovakia	1	0	2	0	3
Slovenia	1	0	0	0	1
Solomon Islands	0	0	1	0	1
Somalia	0	0	1	0	1
South Africa	2	0	12	2	16
Spain	8	6	37	0	51
Sudan	0	0	1	0	1
Switzerland	0	0	3	1	4
Syria	0	0	1	0	1
Taiwan	7	2	1	0	10
Tanzania	3	0	3	1	7
Thailand	1	0	4	0	5
Tonga	1	0	0	0	1
Trinidad and Tobago	2	0	3	0	5
Turkey	2	0	2	0	4
Uganda	1	0	0	0	1
Ukraine	0	0	3	1	4
United Arab Emirates	2	2	5	0	9
United Kingdom	4	2	1	1	8
British Territories	3	3	2	0	8
United States	23	17	45	0	85
U.S. Territories	13	1	14	1	29
Uruguay	0	0	3	0	3
Venezuela	1	2	15	0	18
Yemen	2	0	0	0	2
Zambia	1	0	0	0	1
Zimbabwe	0	0	1	0	1

Table A2. Summary of the number of countries and status of species of parrots (Psittaciformes) outside of their native range.

Scientific Name	Total Countries	Naturalized	Breeding	Introduced	Historic
Agapornis canus	10	6	0	2	2
Agapornis fischeri	13	3	1	9	0
Agapornis lilianae	3	2	0	1	0
Agapornis nigrigenis	1	0	0	1	0
Agapornis personatus	10	4	0	6	0
Agapornis pullarius	3	0	0	3	0
Agapornis roseicollis	18	3	1	14	0
Alipiopsitta xanthops	1	0	0	1	0
Amazona aestiva	9	1	2	5	1
Amazona albifrons	3	1	1	1	0
Amazona amazonica	13	3	1	9	0
Amazona auropalliata	1	0	1	0	0
Amazona autumnalis	4	2	1	1	0
Amazona barbadensis	1	0	0	1	0
Amazona farinosa	5	0	0	5	0
Amazona festiva	4	0	0	4	0
Amazona finschi	3	1	0	2	0
Amazona guildingii	1	0	0	1	0
Amazona kawalli	1	0	0	1	0
Amazona leucocephala	1	0	0	1	0
Amazona mercenarius	1	0	0	1	0
Amazona ochrocephala	10	2	3	5	0
Amazona oratrix	4	3	0	1	0
Amazona pretrei	1	0	0	1	0
Amazona ventralis	3	2	1	0	0
Amazona viridigenalis	3	3	0	0	0
Amazona xantholora	1	0	0	1	0
Anodorhynchus hyacinthinus	2	0	0	2	0
Aprosmictus erythropterus	2	0	0	2	0
Ara ararauna	10	1	1	8	0
Ara chloropterus	4	0	0	4	0
Ara macao	6	0	0	6	0
Ara militaris	1	0	1	0	0
Ara rubrogenys	1	0	0	1	0
Ara severus	5	1	0	4	0
Aratinga jandaya	2	0	0	2	0
Aratinga nenday	12	5	0	7	0
Aratinga weddellii	4	1	0	3	0
Barnardius zonarius	1	1	0	0	0
Brotogeris chiriri	5	1	0	4	0

Table A2. Summary of the number of countries and status of species of parrots (Psittaciformes) outside of their native range, continued.

Scientific Name	Total Countries	Naturalized	Breeding	Introduced	Historic
Brotogeris chrysoptera	1	0	0	1	0
Brotogeris cyanoptera	2	0	0	2	0
Brotogeris jugularis	2	0	0	2	0
Brotogeris pyrrhoptera	2	0	0	1	1
Brotogeris sanctithomae	2	0	0	2	0
Brotogeris tirica	3	0	0	2	1
Brotogeris versicolurus	8	5	1	2	0
Cacatua alba	7	3	0	4	0
Cacatua galerita	22	6	2	12	2
Cacatua goffiniana	8	3	1	4	0
Cacatua moluccensis	6	0	1	5	0
Cacatua ophthalmica	1	0	0	1	0
Cacatua sanguinea	4	2	0	2	0
Cacatua sulphurea	8	4	0	4	0
Cacatua tenuirostris	2	1	0	1	0
Callocephalon fimbriatum	1	1	0	0	0
Calyptorhynchus banksii	1	0	0	1	0
Calyptorhynchus lathami	1	0	0	1	0
Chalcopsitta atra	2	0	0	2	0
Charmosyna multistriata	1	0	0	1	0
Charmosyna papou	2	0	0	2	0
Coracopsis nigra	3	0	0	3	0
Coracopsis vasa	2	0	0	2	0
Cyanoliseus patagonus	5	0	2	3	0
Cyanoramphus novaezelandiae	1	1	0	0	0
Cyanoramphus unicolor	1	0	0	0	1
Diopsittaca nobilis	4	0	0	4	0
Eclectus roratus	7	1	0	6	0
Eolophus roseicapilla	4	1	0	3	0
Eos bornea	6	2	1	3	0
Eos reticulata	1	1	0	0	0
Eupsittula aurea	3	0	0	3	0
Eupsittula cactorum	1	0	0	1	0
Eupsittula canicularis	3	3	0	0	0
Eupsittula nana	2	0	0	2	0
Eupsittula pertinax	15	8	1	6	0
Forpus coelestis	2	0	0	2	0
Forpus passerinus	7	3	0	3	1
Forpus xanthopterygius	3	0	0	3	0
Glossopsitta concinna	1	1	0	0	0

Table A2. Summary of the number of countries and status of species of parrots (Psittaciformes) outside of their native range, continued.

Scientific Name	**Total Countries**	**Naturalized**	**Breeding**	**Introduced**	**Historic**
Guaruba guarouba	1	0	0	1	0
Lathamus discolor	1	0	0	1	0
Lophochroa leadbeateri	2	1	0	1	0
Loriculus galgulus	2	0	0	2	0
Loriculus vernalis	3	0	0	3	0
Lorius garrulus	3	0	0	3	0
Lorius hypoinochrous	1	0	0	1	0
Melopsittacus undulatus	45	12	5	26	2
Myiopsitta monachus	36	26	1	9	0
Nannopsittaca panychlora	1	0	0	0	1
Neophema splendida	1	0	0	1	0
Neopsephotus bourkii	1	0	0	1	0
Northiella haematogaster	1	0	0	1	0
Nymphicus hollandicus	17	1	1	15	0
Orthopsittaca manilatus	4	0	0	4	0
Parvipsitta porphyrocephala	1	0	0	1	0
Pionites melanocephalus	2	0	0	2	0
Pionus fuscus	1	0	0	1	0
Pionus maximiliani	4	0	0	4	0
Pionus menstruus	3	0	0	3	0
Pionus senilis	1	0	0	1	0
Pionus sordidus	1	0	0	1	0
Platycercus adscitus	2	0	0	1	1
Platycercus caledonicus	1	0	0	1	0
Platycercus elegans	6	3	0	3	0
Platycercus eximius	6	2	0	4	0
Platycercus icterotis	1	0	0	1	0
Poicephalus crassus	2	1	0	1	0
Poicephalus cryptoxanthus	1	0	0	1	0
Poicephalus meyeri	2	0	0	1	1
Poicephalus rueppellii	1	0	1	0	0
Poicephalus senegalus	9	1	2	6	0
Polytelis alexandrae	1	0	0	1	0
Polytelis swainsonii	1	0	0	1	0
Primolius auricollis	2	0	0	2	0
Primolius couloni	1	0	0	1	0
Primolius maracana	1	0	0	1	0
Probosciger aterrimus	3	0	0	3	0
Prosopeia splendens	1	1	0	0	0
Prosopeia tabuensis	2	1	0	1	0

Table A2. Summary of the number of countries and status of species of parrots (Psittaciformes) outside of their native range, continued.

Scientific Name	**Total Countries**	**Naturalized**	**Breeding**	**Introduced**	**Historic**
Psephotus haematonotus	3	0	0	3	0
Pseudeos fuscata	2	0	0	2	0
Psittacara chloropterus	2	0	0	2	0
Psittacara erythrogenys	7	2	1	4	0
Psittacara finschi	1	0	1	0	0
Psittacara holochlorus	3	1	0	2	0
Psittacara leucophthalmus	6	0	1	5	0
Psittacara mitratus	7	2	1	4	0
Psittacara wagleri	2	0	1	1	0
Psittacula alexandri	9	5	0	4	0
Psittacula columboides	1	0	0	1	0
Psittacula cyanocephala	6	0	1	5	0
Psittacula eupatria	31	12	1	18	0
Psittacula himalayana	1	0	0	1	0
Psittacula krameri	74	47	4	23	0
Psittacula roseata	7	0	0	7	0
Psittacus erithacus	8	1	0	7	0
Purpureicephalus spurius	1	0	0	1	0
Pyrilia haematotis	1	0	0	1	0
Pyrrhura amazonum	1	0	0	1	0
Pyrrhura devillei	1	0	0	1	0
Pyrrhura frontalis	4	0	1	3	0
Pyrrhura lepida	1	0	0	1	0
Pyrrhura leucotis	1	0	0	1	0
Pyrrhura lucianii	2	0	0	2	0
Pyrrhura molinae	4	0	1	3	0
Pyrrhura perlata	1	0	0	1	0
Pyrrhura picta	2	0	0	2	0
Pyrrhura roseifrons	1	0	0	1	0
Pyrrhura rupicola	2	0	0	2	0
Rhynchopsitta pachyrhyncha	1	1	0	0	0
Rhynchopsitta terrisi	1	0	0	1	0
Strigops habroptila	2	0	0	1	1
Tanygnathus lucionensis	2	2	0	0	0
Tanygnathus megalorynchos	3	0	0	3	0
Thectocercus acuticaudatus	8	3	0	5	0
Touit huetii	1	0	0	1	0
Touit melanonotus	1	0	0	1	0
Trichoglossus chlorolepidotus	2	1	0	1	0

Table A2. Summary of the number of countries and status of species of parrots (Psittaciformes) outside of their native range, continued.

Scientific Name	**Total Countries**	**Naturalized**	**Breeding**	**Introduced**	**Historic**
Trichoglossus flavoviridis	1	0	0	1	0
Trichoglossus haematodus	9	4	1	4	0
Trichoglossus moluccanus	2	0	0	2	0
Trichoglossus ornatus	1	0	0	1	0
Trichoglossus rubritorquis	1	0	0	1	0
Vini kuhlii	4	2	0	2	0
Vini peruviana	1	0	0	1	0

Table A3. Status of parrots (Psittaciformes) in the USA recorded in the databases in this study compared with those in recent and in-depth studies and reviews. Status identifiers have been abbreviated as follows: Naturalized = Nat.; Breeding = Bre.; Introduced = Int.; Observed = Obs.; and Historic = His.

Scientific Name	**Common Name**	**Continental U.S.**		**Hawaiian Islands**		**Puerto Rico**	
		This Study	Uehling et al. 2019, 2021	This Study	VanderWerf & Kalodimos, 2021	This Study	Falcón & Tremblay, 2018
Agapornis fischeri	Fischer's Lovebird	Int.	Obs.			Obs.	Bre.
Agapornis personatus	Yellow-collared Lovebird	Int.	Nat.		Obs.	Obs.	Bre.
Agapornis pullarius	Red-headed Lovebird		Obs.				
Agapornis roseicollis	Rosy-faced Lovebird	Nat.	Nat.	Bre.	Nat.	Obs.	Bre.
Amazona aestiva	Turquoise-fronted Amazon	Bre.	Nat.	Int.	Obs.	Int.	Bre.
Amazona albifrons	White-fronted Amazon	Bre.	Nat.			Int.	Nat.
Amazona amazonica	Orange-winged Amazon	Nat.	Nat.		Obs.	Nat.	Nat.
Amazona auropalliata	Yellow-naped Amazon	Bre.	Obs.				
Amazona autumnalis	Red-lored Amazon	Nat.	Nat.		Obs.		
Amazona barbadensis	Yellow-shouldered Amazon	Int.					
Amazona farinosa	Southern Mealy Amazon	Int.	Obs.				
Amazona festiva	Festive Amazon	Int.					
Amazona finschi	Lilac-crowned Amazon	Nat.	Nat.				
Amazona leucocephala	Cuban Amazon						Bre.
Amazona ochrocephala	Yellow-crowned Amazon	Bre.	Nat.	Int.		Nat.	Nat.
Amazona oratrix	Yellow-headed Amazon	Nat.	Nat.		Obs.	Nat.	Nat.
Amazona pretrei	Red-spectacled Amazon	Int.					
Amazona ventralis	Hispaniolan Amazon	Bre.	Obs.			Nat.	Bre.
Amazona viridigenalis	Red-crowned Amazon	Nat.	Nat.	Nat.	Nat.	Nat.	Nat.
Amazona xantholora	Yucatan Amazon	Int.	Obs.				
Anodorhynchus hyacinthinus	Hyacinth Macaw	Int.	Obs.				
Ara ararauna	Blue-and-yellow Macaw	Bre.	Nat.	Bre.	Obs.	Nat.	Nat.
Ara chloropterus	Red-and-green Macaw	Int.	Obs.			Int.	Bre.
Ara macao	Scarlet Macaw	Int.	Obs.	Int.	Obs.		Nat.

Table A3. Status of parrots (Psittaciformes) in the USA recorded in the databases in this study compared with those in recent and in-depth studies and reviews, continued.

Scientific Name	**Common Name**	**Continental U.S.**		**Hawaiian Islands**		**Puerto Rico**	
		This Study	Uehling et al. 2019, 2021	This Study	VanderWerf & Kalodimos, 2021	This Study	Falcón & Tremblay, 2018
Ara militaris	Military Macaw	Int.	Obs.	Bre.	Obs.		Bre.
Ara severus	Chestnut-fronted Macaw	Nat.	Nat.				
Aratinga jandaya	Jandaya Parakeet		Obs.		Obs.		
Aratinga nenday	Nanday Parakeet	Nat.	Nat.	Nat.	Obs.	Nat.	Bre.
Aratinga weddellii	Dusky-headed Parakeet	Nat.	Obs.				
Bolborhynchus lineola	Barred Parakeet		Obs.				
Brotogeris chiriri	Yellow-chevroned Parakeet	Nat.	Nat.				
Brotogeris jugularis	Orange-chinned Parakeet	Int.		Int.	Obs.		
Brotogeris pyrrhoptera	Grey-cheeked Parakeet	Int.					
Brotogeris sanctithomae	Tui Parakeet	Int.					
Brotogeris versicolurus	White-winged Parakeet	Nat.	Nat.			Nat.	Nat.
Cacatua alba	White Cockatoo	Int.		Obs.	Bre.	Obs.	Bre.
Cacatua galerita	Sulphur-crested Cockatoo	Nat.	Obs.	Bre.	Obs.		Bre.
Cacatua goffiniana	Tanimbar Corella	Int.		Bre.	Bre.		Bre.
Cacatua moluccensis	Salmon-crested Cockatoo	Int.		Int.	Bre.	Obs.	Bre.
Cacatua sulphurea	Yellow-crested Cockatoo				Obs.		
Chalcopsitta atra	Black Lory			Int.			
Cyanoliseus patagonus	Burrowing Parakeet	Int.	Obs.	Bre.	Bre.		
Cyanoramphus novaezelandiae	Red-crowned Parakeet		Obs.				
Diopsittaca nobilis	Red-shouldered Macaw	Int.					
Eclectus roratus	Eclectus Parrot	Int.		Int.	Obs.		
Enicognathus leptorhynchus	Slender-billed Parakeet				Obs.		
Eolophus roseicapilla	Galah	Int.		Int.	Obs.		
Eos bornea	Red Lory	Bre.	Obs.				
Eupsittula aurea	Peach-fronted Parakeet	Int.	Obs.				
Eupsittula canicularis	Orange-fronted Parakeet	Nat.	Obs.		Obs.	Nat.	Nat.
Eupsittula nana	Olive-throated Parakeet		Obs.			Int.	

