A global study of the distribution and richness of alien bird species

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Declaration

I, Ellie Eveness Dyer, confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Ellie Dyer, 4th November 2015

Abstract

Alien species are a major component of human-induced environmental change, yet spatial and temporal variation in the drivers of their introduction, and their subsequent distribution and richness, are poorly understood. Here, I present a global analysis of the drivers of this variation for a major animal group, birds (Class Aves), using the newly-created Global Avian Invasions Atlas (GAVIA) database. GAVIA includes information on introduction successes and failures, enabling me to examine the effect of colonisation pressure (the number of species introduced) on alien bird distributions.

A description of the GAVIA database is given in Chapter 2, with details on its scope and sources, data collation and validation, and the production of alien range maps. Chapter 3 focuses on the early stages of the invasion pathway, and shows that historical introductions tend to originate in Europe, were driven by the global movements of British colonialism, and involved species deemed useful. Modern introductions, in contrast, tend to originate in Southeast Asia and Africa, are driven by factors associated with wealth, and involve species found in the pet trade. Chapter 4 identifies colonisation pressure as the principal determinant of alien bird species richness at a global scale. Additional anthropogenic factors (residence time, distance to historic port) and environmental variables (temperature range, precipitation) also influence richness. Chapter 5 analyses the factors influencing alien geographic range size, with species achieving a larger alien range if they have been introduced more often, have a larger native range and a shorter residence time. Chapter 6 examines latitudinal patterns of alien species richness and range size, and the likelihood of failure relative to latitude and native range limits.

Overall, I demonstrate that alien bird distributions are primarily driven by anthropogenic influences, and highlight in particular the importance of incorporating a measure of colonisation pressure into studies of invasion.

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Chapter 1.

Introduction

1.1 The Invasion Pathway

1.1.1 Overview

An alien species is one which has been introduced by humans into a new environment outside its native range, either accidentally or deliberately (Elton 1958). For some of these species, their new existence is short-lived: the species fails to establish a viable population and dies out. However, some will become established, and some of these populations will grow and spread away from their point of introduction.

The ‘Invasion Pathway’ (Williamson 1996, Duncan *et al*. 2003) describes the process by which a species becomes an alien invader. That process begins in the species’ native range and describes the four stages which individuals from the native population must pass through. First, the species must be transported from its native geographic range to a new location. Second, the species must be released (or escape) into the new environment. Third, the species must successfully establish a self-sustaining population in the new location. Finally, species that do establish successfully may increase in abundance and spread beyond the original point of introduction and become invasive; the extent of this spread determines their alien geographic range in the new location (Duncan *et al*. 2003). These four stages are termed *transport*, *introduction* (release or escape), *establishment* and *spread* (figure 1.1; Blackburn *et al*. 2011b).

Species that are not native to regions may be termed alien, exotic, introduced, non-native, non-indigenous, naturalized, or invasive, amongst others (Colautti & MacIsaac 2004). Most of these terms are interchangeable, but some such as ‘introduced’ and ‘invasive’ may also be used to refer specifically to a certain stage of the invasion pathway (figure 1.1). An introduced species is one that has successfully passed through the first two stages of the pathway (transport and introduction) and is present in the location of introduction. An established species is one that is maintaining a self-sustaining wild population following introduction. If an established species succeeds in spreading beyond the original site of introduction then it is termed invasive (figure 1.1).

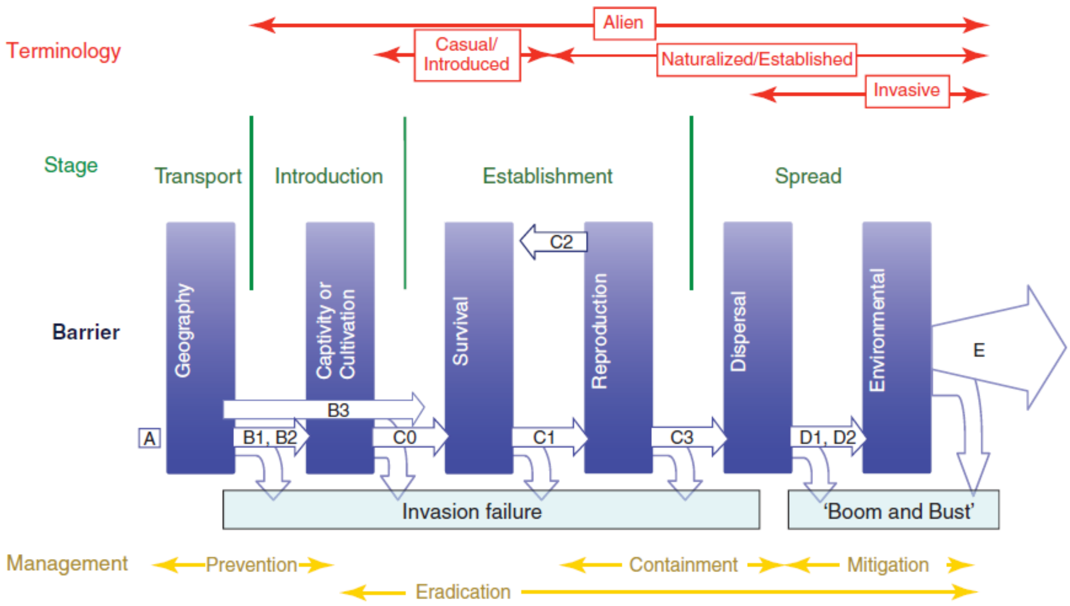


Figure 1.1 The Invasion Pathway (from Blackburn *et al*. 2011b). The process of invasion can be divided into a series of stages, and within each stage there are barriers that the alien species or population must overcome in order to pass onto the next stage. The white arrows represent the movement of species along the invasion pathway with respect to the barriers. The red arrows highlight the different terminology that is used for species depending on which stage they have reached, and the yellow arrows outline the different management strategies that apply at each stage.

The introduction of an alien species to a novel location is termed an introduction event (Duncan *et al*. 2003). Throughout this thesis I will use the term 'alien' as a general descriptor of species that are not naturally occurring in the native fauna of a region, regardless of whether or not they are established. For the sake of clarity, a native population is classified as one inhabiting a region where the species has evolved or to which it has spread without human intervention.

For a species to have reached a given stage in the invasion pathway it must have successfully passed through all prior stages (Duncan *et al*. 2003). A species may fail at any one of the stages in the pathway, although this failure does not preclude the possibility of the same species becoming successful at that or a different location in the future (Blackburn *et al*. 2011b). Identifying the factors that affect the likelihood that a species will move through each stage of the pathway is crucial in achieving an understanding of the overall determinants of alien species distribution, although it is important to bear in mind that invasion is a continuous process. The drivers and processes that influence the early invasion stages will affect the species composition and likelihood of success at the later stages. For example, the number and frequency of species introductions into a novel environment will influence the possibility of successful establishment (Lockwood *et al*. 2005). Therefore, in order comprehensively to understand the invasion process, studies that address all of the stages of invasion are required (Blackburn *et al*. 2011b).

1.1.2 Birds as a focal taxon

Substantial progress in invasion biology has come from studying birds (Blackburn *et al*. 2009a), for which detailed historical and ecological information allows determinants of alien species distributions to be explored (Duncan *et al*. 2003). There has been a range of motivations for humans to transport bird species outside their native ranges, and a diverse selection of bird species have been transported and subsequently introduced (Blackburn *et al*. 2010). The practise of transporting and introducing birds has a long history (West & Zhou 1989) and is a relatively global phenomenon (Cassey *et al*. 2015). Indeed, all but a few countries have at least one alien bird species recorded within their borders (Chapter 2). Birds are also one of the few taxa which we believe to have been almost fully described (most new species are taxonomic splits rather than genuinely novel discoveries) and to have had their native distributions mapped (Orme *et al*. 2005). In addition, thanks to the large number of bird-watchers, ornithologists and scientists collecting sightings data and keeping species lists, there is a wealth of information available, both published and unpublished, showing which species (native and alien) have been recorded in which locations.

1.1.3 Transport and Introduction

Species only have the chance to establish and spread if they are first transported and introduced. Therefore the early stages of invasion are important for understanding the invasion process because they act as filters for species entering the later stages (Blackburn & Duncan 2001b, Cassey *et al*. 2004, Jeschke & Strayer 2006).

There is evidence that people have been moving animals, either purposefully or inadvertently, for thousands of years, and across a wide range of regions and civilisations (Lever 1979, Yalden 1999). For example, the red jungle-fowl (*Gallus gallus*) is believed to have first been transported outside of its native range c.8,000 years ago (West & Zhou 1989). Despite this long history, the real 'golden age' of translocations of bird species did not start until the middle of the nineteenth century, at which point there was a step-change in the rate at which introductions occurred worldwide (Blackburn *et al*. 2015b, Cassey *et al*. 2015). Since this point, two distinct periods of activity have been identified in the transportation and introduction of bird species that influence current alien bird distributions.

The first of these is the era of the acclimatisation societies during the great European diaspora between the eighteenth and twentieth centuries (Thomson 1922). Acclimatisation societies were borne in part out of the homesickness of Europeans who were settling in colonies around the world, and in part out of the desire to augment environments with beneficial species, such as game species or biocontrol agents. In an effort to make their new environment feel more familiar and useful, colonists introduced a range of plants and animals, sparking the transportation of many species across the oceans (McDowall 1994). This transport was in both directions as newly discovered beneficial species from the colonies were sent back for the benefit of the "old country". Acclimatisation societies were particularly popular with the British. For example, one study found that c.40% of known bird introductions could be attributed to activity relating to the British occupation of just four geopolitical regions: Australia, New Zealand, Hawaii, and the continental USA (Blackburn *et al*. 2009a). However, it was eventually recognised that the introduction of alien species was ecologically unsound, and the practice had died out by the end of the Second World War (Simberloff & Rejmanek 2011). The second significant period of activity in the transport and introduction of birds is the era of international trade in wild birds for bird-keeping from the late-twentieth century to the present day (Cassey *et al*. 2015). Most new alien bird introductions now have their origins in the accidental (e.g. escaped pet birds) or recreational (e.g. for religious or festive reasons) release of cage birds, rather than as a result of deliberate introduction efforts (Eguchi & Amano 2004, Lever 2005).

There are a variety of motives behind bird transport and introductions, and each motive dictates the types of species that are introduced, given that it is often only those species deemed desirable which are released or given the opportunity to escape. Consequently the species transported and introduced are likely to be a non-random subset of all species, and will possess certain qualifying characteristics (Blackburn & Duncan 2001b).

Species introduced as game birds tend to be 'larger and tastier' than average (Blackburn *et al*. 2009a), and originate primarily from the families Phasianidae (pheasants) and Anatidae (wildfowl) (Blackburn & Duncan 2001b, Duncan *et al*. 2003).

Those introduced as a potential source of food were usually domesticated species such as the ancestor of the domestic chicken, the red jungle-fowl (*Gallus gallus*), and the rock dove/feral pigeon (*Columba livia*) (West & Zhou 1989, Lever 2005). Many birds have been introduced for the purpose of biological control, usually with the intention of controlling invertebrates. However, these species run the risk of becoming pests themselves: the house sparrow (*Passer domesticus*), originally introduced to the USA, Argentina and Brazil between 1850-1900 to control insect pests (Lever 2005), is now established in 32 countries from Canada south to Argentina, and in 44 additional non-native countries globally (Dyer & Blackburn unpubl.). Black swans (*Cygnus atratus*) were introduced to Christchurch, New Zealand, to control water cress, an introduced plant that was itself feared to hinder the establishment of introduced trout (McDowall 1994). Although in the present day alien species are still occasionally used as biological control agents, it has become commonly accepted that the intentional introduction of generalist vertebrates such as birds is a potentially dangerous practice (Simberloff & Stiling 1996).

It was not only for practical reasons that alien birds were introduced. Some introductions made under the auspices of the acclimatisation societies were driven by sentimentality or nostalgia (Lever 1992). These introductions involved songbirds or those with brightly coloured plumage (mainly from the families Sturnidae, Fringillidae, Passeridae and Emberizidae) imported to North America and the Antipodes by colonists (Dyer & Blackburn unpubl., MacDowall 1994, Lockwood *et al*. 2000, Blackburn & Duncan 2001b). Birds introduced for aesthetic improvement, or to ‘grandify’ surroundings (McDowall 1994), have mostly been wildfowl (Anatidae) and pheasants (Phasianidae) (Dyer & Blackburn unpubl., Banks *et al*. 2008); for example the liberation of golden pheasants (*Chrysolophus pictus*) into Europe (Long 1981).

Occasionally introductions are carried out as part of efforts to save a species from extinction, with some endangered bird species translocated to areas outside of their native range for conservation purposes, usually because their original habitat is no longer suitable or safe (Duncan *et al*. 2003). Examples include the greater bird of paradise (*Paradisea apoda*) introduced from the Aru Islands in Indonesia to Little Tobago in the Caribbean (Anthony 1997); the kakapo (*Strigops habroptila*) introduced to New Zealand’s offshore islands (from the mainland) (Higgins 1999); and Meller’s duck (*Anas melleri*) introduced from Madagascar to boost populations on Mauritius (Jones 1996). Although not an introduced alien species in the typical sense, these species can still provide important information on the factors that affect successful establishment, and likewise lessons learned from other alien bird introductions can aid in the successful translocation of endangered bird species (Cassey *et al*. 2008).

In addition to these purposeful introductions of bird species, as many as 165 species have become established outside of their native range as a result of escaping from captivity or domesticity (Dyer & Blackburn unpubl.). Transport, trade and tourism have consistently been related to the unintentional introduction of alien species (Westphal *et al.* 2008, Hulme 2009, Pyšek *et al.* 2010, Essl *et al.* 2011, Gallardo *et al.* 2015). For instance, roads, canals and railways create pathways along which species can disperse (Hulme 2009). Ports are the entrance point of alien species arriving from other continents as imports, through contamination of a product, or as stowaways (Hulme 2009, Gallardo *et al.* 2015). Several bird species have made use of human transportation as a means of colonising new areas. The most prominent example of this is the house crow (*Corvus splendens*), which has been carried to the Arabian Gulf, eastern and southern Africa, Australia, western Europe and many Indian Ocean islands as a stowaway on ships (Lever 2005).

The transport and introduction of alien species is primarily driven by anthropogenic factors and societal demands (Hulme 2009, Pyšek *et al*. 2010, Essl *et al*. 2011). Differences and changes in societies over time and across the globe are therefore likely to continue to influence the types of species transported and introduced (Blackburn *et al*. 2010), and also the origins from where species are sourced, and the destinations to which they are transported (Blackburn & Duncan 2001a, Duncan *et al*. 2003). However, studies of alien bird invasions to date have largely considered data from European-driven introductions, particularly those from the acclimatisation era as detailed in Long’s (1981) seminal monograph on the subject (Blackburn *et al*. 2015b). These introductions are likely to be very different in time, space and motivation from more recent introductions and from those occurring in other regions, such that conclusions drawn from these studies may not be transferable to more recent introductions (Blackburn *et al*. 2015b). This highlights the need for updated global data on alien bird species, incorporating a more complete spatial and temporal coverage, so that the changing drivers of alien bird species transportation and introduction can be identified.

1.1.4 Establishment

Not all stages in the invasion pathway have been equally well-studied, with a predominance of literature aiming to identify the factors that influence establishment (Duncan *et al*. 2003). Whether or not an alien species will succeed and become established in a new environment is argued to be broadly dependent on three interrelated elements: the characteristics of the introduction event, the characteristics of the species and the characteristics of the novel location (Duncan *et al*. 2003).

The characteristics of the introduction event are arguably the most important when it comes to influencing whether a species will succeed or fail in a new environment (Duncan *et al*. 2014). There is variation in the effects of species characteristics and location characteristics, and although they are likely to play an important role in influencing establishment, as yet there is limited consensus on how (Sol *et al*. 2012). The fact that many introductions fail the first (or first few) times before successfully establishing in a new location, suggests that there are additional elements affecting establishment success, which vary from introduction to introduction independently of the species and location concerned.

One key factor that can vary independently of the species or location and that is expected to affect establishment success is propagule pressure (the number of individuals of a species introduced) (Lockwood *et al*. 2005, Hayes & Barry 2008, Simberloff 2009, Blackburn *et al*. 2011a). The larger the number of individuals that are released, either in one event or through multiple releases, the more likely they are to persist and reproduce successfully in a new environment, overcoming the problems of environmental, demographic and genetic stochasticity that are well known to afflict small populations (Lockwood *et al*. 2005, Uller & Leimu 2011, Duncan *et al*. 2014). Most studies that analyse the effect of propagule pressure on the establishment success of alien bird populations find a significant positive relationship (Blackburn *et al*. 2009a). However, it does not follow that with a continued increase of population size the likelihood of success also increases in a linear fashion. Duncan *et al*. (2014) show that heterogeneity in environmental conditions can change the shape of the relationship between probability of establishment and propagule pressure, through a disproportionate decline in the probability of establishment in larger populations. Unfortunately, avian empirical studies including a measure of propagule pressure are restricted and largely constrained to Australia and New Zealand (Veltman *et al*. 1996, Duncan 1997, Green 1997, Sol & Lefebvre 2000, Duncan *et al*. 2001, Cassey 2001b, Duncan & Blackburn 2002). Without this information, it is difficult to separate out the role that propagule pressure plays from the influence of other characteristics of the introduction event, or characteristics of the species or location.

The impact that the characteristics of the species have on establishment has been widely investigated (see Duncan *et al*. 2003, Sol *et al*. 2005a, Sol 2007, Blackburn *et al*. 2009b), presumably because it involves the most readily available data, yet it is also the most contentious (Sol *et al*. 2012). Some broad generalisations can be made, however, on the basis of studies to date. For an alien species, unfamiliarity and insufficient adaptation to novel resources, enemies and other hazards are likely to increase the chances of reproductive failure (Yeh & Price 2004) and thus the risk of establishment failure. It has recently been shown that an alien species which prioritises future rather than current reproduction is more likely to be successful (Sol *et al*. 2012). Having a high future breeding expectation reduces the costs of reproductive failure under uncertain conditions and increases the opportunities for a species to adapt to the new environment and respond to novel ecological pressures (Sol *et al*. 2012). In addition to this, being a habitat generalist is thought to increase a species' chances of experiencing environmental conditions to which it is already suited, and therefore improve its likelihood of success (Cassey 2001b, Cassey 2002, Cassey *et al*. 2004, Blackburn *et al*. 2009b, Sol *et al*. 2012). It is also generally accepted that a large brain relative to body size promotes establishment, as the species is more likely to have adaptations that can provide a buffer to extrinsic factors (Sol *et al*. 2005a, Sol *et al*. 2007, Blackburn *et al*. 2009a, Sol *et al*. 2012).

Just as some species are likely to establish more readily than others, so too is it likely that some locations will prove more suitable for receiving alien species. Shea and Chesson (2002) identified three aspects of a location that are likely to influence establishment: the physical environment, the availability of resources, and interspecific interactions. Even with propagule pressure accounted for, environmental factors frequently emerge as important predictors of establishment success (Duncan *et al*. 2001, Forsyth *et al*. 2004, Duncan *et al*. 2014). Locations could be unsuitable for the establishment of alien species because temperatures unfavourable to life (e.g. extreme cold) are typical, because broad ranges of environmental conditions such as temperature or precipitation may be encountered on daily or annual timescales, or because there is little available water or foodstuffs (Blackburn *et al*. 2009a). Additionally, predators, parasites, or diseases against which the alien species has no defences may also provide barriers to establishment. Alien bird introductions are more likely to fail to establish on islands where larger numbers of predator species have been introduced (Cassey *et al*. 2005). Therefore locations with a more stable environment, readily available resources, or fewer enemies and more mutualisms, may favour establishment success.

The establishment success of alien bird populations has been found to be higher when the difference between a species' latitude of origin and its latitude of introduction is small (Blackburn & Duncan 2001a, Cassey 2001b), when species are introduced to areas within their native biogeographical range (Blackburn & Duncan 2001a, Cassey 2003), and when the climate in the locations of origin and introduction are more similar (Duncan *et al*. 2001). Therefore, the characteristics of an environment should be assessed from the perspective of the species in question and its respective environmental tolerances (Blackburn *et al*. 2009a), suggesting that components of the physical environment on their own may be less significant than the match between the native and alien environments for each species individually (Cassey *et al*. 2008).

1.1.5 Spread

Once an alien population is successfully established, the next challenge relates to the spread stage of the pathway, and the ability of the population to expand its range. At this stage, the species faces barriers to dispersal and then environmental barriers to establishment in new areas following spread (Blackburn *et al*. 2009a). Relative to other taxa, birds are generally good dispersers, yet following establishment they can differ markedly in the extent to which they spread and in the final extent of their alien distribution (Duncan *et al*. 2003). Some alien species established in a novel location maintain relatively small populations and do not expand far beyond the original release site (Blackburn *et al*. 2009a). This is particularly true when the surrounding areas are unsuitable, for example if a species has been released into a botanic garden within a city (e.g. *Eos bornea* in Singapore Botanic Gardens, Keng & Hails 2007). Physical or climatic barriers can also prevent a species from spreading. Duncan *et al.* (1999, 2001) showed that the range sizes of alien bird species in New Zealand and Australia were determined in part by the area of suitable habitat. If the areas surrounding the introduction site are amenable to the new species, or if they have the dispersal ability to spread to similar locations, then the alien species will likely increase the size of its non-native distribution through a combination of population growth and dispersal (Blackburn *et al*. 2009a). The common starling (*Sturnus vulgaris*) was introduced in New York in the late nineteenth century and has subsequently spread across the entirety of mainland North America, becoming one of the most abundant bird species

(Long 1981, Duncan *et al*. 2003). Nevertheless in the majority of cases, alien distributions actually tend to be relatively small in magnitude, and most aliens have not (yet) spread far from their point of release/escape or reached the distributional extent observed in their native range (Guo *et al.* 2012).

Relative to the establishment stage of the pathway, studies on patterns of spread among alien birds are comparatively rare (Duncan *et al*. 2003, Sol *et al*. 2005b). This is likely due to a lack of suitable data. The species and populations that fail at each stage of the pathway provide a reduction in the available sample size at the latter stages (Blackburn *et al*. 2009a). Therefore, by the time that the spread stage is reached, few species are left on which to focus analyses on aspects of alien species spread such as alien species richness, geographic range size and patterns in latitudinal extent.

The number of species that are able to establish at, or spread to, any given location combine to create the alien species richness of a region. Studies devoted to achieving a better understanding of the factors that govern alien species richness (Evans *et al*. 2005a, Blackburn *et al.* 2008, Chiron *et al.* 2009) have highlighted the importance of various environmental, climatic, socioeconomic and demographic factors, but there is currently limited consensus regarding their relative influence (Westphal *et al.* 2008, Pyšek *et al.* 2010, Essl *et al.* 2011, Gallardo *et al.* 2015). Alien species richness is likely to be predominantly influenced by location- and event-level factors, particularly colonisation pressure (the number of species initially introduced), but as yet no study has examined the determinants of alien bird richness on a global scale. Aside from a couple of examples (e.g. Blackburn *et al.* 2008, Chiron *et al.* 2009), detailed data on colonisation pressure is not often included in invasion studies due to the lack of information for this early stage in the invasion process (Pyšek *et al.* 2010). This is important because the number of species introductions that fail is unlikely to be constant, but instead a function of the abiotic environment, biotic interactions, and aspects such as propagule size (Zenni & Nuñez 2013, Duncan *et al*. 2014).

Geographic range size is a measure of spread in alien species (Duncan *et al*. 2003) and potentially a strong predictor of the level of impact (Parker *et al.* 1999). The determinants of alien bird species range size have been investigated at a regional scale for Australia (Long & Mawson 1991, Duncan *et al*. 2001) and New Zealand (Duncan *et al*. 1999, Duncan & Blackburn 2002), with species achieving larger alien range sizes when they have been introduced more often and have a longer residence time. Native range size has also been found to be correlated with alien range size at a global scale but for a limited number of birds (Guo *et al*. 2012). To date, tests of the determinants of alien range size have either considered variation in restricted taxa (Proçhes *et al.* 2012) or regional assemblages (Duncan *et al.* 1999, 2001, Forsyth *et al.* 2004), and as yet there has been no global assessment of the factors affecting the range sizes attained by alien bird species.

Another means of examining the spatial spread of species is by assessing latitudinal patterns. Latitude integrates many aspects of biotic, abiotic and human influences that may be important in limiting alien species distributions (Guo *et al*. 2012). Consequently, examining alien distributions in the context of latitude can potentially inform the limitations and potential expansion of distributions of alien species, particularly at the global scale. There is evidence that with increasing latitude the number of alien bird species in temperate regions decreases, whilst their geographical range sizes increase (Sax 2001). Currently, analyses concerning the latitudinal patterns of alien bird species have only examined those species with established distributions, and have not fully considered the effects of where species have been introduced, and where introduced species have succeeded or failed. Yet latitudinal gradients in alien species richness or geographic range extent may arise as a result of human actions in introducing species (Blackburn *et al*. 2009a), rather than the abiotic or biotic effects that underlie these patterns in native species (Pyšek *et al*. 2010).

Although the majority of alien species seemingly have low impact, any negative impacts they do have are only compounded when combined with larger range sizes (Parker *et al.* 1999). It is therefore important that the structure and mechanisms driving alien species spread are understood, so that those alien species that are more likely to achieve greater distributions can be identified.

1.1.6 Impacts of alien species

The introduction of an alien species into a new environment can have a number of far-reaching and often unpredictable consequences, and they can pose a significant threat to native species (Sakai *et al*. 2001). Their effects can include the transmission of parasites, pathogens and disease; disturbance and disruption of the native ecosystem; interspecific competition with native species; changes in native populations through hybridisation with non-natives, and within the non-native populations themselves through adaptation to the new environment (Lever 2005, Kumschick & Nentwig 2010, Uller & Leimu 2011). In a survey of 170 extinction events, 54% listed alien species as a contributing event, compared to 48% listing habitat destruction (Clavero & Garcia-

Berthou 2005), and there is no sign that their role in the current extinction crisis is diminishing. The economic costs of managing alien species and mitigating their impacts can be staggering. The total annual cost of alien species to the British economy alone has been estimated at approximately GB£1.7 billion (Williams *et al*. 2010).

Therefore there is a great incentive, both environmentally and economically, to stem the tide of alien species. Once established, the eradication or control of alien species is costly, and so the most effective way to minimise their impact is to prevent establishment and/or spread (Ricciardi & Rassmusen 1998, Mack *et al*. 2000). This requires an understanding of the factors driving alien species distributions at each stage of the invasion process, so that the situations where invasion risk is high can be identified (Duncan *et al*. 2003).

Alien species also represent an opportunity to be exploited (Brown & Sax 2004). They belong to numerous taxa and occur in many different environments, and so the study of alien species allows an array of biological questions to be investigated (Sax *et al*. 2005). For example, alien species enable us to study rapid change in real time, rather than through the inference of past events, and can provide important insights into ecology, evolution, and biogeography (Blackburn *et al*. 2009a, Simberloff *et al*. 2013). The study of the ecology and distribution of alien species is one way in which an understanding of the invasion process can be advanced.

1.2 The Global Avian Invasions Atlas (GAVIA)

Despite the wealth of available data and studies on alien birds, significant gaps in our understanding of the invasion pathway still remain for this group. Most notably, although the necessary stages through which a species passes to become invasive are relatively well documented (figure 1.1), aside from a few case studies (Veit & Lewis 1996, Pithon & Dytham 2002, Silva *et al*. 2002, Stohlgren *et al*. 2006, Chiron *et al*. 2009), the drivers of alien species richness and range size have largely been ignored for birds (Mack *et al*. 2000, Blackburn *et al*. 2009a), particularly with regards to spatial and temporal changes. Understanding these processes is critical in order to mitigate the impacts of alien species, especially given the need to determine the likely effects of global change on the potential for species to invade new regions.

To this end, the Global Avian Invasions Atlas (GAVIA) project was initiated to provide a unified database of records on alien bird species introductions, incorporating records from all stages of the invasion pathway, including those introductions that have failed as well as those that have succeeded. GAVIA currently comprises 27,737 distribution records for 972 alien bird species, based on ~700 published references and substantial unpublished information derived from consultation with over 600 organisations and experts worldwide (for further information see Chapter 2). This database represents the most comprehensive resource on the global distribution of alien species in any major taxon, allowing the spatial and temporal dynamics of alien bird population spread to be examined. Uniquely, the GAVIA database includes information on colonisation pressure (*sensu* Lockwood *et al*. 2009), enabling the impact that this has on all aspects of alien bird distributions to be explored for the first time at a global scale.

1.3 Thesis overview

In this thesis I use the GAVIA database to address key questions on the distribution of alien bird species at each stage of the invasion pathway. First I introduce the GAVIA database in **Chapter 2**, describing in detail how it was collated, validated and curated, and how the alien distribution range maps were produced. In this chapter I also describe its taxonomic, geographic and temporal coverage.

In **Chapter 3** I focus on the first two stages on the invasion pathway – transport and introduction – and directly examine how the spatial distribution of alien bird introductions has changed between the time of the acclimatisation societies and the present day global bird trade. I show how the types of species introduced in each period have changed, reflecting a shift in the motives behind introductions. I also identify the different anthropogenic drivers of alien species transportation and introduction in each time period, and I demonstrate how the origins and destinations of alien species have moved in relation to these drivers.

In **Chapters 4, 5 and 6** I focus on the final stage of the invasion pathway – spread – and investigate whether it is possible to identify factors that are associated with alien species richness, variation in geographic range sizes and latitudinal patterns of alien bird species distributions.

Specifically in **Chapter 4** I investigate whether it is anthropogenic drivers that determine alien species richness at the global scale, or whether attributes relating to the climate and environment become more relevant. Uniquely, the data in GAVIA enables me to include anthropogenic aspects of the introduction event itself, including information on colonisation pressure and residence time.

In **Chapter 5** I address whether the size or location of a species' native range affects the size or location of its alien range, and whether alien range size is a phylogenetically conserved trait. In addition, I try to determine whether there are species characteristics that may predict alien range size.

In **Chapter 6** I examine the latitudinal patterns in the species richness and geographical extents of alien bird distributions at the global scale, and explore how the latitudes where species are introduced and where species fail to establish may help to drive these patterns. I also compare the latitudinal limits of each species in its total recorded alien range, established alien range, and in its native range, in order to determine the direction of any latitudinal shifts that are apparent, and to ascertain whether species recorded beyond the latitudinal limits of their native ranges are more likely to succeed or fail. My aim is to explore the extent to which latitudinal shifts may be a consequence of human actions in introducing species, versus abiotic or biotic environmental effects.

I finish the thesis with a summary in **Chapter 7** of the key findings from my analyses, and I discuss the challenges of alien species research. I also consider the implications of these results for the future study of alien species distributions, and I suggest directions for future research utilising the GAVIA database.

Chapter 2.

The GAVIA database: a global database of alien bird distributions

2.1 INTRODUCTION

The Parties to the Convention on Biological Diversity (CBD) made a commitment in 2002 to develop an adequate knowledge base to address the problem of invasive alien species, including encouraging research on “the history and ecology of invasion (origin, pathways and time-period)” (CBD 2002). Despite this, there continues to be an absence of high-quality, spatially and temporally explicit data available on the distributions of alien species. An evaluation of progress towards the CBD’s 2010 targets (CBD 2010) highlighted the need for datasets with broader taxonomic and geographic coverage than those that currently exist (Walpole *et al*. 2009). Broad taxonomic coverage is necessary because taxa differ in their likelihood to become invasive when introduced, and some will pose a higher impact to the alien environment or entail a greater economic cost to eradicate than others. Broad geographic coverage is needed as currently the majority of data on alien species is skewed towards developed nations (Dana *et al*. 2013). It is therefore impossible to distinguish whether this imbalance is due to a higher incidence of introductions in these regions or just a greater recording effort. In the absence of broad coverage, any pattern apparent in a dataset is inclined to reflect the pattern in recording effort instead of the true global picture.

In order to address this data gap and begin to identify broad patterns and processes of alien invasions, it is clearly necessary to develop a novel, spatially referenced, global data set on the historical introductions and alien distributions of a complete taxonomic group. In response to this need, here I present, to my knowledge, the largest and most complete global database on alien bird introductions and distributions. Birds provide an excellent focal taxon for studies of invasion biology (Blackburn *et al*. 2009a, Cassey *et al*. 2015). The practise of introducing birds is a global phenomenon, and the wide range of motivations for humans to transport bird species outside of their native ranges, has led to a diverse selection of bird species being introduced (Blackburn *et al*. 2009a). In addition, birds are taxonomically well-described, and have had their native distributions mapped at the global scale (Orme *et al.* 2005).

This database on alien bird species distributions derives from both published and unpublished sources, including atlases, country species lists, peer-reviewed articles, websites and via correspondence with in-country experts. The underlying data consist of individual records, each concerning a specific alien bird species introduced to a specific location, and where possible with an associated distribution map. The database forms the core of the GAVIA (Global AVian Invasions Atlas) project. Ultimately, the aim is to make these data available to other interested parties, through existing resources available at ZSL and UCL. The data contained within GAVIA constitute a large evidence base for the analysis of spatial and temporal patterns in alien bird distributions, and will be an important resource for scientists interested in understanding the invasion process. GAVIA should also help conservation bodies and policy makers to understand where and why invasions are continuing to occur, and so ultimately contribute to efforts to stem the process and ameliorate its impacts.

This chapter introduces the database, describes in detail how it was: (1) collated, validated and curated; (2) how the alien distribution range maps were produced; and (3) assesses its taxonomic, geographic and temporal coverage.

2.2 METHODS

2.2.1 Data compilers

I was solely responsible for the database design and all data searching and collation (with the exception of 5,074 records previously collated by a technician working for T.M. Blackburn in 2006/7). A team of four interns and one project assistant were tasked with the data entry, distribution mapping and cross-validation; I was solely responsible for supervising their work (see Acknowledgements).

2.2.2 Criteria for data inclusion

To be included in the database, records had to meet *both* 1) and 2) from the following criteria, and then *either* 3) or 4) or 5):

1. The record related, at the minimum, to the country level presence of an alien bird species
2. The record identified, at the minimum, the genus to which the bird concerned belongs
3. The record referred to a bird species that had been introduced (either purposefully or accidentally) into an area outside of its native range
4. The record referred to a bird species that had spread to a new area beyond its native range from an adjacent introduced population
5. The record referred to a bird species introduced into an area outside of its historical native range for the purposes of conservation

Records excluded from the database included:

- Single escapees (unless there was an introduced population already present), for example, the blue-and-yellow macaw (*Ara ararauna*) seen flying down Berkhamstead High Street (Tim Blackburn, pers.comm. 22/05/15).
- Migratory bird species occurring as vagrants.
- Records referring to bird species that have naturally expanded their native range into areas immediately adjacent to their original range (e.g. the collared dove (*Streptopelia decaocto*) in Europe).

A key feature of the GAVIA database is that it contains information on all introduction events, and not only those resulting in establishment. This will enable future research to incorporate a measure of colonisation pressure into analyses, a variable that is an important determinant of alien species richness (Lockwood *et al*. 2009) but is usually unavailable.

2.2.3 Data searches

To ensure that equal effort was assigned to gathering data from all regions of the globe, and for all species, the globe was divided into the following regions: North America, Central America and the Caribbean, South America and Antarctica, Europe, Africa, Central Asia, Southeast Asia, and Australasia and Oceania (figure 2.1).

Searches were then conducted for each region in turn, and more general searches were undertaken in order to capture data from global resources.

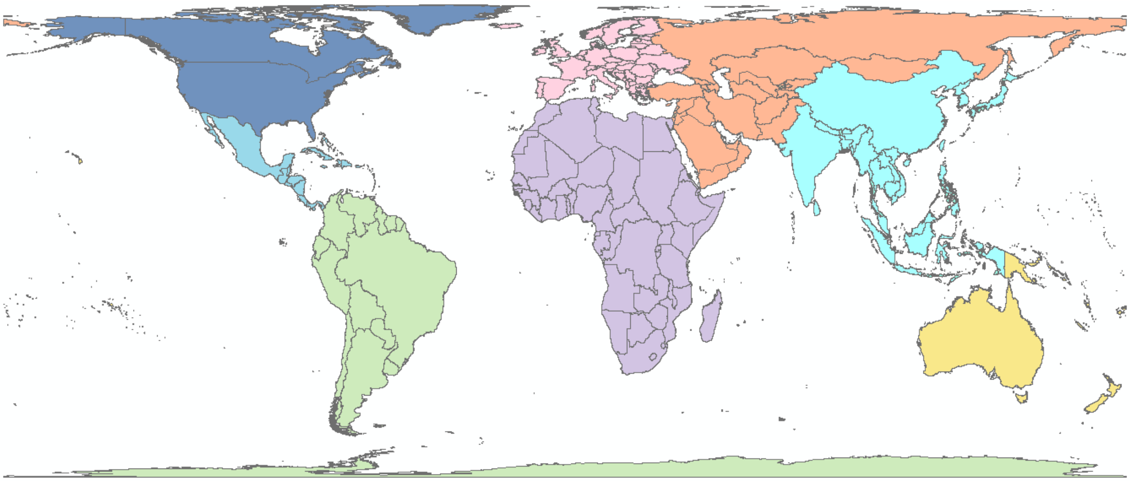


Figure 2.1 A demonstration of how the regions of the world were divided up for the purposes of data searching and collation. Each region was focussed on in turn in order to ensure that no countries were missed. The regions were labelled as follows: North America, Central America and the Caribbean, South America and Antarctica, Europe, Africa, Central Asia, Southeast Asia, and Australasia and Oceania.

Online searches of published literature were conducted using Google Scholar, Science Direct, JSTOR and Web of Science. One by one the words ‘invas*’, ‘introduc*’, ‘alien’, ‘exotic’, ‘non-native’, and ‘establish*’ were used to search the literature, together with the name of the region, or the names of the individual countries within that region. Initially these broader invasion biology terms were used in order to pick up more general multi-species studies. Subsequently, the words ‘bird’, ‘avian’ and ‘ornitholog*’ were included in turn. For widely known introduced bird species, a search was conducted using both their binomial and common name(s), e.g. ‘*Acridotheres tristis*’, ‘Indian myna’, ‘common myna’. If the papers or other sources identified from these searches could not be downloaded digitally, then the COPAC national library catalogue (http://copac.ac.uk) was used to identify libraries at which hard copies could be obtained.

The reference lists in these articles were searched to identify further papers or books which may have contained useful information. Hard copies of references came from the Zoological Society of London’s library, the Natural History Museum libraries in London and Tring, Oxford University’s Bodleian and Ornithological (Alexander) libraries, and the British Library. During visits to the libraries listed above, the zoological and ornithological sections were also searched, as well as every country or taxon-specific bird guide, in addition to books relating to invasion biology. As well as articles written in English, articles written in Spanish, German and Mandarin – languages in which one or more of the team of compilers were proficient – were also considered. In addition to published literature searches, the same search terms described above were entered into Google to identify relevant online datasets or country-level species lists which may have contained records of alien bird species.

The names and contact details of people or organisations that were potential sources of information were gleaned from the above literature, and websites (www.europe-aliens.org/expertSearch.do, www.birdlife.org/worldwide/partnership/birdlife-partners) were also used to identify possible experts on alien bird distributions. These contacts were emailed by or on behalf of myself to inform them about the GAVIA project, and to enquire as to whether they knew of any alien bird resources based in their region, or if they knew of anyone conducting similar work. In total, 603 experts from 155 countries were contacted, and useful replies were received from 201 experts from 85 countries. These personal communications proved to be an invaluable resource providing unpublished data and local information, as well as suggestions of obscure published works, or further contacts interested in similar issues.

2.2.4 Database design

GAVIA was compiled in the programme Microsoft Access 2010. It was completed in March 2014. Each entry in GAVIA corresponds to a single record of a single species recorded as introduced and non-native in a specific location as published in a single reference. The data fields of the GAVIA database are described in table 2.1. For the sake of minimising repetition, it was decided at the design stage that only ‘new’ data on the actual introduction and invasion events themselves would be collated in GAVIA. Data that would be useful for analytical purposes but which was already recorded elsewhere (e.g. life history data) would not be repeated there. To minimise errors and to reduce the size of the resulting database, supplementary datasets for taxonomy and geographical regions were embedded, and linked to the database via ‘look-up’ tables. This meant that each taxonomic or geographical name was selected through a drop-down list and did not have to be typed repeatedly. This not only significantly reduced the size of the database, and therefore the necessary storage capacity, but also reduced the likelihood of inputting errors. The resulting selection is recorded in the database as an ID number which relates to the species name or country.

Table 2.1 Data fields in GAVIA. 'Field Name' shows the GAVIA column headings, 'Field Type' denotes what kind of data entry is possible for that field, and 'Description of Contents' describes what kind of information is recorded in that field. For Field Type, an 'Autofill box' is one which is filled in automatically once a new record is created. For example, each new record is awarded its own unique ID number which cannot be chosen or edited. When a binomial is selected, the respective unique species ID and common name boxes are also automatically filled in and cannot be changed or edited unless a new binomial is selected. A 'Look-up table' field type means that the information in that box has been selected from an embedded table, for example the taxonomic list or the GADM country list. In other words there are a finite number of selections from which to choose, and the contents of these cells cannot deviate from the contents of the respective look-up tables. A 'Free Text' or 'Free Number' box means that the data compiler can freely enter whatever text or number that they wish. A tick box provides the compiler with a certain number of selections, for example island type, and the compiler then ticks the relevant box. An 'EndNote Citation code' relates only to the references recorded in GAVIA, and this information links to the full references recorded in the GAVIA EndNote library.

Field Name	**Field Type**	**Description of Contents**
RecordID	Autofill box	A unique number for that particular record. Each corresponding individual map also carries this number. This number never changes, even if previous records are deleted.
SpeciesID	Autofill box	A unique number for each individual species.
Binomial	Look-up table	The binomial of that species, as per the taxonomy accepted by the IUCN and BirdLife.
Common_name	Autofill box	The common name of that species, as per the IUCN and BirdLife.
CountryName	Look-up table	The name of the country in which that record occurs as per the GADM designations.
AreaName1	Look-up table	The first sub-level down from country, e.g. region/state, in which that record occurs, as per GADM designations.
AreaName2	Look-up table	The second sub-level down from country, e.g. sub-region/city, in which that record occurs, as per GADM designations.
LocationDescription	Free text box	A specific description of where the record occurs, if it cannot be selected from AreaName 1 or 2.
Realm	Look-up table	The biogeographical realm in which that record occurs, as per the Olson *et al.* (2001) delineations.
Island	Tick box	Whether the record occurs on an island or not.
LandType	Look-up table	The type of land that the record occurs on, choices being mainland, continental island or oceanic island.
IntroducedDate	Free text box	The date that the species was first introduced (if known), written exactly as found in the reference, e.g. 'late 17th century'.

IntroducedDateGrouped	Free number box	The date that the species was first introduced (if known), converted to a number, e.g. 'late 17th century' would become 1690. Guidelines were produced to aid this, so that all transformations were consistent (table 2.3).
Mapping_date	Free number box	The date that the map which corresponds to that particular record represents. For example, the introduced date will stay the same for all individual records from that reference, but as the species spreads over time, the mapped date will change to reflect the newly colonised areas. If there are no dates mentioned at all within the reference, then the date that the reference was published is used as the default mapping date.
ReferenceDate	Free number box	Rarely used. If there is no date of introduction recorded, but the reference referred to is a significantly 'old' date, then this is recorded so that it is at least an indication of how long the species has been present in that region.
StatusCat	Look-up table	The status of the species in that record, e.g. established, died out etc. (table 2.2).
IntroMethod	Look-up table	How the species was introduced. For example it was released, or it escaped etc.
IntroPurpose	Look-up table	Why the species was introduced. For example it escaped from a zoo, or was released for hunting purposes.
GISFileName	Free text box	Whether or not the record has a corresponding distribution map. Either Mapped or Not Mapped. If Not Mapped, it means that it will never be mapped, as the data is deemed too broad scale or vague. NB. During the early stages of the project before the maps were created, this box was also used to record whether or not the species had a photocopy of a hard copy map taken from the reference stored for future use.
TaxonomicNotes	Free text box	Any taxonomic information relevant to that record.
Notes	Free text box	Relevant additional notes relating to the record that can't be entered by using one of the above fields, e.g. it might specify numbers of birds released, or specific paths of species spread etc.
Reference	EndNote citation code	Where the information was found, this links to the GAVIA EndNote library.
CompilerFullName	Look-up table	The name of the person responsible for compiling that record in the database (not who created the final map).

Table 2.2 Definitions of alien status categories in GAVIA.

Established	The species has formed self-sustaining populations in the area of introduction
Breeding	The species is known to be breeding/have bred in the area of introduction, but is not thought to be self-sustaining
Unsuccessful	The species has not formed self-sustaining populations (casual, incidental)
Died Out	The species was once established but has now completely died out in the area of introduction.
Extirpated	The species was once established but has now been actively exterminated in the area of introduction.
Unknown	The status of the species in the area of introduction is not known and further clarification is necessary to determine which of the other 5 categories is appropriate.

The full bird taxonomy used in GAVIA was that used by the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species (www.iucnredlist.org, downloaded August 2010). The country and regional designations used in GAVIA were downloaded from the Global Administrative Areas (GADM) database (www.gadm.org, downloaded August 2010). References were recorded using EndNote citation software (version X4, Thomson Reuters 2010). In a further effort to reduce human error and save computational space, only the first surname, year and EndNote code were recorded in GAVIA, which were then linked back to the full reference in the EndNote database.

Six categories were used in GAVIA to describe the invasive status of each alien species, and definitions of these are provided in table 2.2. These categories were chosen to cover all of the ways in which an alien species may be described as being present in a location. An ‘Unknown’ category was necessary as sometimes, even after communicating with experts, it was not possible to assign a species’ status in a certain area to one of the other categories. The opportunity exists to update these cases if and when their status can be clarified.

Table 2.3 demonstrates how dates of introduction were recorded in the GAVIA database. Often in the literature, a date is approximated, or described in a way that is not a four-digit year. In order to maintain the integrity of the reference, the date was first recorded exactly as given in the reference (e.g. ‘early 1700s’). To make the date usable in later analyses, it was also converted to a four-digit number (in the preceding example, this would be 1710) (table 2.3).

Table 2.3 Guidelines used for converting the introduced date given in the reference into a whole number.

Date given	Grouped (converted) date	Rule
1912	1912	Use the four digit number as given
c.1890	1890	Use the four digit number given
1777-1778	1777	Use the earliest date in the range
1930-1940	1935	Use the midpoint of the range
C18th	1750	Use the midpoint of the century
early C18th	1710	Use the date 10 years into the century
mid C18th	1750	Use the midpoint of the century
late C18th	1790	Use the date 10 years before the end of the century
1800s	1850	Use the midpoint of the century
c.1800s	1850	Use the midpoint of the century
1990s	1995	Use the midpoint of the decade
early 1700s	1710	Use the date 10 years into the century
mid 1700s	1750	Use the midpoint of the century
late 1700s	1790	Use the date 10 years before the end of the century
early 1990s	1991	Use the first year of the decade
mid 1990s	1995	Use the midpoint of the decade
late 1990s	1999	Use the last year before the end of the decade
1980s-1990s	1990	Use the midpoint of the two decades
<1965	1964	Use the date immediately before the date given
>1970	1971	Use the date immediately after the date given

All converted dates were Anno Domini, although four records had dates of introduction earlier than 1000AD, and were consequently converted to three digit numbers. All records with dates of introduction Before the Common Era (BCE) were too vague to convert to a usable date. These guidelines ensured that all data compilers recorded dates in the same fashion.

2.2.5 Data entry

At the time of data collection and entry, all information was entered into the database exactly as it was described in each reference, with as much information extracted as possible. Multiple records from different authors who had recorded the same information were still included in the interests of completeness.

In total, seven data recorders were involved with entering data into the GAVIA database including the author, four interns, one project assistant and the previously mentioned technician. To maximise uniformity in data entry, all data recorders were given thorough and consistent training, and each was provided with a set of database guidelines (see appendix A). In addition, spot checks were regularly carried out on all database entries, and weekly meetings of the GAVIA team were held to address inconsistencies.

An Access Database form was created to standardise data entry, and this also enabled multiple members of the team to enter data simultaneously (figure 2.2a,b,c). This form was divided into three sections: Taxonomy, Distribution and Introduction. When a new record was created, the form automatically assigned a unique record ID number. The compiler then selected their own initials from a drop down box, to indicate that they had completed that entry, and they also selected the relevant reference from the EndNote bibliography to add to the form. Where available, the following data were entered into the GAVIA database for each record under each section tab (figure 2.2a,b,c; see table 2.1 for full details):

Taxonomy tab

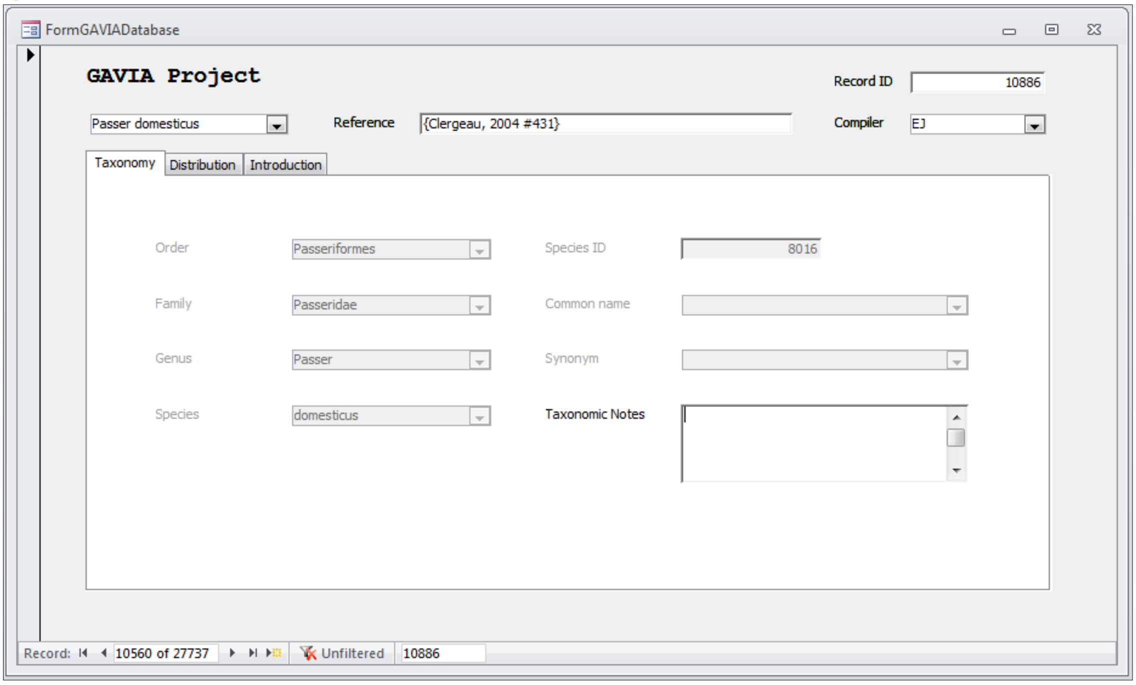
6. The species' binomial was selected from a drop down list, and this then automatically filled in the appropriate Order, Family, Genus, Species, species ID, common (English) name, and any synonyms.
7. A free text box titled 'Taxonomic Notes' allowed the complier to enter any additional information regarding the taxonomy of the species in question, for example if it was thought to be a certain subspecies, or if the identification was uncertain.

Distribution tab

8. The drop down boxes 'Country', 'Area Name 1', and 'Area Name 2' are the country, state and sub-state level delineations available for selection by the compiler. These areas match up to the GADM spatial layers used in the distribution maps relating to each database record.
9. The free text box 'Location Description' is used for additional information regarding the location of the record. For example, it could specify a location not included on the GADM list, or it could provide additional directions such as 'the area of National Park between town A and town B'.
10. The compiler can then select the biogeographical realm within which the record lies, and can also record the land type (mainland, oceanic island or continental island), and select the 'Island' tick box if the record occurs on an island of either type.

Figure 2.2

a)



GAVIA Project

Record ID: 10886

Passer domesticus

Reference: {Clergeau, 2004 #431}

Compiler: EJ

Order: Passeriformes

Species ID: 8016

Family: Passeridae

Common name:

Genus: Passer

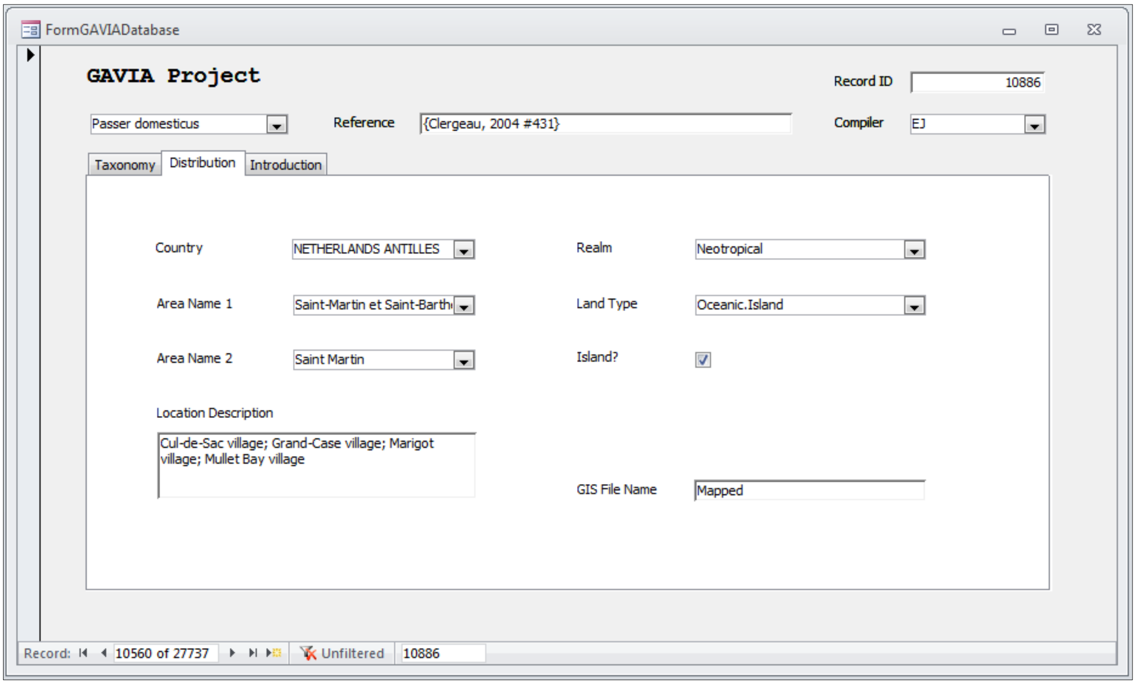
Synonym:

Species: domesticus

Taxonomic Notes:

Record: 10560 of 27737 Unfiltered 10886

b)



GAVIA Project

Record ID: 10886

Passer domesticus

Reference: {Clergeau, 2004 #431}

Compiler: EJ

Country: NETHERLANDS ANTILLES

Realm: Neotropical

Area Name 1: Saint-Martin et Saint-Barth

Land Type: Oceanic.Island

Area Name 2: Saint Martin

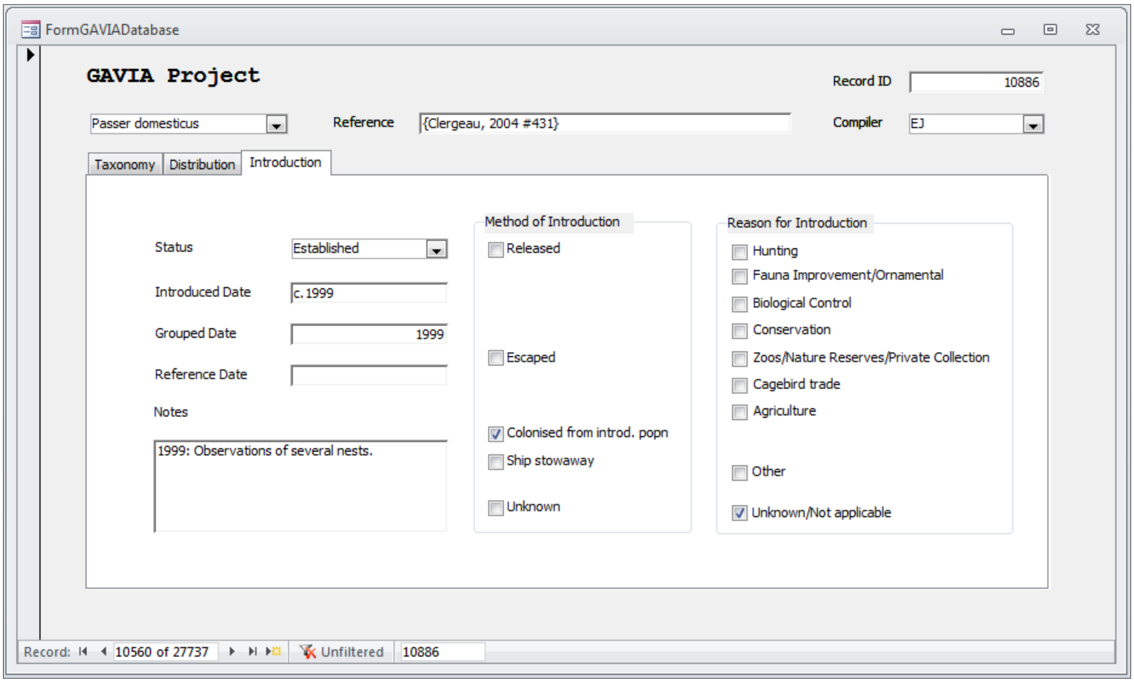
Island? ☑

Location Description: Cul-de-Sac village; Grand-Case village; Marigot village; Mullet Bay village

GIS File Name: Mapped

Record: 10560 of 27737 Unfiltered 10886

c)



GAVIA Project

Record ID: 10886

Passer domesticus

Reference: {Clergeau, 2004 #431}

Compiler: EJ

Status: Established

Introduced Date: c. 1999

Grouped Date: 1999

Reference Date:

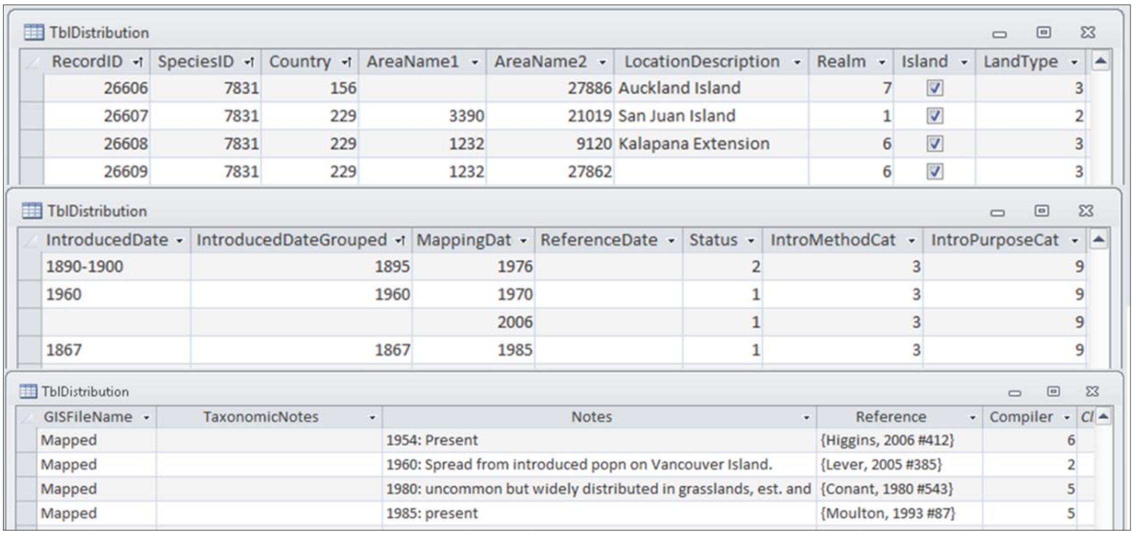
Notes: 1999: Observations of several nests.

Method of Introduction
- ☐ Released
- ☐ Escaped
- ☑ Colonised from introd. popn
- ☐ Ship stowaway
- ☐ Unknown

Reason for Introduction
- ☐ Hunting
- ☐ Fauna Improvement/Ornamental
- ☐ Biological Control
- ☐ Conservation
- ☐ Zoos/Nature Reserves/Private Collection
- ☐ Cagebird trade
- ☐ Agriculture
- ☐ Other
- ☑ Unknown/Not applicable

Record: 10560 of 27737 Unfiltered 10886

Figure 2.2 *(Also previous page)* The GAVIA database data entry form, designed for ease of use, it enabled multiple members of the team to enter data concurrently. **a)** The taxonomy tab for information relating to the species. This was populated automatically once the species binomial was selected from the drop down box in the top left corner. **b)** The distribution tab where information relating to the details of the location of introduction were recorded. **c)** The introduction tab for information relating to details of the introduction event itself.



TblDistribution

RecordID	SpeciesID	Country	AreaName1	AreaName2	LocationDescription	Realm	Island	LandType
26606	7831	156		27886	Auckland Island	7	☑	3
26607	7831	229	3390	21019	San Juan Island	1	☑	2
26608	7831	229	1232	9120	Kalapana Extension	6	☑	3
26609	7831	229	1232	27862		6	☑	3

TblDistribution

IntroducedDate	IntroducedDateGrouped	MappingDat	ReferenceDate	Status	IntroMethodCat	IntroPurposeCat
1890-1900	1895	1976		2	3	9
1960	1960	1970		1	3	9
		2006		1	3	9
1867	1867	1985		1	3	9

TblDistribution

GISFileName	TaxonomicNotes	Notes	Reference	Compiler	Cl
Mapped		1954: Present	{Higgins, 2006 #412}	6	
Mapped		1960: Spread from introduced popn on Vancouver Island.	{Lever, 2005 #385}	2	
Mapped		1980: uncommon but widely distributed in grasslands, est. and	{Conant, 1980 #543}	5	
Mapped		1985: present	{Moulton, 1993 #87}	5	

Figure 2.3 An example of how the 21 columns of information are presented in the main distribution table of the GAVIA database. All information entered into the data entry form (figure 2.2a,b,c) is stored in a numbered format in this table, with the exception of the free text boxes, for example ‘LocationDescription’ which are stored as written.

11. The GIS File Name box is used to identify whether or not that record contains enough detail to be converted into a distribution range map. At the data entry stage, this box was also used to record whether or not the reference included a distribution map of the species, in which case it was photocopied or printed and stored for later use.

Introduction tab

12. The status of the species is selected from a drop down list (table 2.2).
13. There are four different date boxes available to the compiler, although ‘Mapping date’ is not included in the data entry form as it is only relevant at the later mapping stage. The ‘Introduced Date’ is the date exactly as recorded in the reference. ‘Grouped Date’ is the introduced date converted to a whole number (if necessary) using the standardised system as described in table 2.3. ‘Reference date’ is rarely used, but useful if the record does not include a date of introduction, yet the reference in question is sufficiently old enough to warrant the inclusion of the publication date as an indication of timescale. For example, if the reference was written in 1910, even if it does not state a specified date of introduction it is possible to deduce that the bird was present in that location over a hundred years ago. ‘Mapping date’ refers to the date of any associated distribution map(s). For example, a source may describe a species as having been introduced to a location in the year 1900, but also record that the species had spread to a much larger range size by the year 1950. In this case, two records would be created, resulting in two distribution maps. The first record would have both the date of introduction and the mapping date as 1900, and the map would relate to the distribution of the species at this time (i.e. the location of introduction). The second record would also have the date of introduction as 1900, but the mapping date would be 1950, and the associated map would relate to the subsequent (presumably larger) distribution. If there were no dates mentioned at all within the reference, then the date that the reference was published was used as the default mapping date.
14. The free text ‘Notes’ box is for recording additional relevant information, for example details of spread, or an estimate of population health.
15. Under ‘Method of Introduction’ and ‘Reason for Introduction’, tick boxes allow the compiler to record how and why the species was recorded, if this information is available.

The Access form acts as an entry portal for data, but the resulting records are stored in an Access table, with each selection from the drop down menus stored as a number; the only text stored is from the free text boxes (figure 2.3). This reduces the size and complexity of the database, and reduces the likelihood of errors. An Access query can be run to extract specific information, or to view the entire database in its readable text format.

Where a reference provided information for multiple species or countries, individual records were created for each species-country pair. Information sent to us in email form from experts was recorded in the Endnote library as 'pers. comm.' and entered accordingly into the main database.

2.2.6 Taxonomic names and classification

It was necessary to be able to identify taxa in the database as accurately as possible, and without losing any information. It was also necessary to be able to place each species within the avian phylogeny. Therefore, I required a stable and authoritative resource for nomenclature, which included species whose status may be unclear. The database taxonomy was based on that agreed by the IUCN Red List of Threatened Species at the time of database creation (2010). There were several reasons for this choice. First, this taxonomy follows that used by Birdlife International, whose in-country partner organisations were an invaluable source of information during the data collection stage. Second, the taxonomy was easily obtainable and downloadable, in a format that matched the GAVIA database with minimal reformatting required. Third, the taxonomy provided a single accepted classification for each species. Fourth, the taxonomy included species for which taxonomic status was undecided. This was important because I did not want to exclude records of introduced birds because the taxonomy of the species in question was uncertain. Finally, the IUCN taxonomy is a consensus, and not dependent on the views of a particular taxonomist.

Two species with records in GAVIA were not included on the IUCN taxonomy: the Javan myna (*Acridotheres javanicus*) and the Barbary dove (*Streptopelia risoria*). The taxonomy of these species is in dispute (Lovette *et al*. 2008, Sangster *et al*. 2013), but as there were substantial records of individuals assigned to these taxa being introduced, the decision was made to add their names to our taxonomic list. If in the future their species status is agreed upon then the records can be updated accordingly.

Where a species name stated in a reference was a synonym for one included in the IUCN taxonomy, the accepted species name was selected on the Access form, and the synonym used in the reference was written in the ‘Taxonomic Notes’ section. Where a subspecies was mentioned in the reference, the record was listed under the species name, and the subspecies was also recorded in the ‘Taxonomic Notes’ section. There are 11 records in the GAVIA database with no attributed species name. This was generally in cases where the reference referred to a species only by its common name which cannot be matched to a species in our taxonomy, and an online search does not result in a definite identification. Examples include ‘Chinese partridges’ and ‘English pheasant’. When a full species count is performed on the database, these records are excluded.

The use of a drop-down list for selecting the species name on the data entry form, with the higher taxonomy then automatically entered, resulted in minimal errors and inconsistencies when inputting species names. Any typographical errors in the original reference (e.g. misspelling of species names) were again recorded in the ‘Taxonomic Notes’ text box.

2.2.7 Biogeographical coverage

Alien bird records were compiled for 230 countries and administrative areas from all biogeographical realms (although only offshore islands from the Antarctic realm have records - there are no records (yet) for the Antarctic continent). Realm delineations followed those set out in Olson *et al*. (2001) (figure 2.4). There were seven countries for which records were not obtained (appendix B). A concerted effort was made to identify any alien birds introduced to these missing regions, and so I am confident that I can rule out a lack of effort as the reason for the lack of records. However, it is not known whether it is actually the case that no alien birds have been introduced to these places, or whether they have but either no one has recorded them, or these records have not yet found their way into the public domain.

In order to maintain continuity, the list of country units defined in the GADM database were used in the GAVIA database (‘Country’, ‘Area Name 1’ and ‘Area Name 2’), and the corresponding GADM GIS layers were used to produce the resulting range maps.

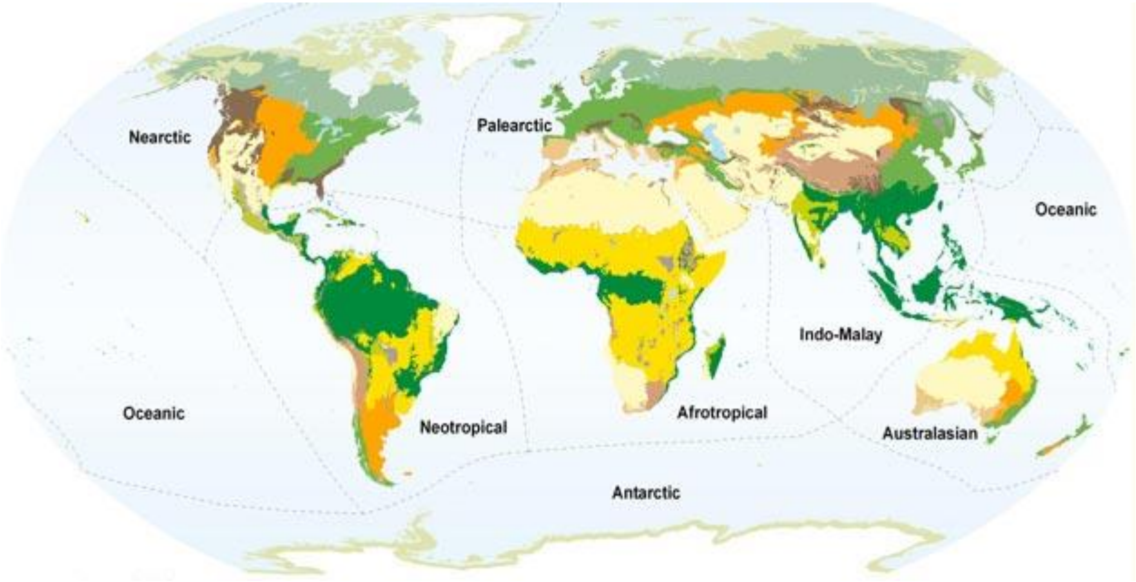


Figure 2.4 The 8 biogeographical realms used in Olson *et al*. (2001), and which were followed by GAVIA for the purposes of assigning alien ranges to realms.

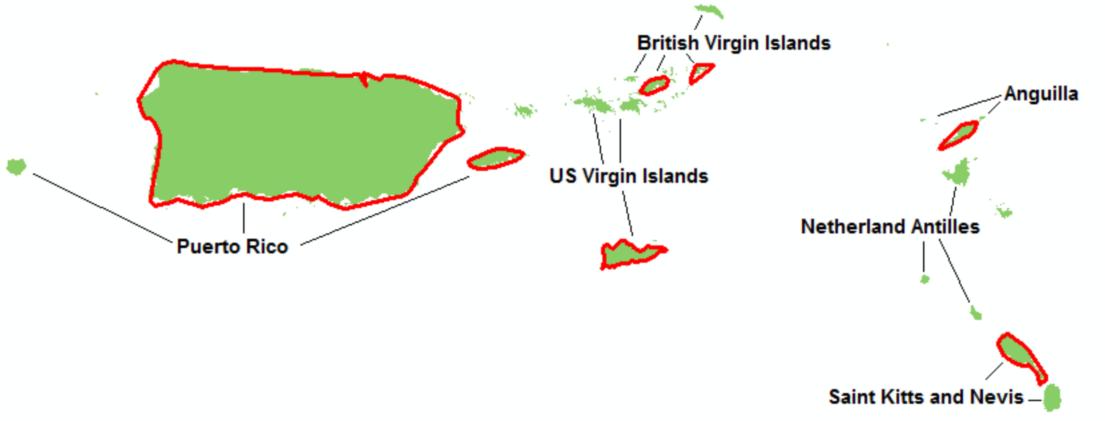


Figure 2.5 A cropped map of islands in the Caribbean demonstrating the variation between a coarse scale GIS base map (red outline), and the fine scale GIS base maps provided by the GADM shapefiles used in GAVIA (green infill). Not only does the coarse scale base map simplify the coastline of landmasses, it also misses out some islands entirely, or in this case an entire administrative area: Netherland Antilles.

These are very fine scale GIS layers, with extremely detailed borders, coasts and island groups. This inevitably led to a considerable increase in the computational memory and storage space required for the maps, and more importantly the processing time for analysis. However, this level of detail was deemed necessary as many alien bird species have been introduced to islands or coastal areas, locations which are simply missing from lower resolution GIS layers (figure 2.5). Had a coarser scale base map been used, not only would it have proved difficult to map some of these coastal or island records, but any subsequent analysis involving range size calculations would have been inaccurate.

2.2.8 Distribution range maps

Introduction records were converted into distribution maps using the software ESRI ArcGIS version 9.3 (2008). All records containing a high enough level of detail to create an accurate estimation of distribution range (as defined in appendix C) were converted into maps, regardless of alien status. All team members involved in this activity received 2-3 days of training beforehand using the training manual created by the Indicators and Assessments Unit for internal use at the Zoological Society of London (Smith *et al*. unpubl.).

In addition to this training, team members received a set of guidelines to follow (appendix C), and I would spot-check a random sample of distribution maps created by the team each week to identify any errors or inconsistencies. Any problems were worked through at weekly meetings. This was to ensure, as far as possible, that all team members created distribution maps in a uniform manner.

At the beginning of the mapping process, a spreadsheet was created called ‘Map Master Sheet’, which contained a list of all of the names of the species recorded in the GAVIA database, together with the number of records for each one. Each member of the team was assigned a set of species with a roughly equal total number of records, and their initials were placed next to their respective species on the spreadsheet. I took responsibility for those species with the highest number of records, for which mapping was likely to be the most complicated.

One of the anticipated problems with having multiple team members accessing the GAVIA database at the same time was the risk of them simultaneously editing the same record, such that one entry would overwrite the other. To prevent this from happening, each member of the team was assigned their own Access query which they could use to extract data from the database. A normal Access query enables the user to view a subset of information from a database, but the data cannot be edited through the query. Therefore there was no risk of a team member accidentally editing records or overwriting another team member's changes. If a team member did want to open or edit the main Distribution table containing the raw data (figure 2.3), they first had to check verbally that no one else was using it or had it open on their screen. In order to keep the team's files and folders as consistent and logical as possible, all team members followed the guidelines provided to them (appendix C) and adhered to a strict system of file and folder labelling and backing-up.

To create a distribution map, a team member would select one of their assigned species from the spreadsheet and create a folder on their desktop labelled with the species' binomial. They would then run their query in the GAVIA database using the ID number of their particular species in order to view all of the information available for that species. The staff member would then review this information to make a decision on which records were to be converted into range maps (based on the level of information provided in the record). After adding this information back into the main distribution table, the query would be re-run and the output would be copied and pasted into an excel spreadsheet, saved in the desktop folder under the name of the species binomial, and used as the basis for the attribute table for the distribution map. A search would then be run through the GAVIA folders to check that no range maps had previously been created for that species, and also whether there were any hard-copy maps printed or photocopied from distribution references. The team member would then use ArcGIS software to create the distribution maps, producing a spatial polygon to correspond with each of the records in the database.

The GIS base-layers used were downloaded from www.gadm.org. The website www.geonames.org was used to identify latitude and longitude points for place names, so that they could be plotted. If a hard copy map existed then it was scanned and georeferenced. If the location description only provided information for a single city or point then a 10km buffer was created around it in order to produce a range polygon. Each map file was labelled with the species' name and record ID. Once all records for a species were converted into range maps, the files were merged together and combined with the previously created attribute table (containing all of the data for that species extracted from the GAVIA database) and saved as a single shapefile uploaded into the main GAVIA folder. All of the earlier versions of the species map were kept in a drafts folder, also uploaded from the desktop onto the server. Team members recorded the number of distribution maps they created each day so that progress could be measured, and a back-up of the database was made at the end of every day, and of the entire GAVIA folder at the end of every week.

Some records in GAVIA needed to be split before they could be mapped. For example, a record may have stated how the distribution of the species has changed over time. In such cases, multiple maps needed to be created to plot this change. Full details of how this was done are given in appendix C. Conversely, some records in GAVIA were deemed not to contain enough detail to warrant conversion into distribution maps. It was important that the resulting distribution maps were as detailed as possible, but were also mapped to a comparable level of detail. If the record only stated the country in which the species was introduced, without further specification of location, then it was recorded as being ‘Not mapped’ in the GISFileName box. Exceptions to this rule were if the country was particularly small (e.g. Singapore, Hong Kong), or if it was a small island (e.g. the majority of the Pacific islands).

Distribution maps were created to the minimum possible range size so as to not over-estimate a species’ distribution. When combined, the distribution maps represent the species’ Extent of Occurrence rather than Area of Occupancy (Gaston & Fuller 2009), and the species are unlikely to be extant in every part of their mapped range, particularly those areas where their status is not established. The distribution maps were projected using the World Behrmann equal area projection so that accurate range size estimates could be calculated. Where a species’ distribution needed clarification (e.g. if two seemingly reliable references contradicted each other), then one of the in-country experts who provided information at the data gathering stage was invited to verify the distribution map.

2.2.9 Cross validation between database and distribution maps

The final stage of the project required all of the distribution maps to be cross validated against the database. This was carried out by a single team member in an effort to lessen any inconsistencies that might be introduced into the database by different team members. Each species was addressed in turn. Consistency checks were carried out on the records in GAVIA, and then the distribution maps were verified to ensure that they corresponded to the information in the database. In addition to these checks, each species’ alien distribution map was checked against its native range map (representing native global breeding range) extracted from the database used by Orme *et al.* (2005). This was to ensure that there was no overlap, for example regions where a species was native but it had been recorded as introduced or vice versa. Necessary changes were made to both the database and the distribution maps, and a new 'final' copy of each species map was saved.

2.3 RESULTS

Between July 2010 and March 2014, 27,737 alien bird records were collated, representing 972 species, from 230 countries and administrative areas across all eight biogeographical realms, spanning the period 6000 BCE – AD 2014. These records are based on 693 published references and substantial unpublished information derived from consultation with more than 600 organisations and experts worldwide.

Data coverage of the globe was extensive. Only seven countries had zero records of introduced birds in GAVIA (figure 2.6). Once the records were converted to distribution maps, areas with relatively low numbers of alien birds or no recorded introductions included areas close to the poles (Greenland, northern Russia, far northern Europe, northern Canada, Antarctica), deserts (parts of the Sahara, western and central Australia, the Gobi desert, the Arabian desert), mountainous areas (parts of the Andes

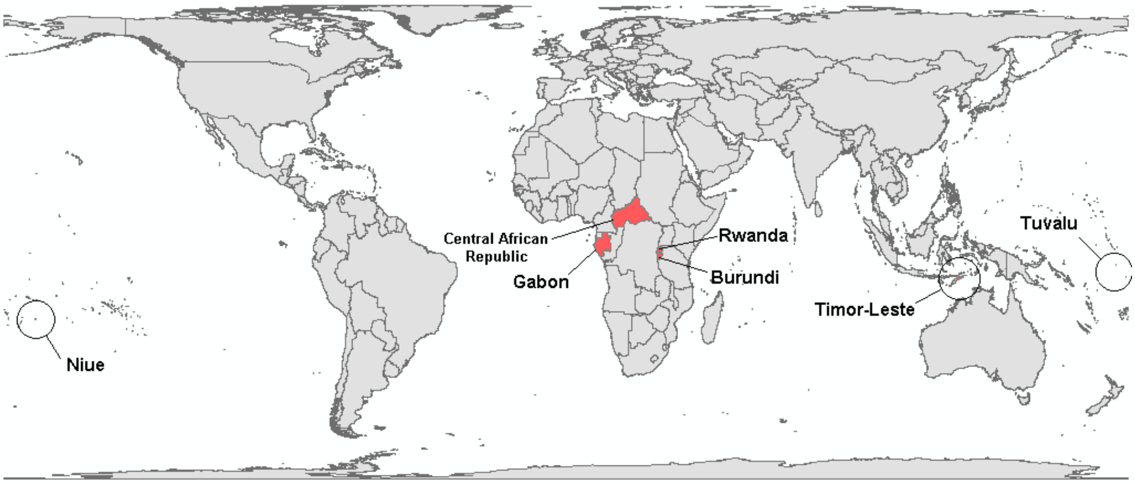


Figure 2.6 The global coverage of the distribution of records in GAVIA at a country level (grey), highlighting the seven countries with zero records of introduced bird species (red).

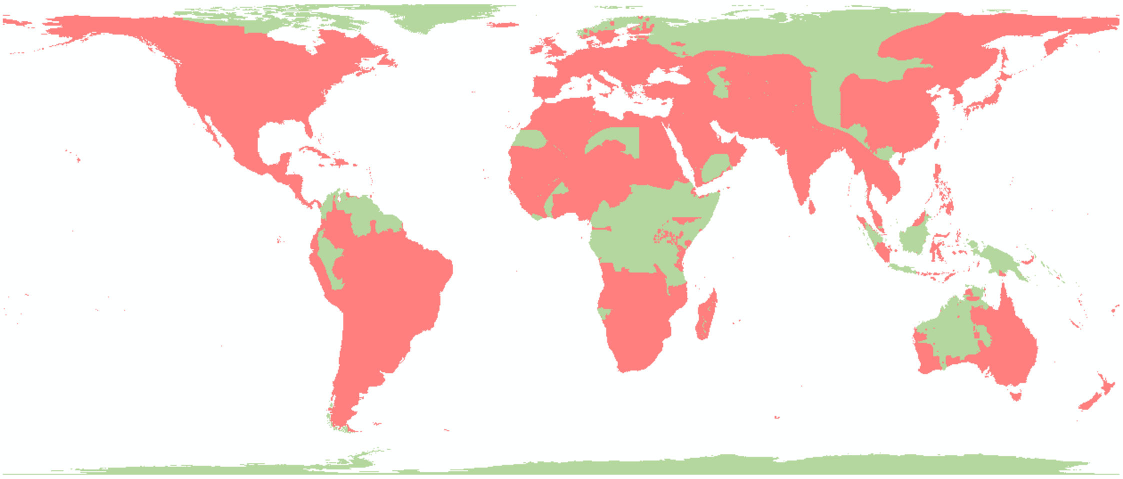


Figure 2.7 The global distribution of those records in GAVIA that contain sufficient information to have been converted into distribution maps. These include all status categories, so introductions that have both succeeded and failed.

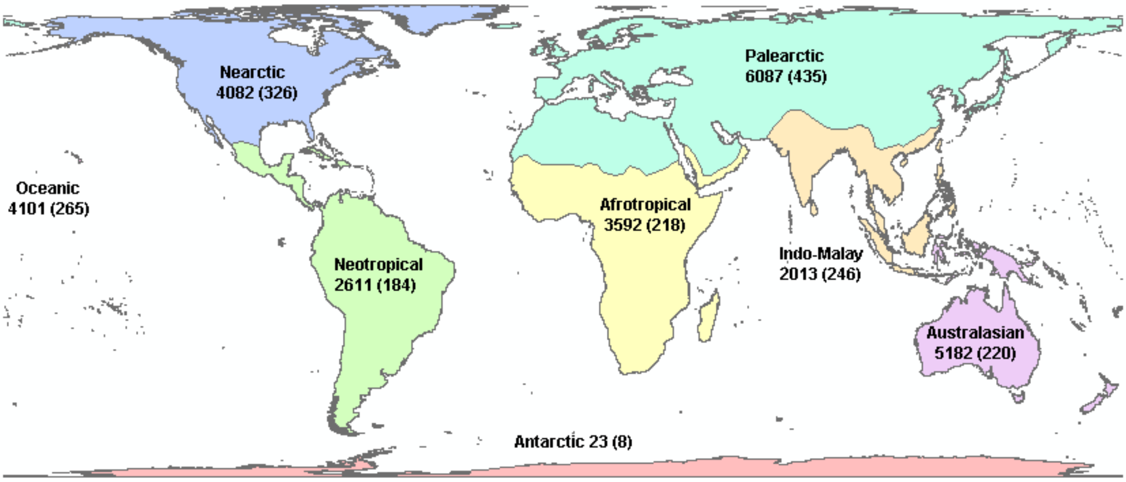


Figure 2.8 The biogeographical realms to which all records in GAVIA are assigned. The first number is the number of records in GAVIA for each realm, and the number in brackets is the number of species recorded as being introduced in each realm.

and the Himalayas), and parts of the tropics (northern South America, central Africa, and parts of Indonesia, Borneo and Papua New Guinea) (figure 2.7). For those records where a land type was assigned, 44% related to oceanic islands (12,196 records), 40% related to mainland locations (11,148 records) and 16% to continental islands (4,260). The best-represented biogeographical realms are the Palearctic (6,087 records, 22% of all records, 435 species), Australasian (5,182, 19%, 220 species), Nearctic (4,082, 15%, 326 species) and Oceanic realms (4,101, 15%, 265 species) (figure 2.8).

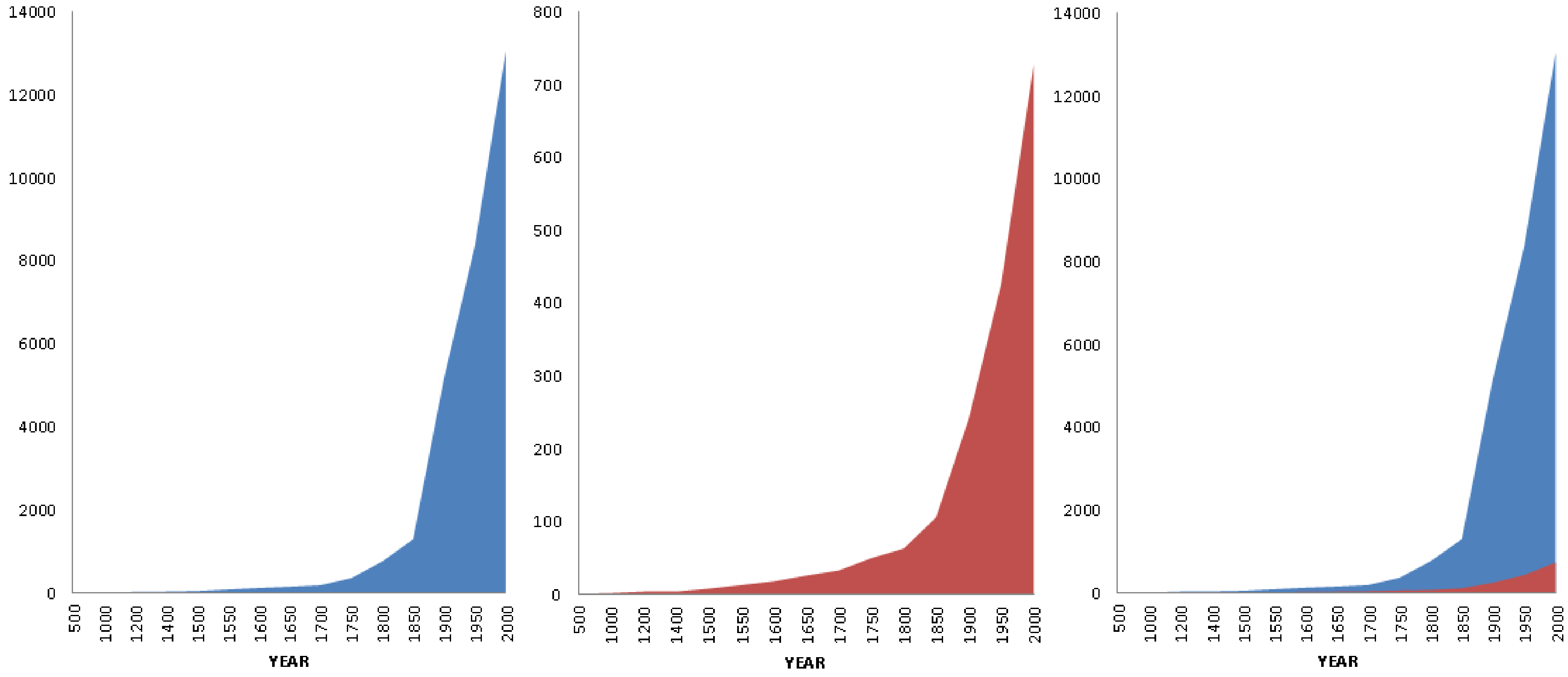


Figure 2.9 (a) The cumulative increase in the number of records in the GAVIA database over time; **(b)** the cumulative number of species recorded in the GAVIA database over time; and **(c)** both the number of records and species plotted together. Blue is the number of records, red is the number of species.

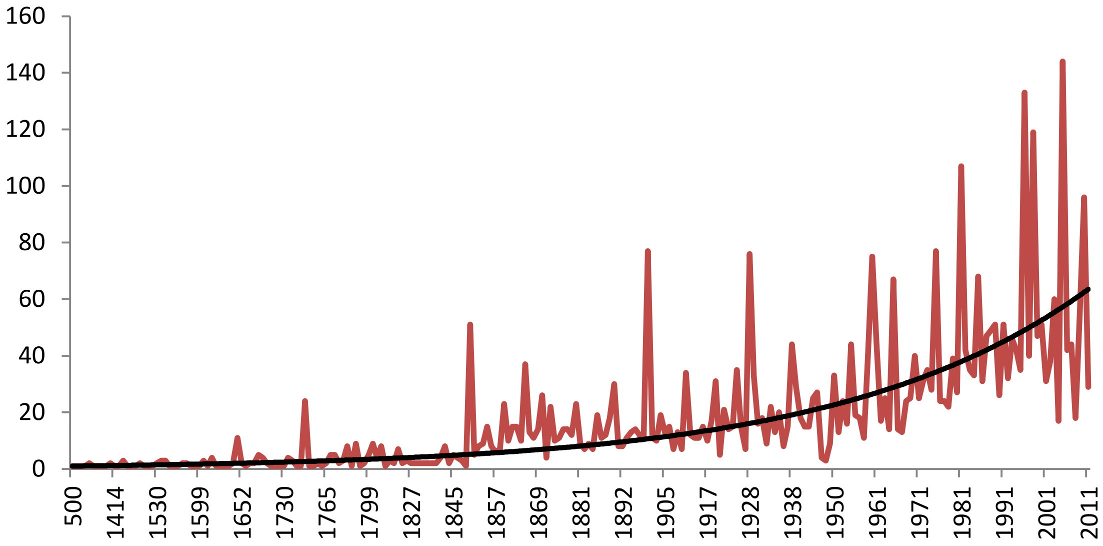


Figure 2.10 The number of records in GAVIA for each year from 500AD – 2011AD.

Four countries have more than one thousand records each: the United States (6,159), New Zealand (2,464), Australia (2,370), and the United Kingdom (1,631) (for a full list see appendix B).

There are records in GAVIA of birds being transported to areas outside of their native distributions *c*. 8,000 years ago (Red Jungle Fowl (*Gallus gallus*), West & Zhou, 1989), such that the earliest record is from ~6000 BCE. However, the earliest record for which there is enough detail for a distribution map to be created is from 500 AD. The most recent date of first introduction (as opposed to the 'Mapping Date' or date of spread) is 2011. Therefore, the records in GAVIA with a first date of introduction at a resolution suitable for mapping span 1,511 years.

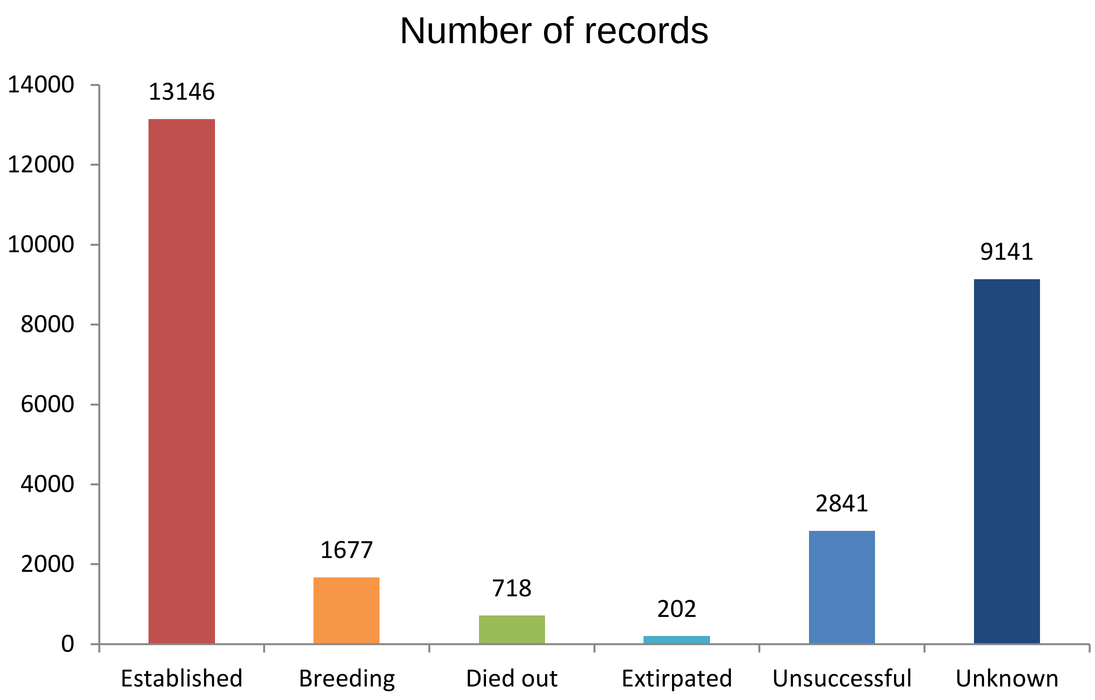
The cumulative number of records in GAVIA increases steadily until 1850, at which point there is a step-change and the cumulative number of records increases by an order of magnitude over the following 150 years (figure 2.9a). An almost identical pattern is apparent in the cumulative number of alien bird species recorded in GAVIA, although on a different scale (figure 2.9b). When plotted together, it is possible to see that the number of records and the number of species do indeed increase in parallel, demonstrating that in the last 150 years in particular, more people have been recording a more diverse variety of alien bird species (figure 2.9c). The number of records in GAVIA for each year also demonstrates an increase in recording effort over time (figure 2.10). The slight dip in recent years is likely a result of the lag effect, where introduced species records have yet to make it into the literature, rather than a true decrease in alien bird species introductions.

The bird families with the highest numbers of species records are Psittacidae (131 species recorded) and Anatidae (92). Seven species have more than five hundred records each in the database: house sparrow (*Passer domesticus*, 1,292 records), common myna (*Acridotheres tristis*, 1,214), rock pigeon (*Columba livia*, 823), rose-ringed parakeet (*Psittacula krameri*, 778), common pheasant (*Phasianus colchicus*, 681), common starling (*Sturnus vulgaris*, 673) and Java sparrow (*Padda oryzivora*, 540) (for a full list see appendix D). The highest proportion of records in GAVIA relate to established species (13,146 records, 47% of all records), followed by records with an unknown status (9,141, 33%) (figure 2.11a).

Note that these numbers cannot be used to calculate establishment probability, as established populations are more likely to generate multiple records in the database. The majority of the 972 species in GAVIA have more than one recorded occurrence, for which the outcomes may be different. Thus, 419 species (43%) have an established population somewhere in the world, 464 (48%) have an unsuccessful population somewhere, 236 (24%) have a breeding population, 178 (18%) have a population that was once established but has now died out, and 76 (8%) had a population that has now been extirpated. The status of one or more of the populations of 817 species (84%) is unknown (figure 2.11b).

Only 8,068 records have a method of introduction listed, and of those, 2,366 have a reason for introduction. The most common methods of introduction were release (4,757 records, 59% of all records with a method of introduction listed), and escape (2,332, 29%) (full list in table 2.4). Of those 1,285 records with a reason for release listed, 356 (28%) were for reasons of biological control, 297 (23%) were for hunting, 254 (20%) were from the cagebird trade, and 218 (17%) were for the purposes of faunal ornamentation. Of the 1,065 escaped records with a source of escape listed, 606 (57%) were from the cagebird trade, and 365 (34%) were from zoological gardens, nature reserves or private collections (full list in table 2.5).

a)



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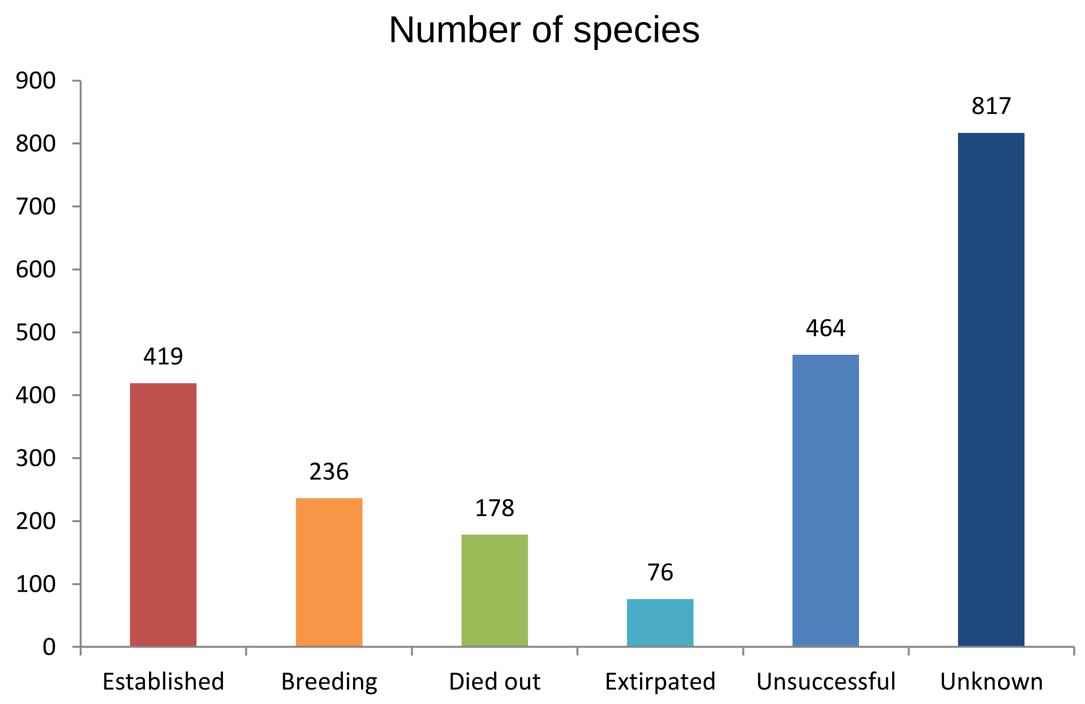


Figure 2.11 How the records in GAVIA are apportioned to introduction status. **(a)** The number of records assigned to each status, and **(b)** the number of species assigned to each status.

Table 2.4 Methods of introduction for the species records in GAVIA and the number of records of each.

Method of Introduction	Num records
Released	4,757
Escaped	2,332
Colonised from an introduced population	798
Ship stowaway	181
Unknown	19,669

Table 2.5 Purposes of introduction for the species records in GAVIA and the number of records of each.

Purpose of Introduction	Num records
Cagebird trade	1,176
Zoos/nature reserves/private collections	540
Biological control	371
Hunting	316
Fauna improvement/ornamental	262
Agriculture	66
Other	53
Conservation	35
Unknown/not applicable	24,918

2.4 DISCUSSION

Understanding the processes governing alien species introduction and spread is critical in order to mitigate their impacts. However, there are inherent difficulties in the study of alien species. Human-mediated invasions represent a classic example of ‘experiments in nature’ (empirical studies in which individuals or populations are exposed to experimental and control conditions determined by nature or other factors outside the control of the investigator) (Diamond 1986), and are a resource that can be exploited to analyse drivers of the invasion process. Nevertheless, this experiment has not been well designed: multiple populations of different species with conflicting characteristics have been introduced into contrasting locations using a variety of methods. This means that the likelihood of success has been driven by a whole suite of uncontrolled factors, which are consequently hard to disentangle (Blackburn *et al*. 2009a). As a result, there is a clear need for a large-scale comprehensive database such as GAVIA, to provide the raw material to explore the invasion process.

A common problem with macroecological and invasive species studies is the bias in locations where biologists conduct their research, both geographically and also in terms of habitats which are inaccessible or difficult to survey. This geographical bias is particularly prevalent in single-species studies (Pyšek *et al*. 2008). Although Europe, the United States and Australia are over-represented in terms of research locales (Dana *et al*. 2013), it is difficult to disentangle whether this is due to a higher number of invasion biologists focussing their studies there, or if it is a justified skew as a result of these areas holding a relatively larger number of alien species. Pyšek *et al*. (2008) also found that invasion research seemed to focus on those species that are perceived to have the potential to produce the most economic or ecological harm. Although GAVIA is based on a systematic and thorough search of all the data available from all regions of the world (where possible), there is still the potential for biases due to the intrinsic biases in the available literature. It is likely that there are regions of the world where invasions are continuing to occur without written records being made, and therefore even if the most thorough search of the literature is made, records will still be missed. This potential bias needs to be taken into consideration when conclusions are being drawn from the results presented here, as it is likely that regions with better written records will be more comprehensively represented that those without.

The use of the GADM layers as a basis for the range maps may have resulted in a small degree of spatial extrapolation of introduction records. For example, if a record states that a species is present in the Australian city of Sydney then the resulting distribution map will encompass the whole of Sydney as delineated by the GADM level 3 layer, although in reality it may only occur in a certain area of the city. This was addressed by producing distribution maps which represented the minimum convex polygon of the range that was described in the record, in order to avoid any unnecessary extrapolation. Where the record was too vague in its spatial description, a distribution map was not created. However, it is possible that for some species, their alien range size may be over-estimated due to this potential extrapolation and the species is unlikely to be extant in every part of its total recorded alien range (as is the case with most commonly used native species range maps).

The sheer number and diversity of the records in GAVIA means that this database should provide a representative portrayal of the global distribution of alien bird species. Indeed, GAVIA doubles the number of bird species known to have been introduced, and also doubles the number known to have established viable populations since Long (1981), the last attempt at a comprehensive catalogue of alien birds (Blackburn *et al*. 2015b). The coverage of the GAVIA database, both geographically (230 countries), taxonomically (~10% of all bird species) and temporally (anecdotal records from ~8,000 years ago, detailed distribution records spanning the last 1,500 years), illustrates the extent of alien bird introductions and spread, and the breadth of available information relating to them. GAVIA represents the first time these data have been collated and compiled into one database, and distribution maps have been created. It is therefore arguably the most comprehensive resource on the global distribution of alien species in any major taxon, and allows the spatial and temporal dynamics of alien bird population spread to be analysed in some detail. I hope that GAVIA will remain dynamic, and will be updated as and when it becomes publically available. Data on alien species are imperfect, and analyses of such data need to take this into account. Nevertheless, such imperfections are not limited to alien species, and are outweighed by the fact that the data exist at all, with the excellent opportunities for novel investigations into all facets of environmental biology that they present. Overlaying this data with datasets of environmental variables or species attributes provides a wealth of additional analytical possibilities, and should significantly increase the breadth of our understanding of invasions as a result.

Chapter 3.

Temporal change of global drivers of alien bird introductions

3.1 INTRODUCTION

It is now widely accepted that the process of biological invasion consists of multiple, normally four, separate and sequential stages (Williamson 1996). First, transport: a species must be transported beyond the boundaries of its native geographical range into a new environment. Second, introduction: the species must be released or escape from captivity into that new environment. Third, establishment: the species must become established following introduction, forming a self-sustaining population. Finally, spread: species that establish successfully may spread beyond the release point, colonising neighbouring alien environments (Duncan *et al*. 2003). The successful management of alien species requires an understanding of the early stages of the invasion pathway, in particular understanding what determines which species are likely to be transported and introduced. Alien species that pose negative impacts (*sensu* Jeschke *et al*. 2014) are likely to be costly and difficult to eradicate (Pimentel *et al*. 2000), and therefore preventing invasions will be cheaper and easier than eliminating them (CBD 2002). These early invasion stages form the focus of this chapter.

Substantial progress in the discipline of invasion biology has been made from quantitative study of the introduction and establishment of alien birds (Blackburn *et al*. 2009a), initially due to the availability of a catalogue of alien birds compiled by Long (1981). Humans have transported birds outside their native geographic ranges for thousands of years, to more or less all ice-free regions of the world (Duncan *et al*. 2003). These translocations have been made for a wide variety of reasons, including planned releases for game hunting, landscape ornamentation, biocontrol, commercial concerns (e.g. for ceremonial feathers), religious reasons, and accidental or deliberate releases of individuals from aviculture or the pet trade (reviewed in Lever 2005, Blackburn *et al*. 2009a, Blackburn *et al*. 2010, Cassey *et al*. 2015). Blackburn and Duncan (2001a) used introduction records from Long (1981) to show that the locations at which alien bird species have been introduced are not randomly distributed across the globe. They suggested that for the most part, this non-random distribution reflected the pattern of movement by European settlers, particularly the British, during the period of colonial expansion (mid 18th – early 20th centuries). Species living in areas from which settlers departed, and those to which settlers emigrated, feature prominently in records of alien birds (Blackburn & Duncan 2001a). Introductions were often associated with the formation of acclimatisation societies whose aims were to establish beneficial or desirable species in the new colonies and also in the old countries of origin (see Thomson 1922, McDowall 1994, Duncan *et al*. 2003). These aims are reflected in the non-randomness of the types of birds introduced, with over-representation of species from certain families suggesting the preferential selection of species for hunting (e.g. from the families Anatidae, Columbidae, Odontophoridae, Phasianidae) or for aesthetic purposes (e.g. Passeridae, Psittacidae) (Lockwood 1999, Lockwood *et al*. 2000, Blackburn & Duncan 2001a, Blackburn *et al*. 2009a).

Colonial expansion is now largely a thing of the past, but the number of alien species, and the rate at which they are transported and introduced to new environments, have continued to grow in the second half of the twentieth century (Westphal *et al*. 2008, Blackburn *et al*. 2015b) (figure 3.1). Therefore, the underlying drivers of alien bird introductions are likely to have changed over time (Blackburn *et al*. 2009a). Planned releases by acclimatisation societies were abolished after the recognition of the undesirable consequences of alien species, and subsequently replaced by legislation promoting their control and management (Blackburn *et al*. 2010, Cassey *et al*. 2015). Yet, the expansion of international trade, travel, and transport networks has maintained the movement of organisms around the globe (Hulme 2009, Pyšek *et al*. 2010, Essl *et al*. 2011), and many of these species may deliberately or accidentally end up in new environments. The on-going trade in live birds kept as pets and for show provides significant opportunities for alien species introduction and establishment (Nentwig 2007, Cassey *et al*. 2015), and new markets for captive birds, opened up by the increase in global trade, may have broadened the range of geographic locations from which alien birds are sourced (Blackburn *et al*. 2010). The types of birds introduced may also have changed in parallel, as planned releases of bird species considered beneficial to the new environment have been replaced with unplanned releases or escapes of species in trade. Blackburn *et al*. (2010) found that the frequency of alien birds differed across families, between those introductions recorded in Long (1981) and those occurring subsequent to its publication. The proportion of introductions likely resulting from the pet trade (from the families Psittacidae, Sturnidae and Sylviidae), were higher in the introductions occurring after Long (1981). They attributed these differences to changes in attitudes, legislation and vectors of transport over the last two

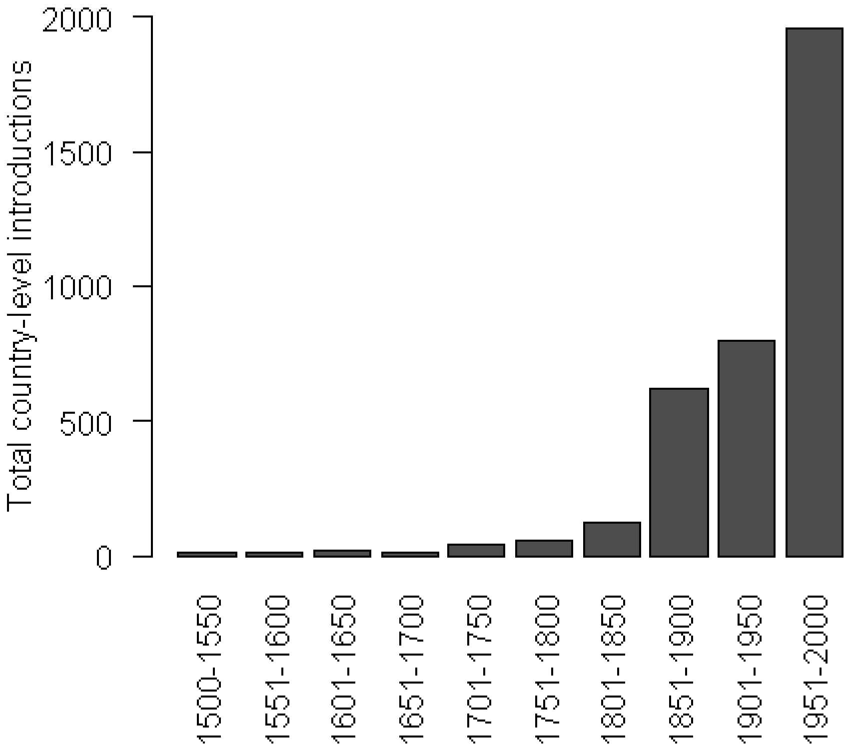


Figure 3.1 The total number of species being introduced at a country level during the period 1500 – 2000.

centuries, as the planned introductions by acclimatisation societies have become increasingly legislated against and superseded by unplanned releases of species from the cage bird trade.

Long (1981) is particularly rich in data on introductions that occurred during the Great European Diaspora (Crosby 1993), yet more than a quarter of the bird introductions recorded in the recently compiled Global Avian Invasions Atlas (GAVIA) database (see Chapter 2) have occurred since Long (1981) was published. The movement patterns of settlers two centuries ago cannot still be determining the composition of alien bird introductions. However, the extent to which likely changes in introduction drivers have resulted in changes in the kinds of species being moved, and the locations to and from which species are being transported, remains unknown. Therefore, there is a clear opportunity to examine how the composition of alien introductions has changed from the early days of mass human movement and acclimatisation societies, to the globalisation of the modern era.