Table A3. Status of parrots (Psittaciformes) in the USA recorded in the databases in this study compared with those in recent and in-depth studies and reviews, continued.

Scientific Name	**Common Name**	**Continental U.S.**		**Hawaiian Islands**		**Puerto Rico**	
		This Study	Uehling et al. 2019, 2021	This Study	VanderWerf & Kalodimos, 2021	This Study	Falcón & Tremblay, 2018
Eupsittula pertinax	Brown-throated Parakeet	Nat.				Bre.	Bre.
Forpus coelestis	Pacific Parrotlet		Obs.				
Lorius garrulus	Chattering Lory	Int.					
Melopsittacus undulatus	Budgerigar	Nat.	Nat.	Int.	Obs.	Nat.	Bre.
Myiopsitta monachus	Monk Parakeet	Nat.	Nat.	Int.	Obs.	Nat.	Nat.
Nymphicus hollandicus	Cockatiel	Intr.	Obs.	Int.	Obs.	Int.	Bre.
Pionites melanocephalus	Black-headed Parrot	Intr.	Obs.				
Pionus maximiliani	Scaly-headed Parrot	Obs.	Obs.				
Pionus senilis	White-crowned Parrot	Int.	Obs.		Obs.		
Platycercus adscitus	Pale-headed Rosella			His.			
Platycercus elegans	Crimson Rosella	Int.	Obs.				
Platycercus eximius	Eastern Rosella	Int.					
Poicephalus crassus	Niam-niam Parrot	Int.					
Poicephalus meyeri	Meyer's Parrot		Obs.	Int.	Obs.		
Poicephalus rueppellii	Rüppell's Parrot	Bre.					
Poicephalus senegalus	Senegal Parrot	Bre.		Int.	Obs.	Int.	Bre.
Primolius auricollis	Golden-collared Macaw	Int.					
Probosciger aterrimus	Palm Cockatoo				Obs.		
Psephotus haematonotus	Red-rumped Parrot	Int.					
Pseudeos fuscata	Dusky Lory	Int.					
Psittacara chloropterus	Hispaniolan Parakeet	Int.				Int.	Nat.
Psittacara erythrogenys	Red-masked Parakeet	Nat.	Nat.	Bre.	Nat.	Obs.	Nat.
Psittacara finschi	Finsch's Parakeet	Bre.	Nat.				
Psittacara holochlorus	Green Parakeet	Nat.	Nat.				
Psittacara leucophthalmus	White-eyed Parakeet	Bre.					
Psittacara mitratus	Mitred Parakeet	Nat.	Nat.	Nat.	Nat.	Bre.	Bre.
Psittacara wagleri	Scarlet-fronted Parakeet	Bre.	Nat.	Bre.			

Table A3. Status of parrots (Psittaciformes) in the USA recorded in the databases in this study compared with those in recent and in-depth studies and reviews, continued.

Scientific Name	**Common Name**	**Continental U.S.**		**Hawaiian Islands**		**Puerto Rico**	
		This Study	Uehling et al. 2019, 2021	This Study	VanderWerf & Kalodimos, 2021	This Study	Falcón & Tremblay, 2018
Psittacula alexandri	Red-breasted Parakeet	Int.					
Psittacula columboides	Blue-winged Parakeet	Int.					
Psittacula cyanocephala	Plum-headed Parakeet	Int.			Obs.		
Psittacula eupatria	Alexandrine Parakeet	Int.	Obs.	Int.			
Psittacula krameri	Rose-ringed Parakeet	Nat.	Nat.	Nat.	Nat.	Nat.	Bre.
Psittacula roseata	Blossom-headed Parakeet	Int.					
Psittacus erithacus	Grey Parrot	Int.	Obs.	Int.	Obs.	Int.	
Pyrrhura frontalis	Maroon-bellied Parakeet	Bre.					
Pyrrhura hoffmanni	Sulphur-winged Parakeet						Bre.
Pyrrhura leucotis	White-eared Parakeet		Nat.				
Pyrrhura molinae	Green-cheeked Parakeet	Bre.					Bre.
Pyrrhura rhodocephala	Rose-crowned Parakeet				Obs.		
Pyrrhura roseifrons	Rose-fronted Parakeet						Bre.
Rhynchopsitta pachyrhyncha	Thick-billed Parrot	Nat.	Obs.				
Rhynchopsitta terrisi	Maroon-fronted Parrot	Int.					
Strigops habroptila	Kakapo	Int.					
Thectocercus acuticaudatus	Blue-crowned Parakeet	Nat.	Nat.	Int.	Bre.	His.	Bre.
Trichoglossus chlorolepidotus	Scaly-breasted Lorikeet	Int.					
Trichoglossus haematodus	Coconut Lorikeet	Int.				Int.	
Trichoglossus moluccanus	Rainbow Lorikeet		Obs.				
Trichoglossus ornatus	Ornate Lorikeet	Int.					
Vini kuhlii	Kuhl's Lorikeet	Nat.					

Figure A1. Distribution of sightings of Monk Parakeets (*Myiopsitta monachus)* based on records in eBird and iNaturalist, outside of the native range of the species and subject to the criteria used in calculating the Area of Occupancy.

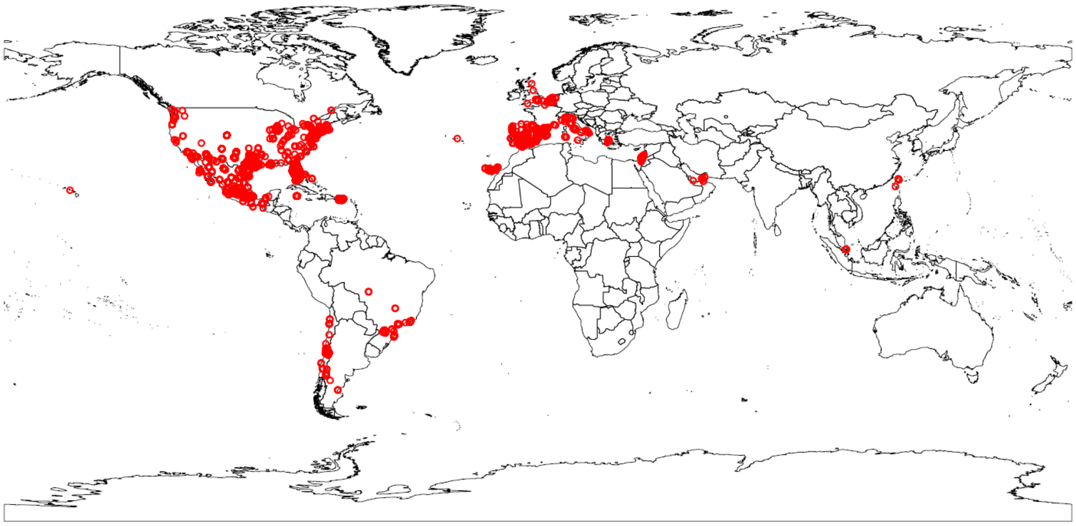


Figure A2. Distribution of sightings of Rose-ringed Parakeets (*Psittacula krameri)* based on records in eBird and iNaturalist, outside of the native range of the species and subject to the criteria used in calculating the Area of Occupancy.

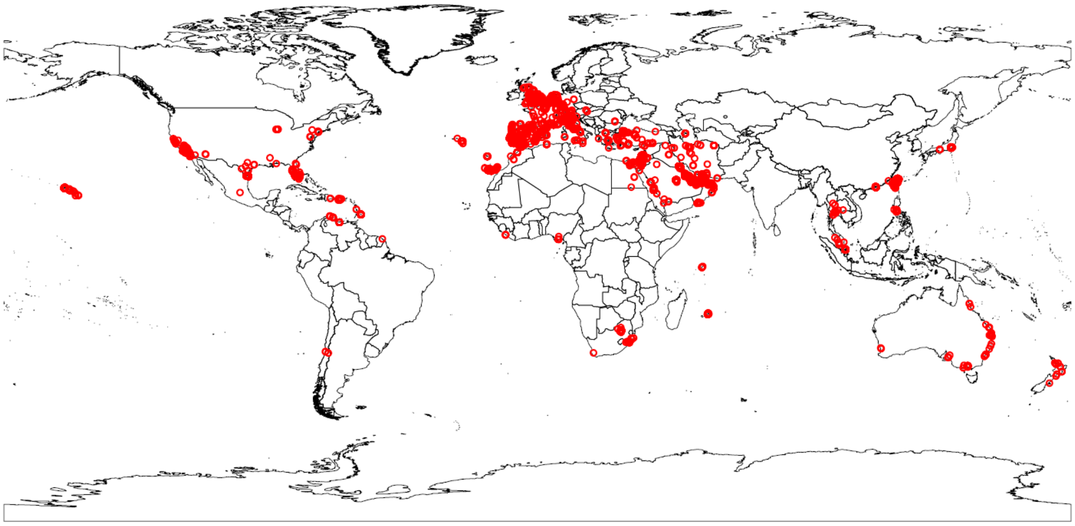


Figure A3. Distribution of sightings of Eastern Rosellas (*Platycercus eximus)* based on records in eBird and iNaturalist, outside of the native range of the species and subject to the criteria used in calculating the Area of Occupancy.

Figure A4. Distribution of sightings of Nanday Parakeets (*Aratinga nenday*) based on records in eBird and iNaturalist, outside of the native range of the species and subject to the criteria used in calculating the Area of Occupancy.

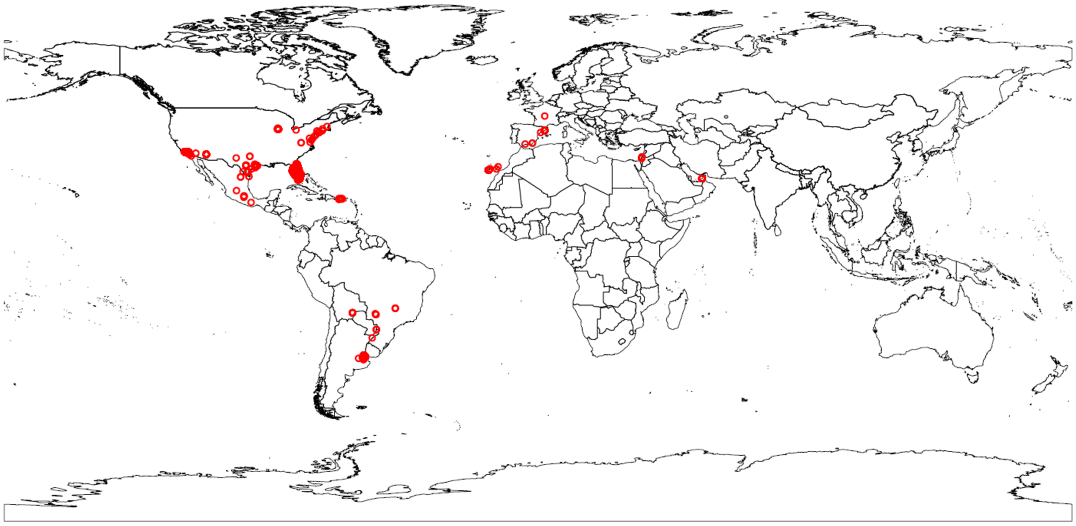
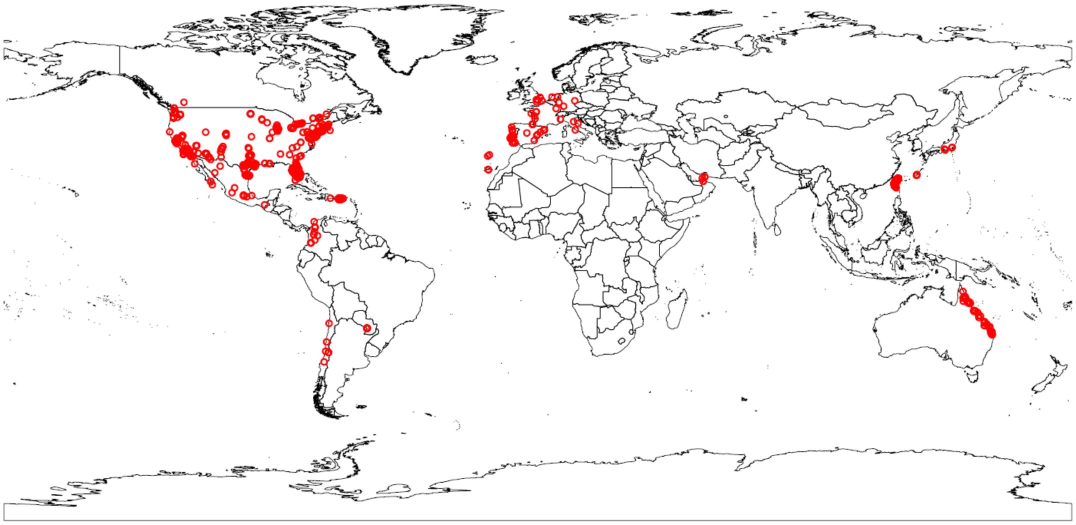


Figure A5. Distribution of sightings of Red-crowned Amazons (*Amazona viridigenalis*) based on records in eBird and iNaturalist, outside of the native range of the species and subject to the criteria used in calculating the Area of Occupancy.

Figure A6. Distribution of sightings of Budgerigar (*Melopsittacus undulatus*) based on records in eBird and iNaturalist, outside of the native range of the species and subject to the criteria used in calculating the Area of Occupancy.



Appendix B: Chapter 2 Data Tables and Supplementary Figures

Following is a collection of two data tables and 36 supplementary figures referred to in Chapter 2.

Table B1. Loadings for the Principal Components of the 19 Bioclimatic and elevational variables available from WorldClim.

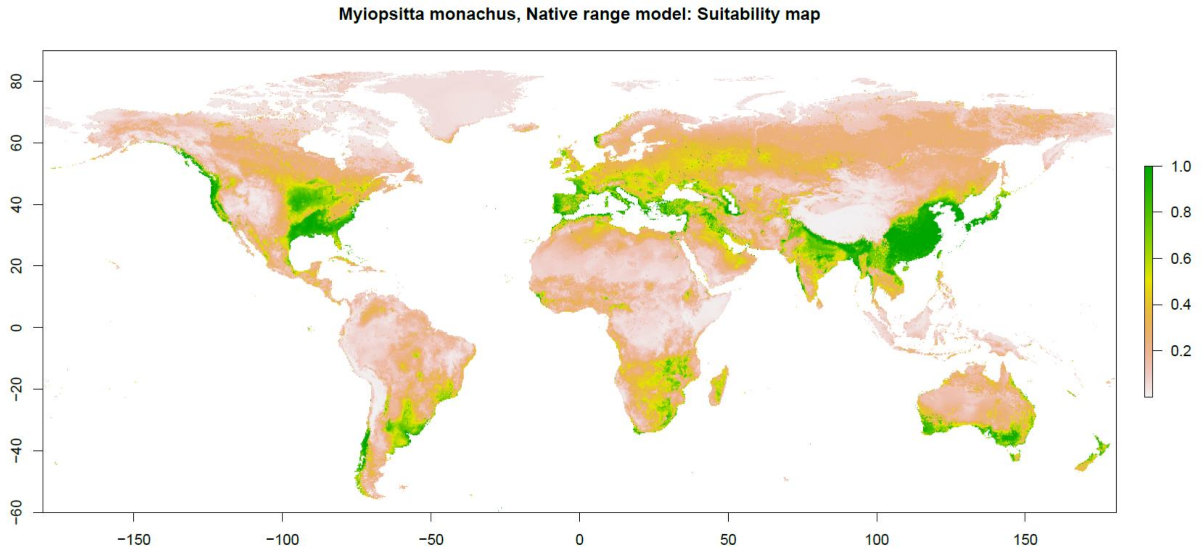
	PC1	PC2	PC3	PC4	PC5
Annual Mean Temperature (bio1)	0.310	0.181	0.029	0.140	0.092
Mean Diurnal Range (bio2)	-0.100	0.272	0.057	-0.203	0.438
Isothermality (bio3)	0.253	-0.092	-0.333	-0.060	0.307
Temperature Seasonality (bio4)	-0.271	0.137	0.385	0.038	-0.072
Max. Temperature of Warmest Month (bio5)	0.161	0.348	0.242	0.142	0.110
Min. Temperature of Coldest Month (bio6)	0.332	0.015	-0.157	0.158	-0.009
Temperature Annual Range (bio7)	-0.241	0.232	0.341	-0.069	0.088
Mean Temperature of Wettest Quarter (bio8)	0.241	0.184	0.192	0.042	0.279
Mean Temperature of Driest Quarter (bio9)	0.252	0.120	-0.164	0.204	-0.135
Mean Temperature of Warmest Quarter (bio10)	0.222	0.289	0.239	0.199	0.049
Mean Temperature of Coldest Quarter (bio11)	0.332	0.084	-0.125	0.098	0.083
Annual Precipitation (bio12)	0.244	-0.265	0.235	-0.157	-0.002
Precipitation of Wettest Month (bio13)	0.262	-0.082	0.244	-0.337	-0.238
Precipitation of Driest Month (bio14)	0.005	-0.370	0.185	0.227	0.306
Precipitation Seasonality (bio15)	0.171	0.304	-0.012	-0.265	-0.179
Precipitation of Wettest Quarter (bio16)	0.267	-0.108	0.248	-0.328	-0.198
Precipitation of Driest Quarter (bio17)	0.018	-0.372	0.194	0.221	0.301
Precipitation of Warmest Quarter (bio18)	0.169	-0.185	0.272	-0.201	0.277
Precipitation of Coldest Quarter (bio19)	0.148	-0.246	0.120	-0.022	-0.276
Elevation	-0.041	0.025	-0.254	-0.578	0.332

Table B2. Percentage of Variable Contribution to the Maxent models.

Species	Model Type	Land Use	PC1	PC2	PC3	PC4	PC5	Urban Dist.
Agapornis fischeri	Native	4.09	35.14	36.63	1.27	4.63	18.23	
Agapornis roseicollis	Native	18.93	7.44	19.35	20.74	21.36	12.19	
Amazona aestiva	Native	53.34	20.46	4.52	11.77	8.18	1.73	
Amazona albifrons	Native	3.66	31.39	20.71	6.91	9.06	28.26	
Amazona amazonica	Native	50.57	5.48	12.59	4.11	26.20	1.05	
Amazona autumnalis	Native	5.78	8.88	22.72	28.37	4.35	29.90	
Ara ararauna	Native	29.48	24.59	18.40	13.20	6.56	7.77	
Aratinga nenday	Native	24.79	36.06	16.60	11.42	8.77	2.36	
Brotogeris chiriri	Native	32.16	12.92	42.17	2.07	4.58	6.11	
Brotogeris versicolurus	Native	22.27	5.79	13.93	8.57	38.61	10.83	
Cacatua galerita	Native	13.42	4.75	65.80	4.29	1.24	10.49	
Cacatua galerita	Native-Urban	8.36	6.46	26.61	5.57	0.42	12.59	39.98
Cacatua galerita	Naturalized	7.48	19.97	12.57	6.91	47.58	5.49	
Cacatua galerita	Naturalized-Urban	12.78	8.64	1.78	9.18	39.84	4.50	23.29
Cacatua tenuirostris	Native	16.71	8.65	29.46	19.57	9.97	15.65	
Cacatua tenuirostris	Naturalized	22.24	8.90	32.40	0.99	22.03	13.44	
Eclectus polychloros	Native	3.68	51.09	4.05	8.54	18.09	14.55	
Forpus coelestis	Native	13.71	1.48	7.53	2.60	16.76	57.92	
Forpus passerinus	Native	20.94	62.03	1.41	4.56	9.20	1.86	
Forpus passerinus	Native-Urban	3.50	5.75	1.03	2.95	0.69	0.44	85.64
Forpus passerinus	Naturalized	7.20	7.99	12.23	15.73	52.32	4.53	
Forpus passerinus	Naturalized-Urban	3.35	9.39	6.18	3.55	25.93	1.38	50.22
Melopsittacus undulatus	Native	13.67	6.82	4.69	5.30	18.86	50.66	
Myiopsitta monachus	Native	45.47	13.27	10.24	5.51	7.04	18.47	
Nymphicus hollandicus	Native	25.59	7.22	41.87	8.07	10.91	6.35	
Platycercus eximius	Native	14.14	1.53	58.54	9.94	14.76	1.09	
Psittacara erythrogenys	Native	12.65	18.19	11.85	1.23	1.85	54.24	
Psittacara holochlorus	Native	16.08	43.38	4.05	5.05	21.96	9.49	
Psittacara holochlorus	Native-Urban	5.47	41.42	6.19	5.62	13.87	5.14	22.30
Psittacara holochlorus	Naturalized	13.24	3.10	0.23	8.08	53.73	21.63	
Psittacara holochlorus	Naturalized-Urban	5.36	1.23	1.71	1.40	30.20	8.00	52.11
Psittacara mitratus	Native	8.41	43.74	3.38	5.04	29.01	10.42	
Psittacara mitratus	Naturalized	69.82	4.07	4.02	2.12	3.56	16.42	
Psittacula eupatria	Native	44.05	30.93	4.44	6.30	12.51	1.77	
Psittacula krameri	Native	37.95	28.90	17.81	3.88	6.22	5.24	
Psittacus erithacus	Native	21.77	13.03	20.38	20.50	16.61	7.71	
Psittacus erithacus	Naturalized	38.95	9.03	26.98	6.39	10.62	8.04	
Thectocercus acuticaudatus	Native	33.19	15.41	4.18	16.47	28.97	1.79	
Trichoglossus moluccanus	Native	13.72	24.89	57.30	2.02	1.45	0.62	

Figure B1. Suitability map a) of native range model for *Myiopsitta monachus* predicted across the entire globe. b) The same suitability map but overlaid with training and test data points and the occurrences for the species in the non-native range.

B1a)



B1b)

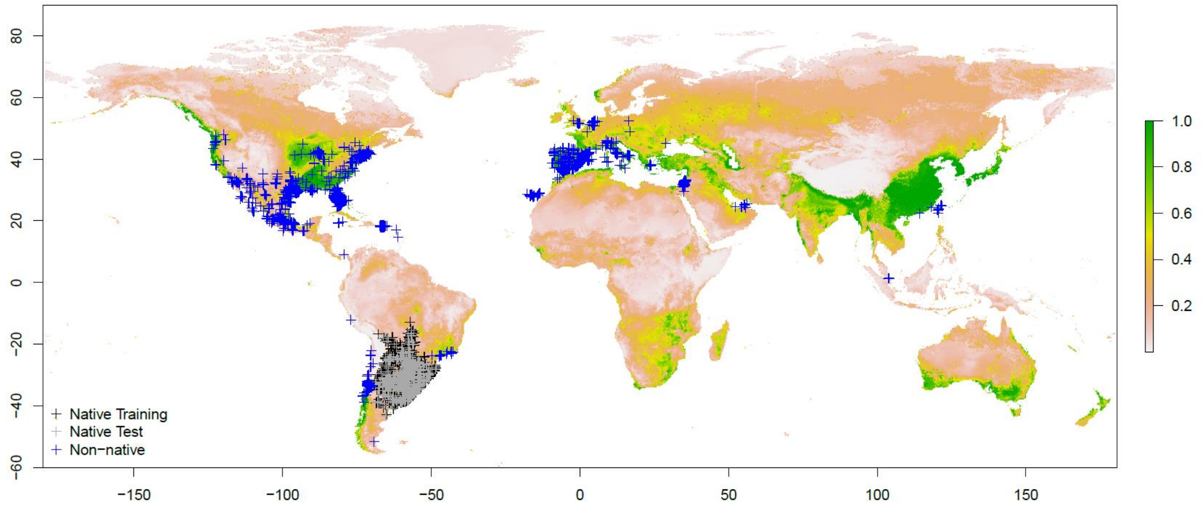
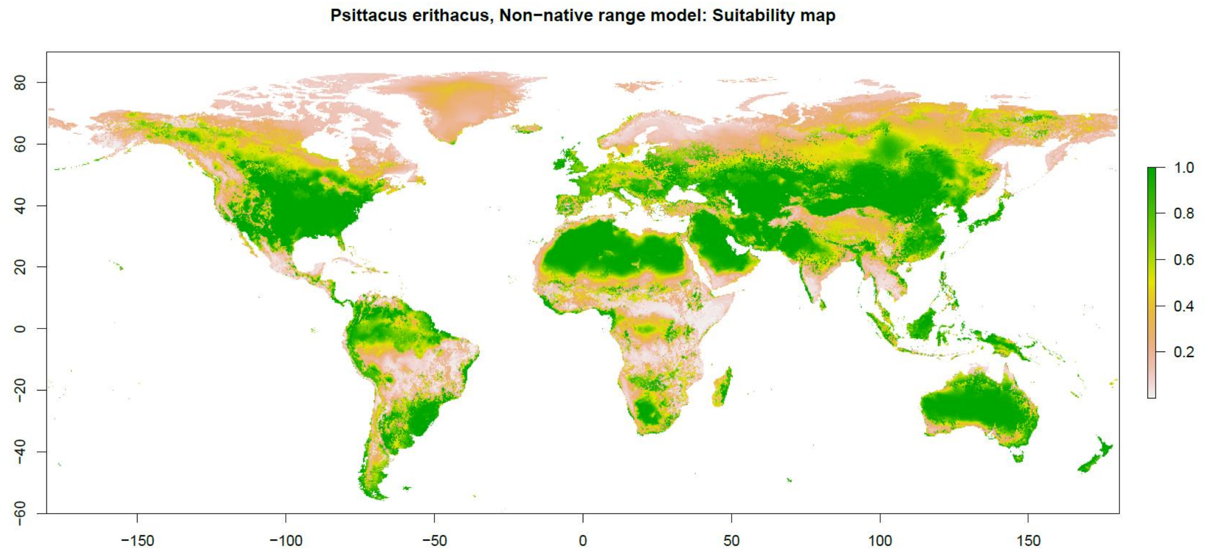


Figure B2. Suitability map a) of non-native range model for *Psittacus erithacus* predicted across the entire globe. b) The same suitability map but overlaid with training and test data points and the occurrences for the species in the non-native range.

B2a)



B2b)

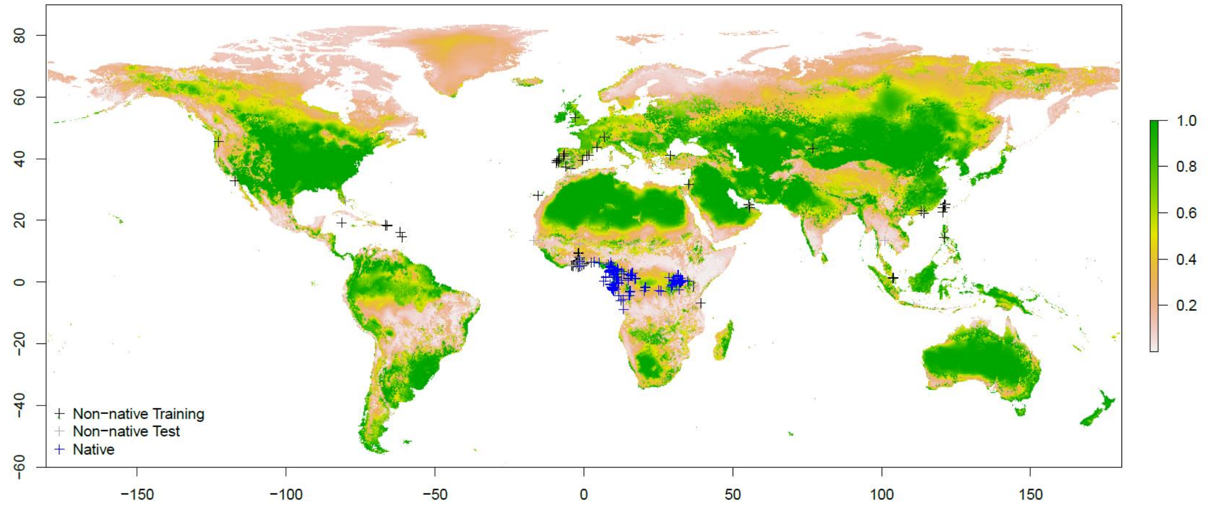
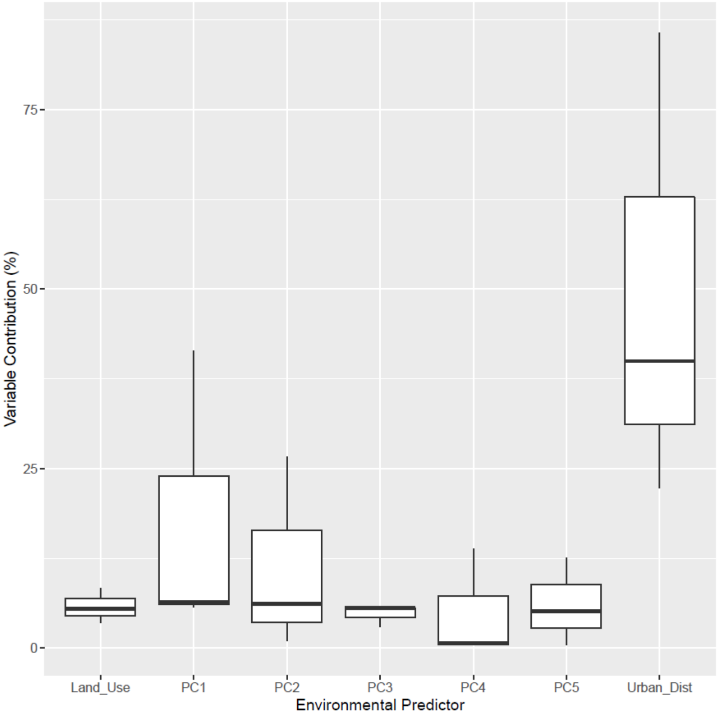


Figure B3. Variable contributions to the species distribution models of three species (*Cacatua galerita*, *Forpus passerinus*, *Psittacara holochlorus*) trained using a) native range occurrences and b) non-native range occurrences that include distance from urban centers (Urban_Dist) as an environmental predictor.