Here I directly examine for the first time how the spatial distribution, tempo, mode, and drivers of alien bird introductions have changed over time. In order to do this I focus on two time periods: the first quartile of the temporal record of introductions from the GAVIA database, which primarily comprise movements associated with the European diaspora and the advent of the acclimatisation societies (termed the historical era), and introductions occurring in the fourth quartile of GAVIA records (termed the modern era), encompassing the period of globalisation and exclusively comprising introductions that post-date the publication of Long (1981).

The era of colonial expansion was particularly dominated by the British, and the establishment of their global empire “on which the sun never sets” (Macartney 1773). Most acclimatisation societies were also formed by the British or their colonial subjects (McDowall 1994). Therefore, I would expect that introductions in the historical era will have been heavily driven by the movement of species between places that were British colonies at the time. Consequently, I test the following hypotheses for the historical era: i) that British colonial status will be an important determinant of the number of introductions to and from a country; ii) that the number of country locations to which species would have been introduced at that time will be relatively low, because while extensive, at its height the British Empire covered only around a quarter of the Earth’s surface; and iii) that the species introduced in the historical era will be mainly derived from ‘beneficial’ taxa, such as the gamebirds, waterfowl and pigeons introduced for hunting or for aesthetic purposes.

As globalisation and economic growth have become widely recognised as important drivers of modern biological invasions (Essl *et al*. 2011), for the modern era I test the following hypotheses: iv) that measures of economic activity will be important determinants of the number of introductions to and from a country; v) that a wider set of countries will be involved in modern era introductions, as international trade now concerns more or less all countries of the world; vi) that regions where desirable pet species are sourced and traded will be well-represented as locations of origin and introduction; vii) that the species composition of modern era introductions will reflect a decline in purposeful introductions of beneficial species, and instead be dominated by species that are unplanned releases from the flourishing global pet trade; and finally viii) that the overlap between both country units and types of species introduced in the two time periods will be small, as a reflection of the different drivers.

In this chapter, I test these various hypotheses, and discuss the implications of my results for understanding the changing drivers of naturalisation in birds.

3.2 METHODS

3.2.1 Data

This analysis concerns human-mediated introductions of species to locations outside their native geographic range. The GAVIA database comprises 27,737 distribution records for 972 alien bird species, based on ~700 published references and substantial unpublished information derived from consultation with over 600 organisations and experts worldwide (see Chapter 2). GAVIA contains records for all statuses of introduction event, from those which were unsuccessful through to those that are deemed to be established, i.e. which have a self-sustaining population in the area of introduction. The subset of introduction records used here are those that represent the first record of a species in each country (or state for Australia, Canada and the USA) hereafter referred to as a ‘country unit’, for the period 1500 – 2000 (i.e. each species is only counted in each country unit once), regardless of whether that introduction was successful or not. This period of time was selected because 1500 is a standard cut-off point for reliable ecological data (Baillie *et al*. 2004), and introductions occurring after the year 2000 may not yet have filtered into the literature, and therefore may represent an incomplete sample. Natural colonisations were excluded from the analysis, as they are not human-mediated, as were translocations for conservation purposes as they represent a small proportion of records. These criteria resulted in a total of 3,661 alien bird introduction records from 715 bird species being extracted from GAVIA.

The 3,661 records were split into four quartiles on the basis of introduction date. The first quartile (hereafter, the ‘historical era’) represents historical introductions and includes 922 records encompassing the period 1500 – 1903, with a total of 245 species from 48 families introduced to 167 country units. The fourth quartile (hereafter, the ‘modern era’) represents modern introductions and encompasses 935 introductions during the period 1983 – 2000, with a total of 324 species from 51 families introduced to 235 country units. Although not analysed here, the second and third quartiles represent the periods 1904 – 1956, and 1957 – 1982 respectively.

Species were classified following the taxonomy used by IUCN (2010). The phylogenetic tree used to create figure 3.2 is a representative avian tree downloaded from www.birdtree.org (Jetz *et al.*, 2012; Hackett backbone, downloaded 26/02/15). All maps were created using ESRI ArcGIS version 10.2.2 (2014). The country-level introduced species richness maps (figures 3.3a and b) use the introduction records

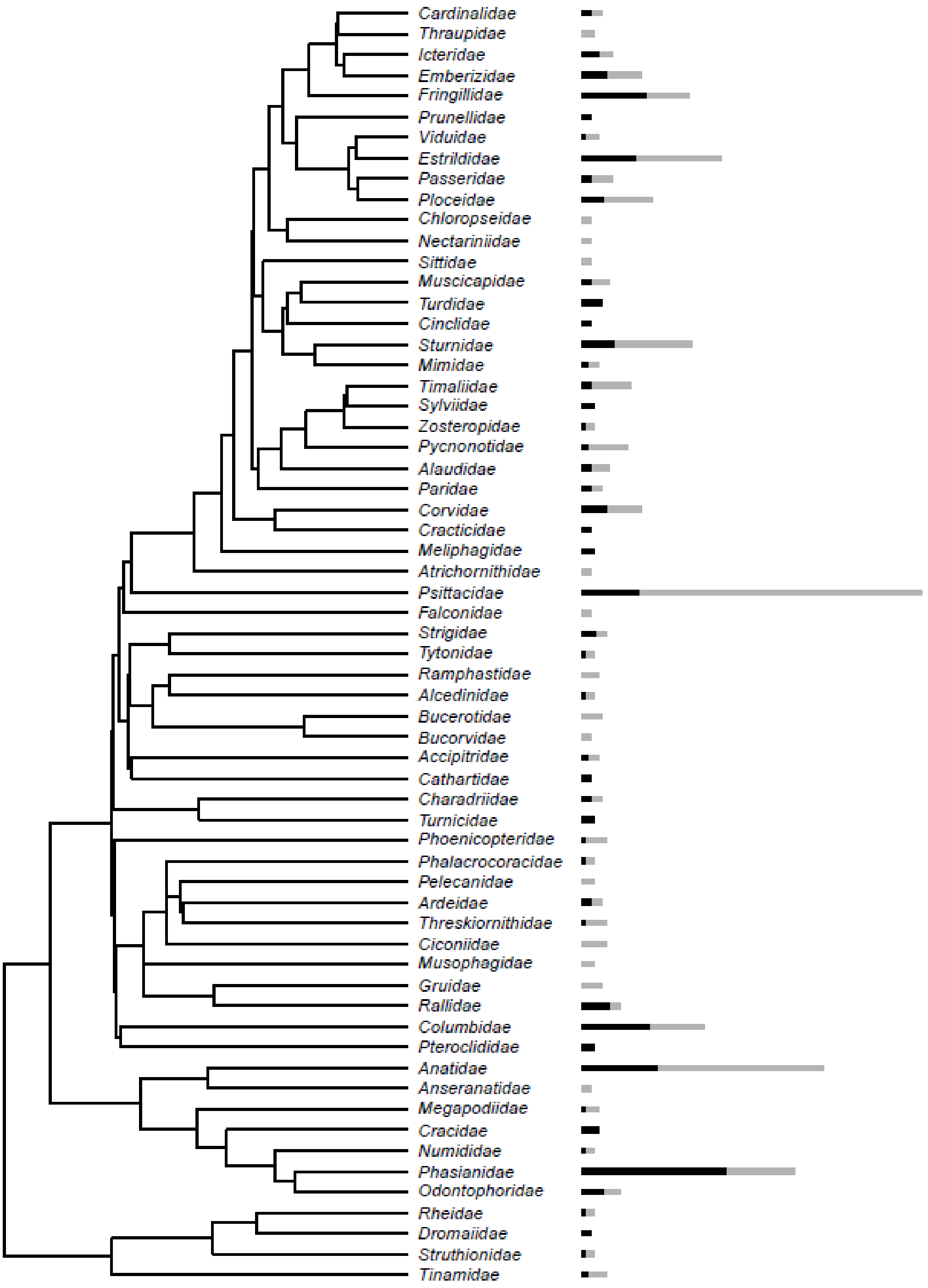


Figure 3.2 A representative avian phylogenetic tree pruned to the family level. Each tip corresponds to a family from which species were introduced in either time period. The black bars represent the number of species from the family introduced during the historical era, and the grey bars represent the number of species from the family introduced during the modern era.

from the GAVIA database. The native richness maps (figures 3.4a and b, and 3.5a-d), which demonstrate the regions from where introduced bird species were sourced, were constructed using native range maps extracted from the database used by Orme *et al.* (2005). Figures 3.4a and b, and 3.5a-d were created by projecting the range maps onto a hexagonal grid of the world, resulting in a geodesic discrete global grid, defined on an icosahedron and projected onto the sphere using the inverse Icosahedral Snyder Equal Area projection. This resulted in a hexagonal grid composed of cells that retain their shape and area (865.5 km^2) throughout the globe.

A list of British colonies was obtained from Marshall (1996). The countries present in both time periods (historic era and modern era) were assigned to either 'British colony' or 'non-British colony' categories, and all countries were used in the analysis. Data on GDP per capita (in 1990 international Geary-Khamis dollars (Int$)) were downloaded from ourworldindata.org (Roser 2014; downloaded 18/03/15). A subset of GDP data for the year 1900 was used for the countries present in the historical era, and the year 2000 for countries present in the modern era. GDP data were not available for all countries, particularly during the historical era, so countries without data were excluded, leaving 32 countries in the historical era analysis and 118 in the modern era. For the historical era, GDP per capita ranged from a minimum of Int$ 545 for China, to a maximum of Int$ 5,899 for Switzerland (mean = Int$ 2,276; median = Int$ 1,980). For the modern era, GDP per capita ranged from a minimum of Int$ 509 for Sierra Leone, to a maximum of Int$ 28,702 for the United States (mean = Int$ 7,162; median = Int$ 4,564).

3.2.2 Statistical analyses

All analyses were conducted in the R software environment for statistical and graphical computing version 3.1.2 (R Core Team 2014).

In order to examine how the source locations of species introduced have changed between the two time periods, the native range of each species was intersected with the eight biogeographic realms defined by the Olson *et al*. (2001), using ESRI ArcGIS version 10.2.2 (2014), and each was assigned to the realm where the native range of that species was found. No species from the Antarctic realm are included in these data, leaving seven realms in the analysis. For those species ranges that spanned more than one realm, the predominant realm was selected.

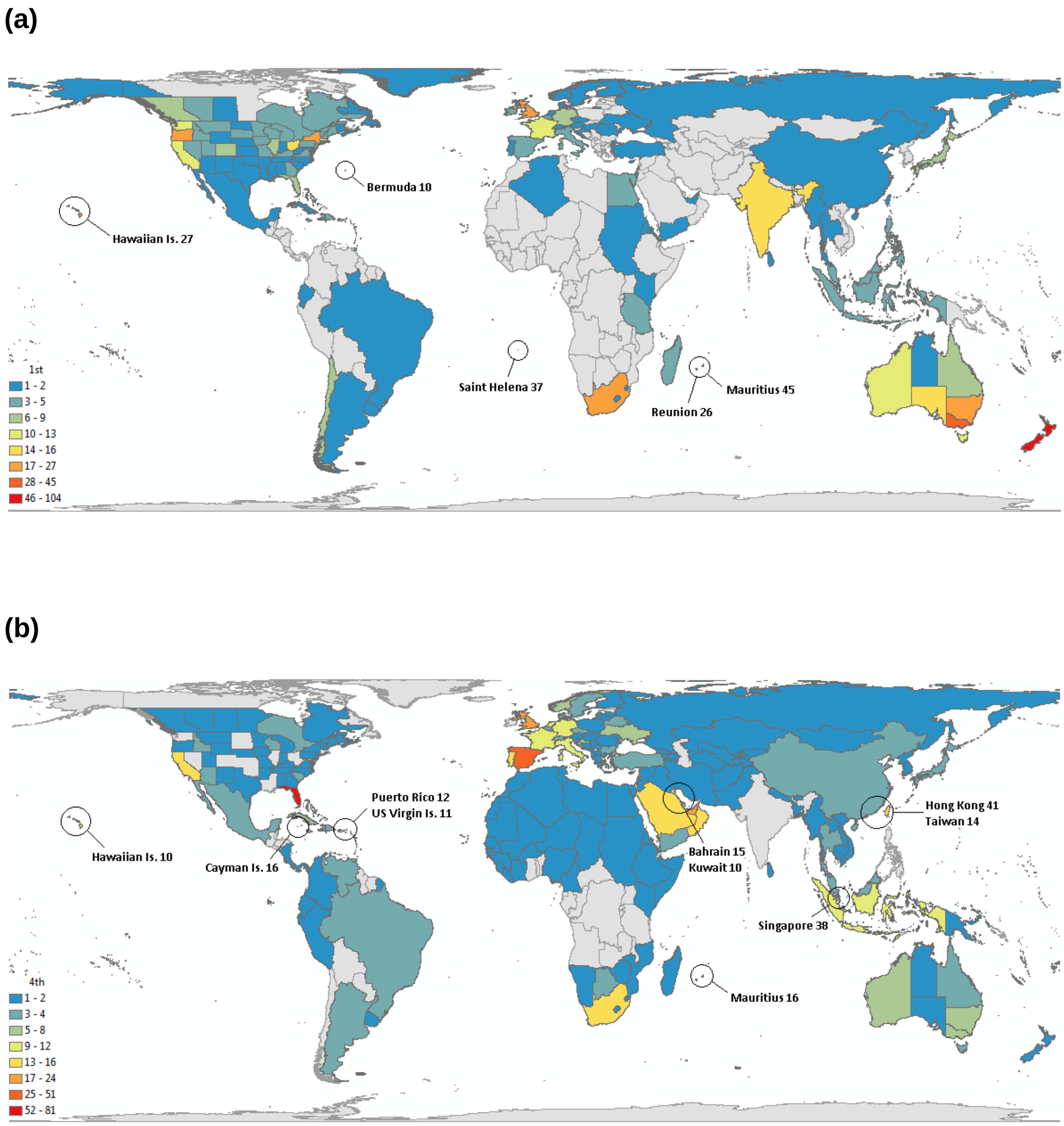
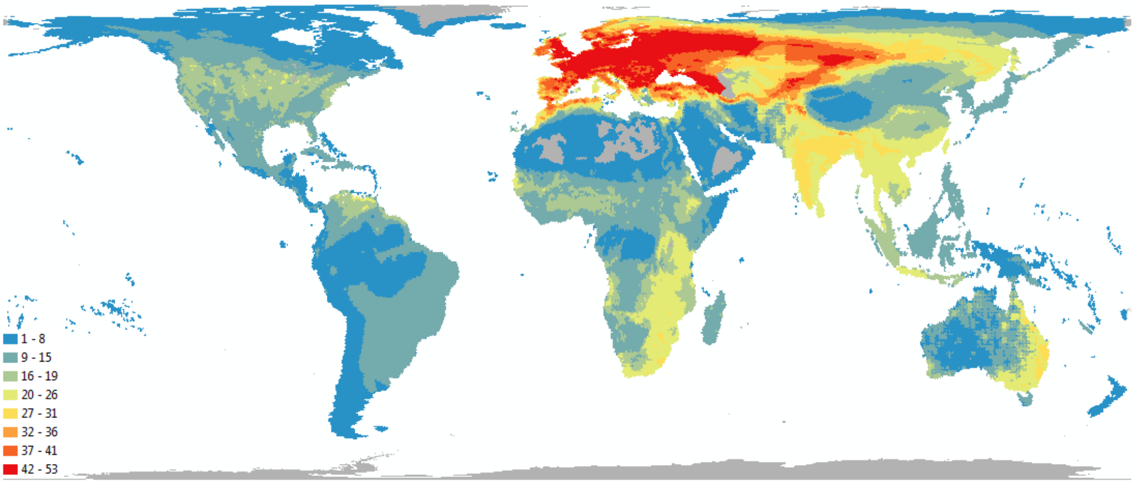


Figure 3.3 Global maps showing the country units where alien bird species were introduced during **(a)** the historical era, and **(b)** the modern era. Cold colours represent low numbers of alien bird species, warm colours represent higher numbers. Grey countries are those without any record of alien birds having been introduced during this period.

(a)



(b)

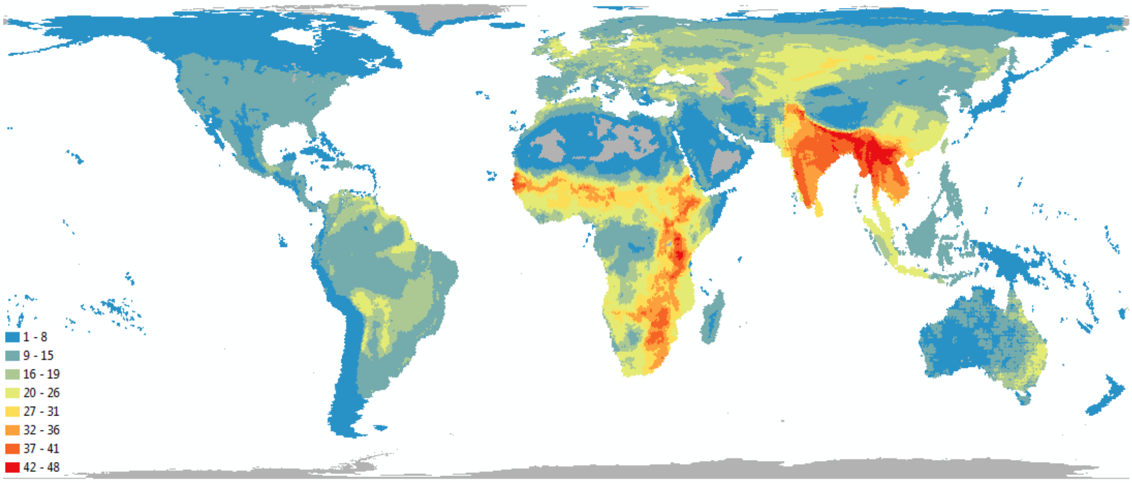
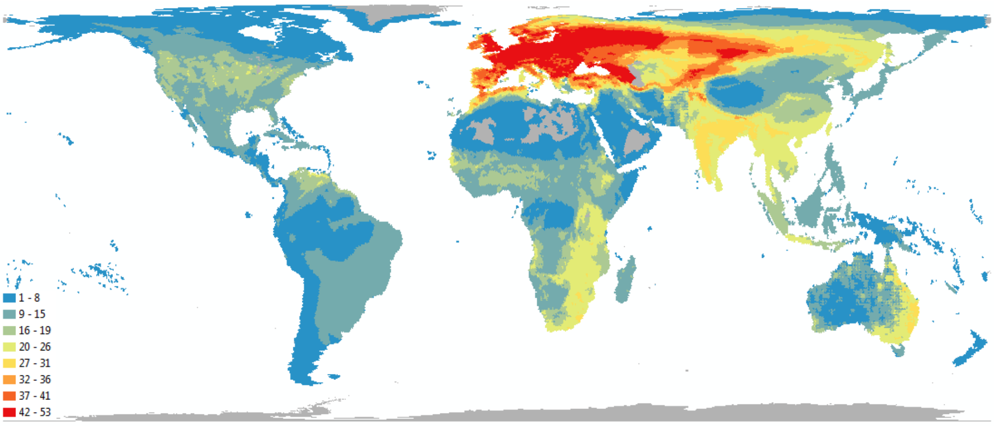


Figure 3.4 Global map showing the richness of the native ranges of the alien bird species introduced during **(a)** the historical era, and **(b)** the modern era. Cold colours represent lower density of bird species, warm colours represent higher density. Grey areas are those not covered by the native ranges of the species.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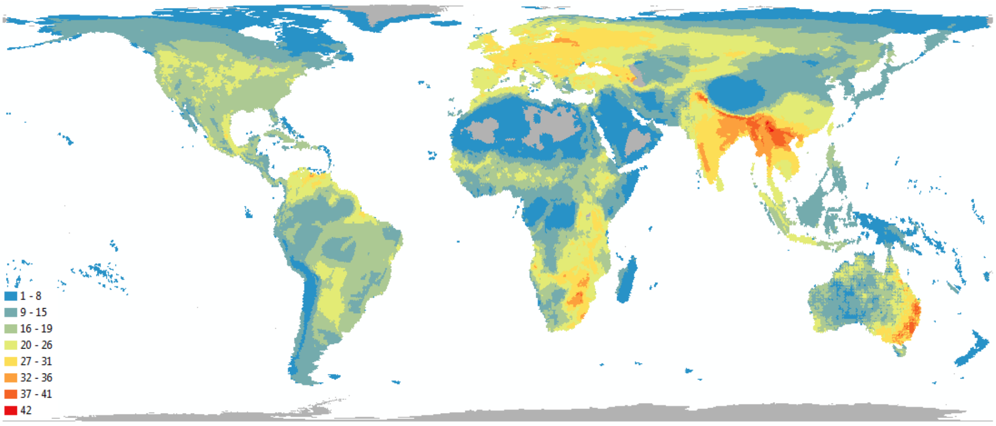
16 - 19
20 - 26
27 - 31
32 - 36
37 - 41
42 - 53

(a)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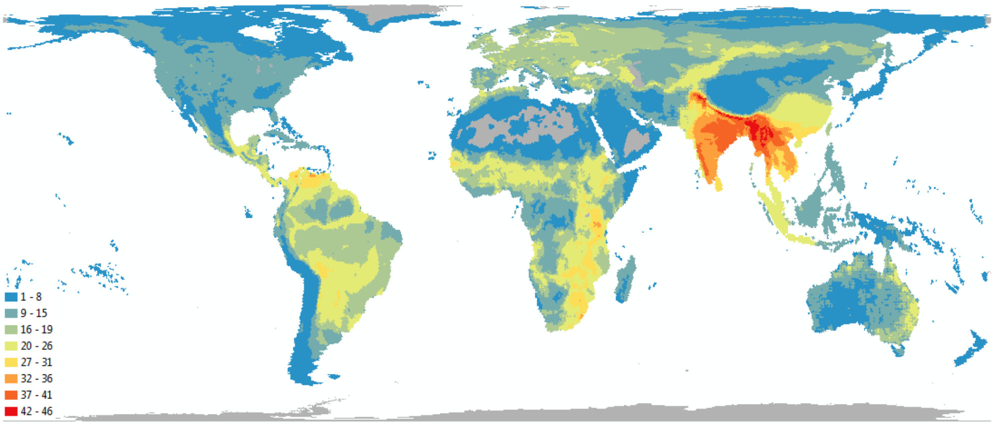
(b)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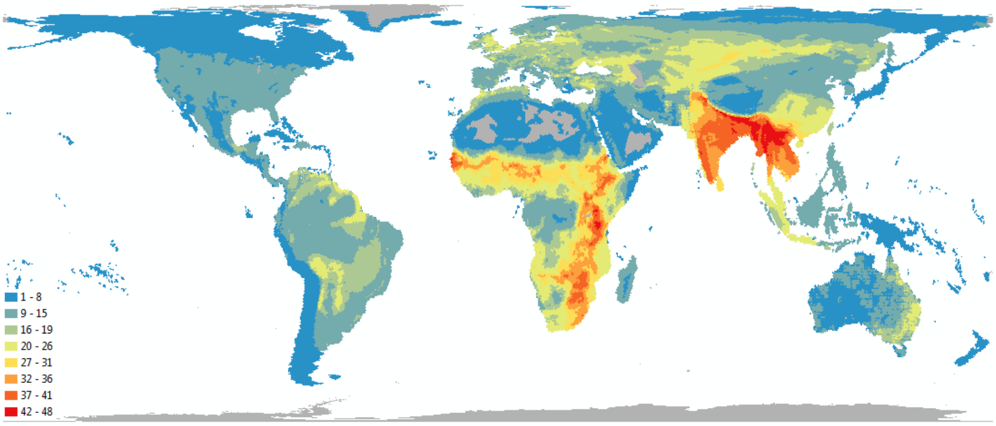
(c)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20 - 26
27 - 31
32 - 36
37 - 41
42 - 48

(d)

Figure 3.5 (*Previous page*) Global maps showing the richness of the native ranges of the alien bird species introduced during all four quartiles of the data. **(a)** The first quartile or the historical era (500-1903), as in figure 3.4a; **(b)** the second quartile (1904-1956); **(c)** the third quartile (1957-1982); and **(d)** the fourth quartile or the modern era (1983-2000), as in figure 3.4b. Cold colours represent lower density of bird species, warm colours represent higher density. Grey areas are those not covered by the native ranges of the species.

Where the range was distributed equally across two or more realms, the species was excluded from the analysis (n = 27). This resulted in 225 species with assigned native realms in the historical era, and 298 species in the modern era. A Pearson's Chi-squared test was used to determine whether the number of species sourced from each biogeographic realm was significantly different to that expected by chance between the historical era and the modern era.

Bespoke simulations were used to establish whether there were differences between the observed and expected number of country units where species had been introduced in either time period. Each iteration of the simulation involved selecting 922 introductions at random, and without replacement, for the historical era (and 935 for the modern era) from the full dataset of all introductions between the period 1500 – 2000 (n = 3,661). For each iteration I summed the number of country units to which introductions in this randomly chosen subset were assigned. This process was repeated 10,000 times for each time period, and the observed number of country units was judged significantly different to the expected if the observed number fell outside of the 2.5 – 97.5 % quantiles. Additionally, the number of overlapping countries between the historical and modern eras was calculated for each of the iterations paired by iteration number (1 – 10,000), in order to determine if species were being introduced into the same or different countries in the different time periods. The observed overlap was judged to be significantly different to the expected if the observed number fell outside of the 2.5 – 97.5 % quantiles. The same procedure was also used to test for differences between the observed and expected number of species introduced in each time period.

To understand how acclimatisation societies and movements of settlers influenced the introduction of birds, a two-sample Wilcoxon test was used to compare the number of alien bird introductions in the historical time period in British colonies, versus the number of introductions in non-British colonies. This was repeated for introductions in the modern era to determine whether the influence remained. To understand the effect of globalisation and economic growth, a linear regression was conducted to compare the number of alien bird introductions in the historical era and GDP per capita in the year 1900 (Int$). This was then repeated for the modern era and GDP per capita in the year 2000 (Int$).

To ascertain whether certain avian families were over- or under-represented in the avifauna introduced in either time period, a slightly different bespoke simulation approach was used to test for differences between the observed and expected number of introduced species from each bird family in both time periods. For these randomisations, a list of the total global avifauna was used (n = 10,245 species, IUCN 2010). Each iteration of the simulation involved selecting 245 species at random, and without replacement, for the historical era (324 for the modern era) from the total global avifauna and summing the number of these randomly chosen species in each family. A total of 10,000 iterations of the simulation procedure were run for each time period, and the observed number of introduced species in any given family was judged significantly greater than expected if at least S% of the randomly derived values for that family were less than the observed, where $S = (\beta/2) \times 100$. The β is calculated by applying a sequential Bonferroni correction to α, and $\alpha = 0.05$ (see Blackburn & Duncan 2001a).

3.3 RESULTS

3.3.1 Locations of introduction

Particular regions with higher levels of introductions during the historical era (1500 – 1903) included New Zealand, Australia, South Africa, India, Mauritius, Saint Helena, Hawaii, the UK and coastal states of the USA (figure 3.3a). Countries with the highest number of introductions during the modern era included southern USA (specifically Florida), Spain, Taiwan, the UK, Hong Kong, South Africa, Bahrain and the UAE (figure 3.3b).

For the historical era, the observed number of country units where species had been introduced was lower than expected by chance (observed: 167; expected median [range]: 212 [189 – 231], $p < 0.0002$). Conversely, the observed number of country units where species had been introduced in the modern era was greater than expected by chance (observed: 235; expected: 214 [194 – 235], $p = 0.0002$). The observed number of country units into which species had been introduced in both time periods was lower than expected by chance (i.e. the country unit overlap: observed: 135; expected: 176 [158 – 196], $p < 0.0002$) (table 3.1).

For those country units where species have been introduced in both time periods, the majority of introductions sometimes occur in the historical era (e.g. New Zealand, Australia, Canada, Bermuda, Reunion and Mauritius), and sometimes in the modern era (Spain, Hong Kong, Singapore, and the United Arab Emirates) (figure 3.6).

More alien bird introductions in the historical era were to British colonies than to non-British colonies (Wilcoxon rank sum test: Statistic = 5,557, $p < 0.01$). However, British colonial status had no discernible effect on the numbers of alien bird species introduced in the modern era sample (Wilcoxon rank sum test: Statistic = 4,424, $p = 0.99$) (figure 3.7). GDP per capita from the year 1900 was not significantly correlated with the numbers of alien birds introduced during the historical era (n = 32; $F_{1, 30} = 2.72$, $r^2_{adj} = 0.05$, $p = 0.1$). However, the numbers of alien bird species introduced during the modern era was significantly greater for countries with a higher GDP per capita in the year 2000 (n = 118; $F_{1, 116} = 50.87$, $r^2_{adj} = 0.29$, $p < 0.001$) (figure 3.8).

Table 3.1 Results from the simulations showing the observed number of species introduced in each time period, the overlap of those sets of species, and the number of countries into which species had been introduced in each period relative to the frequency of expected values.

		Quartile 1 num species	Quartile 4 num species	Q1 vs Q4 species overlap	Quartile 1 num countries	Quartile 4 num countries	Q1 vs Q4 country overlap
	Observed	**245**	**324**	**106**	**167**	**235**	**135**
Simulations	min.	317	316	192	189	194	158
	0.01%	318	316	195	191	194	159
	0.05%	321	320	197	192	196	160
	0.50%	326	329	204	197	199	162
	2.50%	331	334	209	201	202	166
	median	350	353	224	212	214	176
	97.50%	369	372	240	223	225	187
	99.50%	375	378	245	226	228	191
	99.95%	382	385	252	230	232	194
	99.99%	383	389	255	231	233	195
	max.	383	393	257	231	235	196

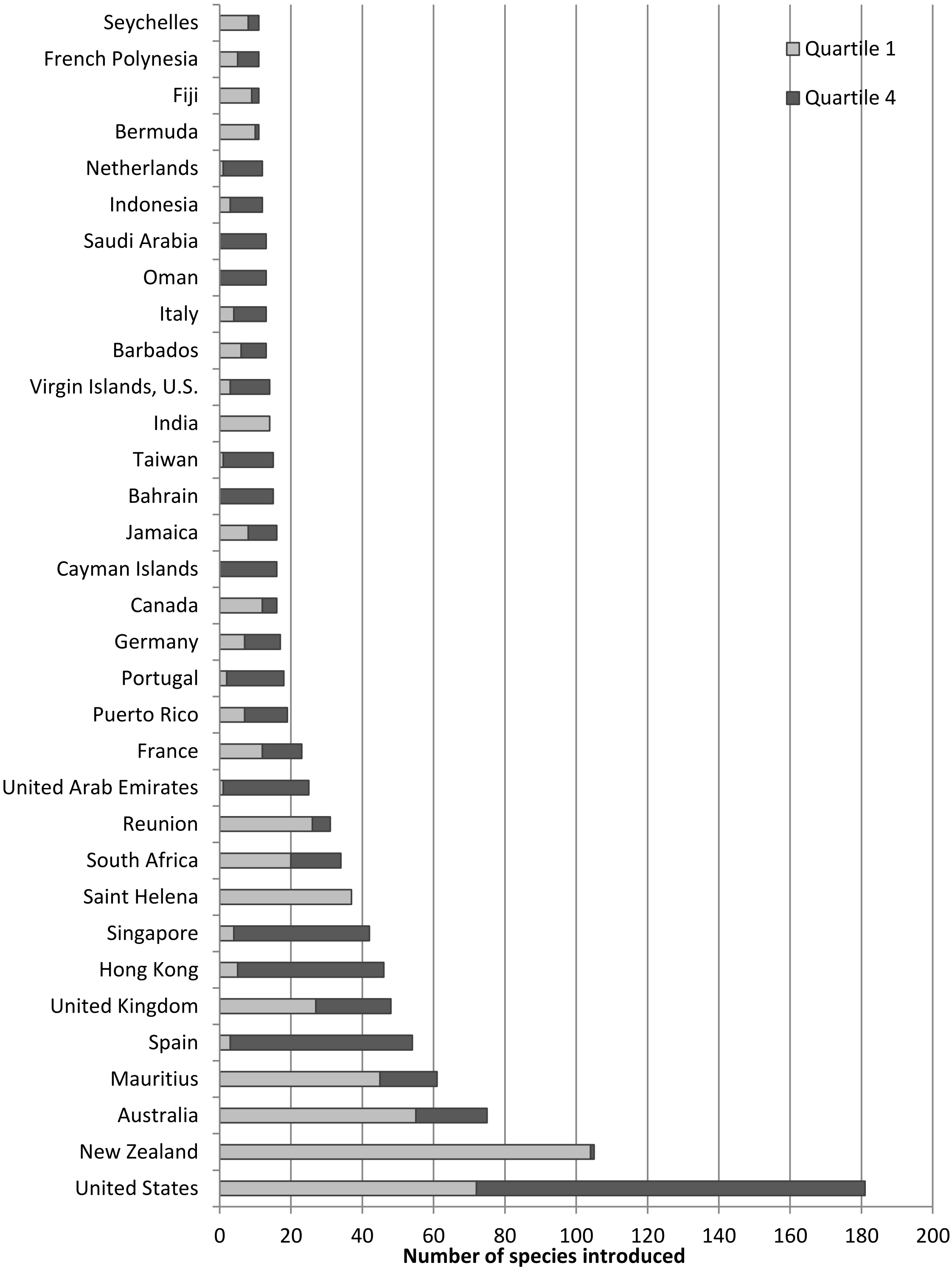
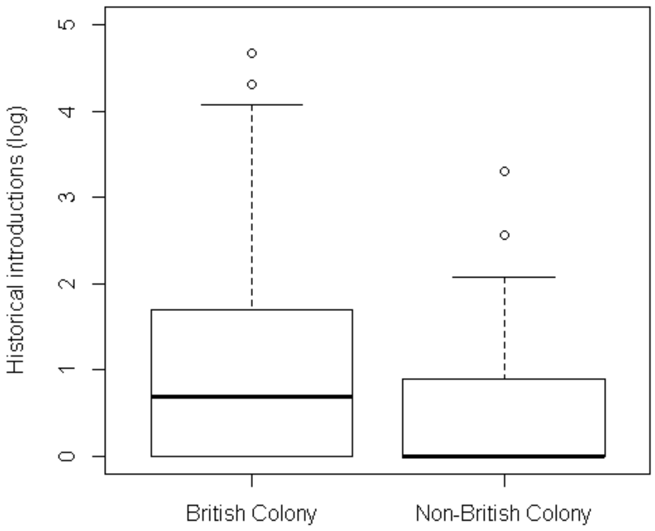
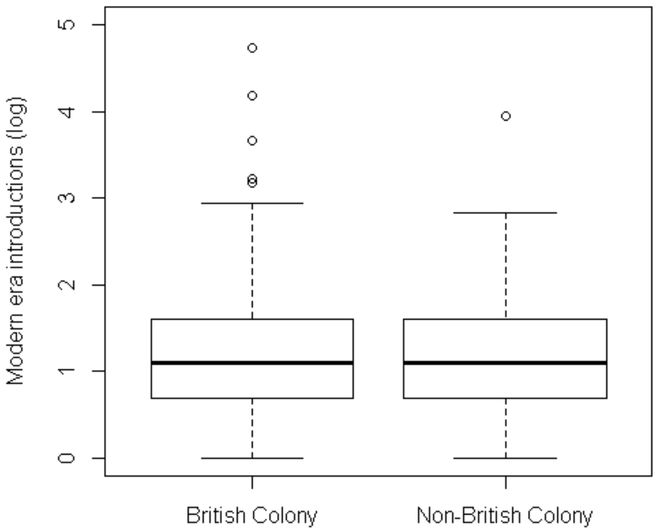


Figure 3.6 Number of alien bird species introduced to countries where >10 total species have been introduced, during the historical era (light grey bar) and the modern era (dark grey bar).

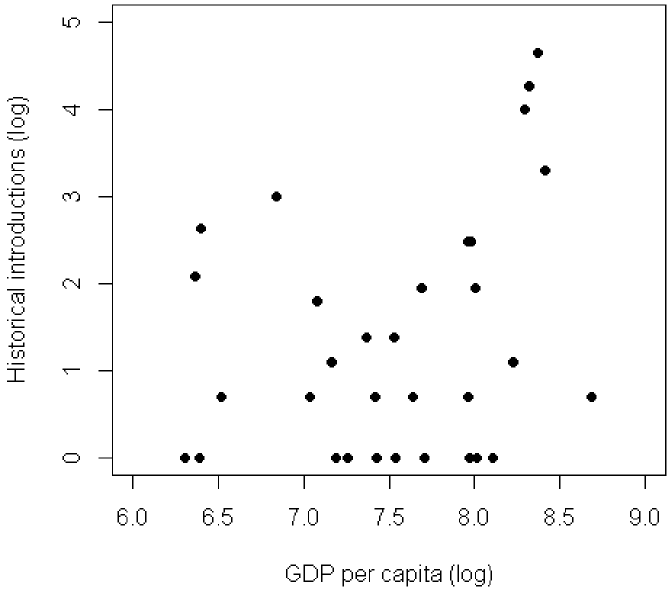


(a)

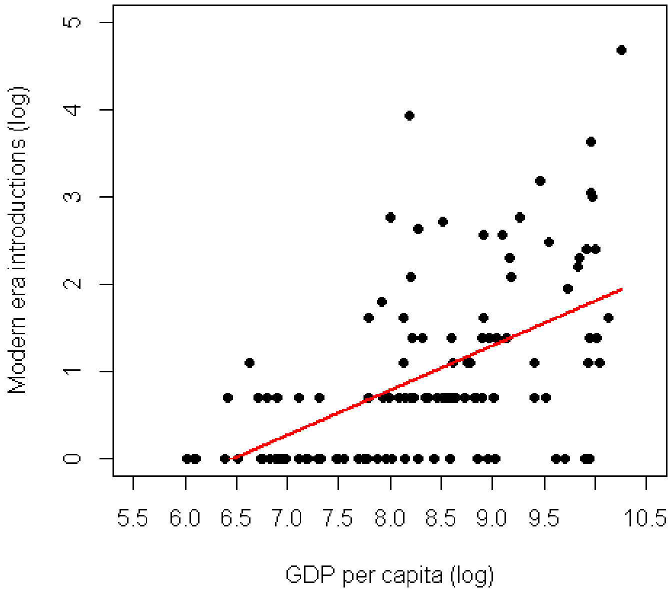


(b)

Figure 3.7 The number of alien bird introductions in British colonies and non-British colonies for **(a)** the historical era and **(b)** the modern era. A constant of 1 was added to each variable prior to log-transformation.



(a)



(b)

Figure 3.8 The relationship between **(a)** log number of species introduced to countries during the historical era and log GDP per capita in the year 1900 (n=32), **(b)** log number of species introduced to countries during the modern era and log GDP per capita in the year 2000 (n=118). The red line represents the coefficients from the linear model (slope estimate).

3.3.2 Source locations

Species introduced in the historical era were sourced primarily from countries in the Palearctic realm (figure 3.4a). In contrast, the areas from which alien birds were being sourced in the modern era have shifted relative to the historical era, and the species now selected for introduction primarily originate in the Indian subcontinent and Indochina, and from sub-Saharan Africa (figure 3.4b). The numbers (and proportions) of species sourced from each biogeographic realm during the two time periods differed significantly (X^2 = 22.88, p <0.001) (table 3.2), as expected from figures 3.4a and b. Figures 3.5a-d demonstrate that the shift in source locations was most abrupt between the first quartile (historic era) and the second quartile of introductions. During the second quartile, far fewer species were sourced from the Palearctic realm, and there is already an apparent shift to Southeast Asia and southern Africa. The third quartile of introductions are similar to the fourth quartile (modern era).

3.3.3 Species introduced

For the historical era, the observed number of species introduced was fewer than would be expected if introductions in this period were a random sample of all introductions (observed: 245; expected: 350 [317 – 383], p < 0.0002). The observed number of species introduced in the modern era was also lower than expected (observed: 324; expected: 353 [316 – 393], p = 0.003), as was the observed number of species which had been introduced to both time periods (i.e. the species overlap: observed: 106; expected: median 224 [192 – 257], p < 0.0002) (table 3.1).

The species chosen for introduction are not a random sample of birds with regards to family membership. Modern era introductions represent a wider range of families compared to those from the historical era. Species from 62 families were introduced in total over both periods. During the historical period, species from 48 families were introduced, 11 of which are not represented in the modern era. This compares to species from 51 families introduced in the modern era, of which 14 were ‘new’ families not represented during the historical era (figure 3.2).

Three families (Anatidae, Estrildidae and Phasianidae) were significantly over-represented in both time periods. A further three families were over-represented only in the historical era (Columbidae, Fringillidae and Odontophoridae), and a further seven only in the modern era (Anseranatidae, Ciconiidae, Phoenicopteridae, Ploceidae, Psittacidae, Sturnidae and Gruidae) (table 3.3). Three bird families were significantly under-represented in the modern era (Tyrannidae, Trochilidae, Sylviidae), and the first two of these families were also under-represented in the historical era (table 3.3).

Table 3.2 The number of species from different biogeographic regions that have been introduced outside of their native distribution in the historical era or the modern era. Prop.historic = the proportion of species introduced in the historical era from each biogeographic region; Prop.modern = the proportion of species introduced in the modern era from each biogeographic region.

Realm	Historical	Modern	Prop.historic	Prop.modern
Afrotropical	34	59	0.15	0.20
Australasian	31	40	0.14	0.13
Indo-Malay	36	65	0.16	0.22
Nearctic	23	18	0.10	0.06
Neotropical	24	57	0.11	0.19
Oceanic	4	3	0.02	0.01
Palearctic	73	56	0.32	0.19

Table 3.3 The number of species introduced from a family in the historical and modern eras, the total number of species in the family (Total; following IUCN 2010), and the probability (*P* $_{\text{sim}}$ calculated using simulations; see Methods) of observing as many or more introductions (or fewer introductions for those in the shaded areas) from that family given the number of species in the family and the proportion of the world's bird species that have been introduced. The families shown are those with probabilities that are significantly lower than expected (α = 0.05), once a sequential Bonferroni correction for multiple statistical tests (Rice 1989) has been applied.

	No. spp. Introduced			*P* sim	
Family	Historical	Modern	Total	Historical	Modern
Anatidae	21	44	173	<0.0001	<0.0001
Estrildidae	15	22	138	<0.0001	<0.0001
Phasianidae	40	17	183	<0.0001	<0.0001
Columbidae	19	13	320	<0.0001	
Fringillidae	18	10	179	<0.0001	
Odontophoridae	6	3	31	<0.0001	
Anseranatidae	0	1	1		<0.0001
Ciconiidae	0	5	19		<0.0001
Phoenicopteridae	1	4	6		<0.0001
Ploceidae	6	12	106		<0.0001
Psittacidae	16	76	374		<0.0001
Sturnidae	9	20	115		<0.0001
Gruidae	0	4	15		0.0002
Tyrannidae	0	0	416	0.0002	<0.0001
Trochilidae	0	0	338	0.0002	0.0002
Sylviidae	2	0	299		0.0002

3.4 DISCUSSION

The number of alien bird species introduced into countries where they are not native has increased during the period 1500 – 2000 (figure 3.1). This is also reflected by the much shorter period of time covered by introductions in the 4th quartile of the data set - the modern era (18 years) - compared to the 1st quartile or historical era (404 years). These introductions have been highly non-random with respect to taxon, location of origin and location of introduction in both the historical and modern eras. Furthermore, the alien bird species introduced have changed between the historical and modern eras, in terms of where they are sourced from and introduced to, and in terms of species composition.

The locations at which alien bird species have been introduced are broadly consistent with my hypotheses based on changes in the likely history of introductions. During the historical era, a high proportion of introductions concerned planned translocations between Europe and colonies around the world settled by emigrants, particularly the British (Cassey *et al*. 2015) (figure 3.3a). A third of all bird species introduced during historical times were sourced from the Palearctic realm (table 3.2; figure 3.4a), and transported to regions including New Zealand, Australia, South Africa, India, the UK, Hawaii and coastal states of the USA, as expected given the importance of the British and their expatriates in the colonies. British colonies were significantly more likely to receive alien birds during the historical era than non-British colonies (figure 3.7). The advent of acclimatisation societies, whose specific aim was to enrich the flora and fauna of a region with beneficial or desirable plants and animals from around the world (Duncan *et al*. 2003), helped to drive this pattern.

In contrast, relative to the historical period, the set of species introduced in the modern era shows increases in representation from Afrotropical, Indo-Malay and Neotropical species, suggesting a shift away from colonialist activities and a move towards the influences from the pet trade (table 3.2). Species now selected for introduction are more likely to originate from the Indian subcontinent and Indochina, and from sub-Saharan Africa (figure 3.4b). Particular regions with high levels of introductions now include Florida, Spain, Taiwan, the UK, South Africa, California, and the UAE and other Arabian nations (figure 3.3b). These changes can broadly be explained in terms of changes in attitudes, legislation and vectors of transport relating to alien species (Blackburn *et al*. 2010, Essl *et al*. 2011), rapidly developing countries (Ding *et al*. 2008), increasing affluence and disposable income (Jenkins 1996, Pyšek *et al*. 2010), and the increasingly lucrative nature of the pet trade broadening the range of geographic locations from which species are sourced. Legislation against the custom of intentional introductions explains the drop in representation of Palearctic species (from 32% to 19%) in the modern era versus the historical period. Nevertheless, Palearctic species still occur in international trade, and can be found for sale in the Taiwanese pet market, for example (Su *et al*. 2014). The origins of species introduced during the time period between the historic and modern eras (quartiles 2 and 3, representing the years 1904 – 1956, and 1957 – 1982) support these results (figures 3.5a-d). The second quartile shows a substantial decrease in the species sourced from the Palearctic realm, and an increase in species being sourced from Southeast Asia and southern Africa (figure 3.5b). This is likely to be a result of the waning popularity of acclimatisation societies, and the increase in international trade and travel. Source locations in the second quartile are much more widespread compared to the other three quartiles, likely due to the increased human movement occurring as a result of the world wars. By the third quartile, very few species are being sourced from the Palearctic realm, and instead are originating from similar locations to those in the modern era (fourth quartile) (figure 3.5c).

As predicted, British colonial status is not related to the number of introductions a country unit has received in the modern era (figure 3.7). Instead, the numbers of alien bird species introduced during the modern era is significantly greater for countries with a higher per capita GDP (figure 3.8). Per capita GDP was not significantly correlated with the numbers of alien birds introduced during the historical era, suggesting that modern day introductions are linked to an increase in country wealth. Ding *et al*. (2008) found that the rate of alien species introductions in China was accelerating in step with surging economic growth there, and with the proliferation of domestic transport networks radiating from ports. Much of Hawaii also stands as an example of the virtual replacement of vulnerable native plants and animals by alien species as trade volume and living standards have increased (Cuddihy & Stone 1990).

The effect that this opening up of transport routes and global trade has had on alien species introductions is further demonstrated by the results of the country-unit simulations (table 3.1). During the historical era, the observed number of country units where species had been introduced was lower than expected by chance, with alien species introductions generally restricted to those countries encompassed by the British Empire. In the modern era, however, the observed number of country units where species have been introduced was higher than would be expected by chance. This shows that the range of countries affected by the proliferation of species introductions (figure 3.1) has expanded with globalisation (figure 3.3a and b). However, the observed overlap of country units into which species had been introduced in both time periods was lower than expected by chance, highlighting the difference in introduction drivers during the two time periods.

The different drivers of bird introductions have led to significantly different sets of species being introduced in each time period. While there may have been a certain level of opportunism in which species were transported and introduced, determined by the local availability of species, people have nevertheless preferentially selected specific types of birds for introduction (Blackburn & Duncan 2001a). Differences in taxonomic composition between the historical and modern eras are largely consistent with a shift from planned attempts by acclimatisation societies to introduce species considered to be beneficial in the historical period, to an increasing proportion of unplanned releases of species from the cage bird trade in the modern era, as deliberate introductions have increasingly become outlawed (Blackburn *et al*. 2010). During the historical period, European settlers and acclimatisation societies favoured ‘useful’ species, which were introduced for the purposes of game hunting, for food, as biocontrol, or for ornamental or aesthetic reasons (Nentwig 2007, Blackburn *et al*. 2010, Cassey *et al*. 2015). This led to an over-representation of species for hunting and ornamental purposes from the families Anatidae (ducks, geese and swans), Phasianidae (pheasants and other fowl), Odontophoridae (quails) and Columbidae (doves and pigeons), and for aesthetic reasons and for their songs from the families Estrildidae and Fringillidae (the finches) (table 3.3, figure 3.2).

In contrast, during the modern era of globalisation and trade, alien bird species are more likely to be the result of releases or escapes from the pet trade (Blackburn *et al*. 2010). Seven families are significantly over-represented in introductions in the modern but not the historical era. Introductions of birds from the Ploceidae (weavers), Psittacidae (parrots) and Sturnidae (starlings) are most likely to be a result of the pet trade, whereas those from Anserantidae (magpie goose), Ciconiidae (storks), Phoenicopteridae (flamingos), and Gruidae (cranes) are more likely as a result of escaped free-ranging birds kept in zoological and private collections (table 3.3, figure 3.2). However, these last four families are small, meaning that when even a few species from them are introduced it represents a high proportion of the entire family, and they may be over-represented in introductions for this reason. Compared to the historical era, introductions during the modern era represent a more diverse set of bird species from a wider range of families (figure 3.2). This supports the shift from planned releases of beneficial species to unplanned releases or escapes from the pet trade.

Certain families are over-represented in both the historical and modern eras: species from Phasianidae and Anatidae may have ongoing appeal for landowners populating private lakes and estates for ornamentation and hunting. Estrildid finches (Estrildidae) may have always held appeal as cage birds in both historical and modern eras. Three bird families were significantly under-represented in the modern era: Tyrannidae (flycatchers), Trochilidae (hummingbirds) and Sylviidae (Old World warblers), and the first two of these families were also under-represented in the historical era (table 3.3). This may be due to their native ranges being generally outside of the realms where alien birds were being sourced and traded. Species in these families may also be more difficult to keep in captivity.

In both the historical and modern eras, significantly fewer bird species were introduced than would be expected were introductions a random sample of all bird species (table 3.1). However, the overlap of species which were introduced during both of the time periods was also significantly less than expected by chance (table 3.1). This further supports the changing drivers of bird introductions. That the compositions of species introduced in each time period were different further supports the hypothesis that the drivers of species introductions have changed over time.

In summary, the basic drivers behind introductions have changed between the historical and modern time periods. Bird introductions are increasing in number, and occur in a wider range of countries as a result of globalisation. The movement of the British was associated with alien bird introductions in the historical period, with species that were deemed to be beneficial sourced primarily from the Palearctic realm for introduction. In the modern era, data are consistent with a shift in drivers towards the burgeoning global pet trade, and an increase in country wealth. Compared to the historical era, a different set of species from different sources are now being selected and introduced into a different set of countries. Taken together, these results suggest that if invasions are to be prevented, then more resources for combating alien species should be directed at the transport and introduction stages of the invasion pathway (Westphal *et al*. 2008). All the available evidence suggests that numbers of introductions, numbers of species introduced, and numbers of countries involved are all on the increase. Given that wealth and trade seem to be driving modern introductions, and wealth and trade are predicted to continue to grow as countries continue to develop, the situation is only going to get worse. Therefore it seems likely that we are going to have to work even harder if we are to achieve our aim (or Aichi target 9 aim (CBD 2010)) of identifying and managing alien species and pathways to prevent invasions before they occur.

Chapter 4.

Determinants of global variation in alien bird species richness

4.1 INTRODUCTION

The number of species naturally inhabiting a location (native species richness) is ultimately driven by the processes of speciation, extinction, immigration and emigration, and proximately by the suite of environmental, ecological, historical and evolutionary factors that determine the interplay of these four processes (Rosenzweig 1995). Yet, the spread of humans around the world has modified this interplay, elevating extinction rates (Duncan *et al*. 2002), potentially altering speciation rates (Rosenzweig 2001, Thomas 2013), and by deliberately or accidentally transporting and introducing species to areas beyond the limits of their native ranges at increasingly high rates (Cassey *et al*. 2015). These species (hereafter termed alien) are a significant component of human induced global change, presenting one of the most substantial environmental challenges of the 21st century (Vitousek *et al.* 1997, Stohlgren *et al.* 2006). Aliens can adversely affect the native biota of a new habitat, driving populations and species to extinction (Clavero & Garcia-Berthou 2005), altering ecosystem processes (Dukes & Mooney 2004), and negatively impacting social and economic activities (Pimentel *et al.* 2000). There is therefore a significant impetus to identify the underlying drivers of the invasion process.

Much research effort has been devoted to achieving a better understanding of the factors that govern global invasions by alien species. The importance of various environmental, climatic, socioeconomic and demographic factors is increasingly being realised, but as yet there is limited consensus regarding their relative influence (Westphal *et al.* 2008, Pyšek *et al.* 2010, Essl *et al.* 2011, Gallardo *et al.* 2015). For the first stages of invasion (transport and introduction), anthropogenic factors relating to the socioeconomic drivers of species' translocation are particularly important in determining alien species distribution (Chapter 3), whilst at later stages (establishment and spread), attributes relating to the climate and environment become more relevant (Stohlgren *et al.* 2006). Introduced species that successfully establish populations contribute to the alien species richness of a location. Therefore, when investigating the factors that influence alien invasions and species richness, it is essential to examine the different pressures from all stages of the invasion pathway, both anthropogenic and environmental.

Data on alien bird introductions provide a unique opportunity to test hypotheses about the drivers of alien species richness. Birds have a long history of translocation and introduction (Long 1981, Blackburn *et al*. 2009a, Blackburn *et al*. 2015b, Cassey *et al*. 2015), have been introduced to all major ice-free regions of the world (Duncan *et al*. 2003), and are also the only large taxon for which sufficiently high quality information on introduction failures is obtainable (Blackburn *et al.* 2008). Usefully for comparison purposes, the determinants of native bird richness have also already been investigated (Orme *et al.* 2005, Davies *et al.* 2007a).

There are many hypotheses regarding the environmental predictors that drive species richness. These can broadly be divided into aspects relating to temperature (ambient energy hypothesis), thought to influence species distributions via physiological constraints (Turner *et al.* 1988); the availability of water, heat and light (productive energy hypothesis), thought to influence species richness by the energy flow through food webs (Waide *et al.* 1999); and the number of habitat types or topographical variability of a region (habitat heterogeneity hypothesis) (Rozensweig 1995, Kerr & Packer 1997, Rahbek & Graves 2001). If these aspects of the environment can affect native species richness, then they are likely also to impact upon alien species richness to some degree.

For native birds, topographical variability and temperature have been identified as the most important global predictors of species richness (Davies *et al.* 2007a), but for alien species, the relative impacts of environmental factors apparently vary depending on scale and taxon. Evans *et al.* (2005a) found the richness of alien bird species in Britain to be related to energy availability, whereas Stohlgren *et al.* (2006) found that low elevation areas close to the coast with high precipitation had the highest richness of alien plants, birds and fishes in the continental USA. The impacts of the native biota of a region must also be taken into consideration when assessing alien species richness. Alien species may follow the richness patterns of their native counterparts, if they respond to similar energy and resource limitations in the same way (Stohlgren *et al.* 2006), or they may have to compete for resources and niche space with native species (Elton 1958), or even risk being predated upon. However, alien species have been found to exhibit an ability to adapt to a wider range of environmental limits than those found in their native range (Li *et al.* 2014), and therefore environmental factors alone are likely to be insufficient in explaining the variation in alien species richness (Gallardo *et al.* 2015).