B3a)



B3b)

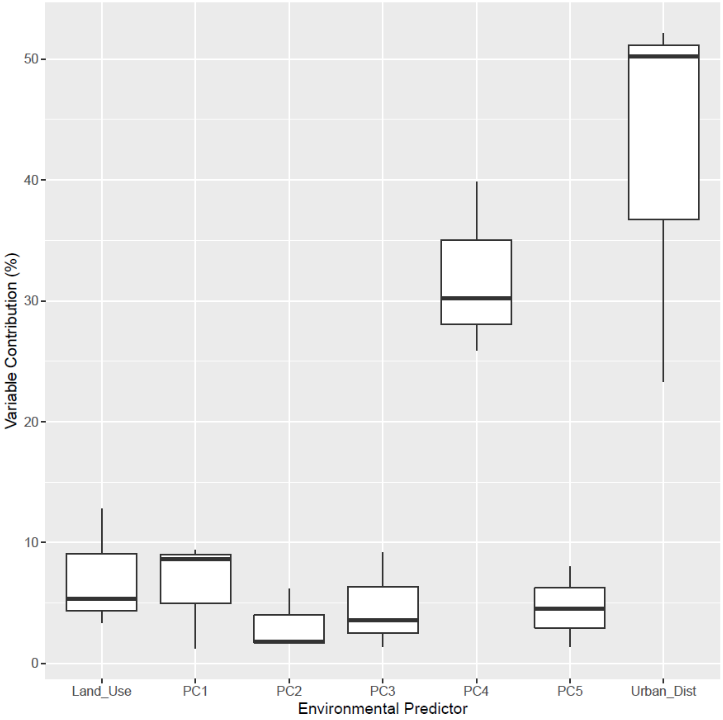
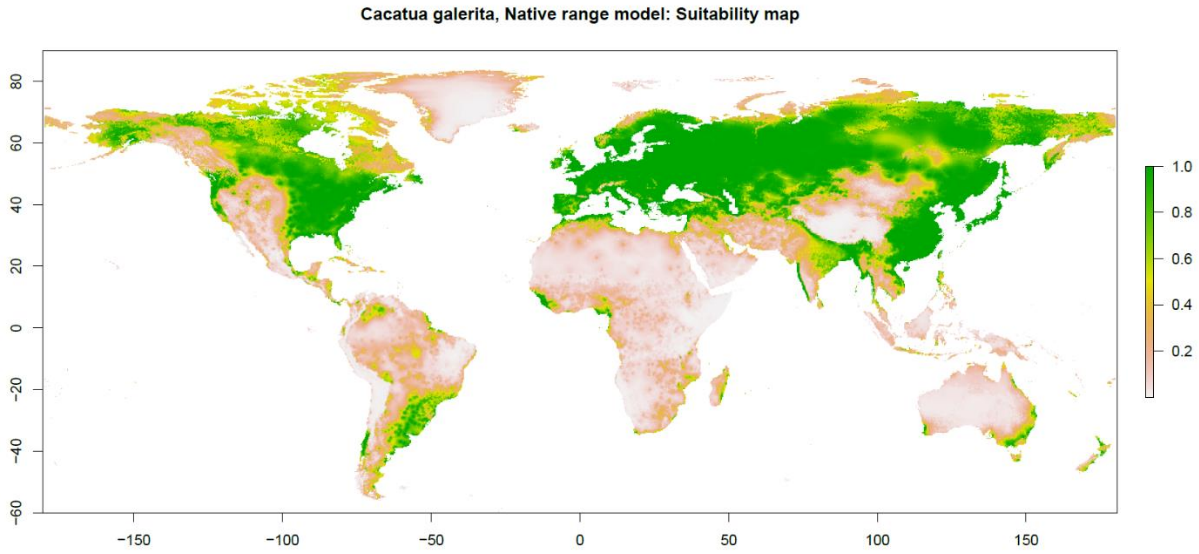


Figure B4. Comparison of suitability maps for *Cacatua galerita* with the a) native range model, b) with occurrence data overlaid and the c) non-native range models, d) with occurrence data overlaid.

B4a)



B4b)

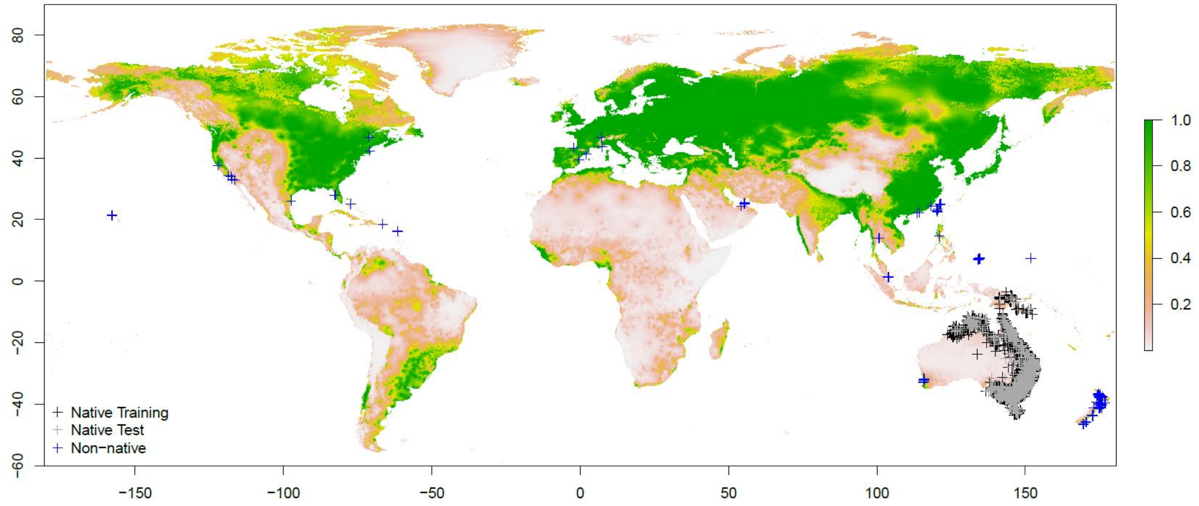
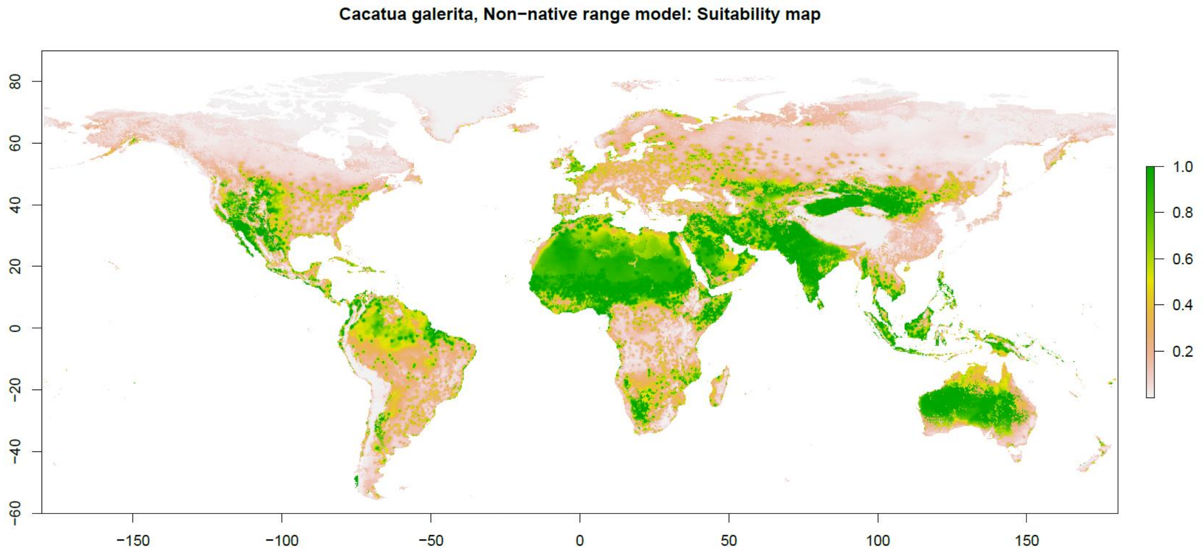
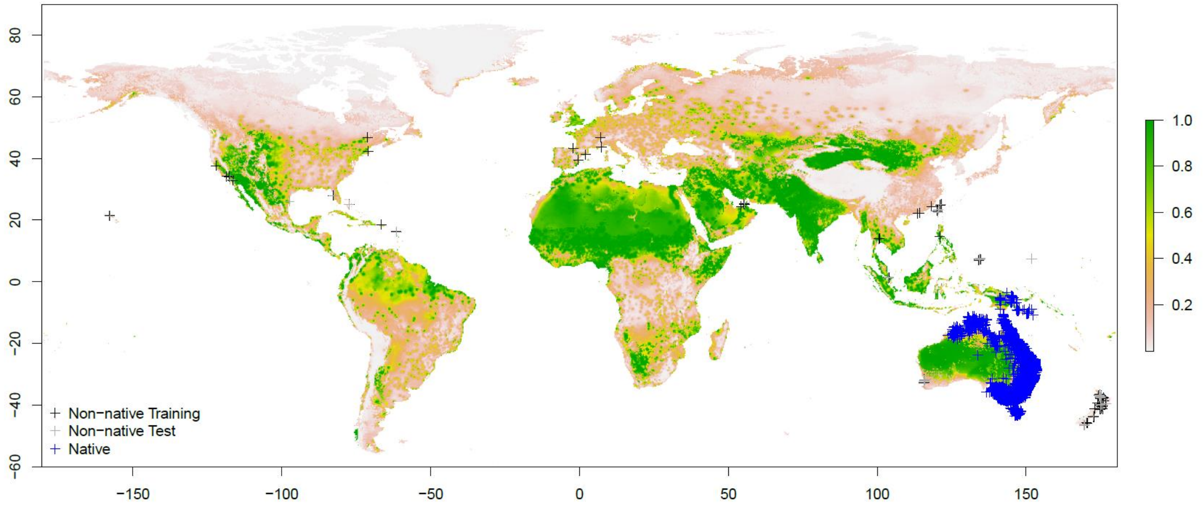


Figure B4. Comparison of suitability maps for *Cacatua galerita* with the a) native range model, b) with occurrence data overlaid and the c) non-native range models, d) with occurrence data overlaid, continued.

B4c)

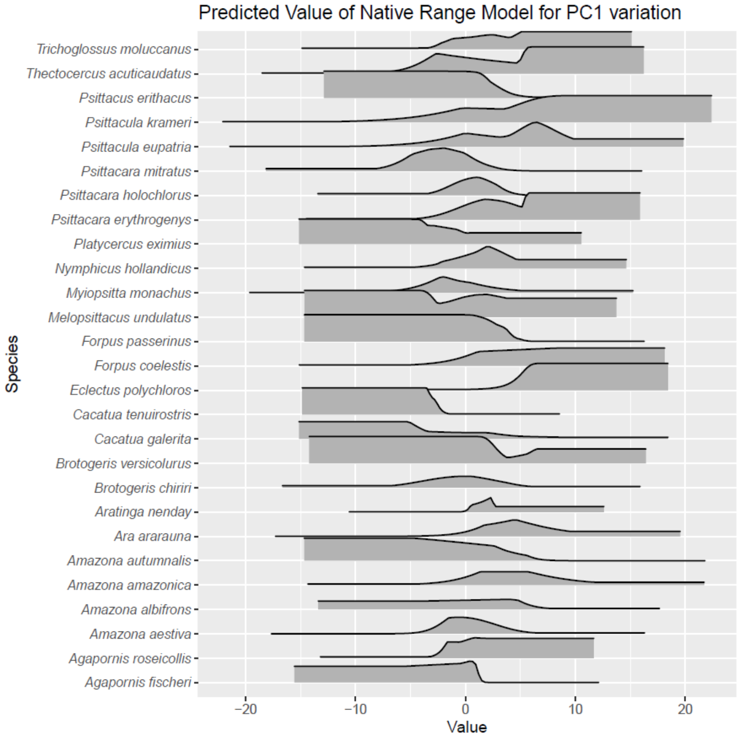


B4d)

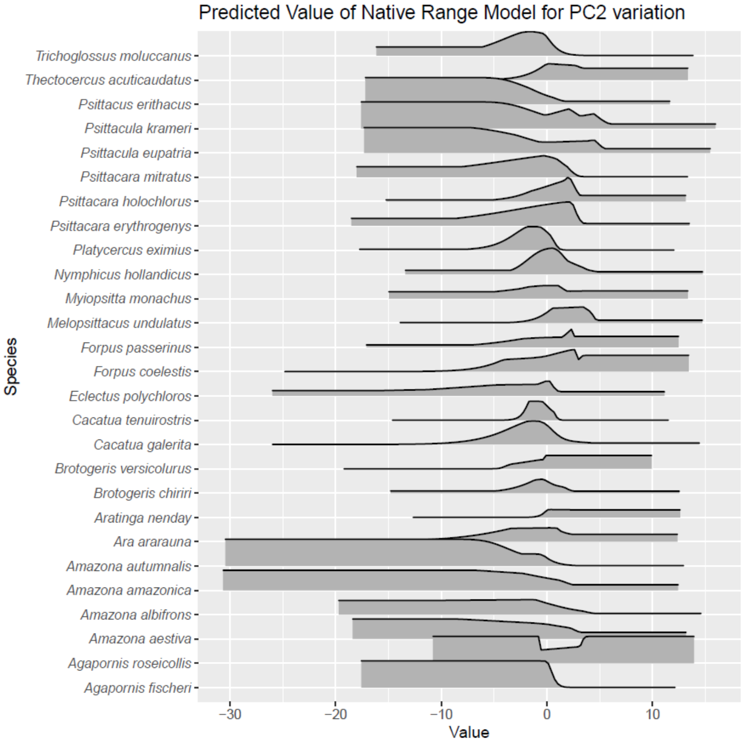


Figures B5a-f. Visual representations of Native Range Model's Predicted Value for each Environmental Predictor.

B5a)

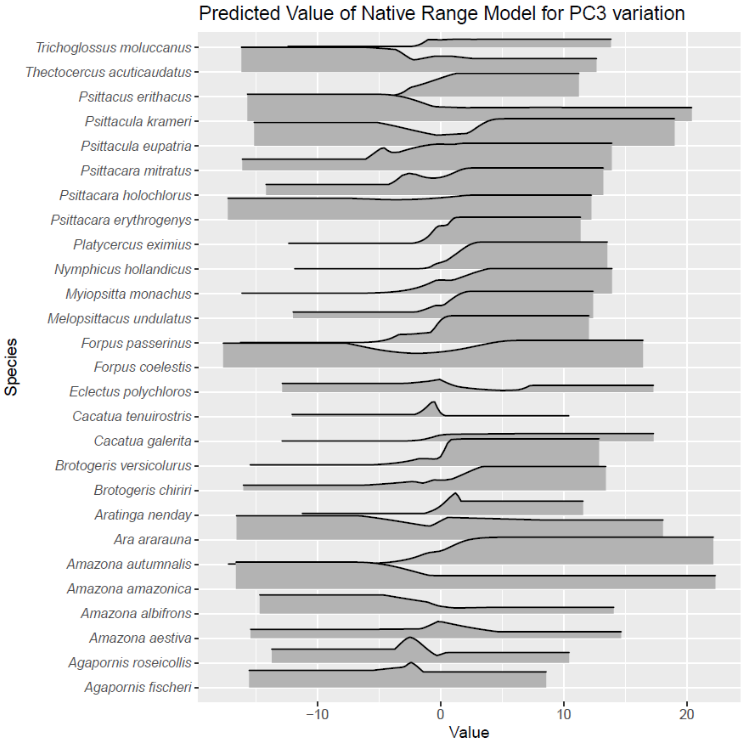


B5b)

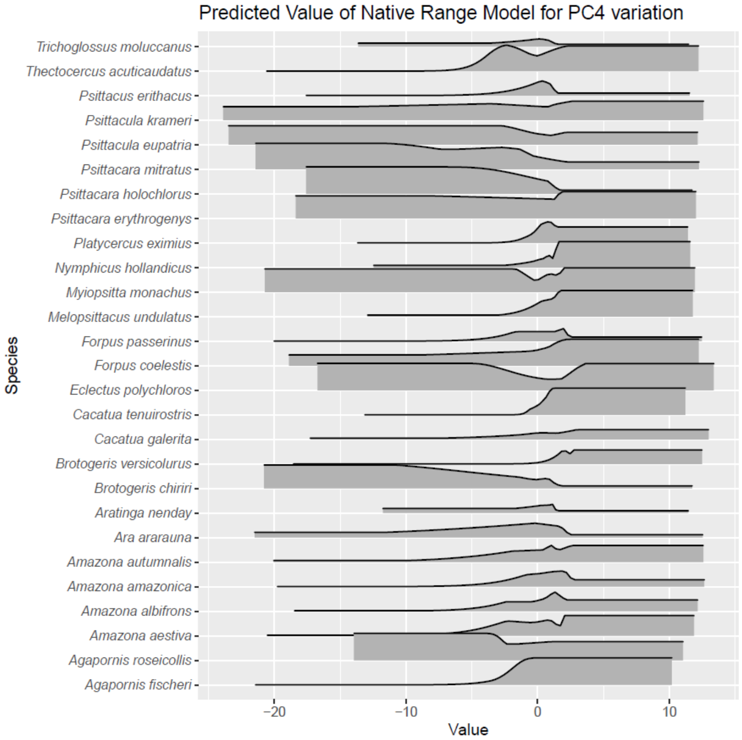


Figures B5a-f. Visual representations of Native Range Model's Predicted Value for each Environmental Predictor, continued.

B5c)

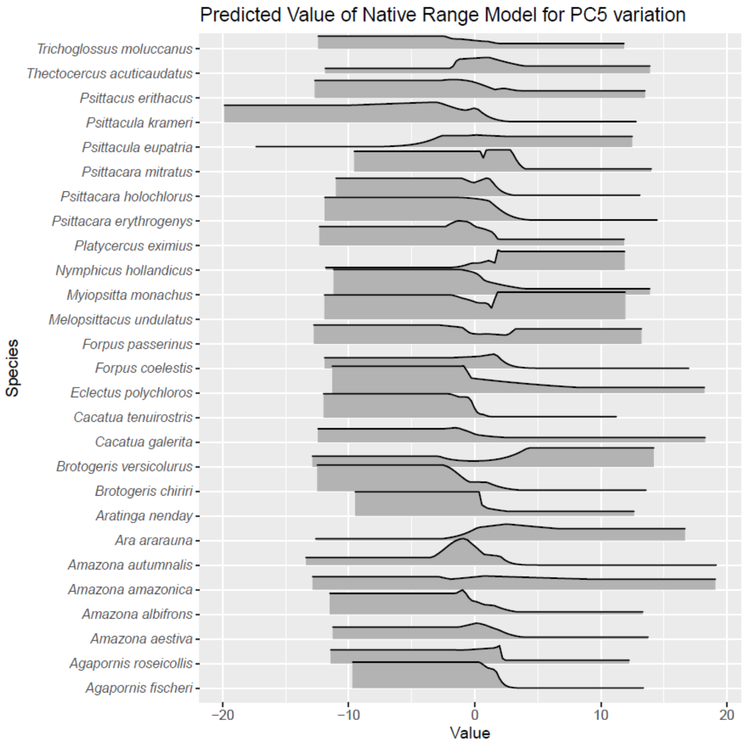


B5d)

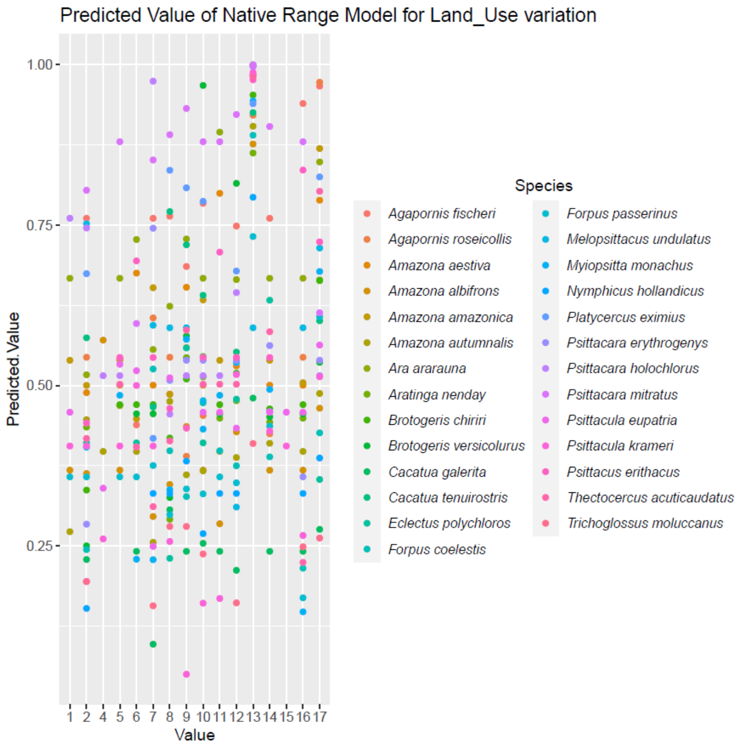


Figures B5a-f. Visual representations of Native Range Model's Predicted Value for each Environmental Predictor, continued.

B5e)



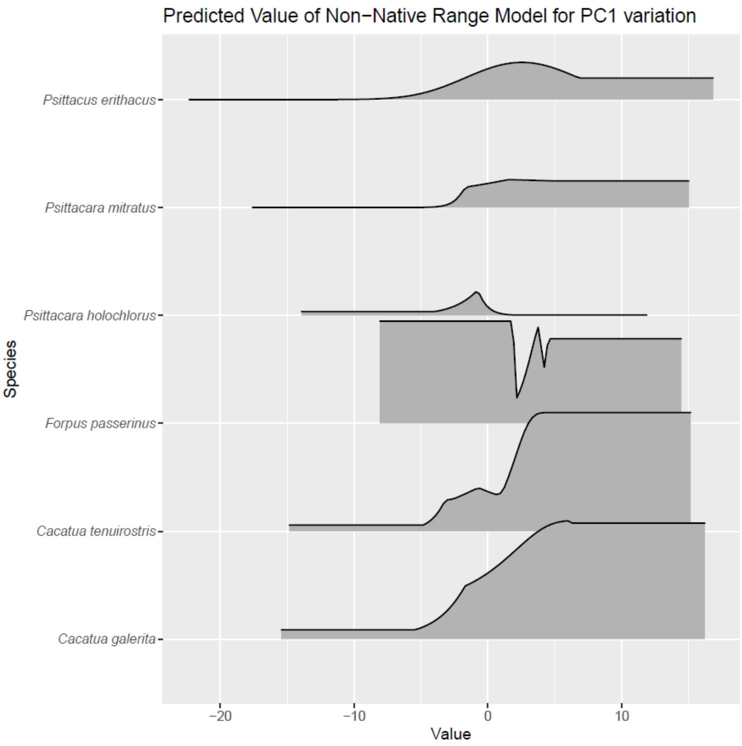
B5f)



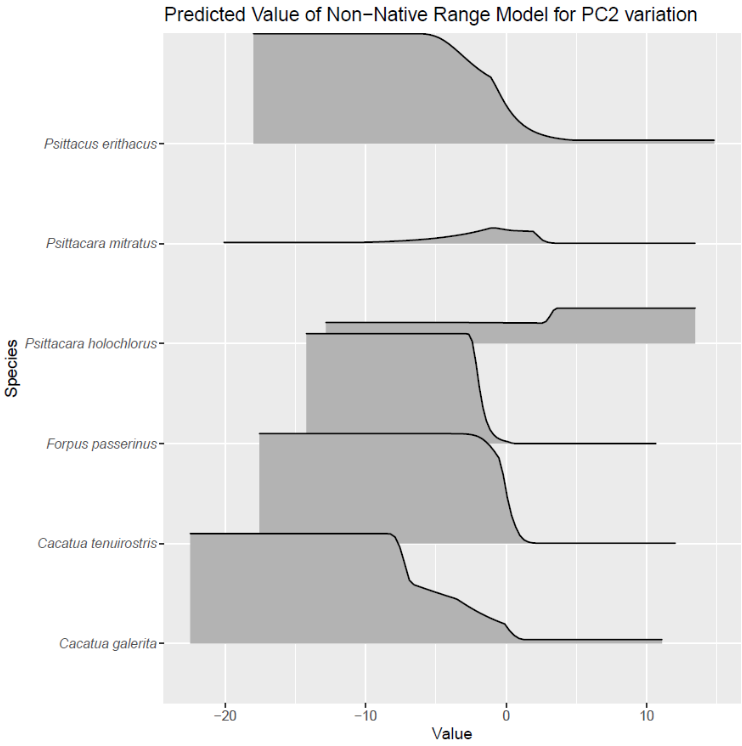
1 = Evergreen Needleleaf Forest
2 = Evergreen Broadleaf Forest
3 = Deciduous Needleleaf Forest
4 = Deciduous Broadleaf Forest
5 = Mixed Forest
6 = Closed Shrublands
7 = Open Shrublands
8 = Woody Savannas
9 = Savannas
10 = Grasslands
11 = Permanent Wetlands
12 = Croplands
13 = Urban and Built-Up
14 = Cropland/Natural Vegetation Mosaic
15 = Snow and Ice
16 = Barren or Sparsely Vegetated
17 = Water Bodies
100 = Missing Data

Figures B6a-f. Visual representations of Non-native Range Models Predicted Value for each Environmental Predictor.

B6a)

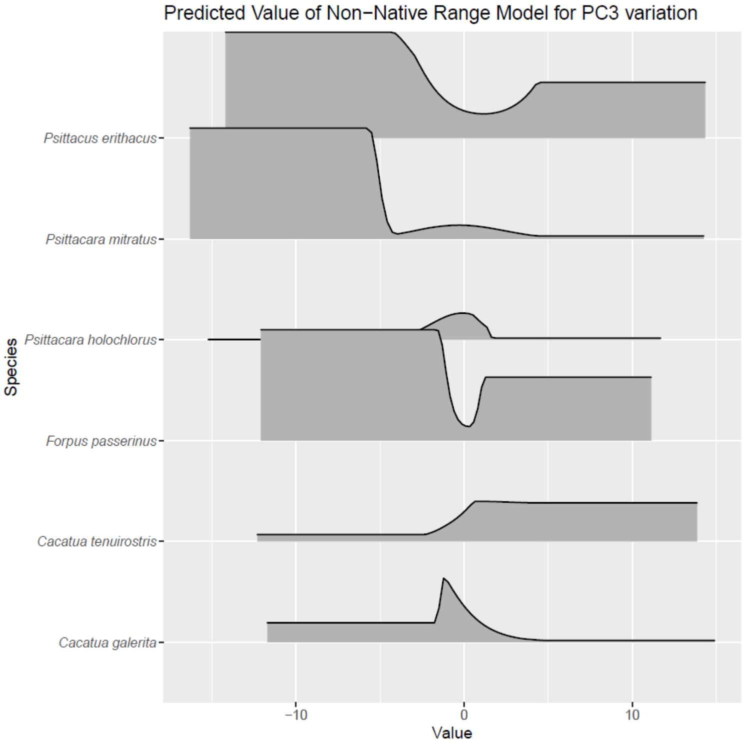


B6b)

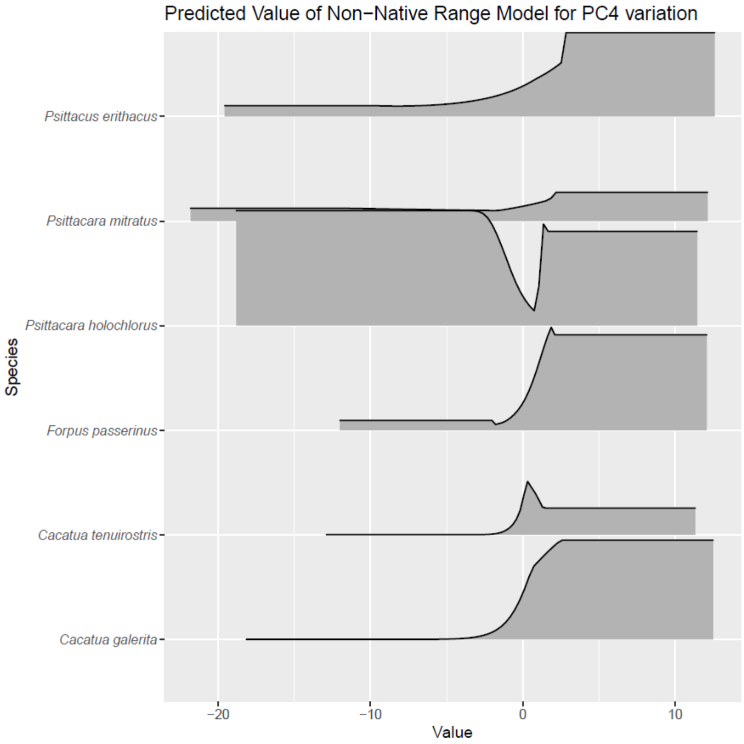


Figures B6a-f. Visual representations of Non-native Range Models Predicted Value for each Environmental Predictor, continued.

B6c)

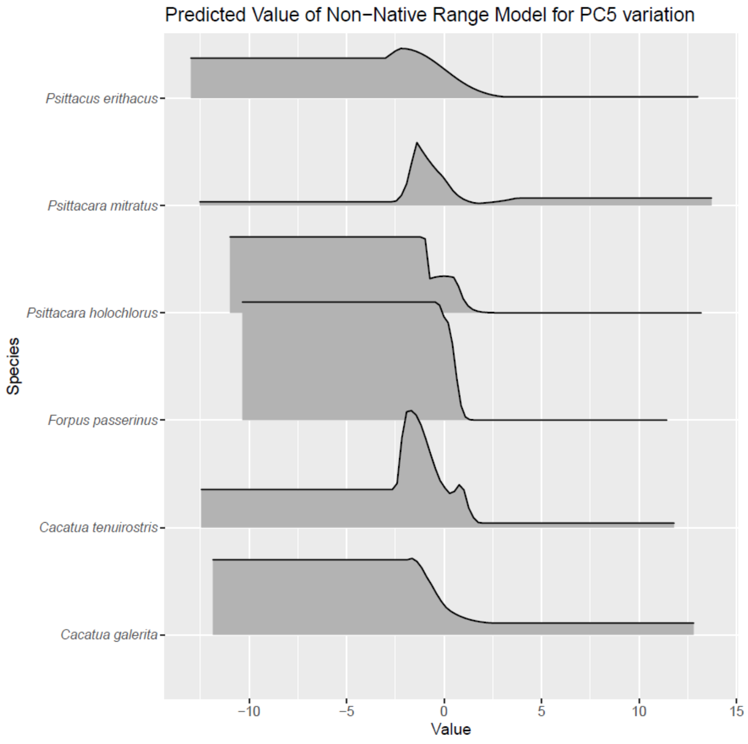


B6d)

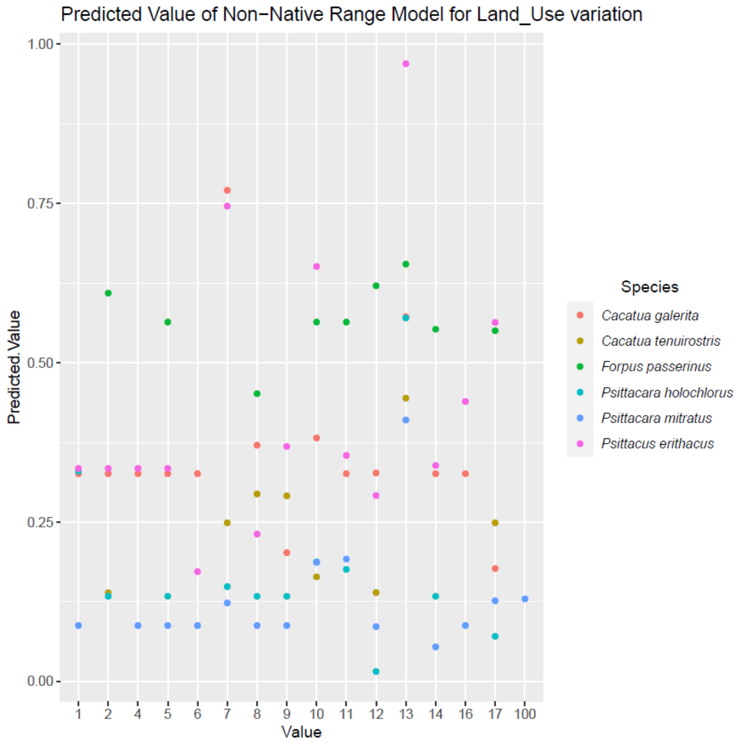


Figures B6a-f. Visual representations of Non-native Range Models Predicted Value for each Environmental Predictor, continued.