Recent studies have demonstrated that on broad spatial scales, the impact of human activities exceeds the influence of biogeography and climate on species invasions (Blackburn *et al.* 2008, Chiron *et al.* 2009, Pyšek *et al.* 2010). Anthropogenic factors, including those associated with transport, trade and tourism, have consistently been related to the spatial distribution of alien species (Westphal *et al.* 2008, Hulme 2009, Pyšek *et al.* 2010, Essl *et al.* 2011, Gallardo *et al.* 2015). For instance, roads, canals and railways create pathways along which species can disperse (Hulme 2009). Ports are the entrance point of alien species arriving from other continents as imports, through contamination of a product, or as stowaways (Hulme 2009, Gallardo *et al.* 2015). Human population pressure and various contemporary indicators of socioeconomic conditions are associated with high rates of species invasion (Stohlgren *et al.* 2006, Blackburn *et al.* 2008, Chiron *et al.* 2009, Hulme 2009, Pyšek *et al.* 2010, Essl *et al.* 2011, Spear *et al.* 2013), and can be related to a more substantive pet trade, resulting in accidental and deliberate releases of species (Su *et al*. 2014). In addition, the environmental legacies of economic development such as loss and fragmentation of natural habitats, agricultural intensification, and horticultural activity are known to foster alien species establishment and spread (Essl *et al.* 2011).

The number of alien species established per site is also influenced by the introduction history of a region, namely the number of species that have had the chance to establish at that site (colonisation pressure, *sensu* Lockwood *et al*. 2009) (Jeschke & Strayer 2005, Blackburn *et al.* 2008, Chiron *et al.* 2009), and the length of time that they have been there (time since introduction), given that this will increase the opportunity for the species to spread (Wilson *et al.* 2007, Li *et al.* 2014, Byers *et al.* 2015). Many studies of invasion ecology assume that the opportunity for biological invasions is similar across regions. However, if colonisation pressure (also termed introduction effort or community level propagule pressure) varies then this may not be the case. Alien species richness cannot be greater than the number of species introduced to a location (allowing for population spread), and therefore there is likely to be a strong positive correlation between the two. However, aside from a couple of examples (e.g. Blackburn *et al.* 2008, Chiron *et al.* 2009), detailed data on colonisation pressure is often not included in invasion studies due to the lack of information for this early stage in the invasion process (Pyšek *et al.* 2010). This is important because the number of species introductions that fail is unlikely to be constant, but instead a function of the abiotic environment, biotic interactions, and aspects of the introduction event such as propagule size (Zenni & Nuñez 2013, Duncan *et al*. 2014). Without this information, ecologists have no way of factoring out the role that colonisation pressure plays from the influence of ecological forces or anthropogenic pressures.

While the determinants of alien species richness have been widely explored, the majority of studies have been conducted at the local or regional level. Studies that have investigated continental or global scale patterns have often been based on coarse or country level datasets (Taylor & Irwin 2004, Pyšek *et al.* 2010), due to a lack of detailed global data for an entire taxonomic group. In addition, a scarcity of information on colonisation pressure has hampered the analysis of the invasion pathway. Without this knowledge, erroneous conclusions about the determinants of alien species richness are likely.

Here I present a global analysis of the importance of anthropogenic and environmental predictors in determining large-scale patterns of alien species richness for a major animal group, birds (Class Aves). I use a newly developed database comprising 27,737 distribution records for 972 alien bird species (Chapter 2). Uniquely, my database includes information on colonisation pressure, allowing me to explore the factors that underpin alien species richness. I combine information on colonisation pressure with environmental and anthropogenic variables hypothesised to influence alien species richness (table 4.1), in order to identify the determinants of alien bird species richness worldwide. I also provide, to my knowledge, the first global map of alien bird richness at a 1° resolution.

4.2 METHODS

4.2.1 Spatial extent

Global analyses were based on the vector range maps and introduction records from the GAVIA database (Chapter 2), supplemented with additional raster data on environmental and anthropogenic variables. For consistency with studies of native bird species richness patterns (Orme *et al.* 2005, Davies *et al.* 2007a), all data were converted to a global grid using a Behrmann equal area projection at a cell resolution of 96.486km, equivalent to 1° longitude and approximately 1° latitude at the equator. This was performed using the *R* packages *sp* (Pebesma & Bivand 2005, Bivand *et al*.

Table 4.1 Predicted relationships between alien bird species richness and anthropogenic and environmental variables, with details of studies that provide support for each prediction.

	Prediction	Predicted relationship	Support
Anthropogenic			
Colonisation pressure	As colonisation pressure (the number of species introduced) increases, so will alien bird richness	+	Jeschke & Strayer 2005; Blackburn *et al*. 2008; Chiron *et al*. 2009; van Wilgen & Richardson 2012
Time since introduction	Species richness will be highest in areas where alien birds have been introduced for the longest	+	Wilson *et al.* 2007; Li *et al.* 2014; Byers *et al.* 2015
Human population density	Alien species richness will be highest in areas where human population density is high	+	Vilà & Pujadas 2001;Taylor & Irwin 2004; Blackburn *et al*. 2008; Leprieur *et al*. 2008; Hulme 2009; Pyšek *et al*. 2010; Essl *et al*. 2011; Spear *et al*. 2013
Human footprint index	Where human footprint is high (including higher human population, greater habitat disturbance and increased access) alien bird richness will also be high	+	Westphal *et al*. 2008; Hulme 2009; Sharma *et al*. 2010; Spear *et al*. 2013; Gallardo *et al*. 2015
Distance to city	As you move further away from cities, alien bird richness will decrease	-	Sharma *et al*. 2010
Distance to historic port	As you move further away from historic ports, alien bird richness will decrease	-	Hulme 2009; Essl *et al*. 2011; Gallardo *et al*. 2015
Environmental			
Biotic			
Native species richness	In areas where native bird richness is high, alien bird richness will also be high	+	Evans *et al*. 2005a; Stohlgren *et al*. 2006; Westphal *et al*. 2008
Habitat complexity	As the number of habitat types in an area increases, as will alien species richness	+	Rosenzweig 1995; Kerr *et al*. 2001
Abiotic			
Altitude	As altitude increases, alien bird richness will also increase	+	Richerson & Lum 1980; Kerr & Packer 1997; Rahbek & Graves 2001; Davies *et al*. 2007a
Temperature	At the extremes of median temperature, alien bird richness will be low, with a peak when it is mid-high. As the temperature range within a grid cell increases, alien richness will decrease	-/+	Turner *et al*. 1988; Currie 1991; Waide *et al.* 1999; Allen *et al*. 2002; Evans *et al*. 2005a; Davies *et al.* 2007a; Essl *et al.* 2015; Gallardo *et al*. 2015
Precipitation	As the level of precipitation increases, as will alien species richness	+	Waide *et al*. 1999; Stohlgren *et al*. 2006; Essl *et al.* 2015

2013b) and *raster* (Hijmans 2015). The global grid contained 360 by 152 cells, omitting the partial cells at latitudes higher than 87.13°. Each grid cell was assigned latitude and longitude values, which represented the centre point of each cell. The global grid contained 54,720 cells, but cells not containing any alien bird species records would inflate covariation measures (the double zero problem: Legendre & Legendre 1998), therefore those cells with no alien bird introductions (i.e. where colonisation pressure = 0), were excluded. Any cell which fell entirely over the ocean, or with an NA value for any of the variables described below was also excluded from the analysis, leaving a total of 8,249 grid cells.

4.2.2 Alien species richness

The GAVIA database contains records for a total of 972 species, of which 419 have established alien populations. The measure of alien species richness used here is based on 362 species with records of established alien populations containing sufficient detail to convert to range maps using the software ESRI ArcGIS version 9.3 (2008) (Chapter 2). The most recently reported established range for each species was used to calculate alien species richness. The range maps were converted to grid cell counts using the *R* packages *rgdal* (Bivand *et al*. 2015)*, sp* (Pebesma & Bivand 2005, Bivand *et al*. 2013b)*,* and *raster* (Hijmans 2015). Species were scored as present in a grid cell if any of the established introduced range fell within the cell boundaries. This ensured that even small established introductions, or those occurring on small islands, were counted. Overall alien species richness was derived by summing all species present within each cell.

4.2.3 Predictor variables

Six anthropogenic predictor variables and five environmental predictor variables were selected for use in model building based on their suitability for hypothesis testing (table 4.1). Available raw data for each of the candidate variables were re-projected and re-sampled to the same equal area grid as the alien species richness data using spatial tools from the statistical software R (version 3.1.1; R Core Team 2015) (for details see table 4.2).

Table 4.2 Details of the anthropogenic and environmental predictor variables selected for use in model building.

Predictor	Variations (per grid cell)	Transformations	Raw resolution	Unit	Source
Anthropogenic					
Colonisation pressure	total	log		No. species introduced	GAVIA database
Time since introduction	earliest	log		Years since first record	GAVIA database
Human population density	mean	log	1x1 km grid	persons per km2	http://sedac.ciesin.columbia.edu/gpw; CIESIN 2005
Human population density	median	log	1x1 km grid	persons per km2	http://sedac.ciesin.columbia.edu/gpw; CIESIN 2005
Human footprint	median	square root	1x1 km grid	Human Influence Index (HII)	http://dx.doi.org/10.7927/H4M61H5F; WCS & CIESIN 2005
Distance to city	median	log	30 arc seconds	minutes of travel time	http://bioval.jrc.ec.europa.eu/products/gam; Nelson 2008
Distance to historic port	median	log(x+1)		kilometres to port	http://pendientedemigracion.ucm.es/info/cliwoc/cliwoc15.htm; García-Herrera *et al*. 2005
Environmental					
Native species richness	total	square root		No. native species	ADHoC database; Orme *et al.* 2005
Altitude	median	log	30 arc seconds	metres above sea level	http://www.worldclim.org; Hijmans *et al.* 2005
Altitude	range	square root	30 arc seconds	metres above sea level	http://www.worldclim.org; Hijmans *et al.* 2005
Temperature	median	log	30 arc seconds	degrees centigrade	http://www.worldclim.org; Hijmans *et al.* 2005
Temperature	minimum		30 arc seconds	degrees centigrade	http://www.worldclim.org; Hijmans *et al.* 2005
Temperature	maximum	log	30 arc seconds	degrees centigrade	http://www.worldclim.org; Hijmans *et al.* 2005
Temperature	range	log	30 arc seconds	degrees centigrade	http://www.worldclim.org; Hijmans *et al.* 2005
Precipitation	median	square root	30 arc seconds	millimetres	http://www.worldclim.org; Hijmans *et al.* 2005
Habitat complexity	8 grid cells		300 m	number of landcover types	http://www.esa-landcover-cci.org/?q=node/158; Arino *et al.* 2012
Habitat complexity	24 grid cells		300 m	number of landcover types	http://www.esa-landcover-cci.org/?q=node/158; Arino *et al.* 2012

4.2.3.1 Anthropogenic variables

(1) *Colonisation pressure*

Colonisation pressure (total number of species recorded in a grid cell) was calculated in a similar way to alien species richness, but additionally included records from GAVIA where the species was considered introduced to an area but its status was listed as breeding (but not yet established), unsuccessful, died out, or extirpated. Records with the status ‘unknown’ were excluded from all analyses. Although GAVIA contains records for a total of 972 introduced species, only records for 719 of those species contain sufficient detail to enable conversion of their areas of introduction to range maps using the software ESRI ArcGIS version 9.3 (2008) (Chapter 2). The range maps were converted to grid cell counts using the *R* packages *rgdal* (Bivand *et al*. 2015)*, sp* (Pebesma & Bivand 2005, Bivand *et al*. 2013b)*, raster* (Hijmans 2015) and *rgeos* (Bivand & Rundel 2015). Species were scored as present in a grid cell if any of the introduced range fell within the cell boundaries, and colonisation pressure was derived by summing all species present within each cell.

(2) *Time since first introduction*

Alien distribution records in GAVIA include a date of introduction, which is the first year that the species was recorded as being present in an area. To calculate the length of time since the first alien bird species was recorded in each grid cell, all of the dates of introduction for each species range map that overlapped each grid cell were extracted using the *R* packages *rgdal* (Bivand *et al*. 2015)*, sp* (Pebesma & Bivand 2005, Bivand *et al*. 2013b)*, raster* (Hijmans 2015), and then the earliest date recorded from each cell was subtracted from the year 2015. This resulted in a single figure for each grid cell, equal to the number of years since the first record of any alien bird species in that cell.

(3) *Human population density*

The Gridded Population of the World: Population Density Grids gives data on global human population densities in 2000, adjusted to match UN totals, measured in persons per square km. It was downloaded from http://sedac.ciesin.columbia.edu/gpw (Version 3 (GPWv3): CIESIN 2005, downloaded 26/04/2013). The *aggregate* function in *R* was used to summarise the mean and median human population density for each grid cell.

(4) *Human footprint index*

The Global Human Footprint Dataset of the Last of the Wild Project is the Human Influence Index (HII) normalized by biome and realm. It was downloaded from http://dx.doi.org/10.7927/H4M61H5F (version 2: WCS and CIESIN 2005, downloaded 26/04/2013). The HII is a global dataset of 1 kilometre grid cells, created from nine global data layers covering human population pressure (population density), human land use and infrastructure (land use/land cover, built-up areas, nighttime lights), and human access (roads, railroads, coastlines, navigable rivers). The *aggregate* function in *R* was used to summarise the median human footprint index for each grid cell.

(5) *Distance to nearest city*

Estimated travel time to the nearest city (>50,000 people in the year 2000) was downloaded from http://bioval.jrc.ec.europa.eu/products/gam/ (Nelson 2008, accessed 10/09/2013) at a resolution of 30 arc seconds measured in minutes of travel time. The *aggregate* function in *R* was used to summarise the median travel time to the nearest city for each grid cell.

(6) *Distance to historic port*

Distance to historic shipping port was based on the Climatological Database for the World's Oceans: 1750-1854 (CLIWOC) dataset, and was downloaded from http://pendientedemigracion.ucm.es/info/cliwoc/cliwoc15.htm (García-Herrera *et al*. 2005, accessed 08/04/2015). The *dist* function in *R* was used to find the distance in metres from each grid cell to the nearest port in the database. Distance to historic port was divided by 1000 to convert it to kilometres.

4.2.3.2 Environmental variables

(1) *Native bird species richness*

Native bird species richness for 9,650 extant bird species was calculated using native breeding range data obtained from the ADHoC (Avian Diversity Hotspots Consortium) database, first published by Orme *et al.* (2005). Native bird species richness was calculated using the *R* packages *rgdal* (Bivand *et al*. 2015), *sp* (Pebesma & Bivand 2005, Bivand *et al*. 2013b), and *raster* (Hijmans 2015), and species were scored as present in a grid cell if any of the native range fell within the cell boundaries.

(2) *Altitude (median and range)*

Altitudinal data were downloaded from http://www.worldclim.org/ (Hijmans *et al.* 2005, downloaded 01/05/2013) at a resolution of 30 arc seconds measured in metres above sea level. The *aggregate* function in *R* was used to summarise the minimum, maximum and median altitudes for the land area within each grid cell. The minimum was subtracted from the maximum to obtain the altitudinal range of each cell. In 30 of the grid cells, median altitude was below sea level, and therefore had a negative value

(0.28% of all cells). The most negative median altitude value was -31.7, therefore 32 was added to all values.

(3) *Temperature (median, minimum, maximum and range)*

Data on temperature were downloaded from http://www.worldclim.org/ (Hijmans *et al.* 2005, downloaded 01/05/2013) at a resolution of 30 arc seconds measured in degrees centigrade multiplied by ten. The *aggregate* function in *R* was used to summarise the median temperature within each cell from the WorldClim bioclimatic variable BIO1 (annual mean temperature), the minimum from bioclimatic variable BIO6 (minimum temperature of coldest month), and the maximum from bioclimatic variable BIO5 (maximum temperature of warmest month). The minimum, maximum and median temperatures were divided by ten in order to convert them back to true centigrade values. The minimum was then subtracted from the maximum in order to obtain the temperature range within each grid cell.

(4) *Precipitation (median)*

Data on precipitation were downloaded from http://www.worldclim.org/ (Hijmans *et al.* 2005, downloaded 01/05/2013) at a resolution of 30 arc seconds measured in millimetres. The *aggregate* function in *R* was used to calculate the median precipitation within each cell from the WorldClim bioclimatic variable BIO12 (annual precipitation).

(5) *Habitat complexity*

Data on land cover types were downloaded from http://www.esa-landcover-cci.org/?q=node/158 (Arino *et al*. 2012, downloaded 02/04/2015) and included 37 categories at a resolution of 300m. The *extract* function from the package *raster* in *R* (Hijmans 2015) was used to extract the number of different land cover types in the surrounding eight and 24 cells of each grid cell as a measure of habitat complexity.

4.2.4 Statistical analyses

The full dataset of alien bird richness was not normally distributed (figure 4.1a). A small number of very successful widely distributed alien birds (e.g. *Columba livia*, *Passer domesticus*) have caused a large proportion of grid cells (n = 4644; 56.3%) to have equal values for alien richness and colonisation pressure (largely where they both equal 1, or both equal 2). Although interesting, these cells were not representative of all species, and gave the impression that alien birds introduced in these areas had a

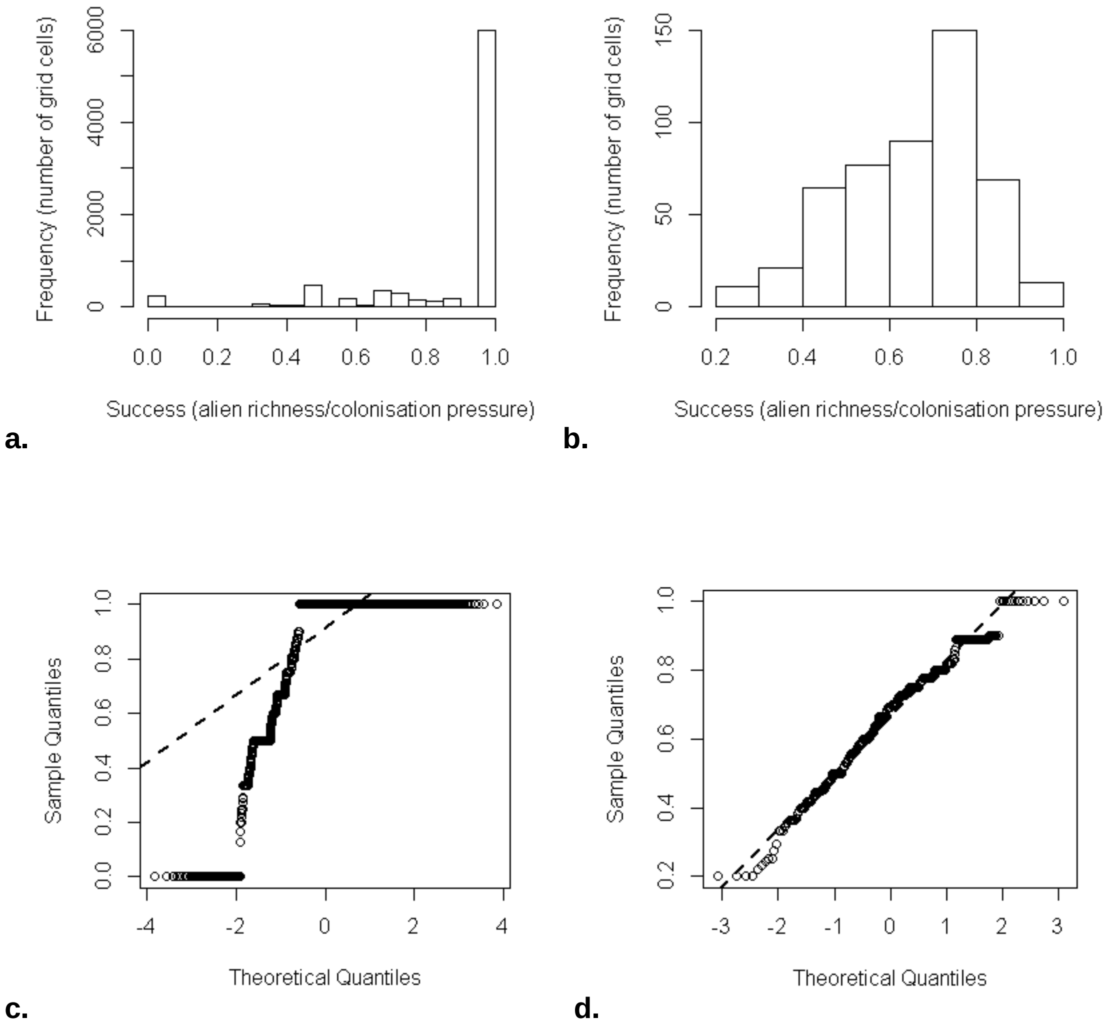


Figure 4.1 The frequency distribution of establishment success (i.e. alien bird species richness/colonisation pressure) for **(a)** the full global dataset and **(b)** the subset of data where colonisation pressure ≥9, and the normal probability plots for establishment success in **(c)** the full dataset, and in **(d)** the subset of data where colonisation pressure ≥9, showing the expectation under a normal distribution (dashed line) and the observed distribution (open circles).

success rate of 100%, when in fact it is just one or two highly successful adaptable species driving the pattern. If all grid cells were used for the analysis then over half of the data points would be assessing the distributions of these few species rather than examining the broad scale richness patterns I am interested in here. To account for this, I used a Shapiro-Wilk test for normality to identify a subset of data where alien bird establishment success (alien species richness/colonisation pressure) had the highest W statistic out of all possible subsets. Although in this study I am not testing establishment success, I used a measure of it in order to identify a subset of data that had the most normal relationship between colonisation pressure and alien richness. The optimum subset identified comprised 496 grid cells, and included only those grid cells with colonisation pressure ≥9 (Shapiro-Wilk test for normality: W = 0.98; n = 496) (figure 4.1). Figure 4.2 demonstrates the spatial distribution of the resulting grid cells.

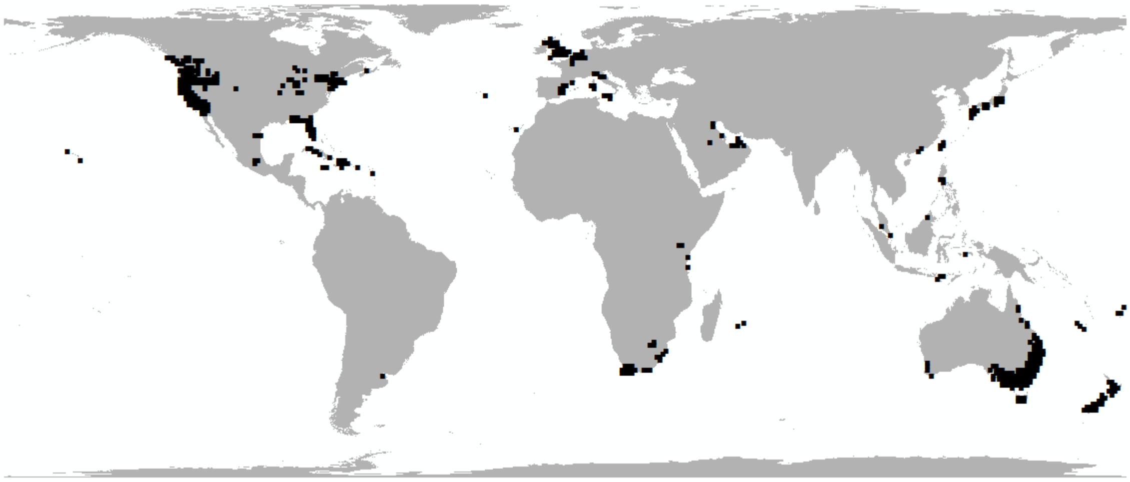


Figure 4.2 The spatial distribution of the cells selected for analysis, where colonisation pressure ≥9. These cells represent the subset of data that had the most normal relationship between colonisation pressure and alien richness, and therefore where the pattern is not simply being driven by one or two highly successful species.

Tests of collinearity between the predictor variables revealed relatively high correlations within the temperature variables, altitude variables and habitat complexity variables, and between human population density, human footprint index and distance to the nearest city (table 4.3). The predictor variables: temperature minimum and maximum; median altitude; and the habitat complexity in the surrounding 24 cells were thus excluded from models *a priori*. As the human footprint index incorporated human population density, human infrastructure and road access, population density mean and median and distance to city were also excluded *a priori*. This resulted in 10 predictor variables for analysis.

Table 4.3 Correlation matrix of all transformed predictor variables from the subset of data that only contains grid cells where colonisation pressure ≥9: r is above the diagonal and P is below it.

	native richness	colonisation pressure	time since introduction	altitude (median)	altitude (range)	temperature °C (median)	temperature °C (max.)	temperature °C (min.)	temperature °C (range)	population (mean)	population (median)	distance to city	human footprint	number of different globecover (8 cells)	number of different globecover (24 cells)	distance to historic port	precipitation (median)
native richness		-0.44	-0.23	0.13	-0.03	0.03	0.16	-0.04	0.14	-0.14	-0.18	0.12	-0.18	0.03	0.03	0.02	-0.20
colonisation pressure	0.000		0.04	-0.20	0.04	0.16	-0.27	0.27	-0.40	0.21	0.17	-0.19	0.18	-0.01	0.05	-0.07	0.25
time since introduction	0.000	0.425		0.14	0.10	-0.37	-0.23	-0.30	0.12	-0.04	-0.06	-0.06	0.00	0.06	0.09	0.02	0.03
altitude (median)	0.003	0.000	0.002		0.76	-0.47	-0.13	-0.46	0.33	-0.35	-0.40	0.39	-0.52	-0.07	-0.16	0.38	-0.21
altitude (range)	0.509	0.394	0.025	0.000		-0.23	-0.18	-0.12	-0.03	-0.06	-0.10	0.24	-0.30	-0.07	-0.15	0.29	0.08
temperature °C (median)	0.446	0.000	0.000	0.000	0.000		0.61	0.88	-0.47	0.22	0.25	-0.08	0.20	0.02	0.02	-0.15	0.07
temperature °C (max.)	0.000	0.000	0.000	0.004	0.000	0.000		0.32	0.29	-0.02	-0.01	0.02	-0.06	-0.04	-0.07	0.09	-0.41
temperature °C (min.)	0.334	0.000	0.000	0.000	0.006	0.000	0.000		-0.79	0.23	0.28	0.01	0.20	0.03	0.02	-0.22	0.25
temperature °C (range)	0.002	0.000	0.009	0.000	0.523	0.000	0.000	0.000		-0.27	-0.31	-0.01	-0.25	-0.06	-0.06	0.27	-0.55
population (mean)	0.001	0.000	0.357	0.000	0.211	0.000	0.708	0.000	0.000		0.94	-0.76	0.85	0.09	0.15	-0.51	0.34
population (median)	0.000	0.000	0.193	0.000	0.029	0.000	0.830	0.000	0.000	0.000		-0.74	0.88	0.10	0.15	-0.50	0.38
distance to city	0.010	0.000	0.162	0.000	0.000	0.086	0.586	0.903	0.848	0.000	0.000		-0.81	-0.09	-0.16	0.45	-0.11
human footprint	0.000	0.000	0.952	0.000	0.000	0.000	0.168	0.000	0.000	0.000	0.000	0.000		0.12	0.20	-0.51	0.28
number of different globecover (8 cells)	0.503	0.784	0.199	0.095	0.113	0.599	0.405	0.437	0.208	0.035	0.020	0.035	0.005		0.76	-0.14	0.07
number of different globecover (24 cells)	0.508	0.236	0.042	0.000	0.001	0.732	0.101	0.627	0.177	0.001	0.001	0.000	0.000	0.000		-0.22	0.13
distance to historic port	0.734	0.096	0.614	0.000	0.000	0.001	0.052	0.000	0.000	0.000	0.000	0.000	0.000	0.002	0.000		-0.10
precipitation (median)	0.000	0.000	0.484	0.000	0.068	0.132	0.000	0.000	0.000	0.000	0.000	0.015	0.000	0.096	0.004	0.029	

4.2.4.1 Spatial autocorrelation

Spatial autocorrelation is a common phenomenon in environmental data, where similarities in the values of predictor and response variables arise as a function of proximity of sampling locations. Species distribution data in particular are inherently spatially structured (Kissling & Carl 2007) due to a combination of intrinsic processes such as population growth and dispersal (Legendre *et al.* 2002), areas of false presence or absence records due to errors in distributional data (Hurlbert & White 2005), or where the environmental processes that drive species richness patterns show spatial autocorrelation themselves (Legendre *et al.* 2002). There is strong spatial autocorrelation in both the response and predictor variables in the data (Moran's I ≥ 0.73; $p < 0.001$ in all cases, with the exception of *time since introduction* where Moran's I ≥ 0.56; $p < 0.001$, and *habitat complexity* which displayed very limited spatial autocorrelation, Moran's I = 0.07; $p = 0.02$), and therefore regression methods that assume each grid cell is an independent data point are not appropriate here.

To address this, spatial autocorrelation was integrated into the models using simultaneous autoregressions (SAR) (Bivand *et al*. 2013a). Neighbourhood size was defined as the distance which captured the centre point of all eight surrounding grid cells (150 km). Neighbourhood connection matrices were calculated with row-standardized weights. Two specifications of the error covariance matrix were considered: SAR_{lag} (spatial autocorrelation in the response), and SAR_{err} (spatial autocorrelation in the error term). A Lagrange multiplier test was used to find the best error specification and the SAR_{err} model showed higher support (SAR_{err}: Lagrange multiplier RLMerr = 348.1, $p < 0.001$; SAR_{lag}: Lagrange multiplier RLMlag = 0.004, $p = 0.95$). SAR_{err} models are recommended for use when dealing with spatially autocorrelated species distribution data and are the most reliable type of SAR model, having been found to perform well and provide the most precise parameter estimates regardless of the kind of spatial autocorrelation induced and whether model selection is via R^2 or AIC (Kissling & Carl 2007).

4.2.4.2 Model selection

I first ran single predictor models of all variables in order to compare the significance and directions of slopes for different predictors modelled in isolation (table 4.4). Quadratic as well as linear terms were included for 5 of the predictors in the models to allow for non-linear relationships (time since introduction, distance to historic port, native species richness, temperature range and precipitation).

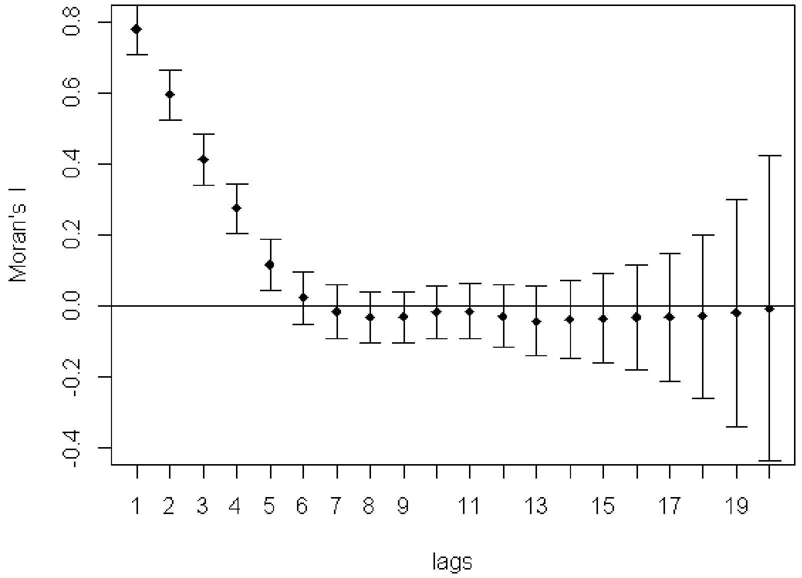
Table 4.4 Outputs from single predictor SAR_{err} models where log alien species richness is the response variable. S.E. = standard error for the variable. R^2 = pseudo-R^2, calculated as the squared Pearson correlation between predicted and observed values.

	Estimate ± S.E.					
Predictor	**Linear**	**Quadratic**	**AIC**	**Δ AIC**	**weight**	**R^2**
Colonisation pressure	0.75 ± 0.02		-541.78	0.00	1.00	0.73
Native richness	-0.17 ± 0.03	0.005 ± 0.001	86.49	628.28	0.00	0.14
Time since introduction	-0.43 ± 0.12	0.06 ± 0.01	94.97	636.76	0.00	0.04
Temperature (range)	1.99 ± 0.85	-0.40 ± 0.14	100.04	641.82	0.00	0.09
Human footprint index	0.09 ± 0.02		114.33	656.12	0.00	0.00
Precipitation	0.03 ± 0.01	-0.0004 ± 0.0001	130.32	672.11	0.00	0.09
Distance to historic port	-0.17 ± 0.04	0.02 ± 0.004	131.97	679.81	0.00	0.06
Temperature (median)	0.18 ± 0.05		133.41	675.19	0.00	0.00
Altitude (range)	0.003 ± 0.002		142.29	684.07	0.00	0.00
Habitat complexity	0.02 ± 0.01		142.73	684.52	0.00	0.00

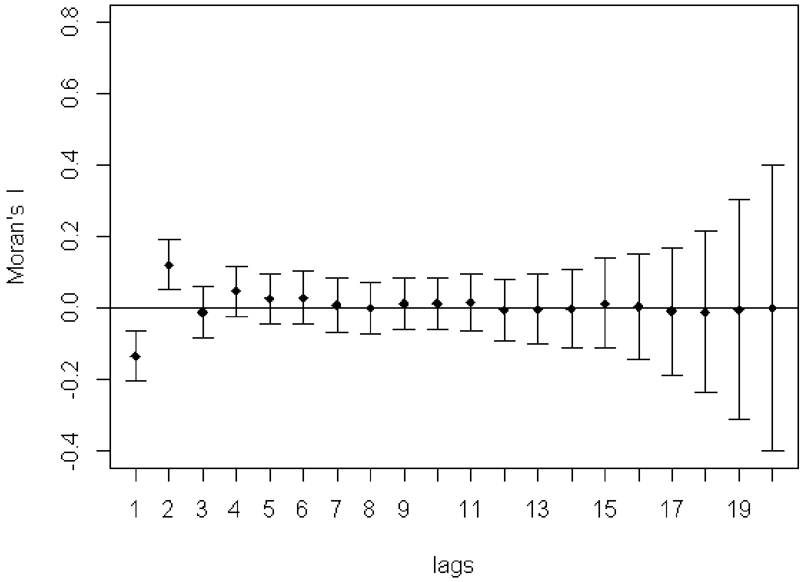
The inclusion of quadratic terms was determined by comparing single predictor models for each linear term with a model containing both the linear and quadratic form. If the AIC (Akaike's information criterion; Burnham & Anderson 2002) improved by >4 then the quadratic form was included in model building.

A multivariate minimum adequate model (MAM) was devised by forward stepwise procedures. The single predictor model with the lowest AIC value was used as a starting model, with each predictor added in turn. The criterion for inclusion of additional model terms was improvement of the AIC value by >4. The use of AIC in model selection procedures observes principles of parsimony and avoids the model over-fitting that can be a result of data dredging (Burnham & Anderson 2002). Once the MAM with the lowest overall AIC score was identified, each predictor not included was once again added in turn to ensure that the best combination of predictor variables was selected. Goodness-of-fit of the SAR_{err} models was evaluated by calculating Pearson's correlation coefficients between the response variables and the fitted values of the models (Essl *et al.* 2011). Spatial correlograms were used to examine the patterns of spatial autocorrelation for alien bird species richness, and for the model residuals, and to confirm that the method largely eliminates spatial autocorrelation in the MAM (figure 4.3).

To assess model performance and predictive capabilities, holdout cross validation was performed. Each of the 496 grid cells was assigned to a biogeographic realm (Olson *et al*. 2001). The grid cells from the Antarctic, Indo-Malay, Neotropical and Oceanic realms were excluded from this part of the analysis due to low sample size.



a.



b.

Figure 4.3 Correlograms to examine the patterns of spatial autocorrelation within **(a)** alien bird richness from the subset of data that only contains grid cells where colonisation pressure ≥9; **(b)** the residuals of the most likely SAR_{err} model.

Three of the four remaining realms were used as the training set upon which stepwise model selection was conducted, as described above. The fourth realm was then used as the testing set and a cross validation metric, root mean squared error (RMSE), was calculated to assess the ability of the model at predicting the held-out realm. Goodness-of-fit of the model was also evaluated by calculating Pearson's correlation coefficients between the response variables of the testing set and the fitted values of the model (Essl *et al.* 2011). This process was repeated three more times with a different realm being used as the testing set each time, and then the RMSE across all samples was averaged to get the cross validation error. This allowed me to evaluate not only how much variance was explained, but also the predictive accuracy of the global-scale model. I used cross validation to assess the robustness of model parameter estimates in a manner akin to k-fold cross validation (Arlot & Celisse 2010), but following Newbold *et al*. (2015) using realms to test the biological predictions of the models. This allowed me to provide a more realistic biological test of model predictions, rather than using holdout models on randomly divided sets of data.

R^2 values are not directly provided for SAR models, and a maximum model fit was thus assessed with a pseudo-R^2 value calculated as the squared Pearson correlation between predicted and observed values (hereafter simply referred to as R^2) (Kissling & Carl 2007). All SAR models were built with the *R* package *spdep* (Bivand *et al*. 2013a, Bivand & Piras 2015) from statistical software R (version 3.2.1; R Core Team 2015).

4.3 RESULTS

In total, 362 bird species have been recorded as having at least one established alien population (at a resolution high enough to result in production of a range map), from a total of 719 species which have been recorded as introduced somewhere in the world (ditto). The global map of alien bird richness shows higher species richness at mid-latitudes, in coastal areas and on island nations in both the northern and southern hemispheres. Notable peaks in alien bird species richness are observed in North America (particularly California and Florida), the Hawaiian Islands, the Caribbean, the United Kingdom, the Mascarene islands, Taiwan, Hong Kong, Singapore, southeast Australia and New Zealand, and to a lesser extent South Africa and the Persian Gulf states (figure 4.4).

Single predictor SAR models revealed that colonisation pressure was the strongest predictor and positively correlated to alien species richness, explaining 73% of variation on its own. Native species richness, time since introduction, the quadratic form of temperature range and distance to historic port, were negatively correlated to alien species richness, explaining 14%, 4%, 9% and 6% of the variation respectively. Precipitation was positively correlated with alien species richness and explained 9% of the variation. All other predictor variables had R^2 values indiscernible from zero (table 4.4). The relationships between the response and predictor variables are plotted in figure 4.5.

A minimum adequate SAR model (MAM) explained 94% of the spatial variation in alien bird species richness, and showed colonisation pressure to be the strongest predictor, with time since introduction, and linear and quadratic terms for temperature range, precipitation and distance to historic port also included (table 4.5). Pearson's correlation coefficients between the response variables and the fitted values of the MAM demonstrated excellent goodness-of-fit (Pearson's product-moment correlation = 0.97, $p < 0.001$).

When the model selection process was repeated with the predictor variable colonisation pressure excluded, the influence of distance to historic port on alien species richness strengthens substantially, and the resulting MAM also includes a strong positive effect of the human footprint index. The model also identifies a strong negative effect of native species richness (table 4.6). The model is a worse fit to the data compared to the MAM including colonisation pressure (Pearson's product-moment correlation = 0.91, $p < 0.001$). The curvilinear term for distance to historic port (table 4.5) was substituted with an interaction between distance to historic port and time since introduction with little loss of explanatory power (table 4.7), therefore the original MAM was kept.

The results from the holdout cross validation had high predictive power and goodness-of-fit (Pearson's product-moment correlation: 0.80 – 0.97, $p < 0.001$ in all cases). Although the components of the MAMs varied somewhat between realms, they all contained combinations of those predictor variables included in the full data MAM. Three predictor variables - colonisation pressure, time since introduction and temperature range - were included in all of the four models. In addition to this, precipitation was included in three models, and native species richness in two (table 4.8). The average RMSE of the predictive capabilities for the four realms was 0.51, compared to 0.12 for the full data MAM.

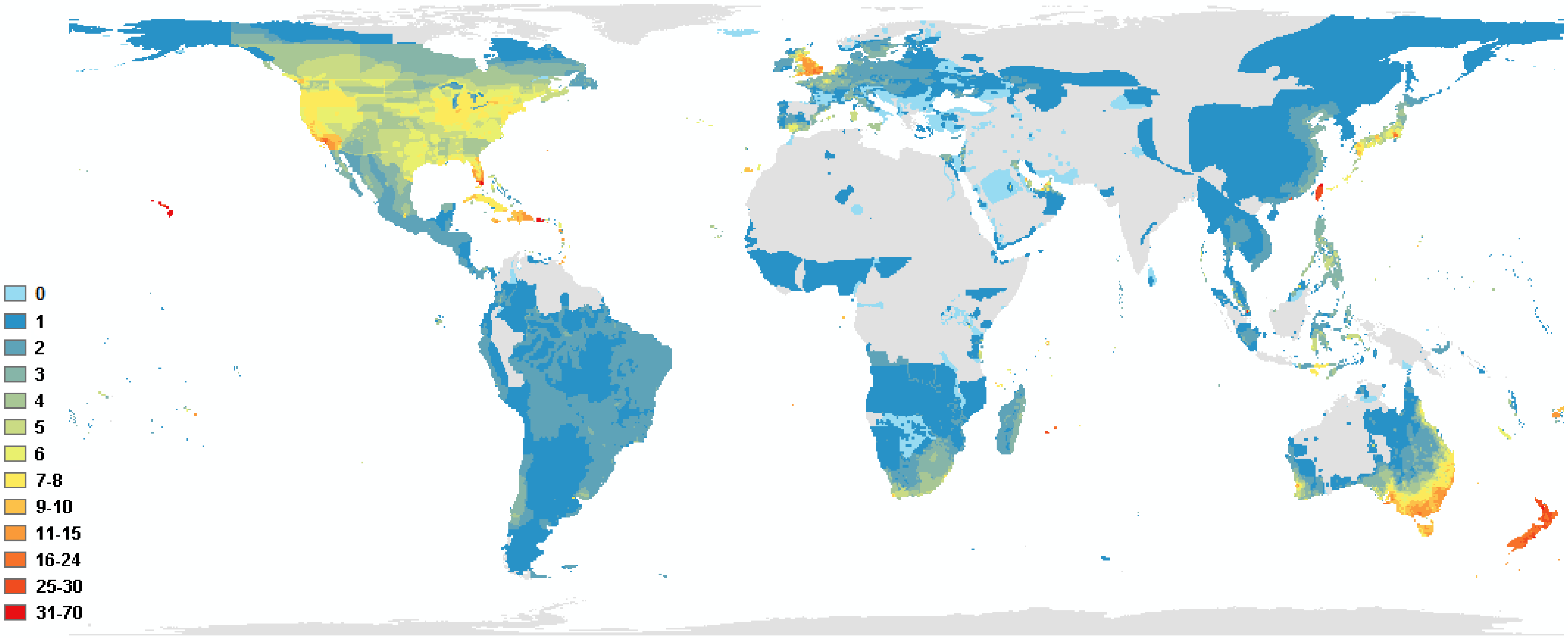


Figure 4.4 The global map of alien bird species richness for the 362 bird species with established alien distributions. Colder colours indicate lower bird species richness, while warmer colours represent higher richness. Grey areas are those where there are no recorded bird introductions (or at least no recorded introductions with enough detail to warrant creation of a range map, see Chapter 2).

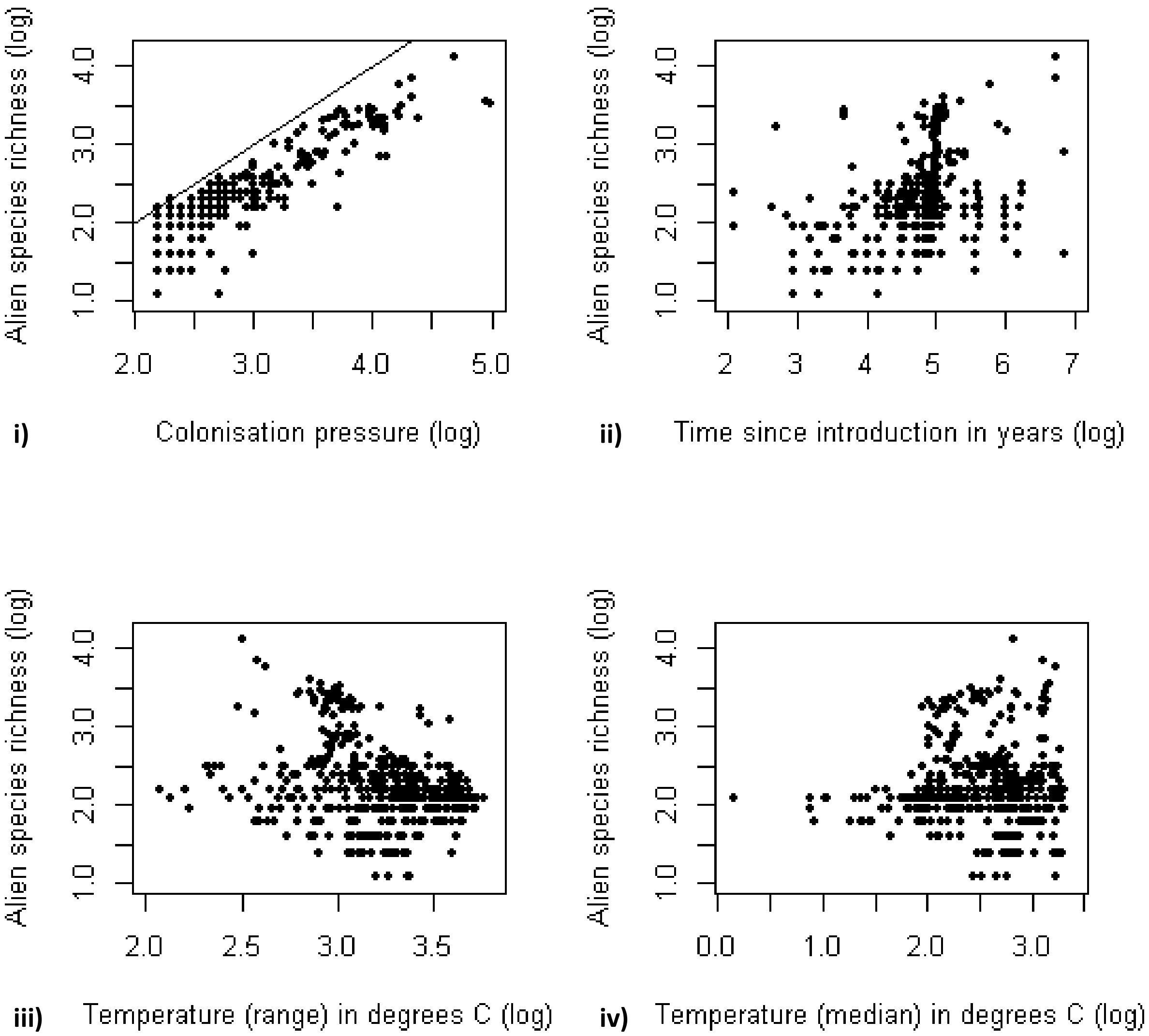


Figure 4.5 *(This and subsequent page)* The relationship between log alien richness and **i)** log colonisation pressure; **ii)** log time since introduction (years); **iii)** log temperature range (°C); **iv)** log median temperature (°C); **v)** square-root native species richness; **vi)** square-root median annual precipitation (mm); **vii)** square-root altitudinal range (msl = metres above sea-level); **viii)** habitat complexity (number of landcover types in surrounding 8 grid cells); **ix)** square-root human footprint; and **x)** log distance to historic port (km). The thin black line in **(i)** is the 1:1 line (alien species richness = colonisation pressure).

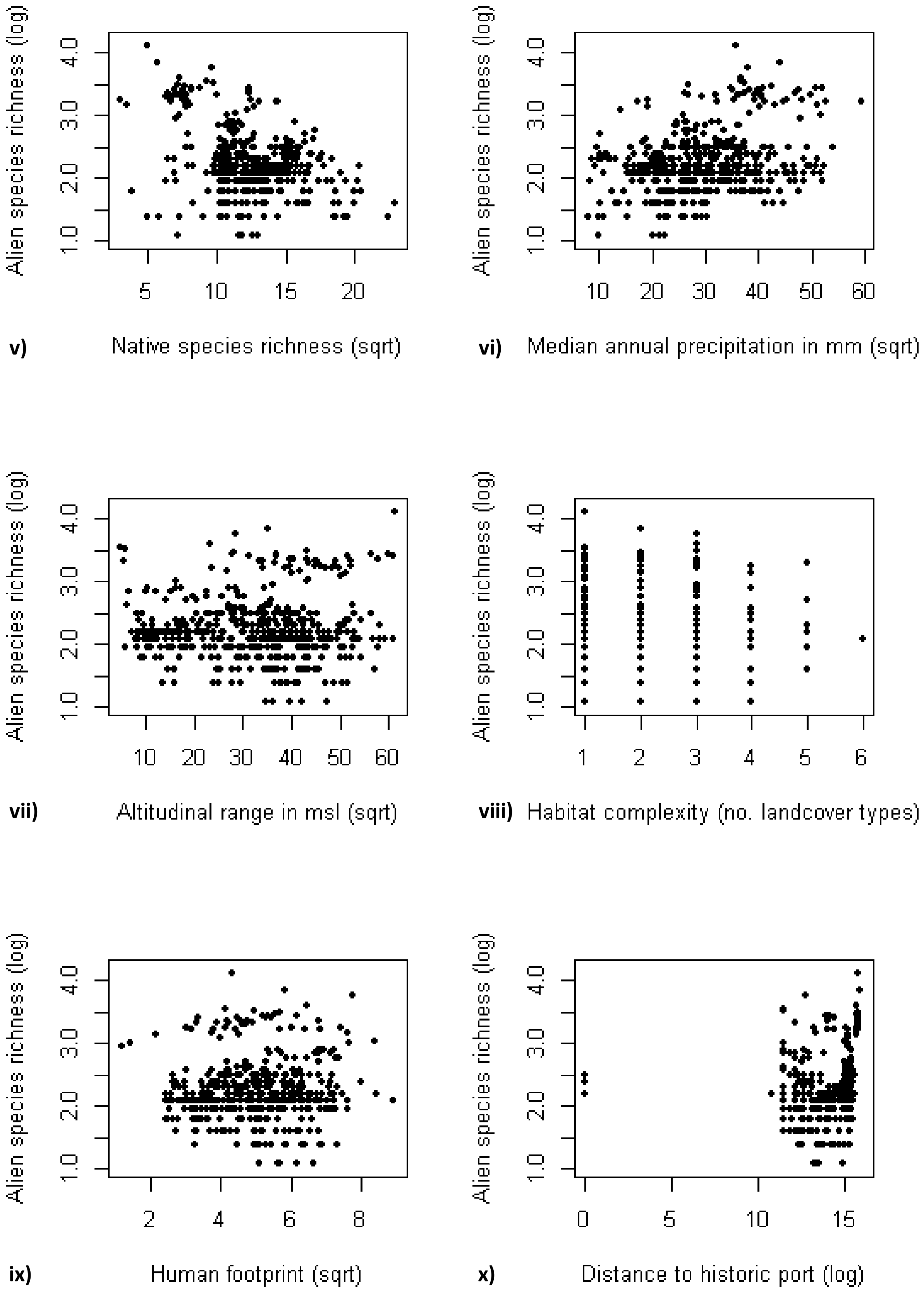

Alien species richness (log)
1.0
2.0
3.0
4.0
5
10
15
20
v)
Native species richness (sqrt)
Alien species richness (log)
10
20
30
40
50
60
vi)
Median annual precipitation in mm (sqrt)
Alien species richness (log)
10
20
30
40
50
60
vii)
Altitudinal range in msl (sqrt)
Alien species richness (log)
1
2
3
4
5
6
viii)
Habitat complexity (no. landcover types)
Alien species richness (log)
2
4
6
8
ix)
Human footprint (sqrt)
Alien species richness (log)
0
5
10
15
x)
Distance to historic port (log)

Table 4.5 Spatial correlates of alien bird richness for the minimum adequate model (MAM). Parameter estimates are given for spatial autoregressive error (SAR_{err}) models. AIC = -575.31. R^2 = 0.94 (pseudo-R^2, calculated as the squared Pearson correlation between predicted and observed values). S.E.: standard error. n = 362 species. * = p <0.05, ** = p <0.01, *** = p < 0.001.

Parameter	**Estimate**	**S.E.**	**z value**	
Intercept	1.86	0.65	2.87	**
Anthropogenic				
Colonisation pressure	0.73	0.02	35.33	***
Time since introduction	0.04	0.01	3.37	***
Distance to historic port	-0.03	0.02	-1.17	
Distance to historic port²	0.005	0.002	2.37	*
Environmental				
Temperature range	-1.45	0.44	-3.29	***
Temperature range²	0.23	0.07	3.19	**
Precipitation	0.02	0.005	4.14	***
Precipitation²	-0.0003	0.00007	-3.70	***

Table 4.6 Spatial correlates of alien bird richness for the minimum adequate model excluding colonisation pressure. Parameter estimates are given for spatial autoregressive error (SAR_{err}) models, using the same methods as for table 4.5. AIC = -12.16. R^2 = 0.84 (pseudo-R^2, calculated as the squared Pearson correlation between predicted and observed values). S.E.: standard error. n = 362 species. * = p <0.05, ** = p <0.01, *** = p < 0.001.

Parameter	**Estimate**	**S.E.**	**z value**	
Intercept	1.36	1.13	1.20	
Anthropogenic				
Time since introduction	-0.18	0.12	-1.55	
Time since introduction²	0.03	0.01	2.48	*
Human footprint index	0.07	0.01	5.22	***
Distance to historic port	-0.17	0.04	-4.55	***
Distance to historic port²	0.02	0.004	5.80	***
Environmental				
Native species richness	-0.03	0.01	-4.20	***
Temperature range	1.12	0.76	1.46	
Temperature range²	-0.25	0.13	-1.99	*

Table 4.7 Spatial correlates of alien bird richness for the minimum adequate model. The model is as given in table 4.5, except that the curvilinear term for distance to historic port is substituted by the interaction between distance to historic port and time since introduction. Parameter estimates are given for spatial autoregressive error (SAR$_{err}$) models, using the same methods as for table 4.5. AIC = –575.07. R^2 = 0.94 (pseudo-R^2, calculated as the squared Pearson correlation between predicted and observed values). S.E.: standard error. n = 362 species. * = p <0.05, ** = p <0.01, *** = p < 0.001.