B6e)



B6f)



1 = Evergreen Needleleaf Forest
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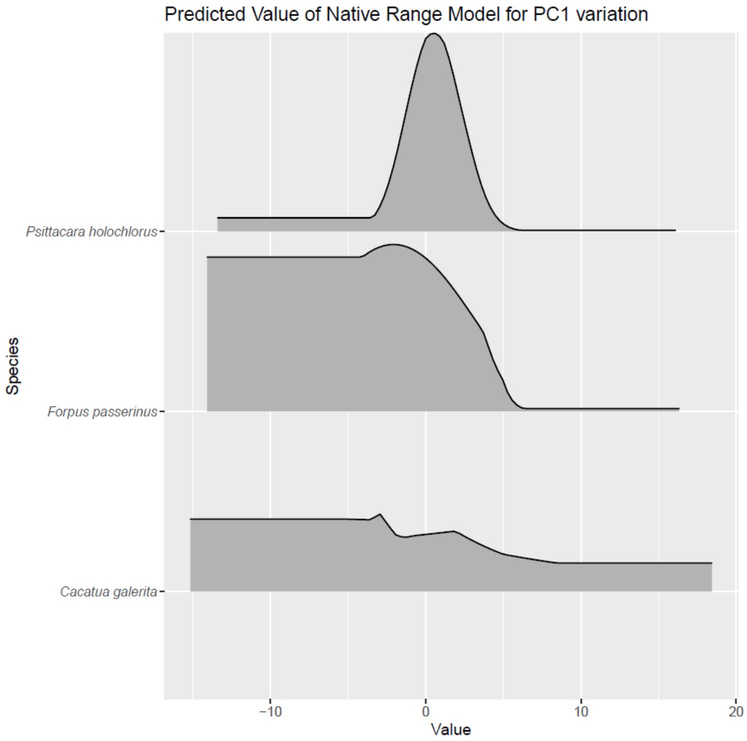
4 = Deciduous Broadleaf Forest
5 = Mixed Forest
6 = Closed Shrublands
7 = Open Shrublands
8 = Woody Savannas
9 = Savannas
10 = Grasslands
11 = Permanent Wetlands
12 = Croplands
13 = Urban and Built-Up
14 = Cropland/Natural Vegetation Mosaic
15 = Snow and Ice
16 = Barren or Sparsely Vegetated
17 = Water Bodies
100 = Missing Data

Figure B7a-n. Visual representations of Native and Non-native Range Models Predicted Value for each Environmental Predictor when Urban_Dist environmental layer is included.

B7a)



B7b)

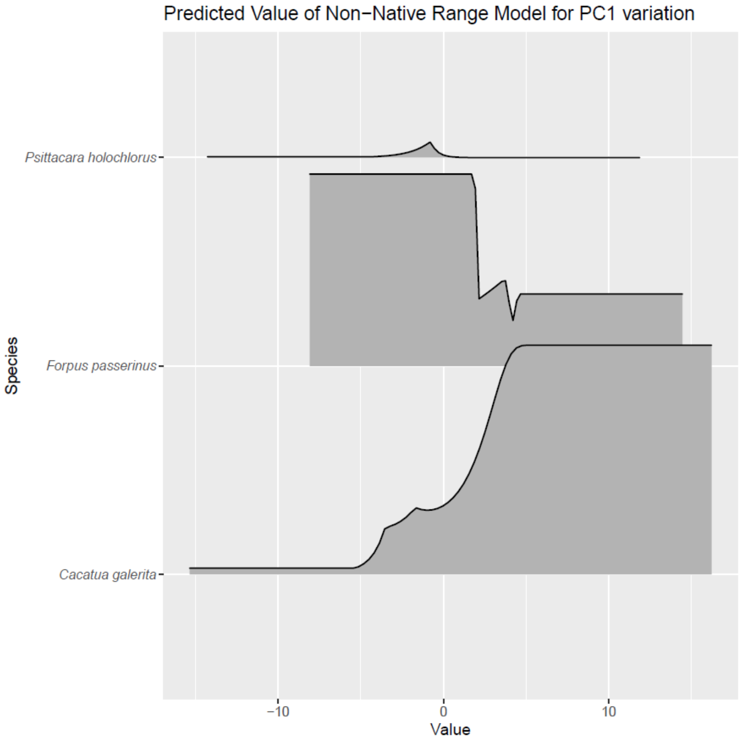
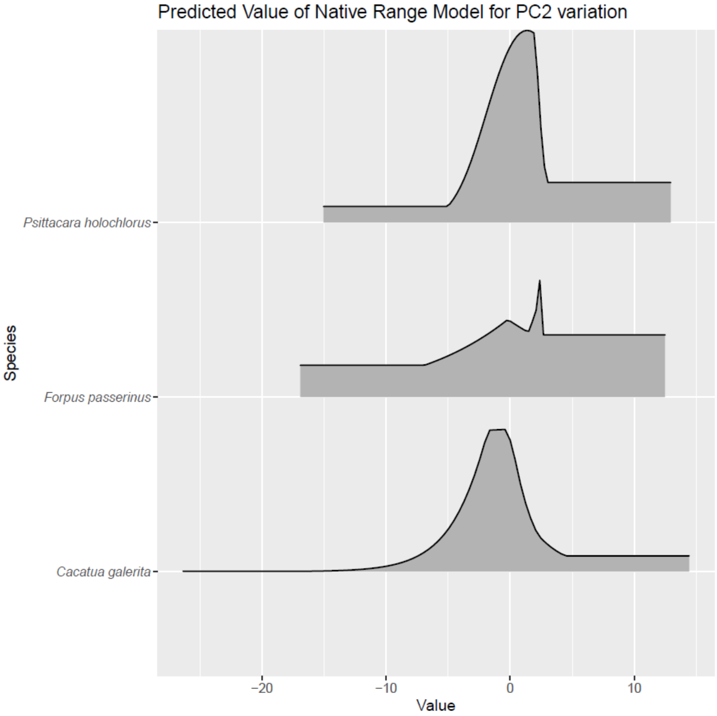


Figure B7a-n. Visual representations of Native and Non-native Range Models Predicted Value for each Environmental Predictor when Urban_Dist environmental layer is included, continued.

B7c)



B7d)

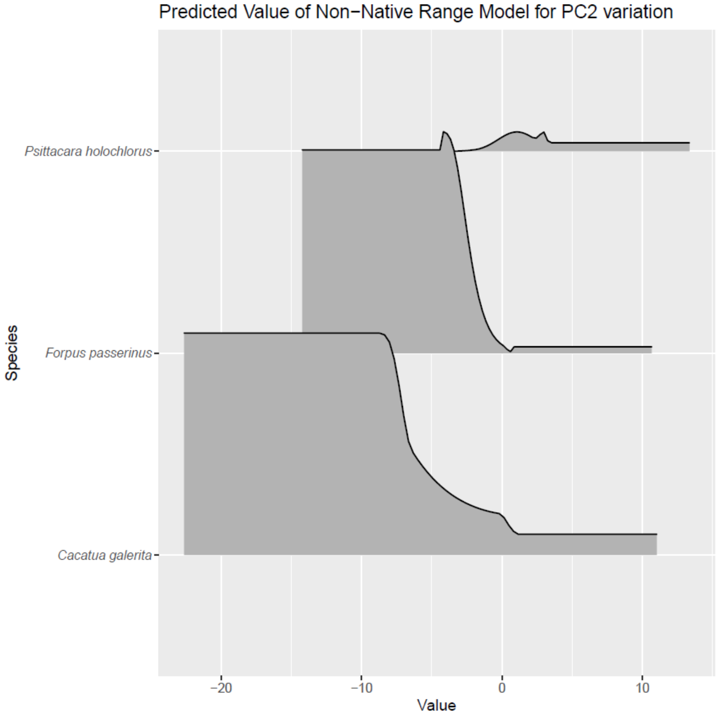
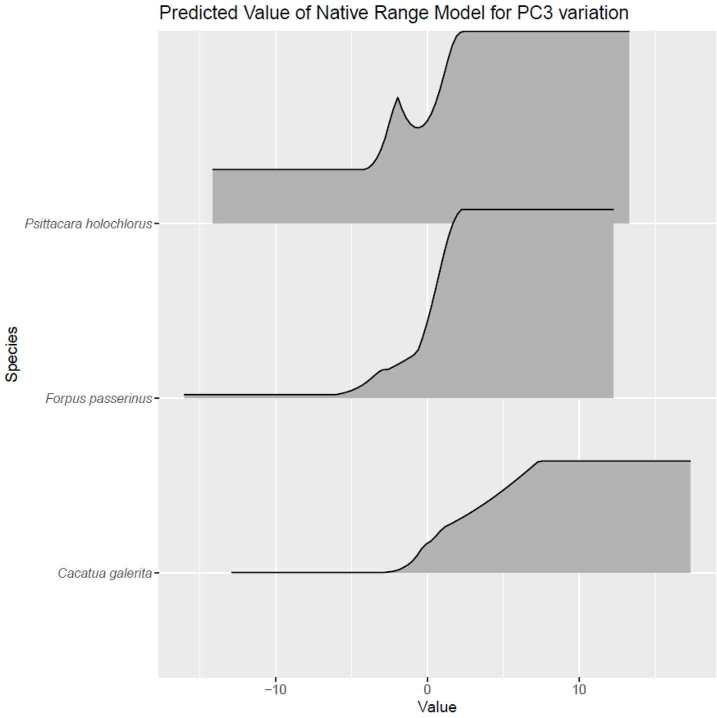


Figure B7a-n. Visual representations of Native and Non-native Range Models Predicted Value for each Environmental Predictor when Urban_Dist environmental layer is included, continued.

B7e)



B7f)

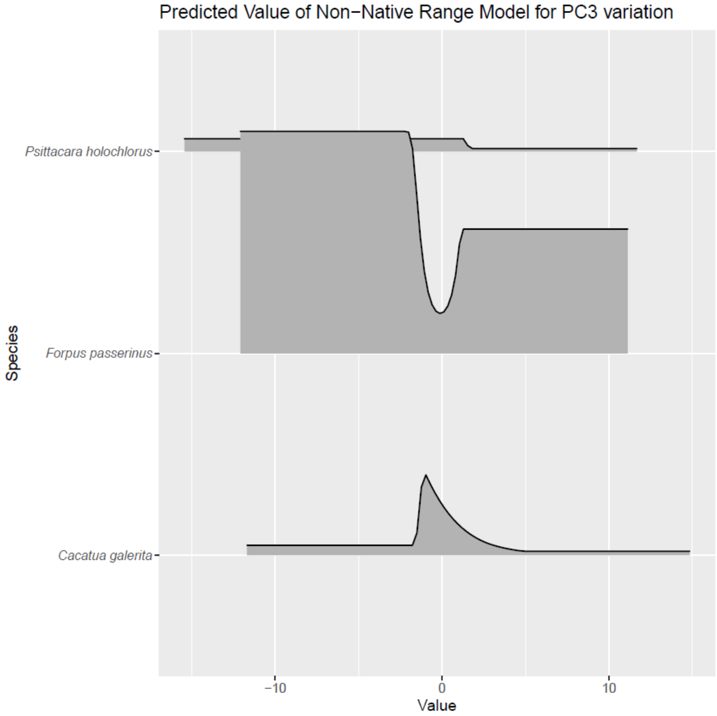
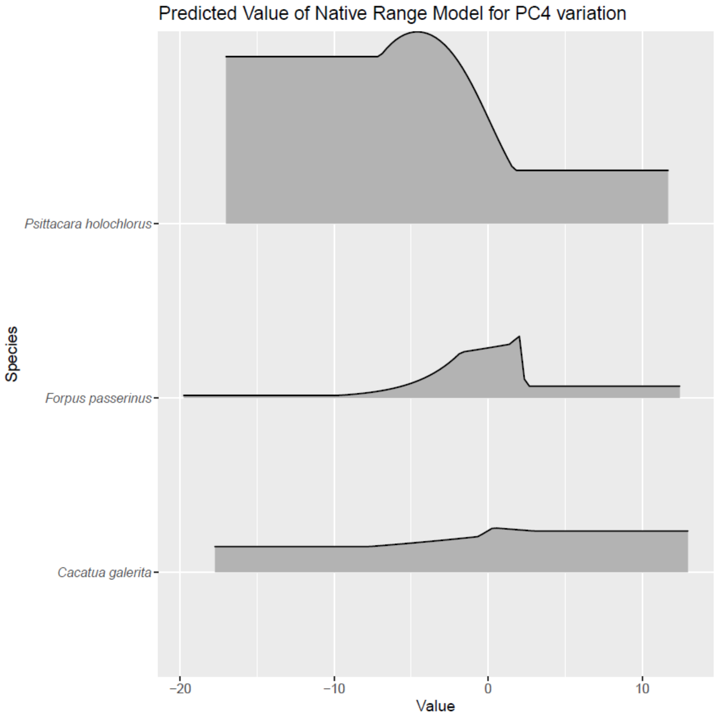


Figure B7a-n. Visual representations of Native and Non-native Range Models Predicted Value for each Environmental Predictor when Urban_Dist environmental layer is included, continued.

B7g)



B7h)

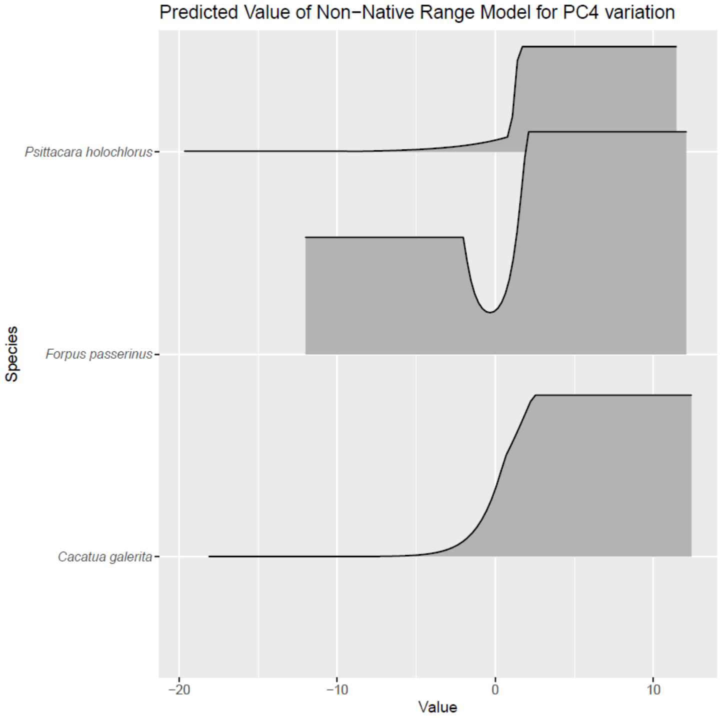
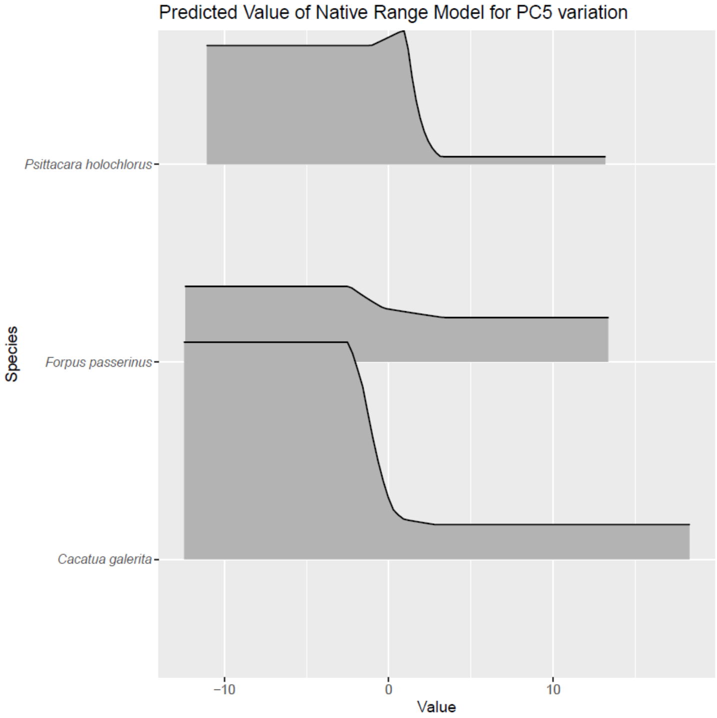


Figure B7a-n. Visual representations of Native and Non-native Range Models Predicted Value for each Environmental Predictor when Urban_Dist environmental layer is included, continued.
B7i)



B7j)

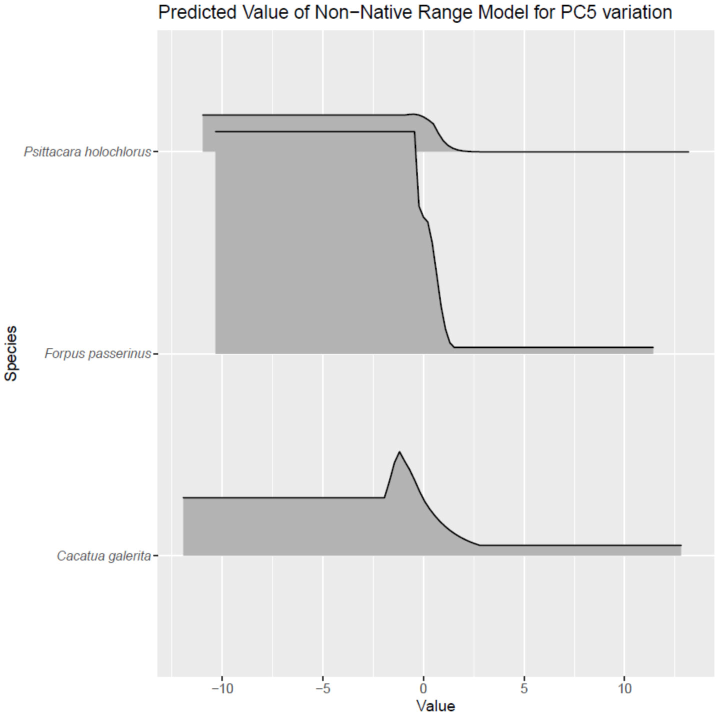
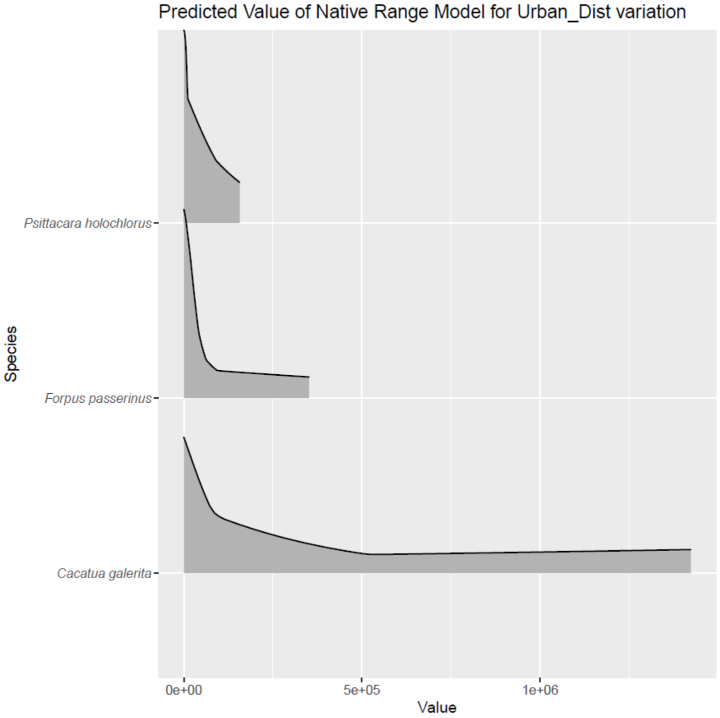


Figure B7a-n. Visual representations of Native and Non-native Range Models Predicted Value for each Environmental Predictor when Urban_Dist environmental layer is included, continued.

B7k)



B7l)

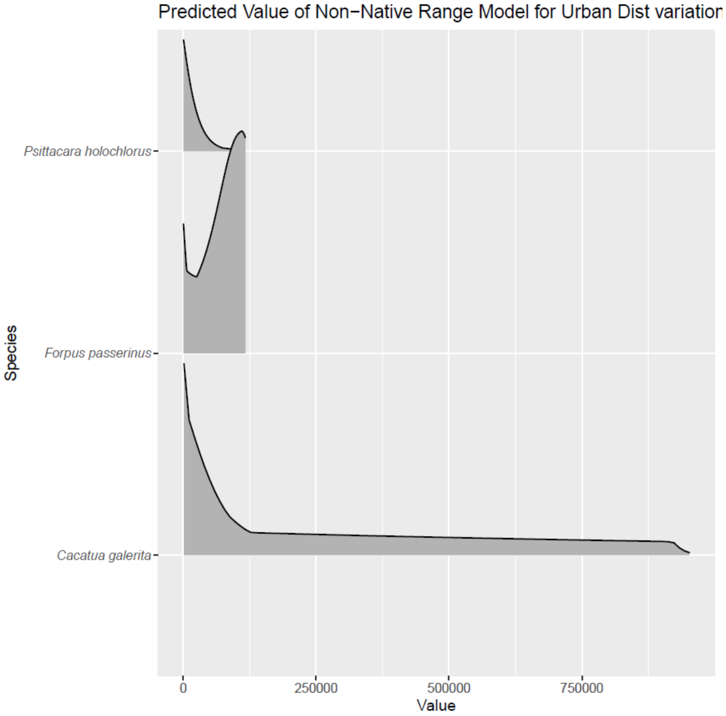
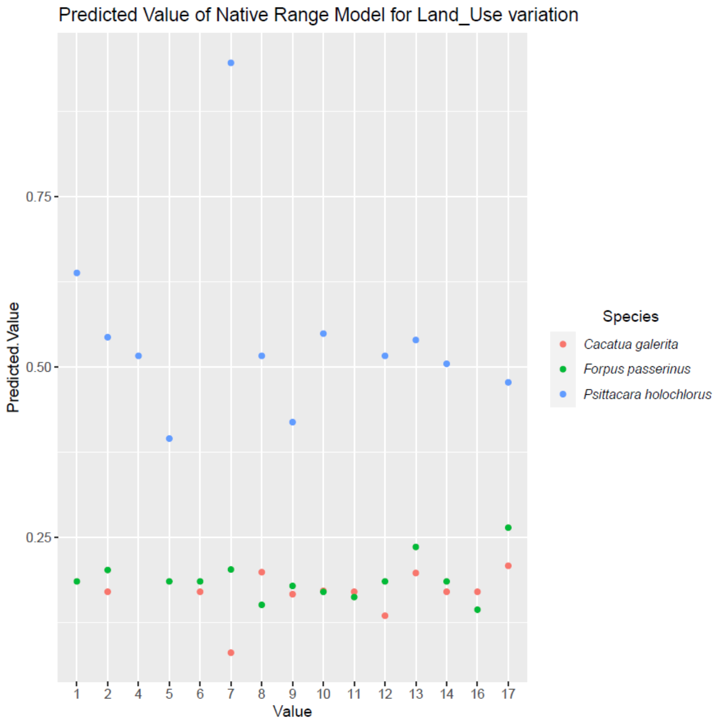


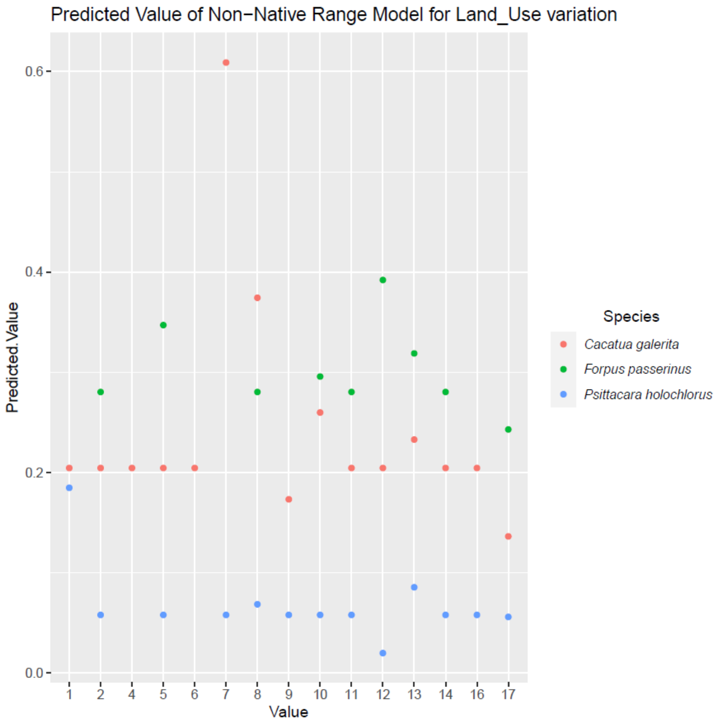
Figure B7a-n. Visual representations of Native and Non-native Range Models Predicted Value for each Environmental Predictor when Urban_Dist environmental layer is included, continued.

B7m)



1 = Evergreen Needleleaf Forest
2 = Evergreen Broadleaf Forest
3 = Deciduous Needleleaf Forest
4 = Deciduous Broadleaf Forest
5 = Mixed Forest
6 = Closed Shrublands
7 = Open Shrublands
8 = Woody Savannas
9 = Savannas
10 = Grasslands
11 = Permanent Wetlands
12 = Croplands
13 = Urban and Built-Up
14 = Cropland/Natural Vegetation Mosaic
15 = Snow and Ice
16 = Barren or Sparsely Vegetated
17 = Water Bodies
100 = Missing Data

B7n)



1 = Evergreen Needleleaf Forest
2 = Evergreen Broadleaf Forest
3 = Deciduous Needleleaf Forest
4 = Deciduous Broadleaf Forest
5 = Mixed Forest
6 = Closed Shrublands
7 = Open Shrublands
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9 = Savannas
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12 = Croplands
13 = Urban and Built-Up
14 = Cropland/Natural Vegetation Mosaic
15 = Snow and Ice
16 = Barren or Sparsely Vegetated
17 = Water Bodies
100 = Missing Data

Appendix C: Chapter 3 Data Tables and Supplementary Figures

Following is a collection of two data tables and two supplementary figures referred to in Chapter 3.

Figure C1. Values of Delta K for their corresponding K cluster value.

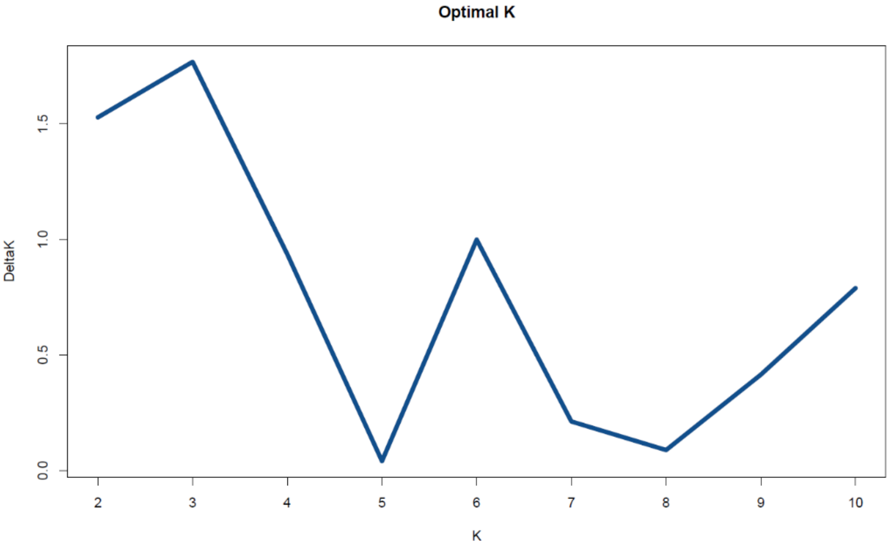

Figure C2. Map of the admixture proportions clusters within the native range with major rivers overlaid (Source: mapdata R package).

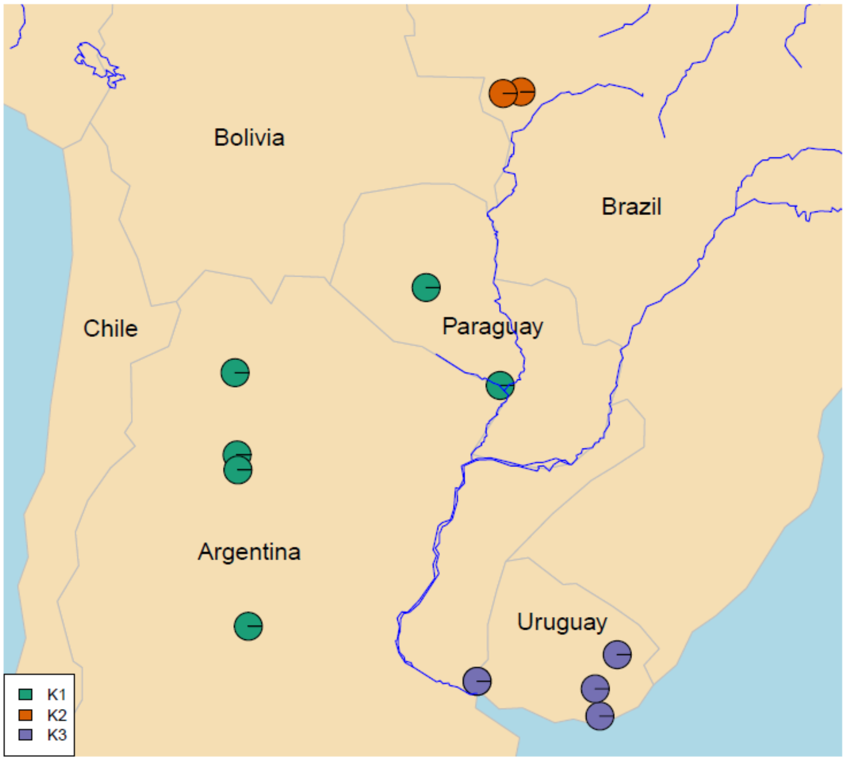

Table C1. List of native range samples and their associated locality and collection information.