Parameter	**Estimate**	**S.E.**	**z value**	
Intercept	2.14	0.68	3.15	**
Anthropogenic				
Colonisation pressure	0.73	0.02	35.27	***
Time since introduction	-0.07	0.05	-1.44	
Distance to historic port	-0.06	0.04	-1.61	
Time*historic port	0.02	0.007	2.24	*
Environmental				
Temperature range	-1.29	0.45	-2.89	**
Temperature range^2	0.21	0.07	2.79	**
Precipitation	0.02	0.005	3.73	***
Precipitation^2	-0.0002	0.00007	-3.33	***

Table 4.8 Predictor variables included in each of the holdout cross validation SAR_{err} models. The shaded column indicates the selected predictors and values for the minimum adequate SAR_{err} model using all of the data. MAM = minimum adequate model. RMSE = root mean squared error. Goodness-of-fit calculated with Pearson's correlation coefficients between the response variables and the fitted values of the models. Average RMSE of holdout models = 0.51.

Predictors	**MAM of full data**	**Holdout Afrotropical**	**Holdout Australasian**	**Holdout Nearctic**	**Holdout Palearctic**
Colonisation pressure	X	X	X	X	X
Native species richness					X
Native species richness + native species richness^2				X	
Time since introduction	X	X	X	X	
Time since introduction + time since introduction^2					X
Temperature range				X	X
Temperature range + temperature range^2	X	X	X		
Human footprint index					
Precipitation					
Precipitation + precipitation^2	X	X	X	X	
Temperature median					
Distance to historic port					
Distance to historic port + distance to historic port^2	X				
Human footprint index					
Temperature median					
Habitat complexity					
Altitude median					
RMSE	0.12	0.38	0.23	0.26	0.44
Goodness-of-fit	0.97	0.94	0.97	0.82	0.80

4.4 DISCUSSION

Socioeconomic drivers determine the regions from which alien bird species are sourced, and the areas to which they are translocated and introduced (Chapter 3). The results here demonstrate that it is then a combination of anthropogenic and environmental conditions that influence alien species richness. Colonisation pressure and the length of time since introduction, both anthropogenic elements of the introduction history of the region, together with distance to historic port, are the most important predictors of alien species richness. Confirming observations made in previous studies (Stohlgren *et al*. 2006, Davies *et al*. 2007b, Gallardo & Aldridge 2013), environmental (specifically climate-related) predictors, namely temperature and precipitation, also play a significant role in explaining some of the global distribution of alien bird richness, indicating the importance of productive and ambient energy.

Global variation in alien bird species richness is primarily driven by the strong positive relationship with colonisation pressure (the number of species introduced). Colonisation pressure is the variable most closely associated with alien bird species richness in both the single predictor models and the global MAM, and it is present in all of the realm-level holdout cross validation models (tables 4.4, 4.5, 4.8). Studies that include a true measure of colonisation pressure when modelling alien species distributions are relatively limited, and most focus on one or a few taxonomic groups or regions (Blackburn *et al*. 2008, Chiron *et al*. 2009). Due to the lack of information of this key variable in the invasion process, other studies have used proxies for colonisation pressure including human population size or density (Taylor & Irwin 2004, Westphal *et al*. 2008, Essl *et al*. 2015); the amount of tourism and trade (Leprieur *et al*. 2008, Westphal *et al*. 2008); the extent and density of transport networks (Vilà & Pujadas 2001, Westphal *et al*. 2008); the number of countries where a species was introduced (Jeschke & Strayer 2006); and the coverage of species in the literature (Proçhes *et al*. 2012). However, in concordance with the results of this study, all found a positive correlation between colonisation pressure (or proxies thereof) and alien species richness. The availability of data on colonisation pressure has enabled me to incorporate the effect that the number of species introduced has on the determinants of alien bird richness (Blackburn *et al*. 2008), and therefore better understand the mechanisms shaping biological invasions.

Alien bird species richness is also higher in areas with a longer history of introductions, as shown by a significant effect of the number of years since the first bird introduction to a region (present in the global MAM and all of the models in the realm-level holdout cross validation), and shows a U-shaped relationship with distance to historic ports (only present in the global MAM) (tables 4.5 & 4.8). These relationships reflect the direct effect of socioeconomic drivers on alien species distributions. Alien species richness is higher where bird species have had more time to establish and spread following introduction. The early trade in alien birds was conducted largely by sea, and areas situated nearer to the source of historically imported birds, and therefore where bird species have had more time to establish and spread following introduction, have higher alien richness as a result. Proximity to ports has been shown to be an important predictor in other alien species groups, particularly for aquatic invasives, but also for some terrestrial plants and animals (Hulme 2009, Gallardo *et al*. 2015). However, the recent growth in colonisation pressure is in areas distant from historic ports, such that the curvilinear term for distance to historic port (table 4.5) can be substituted with an interaction between distance to historic port and time since introduction with little loss of explanatory power (table 4.7). Many alien species are not recent arrivals but were introduced decades or centuries ago. Therefore factoring in a measure of time can be expected to better predict current levels of alien species richness.

The effects of time and proximity to port are not simply a consequence of higher overall levels of human activity (higher population size or density, greater habitat disturbance and increased access) in some regions, as they are independent of the human footprint index (table 4.5). Surprisingly, and in contrast to previous findings, the human footprint index was not significantly correlated with alien bird richness in the single predictor models, nor was it included in the global MAM or any of the realm-level holdout cross validation models (tables 4.4, 4.5, 4.8). In contrast to the results here, Chiron *et al*. (2009) found human footprint to be positively correlated with alien bird richness in Europe. Blackburn *et al*. (2008) also found that the number of alien birds introduced to islands increased with human population size. Both of these studies accounted for colonisation pressure, and therefore the discrepancy in findings cannot be explained by the inclusion of that variable (nor indeed could it explain the lack of a univariate relationship). It may be that human influence is more instrumental in the initial establishment of alien species (Chapter 3), and environmental factors become more important in determining the extent of spread and ultimate distribution (Stohlgren *et al*. 2006). This may explain the limited number of human-related anthropogenic variables (rather than facets of the introduction history) in the global MAM. Alternatively it may be that the human footprint index failed to explain alien richness due to the lag effect, and if I had been able to use historical human influence data (as I did for ports) it may have become significant (Essl *et al*. 2011).

Alien bird species richness is not just a function of anthropogenic factors, but is also significantly influenced by the abiotic environment. Stohlgren *et al*. (2006) concluded that the final distributions of alien species were primarily determined by environmental factors, much like their native species counterparts. Native species richness tends to be higher in warmer, wetter regions. Many theories have been proposed to explain these associations, and they may arise due these areas having higher levels of energy availability (Evans *et al*. 2005b, Rabosky & Hurlbert 2015), or less physiologically stressful environments (Wiens & Donoghue 2004). I show that alien bird species richness follows these trends, as regions with low to medium ranges of temperatures, and with medium to high levels of precipitation, contain more alien bird species, even when controlling for anthropogenic pressures.

Native bird richness has been found to be significantly correlated with annual median temperature (Davies *et al*. 2007a). However, annual temperature range is negatively correlated with, and outperforms, median temperature as a determinant of alien species richness in the models (tables 4.3 - 4.5, 4.8), and was included in the global MAM and all realm-level holdout cross validation models. This suggests that a lack of extremes matters more than high temperatures in the range of (largely temperate) environments inhabited by alien birds; this effect may also contribute to the high alien species richness of islands (figure 4.4). Alien species richness was also significantly correlated with precipitation, which was present in the global MAM and three of the four realm-level holdout cross validation models. Together, these results support the findings of studies on other alien species groups. Gallardo *et al*. (2015) found that temperature-related variables explained the largest amount of the potential distribution of 72 terrestrial, freshwater and marine alien species. Essl *et al*. (2015) showed that the climate of the recipient region (mean temperature, mean precipitation), independent of its similarity with the climatic conditions of the species' native range, appeared to be an important determinant of whether an introduced bryophyte became established.

Conversely, features of the biotic environment have a limited effect on alien species richness. Single predictor models suggest that alien species richness is lower in areas rich in native species (table 4.4), as would be expected from biotic resistance (Elton 1958). However, native and alien bird richness is not associated independently of colonisation pressure and native bird richness is not included in the global MAM (table 4.5), although it is present in two of the four realm-level holdout cross validation models (table 4.8). The literature contains conflicting results on the relationship between native and alien species richness. Intact native communities may be harder to invade since there would be little or no opportunity to capitalise on unused resources (Blackburn *et al*. 2009a), or the native species themselves may be in some way preventing alien species from establishing (Elton 1958). Indeed some studies support my results in finding a negative relationship between the number of alien and native species (Case 1996). However, Stohlgren *et al*. (2006) evaluated the relationship between alien and native birds across the USA, and found native bird richness to be positively correlated to alien bird richness. They suggest that both native and alien bird species appear to be responding in a similar way to basic biophysical properties of the landscape. Blackburn *et al*. (2008) found that islands with a greater number of native bird species had a higher number of alien bird species introduced and subsequently establish. Similarly, Chiron *et al*. (2009) showed that for the UK, native bird richness is an important predictor of alien bird richness, even after controlling for other factors. Other studies have found no significant relationship between native and alien bird species (on islands; Cassey *et al*. 2005).

The habitat heterogeneity hypothesis predicts that high species richness is promoted by greater habitat heterogeneity at the mesoscale, enabling more species to coexist (Davies *et al*. 2007b). This has been tested as topographic variability (altitude), which has been reported as showing association with native bird species richness in warm climates (Davies *et al*. 2007a). It has also been tested as the number of landcover types, which has been shown to be a positive predictor of native species richness in some (e.g. Kerr *et al*. 2001) but not all cases (e.g. Hawkins and Porter 2003). However, in this study, both altitude and habitat complexity had no significant effect on alien bird richness in the single predictor models (table 4.4), nor were they included in the global MAM (table 4.5) or any of the realm-level holdout cross validation models (table 4.8). It would seem that for alien birds, measures of habitat heterogeneity are of secondary importance as predictors of species richness when tested alongside abiotic and anthropogenic factors.

When I repeated the analyses excluding colonisation pressure, the influence of distance to historic port on alien species richness strengthened substantially, and the resulting MAM also included a strong positive effect of the human footprint index (table 4.6). This model is a worse fit to the data, but does identify that human activities matter to global variation in alien species richness. Nevertheless, the analysis in this chapter demonstrates that colonisation pressure is the key human activity (tables 4.4 – 4.6). The model also identified a strong negative effect of native species richness (table 4.6), suggesting that native birds resist incursions by aliens. The distribution of alien species richness, and in particular the dearth of alien bird species in the tropics (figure 4.4), would indeed seem to imply that biotic resistance is an important influence on where alien species can succeed (Elton 1958). However, there is little evidence for biotic resistance when colonisation pressure is included (tables 4.4, 4.5, 4.8), suggesting instead that, at least for birds, there were fewer attempts to establish alien species in areas already rich in natives.

Although the data utilised in this study are the best currently available from an entire major taxon, these analyses still have certain caveats. The application of SAR and other autoregressive models in ecology and species distribution is limited. This may be because the implementation of autoregressive models is mathematically complex and computationally intensive. In addition, model selection procedures are largely absent for spatially autocorrelated data (Kissling & Carl 2007). The subset of data used in these analyses is spatially disjunct, and in addition to purposefully encompassing those regions with higher colonisation pressure, it is also likely to be indicative of regions with higher recording effort. This should be taken into consideration when interpreting these results. However, the subset of data does have a circum-global distribution (figure 4.2), and is a good representation of those areas with high numbers of introduced species. In addition, cross validation holding out individual biogeographic realms confirmed that the models have high goodness-of-fit and are robust to sub-sampling of the data.

The measure of colonisation pressure will by no means be comprehensive, as many failed introductions leave no trace of their presence. However, the GAVIA database is based on a systematic and thorough search of all the data available for alien bird introductions from all regions of the world (where possible), and so I can be confident that the measure of colonisation pressure is as accurate as it can be at this time. It should also be borne in mind that the species included in this analysis are not at equilibrium, some will go on to establish, others will spread, others still will die out or be eradicated. In addition, this analysis does not take into account increasing measures to eradicate or prevent invasions. If such actions tend to occur more readily or are more effective in areas of higher human footprint then this could reduce the correlation between anthropogenic variables and alien richness. However, as such measures mainly concentrate on especially harmful alien species which have a high economic or environmental impact, they probably have minimal bearing on the bulk of species analysed here.

Here I have shown that alien bird richness is the product of both anthropogenic and environmental drivers of species establishment and spread. My analyses suggest that alien bird richness is ultimately determined by colonisation pressure and time since introduction, but that it is also limited by temperature range and precipitation, and can be predicted to some degree by distance to historic port. My results raise questions regarding the validity of studies that, in the absence of introduction history data (such as colonisation pressure and time since introduction), conclude that environmental or socioeconomic factors are the main determinants of variation in the numbers of alien species at the regional and continental scale. Information relating to introduction history, where available, should routinely be considered when analysing aspects of the invasion process. Without it, erroneous conclusions about the determinants of alien species richness are likely. That colonisation pressure is a major determinant of alien species richness is a clear cause for concern given the negative impacts of some alien species (Evans *et al*. 2014) and the increasing rate at which introductions are occurring (Chapter 3). Therefore my results reinforce the need for controls at the early stages of the introduction pathway in order to reduce species introductions and prevent invasions.

Chapter 5.

A global analysis of the determinants of alien geographic range size in birds

5.1 INTRODUCTION

The ongoing influences of human settlement, acclimatization, recreation and commerce have led to repeated introductions of bird species into areas to which they are not native (Long 1981). Substantial progress in invasion biology has come from studying these alien birds (Blackburn *et al.* 2009a), but significant gaps in our understanding remain. Most notably, aside from a few case studies (e.g. Liversidge 1962, Silva *et al.* 2002), the processes determining the geographic spread of alien bird species, and their resulting geographic range sizes, have largely been ignored (Mack *et al.* 2000, Blackburn *et al.* 2009a). Geographic range size is one of the fundamental ecological and evolutionary characteristics of a species. It is a strong predictor of extinction risk (Gaston 2003) and, with regards to an alien species, the potential for impact (Parker *et al.* 1999). Range expansions are inextricably linked to global environmental and economic issues of increasing importance: climate change, habitat fragmentation, declining biodiversity, and genetic introgression (Vitousek *et al.* 1997, Kolar & Lodge 2001). An obvious question, therefore, is whether it is possible to identify the factors that are associated with the variation in geographic range sizes of alien bird species?

The establishment success of alien bird species relates to characteristics of the species introduced, of the location of introduction, and of the introduction event itself (Duncan *et al.* 2003). The same categories of factors have also been hypothesised to influence the extent of spread following establishment. As far as I am aware, only two global scale analyses have considered the effects that event level factors have on alien range size. These studies found that pine tree species (Proçhes *et al*. 2012) and reptiles and amphibians (Li *et al.* 2014) that have been introduced more often have larger alien ranges. Regional studies find similar relationships for bird species introduced to New Zealand (Duncan *et al.* 1999, Duncan & Blackburn 2002), and Australia (Long & Mawson 1991, Duncan *et al.* 2001), and reportedly also in North

America (Johnston & Garrett 1994). Regional studies have also demonstrated that the length of time since those introductions occurred (residence time, *sensu* Wilson *et al.* 2007) is positively related to alien range size (Williamson *et al.* 2009), total latitudinal extent (Guo *et al.* 2012), and likelihood of invasion and spread (Pyšek *et al.* 2009a) in plants. Conversely, Duncan *et al.* (1999) found no relationship between residence time and range size for bird species introduced to New Zealand.

Characteristics of the species can affect native geographic range sizes, and so may also influence the sizes of their alien distributions. There is as yet little consensus on the factors that determine native range sizes, although it is likely that generalist species, which can tolerate a wider range of climatic, habitat and dietary variables (Brown 1984), or species that utilise more commonly encountered environments or resources, are likely to be more widespread as a result (Long & Mawson 1991, Gaston 2003). Regardless of the actual drivers, however, native range size itself may be a useful proxy for what determines alien range size, and so if the same factors also influence alien range size, a positive correlation would be expected between the two. Indeed, native range size has been demonstrated to be an indicator of probability of invasiveness in plant species (Pyšek *et al.* 2009b), and global native and alien range sizes have been shown to be correlated in introduced tree species in the genus *Pinus* (Proçhes *et al.* 2012), and for a limited sample of alien bird species (Guo *et al.* 2012).

Life history traits have also been shown to influence the extent to which established species can spread. For example, there is a relationship between the sizes of alien bird ranges in New Zealand and Australia and life history traits associated with higher rates of population growth (Duncan *et al.* 1999, Duncan *et al.* 2001). Small body mass and high reproductive rate influenced the spread of alien birds in Florida (Allen *et al.* 2013), and adult survival has been found to impact upon the potential of alien birds to succeed and spread in the Mediterranean (Blondel 1991). Species with faster growth rates may be less vulnerable to local extinction when their population is small, and able to colonize new sites more quickly following establishment (Duncan *et al.* 2001).

Characteristics of the location may affect the range size of an alien species through the availability of suitable habitat or climate, or the presence of barriers to range expansion such as oceans or mountain ranges. In a global study, Orme *et al.* (2006) showed that the geographic range sizes of native bird species are smaller on islands, and on mountain ranges in the tropics and sub-tropics. This suggests that, for native ranges at least, size is constrained by the availability of land area within the climatic zones to which species are best adapted (Chown & Gaston 1999). It could therefore be expected that alien range sizes would be larger in areas that are more environmentally similar to the native distribution, and that are less spatially restricted. Duncan *et al.* (1999, 2001) showed that the range sizes of alien bird species in New Zealand and Australia were determined in part by the area of suitable habitat, while Forsyth *et al.* (2004) showed the same for alien mammals in Australia.

To date, tests of determinants of alien geographic range sizes have generally considered variation in relatively few taxa (e.g. a single genus: Proçhes *et al.* 2012) or restricted regional assemblages (e.g. New Zealand, Australia: Duncan *et al.* 1999, Duncan *et al.* 2001, Forsyth *et al.* 2004). Here, I present the first global-scale analysis of spatial variation in the geographic range sizes of all extant alien species with a known established population, for a major taxon, birds. I simultaneously explore event-, species- and location-level predictors of alien range size. Specifically, I test the hypotheses that bird species will achieve larger alien geographic range sizes when (i) they have been successfully introduced more times, (ii) they have longer residence times, (iii) they have larger native geographic range sizes, (iv) they have faster life histories, (v) they are diet and habitat generalists, (vi) they have close relatives with large alien geographic range sizes, (vii) they have been introduced to regions in the same climatic zone (tropical or temperate) as their native distributions, and (viii) they have been introduced to larger geographic regions.

5.2 METHODS

5.2.1 Data

The total alien geographic range size for 327 bird species with established alien populations was extracted from the Global Avian Invasions Atlas (GAVIA) database (Chapter 2). For this study, alien geographic range size was calculated as the total size in km^2 of the global alien range for each species, based on extent-of-occurrence polygon maps of the most recent data for populations known to be established. The total alien range sizes for the 327 species varied from 0.48 km^2 (*Cacatua sanguinea* on Saint John’s Island, Singapore) to 49.99 x 10^6 km^2 (*Columba livia*) (mean = 0.52 x 10^6 km^2; median 10,460 km^2). The frequency distribution of natural log-transformed alien range sizes is shown in figure 5.1 (Shapiro-Wilk test for normality: W = 0.99, p = 0.08).

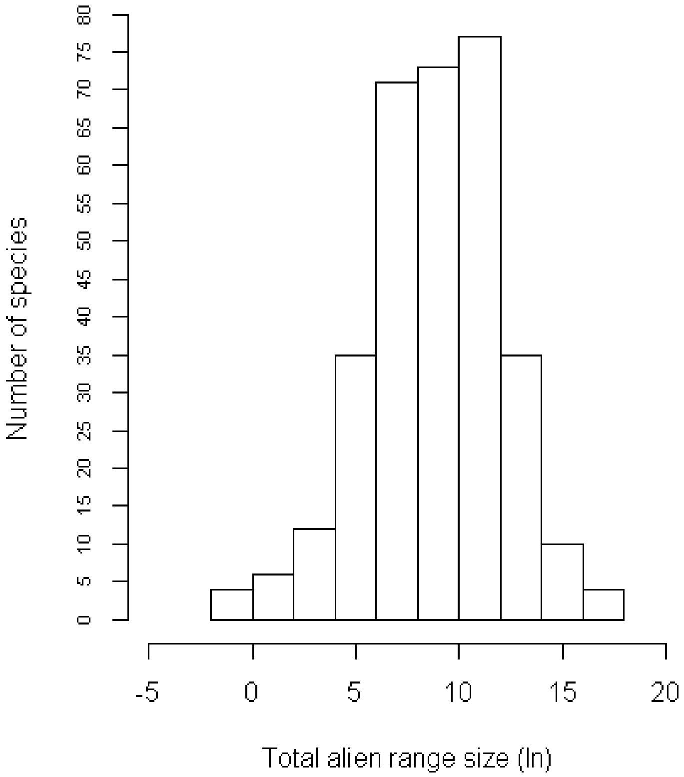


Figure 5.1 The frequency distribution of log-transformed total alien range sizes (km^2) for the 327 species included in the analysis.

5.2.1.1 Event-level variables

Estimates of the number of times that a species has been successfully introduced to different locations were calculated as the number of independent state-level references for each species in GAVIA, where the species has been recorded as established in that location. A 'state' in this instance is defined as the units in the first lower-level sub-division from the Global Administrative Areas database (www.gadm.org, downloaded August 2010; Global Administrative Areas 2012); for example, this level includes US states, and countries within the United Kingdom. The number of successful introductions varied from 1 to 440 (mean = 27.73; median = 6).

Residence times were calculated as the number of years from the earliest GAVIA record for that species to the year 2014, when the database was completed. Where there was no information available on the first date recorded, residence time was calculated from the date of the earliest published reference in which that species was mentioned. The longest recorded residence time of an established species was 1513 years (*Gallus gallus*, earliest record 500AD), and the shortest 7 years (*Polyplectron napoleonis* and *Sturnus malabaricus*, earliest record 2006) (mean = 141; median = 96.5 years).

5.2.1.2 Species-level variables

Native range sizes were extracted from the database of extent-of-occurrence avian range maps used by Orme *et al.* (2005), and were calculated as the total global breeding range size. The native range sizes of the species in the dataset showed similar variation to the alien ranges, from 3.32 km^2 (*Foudia sechellarum*) to 58.19 x 10^6 km^2 (*Tyto alba*), but with higher mean (6.03 x 10^6 km^2) and median (2.87 x 10^6 km^2).

Body mass was used as a proxy for life history variation, as it is known to be highly correlated with many other reproductive, timing, physiological and ecological traits (Peters 1983, Cassey 2002), and relationships have been found between body mass and both native and alien range size (Gaston & Blackburn 1996, Duncan *et al.* 2001). Body masses were taken from the database used by Olson *et al.* (2009), and were calculated as the geometric mean body mass in grams. Body masses in the sample varied from 6.2 g (*Collocalia bartschi*) to 109.65 kg (*Struthio camelus*) (mean = 1.08 kg; median = 117.5 g).

In order to address the effect of the level of specialism (or inversely, generalism) of a species, a specialisation index was calculated using the number of food types (diets) that a species is known to consume, and the number of habitats that it is known to utilise, where specialisation index = ln[100/(number of diets x number of habitats)] (after Sekercioglu 2011). Bird habitat and diet data were obtained from a global bird ecology database covering all the bird species of the world (see Sekercioglu *et al*. 2004). The specialisation index in the sample varied from 0.87 (*Alectura lathami* and *Corvus frugilegus*) to 4.6 (*Polyplectron napoleonis*, *Agapornis personatus* and *Pomarea dimidiata*) (mean = 2.3; median = 2.4). A low specialisation index indicates that a species is more of a generalist in terms of its diet and habitat preferences, whereas a high specialisation index indicates that a species is a specialist and utilises fewer habitats and dietary resources.

5.2.1.3 Location-level variables

Species ranges were assigned to biogeographic realms (Afrotropical, Australasian, Indomalayan, Nearctic, Neotropical, Oceanic and Palearctic) following Olson *et al*. (2001). A spatial layer depicting the biogeographic realms was created using ESRI ArcGIS version 9.3 (2008), and realm-level alien range sizes, residence time and number of successful introductions were extracted from GAVIA, as was the total land area of each realm. The Antarctic realm was excluded from the analysis due to a small sample size.

In order to explore the effects on range size of a species' native and alien climatic zones, species' ranges were split into temperate and tropic regions based on the geographical delineation of the Tropics of Cancer (23° 26′ 16″ N) and Capricorn (23° 26′ 16″ S). As with the realms, a spatial layer depicting the temperate and tropic regions was created using ESRI ArcGIS version 9.3 (2008), and the extent of alien and native range sizes in the different regions were extracted from GAVIA and from Orme *et al.* (2005).

5.2.2 Statistical analyses

The parameters were tested to see if they were phylogenetically correlated using Pagel's λ calculated using function *phylosig* from the *R* package *phytools* (Revell 2012). To account for uncertainty in the avian phylogeny, these tests were repeated for a random selection of 100 bird trees for the 327 species with alien ranges, downloaded from www.birdtree.org (Jetz *et al.* 2012; Hackett backbone, downloaded 15/12/14). Alien range size and number of successful introductions showed a low phylogenetic correlation for the 327 species in the data (mean λ [5th percentile, 95th percentile]: alien range size: $6.62\ \mathrm{x}10^{-5}$, [$6.61\ \mathrm{x}10^{-5}$, $6.64\ \mathrm{x}10^{-5}$]; successful introductions: $6.62\ \mathrm{x}10^{-5}$, [$6.61\ \mathrm{x}10^{-5}$, $6.64\ \mathrm{x}10^{-5}$], whereas the phylogenetic correlations for native range size, body mass and specialisation index were all much higher (native range size: 0.70 [0.61, 0.77]; body mass: 1.00 [1.00, 1.00]; specialisation index: 0.64 [0.59, 0.68]). Therefore, in order to account for any phylogenetic autocorrelation in my analyses, the tests of the determinants of alien range size were based on phylogenetic generalised least squares models (PGLS) applied by the function *pgls* from the *R* package *caper* (Orme *et al.* 2013).

Table 5.1 Correlation matrix of all log-transformed predictor variables. Numbers above the diagonal are correlation coefficients (r); numbers below the diagonal are associated P values. N = 327 in all cases.

	Native range size	**Successful introductions**	**Residence time**	**Body mass**	**Specialisation Index**
Native range size		0.26	0.23	0.05	-0.35
Successful intros	0.22		0.58	-0.07	-0.21
Residence time	0.27	0.00		0.07	-0.30
Body mass	0.80	0.73	0.73		-0.26
Specialisation Index	0.08	0.32	0.17	0.21	

Tests of collinearity between the predictor variables using *R* functions *cor* and *corr.p* found these to be only weakly correlated (table 5.1) and therefore all variables were used in subsequent analyses. I initially examined the relationship between alien range size and successful introductions, (successful introductions)^2, native range size, residence time, (residence time)^2, body mass and specialisation index separately, using univariate PGLS models (table 5.2). My *a priori* expectation was that the number of successful introduction events would be positively related to alien range size. Therefore I specified models that included successful introductions, and (residence time)^2 only when residence time was present, and then compared the fits of all models that fulfilled these criteria. The most likely multivariate model was identified using the function *model.sel* from the *R* package *MuMIn* (Barton 2014), assessing the support for different models using the small sample version of Akaike's Information Criterion (AICc).

A species with alien population(s) can attain its global alien range size in a variety of ways. For example, a species may have been introduced to a single area and spread out to attain a range size of 1000 km^2, or to five different locations, each time spreading to 200 km^2. The global scale multivariate model treats these two hypothetical species as the same, as the global alien range size is the sum of the ranges overall alien populations, regardless of the number of separate areas to which a species has been introduced. I address the effect of multiple introductions by conducting the analysis of total number of successful introductions for each species with at least one alien population. However, I additionally explored the effect of different routes to an overall alien range size by dividing the global data into realm level ranges, and repeating the specified models separately on the data for each realm. This tested the robustness of

Table 5.2 Outputs from univariate PGLS models where log alien range size (km^2) is the response variable. Each variable is tested at the global level (all data), and then split by realm. This was in order to test whether the global patterns remained when the data was addressed at a regional/population level. The numbers in the second column are PGLS model estimates ± standard error for the variable.

	Estimate ± s.e.	***P***	**R^2**
No. of SUCCESSFUL INTRODUCTIONS (log)			
GLOBAL	**1.59 ± 0.08**	**<0.001**	**0.54**
Afrotropical	1.61 ± 0.18	<0.001	0.54
Australasian	2.17 ± 0.18	<0.001	0.63
IndoMalay	0.99 ± 0.22	<0.001	0.18
Nearctic	2.12 ± 0.23	<0.001	0.52
Neotropical	1.43 ± 0.17	<0.001	0.45
Oceanic	0.81 ± 0.16	<0.001	0.19
Palearctic	1.55 ± 0.17	<0.001	0.49
(No. of SUCCESSFUL INTRODUCTIONS (log))^2			
GLOBAL	**0.31 ± 0.02**	**<0.001**	**0.52**
Afrotropical	0.34 ± 0.04	<0.001	0.50
Australasian	0.49 ± 0.04	<0.001	0.60
IndoMalay	0.27 ± 0.06	<0.001	0.21
Nearctic	0.67 ± 0.06	<0.001	0.59
Neotropical	0.40 ± 0.04	<0.001	0.49
Oceanic	0.24 ± 0.05	<0.001	0.19
Palearctic	0.32 ± 0.03	<0.001	0.49
NATIVE RANGE (log)			
GLOBAL	**0.54 ± 0.06**	**<0.001**	**0.17**
Afrotropical	0.34 ± 0.15	<0.05	0.06
Australasian	0.78 ± 0.12	<0.001	0.33
IndoMalay	0.33 ± 0.16	<0.05	0.04
Nearctic	0.64 ± 0.22	<0.01	0.09
Neotropical	0.65 ± 0.15	<0.001	0.17
Oceanic	0.38 ± 0.07	<0.001	0.23
Palearctic	0.27 ± 0.20	0.17	0.01
RESIDENCE TIME (log)			
GLOBAL	**1.30 ± 0.18**	**<0.001**	**0.14**
Afrotropical	0.87 ± 0.32	<0.01	0.09
Australasian	2.47 ± 0.46	<0.001	0.25
IndoMalay	0.25 ± 0.29	0.39	0.00
Nearctic	1.96 ± 0.45	<0.001	0.18
Neotropical	0.97 ± 0.25	<0.001	0.14
Oceanic	0.48 ± 0.31	0.12	0.01
Palearctic	1.27± 0.21	<0.001	0.30
(RESIDENCE TIME (log))^2			
GLOBAL	**0.16 ± 0.02**	**<0.001**	**0.15**
Afrotropical	0.12 ± 0.04	<0.01	0.11
Australasian	0.49 ± 0.04	<0.001	0.60
IndoMalay	0.05 ± 0.04	0.19	0.01
Nearctic	0.23 ± 0.06	<0.001	0.18
Neotropical	0.13 ± 0.03	<0.001	0.18
Oceanic	0.06 ± 0.04	0.11	0.01
Palearctic	0.14 ± 0.02	<0.001	0.30

BODY MASS (log)				
	GLOBAL	**0.04 ± 0.10**	**0.66**	**0.00**
	Afrotropical	-0.19 ± 0.23	0.42	0.00
	Australasian	-0.15 ± 0.25	0.54	0.00
	IndoMalay	-0.03 ± 0.20	0.88	0.00
	Nearctic	0.22 ± 0.24	0.37	0.00
	Neotropical	-0.14 ± 0.17	0.42	0.00
	Oceanic	0.13 ± 0.12	0.27	0.00
	Palearctic	0.16 ± 0.15	0.30	0.00
SPECIALISATION INDEX				
	GLOBAL	**-0.98 ± 0.25**	**<0.001**	**0.04**
	Afrotropical	-0.10 ± 0.57	0.86	0.00
	Australasian	-1.22 ± 0.56	<0.05	0.04
	IndoMalay	-0.51 ± 0.42	0.23	0.00
	Nearctic	-0.72 ± 0.63	0.26	0.00
	Neotropical	-0.89 ± 0.48	<0.1	0.03
	Oceanic	-0.65 ± 0.29	<0.05	0.03
	Palearctic	-1.22 ± 0.47	<0.05	0.06

my global model and the extent to which global patterns are driven by species introduced to multiple realms, and also whether the same variables determine alien range sizes in different realms. ANOVA was used to test for differences in the mean alien range sizes between realms, and also to test whether the land area of the realm influenced the mean alien range size.

Two-sample t-tests were used to compare the alien range sizes of species that had been introduced to the same climatic zone as their native range, versus the alien range sizes of species that had been introduced to a different climatic zone. Paired t-tests were used to compare the alien range sizes of species that had been introduced to both the same and to different zones as their native ranges, and to compare alien ranges in the temperate zone versus the tropical zone for species introduced to both zones.

All analyses were conducted in R version 3.1.2 (R Core Team 2014). Alien range size, native range size, number of successful introductions, residence time and body mass were logarithmically transformed.

5.3 RESULTS

5.3.1 Global-scale analysis

Native range sizes were significantly larger than alien range sizes for the species in my dataset (paired t-test: t = -31.2, d.f. = 327, p <0.001). Univariate PGLS models showed that successful introductions, (successful introductions)^2, native range size, residence time, (residence time)^2 and the specialisation index were related to alien range size, whereas body mass was not (figure 5.2). Model selection identified a multivariate model containing four of the five predictor variables, plus the quadratic form of successful introductions, as the most likely, such that species with large native range sizes, which had been successfully introduced more times, with shorter residence times and larger body masses had larger alien range sizes (table 5.3). Eight other models were also well supported by the analysis (ΔAICc < 4). Number of successful introduction events and native range size had variable importance values equal to 1, while that for residence time was 0.95, body mass was 0.74, (successful introductions)^2 was 0.72, specialisation index was 0.30 and (residence time)^2 was 0.26.

5.3.2 Realm-level analysis

Mean log-transformed alien range size differed between realms ($F_{1,\ 1150}$ = 20.61, p <0.001), but was not related to land area within each realm ($F_{1,\ 5}$ = 0.77, p = 0.42). Univariate PGLS models at the realm level showed that successful introductions, (successful introductions)^2, and native range size were consistently related to alien range size (table 5.2, figure 5.3). Model selection identified the best-supported multivariate model for each of the seven biogeographic realms (table 5.4, full outputs from the model selection process are given in appendix E). The best model varies across realms, with the order of importance of variables other than number of successful introductions also varying (table 5.4). Ranking predictor variables within realms in terms of their variable importance allowed us to calculate median rankings across the realms, which were 1 for number of successful introductions, 2 for native range size, 3 for residence time, 4 for (successful introductions)^2, 5 for body mass, 6 for specialisation index and 7 for (residence time)^2. Thus, alien range size was associated with a high number of successful introduction events, large native range sizes, short residence time, and larger body mass, in agreement with the global results.

Figure 5.2

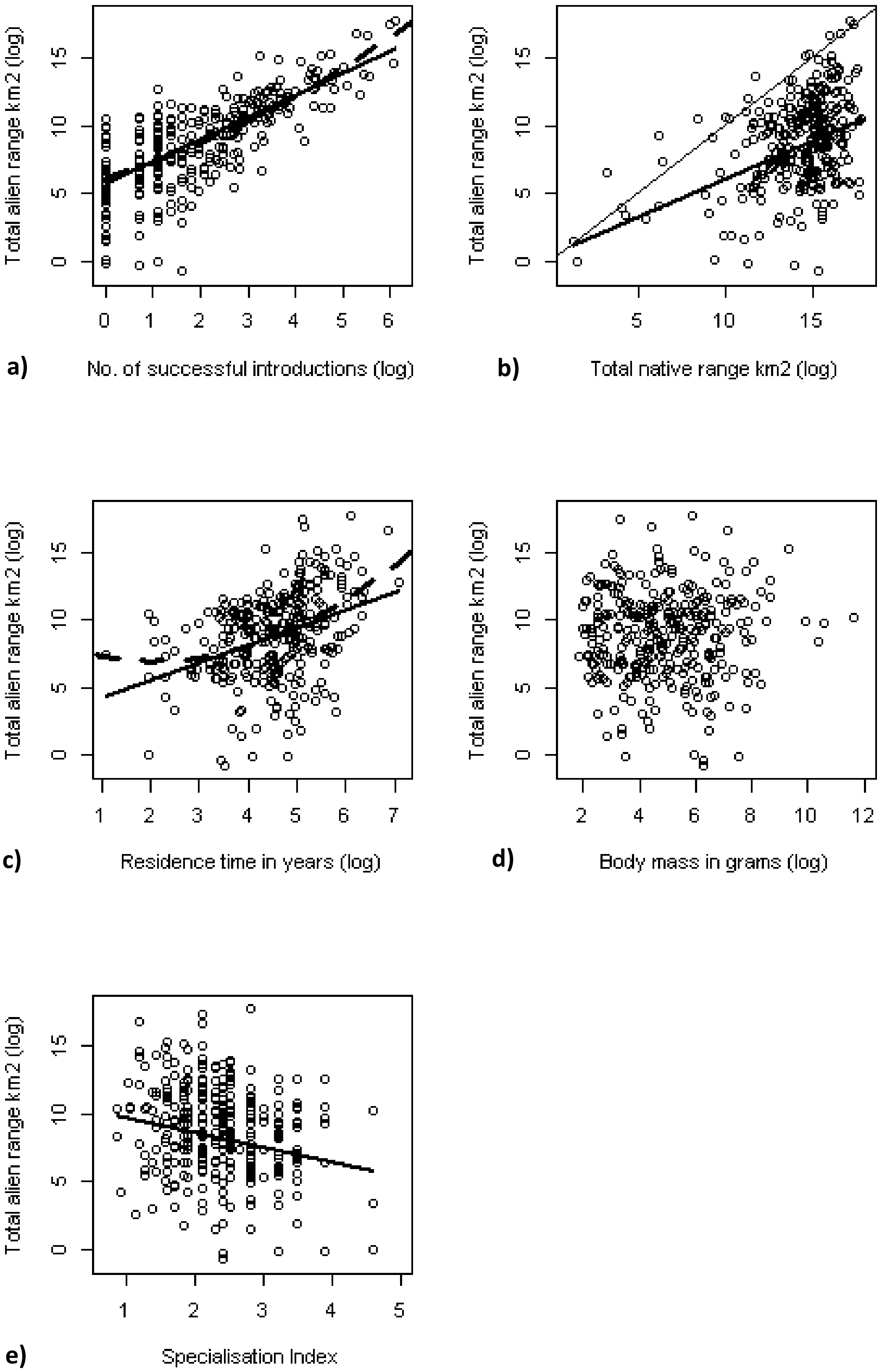

Total alien range km2 (log)
0
5
10
15
0
1
2
3
4
5
6
a)
No. of successful introductions (log)
Total alien range km2 (log)
5
10
15
b)
Total native range km2 (log)
Total alien range km2 (log)
1
2
3
4
5
6
7
c)
Residence time in years (log)
Total alien range km2 (log)
2
4
6
8
10
12
d)
Body mass in grams (log)
Total alien range km2 (log)
1
2
3
4
5
e)
Specialisation Index

Figure 5.2 *(Previous page)* The relationship between log total alien range size (km^2) and **a)** log number of successful introductions (slope estimate ± s.e. = 1.59 ± 0.08; $R^2 = 0.54$, n = 327, p <0.001, *p*CI = 9.8 x 10^{-4}), (log number of successful introductions)^2 (slope estimate ± s.e. = 0.31 ± 0.02; $R^2 = 0.52$, n = 327, p <0.001, *p*CI = 1.0 x 10^{-6}); **b)** log total native range size (km^2) (0.54 ± 0.06; $R^2 = 0.17$, n = 327, p <0.001, *p*CI = 0.002); **c)** log residence time (years) (1.30 ± 0.18; $R^2 = 0.14$, n = 327, p <0.001, *p*CI = 3.7 x 10^{-8}), (log residence time)^2 (years) (0.16 ± 0.02; $R^2 = 0.15$, n = 327, p <0.001, *p*CI = 3.3 x 10^{-4}); **d)** log body mass (g) (0.04 ± 0.1; $R^2 = 0.00$, n = 327, p = 0.66, *p*CI = 0.01); and **e)** specialisation index (-0.98 ± 0.25; $R^2 = 0.04$, n = 327, p <0.001, *p*CI = 0.008). The solid lines represent the univariate phylogenetic generalised least squares models (slope estimate), the dashed lines the models with a squared term, and the thin black line in **(b)** is the 1:1 line (alien range size = native range). s.e. = standard error. *p*CI = phylogenetic confidence interval.

Table 5.3 The results of model selection identifying the most likely models for log alien range size using the seven predictors in columns 2 – 8, with number of successful introductions included in all models, and (residence time)^2 only included when residence time was present. The numbers in each cell are PGLS model estimates ± standard error for the variable if it is included in the model. *p*CI = phylogenetic confidence interval, demonstrating the variation that the uncertainty in the phylogenetic tree makes on each parameter in each model. All models with ΔAICc < 4 are included. Number of successful introductions, native range size, residence time and body mass are all log transformed. N = 327 species.

	No. of successful introductions	**(No. of successful introductions)^2**	**Native range size**	**Residence time**	**(Residence time)^2**	**Body mass**	**Specialisation Index**	**AICc**	**ΔAICc**	**Akaike weight**	**R^2**
Model 31	1.21 ± 0.23 *p*CI 2.8x10^{-8}	0.09 ± 0.04 *p*CI 3.8x10^{-9}	0.31 ± 0.05 *p*CI 8.9x10^{-9}	-0.43 ± 0.15 *p*CI 2.6x10^{-8}		0.13 ± 0.06 *p*CI 1.9x10^{-8}		1387.89	0.00	0.26	0.61
Model 32	1.21 ± 0.23 *p*CI 2.6x10^{-8}	0.09 ± 0.04 *p*CI 3.6x10^{-9}	0.32 ± 0.05 *p*CI 8.7x10^{-9}	-0.42 ± 0.15 *p*CI 2.5x10^{-8}		0.14 ± 0.07 *p*CI 1.9x10^{-8}	0.12 ± 0.18 *p*CI 1.1x10^{-8}	1389.56	1.67	0.11	0.61
Model 29	1.62 ± 0.10 *p*CI 1.0x10^{-8}		0.32 ± 0.05 *p*CI 8.1x10^{-9}	-0.43 ± 0.15 *p*CI 2.5x10^{-8}		0.13 ± 0.06 *p*CI 2.1x10^{-8}		1389.81	1.92	0.10	0.60
Model 63	1.20 ± 0.23 *p*CI 2.3x10^{-8}	0.09 ± 0.05 *p*CI 3.0x10^{-9}	0.31 ± 0.05 *p*CI 8.4x10^{-9}	-0.20 ± 0.77 *p*CI 8.1x10^{-8}	-0.03 ± 0.09 *p*CI 1.2x10^{-8}	0.13 ± 0.06 *p*CI 1.8x10^{-8}		1389.88	1.99	0.10	0.61
Model 27	1.18 ± 0.23 *p*CI 3.6x10^{-4}	0.09 ± 0.05 *p*CI 6.2x10^{-5}	0.32 ± 0.05 *p*CI 1.6x10^{-4}	-0.40 ± 0.15 *p*CI 4.9x10^{-4}				1389.94	2.04	0.09	0.60
Model 30	1.62 ± 0.09 *p*CI 9.5x10^{-9}		0.33 ± 0.05 *p*CI 7.6x10^{-9}	-0.42 ± 0.15 *p*CI 2.4x10^{-8}		0.14 ± 0.07 *p*CI 2.0x10^{-8}	0.12 ± 0.18 *p*CI 1.1x10^{-8}	1391.49	3.60	0.04	0.60
Model 64	1.20 ± 0.23 *p*CI 2.3x10^{-8}	0.09 ± 0.05 *p*CI 3.1x10^{-9}	0.32 ± 0.05 *p*CI 8.8x10^{-9}	-0.16 ± 0.77 *p*CI 8.0x10^{-8}	-0.03 ± 0.09 *p*CI 1.2x10^{-8}	0.15 ± 0.07 *p*CI 1.9x10^{-8}	0.12 ± 0.18 *p*CI 1.1x10^{-8}	1391.55	3.66	0.04	0.60
Model 61	1.62 ± 0.10 *p*CI 1.2x10^{-8}		0.32 ± 0.05 *p*CI 7.8x10^{-9}	-0.59 ± 0.75 *p*CI 8.1x10^{-8}	0.02 ± 0.09 *p*CI 1.2x10^{-8}	0.13 ± 0.06 *p*CI 2.0x10^{-8}		1391.84	3.95	0.04	0.60
Model 25	1.60 ± 0.10 *p*CI 0.6x10^{-3}		0.33 ± 0.05 *p*CI 0.1x10^{-3}	-0.40 ± 0.15 *p*CI 0.6x10^{-3}				1391.86	3.97	0.04	0.60

Figure 5.3

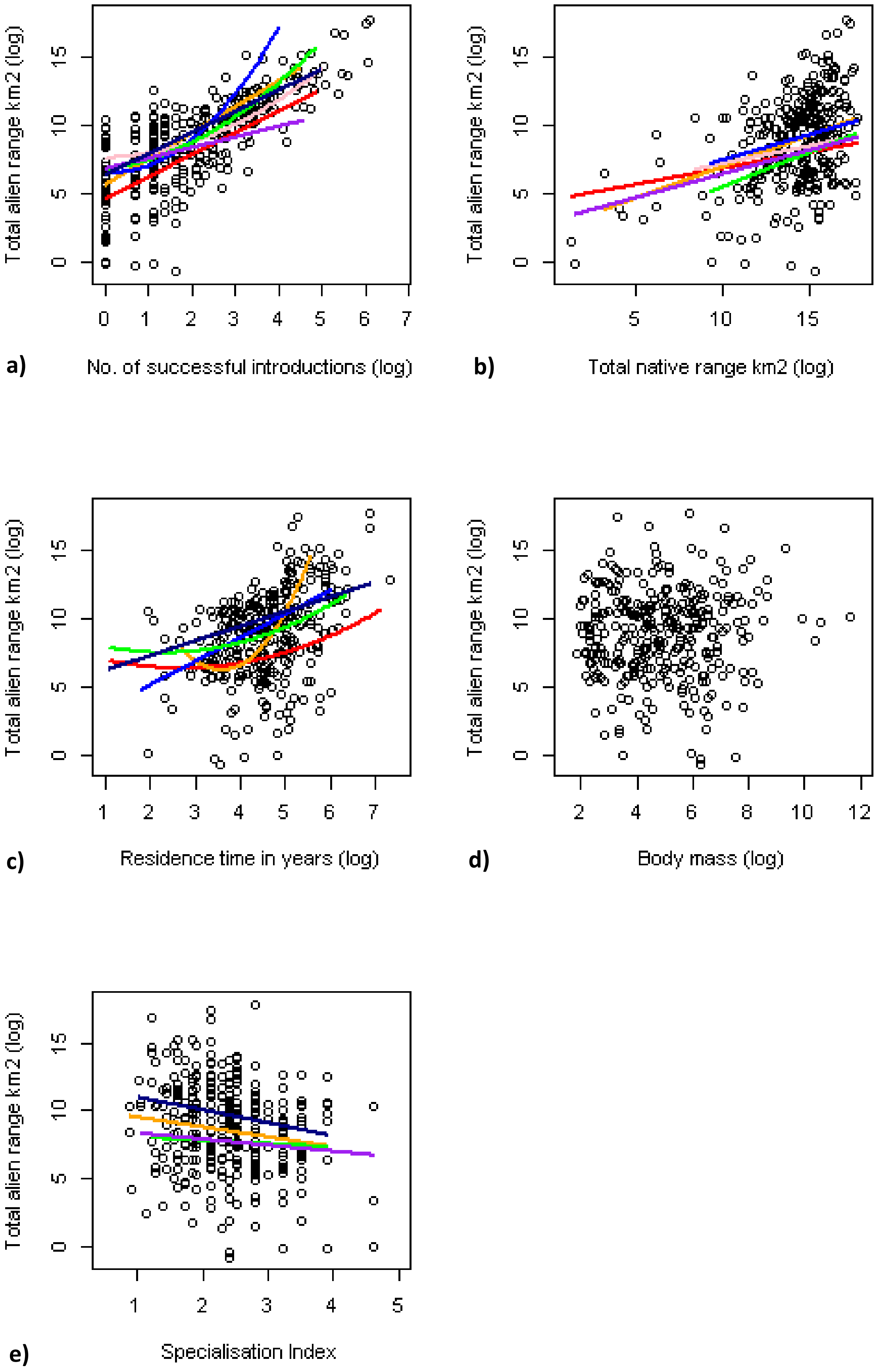

Total alien range km2 (log)
0
5
10
15
0
1
2
3
4
5
6
7
a)
No. of successful introductions (log)
Total alien range km2 (log)
0
5
10
15
5
10
15
b)
Total native range km2 (log)
Total alien range km2 (log)
0
5
10
15
1
2
3
4
5
6
7
c)
Residence time in years (log)
Total alien range km2 (log)
0
5
10
15
2
4
6
8
10
12
d)
Body mass (log)
Total alien range km2 (log)
0
5
10
15
1
2
3
4
5
e)
Specialisation Index

Figure 5.3 *(Previous page)* The relationship between log total alien range size (km^2) and **a)** log number of successful introductions; **b)** log total native range size (km^2); **c)** log residence time (years); **d)** log body mass (g); and **e)** specialisation index, for each realm separately. The coloured lines represent the fitted realm-level univariate PGLS models (with a squared term where significant): Afrotropical = red; Australasian = orange; Indomalayan = pink; Nearctic = blue; Neotropical = green; Oceanic = purple; Palearctic = navy.

Table 5.4 The most likely models for log alien range size as a function of the predictor variables in the top row, for each realm separately, with number of successful introductions included in all models, and (residence time)^2 only included when residence time was present. The upper numbers in each cell are PGLS model estimates ± standard error for the variable if it is included in the best model; the lower number in each cell is the variable weight for that realm, calculated as the sum of the Akaike weights across all models that included that variable as a term. *p*CI = phylogenetic confidence interval. Number of successful introductions, native range size, residence time and body mass are all log transformed.

	No. of successful introductions	**(No. of successful introductions)^2**	**Native range size**	**Residence time**	**(Residence time)^2**	**Body mass**	**Specialisation Index**	**AICc**	**ΔAICc**	**Akaike weight**	**R^2**
AFROTROPICAL	1.61 ± 0.18 *p*CI $3.4\text{x}10^{-8}$		0.24 ± 0.11 *p*CI $1.1\text{x}10^{-8}$				0.71 ± 0.39 *p*CI $5.6\text{x}10^{-8}$	283.46	0.00	0.13	0.57
Weights	1.00	0.25	0.72	0.48	0.12	0.25	0.53				
AUSTRALASIAN	1.83 ± 0.19 *p*CI $2.0\text{x}10^{-3}$		0.33 ± 0.10 *p*CI $2.0\text{x}10^{-3}$					360.20	0.00	0.12	0.68
Weights	1.00	0.28	0.98	0.61	0.38	0.32	0.35				
INDOMALAYAN	1.56 ± 0.27 *p*CI $2.0\text{x}10^{-8}$		0.41 ± 0.14 *p*CI $1.6\text{x}10^{-8}$	-1.05 ± 0.32 *p*CI $3.8\text{x}10^{-8}$				397.06	0.00	0.18	0.30
Weights	1.00	0.46	0.93	0.99	0.28	0.28	0.27				
NEARCTIC	-0.09 ± 0.66 *p*CI 0.03	0.67 ± 0.19 *p*CI 0.01	0.28 ± 0.16 *p*CI 0.01					354.03	0.00	0.15	0.61
Weights	1.00	0.99	0.58	0.31	0.08	0.53	0.26				
NEOTROPICAL	0.38 ± 0.45 *p*CI $6.4\text{x}10^{-3}$	0.27 ± 0.12 *p*CI $2.2\text{x}10^{-3}$	0.30 ± 0.13 *p*CI $2.0\text{x}10^{-3}$					361.62	0.00	0.19	0.51
Weights	1.00	0.81	0.82	0.36	0.09	0.35	0.31				
OCEANIC	0.74 ± 0.16 *p*CI $5.0\text{x}10^{-3}$		0.34 ± 0.06 *p*CI $7.7\text{x}10^{-4}$	-0.36 ± 0.28 *p*CI $5.2\text{x}10^{-3}$				446.07	0.00	0.1	0.35
Weights	1.00	0.47	0.99	0.60	0.16	0.45	0.34				
PALEARCTIC	1.27 ± 0.20 *p*CI $2.0\text{x}10^{-8}$			0.52 ± 0.21 *p*CI $4.9\text{x}10^{-8}$				360.31	0.00	0.13	0.52
Weights	1.00	0.43	0.33	0.87	0.22	0.30	0.28				

5.3.3 Climatic zone analysis

There was no difference in the alien range sizes of species that had been introduced to the same climatic zone as their native range (n = 85) versus the alien range sizes of species that had been introduced to a different climatic zone (n = 10) (Welch two sample t-test: $t = 1.19$, d.f. = 14.4, $p = 0.25$). The same was true comparing the alien range sizes in the tropical and temperate zones of the 26 species that had been introduced to both zones (same zone as native range versus different zone to native range: paired t-test: $t = 0.93$, d.f. = 25, $p = 0.36$). However, alien range sizes in the temperate zone are significantly larger than those in the tropical zone for those species introduced to both zones (tropical alien range size versus temperate alien range size: paired t-test: $t = 2.91$, d.f. = 25, $p < 0.01$).

5.4 DISCUSSION

Birds possess some of the greatest dispersal abilities of animals in the terrestrial environment (Wernham *et al.* 2002). Nevertheless, in the majority of cases, alien distributions actually tend to be relatively small, and most aliens have not reached the distributional extent observed in their native range (Guo *et al.* 2012). Indeed, the median non-native range size of the 327 established alien bird species is just 0.5% of the median for the native geographic ranges of those same species (10,457 km^2 vs 2,937,899 km^2, respectively). Therefore, despite being able to maintain a self-sustaining population in a new environment, in most instances alien bird species have not (yet) spread far from their point of introduction (Blackburn *et al.* 2009a). There are, of course, exceptions to this rule, with species such as the rock pigeon (*C. livia*), common pheasant (*Phasianus colchicus*), common starling (*S. vulgaris*), mute swan (*Cygnus olor*), and house sparrow (*P. domesticus*) having alien range sizes more than one million km^2 larger than their native geographic ranges. My aim here was to take the first steps towards understanding the causes of this variation.

Characteristics of the introduction event and the species best explain current variation in alien geographic range size in birds. Event-level predictors can vary independently of species and location. Number of successful introductions was the strongest predictor for both global and realm analyses, explaining 54% of the variation in alien range size in univariate analyses (table 5.2). This confirmed the *a priori* expectation, and justified the inclusion of this variable in all models of alien range size. It is also consistent with relationships found in regional studies (Long & Mawson 1991, Johnston & Garrett 1994, Duncan *et al.* 1999, Duncan *et al.* 2001), and suggests that this effect is general and global. Species with more successful introduction events are likely to have been introduced to a larger number of areas, and therefore likely to attain a larger alien range. Multiple introductions also tend to involve larger overall propagule pressures (Blackburn *et al.* 2015a) which increase the likelihood of successful establishment (Lockwood *et al.* 2005), and also may encompass greater genetic variation, enabling the population better to adapt (or to include genotypes pre-adapted) to local conditions and to realise a broader geographic range (Blackburn *et al.* 2009a, Blackburn *et al.* 2015a). This may enable the species to capture a greater proportion of available resources than species with smaller founding populations (Duncan *et al.* 1999), leading to faster population growth and spread rates (Duncan *et al.* 2003).

Residence time was also a strong indicator of alien range size, present in all of the most likely global models (table 5.3) and in the most likely models for three of the seven realms (table 5.4). Range sizes will tend to be smaller for all species in the period immediately following introduction, while species with longer residence times will have had longer to adapt to and spread across the recipient environment. A positive relationship between residence time and alien range size would therefore be expected (Wilson *et al.* 2007), and the results from the univariate analyses match this expectation (table 5.2, figures 5.2 & 5.3). Nevertheless, evidence for an effect of residence time on alien range size to date has been mixed (c.f. Duncan *et al.* 1999 with Pyšek *et al.* 2009a, Williamson *et al.* 2009), and I actually found a negative effect of residence time in the global multivariate model (table 5.3), and in most of the realm-level multivariate models that also included this variable (table 5.4). This result was unexpected. One possibility is that it is a consequence of changing drivers of bird introductions. Historical introductions (those with a longer residence time) were more likely to be deliberate, and to be targeted to specific regions through the efforts of acclimatisation societies (Blackburn *et al.* 2009a). More recent introductions are more likely to be a result of unintentional and untargeted releases from the pet trade (Chapter 3), and may therefore be more likely to occur over a larger area for a given number of successful introductions.

Native range size was the second strongest predictor of alien range size in my analyses: it explained 17% of the variance in alien range size on its own (table 5.2), and was present in all of the most likely global models (table 5.3) and the most likely models for six of the seven realms (table 5.4). Even with the effect of the number of successful introductions taken into account, species with larger native ranges were more likely to achieve larger alien ranges. This positive relationship suggests that whatever factor(s) allow a species to attain a large native range also enables a species to achieve a large alien range.

The lack of phylogenetic correlation in alien range sizes also appears to match that for native range sizes, as it is generally observed that closely related species tend not to have similar geographic range sizes (Gaston 2003). Surprisingly, however, the results revealed a reasonably strong phylogenetic correlation in the native range sizes of the 327 established alien bird species in my study, with a value of Pagel’s lambda of 0.7. Waldron (2007) reviewed published lambda values for native range sizes, finding a mean of 0.38 (Waldron 2007). Why the species in my sample show such a high lambda value is unclear, although it may be the result of phylogenetic clustering evident in introduced species (Blackburn *et al*. 2009b).

The causes of variation in native range size are still debated (Gaston 2003), but the current best evidence suggests that niche position (i.e. how typical of the environment are a species’ favoured resources) is the most likely determinant. For alien ranges, an effect of niche position is suggested by studies showing that climate matching increases both establishment success (Blackburn & Duncan 2001a) and the extent of alien range sizes at the regional level (Duncan *et al.* 1999, Duncan *et al.* 2001, Forsyth *et al.* 2004). Interestingly, my analyses did not support the hypothesis that species would attain a larger alien range if they had been introduced to regions in the same climatic zone as their native range. Rather, range sizes in the temperate zone were found to be significantly larger than those in the tropic zone for species that had been introduced to both zones, regardless of the location of their native range. This broadly matches variation in native bird geographic ranges, which tend to be larger at higher latitudes (Olson *et al.* 2009), a pattern known as Rapoport’s rule (Stevens 1989). This fits with the observations of Lonsdale (1999) and others that temperate mainlands are more easily invaded than tropical ones, as there is greater biotic resistance at lower latitudes (Guo *et al.* 2012).

The relationship between alien and native range sizes does not seem to be a consequence of generalist species (those with greater niche breadth; Gaston 2003) being able to attain larger range sizes. Species that can tolerate a wider range of conditions have been hypothesised to be able to have larger range sizes as a result, and in native bird assemblages the degree of habitat specialism has been found to correlate with range size (e.g. Davies *et al.* 2009), with specialist species usually occupying narrow ranges (Belmaker *et al.* 2011). However, the specialisation index was a weak predictor of alien range size in the multivariate analyses: while it was negatively correlated to alien range size at the univariate level (figure 5.2), it had the second lowest variable importance of the predictor variables in the most likely global models (table 5.3), and was present in the most likely model for just one of the seven realms (table 5.4). Thus, the relationship between alien and native range size persists when accounting for the degree of specialism. It is difficult to determine if these results are a result of a weak influence of niche breadth or if they reflect the noise associated with using coarse measures to quantify the specialisation index. Calculating the index through a combination of the number of diets and habitats that a species utilises gives no weight to the proportion of those resources that are used.

Body mass was included in my analyses as a proxy for life history variation, as previous studies have shown that species with fast life histories (smaller body size, shorter development times, higher fecundity) tend to have larger alien range sizes (e.g. Duncan *et al.* 1999, Duncan *et al.* 2001, Allen *et al.* 2013). However, I found body mass to be an inconsistent predictor of alien range size. The positive effect of body mass on alien range size in the multivariate global models runs counter to previous studies at the regional level, but does concur with the general trend for large-bodied species to have larger native geographic ranges (Gaston 2003). However, while body mass had a relatively high variable importance in the global models (table 5.3), it was present in none of the most likely models for the seven realms (table 5.4).

Alien range sizes were not correlated with the extent of land in a realm (c.f. Orme *et al.* 2006), and species did not tend to attain larger alien range sizes in the climatic zone (tropical or temperate) from which they originated. In general, my analyses of factors relating to location of establishment revealed little effect. Nevertheless, the alien range sizes of most species are still small relative to their native range sizes (figure 5.2), suggesting that it may be too early in the process of range expansion for geographic limits to have been reached for most species. Furthermore, my analyses of location-level factors were relatively crude, considering only broad climatic zones and biogeographic realms. Finer-scale analyses in the future may reveal effects that I failed to identify. My analyses of range sizes at the realm level did not reveal constraints of different land areas, but did reveal differences in alien range sizes between realms. They also showed that the variables included within the best models for alien range size varied across realms (table 5.4). However, the median rankings for variable importance across the realms matched those included in the full global model, and in general there was good consistency in the global (table 5.3) and realm-level (table 5.4) predictors of alien range size.

The data used in this study are the best currently available for an entire major taxon, but nonetheless come with caveats. The maps of alien ranges on which these analyses are based represent Extents of Occurrence, rather than Areas of Occupancy (Gaston & Fuller 2009), and species are unlikely to be extant in every part of their total recorded alien range (as is the case with most commonly used native species range maps). The species analysed are likely to be at different stages in their alien range expansion (Blackburn *et al.* 2009a), and many (or most) therefore may still be spreading from their point of introduction. Others may yet die out in the future. The measure of the number of successful introductions may be influenced by higher or lower recording effort in certain regions. All of these issues add noise into my analyses, although I do not believe that they will have generated any of the results I present here as artefacts. The general consistency of my results across different biogeographic realms also suggests that my analyses are robust.

Human activities are influencing range size dynamics by disrupting local assemblages, causing problems for some species but opportunities for others, altering the shapes, sizes and locations of geographic ranges, with consequences which ripple out to cause further alterations (Gaston 2003). The result is that naturally occurring variations in species distributions have been taken over by the establishment of alien species that are globally widespread and often closely associated with mankind (McKinney & Lockwood 1999). Although the majority of alien species seemingly have low impact, they can have unpredictable consequences and negative impacts, which are only compounded when combined with larger range sizes (Parker *et al.* 1999).

Here, I have shown that the strongest determinant of the extent of alien bird species spread is the number of successful introductions of a species, but that species with larger native ranges also tend to have larger alien ranges. This information can be combined with studies concerning predictors of the impact of alien birds (e.g. Evans *et al.* 2014) in order to identify those species that have the potential to have a high impact on native ecosystems. It is important that we understand the structure and mechanisms behind alien geographic ranges, so that we can more readily identify those alien species likely to spread. This will help to inform policy and conservation action by highlighting which species pose the greatest overall threat (Parker *et al.* 1999), and therefore where limited management funds should be targeted.

Chapter 6.

Latitudinal patterns in the distribution of alien bird species

6.1 INTRODUCTION

It has long been recognised that biodiversity shows systematic patterns of spatial variation (von Humboldt 1850, Arrhenius 1921, Dobzhansky 1950, Fischer 1960, Pianka 1966, Rapoport 1982). Some of the most studied associations relate to latitude. For example, species richness tends to be negatively correlated with latitude, decreasing from the tropics to the poles (Rohde 1992). The reason for this association is yet to be determined, but is thought to be due to a combination of the effects of availability of energy or temperature on population dynamics (Rohde 1992, Hawkins *et al*. 2003, Whittaker *et al*. 2003, Davies *et al.* 2007a), coupled with the time available for the process of diversification to occur (Pianka 1966, Rohde 1992). Conversely, native range size tends to be positively correlated with latitude, a phenomenon known as Rapoport's rule (Rapoport 1982, Stevens 1989). The generality of the rule has been much debated, and has received considerable attention in the literature with a range of hypotheses proposed to explain the pattern (see Rohde 1992). Candidate explanations include climatic variability (Dobzhansky 1950, Stevens 1989, France 1992), climatic extremes (Pither 2003), competition (Pianka 1989, Stevens 1996), biogeographical boundaries (Roy *et al*. 1994, Smith *et al*. 1994, Blackburn & Gaston 1996) and differential extinction or glacial history (Brown 1995, Jansson 2003, Araújo *et al*. 2008).

Differentiating between the hypotheses put forward to explain latitudinal patterns is difficult. This is because there is a limited quantity of suitable data, manipulative experiments are almost impossible to undertake, and few replicates exist (Sax 2001) at the large scales over which these patterns are expressed. There are a dearth of studies from low latitudes and from the southern hemisphere, which hampers our understanding of both the pattern and the process (Gaston *et al*. 1998). To address these issues, some authors have turned to alien species as a form of natural experiment to test the mechanisms driving latitudinal patterns (e.g. Sax 2001, Guo *et al*. 2012). Similarities and differences in the patterns expressed by alien and native species may be informative about the drivers of patterns in the latter group. Birds are a suitable alien taxon with which to explore these patterns, as they have been introduced globally to all ice-free latitudes (Chapters 3, 4), and there is a wealth of information available on their alien distributions (Long 1981, Lever 2005).

There is evidence that alien bird species richness varies with latitude, as is the case for native bird species. Sax (2001) showed that established alien bird species richness on continents (excluding Australia) increases from the poles to the edges of the tropics in both the northern and southern hemispheres, but attains only relatively low levels throughout the tropics. He argued that in the temperate zone, this was due to the primarily environmental (abiotic) determinants of native species richness also impacting upon the richness of alien bird species. In the tropics, he postulated that the low alien bird richness may be a result of biotic resistance from the high diversity of native species found there (Sax 2001).

Sax (2001) also demonstrated that the latitudinal range extents of established alien bird species introduced to North America increased with latitude north of the tropical zone, in concordance with Rapoport's rule, but were consistently large in the tropics. He used variations in the upper (i.e. poleward) and lower latitudinal range limits of the native and alien distributions of these species to assess likely causes, arguing that established alien latitudinal range extents could be explained in terms of the response of species to contemporary ecological conditions. Sax (2001) found that whilst the highest latitudes in the native and alien ranges of bird species tended to be correlated, species were more likely to exceed their natural high latitude range limits than their natural lower latitude range limits in their alien range.

Subsequently, Guo *et al.* (2012) found similar patterns to Sax (2001) in alien bird species, with strong correlations between the latitudinal distributions of a species' established alien and native ranges, and relatively more alien species occurring poleward in relation to their native ranges, with fewer occurring equatorward. They showed that although a small fraction of alien species occurred beyond both their upper and lower native latitudinal limits, most had not yet reached the latitudinal extent observed in their native range. They proposed that these shifts may be due to climate change, historical limitations on native ranges, greater biotic resistance at lower latitudes, and the impacts of humans on species distributions (Guo *et al*. 2012).

The geographic patterns described by Sax (2001) and Guo *et al*. (2012) assume that the opportunity for biological invasion is similar across latitudes. Yet, these analyses only examine those species with established distributions, and do not fully consider the effects of where species have been introduced, and where introduced species have succeeded or failed. Their transitory nature means that data on failed introductions are harder to obtain than data on successfully established species (Chapters 1 & 4; Blackburn *et al*. 2009a, Pyšek *et al*. 2010), and therefore patterns in alien species latitudinal distributions have generally been described without fully taking them into account. Yet, latitudinal gradients in alien species richness or geographic range extent may arise as a result of human actions in introducing species (Chapter 4 & 5), rather than the abiotic or biotic effects that underlie these patterns in native species (Pyšek *et al*. 2010). Sax (2001) rejected an association between the distribution of species introductions and alien species richness, arguing that the latitudinal pattern of introduction events for alien birds in North America did not match the latitudinal pattern of established species richness. However, Blackburn *et al*. (2009a, from data analysed by Blackburn *et al*. 2004 and Cassey *et al*. 2005) found that latitudes where islands have higher established alien bird species richness are also those latitudes that have had more alien bird species introduced. Guo *et al*. (2012) suggested that biases in the location of introductions may explain the latitudinal patterns that they found, but did not test this.

In this chapter, I examine the latitudinal patterns in the richness and geographical extents of both recorded and established alien bird distributions in relation to their native ranges at the global scale, and explore whether where species are introduced and where species fail to establish may help to drive these observed patterns. Recorded distributions encompass the locations of all alien records of a species regardless of whether or not it established, and the differences between recorded and established distributions enable me to assess where failures occurred (figure 6.1). Using the GAVIA database (Chapter 2), I test the relationships between latitude and recorded and established alien species richness, and between latitude and recorded and established alien range extent at the global scale. I compare the latitudinal range extent, latitudinal midpoint, and the lowest and highest latitudinal limits of each species in its total recorded alien range, established alien range, and in its native range, to determine the direction of any latitudinal shifts that are apparent. Incorporating data on recorded distributions in addition to established distributions enables me to ascertain whether species recorded beyond the latitudinal limits of their native ranges are more likely to succeed or fail. This helps me to explore the extent to which latitudinal shifts may be a consequence of human actions in introducing species versus abiotic or biotic environmental effects.

6.2 METHODS

6.2.1 Data

Alien range data for 719 species (the number of alien bird species recorded globally, regardless of status, with sufficient introduction information recorded to enable a range map to be created) were extracted from the GAVIA database (Chapter 2). Of these species, 359 had at least one successfully established population for which a native range map existed. Native range metrics for the 359 established species were calculated using native breeding range information obtained from the ADHoC (Avian Diversity Hotspots Consortium) database, first published by Orme *et al.* (2005).

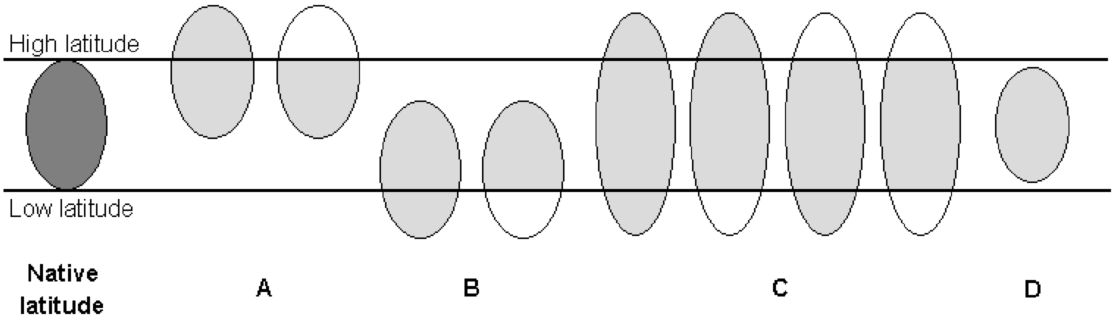


Figure 6.1 The four possible scenarios **(A-D)** of latitudinal shifts of a species' established alien range relative to its native range (after Guo *et al*. 2012). The darkest grey oval represents the native range of the species with its high and low latitudinal limits. **(A)** *Poleward range*, where the pale grey shading shows the established alien range under two scenarios: i) where the species is recorded and is successful in establishing a range higher than its native highest latitude, and ii) where the species is recorded but has failed to establish in the proportion of the alien range that is higher than its native highest latitude. **(B)** *Equatorward range*, with the pale grey shading representing the same two scenarios but at the lower latitude. **(C)** *Bidirectional range*, where the species has been recorded in regions both higher and lower than its native latitudinal limits. The grey shading shows the four possible establishment outcomes. **(D)** *No range change*, where the species has only been recorded as alien within the latitudinal limits of its native range, and is currently only established between the high and low bounds.

Using ESRI ArcGIS version 10.2.2 (2014), the native and alien range maps were intersected with a shapefile delineating 5° bands of latitude (following Sax 2001). For each of these 5° bands, four metrics were calculated:

1) The *number of recorded alien species* was calculated by counting the number of alien species with a range within or overlapping each band, regardless of whether they were successfully established or not.

2) The *number of established alien species* was calculated by counting the number of established alien species with a range within or overlapping each band. For both 1) and 2), if the same species was present on multiple continents, at the same band of latitude, it was only counted once for that band.

3) The *mean latitudinal range extent of the recorded range* (a measure of geographic range size) for all the alien species in each band was extracted. This was calculated by summing the number of 5° bands of latitude between (and including) the northernmost and southernmost point of the range of each recorded alien species within each band, regardless of whether or not it crossed the equator, to produce a maximum latitudinal range extent. For example, if the northernmost and southernmost points of a species' introduced range covered four 5° bands of latitude, then its range extent would be recorded as 20°. The introduced range extents were then averaged across all the species present in each band.

4) The *mean latitudinal range extent of the established range (*a measure of geographic range size) for all the established alien species in each band was extracted. This was calculated by summing the number of 5° bands of latitude between (and including) the northernmost and southernmost point of the range of each established alien species within each band, regardless of whether or not it crossed the equator, to produce a maximum latitudinal range extent. As above, if the northernmost and southernmost points of a species range covered four 5° bands of latitude, then its range extent would be recorded as 20°. The range extents were then averaged across all the species present in each band. For both 3) and 4), the actual range extent may be discontinuous; the species may not be recorded or established in every band between the northernmost and southernmost point, yet the range extent is calculated as the total number of bands between (and including) the northernmost and southernmost points.

Three of the most poleward latitudinal bands were excluded from the analysis due to low sample size: the band between 65°N and 70°N in which five species were recorded and three species established, and the bands between 70°N and 75°N, and 55°S and 60°S which both had four species recorded and two species established. This left 13 latitudinal bands in the northern hemisphere, from 0°-65°N, and 11 latitudinal bands in the southern hemisphere, from 0°-55°S.

For each species, I extracted the following information from their native range, recorded alien range and established alien range:

5) The *absolute lowest latitudinal range limit* was recorded for each species for its native range, recorded alien range, and established alien range. This was calculated irrespective of the hemisphere in which a species occurred. For example, if a species occurred only in the 5° band spanning 10°-15°N, then its lowest latitudinal range limit would be 10°, and likewise if it occurred only in the 5° band spanning 10°-15°S. If a species occurred in different locations, only a single global lowest latitudinal limit was recorded. For species present in separate populations in both the northern and southern hemisphere, the lowest latitude was recorded as the lowest latitudinal range limit of the population closest to the equator. If a species' distribution spanned the equator then its lowest latitude was recorded as 0°.

6) The *absolute highest latitudinal range limit* was recorded for each species in its native range, recorded alien range, and established alien range. Again this was calculated irrespective of the hemisphere in which a species occurred, such that the 5° band range boundary closest to the poles was 'highest'. For example, for a species occurring only in the 5° band that spanned 10°-15°N, then its highest latitudinal range limit would be 15°. If a species occurred in different locations, only a single global highest latitudinal limit was recorded. For species present in separate populations in both hemispheres, the highest latitude was recorded as the highest latitudinal range limit of the population closest to the poles.

7) The *latitudinal midpoint* was recorded for each species for its native range, recorded alien range, and established alien range. Latitudinal midpoint values were calculated as the point equidistant between a species' lowest and highest latitudinal range (values from 5 and 6 above). If a species' distribution spanned the equator then its latitudinal midpoint value was calculated relative to the single hemisphere where it had the largest latitudinal extent, such that the value equals the average of its lowest (i.e., 0°) and its highest latitudinal range limits.

8) The *absolute latitudinal range extent* for each species was calculated by subtracting the lowest latitudinal range limit from the highest latitudinal limit (values from 5 and 6 above) of each species' native range, recorded alien range, and established alien range, even if the range was discontinuous.

6.2.2 Statistical analysis

Ordinary least squares regressions were used to assess the relationship between latitude and: i) the mean latitudinal extent of the established range within each 5° band (termed Stevens' method; Stevens 1989), ii) the mean latitudinal extent for the recorded range within each 5° band, and iii) the proportion of alien bird species that have successfully established (out of the total recorded) within each 5° band. A quadratic term for latitude was included as the relationship may be non-linear.

Paired t-tests and Pearson's rank correlations were used to examine the relationships between four metrics of each species' native range, recorded alien range, and established alien range. These were the lowest latitudinal extent, latitudinal midpoint, highest latitudinal extent and absolute latitudinal extent.

Following Guo *et el.* (2012), I determined whether the latitudinal range of each alien species was shifted poleward, equatorward, or both, relative to its native range, or whether there was no shift. This process was repeated for each species' established alien range relative to its native range, and also relative to its recorded range. This was to ascertain whether each alien species had i) been recorded beyond the latitudinal bounds of its native range and had succeeded in establishing (both the recorded range and established range are beyond the limits of the native range); ii) been recorded beyond the latitudinal bounds of its native range but had failed (the recorded range is beyond the limits of the native range, but the established range is within those limits); or iii) the species has not been recorded beyond the latitudinal bounds of its native range at all (both the recorded range and established range lie within the limits of the native range) (figure 6.1). I used exact binomial tests to determine whether the difference in the number of species with alien ranges shifted poleward or equatorward relative to their native ranges was significant.

6.3 RESULTS

Alien bird introductions have occurred at the majority of latitudes with ice-free land (figure 6.2). The pattern of variation is multimodal, with the greatest peaks in both the number of species recorded and the number of species established between 20-25°N, but with further smaller peaks between 0-5°N, 15-25°S and 30-45°S.

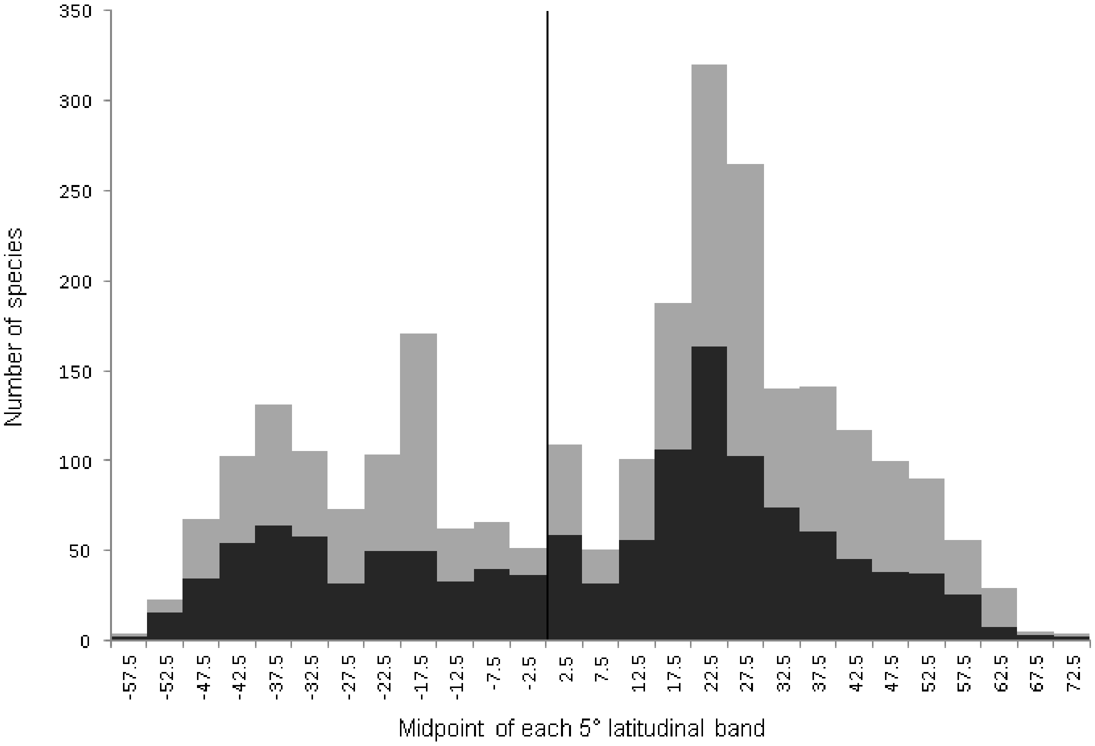


Figure 6.2 The frequency distribution of the number of species recorded (pale grey), and the number established (dark grey) in each 5° latitudinal band. The central vertical black line represents the equator, negative latitudes are in the southern hemisphere. The bars in this figure are not stacked.

Outside of the tropics, the number of recorded alien bird species show gradients of species richness in both the northern and southern hemisphere, with richness negatively correlated with latitude (figures 6.3a,b). In the northern hemisphere, recorded alien bird richness peaks at the Tropic of Cancer, and decreases towards the poles and the equator ([latitude slope ± standard error; latitude^2 slope ± standard error] 6.57 ± 2.99; -0.12 ± 0.04; $r^2 = 0.52$, $p < 0.01$). A similar pattern exists in the southern hemisphere, albeit with a peak in richness south of the Tropic of Capricorn at 40°S (6.58 ± 2.08; -0.12 ± 0.03; $r^2 = 0.55$, $p < 0.01$).

Figure 6.3

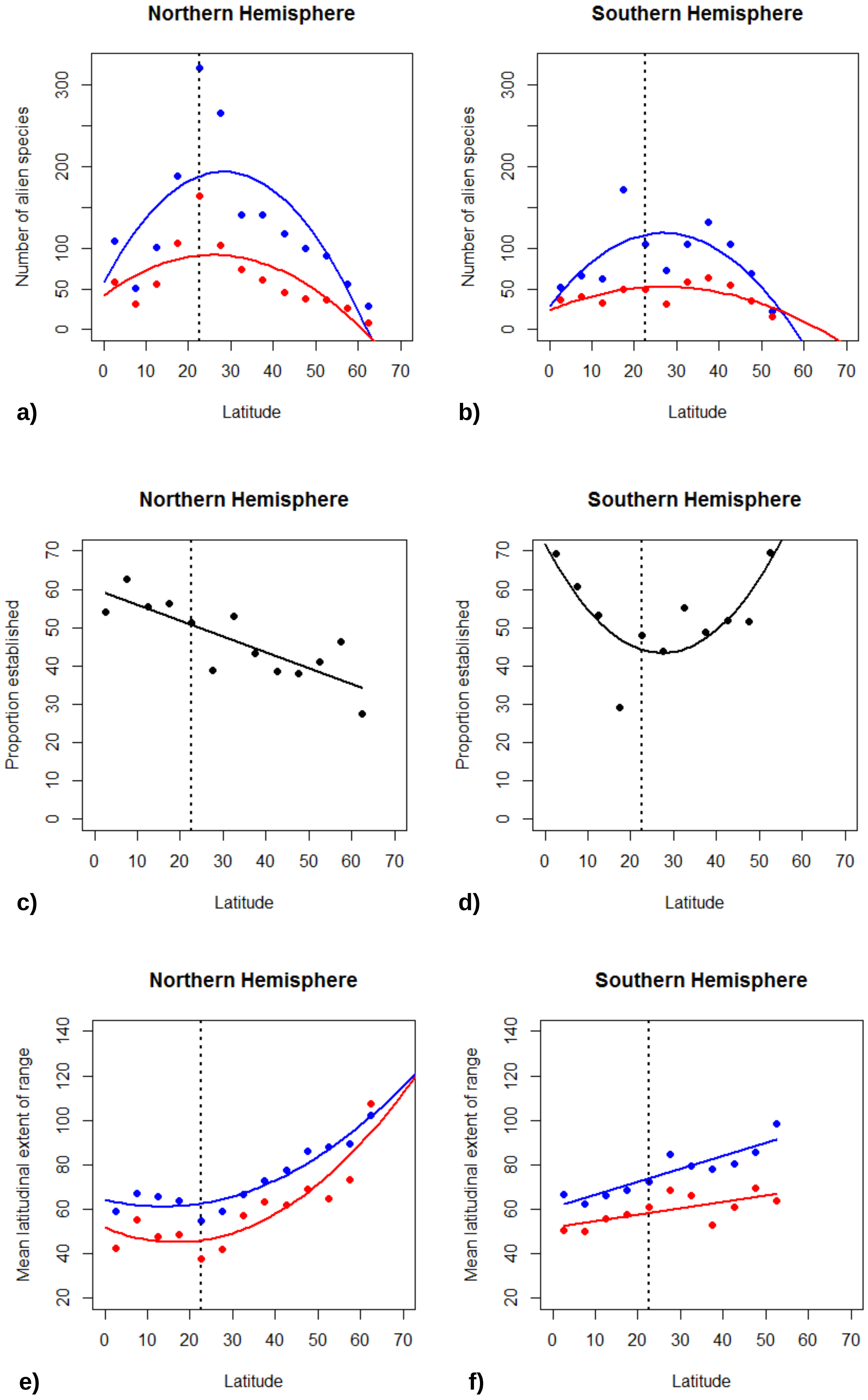

Northern Hemisphere
Southern Hemisphere
Number of alien species
0
50
100
200
300
Latitude
0 10 20 30 40 50 60 70
a)
b)
Northern Hemisphere
Southern Hemisphere
Proportion established
0 10 20 30 40 50 60 70
Latitude
0 10 20 30 40 50 60 70
c)
d)
Northern Hemisphere
Southern Hemisphere
Mean latitudinal extent of range
20 40 60 80 100 120 140
Latitude
0 10 20 30 40 50 60 70
e)
f)

Figure 6.3 *(Previous page)* The relationships between latitude and the number of alien species that have been recorded (blue) and that are established (red) in **a)** the northern and **b)** southern hemispheres; the proportion of alien species that have successfully established out of the total number recorded in **c)** the northern and **d)** southern hemispheres; and mean total latitudinal range extent of the alien species that have been recorded (blue) and that are established (red) in **e)** the northern and **f)** southern hemispheres. Latitude is measured in 5° latitudinal bands. The dotted lines indicate the Tropic of Cancer or Capricorn, dividing the tropical and temperate latitudes. The solid lines represent the coefficients from the fitted ordinary least squares models (slope estimate).

The number of established alien species is also negatively correlated with latitude (northern hemisphere: 2.25 ± 1.50; -0.05 ± 0.02; $r^2 = 0.50$, $p < 0.01$. Southern hemisphere: 2.46 ± 0.79; -0.05 ± 0.01; $r^2 = 0.56$, $p < 0.01$), with peaks that mirror those of recorded alien species richness (figures 6.3a,b).

In the northern hemisphere there is a significant negative relationship between latitude and the proportion of recorded alien bird species that are established (figure 6.3c; [latitude slope ± standard error] -0.41 ± 0.09; $r^2 = 0.64$, $p < 0.001$). In the southern hemisphere the relationship is U-shaped, with the proportion of recorded alien bird species that are established lowest near the Tropic of Capricorn (figure 6.3d; [latitude slope ± standard error; latitude^2 slope ± standard error] -2.07 ± 0.63; 0.04 ± 0.01; $r^2 = 0.49$, $p < 0.05$).

The mean recorded alien range extent within each 5° latitudinal band is positively correlated with latitude (figures 6.3e,f). The relationship is curved upwards in the northern hemisphere (figure 6.3e; [latitude slope ± standard error; latitude^2 slope ± standard error]: -0.46 ± 0.28; 0.02 ± 0.004; $r^2 = 0.89$, $p < 0.001$) but linear in the southern hemisphere, where a quadratic term for latitude was not included in the best model (figure 6.3f; [latitude slope ± standard error] 0.58 ± 0.09: $r^2 = 0.78$, $p < 0.001$).

The mean established alien range extent within each 5° latitudinal band is also positively correlated with latitude (figures 6.3e,f). As with recorded alien range extent, this relationship is curvilinear in the northern hemisphere (figure 6.3e; [latitude slope ± standard error; latitude^2 slope ± standard error]: -0.79 ± 0.52; 0.02 ± 0.01; $r^2 = 0.78$, $p < 0.001$) and linear in the southern hemisphere, where a quadratic term for latitude was again not included in the model (figure 6.3f; [latitude slope ± standard error] 0.29 ± 0.10: $r^2 = 0.41$, $p < 0.05$).

Table 6.1 The relationship between the latitudinal extent, lowest latitudinal limit, mid-latitude, and highest latitudinal limit of **a)** the recorded alien range and native range and **b)** the established alien range and native range. n = 359. * = p <0.05, ** = p <0.01, *** = p < 0.001.

a) Recorded alien range and native range

	Pearson's correlation		**Paired t-test '*t*' statistic**	
Latitudinal extent	0.31	***	-3.23	**
Lowest latitudinal limit	0.51	***	4.70	***
Mid-latitude	0.62	***	2.12	*
Highest latitudinal limit	0.52	***	-0.60	

b) Established alien range and native range

	Pearson's correlation		**Paired t-test '*t*' statistic**	
Latitudinal extent	0.26	***	-13.27	***
Lowest latitudinal limit	0.54	***	11.42	***
Mid-latitude	0.63	***	1.56	
Highest latitudinal limit	0.54	***	-6.40	***

In general, alien species are more likely to be recorded towards the higher latitudes of their native ranges than the lower latitudes, and subsequently have smaller absolute latitudinal extents in the recorded range compared to the native range, but with higher overall mid-latitude values. Comparisons of individual species latitudinal distributions showed that the lowest latitudinal limits, highest latitudinal limits, mid-latitudes and absolute latitudinal extents of species' native and recorded ranges are significantly positively correlated in each case (table 6.1a, figures 6.4a-d): species with their highest native latitudinal limits at higher latitudes also tend to have their highest recorded latitudinal limits at higher latitudes, and so on. However, paired t-tests show that the lowest latitudinal limits of recorded alien ranges tend to be at higher latitudes than the lowest native range latitudinal limits, whilst there is no difference between the highest latitudinal limits of recorded and native ranges (table 6.1a). This results in a significant positive difference between the mid-latitudes of recorded and native ranges and a smaller latitudinal extent in the recorded than the native ranges (table 6.1a).

Similarly, all four metrics of species' native range and established alien ranges are significantly positively correlated (table 6.1b, figures 6.5a-d): species with their highest native latitudinal limits at higher latitudes also tend to have their highest established alien latitudinal limits at higher latitudes, and so on.

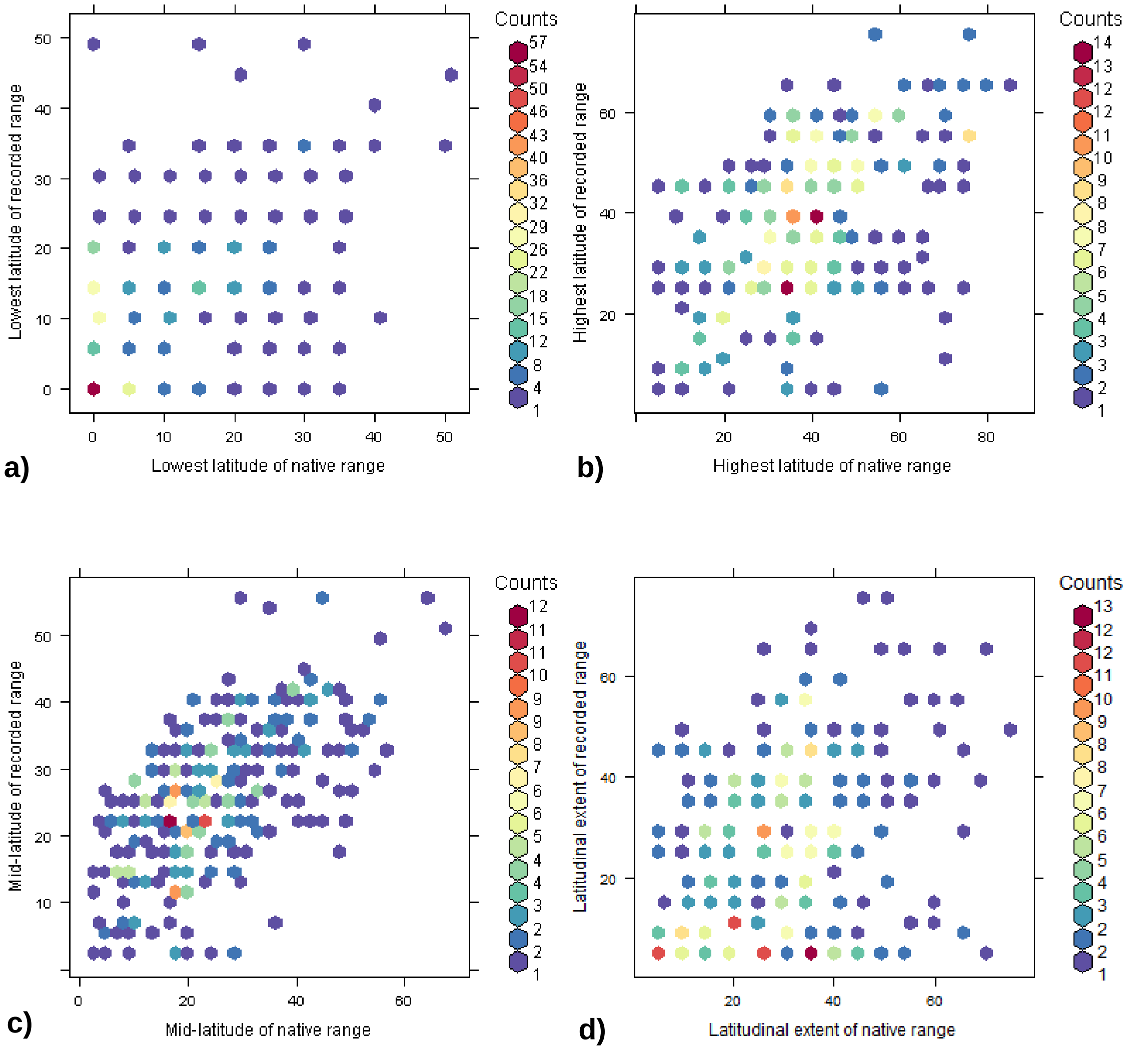


Figure 6.4 The relationship between **a)** the absolute lowest latitude of a species' recorded alien range and the absolute lowest latitude of its native range; **b)** the absolute highest latitude of a species' recorded alien range and the absolute highest latitude of its native range; **c)** the absolute latitudinal midpoint of a species' recorded alien range and the absolute latitudinal midpoint of its native range; **d)** the absolute latitudinal extent of a species' recorded alien range and the absolute latitudinal extent of its native range.

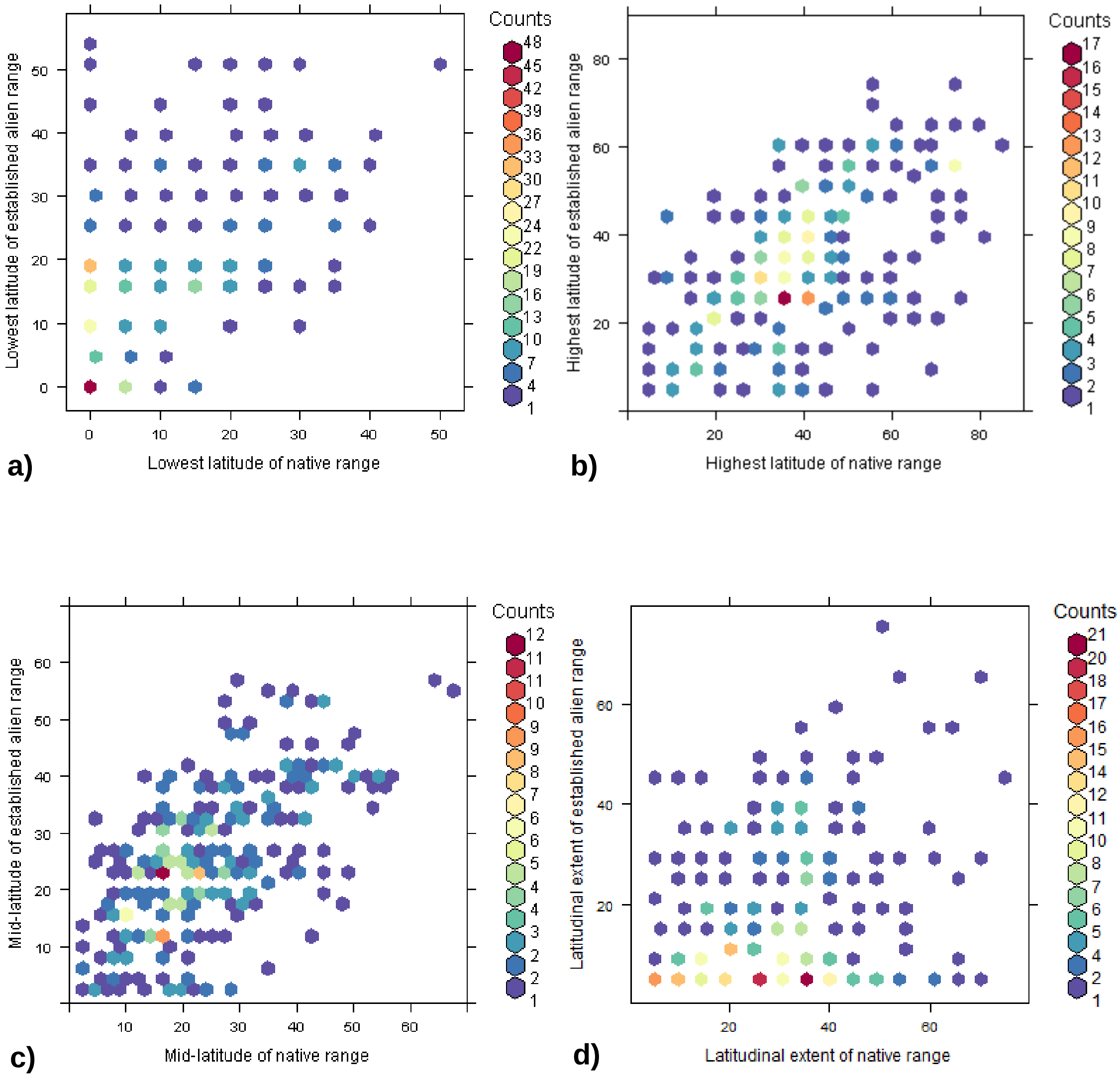


Figure 6.5 The interspecific relationship between **a)** the absolute lowest latitude of a species' established alien range and the absolute lowest latitude of its native range; **b)** the absolute highest latitude of a species' established alien range and the absolute highest latitude of its native range; **c)** the absolute latitudinal midpoint of a species' established alien range and the absolute latitudinal midpoint of its native range; **d)** the absolute latitudinal extent of a species' established alien range and the absolute latitudinal extent of its native range.

However, paired t-tests show that the lowest latitudinal limits of established alien ranges tend to be at higher latitudes than the lowest native latitudinal limits, while the highest latitudinal limits of established alien ranges tend to be at lower latitudes than the highest native latitudinal limits (table 6.1b). This translates into smaller latitudinal extents in the established alien than the native ranges, and no difference in the mid-latitudes of established alien and native ranges (table 6.1b).

More than half of alien bird species (n = 209; 58.2%) have been recorded (successfully or unsuccessfully) beyond one or both of the latitudinal limits of their native range (i.e. the sum of categories A_r, B_r and C_r; table 6.2a), with fewer (n = 150; 41.8%) recorded within the latitudinal bounds of their native range (category D_r; table 6.2a). Of those species recorded beyond the limits of their native range, the majority were recorded only poleward (n = 111; 30.9% of all species; 53.1% of species recorded beyond native limits; table 6.2a), with fewer recorded only equatorward (n = 58; 16.2% of all species; 27.8% of species recorded beyond native limits; table 6.2a), and a smaller number recorded beyond both latitudinal bounds (n = 40; 11.1% of all species; 19.1% of species recorded beyond native limits; table 6.2a). The exact binomial test showed that relative to a 50% expectation, more alien species have been recorded poleward relative to their native range than equatorward (151 vs 98; $p < 0.001$).

Fewer than half of alien bird species (n = 150; 41.8%) have successfully established distributions beyond one or both of the latitudinal limits of their native range (i.e. the sum of categories A_e, B_e and C_e; table 6.2a), meaning that the majority (n = 209; 58.2%) of established alien bird species occur within the same latitudinal bounds as they do in their native range (category D_e; table 6.2a). Of those species that have established alien populations beyond the limits of their native range, the majority have established only poleward (n = 92; 25.6% of all species; 61.3% of species established beyond native limits; table 6.2a), with fewer establishing only equatorward (n = 42; 11.7% of all species; 28% of species established beyond native limits; table 6.2a), and an even smaller number establishing beyond both latitudinal bounds (n = 16; 4.5% of all species; 10.7% of species established beyond native limits; table 6.2a). The exact binomial test showed that relative to a 50% expectation, more alien species have established populations poleward relative to their native range than equatorward (108 vs 58; $p < 0.001$).

Table 6.2 a) The proportion of bird species with a recorded alien range which has shifted relative to the latitudinal boundaries of their native range (A_r – D_r), and how this corresponds to where the species have established relative to the latitudinal boundaries of their native range (A_e – D_e). The values represent the number or percentage of birds with a recorded or established alien range that has shifted by more than 5° beyond ($A_{r,e}$) the high-latitudinal limit of their native range, ($B_{r,e}$) the low-latitudinal limit of their native range, ($C_{r,e}$) both high- and low-latitudinal limits, or ($D_{r,e}$) that remains within the latitudinal limits of their native range (after Guo *et al*. 2012). **b)** The bird species recorded beyond the latitudinal limits of their native range (A_r – C_r), and the number and proportion in each category that succeeded and failed. n = 359.

a)

		Recorded alien range			**Established alien range**	
		No. of species	% of species		No. of species	% of species
Poleward	A_r	111	30.9	A_e	92	25.6
Equatorward	B_r	58	16.2	B_e	42	11.7
Bidirectional	C_r	40	11.1	C_e	16	4.5
No shift	D_r	150	41.8	D_e	209	58.2

b)

Recorded alien range relative to native range	**Successful establishment**	**No. species**	**%**
A_r. Poleward	A_e. Poleward	79	71.2
	D_e. No shift	32	28.8
B_r. Equatorward	B_e. Equatorward	34	58.6
	D_e. No shift	24	41.4
C_r. Bidirectional	A_e. Poleward	13	32.5
	B_e. Equatorward	8	20
	C_e. Bidirectional	16	40
	D_e. No shift	3	7.5

Of those alien bird species recorded beyond the poleward limit of their native range, the majority have successfully established (71.2% of species recorded only poleward, 71.5% of species recorded both poleward and bidirectionally; table 6.2b), with the remainder failing to establish at a higher latitude than occupied in their native range. Of those species recorded beyond the equatorward limit of their native ranges, a smaller majority successfully established (58.6% of species recorded equatorward, 59.2% of species recorded both equatorward and bidirectionally; table 6.2b), with the remainder failing to establish at a lower latitude than occupied in their native range. Of those species recorded beyond both the poleward and equatorward limits of their native range, the largest proportion maintained this bidirectional range extension (40% of species recorded bidirectionally; table 6.2b), with 32.5% succeeding in maintaining only the poleward range, 20% maintaining only the equatorward range, and 7.5% failing to succeed beyond either limit of their native range (table 6.2b). In other words, 28.5% of all species recorded poleward to their native range failed to maintain the poleward extension, while 40.8% of all species recorded equatorward to their native range failed to maintain the equatorward extension.

6.4 DISCUSSION

Here I have revisited the analyses conducted by Sax (2001) and Guo *et al*. (2012), but importantly with the inclusion of data on introductions that failed to establish. I expanded the analyses by conducting them at a global scale and with a wider range of species (359 species compared to 147 in Guo *et al*. (2012), the number of bird species included in Sax (2001) is unknown). I show that established alien bird species richness increases from the poles to the edges of the tropics in both the northern and southern hemispheres (figures 6.3a,b), but within the tropics then decreases towards the equator. The latitudinal range extents of established alien bird species increase with latitude in the southern hemisphere, in accordance with Rapoport's rule (figure 6.3f). Latitudinal range extents increase with latitude north of the tropics in the northern hemisphere, but are more or less constant in size from the Tropic of Cancer to the equator (figure 6.3e). Recorded alien species show similar latitudinal patterns of species richness and latitudinal range size (figures 6.3a,b,e,f). However, there is latitudinal variation in the likelihood that a recorded alien species becomes established, with alien bird species in general more likely to establish nearer the equator (6.3c,d). Conversely, of those species introduced beyond the latitudinal limits of their native range, more are likely to fail beyond the equatorward limits than beyond the poleward limits (table 6.2a,b).

The alien species richness gradients in the northern and southern hemispheres differ in terms of the number of alien bird species recorded and the number established (figure 6.2). The highest values of both recorded and established alien species richness are between 15-30°N, coinciding with the geographic locations of the Hawaiian Islands, Florida, the Caribbean islands, the UAE, Hong Kong and Taiwan, where many bird species have been introduced and have established (Chapter 4). The two lesser peaks in the southern hemisphere between 15-25°S and 30-45°S, coincide with the

Mascarene Islands, and New Zealand and southeast Australia respectively. The peak just north of the equator between 0-5°N is driven primarily by introductions in Singapore.

The results here show that in general, alien bird species richness increases from the poles to the tropics in both hemispheres but attains relatively low levels throughout the tropics (figures 6.3a,b). Sax (2001) proposed that this pattern was due to abiotic factors in the temperate zone (reduced energy availability, climatic variation, colder temperatures: MacArthur 1972, Kaufman 1995), whereas the lower alien bird richness found in the tropics was a result of biotic resistance (predation, competition, parasitism and disease: Dobzhansky 1950). However, incorporating data on the total numbers of recorded alien species at different latitudes (established species and failures) shows that the latitudinal patterns of recorded and established alien species richness are almost identical in shape (figures 6.3a,b), with latitudes that have more established alien bird species also having more failed alien bird species. This suggests that although environmental factors may explain some of the variability in alien species richness at any given latitude (Chapter 4, Stohlgren *et al.* 2006), latitudinal patterns of established alien bird species richness are most likely to be a simple consequence of where species have been introduced.

Despite the congruence in latitudinal patterns of recorded and established alien bird species richness, there is nevertheless variation in the proportion of recorded alien bird species that are established at different latitudes. Previous studies addressing latitudinal patterns of establishment have generally either focussed on the effect of the latitudinal difference between native and alien ranges (Cassey *et al*. 2004, Mahoney *et al*. 2015), or have not considered where species have been introduced and therefore have quantified establishment in terms of alien richness rather than as a proportion of total species introduced (Blackburn & Duncan 2001a). The inclusion of data on total recorded species means that I have been able to calculate the proportion of recorded alien birds that are established at each latitude (and conversely the proportion that have failed); this is not the same as establishment success as it is classically defined because these data do not distinguish between species that were introduced to a latitudinal band and those that were introduced elsewhere and subsequently spread. Nevertheless, these data do identify that higher latitudes are where alien bird species are more likely to fail (and/or less likely to spread to, after establishment) (figure 6.3c,d). These findings again contradict previous studies that have suggested that the low prevalence of alien bird species in the tropics is because of intrinsic features of the environment there, and in particular biotic resistance (Sax 2001, Guo *et al*. 2012), that depress the likelihood of establishment. Instead, alien bird species seem more likely to establish or spread into tropical regions, relative to the number of species recorded there (figure 6.3). These findings do, however, concur with those from Chapter 4 suggesting that a lack of temperature extremes and high precipitation contribute to high alien species richness, while biotic resistance (at least as measured by native bird species richness) does not. It seems likely that these abiotic factors also enable alien species to persist more readily in the tropics.

The mean total latitudinal extents (most northerly point to most southerly point) of established alien bird species ranges increase with latitude poleward of the tropics (figures 6.3e,f). This is consistent with Rapoport's rule (Stevens 1989) and broadly conforms to the variation in alien bird range size observed by Sax (2001) in North America, and also to the variation in range size of native avifauna (Blackburn & Gaston 1996, Orme *et al*. 2006). However, the results here show alien latitudinal range extents to be uniformly small in the tropics. This pattern is also in general concordance with range size and latitudinal range extents of native bird species (Orme *et al*. 2006, Olson *et al.* 2009), and with Rapoport's rule (Stevens 1989). In contrast, Sax (2001) found alien latitudinal range extents to be large across the tropics. Sax's (2001) analysis of latitudinal extents was confined to those alien birds introduced to mainland North America, and he explained the pattern by the status of most of the tropical mainland species as human commensals, i.e. species that inhabit anthropogenic environments and as such have broad alien ranges. This analysis is global, including a larger number of species, and more importantly incorporating many alien species with restricted island populations in the tropics. Figure 4.4 in Chapter 4 supports the suggestion by Sax (2001) that large tropical mainland alien ranges are a result of a few wide-ranging species, so it would seem that the inclusion of islands in this analysis may explain why the results in Sax (2001) differ from the global patterns found here.

The species-level analyses demonstrate variation in both the extents and positions of species' recorded and established alien latitudinal ranges relative to their native latitudinal ranges. The upper latitudinal limits of species' alien and native ranges are positively correlated, as too are the lower latitudinal limits, in concordance with the findings of Guo *et al*. (2012): species found at high latitudes in their native ranges also tend to be found at high latitudes in their alien ranges, and vice versa for the lower latitudinal range limits (figure 6.5). Species with larger native range extents also tend to have larger alien range extents (c.f. Chapter 5). However, in general the lower latitudinal limits of the established alien range are positioned at higher latitudes than for the native range, while the higher latitudinal limits of the established alien range at lower latitudes than for the native range: this means that species have narrower latitudinal extents in their established alien than native ranges, albeit that the latitudinal mid-points of established alien and native ranges do not differ (table 6.1). To a degree, these narrower established alien latitudinal extents reflect where species have been introduced, as most species also have narrower recorded than native latitudinal range extents. Nevertheless, there is evidence of range contraction after introduction, as the higher latitudinal limits of native and recorded alien ranges do not differ, while they are lower for established alien than native ranges (table 6.1). The differences between native and established alien latitudinal extents are also greater than between native and recorded alien latitudinal extents, as indicated by the larger t statistic for the former (table 6.1; mean absolute latitudinal extent for native ranges: 29°; recorded ranges: 26°; established ranges: 17°). Overall, alien bird species are more likely to occur within the latitudinal confines of their native ranges.