Sample ID	Year	Country	Locality	Sub-species	Sex	Institution ID	Mean Coverage	Library Type
FMNH 64410	1927	Brazil	Mato Grosso: Descalvado	cotorra	Male	FMNH	7.9X	WGS
FMNH 296940	1973	Brazil	Mato Grosso: Rio Claro	cotorra	Male	FMNH	9.5X	WGS
FMNH 152012	1944	Paraguay	Chaco: Rio Pilcomayo	cotorra	Female	FMNH	8.6X	WGS
FMNH 152841	1945	Paraguay	Boqueron: Colonia Fernheim	cotorra	Female	FMNH	8.3X	WGS
FMNH 56578	1903	Argentina	Tucuman: Estacion Rio Colorado	calita	Female	FMNH	7.8X	WGS
FMNH 57390	1915	Argentina	Cordoba: El Carrizal	calita	Male	FMNH	8.8X	WGS
FMNH 58142	1918	Argentina	Tucuman: Toro Muerto	calita	Male	FMNH	7.1X	WGS
FMNH 255946	1956	Argentina	Salta	calita	Female	FMNH	9.4X	WGS
FMNH 48994	1908	Argentina	Buenos Aires: General Lavalle	monachus	Female	FMNH	9.8X	WGS
FMNH 64401	1926	Uruguay	Maldonado: Estancia El Corte	monachus	Male	FMNH	7.6X	WGS
FMNH 64403	1926	Uruguay	Treinta y Tres: Quebrada de los Cuervos	monachus	Female	FMNH	11.0X	WGS
FMNH 64404	1926	Uruguay	Lavalleja: Arroyo Polanco	monachus	Male	FMNH	9.9X	WGS
FMNH 64408	1927	Uruguay	Soriano: Dolores	monachus	Female	FMNH	9.9X	WGS
FMNH 64409	1927	Uruguay	Soriano: Dolores	monachus	Male	FMNH	8.7X	WGS

Table C2. List of non-native range samples and their associated locality and collection information.

Sample ID	Year	Country	Locality	Sex	Institution ID	Mean Coverage	Library Type
PR001	2019	Puerto Rico	Aguada			5.7X	3RAD
PR002	2019	Puerto Rico	Aguada			4.8X	3RAD
PR003	2019	Puerto Rico	Aguada			5.6X	3RAD
PR004	2019	Puerto Rico	Aguada			24.8X	3RAD
PR005	2019	Puerto Rico	Aguada			5.2X	3RAD
PR006	2019	Puerto Rico	Aguada			26.5X	3RAD
PR007	2019	Puerto Rico	Aguada			57.1X	3RAD
PR008	2019	Puerto Rico	Aguada			19.9X	3RAD
PR009	2019	Puerto Rico	Aguada			20.4X	3RAD
PR010	2019	Puerto Rico	Aguada			31.2X	3RAD
PR011	2019	Puerto Rico	Aguada			40.9X	3RAD
PR012	2019	Puerto Rico	Aguada			32.2X	3RAD
PR013	2019	Puerto Rico	Aguada			31.9X	3RAD
PR014	2019	Puerto Rico	Aguada			4.4X	3RAD
PR015	2019	Puerto Rico	Aguada			77.7X	3RAD
PR016	2019	Puerto Rico	Aguada			34.4X	3RAD
PR017	2019	Puerto Rico	Aguada			40.3X	3RAD
PR018	2019	Puerto Rico	Aguada			64.5X	3RAD
MZB 2019-1704	2019	Spain	Cataluña: Barcelona, Parc de la Ciutadella		MCNB	57.5X	3RAD
MZB 2018-0106	2018	Spain	Cataluña: Barcelona, Parc de la Ciutadella		MCNB	41.6X	3RAD
MZB 98-0834	1998	Spain	Cataluña: Barcelona, Parc de la Ciutadella		MCNB	37.5X	3RAD
MZB 2011-0858	2011	Spain	Cataluña: Lleida	Female	MCNB	39.4X	3RAD
MZB 2015-1740	2015	Spain	Cataluña: Barcelona, Sant Cugat del Vallès	Female	MCNB	23.5X	3RAD
MZB 2018-0848	2018	Spain	Cataluña: Barcelona, Gavà		MCNB	23.4X	3RAD
MZB 2011-0859	2011	Spain	Cataluña: Lleida	Male	MCNB	28.5X	3RAD
MZB 2011-0857	2011	Spain	Cataluña: Lleida	Female	MCNB	49.8X	3RAD
MZB 2017-1666	2017	Spain	Cataluña: Barcelona, Parc de la Ciutadella		MCNB	61.4X	3RAD
MZB 2017-1254	2017	Spain	Cataluña: Barcelona, Parc de la Ciutadella		MCNB	35.7X	3RAD
MZB 2016-3087	2016	Spain	Cataluña: Tarragona, Almoster	Male	MCNB	18.2X	3RAD
MZB 2011-0856	2011	Spain	Cataluña: Lleida	Male	MCNB	49.0X	3RAD
MZB 2019-1705	2019	Spain	Cataluña: Barcelona, Parc de la Ciutadella		MCNB	74.4X	3RAD

Table C2. List of non-native range samples and their associated locality and collection information, continued.

Sample ID	Year	Country	Locality	Sex	Institution ID	Mean Coverage	Library Type
MZB 2013-4598	2013	Spain	Cataluña: Barcelona, Mollet del Vallès	Male	MCNB	19.6X	3RAD
MZB 2010-1144	2010	Spain	Cataluña: Barcelona, Horta - Guinardó	Male	MCNB	11.5X	3RAD
MZB 2016-3132	2016	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona		MCNB	10.0X	3RAD
MZB 2017-1662	2017	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona		MCNB	35.1X	3RAD
MZB 2011-0868	2011	Spain	Cataluña: Lleida	Female	MCNB	55.9X	3RAD
MZB 2011-0866	2011	Spain	Cataluña: Lleida		MCNB	56.7X	3RAD
MZB 2011-0994	2011	Spain	Cataluña: Lleida	Male	MCNB	37.4X	3RAD
MZB 2011-0996	2011	Spain	Cataluña: Lleida		MCNB	28.9X	3RAD
MZB 2011-0863	2011	Spain	Cataluña: Lleida	Female	MCNB	33.0X	3RAD
MZB 2018-0476	2018	Spain	Cataluña: Barcelona, Parc de la Ciutadella		MCNB	43.8X	3RAD
MZB 2011-0854	2011	Spain	Cataluña: Lleida	Male	MCNB	31.7X	3RAD
MZB 2020-0516	2020	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona	Male	MCNB	1.5X	3RAD
MZB 2021-0898	2015	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona		MCNB	29.8X	3RAD
MZB 2011-0873	2011	Spain	Cataluña: Lleida	Female	MCNB	45.9X	3RAD
MZB 2011-0867	2011	Spain	Cataluña: Lleida	Female	MCNB	97.7X	3RAD
MZB 2004-0922	2004	Spain	Cataluña: Barcelona, Parc de la Ciutadella		MCNB	26.3X	3RAD
MZB 2012-0075	2011	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona	Male	MCNB	1.4X	3RAD
MZB 2011-1175	2011	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona		MCNB	2.5X	3RAD
MZB 2020-0479	2020	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona	Female	MCNB	38.1X	3RAD
MZB 2016-3092	2016	Spain	Cataluña: Tarragona	Male	MCNB	17.9X	3RAD
MZB 2017-0148	2017	Spain	Cataluña: Barcelona, Parc de la Ciutadella		MCNB	5.0X	3RAD

Table C2. List of non-native range samples and their associated locality and collection information, continued.

Sample ID	Year	Country	Locality	Sex	Institution ID	Mean Coverage	Library Type
MZB 2016-3091	2016	Spain	Cataluña: Tarragona, Almoster	Female	MCNB	23.1X	3RAD
MZB 2011-0865	2011	Spain	Cataluña: Lleida	Male	MCNB	35.4X	3RAD
MZB 2011-0989	2011	Spain	Cataluña: Lleida	Male	MCNB	33.5X	3RAD
MZB 2014-7351	2014	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona		MCNB	30.6X	3RAD
MZB 2017-1664	2017	Spain	Cataluña: Barcelona, Parc de la Ciutadella		MCNB	12.9X	3RAD
MZB 2011-0995	2011	Spain	Cataluña: Lleida	Male	MCNB	17.2X	3RAD
MZB 2011-0998	2011	Spain	Cataluña: Lleida	Male	MCNB	37.3X	3RAD
MZB 2011-0869	2011	Spain	Cataluña: Lleida	Female	MCNB	51.2X	3RAD
MZB 2011-0852	2011	Spain	Cataluña: Lleida	Male	MCNB	4.0X	3RAD
MZB 2014-1951	2013	Spain	Cataluña: Barcelona, Parc de la Ciutadella	Male	MCNB	45.1X	3RAD
MZB 2015-1716	2014	Spain	Cataluña: Barcelona, Parc de la Ciutadella	Male	MCNB	3.7X	3RAD
MZB 2014-2027	2013	Spain	Cataluña: Barcelona		MCNB	45.3X	3RAD
MZB 2016-3094	2016	Spain	Cataluña: Tarragona, Almoster	Male	MCNB	6.9X	3RAD
MZB 2011-0876	2011	Spain	Cataluña: Lleida	Female	MCNB	39.7X	3RAD
MZB 2018-0843	2018	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona	Female	MCNB	21.0X	3RAD
MZB 2020-1199	2020	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona	Male	MCNB	3.2X	3RAD
MZB 2018-0088	2016	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona		MCNB	32.8X	3RAD
MZB 2010-1139	2010	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona	Male	MCNB	7.1X	3RAD
MZB 2018-0456	2018	Spain	Cataluña: Barcelona, Parc de la Ciutadella		MCNB	30.0X	3RAD
MZB 2011-0875	2011	Spain	Cataluña: Lleida	Male	MCNB	117.1X	3RAD
MZB 2016-2988	2016	Spain	Cataluña: Tarragona, Almoster	Male	MCNB	3.3X	3RAD
MZB 2016-4241	2016	Spain	Cataluña: Barcelona, Parc de la Ciutadella		MCNB	6.7X	3RAD

Table C2. List of non-native range samples and their associated locality and collection information, continued.

Sample ID	Year	Country	Locality	Sex	Institution ID	Mean Coverage	Library Type
MZB 2011-0874	2011	Spain	Cataluña: Lleida	Male	MCNB	72.9X	3RAD
MZB 2012-0332	2012	Spain	Cataluña: Barcelona	Female	MCNB	3.5X	3RAD
MZB 2011-0860	2011	Spain	Cataluña: Lleida	Female	MCNB	53.1X	3RAD
MZB 2011-0877	2011	Spain	Cataluña: Lleida	Female	MCNB	1.3X	3RAD
MZB 2011-0872	2011	Spain	Cataluña: Lleida	Female	MCNB	4.8X	3RAD
MZB 2011-0997	2011	Spain	Cataluña: Lleida	Male	MCNB	48.3X	3RAD
MZB 2017-1663	2017	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona		MCNB	2.4X	3RAD
MZB 2006-0036	2006	Spain	Cataluña: Lleida	Female	MCNB	5.8X	3RAD
MZB 2006-0643	2006	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona		MCNB	2.2X	3RAD
MZB 2007-0488	2007	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona		MCNB	1.8X	3RAD
MZB 2007-0485	2007	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona		MCNB	1.1X	3RAD
MZB 2016-3093	2016	Spain	Cataluña: Tarragona, Almoster	Male	MCNB	1.3X	3RAD
MZB 2006-0642	2006	Spain	Cataluña: Barcelona, Museu de Zoologia de Barcelona		MCNB	1.4X	3RAD
UF 51737	NA	USA	Florida: Broward Co.		FLMNH	11.2X	3RAD
UF 50956	2015	USA	Florida: Indian Shores		FLMNH	21.7X	3RAD
UF 51064	2007	USA	Florida: Brevard Co.		FLMNH	21.8X	3RAD
UF 51069	2012	USA	Florida: Miami, Goulds Substation		FLMNH	17.3X	3RAD
UF 48281	2011	USA	Florida: Sunrise	Female	FLMNH	33.2X	3RAD
UF 51066	2012	USA	Florida: Miami, Perrine Substation		FLMNH	30.0X	3RAD
UF 43925	2003	USA	Florida: West Palm Beach	Female	FLMNH	44.2X	3RAD
UF 50168	2013	USA	Florida: Lighthouse Point	Female	FLMNH	39.3X	3RAD
UF 51068	2014	USA	Florida: Gainesville		FLMNH	28.4X	3RAD
UF 51104	2003	USA	Florida: Broward Co.		FLMNH	32.6X	3RAD
UF 51063	2002	USA	Florida: Patrick Air Force Base		FLMNH	15.3X	3RAD
UF 42973	1999	USA	Florida: Sarasota	Male	FLMNH	29.1X	3RAD

Table C2. List of non-native range samples and their associated locality and collection information, continued.

Sample ID	Year	Country	Locality	Sex	Institution ID	Mean Coverage	Library Type
UF 43879	2003	USA	Florida: Miami	Female	FLMNH	33.6X	3RAD
UF 51065	2012	USA	Florida: Miami, Perrine Substation		FLMNH	47.0X	3RAD
UF 43926	2003	USA	Florida: Miami-Dade Co.	Female	FLMNH	32.1X	3RAD
FMNH 432980	2000	USA	Florida: Shore Acres		FMNH	24.6X	3RAD
UF 40239	1998	USA	Florida: Coconut Creek	Male	FLMNH	8.8X	WGS
UF 40659	1998	USA	Florida: Ft. Lauderdale	Female	FLMNH	8.8X	WGS
FMNH 428622	2001	USA	Illinois: Chicago, Hyde Park	Male	FMNH	32.4X	3RAD
FMNH 458891	2006	USA	Illinois: Chicago, Hyde Park	Female	FMNH	17.1X	3RAD
FMNH 385941	NA	USA	Illinois: Chicago, Hyde Park	Female	FMNH	43.6X	3RAD
FMNH 470018	2009	USA	Illinois: Chicago	Female	FMNH	40.1X	3RAD
FMNH 470019	2009	USA	Illinois: Chicago	Female	FMNH	1.5X	3RAD
FMNH 454251	2007	USA	Illinois: Chicago	Female	FMNH	32.0X	3RAD
FMNH 458054	2008	USA	Illinois: Chicago, Hyde Park	Male	FMNH	30.4X	3RAD
FMNH 385974	1995	USA	Illinois: Chicago, Hyde Park	Male	FMNH	28.9X	3RAD
FMNH 478898	2011	USA	Illinois: Chicago	Female	FMNH	29.8X	3RAD
FMNH 452418	2005	USA	Illinois: Chicago	Female	FMNH	2.3X	3RAD
FMNH 351080	1985	USA	Illinois: Chicago, Hyde Park	Female	FMNH	8.6X	WGS
UF 51105	2015	Captive	Captive: Gainesville, USDA Lab		FLMNH	35.0X	3RAD
UF 51067	2013	Captive	Captive: Gainesville, USDA Lab		FLMNH	8.8X	3RAD

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