Although the majority of established alien populations fall within the latitudinal bounds of their native ranges, more than half of alien bird species have been recorded beyond one or both of the latitudinal limits of their native range (table 6.2a). Significantly more alien bird species have been recorded poleward relative to their native range than equatorward, and those that have been recorded beyond the equatorward limit are more likely to fail (table 6.2b). Guo *et al*. (2012) found that relatively more alien bird species (and mammal and plant species) occurred at latitudes higher than those in their native ranges, with fewer occurring at latitudes lower than those in their native ranges. They proposed that these patterns were due to climate change, historical limitations on native ranges, greater biotic resistance at lower latitudes, and the impacts of humans on species distributions. However, they did not specifically consider the total number of alien bird species recorded at each latitude. MacArthur (1972) postulated that the lower latitudinal range limits of many northern hemisphere species are determined by biotic interactions, whilst many higher limits are determined by abiotic conditions. Sax (2001) used this theory to explain his findings that only a small proportion of bird (and mammal) species extend to a lower latitude in their alien range than their native range, arguing that they were indicative of biotic resistance on southern range limits. However, to understand the nature of alien species latitudinal shifts, it is useful to know where species have been recorded and where they have failed. My analyses show that while many bird species have been introduced or spread to areas outside the native latitudinal limits, the difference between the number of species recorded and the number established is greater at low latitudes than at high latitudes (table 6.2). This shows that there is a lower tendency for alien species to succeed beyond the lower limits of their native distributions, than beyond the upper (poleward) limits.

The species-level and latitudinal band approaches produce an apparent paradox: the latter shows that alien species are less likely to fail to colonise low latitudes (figure 6.3c,d), while the former shows that alien species are more likely to contract from latitudes beyond the lower limits of their native distributions (table 6.2). The paradox may be resolved by considering differences in species responses within and outside their native latitudinal ranges: species that do not naturally occur at low latitudes can be less likely to succeed there, but if a species can live at low latitudes, it is more likely to persist (or spread) there than a species that can live at higher latitudes is likely to persist (or spread) at high latitudes. The former result may identify where biotic resistance can influence success, because species that do not live in the tropics may typically tolerate a wide range of abiotic conditions (which is likely to include tropical conditions). The latter result may identify an effect of environmental variation on success, because species that can live at higher latitudes are still less likely to be successful there. Small populations may be more likely to fall foul of stressful environmental conditions than in the more benign tropics (c.f. Duncan *et al*. 2014). Overall, this suggests that whether biotic or abiotic conditions matter more to alien species distributions may depend on whether introductions are within or beyond their native latitudinal range limits. This suggests an interesting area for future investigation.

Although whilst collating the data I strived to take into account the biases of similar analyses, certain caveats remain. The species analysed are likely to be at different stages of their alien range expansion (Blackburn *et al.* 2009a), and many (or most) may spread beyond their currently recorded established alien ranges, while some may yet contract and fail. The number of recorded introductions may be influenced by higher or lower recording effort in certain regions – albeit that birds tend to be relatively well recorded, especially in temperate zones. The method used to calculate latitudinal range (the Stevens method; Stevens 1989) has the disadvantage that the mean latitudinal range extents for different bands are not independent, with bands that are closer together sharing a higher proportion of the same species (and therefore the same range extents) (Letcher & Harvey 1994, Gaston *et al*. 1998). However, this method was deemed the most suitable for use with alien bird distributions, as the alternative ‘midpoint method’ (Rohde *et al*. 1993), would provide a meaningless value if the species had spatially disjunct populations (which is the case for many alien bird species). One should not read too much into the significance of the trends in figure 6.3 as a result, although the trends themselves are still interpretable.

Many studies of invasion ecology assume that the opportunity for biological invasions is similar across regions. However, as I have shown here, this is not always the case. The latitudinal patterns apparent in alien bird species distributions are in part a result of where species are introduced to, but there is also variation in the likelihood of alien species persistence with latitude, and relative to the latitudinal distribution of the native range. Hence, whilst there may be intrinsic differences in the ability of species to extend their latitudinal limits, and differences in the inherent invasibility of specific locations and latitudes, human influence is likely also to be a key factor determining the number of alien species found at any particular latitude.

Chapter 7.

Discussion

7.1 In summary

Alien species present a considerable threat to native species and habitats (Clavero & Garcia-Berthou 2005, Evans *et al*. 2014), and pose a substantial economic risk to recipient countries (Pimentel *et al*. 2001, Williams *et al*. 2010). Yet, there is no sign that their influx and spread is diminishing (Pyšek *et al*. 2010, Seebens *et al*. in prep.). Increasing global trade continues to facilitate the movement of many species, and species adaptations and changing environmental factors continue to affect the potential distribution of alien species (Westphal *et al*. 2008, Blackburn *et al*. 2009a). Thus, it will become increasingly challenging to predict alien species' potential distributions and subsequent environmental and economic effects (Stohlgren *et al*. 2006). Jared Diamond included invasive species as one of the "Four Horsemen" of the current environmental apocalypse, along with habitat destruction, over-exploitation by people, and extinction cascades (when one extinction leads to another) (Diamond 1989). Arguably, invasive species will be the most difficult of these horsemen to unseat. Stop hunting or cutting down forests and these pressures on native species immediately cease. Stop introducing alien species and those already present will continue to reproduce and spread, with no let up to their impacts. Alien species are worms (sometimes literally) that will be very difficult to get back in to the can. Gaining a better understanding into the varying drivers of introductions, the numbers of species that become established relative to the number introduced, the potential spread of alien species, and how these aspects vary across taxonomic groups and regions, is therefore an essential starting point for the formulation of effective policy and management approaches (Spear *et al*. 2013).

The majority of literature on biological invasions is biased in favour of invasive alien species – those that have established and spread (Pyšek *et al*. 2008). However, all introduced alien species are potential invaders and each one has to pass through four stages of the invasion pathway before becoming successfully established (Chapter 1). Without examining the different pressures mediating progression at each stage of the pathway, the ability to interpret the full suite of drivers of invasion is impeded (Richardson & Pyšek 2012). The scope of the GAVIA database, both spatially and temporally, and its inclusion of all levels of alien species status (Chapter 2), has enabled me to address the factors that influence the distribution of alien bird species at the least documented stages of this continuum: transportation, introduction and spread. Crucially, I have been able to include a measure of colonisation pressure into my analyses, and emphasise the importance of a metric that is often missing from alien species research.

Focussing on the early stages on the invasion pathway, I showed that the main drivers of alien bird species transportation and introduction have changed between the historical and modern time periods (Chapter 3). Introductions have increased in number, and are occurring in a wider range of countries as a result of globalisation. In the historical period, alien bird introductions were related to the movement of the British around the world, with species that were deemed to be beneficial sourced primarily from the Palearctic realm for introduction. In the modern era, the burgeoning global pet trade and increase in country wealth are now the main drivers of alien bird introductions, with species sourced from Southeast Asia and Africa. Compared to the historical era, the numbers of introductions, numbers of species introduced, and numbers of countries involved are all on the increase. These results suggest that if invasions are to be prevented, then more resources for combating alien species should be directed at the transport and introduction stages of the invasion pathway (Westphal *et al*. 2008). This is critical, as the introduction of alien species is accelerating in step with surging economic growth and international trade (Ding *et al*. 2008, Seebens *et al*. in prep.), factors which are unlikely to diminish.

I then examined the relative importance of the various anthropogenic and environmental conditions that influence a measure of alien species spread in a location - alien species richness (Chapter 4). Anthropogenic elements of the introduction history of the region were the most important predictors of alien species richness: especially colonisation pressure, but also time since introduction and distance to historic port. This demonstrated the ongoing human influence at this later stage of the invasion process. Climate-related environmental predictors, specifically temperature and precipitation, also played a significant role in explaining some of the global distribution of alien bird richness. These analyses also showed that in the absence of data relating to the introduction history of the species (such as colonisation pressure and residence time), studies may mistakenly conclude that environmental or socioeconomic factors are the main determinants of variation in alien species richness. Therefore, the inclusion of information relating to introduction history, where available, should become normal practice when analysing aspects of the invasion process.

I went on to show that the strongest determinant of another representation of alien bird species spread - alien geographic range size - was the number of times that a species had been successfully introduced globally, but that species with larger native ranges and shorter residence times also tended to have larger alien ranges (Chapter 5). This result is important as alien species that are able to spread and achieve a large alien range extent are more likely to have a greater impact on native species and the environment (Parker *et al.* 1999), and consequently a larger economic cost (Williams *et al*. 2010). Therefore gaining an understanding of the structure and mechanisms behind alien range sizes is vital as it can help to identify those species that are likely to spread once introduced to a new region.

I then explored how these patterns of alien species richness and range size changed spatially in relation to latitude (Chapter 6). I showed that both recorded and established alien species richness increases from the poles to the edges of the tropics, but within the tropics then decreases towards the equator. This suggests that although environmental factors may explain some of the variability in alien species richness at any given latitude (as shown in Chapter 4), latitudinal patterns of established alien bird species richness are most likely to be a simple consequence of where species have been introduced. The latitudinal range extents (range size) of both recorded and established alien bird species in general increase with latitude, in accordance with Rapoport's rule (Stevens 1989) and with range size and latitudinal range extents of native bird species (Orme *et al*. 2006, Olson *et al.* 2009). I also found that of those species introduced beyond the latitudinal limits of their native range, more are likely to fail beyond the equatorward limits than beyond the poleward limits. Conversely I demonstrated that alien bird species are in general more likely to establish nearer the equator than the poles. This supports the findings from Chapter 4, suggesting that abiotic factors (e.g. a lack of temperature extremes and high precipitation) contribute to high alien species richness. Overall these results reinforce the importance of the inclusion of elements of the introduction history in alien species analysis (such as the total number of species recorded), to avoid erroneous conclusions from being made.

7.2 The challenges of alien species research

Human-mediated avian invasions represent a classic example of ‘experiments in nature’: empirical studies in which individuals or populations are exposed to experimental conditions determined by nature or other factors outside the control of the investigators (Diamond 1986). Nevertheless, the experiment has not been well designed: multiple populations of different species with conflicting characteristics have been introduced into contrasting locations using a variety of methods. This means that the likelihood of a species establishing a population in a specific location has been driven by a whole suite of uncontrolled factors which are hard to disentangle (Blackburn *et al*. 2009a).

One particular shortcoming of the available alien species data is the lack of a control treatment. This makes it much harder to assess which process or processes are actually driving the change in the study system. For example, if we were to observe higher establishment success and greater spread in species introduced to certain habitats, we might infer that establishment is easier in these habitats. But without experimental controls it is difficult to discern whether it is actually the habitat affecting establishment success, or in fact a different feature of the environment such as fewer competitors or increased resources.

A second problem is one of consistency of data. Studies of avian invasions differ in their definitions of an invader (Hulme & Weser 2011). Some may be reporting those species that have been released into a novel location through an anthropogenic vector and have formed a self-sustaining population, whilst others may be recording species which are single escapees from captivity with no chance of establishing, or natural vagrants or migrants blown off course. Sometimes it is impossible to tell into which category an individual or propagule belongs. This makes it difficult when collating data to ascertain the status of a recorded species, and then further down the line to be able to compare like for like.

In addition to these issues, a third problem is that many of the data needed for a comprehensive understanding of the invasion process are simply lacking. For example, the majority of data involving alien birds does not include information describing exactly how the species came to be in that location, or how many individuals and in what proportions (for example the sex ratio and maturity of individuals) made up the original population. All of these factors can determine whether or not a species establishes and spreads, even before the characteristics of the location or the species itself are considered.

Fourth, there is also a bias in the available data on alien birds. Pyšek *et al*. (2008) demonstrate that there is an acute geographical bias in the locations where invasion biologists conduct their research. Although Europe, the United States and Australia are over-represented in terms of research locales (Dana *et al*. 2013), it is difficult to determine whether this is due to a higher number of invasion biologists focussing their research there, or if it is a justified skew as a result of these areas holding a relatively larger number of alien species. Pyšek *et al*. (2008) also found that invasion research seemed to focus on those species that are perceived to have the potential to produce the most economic or ecological harm, rather than a representative subset.

Data involving alien bird species therefore will be imperfect, and analyses of such data need to take this into account. Nevertheless, the imperfections are outweighed by the fact that the data exist at all and the opportunities for novel investigations into all facets of environmental biology that they present.

7.3 The applicability of this research and future directions

In due course, the GAVIA database will be published online as an important resource for invasion biologists. The data contained within GAVIA constitutes a large evidence base for the analysis of spatial and temporal patterns in alien bird distributions, and will be a useful repository for scientists interested in understanding the invasion process. The results from research undertaken using GAVIA will also help conservation bodies and policy makers to understand where and why invasions are continuing to occur, and so ultimately contribute to efforts to stem the process and ameliorate its impacts.

Combining the data in GAVIA with similar data on other alien taxa would be an expedient next stage of research. It would be interesting to test the wider generality of the relationships shown for birds, as data for other alien taxa become available. For example, an assessment of the general determinants of alien species richness for a wide range of taxonomic groups, weighing the relative importance of environmental and anthropogenic factors, would be useful for identifying alien species hotspots and dictating their future management. Understanding these processes at a cross-taxon level is critical in order to mitigate the impacts of alien species, especially given the need to determine the likely effects of global change on the potential for species to invade new regions.

In addition, combining the results shown here with studies concerning the predictors of the impacts of alien birds (e.g. Evans *et al.* 2014) would enable the identification of those species that have the greatest potential of having a high impact on native ecosystems. The relatively restricted distribution of most species in their alien range relative to their native range highlights the risk of future spread of many introduced species, and calls for their close monitoring under climate change. Combining effort in this way would further help to inform policy and conservation action by identifying which species pose the greatest overall threat, and therefore where limited management funds should be targeted.

7.4 In conclusion

This thesis has emphasised how the quantity and quality of data for an alien species group can enable key hypotheses about the drivers of alien species distributions to be explored. I have highlighted the pivotal role that anthropogenic factors play in determining the distributions of alien bird species, and the importance of including aspects of the introduction history of a species, such as colonisation pressure and residence time, into analyses. I suggest that there is a need to shift attention away from a dominant focus on the properties of invading organisms, to an emphasis on research that considers the influence that anthropogenic factors have on all stages of the invasion pathway. In addition, information relating to introduction history, where available, should routinely be considered when analysing aspects of the invasion process, otherwise the species and areas with the highest risk of invasion may be misidentifed.

References

Allen, A. P., Brown, J. H., & Gillooly, J. F. (2002). Global biodiversity, biochemical kinetics, and the energetic equivalence rule. *Science, 297*(1545-1548).

Allen, C. R., Nemec, K. T., Wardwell, D. A., Hoffman, J. D., Brust, M., Decker, K. L., *et al*. (2013). Predictors of regional establishment success and spread of introduced non-indigenous vertebrates. *Global Ecology and Biogeography, 22*, 889-889.

Anthony, M. (1997). *Historical Dictionary of Trinidad and Tobago*. London: The Scarecrow Press, Inc.

Araújo, M. B., Nogúes-Bravo, D., Diniz-Filho, J. A. F., Haywood, A. M., Valdes, P. J., & Rahbek, C. (2008). Quaternary climate changes explain diversity among reptiles and amphibians. *Ecography, 31*, 8-15.

Arino, O., Ramos Perez, J. J., Kalogirou, V., Bontemps, S., Defourny, P., & Van Bogaert, E. (Cartographer). (2012). *Global Land Cover Map for 2009 (GlobCover 2009)*.

Arlot, S., & Celisse, A. (2010). A survey of cross-validation procedures for model selection. *Statistics Surveys, 4*, 40-79.

Arrhenius, O. (1921). Species and area. *Journal of Ecology, 9*, 95-99.

Baillie, J. E. M., Hilton-Taylor, C., & Stuart, S. N. (Eds.). (2004). *2004 IUCN Red List of Threatened Species. A Global Species Assessment.* Cambridge, UK: IUCN.

Banks, A. N., Wright, L. J., Maclean, I. M. D., & Rehfisch, M. M. (2008). *Review of the Status of Introduced Non-Native Waterbird Species in the Area of the African-Eurasian Waterbird Agreement: 2007 Update*. Thetford, UK: BTO.

Barton, K. (2014). MuMIn: Multi-model inference. R package version 1.10.0. http://CRAN.R-project.org/package=MuMIn

Belmaker, J., Sekercioglu, C. H., & Jetz, W. (2011). Global patterns of specialization and coexistence in bird assemblages. *Journal of Biogeography, 39*(1), 193-203.

Bivand, R.S., Hauke, J., & Kossowski, T. (2013a). Computing the Jacobian in Gaussian spatial autoregressive models: An illustrated comparison of available methods. *Geographical Analysis*, 45(2), 150-179.

Bivand, R. S., Pebesma, E., & Gomez-Rubio, V. (2013b). *Applied spatial data analysis with R*, Second edition. Springer, NY. http://www.asdar-book.org/

Bivand, R. S., & Piras, G. (2015). Comparing Implementations of Estimation Methods for Spatial Econometrics. *Journal of Statistical Software*, 63(18), 1-36. URL http://www.jstatsoft.org/v63/i18/

Bivand, R. S., & Rundel, C. (2015). rgeos: Interface to Geometry Engine - Open Source (GEOS). R package version 0.3-12. http://CRAN.R-project.org/package=rgeos

Bivand, R. S., Keitt, T., & Rowlingson, B. (2015). rgdal: Bindings for the Geospatial Data Abstraction Library. R package version 1.0-7. http://CRAN.R-project.org/package=rgdal

Blackburn, T. M., & Gaston, K. J. (1996). Spatial patterns in the geographic range sizes of bird species in the New World. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 351*, 897-912.

Blackburn, T. M., & Duncan, R. P. (2001a). Determinants of establishment success in introduced birds. *Nature, 414*, 195-197.

Blackburn, T. M., & Duncan, R. P. (2001b). Establishment patterns of exotic birds are constrained by non-random patterns in introduction. *Journal of Biogeography, 28*, 927-939.

Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L., & Gaston, K. J. (2004). Avian extinction and mammalian introductions on oceanic islands. *Science, 305*, 1955-1958.

Blackburn, T. M., Cassey, P., & Lockwood, J. L. (2008). The island biogeography of exotic bird species. *Global Ecology and Biogeography, 17*, 246-251.

Blackburn, T. M., Lockwood, J. L., & Cassey, P. (2009a). *Avian Invasions*. Oxford: Oxford University Press.

Blackburn, T. M., Cassey, P., & Lockwood, J. L. (2009b). The role of species traits in the establishment success of exotic birds. *Global Change Biology, 15*, 2852-2860.

Blackburn, T. M., Gaston, K. J., & Parnell, M. (2010). Changes in non-randomness in the expanding introduced avifauna of the world. *Ecography, 33*, 168-174.

Blackburn, T. M., Prowse, T. A. A., Lockwood, J. L., & Cassey, P. (2011a). Passerine introductions to New Zealand support a positive effect of propagule pressure on establishment success. *Biodiversity Conservation, 20*, 2189-2199.

Blackburn, T. M., Pyšek, P., Bacher, S., Carlton, J. T., Duncan, R. P., Jarošík, V., *et al*. (2011b). A proposed unified framework for biological invasions. *Trends in Ecology & Evolution, 26*(7), 333-339.

Blackburn, T. M., Lockwood, J. L., & Cassey, P. (2015a). The influence of numbers on invasion success. *Molecular Ecology, 9*, 1942-1953.

Blackburn, T. M., Dyer, E., Su, S., & Cassey, P. (2015b). Long after the event, or four things we (should) know about bird invasions. *Journal of Ornithology, In Press*.

Blondel, J. (1991). Invasions and range modifications of birds in the Mediterranean Basin. In R. Groves & F. di Castri (Eds.), *Biogeograpy of Mediterranean Invasions* (pp. 311-326). Cambridge: Cambridge University Press.

Brown, J. H. (1984). On the relationship between abundance and distribution of species. *The American Naturalist, 124*, 255–279.

Brown, J. H. (1995). *Macroecology*. Chicago: University of Chicago Press.

Brown, J. H., & Sax, D. (2004). An essay on some topics concerning invasive species. *Austral Ecology, 29*, 530-536.

Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach* (2nd ed.). New York: Springer-Verlag.

Byers, J. E., Smith, R. S., Pringle, J. M., Clark, G. F., Gribben, P. E., Hewitt, C. L., *et al*. (2015). Invasion expansion: Time since introduction best predicts global ranges of marine invaders. *Scientific Reports, 5*(12436), 1-9.

Case, T. J. (1996). Global patterns in the establishment and distribution of exotic birds. *Biological Conservation, 78*, 69-96.

Cassey, P. (2001a). Are there body size implications for the success of globally introduced land birds? *Ecography, 24*, 413-420.

Cassey, P. (2001b). Determining variation in the success of New Zealand land birds. *Global Ecology and Biogeography, 10*, 161-172.

Cassey, P. (2002). Life history and ecology influences establishment success of introduced land birds. *Biological Journal of the Linnean Society, 76*, 465-480.

Cassey, P. (2003). A comparative analysis of the relative success of introduced landbirds on islands. *Evolutionary Ecology Research, 5*, 1011-1021.

Cassey, P., Blackburn, T. M., Russell, G. J., Jones, K. E., & Lockwood, J. L. (2004a). Influences on the transport and establishment of exotic bird species: an analysis of the parrots (Psittaciformes) of the world. *Global Change Biology, 10*, 417-426.

Cassey, P., Blackburn, T. M., Sol, D., Duncan, R. P., & Lockwood, J. L. (2004b). Global patterns of introduction effort and establishment success in birds. *Proceedings of the Royal Society, London, B (supplement), 271*, S405-S408.

Cassey, P., Blackburn, T. M., Duncan, R. P., & Gaston, K. J. (2005). Causes of exotic bird establishment across oceanic islands. *Proceedings of the Royal Society, London, B, 272*(1576), 2059-2063.

Cassey, P., Blackburn, T. M., Duncan, R. P., & Lockwood, J. L. (2008). Lessons from introductions of exotic species as a possible information source for managing translocations of birds. *Wildlife Research, 35*, 193-201.

Cassey, P., Vall-llosera, M., Dyer, E., & Blackburn, T. M. (2015). The biogeography of avian invasions: history, accident and market trade. In J. Canning Clode (Ed.), *Biological Invasions in Changing Ecosystems: Vectors, Ecological Impacts, Management and Predictions*. Warsaw: de Gruyter Open.

CBD (2002). COP 6 Decision: Alien species that threaten ecosystems, habitats or species. VI/23. Sixth Meeting of the Conference of the Parties to the Convention on Biological Diversity, *the Hague, Netherlands.* 7 - 19 April 2002 https://www.cbd.int/decision/cop/default.shtml?id=7197

CBD (2010). Strategic Goal B: Target 9. Strategic Plan for Biodiversity 2011-2020: Aichi Biodiversity Targets. https://www.cbd.int/sp/targets/default.shtml

CIESIN (Center for International Earth Science Information Network), Columbia University; and Centro Internacional de Agricultura Tropical (CIAT). (2005). Gridded Population of the World Version 3 (GPWv3): Population Density Grids. Palisades, NY: Socioeconomic Data and Applications Center (SEDAC), Columbia University. Available at http://sedac.ciesin.columbia.edu/gpw. (26/04/2013).

Chiron, F., Shirley, S. M., & Kark, S. (2009). Human-related processes drive the richness of exotic birds in Europe. *Proc. R. Soc. Lond. B, 276*, 47-53.

Chown, S. L., & Gaston, K. J. (1999). Exploring links between physiology and ecology at macro-scales: The role of respiratory metabolism in insects. *Biological Reviews, 74*, 87-120.

Clavero, M., & Garcia-Berthou, E. (2005). Invasive species are a leading cause of animal extinctions. *TRENDS in Ecology and Evolution, 20*(3), 110.

Colautti, R. I., & MacIsaac, H. J. (2004). A neutral terminology to define 'invasive' species. *Diversity and Distributions, 10*, 135-141.

Crosby, A. W. (1993). *Ecological imperialism : the biological expansion of Europe, 900-1900.* Cambridge: Cambridge University Press.

Cuddihy, L. W., & Stone, C. P. (1990). *Alteration of native Hawaiian vegetation: effects of humans, their activities and introductions.* Honolulu: University of Hawaii Press.

Currie, D. J. (1991). Energy and large-scale patterns of animal and plant-species richness. *American Naturalist, 137*(27-49).

Dana, E. D., Jeschke, J. M., & Garcia-de-Lomas, J. (2013). Decision tools for managing biological invasions: existing biases and future needs. *Oryx*, 1-8.

Davies, R. G., Orme, C. D. L., Storch, D., Olson, V. A., Thomas, G. H., Ross, S. G., *et al*. (2007a). Topography, energy and the global distribution of bird species richness. *Proceedings of the Royal Society, London, B, 274*, 1189-1197.

Davies, R. G., Orme, C. D. L., Webster, A. J., Jones, K. J., Blackburn, T. M., & Gaston, K. J. (2007b). Environmental predictors of global parrot (Aves: Psittaciformes) species richness and phylogenetic diversity. *Global Ecology and Biogeography, 16*, 220-233.

Davies, T. J., Purvis, A., & Gittleman, J. L. (2009). Quaternary climate change and the geographic ranges of mammals. *The American Naturalist, 174*, 297-307.

Diamond, J. M. (1986). Overview: laboratory experiments, field experiments, and natural experiments. In J. M. Diamond & T. J. Case (Eds.), *Community ecology* (pp. 3- 22). New York: Harper Row.

Diamond, J. M. (1989). The present, past and future of human-caused extinctions. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences, 325*, 469-476.

Ding, J., Mack, R. N., Lu, P., Ren, M., & Huang, H. (2008). China's booming economy is sparking and accelerating biological invasions. *BioScience, 58*(4), 317-324.

Dobzhansky, T. (1950). Evolution in the tropics. *American Scientist, 38*, 209-221.

Dukes, J. S., & Mooney, H. A. (2004). Disruption of ecosystem processes in western North America by invasive species. *Revista Chilena de Historia Natural, 77*, 411-437.

Duncan, R. P. (1997). The role of competition and introduction effort in the success of Passeriform birds introduced to New Zealand. *The American Naturalist, 149*(5), 903-915.

Duncan, R. P., Blackburn, T. M., & Veltman, C. J. (1999). Determinants of Geographical Range Sizes: A Test Using Introduced New Zealand Birds. *Journal of Animal Ecology, 68*(5), 963-975.

Duncan, R. P., Bomford, M., Forsyth, D. M., & Conibear, L. (2001). High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. *Journal of Animal Ecology, 70*, 621-632.

Duncan, R. P., & Blackburn, T. M. (2002). Morphological over-dispersion in game birds (Aves: Galliformes) successfully introduced to New Zealand was not caused by interspecific competition. *Evolutionary Ecology Research, 4*, 551-561.

Duncan, R. P., Blackburn, T. M., & Worthy, T. H. (2002). Prehistoric bird extinctions and human hunting. *Proceedings of the Royal Society, London, B, 269*, 517-521.

Duncan, R. P., Blackburn, T. M., & Sol, D. (2003). The ecology of bird introductions. *Annual Review of Ecology, Evolution, and Systematics, 34*, 71-98.

Duncan, R. P., Blackburn, T. M., Rossinelli, S., & Bacher, S. (2014). Quantifying invasion risk: the relationship between establishment probability and founding population size. *Methods in Ecology and Evolution, 5*(11), 1255-1263.

Eguchi, K., & Amano, H. E. (2004). Spread of exotic birds in Japan. *Ornithological Science, 3*(1), 3-11.

Elton, C. S. (1958). *The ecology of invasions by animals and plants* (1st ed.). London: Methuen.

EndNote citation software (2010). Thomson Reuters (version X4). Available at: www.endnote.com

ESRI (2008). ArcGIS Desktop: Release 9.3. Redlands, CA: Environmental Systems Research Institute.

ESRI (2010). ArcGIS Desktop: Release 10.2.2. Redlands, CA: Environmental Systems Research Institute.

Essl, F., Dullinger, S., Rabitsch, W., Hulme, P. E., Hulber, K., Jarošík, V., *et al*. (2011). Socioeconomic legacy yields an invasion debt. *PNAS, 108*(1), 203-207.

Essl, F., Dullinger, S., Moser, D., Steinbauer, K., & Mang, T. (2015). Macroecology of global bryophyte invasions at different invasion stages. *Ecography, 38*, 488-498.

Evans, K. L., Warren, P. H., & Gaston, K. J. (2005a). Does energy availability influence classical patterns of spatial variation in exotic species richness? *Global Ecology and Biogeography, 14*, 57-65.

Evans, K. L., Warren, P. H., & Gaston, K. J. (2005b). Species-energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews, 80*, 1-25.

Evans, T., Kumschick, S., Dyer, E., & Blackburn, T. (2014). Comparing determinants of alien bird impacts across two continents: implications for risk assessment and management. *Ecology and Evolution, 4*(14), 2957-2967.

Fischer, A. G. (1960). Latitudinal variations in organic diversity. *Evolution, 14*, 64-81.

Forsyth, D. M., Duncan, R. P., Bomford, M., & Moore, G. (2004). Climatic suitability, life-history traits, introduction effort, and the establishment and spread of introduced mammals in Australia. *Conservation Biology, 18*, 557-569.

France, R. (1992). The North American latitudinal gradient in species richness and geographical range of freshwater crayfish and amphipods. *The American Naturalist, 139*, 342-354.

Gallardo, B., & Aldridge, D. C. (2013). The ‘dirty dozen’: socio-economic factors amplify the invasion potential of 12 high rick aquatic invasive species in Great Britain and Ireland. *Journal of Applied Ecology, 50*, 757-766.

Gallardo, B., Zieritz, A., & Aldridge, D. C. (2015). The importance of the human footprint in shaping the global distribution of terrestrial, freshwater and marine invaders. *PLoS One, 10*(5), 1-17.

García-Herrera, R., Können, G. P., Wheeler, D. A., Prieto, M. R., Jones, P. D., & Koek, F. B. (2005). CLIWOC: A Climatological Database for the World's Oceans 1750-1854. *Climatic Change, 73*(1), 1-12.

Gaston, K. J., & Blackburn, T. M. (1996). Global scale macroecology: interactions between population size, geographic range size and body size in the Anseriformes. *Journal of Animal Ecology, 65*, 701-714.

Gaston, K. J., Blackburn, T. M., & Spicer, J. I. (1998). Rapoport's rule: time for an epitaph? *Trends in Ecology & Evolution, 13*(2), 70-74.

Gaston, K. J. (2003). *The structure and dynamics of geographic ranges*. Oxford: Oxford University Press.

Gaston, K. J., & Fuller, R. A. (2009). The sizes of species' geographic ranges. *Journal of Applied Ecology, 46*(1), 1-9.

Global Administrative Areas. Available at: www.gadm.org, downloaded August 2010.

Green, R. E. (1997). The Influence of Numbers Released on the Outcome of Attempts to Introduce Exotic Bird Species to New Zealand. *Journal of Animal Ecology, 66*(1), 25-35.

Guo, Q., Sax, D. F., Qian, H., & Early, R. (2012). Latitudinal shifts of introduced species: possible causes and implications. *Biological Invasions, 14*, 547-556.

Hawkins, B. A., & Porter, E. E. (2003). Relative influences of current and historical factors on mammal and bird diversity patterns in deglaciated North America. *Global Ecology and Biogeography, 12*, 475–481.

Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J.-F., Kaufman, D. M., *et al*. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology, 84*, 3105-3117.

Hayes, K. R., & Barry, S. C. (2008). Are there consistent predictors of invasion success? *Biological Invasions, 10*, 483-506.

Higgins, P. J. (1999). *Handbook of Australian, New Zealand and Antarctic Birds. Vol 4: Parrots to Dollarbirds* (Vol. 4: Parrots to Dollarbirds). Melbourne: Oxford Univeristy Press.

Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G., & Jarvis, A. (2005). Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology, 25*, 1965-1978.

Hijmans, R. J. (2015). raster: Geographic data analysis and modeling. R package version 2.3-24. http://CRAN.R-project.org/package=raster

Hulme, P. E. (2009). Trade, transport and trouble: managing invasive species pathways in an era of globalization *Journal of Applied Ecology, 46*, 10-18.

Hulme, P. E., & Weser, C. (2011). Mixed messages from multiple information sources in invasive species: a case of too much of a good thing? *Diversity and Distributions, 17*, 1152-1160.

Hurlbert, A. H., & White, E. P. (2005). Disparity between range map and survey-based analyses of species richness: patterns, processes and implications. *Ecology Letters, 8*, 319–327.

IUCN (2010) IUCN Red List of Threatened Species. Version 2010.1. IUCN, Gland, Switzerland. Available at: www.iucnredlist.org, downloaded August 2010.

Jansson, R. (2003). Global patterns in endemism explained by past climatic change. *Proceedings of the Royal Society of London B: Biological Sciences, 270*(1515), 583-590.

Jenkins, P. T. (1996). Free trade and exotic species introductions. *Conservation Biology, 10*(1), 300-302.

Jeschke, J. M., & Strayer, D. L. (2005). Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences, 102*(20), 7198-7202.

Jeschke, J. M., & Strayer, D. L. (2006). Determinants of vertebrate invasion success in Europe and North America. *Global Change Biology, 12*, 1608-1619.

Jeschke, J. M., Bacher, S., Blackburn, T. M., Dick, J. T. A., Essl, F., Evans, T., *et al*. (2014). Defining the impact of non-native species. *Conservation Biology, 28*(5), 1188-1194.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature, 491*, 444-448.

Johnston, R. F., & Garrett, K. L. (1994). Population Trends of Introduced Birds in Western North America. *Studies in Avian Biology, 15*, 221-231.

Jones, C. (1996). Bird introductions to Mauritius: status and relationships with native birds. In J. Holmes & J. Simons (Eds.), *The Introduction and Naturalisation of Birds* (pp. 113-123). London: HMSO.

Kaufman, D. M. (1995). Diversity if New World mammals: universality of the latitudinal gradient of species and bauplans. *Journal of Mammalogy, 76*, 322-334.

Keng, W. L., & Hails, C. J. (2007). An annotated checklist of the birds of Singapore. *The Raffles Bulletin of Zoology, Suppl. 15*, 1-179.

Kerr, J. T., & Packer, L. (1997). Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. *Nature, 385*, 252–254.

Kerr, J. T., Southwood, T. R. E., & Cihlar, J. (2001). Remotely sensed habitat diversity predicts butterfly richness and community similarity in Canada. *Proceedings of the National Academy of Sciences, USA, 98*, 11365–11370.

Kissling, W. D., & Carl, G. (2007). Spatial autocorrelation and the selection of simultaneous autoregressive models. *Global Ecology and Biogeography, 17*(1), 59-71.

Kolar, C. S., & Lodge, D. M. (2001). Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution, 16*(4), 199-204.

Kumschick, S., & Nentwig, W. (2010). Some alien birds have as severe an impact as the most effectual alien mammals in Europe. *Biological Conservation, 143*, 2757-2762.

Legendre, L., & Legendre, P. (1998). *Numerical Ecology* (2nd ed.). Amsterdam, Netherlands: Elsevier Science.

Legendre, P., Dale, M. R. T., Fortin, M.-J., Gurevitch, J., Hohn, M., & Myers, D. (2002). The consequences of spatial structure for the design and analysis of ecological field experiments. *Ecography, 25*, 601–615.

Leprieur, F., Beauchard, O., Blanchet, O., Oberdorff, T., & Brosse, S. (2008). Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS Biology, 6*, 404–410.

Letcher, A. J., & Harvey, P. H. (1994). Variation in geographical range size among mammals of the Palearctic. *American Naturalist, 144*, 30-42.

Lever, C. (1979). *The Naturalized Animals of the British Isles*. London: Granada.

Lever, C. (1992). *They dined on eland: the story of the acclimatisation societies.* London: Quiller Press Ltd.

Lever, C. (2005). *Naturalised Birds of the World*. London: T & A D Poyser.

Li, Y., Liu, X., Li, X., Petitpierre, B., & Guisan, A. (2014). Residence time, expansion toward the equator in the invaded range and native range size matter to climatic niche shifts in non-native species. *Global Ecology and Biogeography, 23*, 1094-1104.

Liversidge, R. (1962). The spread of the European Starling in the Eastern Cape. *The Ostrich, 33*(3), 13-16.

Lockwood, J. L. (1999). Using taxonomy to predict success among introduced avifauna: Relative importance of transport and establishment. *Conservation Biology, 13*(3), 560-567.

Lockwood, J. L., Brooks, T. M., & McKinney, M. L. (2000). Taxonomic homogenization of the global avifauna. *Animal Conservation, 3*, 27-35.

Lockwood, J. L., Cassey, P., & Blackburn, T. (2005). The role of propagule pressure in explaining species invasions. *Trends In Ecology & Evolution, 20*(5), 223-228.

Lockwood, J. L., Cassey, P., & Blackburn, T. M. (2009). The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions, 15*(5), 904-910.

Long, J. L. (1981). *Introduced birds of the world*. Newton Abbot, England: David & Charles.

Long, J. L., & Mawson, P. R. (1991). Species of introduced birds in mediterranean Australia. In R. Groves & F. di Castri (Eds.), *Biogeography of Mediterranean Invasions*: Cambridge University Press.

Lonsdale, W. M. (1999). Global patterns of plant invasions and the concept of invasibility. *Ecology, 80*, 1522-1536.

Lovette, I. J., McCleery, B. V., Talaba, A. L., & Rubenstein, D. R. (2008). A complete species-level molecular phylogeny for the "Eurasian" starlings (Sturnidae: *Sturnus*, *Acridotheres*, and allies): Recent diversification in a highly social and dispersive avian group. *Molecular Phylogenetics and Evolution, 47*, 251-260.

MacArthur, R. H. (1972). *Geographic ecology: patterns in the distribution of species*. New York: Harper & Row.

Macartney, G. (1773). *An Account of Ireland in 1773 by a Late Chief Secretary of that Kingdom*. p. 55.; cited in Kenny, K. (2006). *Ireland and the British Empire*. Oxford University Press. p. 72, fn.22

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M., & Bazzaz, F. A. (2000). Biotic invasions: Causes, epidemiology, global consequences, and control. *Ecological Applications, 10*(3), 689-710.

Mahoney, P. J., Beard, K. H., Durso, A. M., Tallian, A. G., Long, A. L., Kindermann, R. J., *et al*. (2015). Introduction effort, climate matching and species traits as predictors of global establishment success in non-native reptiles. *Diversity and Distributions, 21*, 64-74.

Marshall, P. J. (1996). *The Cambridge illustrated history of the British Empire*. Cambridge, UK: Cambridge University Press.

McDowall, R. M. (1994). *Gamekeepers for the nation: the story of New Zealand's acclimatisation societies 1861-1990*. Christchurch, New Zealand: Canterbury University Press.

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution, 14*, 450-453.

Nelson, A. (2008). Estimated travel time to the nearest city of 50,000 or more people in year 2000. Retrieved 10/09/2013, from Global Environment Monitoring Unit - Joint Research Centre of the European Commission, Ispra Italy: http://bioval.jrc.ec.europa.eu/products/gam/

Nentwig, W. (2007). Pathways in animal invasions. In W. Nentwig (Ed.), *Biological Invasions* (Vol. 193, pp. 11-27). Berlin: Springer.

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., *et al*. (2015). Global effects of land use on local terrestrial biodiversity. *Nature, 520*(7545), 45-50.

Olson, D. M., Dinerstein, E., Wikramanayake, E. D., Burgess, N. D., Powell, G. V. N., Underwood, E. C., *et al*. (2001). Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience, 51*, 933-938.

Olson, V. A., Davies, R. G., Orme, C. D., Thomas, G. H., Meiri, S., Blackburn, T. M., *et al*. (2009). Global biogeography and ecology of body size in birds. *Ecology Letters, 12*(3), 249-259.

Orme, C. D. L., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V., *et al*. (2005). Global biodiversity hotspots of species richness, threat and endemism are not congruent. *Nature, 436*, 1016-1019.

Orme, C. D. L., Davies, R. G., Olson, V. A., Thomas, G. H., Ding, T.-S., Rasmussen, P. C., *et al*. (2006). Global patterns of geographic range size in birds. *PLoS Biology, 4*(7), 1276-1283.

Orme, C.D.L., Freckleton, R., Thomas, G., Petzoldt, T., Fritz, S., Isaac, N., & Pearse, W. (2013). caper: Comparative Analyses of Phylogenetics and Evolution in R. R package version 0.5.2. http://CRAN.R-project.org/package=caper

Parker, I. M., Simberloff, D., Lonsdale, W. M., Goodell, K., Wonham, M., Kareiva, P. M., *et al*. (1999). Impact: towards a framework for understanding the ecological effects of invaders. *Biological Invasions, 1*, 3-19.

Pebesma, E.J., & Bivand, R.S. (2005). Classes and methods for spatial data in R. R News 5 (2), http://cran.r-project.org/doc/Rnews/

Peters, R. H. (1983). *The ecological implications of body size*. New York: Cambridge University Press.

Pianka, E. R. (1966). Latitudinal gradients in species diversity: a review of the concepts. *The American Naturalist, 100*, 33-46.

Pianka, E. R. (1989). Latitudinal gradients in species diversity. *Trends in Ecology & Evolution, 4*, 223.

Pimentel, D., Lach, L., Zuniga, R., & Morrison, D. (2000). Environmental and economic costs of nonindigenous species in the United States. *Bioscience, 50*(1), 53-65.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., *et al*. (2001). Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environment, 84*, 1-20.

Pither, J. (2003). Climate tolerance and interspecific variation in geographic range size. *Proceedings of the Royal Society, London, B, 270*, 475-481.

Pithon, J. A., & Dytham, C. (2002). Distribution and population development of introduced Ring-necked Parakeets *Psittacula krameri* in Britain between 1983 and 1998. *Bird Study, 49*, 110-117.

Proçhes, S., Wilson, J. R. U., Richardson, D. M., & Rejmánek, M. (2012). Native and naturalized range size in Pinus: relative importance of biogeography, introduction effort and species traits. *Global Ecology and Biogeography, 21*, 513-523.

Pyšek, P., Richardson, D. M., Pergl, J., Jarošík, V., Sixtova, Z., & Weber, E. (2008). Geographical and taxonomic biases in invasion ecology. *Trends in Ecology & Evolution, 23*(5), 237-244.

Pyšek, P., Křivánek, M., & Jarošík, V. (2009a). Planting intensity, residence time, and species traits determine invasion success of alien woody species. *Ecology, 90*, 2734-2744.

Pyšek, P., Jarošík, V., Pergl, J., Randall, R., Chytrý, M., Kühn, I., *et al*. (2009b). The global invasion success of Central European plants is related to distribution characteristics in their native range and species traits. *Diversity and Distributions, 15*, 891-903.

Pyšek, P., Jarošík, V., Hulme, P. E., Kühn, I., Wild, J., Arianoutsou, M., *et al*. (2010). Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Science, 107*(27), 12157-12162.

R Core Team (2014). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Rabosky, D. L., & Hurlbert, A. H. (2015). Species Richness at Continental Scales Is Dominated by Ecological Limits. *American Naturalist, 185*, 572-583.

Rahbek, C., & Graves, G. R. (2001). Multiscale assessment of patterns of avian species richness. *Proceedings of the National Academy of Sciences, USA, 98*, 4534–4539.

Rapoport, E. H. (1982). *Areography: geographical strategies of species.* Oxford: Pergamon.

Ricciardi, A., & Rasmussen, P. C. (1998). Predicting the identity and impact of future biological invaders: a priority ofr aquatic resource management. *Canadian Journal of Fisheries and Aquatic Sciences, 55*, 1759-1765.

Rice, W. R. (1989). Analyzing tables of statistical tests. *Evolution, 43*, 223-225.

Richardson, D. M., & Pyšek, P. (2012). Naturalization of introduced plants: ecological drivers of biogeographical patterns. *New Phytologist, 196*(2), 383-396.

Richerson, P. J., & Lum, K. (1980). Patterns of plant species diversity in California: relation to weather and topography. *American Naturalist, 116*, 504–536.

Rohde, K. (1992). Latitudinal gradients in species diversity: The search for the primary cause. *Oikos, 65*(3), 514-527.

Rohde, K., Heap, M., & Heap, D. (1993). Rapoport's rule does not apply to marine teleosts and cannot explain latitudinal gradients in species richness. *American Naturalist, 142*(1-16).

Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge, UK: Cambridge University Press.

Rosenzweig, M. L. (2001). Loss of speciation rate will impoverish future diversity. *Proceedings of the National Academy of Science, 98*(10), 5404-5410.

Roser, M. (2014). GDP Growth Over the Last Centuries. *Published online at OurWorldInData.org.* Retrieved from: http://ourworldindata.org/data/growth-and-distribution-of-prosperity/gdp-growth-over-the-last-centuries/ (18.03.15)

Roy, K., Jablonski, D., & Valentine, J. W. (1994). Eastern Pacific molluscan provinces and latitudinal diversity gradient: no evidence for Rapoport's Rule. *Proceedings of the National Academy of Sciences, USA, 91*, 8871-8874.

Sakai, A. K., Allendorf, F. W., Holt, J. S., Lodge, D. M., Molofsky, J., With, K. A., *et al*. (2001). The population biology of invasive species. *Annual Review of Ecology, Evolution and Systematics, 32*, 305-332.

Sangster, G., Collinson, J. M., Crochet, P.-A., Knox, A. G., Parkin, D. T., & Votier, S. C. (2013). Taxonomic recommendations for Western Palearctic birds: ninth report. *Ibis, 155*, 898-907.

Sax, D. F. (2001). Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *Journal of Biogeography, 28*, 139-150.

Sax, D. F., Gaines, S. D., & Stachowicz, J. J. (2005). *Exotic species: a source of insight into ecology, evolution, and biogeography*. Sunderland, Massachussets: Academic Press.

Sekercioglu, C. H., Daily, G. C., & Ehrlich, P. R. (2004). Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences, USA, 101*, 18042-18047.

Sekercioglu, C. H. (2011). Functional extinctions of bird pollinators cause plant declines. *Science, 331*, 1019-1020.

Sharma, G. P., Esler, K. J., & Blignaut, J. N. (2010). Determining the relationship between invasive alien species density and a country's socio-economic status. *South African Journal of Science, 106*(3/4), 1-6.

Shea, K., & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution, 17*, 170-176.

Silva, T., Reino, L. M., & Borralho, R. (2002). A model for range expansion of an introduced species: the common waxbill *Estrilda astrild* in Portugal. *Diversity and Distributions, 8*, 319-326.

Simberloff, D., & Stiling, P. (1996). Risks of species introduced for biological control. *Biological Conservation, 78*, 185-192.

Simberloff, D. (2009). The role of propagule pressure in biological invasions. *The Annual Review of Ecology, Evolution, and Systematics, 40*, 81-102.

Simberloff, D., & Rejmanek, M. (2011). *Encyclopedia of Biological Invasions*. Berkeley: University of California Press.

Simberloff, D., Martin, J.-L., Genovesi, P., Maris, V., Wardle, D. A., Aronson, J., *et al*. (2013). Impacts of biological invasions: What's what and the way forward. *Trends in Ecology & Evolution, 28*(1), 58-66.

Smith, F. D., May, R. M., & Harvey, P. H. (1994). Geographical ranges of Australian mammals. *Journal of Animal Ecology*, 441-450.

Sol, D., & Lefebvre, L. (2000). Behavioural Flexibility Predicts Invasion Success in Birds Introduced to New Zealand. *Oikos, 90*(3), 599-605.

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P., & Lefebvre, L. (2005a). Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences, USA, 102*(15), 5460-5465.

Sol, D., Blackburn, T. M., Cassey, P., Duncan, R. P., & Clavell, J. (2005b). The ecology and impact of non-indigenous birds. . In J. del Hoyo, A. Elliott & J. Sargatal (Eds.), *Handbook of the birds of the world, volume 10, cuckoo-shrikes to thrushes* (pp. 13-35). Cambridge: Lynx Ediçions and BirdLife International.

Sol, D. (2007). Do successful invaders exist? Pre-adaptations to novel environments in terrestrial vertebrates. In W. Nentwig (Ed.), *Biological invasions* (pp. 127-144). Berlin: Springer-Verlag.

Sol, D., Maspons, J., Vall-llosera, M., Bartomeus, I., García-Peña, G. E., Piñol, J., *et al*. (2012). Unraveling the Life History of Successful Invaders. *Science, 337*(6094), 580-583.

Spear, D., Foxcroft, L. C., Bezuidenhout, H., & McGeoch, M. A. (2013). Human population density explains alien species richness in protected areas. *Biological Conservation, 159*, 137-147.

Stevens, G. C. (1989). The latitudinal gradient in geographical range: how so many species co-exist in the tropics. *American Naturalist, 133*, 240-256.

Stevens, G. C. (1996). Extending Rapoport's rule to Pacific marine fishes. *Journal of Biogeography, 23*, 149-154.

Stohlgren, T. J., Barnett, D., Flather, C., Fuller, P., Peterjohn, B., Kartesz, J., *et al*. (2006). Species richness and patterns of invasion in plants, birds, and fishes in the United States. *Biological Invasions, 8*, 427-447.

Su, S., Cassey, P., & Blackburn, T. M. (2014). Patterns of non-randomness in the composition and characteristics of the Taiwanese bird trade. *Biological Invasions, 16*(12), 2563-2575.

Taylor, B. W., & Irwin, R. E. (2004). Linking economic activities to the distribution of exotic plants. *Proceedings of the National Academy of Sciences, USA, 101*, 17725–17730.

Thomas, C. D. (2013). The anthropocene could raise biological diversity. *Nature, 502*(7).

Thomson, G. M. (1922). *The naturalization of plants and animals in New Zealand*. Cambridge, UK: Cambridge University Press.

Turner, J. R. G., Lennon, J. J., & Lawrenson, J. A. (1988). British bird species distributions and the energy theory. *Nature, 335*, 539–541.

Uller, T., & Leimu, R. (2011). Founder events predict changes in genetic diversity during human-mediated range expansions. *Global Change Biology, 17*, 3478-3485.

van Wilgen, N. J., & Richardson, D. M. (2012). The roles of climate, phylogenetic relatedness, introduction effort, and reproductive traits in the establishment of non-native reptiles and amphibians. *Conservation Biology, 26*(2), 267-277.

Veit, R. R., & Lewis, M. A. (1996). Dispersal, population growth, and the Allee effect: dynamics of the house finch invasion of eastern North America. *American Naturalist, 148*, 255-274.

Veltman, C. J., Nee, S., & Crawley, M. J. (1996). Correlates of introduction success in exotic New Zealand birds. *The American Naturalist, 147*(4), 542-557.

Vilà, M., & Pujadas, J. (2001). Land-use and socio-economic correlates of plant invasions in European and North African countries. *Biological Conservation, 100*, 397–401.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmanek, M., & Westbrooks, R. (1997). Introduced species: a significant component of human-caused global change. *New Zealand Journal of Ecology, 21*(1), 1-16.

von Humboldt, A. (1850). *Views of nature: or contemplations on the sublime phenomena of creation; with scientific illustrations* (E. C. Otte & H. G. Bohn, Trans.). London: Henry G. Bohn.

Waide, R. B., Willig, M. R., Steiner, C. F., Mittelbach, G. C., Gough, L., Dodson, S. I., *et al*. (1999). The relationship between net primary productivity and species richness. *Annual Review of Ecology and Systematics, 30*, 257–300.

Waldron, A. (2007). Null models of geographic range size evolution reaffirm its heritability. *The American Naturalist, 170*, 221-231.

Walpole, M., Almond, R. E. A., Besançon, C., Butchart, S. H. M., Campbell-Lendrum, D., Carr, G. M., *et al*. (2009). Tracking progress toward the 2010 biodiversity target and beyond. *Science, 325*, 1503-1504.

Wernham, C. V., Toms, M. P., Marchant, J. H., Clark, J. A., Siriwardena, G. M., & Baillie, S. R. (Eds.). (2002). *The Migration Atlas: movements of the birds of Britain and Ireland*. London: T. & A.D. Poyser.

West, B., & Zhou, B.-X. (1989). Did chickens go north? New evidence for domestication. *World's Poultry Science Journal, 45*(3), 205-218.

Westphal, M. I., Browne, M., MacKinnon, K., & I, N. (2008). The link between international trade and the global distribution of invasive alien species. *Biological Invasions, 10*, 391-398.

Whittaker, R. J., Willis, K. J., & Field, R. (2003). Climate-energetic explanations of diversity: a macroscopic perspective. In T. M. Blackburn & K. J. Gaston (Eds.), *Macroecology: concepts and consequences* (pp. 107-129.). Oxford: Blackwell Science.

Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*(9), 639-644.

WCS (Wildlife Conservation Society), and CIESIN (Center for International Earth Science Information Network), Columbia University. (2005). Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Footprint Dataset (Geographic). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). http://dx.doi.org/10.7927/H4M61H5F. Accessed 26/04/2013.

Williams, F. E., Eschen, R., Harris, A., Djeddour, D. H., Pratt, C. F., Shaw, R. S., *et al*. (2010). *The Economic Cost of Invasive Non-Native Species on Great Britain*: CABI.

Williamson, M. (1996). *Biological Invasions*. London: Chapman & Hall.

Williamson, M., Dehnen-Schmutz, K., Kühn, I., Hill, M., Klotz, S., Milbau, A., *et al*. (2009). The distribution of range sizes of native and alien plants in four European countries and the effects of residence time. *Diversity and Distributions*(15), 155-166.

Wilson, J. R. U., Richardson, D. M., Rouget, M., Proches, S., Amis, M. A., Henderson, L. S., *et al*. (2007). Residence time and potential range: crucial considerations in modelling plant invasions. *Diversity and Distributions, 13*, 11-22.

Yalden, D. W. (1999). *History of British Mammals*. London: T. & A.D. Poyser.

Yeh, P. J., & Price, T. D. (2004). Adaptive Phenotypic Plasticity and the Successful Colonization of a Novel Environment. *The American Naturalist, 164*(4), 531-542.

Zenni, R. D., & Nuñez, M. A. (2013). The elephant in the room: the role of failed invasions in understanding invasion biology. *Oikos, 122*, 801-815.

Appendix A. The guidelines given to each member of the team for them to consult during the data entry stage. This helped to ensure that all records were entered in the same format and the correct information was recorded in the appropriate place.

GAVIA DATABASE GUIDELINES

RecordID: A unique number for that particular record. Each individual map also carries this number.

SpeciesID: A unique number for each individual species.

Binomial: The binomial of that species, as per the IUCN Red List of Threatened Species.

Common_name: The common name of that species, as per the IUCN Red List of Threatened Species.

CountryName: The name of the country in which that record occurs.

AreaName1: The first sublevel down from country, e.g. region/state, in which that record occurs.

AreaName2: The second sublevel down from country, e.g. subregion/city, in which that record occurs.

LocationDescription: A specific description of where the record occurs, if it cannot be selected from AreaName 1 or 2.

Realm: The biogeographical realm in which that record occurs, as per the definitions from Olson *et al*. (2001).

Island: Whether the record occurs on an island or not.

LandType: The type of land that the records occurs on, e.g. mainland, continental island or oceanic island.

IntroducedDate: The date that the species was first introduced (if known), written exactly as found in the reference, e.g. could be 'late 17th century'.

IntroducedDateGrouped: The date that the species was first introduced (if known), written as a number, e.g. 'late 17th century' would become 1690 (see additional guidelines if uncertain).

Mapping_date: The date that the map for that particular record represents. For example, the introduced date will stay the same for all individual records from that reference, but as the species spreads over time, the mapped date will change.

ReferenceDate: Rarely used. If there is no date of introduction recorded, but the reference referred to is a significantly 'old' date, then this is recorded so that it is at least an indication of how long the species has been present.

StatusCat: The status of the species in that record, e.g. established, died out etc.

IntroMethod: How the species was introduced. For example it was released, or it escaped etc.

IntroPurpose: Why the species was introduced. For example it escaped from a zoo, or was released for hunting purposes.

GISFileName: Whether that record has been Mapped or Not Mapped. In this case Not Mapped means that it will never be mapped, as the data is deemed too broad scale.

TaxonomicNotes: Any relevant taxonomic information relevant to the record.

Notes: Relevant notes relating to the record, e.g. it might specify numbers of birds released, or specific paths of species spread etc.

Reference: Where the information was found, this links to the GAVIA Endnote library.

CompilerFullName: Who was responsible for compiling that record in the database (not who created the final map).

Appendix B. A list of all the countries and administrative areas used in GAVIA (as downloaded from the GADM database of Global Administrative Areas www.gadm.org), together with the number of records from each country and the number of species to which these records relate, sorted highest to lowest by number of records.

Country	Num of Records	Num of Species
United States	6159	396
New Zealand	2464	142
Australia	2370	147
United Kingdom	1631	161
Mauritius	836	72
South Africa	735	83
Spain	678	207
French Polynesia	528	71
Reunion	426	44
United Arab Emirates	426	94
Puerto Rico	421	68
Canada	412	47
Singapore	383	82
Hong Kong	376	135
Japan	366	68
Indonesia	341	42
Saint Helena	321	60
Fiji Island	288	30
Seychelles	272	29
France	242	76
Portugal	239	46
Italy	230	63
Germany	206	77
Malaysia	188	28
Taiwan, Province of China	181	75
Philippines	171	24
Chile	154	21
Bermuda	153	26
Netherlands	146	36
Israel	141	34
Bahamas	132	22
Virgin Islands, U.S.	131	34
Jamaica	127	30
Saudi Arabia	125	30
Barbados	118	35
Belgium	115	29
Tanzania, United Republic of	110	16
India	107	23
Cuba	106	26
Cape Verde	104	14

Kuwait	103	39
Mexico	103	29
Oman	102	34
Bahrain	98	29
Dominican Republic	96	22
Cayman Islands	95	23
Argentina	90	23
Brazil	90	19
Martinique	87	22
Kenya	85	9
Ecuador	84	15
Netherlands Antilles	84	25
Tonga	82	9
Comoros	81	14
Austria	78	27
Switzerland	78	46
Guadeloupe	75	19
Samoa	75	6
Ireland	70	22
Sweden	68	21
British Indian Ocean Territory	65	12
New Caledonia	65	11
Norfolk Island	64	16
Trinidad and Tobago	64	30
Vanuatu	63	13
Madagascar	60	14
Yemen	59	8
Egypt	57	11
Guam	57	15
Ukraine	57	22
Palau	55	8
Northern Mariana Islands	54	11
Norway	54	22
Cocos (Keeling) Islands	53	9
Venezuela	51	13
Czech Republic	50	20
Qatar	49	21
China	48	18
Thailand	48	16
Christmas Island	47	7
Falkland Islands (Malvinas)	46	6
Colombia	44	20
Haiti	44	12
Mozambique	44	6
Denmark	42	14

Uruguay	42	8
Turkey	41	10
Cook Islands	40	5
Finland	40	14
Sao Tome and Principe	39	11
Antigua and Barbuda	38	10
Saint Vincent and the Grenadines	37	8
French Southern Territories	36	8
Papua New Guinea	36	8
American Samoa	35	5
Namibia	35	7
Solomon Islands	33	3
Marshall Islands	32	7
Micronesia, Federated States of	31	7
Cyprus	29	13
Gibraltar	29	12
Panama	29	9
Botswana	28	12
Russian Federation	28	10
Algeria	27	9
Peru	26	9
Zimbabwe	26	8
Poland	25	9
Croatia	24	11
Jordan	24	10
Iran, Islamic Republic of	23	10
Greece	22	8
Mayotte	21	12
Saint Kitts and Nevis	21	7
Sri Lanka	21	8
Estonia	20	13
Kiribati	20	7
Iceland	19	5
Latvia	18	10
United States Minor Outlying Island	18	9
Vietnam	18	6
British Virgin Islands	17	10
Dominica	17	6
Lebanon	17	9
Zambia	17	3
Aruba	16	8
Bolivia	16	3
Iraq	16	3
Maldives	16	5
Myanmar	16	4

Somalia	16	5
Swaziland	16	3
Brunei Darussalam	15	6
Grenada	15	6
Hungary	15	9
Turks and Caicos Islands	15	10
Faroe Islands	14	6
Luxembourg	14	6
Bulgaria	13	9
Costa Rica	13	4
Morocco	13	4
Paraguay	13	3
Slovenia	13	7
Saint Lucia	12	4
Sudan	12	2
Djibouti	11	3
Pakistan	11	6
Belize	10	4
Lesotho	10	3
Lithuania	10	4
Malta	10	6
Mauritania	10	3
Romania	10	7
South Georgia and the South Sandwich Islands	10	4
Syrian Arab Republic	10	6
Wallis and Futuna	10	4
Belarus	9	5
Guatemala	9	4
Kazakhstan	9	5
Slovakia	9	5
Eritrea	8	3
Macao	8	1
Montserrat	8	3
Nicaragua	8	2
El Salvador	7	3
Equatorial Guinea	7	5
French Guiana	7	2
Honduras	7	4
Lao, People's Democratic Republic	7	4
Liechenstein	7	4
Palestinian Territory, Occupied	7	5
Senegal	7	3
Afghanistan	6	4
Andorra	6	4
Guyana	6	3

Korea, Democratic People's Republic of	6	4
Korea, Republic of	6	3
Tunisia	6	4
Uganda	6	3
Åland Islands	5	3
Anguilla Island	5	4
Azerbaijan	5	5
Georgia	5	4
Greenland	5	2
Moldova, Republic of	5	3
Monaco	5	4
Niger	5	3
Serbia	5	3
Angola	4	3
Bhutan	4	3
Cambodia	4	3
Malawi	4	1
Nauru	4	2
Suriname	4	2
Uzbekistan	4	2
Albania	3	2
Bangladesh	3	2
Bosnia and Herzegovina	3	2
Chad	3	2
Congo, The Democratic Republic of the	3	1
Côte D'Ivoire	3	2
Gambia	3	2
Liberia	3	2
Macedonia, The Former Yugoslav Republic of	3	2
Mali	3	2
Montenegro	3	2
Nigeria	3	2
Saint Pierre and Miquelon	3	3
Cameroon	2	1
Ethiopia	2	2
Guinea	2	1
Guinea-Bissau	2	2
Kyrgyzstan	2	2
Mongolia	2	2
Nepal	2	2
San Marino	2	2
Sierra Leone	2	1
Antarctica	1	1
Armenia	1	1
Benin	1	1

Burkina Faso	1	1
Congo, Republic of	1	1
Ghana	1	1
Libyan Arab Jamahiriya	1	1
Pitcairn Islands	1	1
Tajikistan	1	1
Togo	1	1
Tokelau	1	1
Turkmenistan	1	1
Western Sahara	1	1
Burundi	0	0
Central African Republic	0	0
Gabon	0	0
Niue	0	0
Rwanda	0	0
Timor-Leste	0	0
Tuvalu	0	0

Appendix C. The mapping guidelines given to each member of the team for use during the mapping stage of the project. They provided detailed instructions on how distribution maps were to be created and saved, so as to ensure consistency amongst the maps created by different team members.

GAVIA MAPPING GUIDELINES

Initial set up:

- Make a folder on your desktop called 'GAVIA Mapping Desktop [Your initials]' e.g. GAVIA Mapping Desktop ED.
- Copy the following layers from T:\GAVIA Project\GAVIA Maps\Basic layers into your new folder:
    - admin_GADM
    - Country_Outline_GADM
    - cities1m_vmap_Behrmann

MAPPING

1. Select one of your species from the spreadsheet 'MAP MASTER SHEET' and make a note of the SpeciesID.
2. Make a new folder within 'GAVIA Mapping Desktop' and call it the Latin name of whichever species you are mapping.
3. Open the GAVIA database and select the query QrySpeciesReport_[your initials]. Input the SpeciesID number for your chosen species and run the query.
4. Make a note of which records you will map and which you won't (see notes below for rules on this), and then go back to the Distribution table (first checking to see whether anyone else is currently editing it) and change the relevant 'Mapped Date' and in the GISFileName column write Mapped or Not mapped. If there is no date relating to the species at all then enter the reference date into the mapped date column.
5. Rerun the query so that it includes this new information and then copy all of the data from the query and paste it into a new empty spreadsheet. Save the spreadsheet in your newly created species folder on your desktop with the name '[Genus species] attribute'.
6. Run a search in the folder T:\GAVIA Project\GAVIA Maps\ALL Additional DB Maps FINAL to identify whether any maps have previously been created for your species.
7. Check the folder T:\GAVIA Project\GAVIA Maps\Ellie edits of MP maps to see if Mark Parnell has previously created a map for the species.
8. In your '[Genus species] attribute' spreadsheet check the column GISFileName to see if there is a hard copy of the map in the map box.
9. Open ArcGIS and add the 3 layers listed above (cities can be turned off until needed), and any of the maps previously created for the species.
10. Create your map in a way that is appropriate. This can be either by drawing a polygon, selecting a region or island from a base layer, or by making a 10km buffer around a point. Alternatively if different distribution records are identical then you can simply make a copy of that shapefile and edit the filename and attribute table accordingly.
11. If you are using a hard copy map from the map box and it is very detailed then it can be georeferenced (i.e. you scan in the map and load it up behind your own GIS map so that you can trace it).
12. It is very important to name your shapefiles carefully and consistently. 'Genus_species_[RecordID]_1' is a good place to start. Then change the end of the filename to '_clip' or '_merge' etc. depending what you've just done to it.

13. Each distribution record must relate to a polygon. A single distribution record can have more than one polygon linked to it, but a single polygon can't have more than one distribution record.
14. *Smooth* any polygons which you drew by hand (do not smooth any which were selected or clipped to a region or country).
15. If necessary *Clip* any polygons to the country layer.
16. *Merge* all of your different shapefiles together including those created from the other databases (NBN, SABAP etc.).
17. *Dissolve* all of the different polygons together so you have one line for each distribution record and so that the attribute table has only three fields:

FID	Shape	Id

18. VERY IMPORTANT – right click on your shapefile and select *Zoom to Layer* so that you can see the full extent of your map and make sure that you haven't accidentally selected any random countries.
19. Click on *Start Editing* and in the *Id* field copy and paste the related RecordID from your spreadsheet. Click *Stop Editing* and save edits. If you are mapping a species which has many distribution records then add *Id* numbers as you go along to avoid confusion.
20. Go back to your '[Genus species] attribute' and click on the top left hand corner so that all the cells are selected, then right click and uncheck the 'wrap text' tick box. Then double click on one of the lines dividing the columns to that all the cells expand to fit their contents. Save the spreadsheet.
21. Go back to ArcGIS and click on *Add Data* and select your excel file '[Genus species] attribute'.
22. Right click on your finished layer and select *Joins and Relates*, then *Join*…
23. For 1. choose Id, for 2. the excel file and for 3. RecordID. Then click OK.
24. Open the attribute table of your finished layer to check that the attribute data has joined correctly and that the right information relates to the appropriate polygon.
25. If everything is as it should be then right click on the finished layer and select *Data – Export data*… Ensure that *Export All Features* is selected and then save it in your species folder on your desktop as 'GAVIA_Genus_species_EXPORT'
26. Copy and Paste the entire species folder from your desktop into T:\GAVIA Project\GAVIA Maps_Not final.
27. Then using Arc Catalog copy and paste your 'GAVIA_Genus_species_EXPORT' shapefile into T:\GAVIA Project\GAVIA Maps_FINAL and rename it 'GAVIA_Genus_species'.
28. Make a note of how many distribution records you created (not including those 'not mapped') so that you can keep a running tally on the MAP QUOTAS spreadsheet.

SPLITTING

NOTE: Anything changed in the 'Distributions' table of the GAVIA database cannot be undone. By editing records in this way you are essentially editing the raw base data. Therefore I cannot emphasise strongly enough how careful you need to be - please tell me *immediately* if you think you have made an error.

1. Open the GAVIA database and select the query QrySpeciesReport_[your initials]. Input the SpeciesID number for your chosen species and run the query.
2. Copy all of the data from the query and paste it into a new empty spreadsheet. Save the spreadsheet in your newly created species folder on your desktop with the name '[Genus species] attribute'.
3. Filter the Notes column in ascending order and highlight the records which need splitting in yellow. Any record that contains more than one date needs to be split. For example:

Introd date	Grouped date	Mapped date	Notes
1870s	1875		1870s: 90+ birds released in Wellington and Hawke's Bay. 1890: abundant around Hawke's Bay, in Napier and Tutira. 1912: plentiful at Tuparoa 1922: spread up coast from Wellington to Wanganui and New Plymouth

4. Make a note of the RecordID for your first record which needs splitting, then check that no-one else has the Distributions table of the GAVIA database open. If they don't then you can open it.
5. Make sure the Distributions table is sorted by the RecordID and scroll down to your relevant RecordID number.
6. Enter the Mapping Date as the first date on the record (should be the same as the Grouped date).

Introd date	Grouped date	Mapped date	Notes
1870s	1875	**1875**	1870s: 90+ birds released in Wellington and Hawke's Bay. 1890: abundant around Hawke's Bay, in Napier and Tutira. 1912: plentiful at Tuparoa 1922: spread up coast from Wellington to Wanganui and New Plymouth

7. Then open the Office Clipboard and copy the entire record (make sure it has definitely copied).
8. Then delete out the information from the record that relates to any date after the first:

Introd date	Grouped date	Mapped date	Notes
1870s	1875	1875	1870s: 90+ birds released in Wellington and Hawke's Bay. 1890: abundant around Hawke's Bay, in Napier and Tutira. 1912: plentiful at Tuparoa 1922: spread up coast from Wellington to Wanganui and New Plymouth

9. Scroll down to the bottom of the Distribution table and paste in as many copies of the record as you will need in total. So for the example record we would need to paste in three copies.
10. Edit the copies to reflect the expansion of the species over time, **make sure you change the mapping date as well as the notes column**. DO NOT change the status column, leave that the same throughout.

Introd date	Grouped date	Mapped date	Notes
1870s	1875	1875	1870s: 90+ birds released in Wellington and Hawke's Bay. 1890: abundant around Hawke's Bay, in Napier and Tutira. 1912: plentiful at Tuparoa 1922: spread up coast from Wellington to Wanganui and New Plymouth
1870s	1875	**1890**	1870s: 90+ birds released in Wellington and Hawke's Bay. 1890: abundant around Hawke's Bay, in Napier and Tutira. 1912: plentiful at Tuparoa 1922: spread up coast from Wellington to Wanganui and New Plymouth
1870s	1875	**1912**	1870s: 90+ birds released in Wellington and Hawke's Bay. 1890: abundant around Hawke's Bay, in Napier and Tutira. 1912: plentiful at Tuparoa 1922: spread up coast from Wellington to Wanganui and New Plymouth
1870s	1875	**1922**	1870s: 90+ birds released in Wellington and Hawke's Bay. 1890: abundant around Hawke's Bay, in Napier and Tutira. 1912: plentiful at Tuparoa 1922: spread up coast from Wellington to Wanganui and New Plymouth

11. Have a read over your edits and make sure everything is as it should be, then *save* the Distribution table.
12. Now go back to your original spreadsheet and take off the yellow highlighted colour for that record.
13. Move onto the next record that needs splitting and repeat the process.
14. Once you have split all of the records for that species, rerun the original query (as per step 1) and then copy and paste this new set of records into a new spreadsheet (you can delete your original spreadsheet).
15. Filter the Notes column into ascending order so that you can check that everything is split correctly.
16. Map as per usual. When mapping a split record map the earliest date first. Then with the next record make a copy of the first map and expand it to cover the new regions. Continue this for all split records, so that you end up with a series of maps showing the distribution expanding over time.
17. Even if the split records do not provide any additional area data still map each one as it is important to know that the species was still present in that location at a later date. This is the same for if the species has died out or is unsuccessful, still map the region for the date that it died out as we need the record to show that it was in that specific area.

WHEN TO MAP AND WHEN NOT TO MAP

We want to use the most specific information available to us so that we can produce the most precise maps.

1. If the record only goes down to Country level then mark it as ‘Not mapped’ in the GISFileName box. Exceptions to this rule are if the country is particularly small (e.g. Singapore, Hong Kong), if it is a small island (e.g. any of the Pacific islands), or if it is Taiwan (we are mapping all Taiwan records, but if it is to country level then make a note of this in the Notes column of the spreadsheet).
2. If the detail goes down to an administrative district level (e.g. a county in England) then that is okay to make, but for example the states of the US would be at too large a scale. Always ask me if you are not sure.

3. Do not map a record if it is obviously a single escapee record, or just an occasional vagrant.
4. Mark it on the MASTER MAP SHEET spreadsheet if you have not mapped any of the records at all for a particular species. In the column ‘Completely not mapped’ write *Yes* and in the notes box explain why. For example ‘Only detailed to US state level’.

Appendix D. A list of all the species with records in the GAVIA database, where each species has been recorded as being introduced somewhere in the world (n = 972), together with their higher taxonomy. Taxonomy and common names follows that which was agreed upon by the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species and BirdLife International (www.iucnredlist.org, downloaded August 2010). The list is sorted high – low by the number of records for each species in the database.

Order	Family	Binomial	Common name	Num records
Passeriformes	Passeridae	Passer domesticus	House Sparrow	1292
Passeriformes	Sturnidae	Acridotheres tristis	Common Myna	1214
Columbiformes	Columbidae	Columba livia	Rock Pigeon	823
Psittaciformes	Psittacidae	Psittacula krameri	Rose-ringed Parakeet	778
Galliformes	Phasianidae	Phasianus colchicus	Common Pheasant	681
Passeriformes	Sturnidae	Sturnus vulgaris	Common Starling	673
Passeriformes	Estrildidae	Padda oryzivora	Java Sparrow	540
Passeriformes	Corvidae	Corvus splendens	House Crow	479
Passeriformes	Fringillidae	Carduelis carduelis	European Goldfinch	386
Passeriformes	Estrildidae	Estrilda astrild	Common Waxbill	386
Psittaciformes	Psittacidae	Myiopsitta monachus	Monk Parakeet	386
Passeriformes	Alaudidae	Alauda arvensis	Eurasian Skylark	354
Anseriformes	Anatidae	Branta canadensis	Canada Goose	349
Passeriformes	Turdidae	Turdus merula	Eurasian Blackbird	334
Passeriformes	Estrildidae	Amandava amandava	Red Avadavat	326
Passeriformes	Passeridae	Passer montanus	Eurasian Tree Sparrow	309
Galliformes	Phasianidae	Gallus gallus	Red Junglefowl	307
Columbiformes	Columbidae	Stigmatopelia chinensis	Spotted Dove	296
Passeriformes	Pycnonotidae	Pycnonotus jocosus	Red-whiskered Bulbul	283
Passeriformes	Estrildidae	Lonchura punctulata	Scaly-breasted Munia	283
Galliformes	Numididae	Numida meleagris	Helmeted Guineafowl	263
Anseriformes	Anatidae	Oxyura jamaicensis	Ruddy Duck	262
Passeriformes	Pycnonotidae	Pycnonotus cafer	Red-vented Bulbul	252
Passeriformes	Fringillidae	Carduelis chloris	European Greenfinch	234
Galliformes	Odontophoridae	Colinus virginianus	Northern Bobwhite	233
Psittaciformes	Psittacidae	Melopsittacus undulatus	Budgerigar	227
Anseriformes	Anatidae	Cygnus olor	Mute Swan	225
Galliformes	Odontophoridae	Callipepla californica	California Quail	223
Galliformes	Phasianidae	Alectoris chukar	Chukar	218
Columbiformes	Columbidae	Geopelia striata	Zebra Dove	214
Anseriformes	Anatidae	Anas platyrhynchos	Mallard	214
Passeriformes	Turdidae	Turdus philomelos	Song Thrush	210
Columbiformes	Columbidae	Streptopelia decaocto	Eurasian Collared-dove	209
Passeriformes	Estrildidae	Lonchura malacca	Tricoloured Munia	201
Galliformes	Phasianidae	Pavo cristatus	Indian Peafowl	175
Anseriformes	Anatidae	Alopochen aegyptiaca	Egyptian Goose	175
Passeriformes	Ploceidae	Ploceus cucullatus	Village Weaver	170
Anseriformes	Anatidae	Cygnus atratus	Black Swan	165
Galliformes	Phasianidae	Perdix perdix	Grey Partridge	163
Anseriformes	Anatidae	Aix galericulata	Mandarin Duck	150
Passeriformes	Fringillidae	Fringilla coelebs	Eurasian Chaffinch	150
Galliformes	Phasianidae	Alectoris rufa	Red-legged Partridge	149
Passeriformes	Fringillidae	Serinus mozambicus	Yellow-fronted Canary	147
Passeriformes	Ploceidae	Foudia madagascariensis	Madagascar Red Fody	141
Passeriformes	Sturnidae	Acridotheres	Crested Myna	141

		cristatellus		
Passeriformes	Fringillidae	Carpodacus mexicanus	House Finch	133
Galliformes	Phasianidae	Francolinus pondicerianus	Grey Francolin	131
Strigiformes	Strigidae	Athene noctua	Little Owl	126
Passeriformes	Timaliidae	Leiothrix lutea	Red-billed Leiothrix	122
Ciconiiformes	Threskiornithidae	Threskiornis aethiopicus	African Sacred Ibis	119
Ciconiiformes	Ardeidae	Bubulcus ibis	Cattle Egret	117
Galliformes	Phasianidae	Meleagris gallopavo	Wild Turkey	111
Passeriformes	Estrildidae	Lonchura malabarica	White-throated Munia	108
Passeriformes	Emberizidae	Paroaria coronata	Red-crested Cardinal	106
Passeriformes	Estrildidae	Lonchura castaneothorax	Chestnut-breasted Munia	105
Passeriformes	Estrildidae	Estrilda melpoda	Orange-cheeked Waxbill	105
Passeriformes	Timaliidae	Garrulax canorus	Chinese Hwamei	105
Galliformes	Phasianidae	Chrysolophus pictus	Golden Pheasant	104
Passeriformes	Cracticidae	Gymnorhina tibicen	Australian Magpie	103
Passeriformes	Emberizidae	Emberiza citrinella	Yellowhammer	103
Anseriformes	Anatidae	Cairina moschata	Muscovy Duck	102
Passeriformes	Cardinalidae	Cardinalis cardinalis	Northern Cardinal	101
Psittaciformes	Psittacidae	Nandayus nenday	Nanday Parakeet	99
Psittaciformes	Psittacidae	Amazona viridigenalis	Red-crowned Amazon	94
Galliformes	Phasianidae	Francolinus francolinus	Black Francolin	93
Passeriformes	Mimidae	Mimus polyglottos	Northern Mockingbird	93
Passeriformes	Sturnidae	Gracula religiosa	Hill Myna	93
Galliformes	Phasianidae	Syrmaticus reevesii	Reeves's Pheasant	92
Psittaciformes	Psittacidae	Psittacula eupatria	Alexandrine Parakeet	92
Anseriformes	Anatidae	Aix sponsa	Wood Duck	91
Passeriformes	Prunellidae	Prunella modularis	Hedge Accentor	91
Passeriformes	Zosteropidae	Zosterops japonicus	Japanese White-eye	91
Psittaciformes	Psittacidae	Brotogeris versicolurus	White-winged Parakeet	87
Psittaciformes	Psittacidae	Cacatua galerita	Sulphur-crested Cockatoo	86
Passeriformes	Estrildidae	Estrilda troglodytes	Black-rumped Waxbill	84
Psittaciformes	Psittacidae	Agapornis canus	Grey-headed Lovebird	84
Passeriformes	Fringillidae	Carduelis flammea	Common Redpoll	83
Anseriformes	Anatidae	Tadorna ferruginea	Ruddy Shelduck	82
Passeriformes	Corvidae	Corvus frugilegus	Rook	82
Passeriformes	Ploceidae	Euplectes orix	Red Bishop	79
Passeriformes	Icteridae	Molothrus bonariensis	Shiny Cowbird	78
Passeriformes	Ploceidae	Euplectes afer	Yellow-crowned Bishop	78
Coraciiformes	Alcedinidae	Dacelo novaeguineae	Laughing Kookaburra	77
Columbiformes	Columbidae	Stigmatopelia senegalensis	Laughing Dove	77
Passeriformes	Icteridae	Icterus icterus	Venezuelan Troupial	73
Passeriformes	Emberizidae	Sicalis flaveola	Saffron Finch	71
Passeriformes	Sturnidae	Acridotheres fuscus	Jungle Myna	68
Passeriformes	Callaeatidae	Philesturnus carunculatus	Saddleback	67
Anseriformes	Anatidae	Anser indicus	Bar-headed Goose	66
Columbiformes	Columbidae	Streptopelia risoria	Barbary Dove	66
Passeriformes	Estrildidae	Neochmia temporalis	Red-browed Finch	65
Galliformes	Phasianidae	Coturnix ypsilophora	Brown Quail	62

Passeriformes	Icteridae	Icterus pectoralis	Spot-breasted Oriole	62
Strigiformes	Tytonidae	Tyto alba	Barn Owl	61
Psittaciformes	Psittacidae	Aratinga acuticaudata	Blue-crowned Parakeet	60
Psittaciformes	Psittacidae	Aratinga pertinax	Brown-throated Parakeet	59
Galliformes	Phasianidae	Chrysolophus amherstiae	Lady Amherst's Pheasant	59
Galliformes	Phasianidae	Coturnix coturnix	Common Quail	58
Galliformes	Phasianidae	Alectoris barbara	Barbary Partridge	57
Psittaciformes	Psittacidae	Aratinga mitrata	Mitred Parakeet	55
Strigiformes	Strigidae	Bubo bubo	Eurasian Eagle-owl	55
Passeriformes	Sturnidae	Acridotheres ginginianus	Bank Myna	55
Galliformes	Phasianidae	Bonasa umbellus	Ruffed Grouse	55
Galliformes	Phasianidae	Coturnix chinensis	Blue Quail	55
Passeriformes	Sturnidae	Acridotheres javanicus	Javan Myna	54
Anseriformes	Anatidae	Netta rufina	Red-crested Pochard	53
Galliformes	Phasianidae	Alectoris graeca	Rock Partridge	52
Gruiformes	Rallidae	Porphyrio porphyrio	Purple Swamphen	51
Passeriformes	Sylviidae	Cettia diphone	Japanese Bush-warbler	49
Passeriformes	Estrildidae	Uraeginthus bengalus	Red-cheeked Cordonbleu	49
Passeriformes	Fringillidae	Serinus canicollis	Cape Canary	48
Passeriformes	Ploceidae	Ploceus manyar	Streaked Weaver	48
Anseriformes	Anatidae	Branta leucopsis	Barnacle Goose	47
Passeriformes	Ploceidae	Euplectes franciscanus	Orange Bishop	47
Galliformes	Phasianidae	Lophura nycthemera	Silver Pheasant	46
Anseriformes	Anatidae	Anser anser	Greylag Goose	45
Columbiformes	Columbidae	Streptopelia roseogrisea	African Collared-dove	44
Passeriformes	Muscicapidae	Copsychus malabaricus	White-rumped Shama	43
Passeriformes	Viduidae	Vidua macroura	Pin-tailed Whydah	43
Galliformes	Phasianidae	Bambusicola thoracicus	Chinese Bamboo-partridge	42
Passeriformes	Fringillidae	Serinus canaria	Island Canary	42
Passeriformes	Muscicapidae	Erithacus rubecula	European Robin	42
Phoenicopteriformes	Phoenicopteridae	Phoenicopterus chilensis	Chilean Flamingo	41
Passeriformes	Zosteropidae	Zosterops lateralis	Silvereye	41
Galliformes	Odontophoridae	Oreortyx pictus	Mountain Quail	40
Phoenicopteriformes	Phoenicopteridae	Phoenicopterus ruber	American Flamingo	40
Psittaciformes	Psittacidae	Agapornis roseicollis	Rosy-faced Lovebird	40
Columbiformes	Columbidae	Nesoenas picturata	Madagascar Turtle-dove	40
Galliformes	Phasianidae	Francolinus pintadeanus	Chinese Francolin	40
Passeriformes	Paridae	Parus varius	Varied Tit	40
Psittaciformes	Psittacidae	Nymphicus hollandicus	Cockatiel	40
Psittaciformes	Psittacidae	Aratinga erythrogenys	Red-masked Parakeet	39
Anseriformes	Anatidae	Chen caerulescens	Snow Goose	39
Psittaciformes	Psittacidae	Amazona ochrocephala	Yellow-crowned Amazon	39
Psittaciformes	Psittacidae	Forpus passerinus	Green-rumped Parrotlet	39
Psittaciformes	Psittacidae	Psittacula alexandri	Red-breasted Parakeet	39
Galliformes	Phasianidae	Margaroperdix	Madagascar Partridge	38

		madagascariensis		
Psittaciformes	Psittacidae	Agapornis personatus	Yellow-collared Lovebird	38
Passeriformes	Estrildidae	Lonchura atricapilla	Chestnut Munia	37
Passeriformes	Emberizidae	Sicalis luteola	Grassland Yellow-finch	37
Galliformes	Odontophoridae	Callipepla gambelii	Gambel's Quail	37
Columbiformes	Columbidae	Ocyphaps lophotes	Crested Pigeon	36
Psittaciformes	Psittacidae	Agapornis fischeri	Fischer's Lovebird	36
Psittaciformes	Psittacidae	Amazona amazonica	Orange-winged Amazon	36
Anseriformes	Anatidae	Dendrocygna autumnalis	Black-bellied Whistling-duck	36
Passeriformes	Monarchidae	Grallina cyanoleuca	Magpie-lark	35
Gruiformes	Rallidae	Gallirallus australis	Weka	34
Passeriformes	Dicruridae	Dicrurus macrocercus	Black Drongo	34
Columbiformes	Columbidae	Geopelia cuneata	Diamond Dove	34
Psittaciformes	Psittacidae	Amazona oratrix	Yellow-headed Amazon	33
Passeriformes	Estrildidae	Lonchura cantans	African Silverbill	33
Psittaciformes	Psittacidae	Strigops habroptila	Kakapo	33
Passeriformes	Icteridae	Sturnella neglecta	Western Meadowlark	32
Passeriformes	Emberizidae	Emberiza cirlus	Cirl Bunting	32
Psittaciformes	Psittacidae	Cacatua sulphurea	Yellow-crested Cockatoo	32
Psittaciformes	Psittacidae	Amazona aestiva	Blue-fronted Amazon	31
Galliformes	Phasianidae	Lophura leucomelanos	Kalij Pheasant	30
Psittaciformes	Psittacidae	Eclectus roratus	Eclectus Parrot	30
Passeriformes	Pycnonotidae	Pycnonotus aurigaster	Sooty-headed Bulbul	30
Galliformes	Phasianidae	Coturnix japonica	Japanese Quail	30
Passeriformes	Estrildidae	Estrilda caerulescens	Lavender Waxbill	30
Passeriformes	Thraupidae	Thraupis episcopus	Blue-grey Tanager	29
Passeriformes	Estrildidae	Lonchura cucullata	Bronze Munia	29
Psittaciformes	Psittacidae	Brotogeris chiriri	Yellow-chevroned Parakeet	29
Anseriformes	Anatidae	Anas melleri	Meller's Duck	29
Passeriformes	Sturnidae	Sturnus contra	Asian Pied Starling	29
Anseriformes	Anatidae	Anser cygnoides	Swan Goose	29
Columbiformes	Columbidae	Streptopelia bitorquata	Island Collared-dove	29
Psittaciformes	Psittacidae	Cacatua goffiniana	Tanimbar Cockatoo	28
Passeriformes	Estrildidae	Taeniopygia guttata	Zebra Finch	28
Passeriformes	Fringillidae	Carduelis cannabina	Eurasian Linnet	28
Galliformes	Phasianidae	Phasianus versicolor	Green Pheasant	28
Cuculiformes	Cuculidae	Crotophaga ani	Smooth-billed Ani	28
Passeriformes	Estrildidae	Lonchura striata	White-rumped Munia	28
Passeriformes	Timaliidae	Garrulax pectoralis	Greater Necklaced Laughingthrush	28
Passeriformes	Estrildidae	Amandava subflava	Zebra Waxbill	28
Ciconiiformes	Ardeidae	Nycticorax nycticorax	Black-crowned Night-heron	27
Passeriformes	Estrildidae	Lonchura maja	White-headed Munia	27
Passeriformes	Icteridae	Quiscalus lugubris	Carib Grackle	26
Passeriformes	Estrildidae	Uraeginthus angolensis	Blue-breasted Cordonbleu	26
Anseriformes	Anatidae	Cereopsis novaehollandiae	Cape Barren Goose	25
Psittaciformes	Psittacidae	Prosopeia tabuensis	Red Shining-parrot	25

Gruiformes	Turnicidae	Turnix nigricollis	Madagascar Buttonquail	25
Passeriformes	Fringillidae	Serinus flaviventris	Yellow Canary	25
Psittaciformes	Psittacidae	Aratinga holochlora	Green Parakeet	25
Psittaciformes	Psittacidae	Platycercus elegans	Crimson Rosella	25
Psittaciformes	Psittacidae	Psittacula cyanocephala	Plum-headed Parakeet	25
Psittaciformes	Psittacidae	Platycercus eximius	Eastern Rosella	25
Passeriformes	Ploceidae	Ploceus intermedius	Lesser Masked Weaver	24
Passeriformes	Muscicapidae	Copsychus saularis	Oriental Magpie-robin	24
Galliformes	Phasianidae	Francolinus erckelii	Erckel's Francolin	24
Passeriformes	Ploceidae	Ploceus philippinus	Baya Weaver	24
Psittaciformes	Psittacidae	Trichoglossus haematodus	Rainbow Lorikeet	24
Passeriformes	Estrildidae	Lagonosticta senegala	Red-billed Firefinch	24
Psittaciformes	Psittacidae	Ara ararauna	Blue-and-yellow Macaw	24
Galliformes	Phasianidae	Tympanuchus cupido	Greater Prairie-chicken	24
Passeriformes	Passeridae	Passer hispaniolensis	Spanish Sparrow	24
Psittaciformes	Psittacidae	Aratinga canicularis	Orange-fronted Parakeet	24
Psittaciformes	Psittacidae	Ara severus	Chestnut-fronted Macaw	24
Passeriformes	Emberizidae	Passerina cyanea	Indigo Bunting	23
Columbiformes	Pteroclididae	Pterocles exustus	Chestnut-bellied Sandgrouse	23
Anseriformes	Anatidae	Dendrocygna viduata	White-faced Whistling-duck	23
Galliformes	Phasianidae	Tetrao tetrix	Black Grouse	23
Psittaciformes	Psittacidae	Amazona autumnalis	Red-lored Amazon	23
Passeriformes	Corvidae	Pica pica	Black-billed Magpie	22
Passeriformes	Muscicapidae	Luscinia megarhynchos	Common Nightingale	22
Passeriformes	Timaliidae	Garrulax chinensis	Black-throated Laughingthrush	22
Passeriformes	Mimidae	Mimus gilvus	Tropical Mockingbird	22
Columbiformes	Columbidae	Leucosarcia melanoleuca	Wonga Pigeon	21
Psittaciformes	Psittacidae	Poicephalus senegalus	Senegal Parrot	21
Galliformes	Phasianidae	Perdicula asiatica	Jungle Bush-quail	21
Passeriformes	Fringillidae	Pyrrhula pyrrhula	Eurasian Bullfinch	21
Columbiformes	Columbidae	Geopelia humeralis	Bar-shouldered Dove	21
Passeriformes	Emberizidae	Tiaris olivaceus	Yellow-faced Grassquit	21
Passeriformes	Estrildidae	Lonchura leucogastroides	Javan Munia	21
Passeriformes	Meliphagidae	Manorina melanocephala	Noisy Miner	20
Passeriformes	Ploceidae	Ploceus jacksoni	Golden-backed Weaver	20
Passeriformes	Fringillidae	Carduelis spinus	Eurasian Siskin	20
Columbiformes	Columbidae	Streptopelia tranquebarica	Red Collared-dove	20
Anseriformes	Anatidae	Callonetta leucophrys	Ringed Teal	20
Psittaciformes	Psittacidae	Amazona ventralis	Hispaniolan Amazon	20
Struthioniformes	Struthionidae	Struthio camelus	Ostrich	19
Columbiformes	Columbidae	Zenaida asiatica	White-winged Dove	19
Passeriformes	Estrildidae	Stagonopleura guttata	Diamond Firetail	19
Passeriformes	Sturnidae	Sturnus pagodarum	Brahminy Starling	19
Psittaciformes	Psittacidae	Psittacus erithacus	Grey Parrot	19

Passeriformes	Pycnonotidae	Pycnonotus leucogenys	Himalayan Bulbul	19
Psittaciformes	Psittacidae	Brotogeris jugularis	Orange-chinned Parakeet	18
Passeriformes	Sturnidae	Sturnus nigricollis	Black-collared Starling	18
Psittaciformes	Psittacidae	Amazona finschi	Lilac-crowned Amazon	18
Galliformes	Odontophoridae	Colinus cristatus	Crested Bobwhite	18
Anseriformes	Anatidae	Anas bahamensis	White-cheeked Pintail	18
Galliformes	Phasianidae	Perdix dauurica	Daurian Partridge	18
Psittaciformes	Psittacidae	Cacatua roseicapilla	Galah	18
Passeriformes	Timaliidae	Garrulax leucolophus	White-crested Laughingthrush	17
Psittaciformes	Psittacidae	Cyanoliseus patagonus	Burrowing Parakeet	17
Anseriformes	Anatidae	Anser albifrons	Greater White-fronted Goose	17
Galliformes	Odontophoridae	Callipepla squamata	Scaled Quail	17
Passeriformes	Ploceidae	Ploceus velatus	Southern Masked-weaver	17
Galliformes	Phasianidae	Tympanuchus phasianellus	Sharp-tailed Grouse	17
Psittaciformes	Psittacidae	Cacatua moluccensis	Salmon-crested Cockatoo	17
Passeriformes	Emberizidae	Paroaria dominicana	Red-cowled Cardinal	17
Columbiformes	Columbidae	Geophaps plumifera	Spinifex Pigeon	16
Falconiformes	Accipitridae	Parabuteo unicinctus	Harris's Hawk	16
Passeriformes	Sturnidae	Sturnus burmannicus	Vinous-breasted Starling	16
Tinamiformes	Tinamidae	Rhynchotus rufescens	Red-winged Tinamou	16
Passeriformes	Menuridae	Menura novaehollandiae	Superb Lyrebird	16
Passeriformes	Muscicapidae	Erithacus akahige	Japanese Robin	16
Ciconiiformes	Threskiornithidae	Eudocimus ruber	Scarlet Ibis	16
Psittaciformes	Psittacidae	Aratinga weddellii	Dusky-headed Parakeet	16
Anseriformes	Anatidae	Chloephaga picta	Upland Goose	16
Galliformes	Phasianidae	Francolinus afer	Red-necked Spurfowl	16
Passeriformes	Corvidae	Urocissa erythrorhyncha	Blue Magpie	16
Passeriformes	Timaliidae	Garrulax albogularis	White-throated Laughingthrush	15
Passeriformes	Fringillidae	Carduelis cucullata	Red Siskin	15
Psittaciformes	Psittacidae	Eos bornea	Red Lory	15
Passeriformes	Meliphagidae	Notiomystis cincta	Stitchbird	15
Psittaciformes	Psittacidae	Cacatua tenuirostris	Long-billed Corella	15
Anseriformes	Anatidae	Tadorna tadorna	Common Shelduck	15
Passeriformes	Sturnidae	Lamprotornis superbus	Superb Starling	15
Columbiformes	Columbidae	Phaps chalcoptera	Common Bronzewing	15
Galliformes	Phasianidae	Tetrao urogallus	Western Capercaillie	15
Psittaciformes	Psittacidae	Tanygnathus lucionensis	Blue-naped Parrot	15
Passeriformes	Tyrannidae	Pitangus sulphuratus	Great Kiskadee	14
Passeriformes	Viduidae	Vidua paradisaea	Eastern Paradise-whydah	14
Passeriformes	Corvidae	Corvus albus		14
Falconiformes	Accipitridae	Circus approximans	Swamp Harrier	14
Passeriformes	Corvidae	Corvus monedula	Eurasian Jackdaw	14
Psittaciformes	Psittacidae	Amazona albifrons	White-fronted Amazon	14
Columbiformes	Columbidae	Oena capensis	Namaqua Dove	14

Passeriformes	Muscicapidae	Cyanoptila cyanomelana	Blue-and-white Flycatcher	14
Passeriformes	Fringillidae	Telespiza cantans	Laysan Finch	14
Galliformes	Phasianidae	Coturnix pectoralis	Stubble Quail	14
Columbiformes	Columbidae	Geophaps smithii	Partridge Pigeon	14
Passeriformes	Ploceidae	Euplectes albonotatus	White-winged Widowbird	14
Galliformes	Phasianidae	Lagopus leucura	White-tailed Ptarmigan	14
Psittaciformes	Psittacidae	Cacatua alba	White Cockatoo	14
Passeriformes	Emberizidae	Paroaria capitata	Yellow-billed Cardinal	14
Galliformes	Phasianidae	Lagopus lagopus	Willow Ptarmigan	14
Galliformes	Phasianidae	Tetraogallus himalayensis	Himalayan Snowcock	13
Passeriformes	Petroicidae	Petroica australis	New Zealand Robin	13
Psittaciformes	Psittacidae	Amazona farinosa	Mealy Amazon	13
Passeriformes	Timaliidae	Garrulax caerulatus	Grey-sided Laughingthrush	13
Anseriformes	Anatidae	Anser fabalis	Bean Goose	13
Passeriformes	Emberizidae	Passerina ciris	Painted Bunting	13
Anseriformes	Anatidae	Anas eatoni	Eaton's Pintail	12
Anseriformes	Anatidae	Aythya ferina	Common Pochard	12
Passeriformes	Zosteropidae	Zosterops natalis	Christmas White-eye	12
Psittaciformes	Psittacidae	Ara macao	Scarlet Macaw	12
Falconiformes	Accipitridae	Circus aeruginosus	Western Marsh-harrier	12
Columbiformes	Columbidae	Chalcophaps indica	Emerald Dove	12
Falconiformes	Cathartidae	Cathartes aura	Turkey Vulture	12
Passeriformes	Sturnidae	Acridotheres albocinctus	Collared Myna	12
Anseriformes	Anatidae	Anas falcata	Falcated Duck	12
Passeriformes	Atrichornithidae	Atrichornis clamosus	Noisy Scrub-bird	12
Passeriformes	Timaliidae	Garrulax sannio	White-browed Laughingthrush	12
Anseriformes	Anatidae	Branta hutchinsii	Cackling Goose	12
Struthioniformes	Apterygidae	Apteryx owenii	Little Spotted Kiwi	12
Passeriformes	Fringillidae	Fringilla montifringilla	Brambling	12
Passeriformes	Emberizidae	Passerina leclancherii	Orange-breasted Bunting	12
Galliformes	Megapodiidae	Alectura lathami	Australian Brush-turkey	12
Passeriformes	Emberizidae	Emberiza hortulana	Ortolan Bunting	12
Anseriformes	Anatidae	Dendrocygna bicolor	Fulvous Whistling-duck	12
Galliformes	Phasianidae	Dendragapus obscurus	Dusky Grouse	11
Galliformes	Cracidae	Ortalis vetula	Plain Chachalaca	11
Passeriformes	Sturnidae	Sturnus melanopterus	Black-winged Starling	11
Passeriformes	Corvidae	Cyanocorax yncas	Green Jay	11
Psittaciformes	Psittacidae	Psittacula roseata	Blossom-headed Parakeet	11
Psittaciformes	Psittacidae	Agapornis lilianae	Lilian's Lovebird	11
Passeriformes	Fringillidae	Serinus leucopygius	White-rumped Seedeater	11
Passeriformes	Ploceidae	Quelea quelea	Red-billed Quelea	11
Anseriformes	Anatidae	Anser brachyrhynchus	Pink-footed Goose	11
Passeriformes	Fringillidae	Carduelis flavirostris	Twite	11
Pelecaniformes	Phalacrocoracidae	Phalacrocorax carbo	Great Cormorant	11
Galliformes	Phasianidae	Syrmaticus soemmerringii	Copper Pheasant	11
Psittaciformes	Psittacidae	Vini kuhlii	Rimitara Lorikeet	10
Psittaciformes	Psittacidae	Barnardius zonarius	Ringneck Parrot	10

Phoenicopteriformes	Phoenicopteridae	Phoenicopterus roseus	Greater Flamingo	10
Passeriformes	Thraupidae	Ramphocelus dimidiatus	Crimson-backed Tanager	10
Passeriformes	Muscicapidae	Erithacus komadori	Ryukyu Robin	10
Anseriformes	Anatidae	Anas acuta	Northern Pintail	10
Passeriformes	Turdidae	Turdus poliocephalus	Island Thrush	10
Anseriformes	Anatidae	Netta peposaca	Rosy-billed Pochard	10
Gruiformes	Gruidae	Balearica regulorum	Grey Crowned-crane	10
Gruiformes	Rallidae	Porphyrio mantelli	North Island Takahe	10
Columbiformes	Columbidae	Gallicolumba luzonica	Luzon Bleeding-heart	10
Apodiformes	Apodidae	Collocalia bartschi	Guam Swiftlet	10
Passeriformes	Icteridae	Sturnella loyca	Long-tailed Meadowlark	10
Passeriformes	Alaudidae	Melanocorypha mongolica	Mongolian Lark	10
Anseriformes	Anatidae	Aythya fuligula	Tufted Duck	10
Passeriformes	Rhipiduridae	Rhipidura leucophrys	Willie-wagtail	10
Passeriformes	Estrildidae	Erythrura psittacea	Red-throated Parrotfinch	10
Gruiformes	Gruidae	Grus antigone	Sarus Crane	10
Anseriformes	Anatidae	Cygnus cygnus	Whooper Swan	10
Passeriformes	Zosteropidae	Zosterops palpebrosus	Oriental White-eye	10
Anseriformes	Anatidae	Chen canagica	Emperor Goose	10
Psittaciformes	Psittacidae	Eos reticulata	Blue-streaked Lory	9
Psittaciformes	Psittacidae	Aratinga chloroptera	Hispaniolan Parakeet	9
Passeriformes	Emberizidae	Paroaria gularis	Red-capped Cardinal	9
Psittaciformes	Psittacidae	Ara militaris	Military Macaw	9
Galliformes	Cracidae	Ortalis ruficauda	Rufous-vented Chachalaca	9
Psittaciformes	Psittacidae	Amazona auropalliata	Yellow-naped Amazon	9
Psittaciformes	Psittacidae	Platycercus adscitus	Pale-headed Rosella	9
Psittaciformes	Psittacidae	Aratinga leucophthalma	White-eyed Parakeet	9
Passeriformes	Pycnonotidae	Pycnonotus goiavier	Yellow-vented Bulbul	9
Gruiformes	Rallidae	Aramides cajanea	Grey-necked Wood-rail	9
Columbiformes	Columbidae	Caloenas nicobarica	Nicobar Pigeon	9
Passeriformes	Timaliidae	Leiothrix argentauris	Silver-eared Mesia	9
Passeriformes	Ploceidae	Euplectes aureus	Golden-backed Bishop	9
Falconiformes	Falconidae	Milvago chimango	Chimango Caracara	9
Passeriformes	Emberizidae	Tiaris canorus	Cuban Grassquit	9
Galliformes	Phasianidae	Ammoperdix griseogularis	See-see Partridge	9
Anseriformes	Anatidae	Anas strepera	Gadwall	9
Passeriformes	Icteridae	Sturnella militaris	Red-breasted Blackbird	9
Passeriformes	Alaudidae	Lullula arborea	Wood Lark	9
Tinamiformes	Tinamidae	Nothoprocta perdicaria	Chilean Tinamou	9
Passeriformes	Timaliidae	Pomatorhinus ruficollis	Streak-breasted Scimitar-babbler	9
Psittaciformes	Psittacidae	Aratinga wagleri	Scarlet-fronted Parakeet	8
Falconiformes	Accipitridae	Buteogallus anthracinus	Common Black-hawk	8
Anseriformes	Anatidae	Chen rossii	Ross's Goose	8
Columbiformes	Columbidae	Streptopelia turtur	European Turtle-dove	8
Columbiformes	Columbidae	Columbina inca	Inca Dove	8
Passeriformes	Paradisaeidae	Paradisaea apoda	Greater Bird-of-paradise	8

Strigiformes	Tytonidae	Tyto novaehollandiae	Australian Masked-owl	8
Galliformes	Phasianidae	Dendragapus canadensis	Spruce Grouse	8
Psittaciformes	Psittacidae	Pyrrhura molinae	Green-cheeked Parakeet	8
Passeriformes	Emberizidae	Oryzoborus angolensis	Lesser Seed-finch	8
Passeriformes	Corvidae	Corvus brachyrhynchos	American Crow	8
Galliformes	Cracidae	Crax rubra	Great Curassow	8
Passeriformes	Estrildidae	Stagonopleura bella	Beautiful Firetail	8
Passeriformes	Sturnidae	Lamprotornis caudatus	Long-tailed Glossy-starling	8
Passeriformes	Estrildidae	Amadina fasciata	Cut-throat	8
Psittaciformes	Psittacidae	Lorius garrulus	Chattering Lory	8
Psittaciformes	Psittacidae	Pyrrhura frontalis	Maroon-bellied Parakeet	8
Passeriformes	Sturnidae	Acridotheres cinereus	Pale-bellied Myna	8
Psittaciformes	Psittacidae	Trichoglossus chlorolepidotus	Scaly-breasted Lorikeet	8
Passeriformes	Sittidae	Sitta frontalis	Velvet-fronted Nuthatch	8
Passeriformes	Fringillidae	Carduelis tristis	American Goldfinch	8
Psittaciformes	Psittacidae	Callocephalon fimbriatum	Gang-gang Cockatoo	8
Anseriformes	Anatidae	Cygnus melancoryphus	Black-necked Swan	8
Passeriformes	Sylviidae	Sylvia atricapilla	Blackcap	8
Gruiformes	Gruidae	Balearica pavonina	Black Crowned-crane	8
Galliformes	Phasianidae	Gallus varius	Green Junglefowl	8
Passeriformes	Thraupidae	Cyanerpes cyaneus	Red-legged Honeycreeper	8
Galliformes	Phasianidae	Perdicula argoondah	Rock Bush-quail	8
Passeriformes	Icteridae	Agelaius phoeniceus	Red-winged Blackbird	7
Struthioniformes	Dromaiidae	Dromaius novaehollandiae	Emu	7
Charadriiformes	Charadriidae	Vanellus chilensis	Southern Lapwing	7
Psittaciformes	Psittacidae	Vini peruviana	Blue Lorikeet	7
Passeriformes	Emberizidae	Emberiza schoeniclus	Reed Bunting	7
Passeriformes	Estrildidae	Taeniopygia bichenovii	Double-barred Finch	7
Passeriformes	Corvidae	Cyanopica cyanus	Azure-winged Magpie	7
Passeriformes	Icteridae	Molothrus ater	Brown-headed Cowbird	7
Columbiformes	Pteroclididae	Syrrhaptes paradoxus	Pallas's Sandgrouse	7
Passeriformes	Paridae	Parus major		7
Columbiformes	Columbidae	Zenaida macroura	Mourning Dove	7
Pelecaniformes	Pelecanidae	Pelecanus rufescens	Pink-backed Pelican	7
Passeriformes	Timaliidae	Garrulax formosus	Red-winged Laughingthrush	7
Passeriformes	Estrildidae	Erythrura gouldiae	Gouldian Finch	7
Anseriformes	Anatidae	Bucephala albeola	Bufflehead	7
Passeriformes	Estrildidae	Lonchura fringilloides	Magpie Munia	7
Struthioniformes	Rheidae	Rhea americana	Greater Rhea	7
Psittaciformes	Psittacidae	Aratinga aurea	Peach-fronted Parakeet	7
Passeriformes	Timaliidae	Paradoxornis alphonsianus	Ashy-throated Parrotbill	7
Psittaciformes	Psittacidae	Cyanoramphus novaezelandiae	Red-fronted Parakeet	7
Psittaciformes	Psittacidae	Amazona barbadensis	Yellow-shouldered Amazon	7
Anseriformes	Anatidae	Anas rubripes	American Black Duck	7

Passeriformes	Muscicapidae	Copsychus sechellarum	Seychelles Magpie-robin	7
Passeriformes	Sturnidae	Lamprotornis chalybaeus	Greater Blue-eared Glossy-starling	7
Passeriformes	Paridae	Parus spilonotus	Yellow-cheeked Tit	7
Passeriformes	Sturnidae	Acridotheres grandis	White-vented Myna	7
Anseriformes	Anatidae	Branta ruficollis	Red-breasted Goose	6
Passeriformes	Emberizidae	Diuca diuca	Common Diuca-finch	6
Anseriformes	Anatidae	Anas hottentota	Hottentot Teal	6
Anseriformes	Anatidae	Marmaronetta angustirostris	Marbled Teal	6
Phoenicopteriformes	Phoenicopteridae	Phoeniconaias minor	Lesser Flamingo	6
Galliformes	Megapodiidae	Megapodius pritchardii	Polynesian Megapode	6
Columbiformes	Pteroclididae	Pterocles alchata	Pin-tailed Sandgrouse	6
Passeriformes	Meliphagidae	Manorina melanophrys	Bell Miner	6
Passeriformes	Pycnonotidae	Pycnonotus melanicterus	Black-crested Bulbul	6
Pelecaniformes	Pelecanidae	Pelecanus crispus	Dalmatian Pelican	6
Galliformes	Megapodiidae	Macrocephalon maleo	Maleo	6
Gruiformes	Rallidae	Porzana palmeri	Laysan Rail	6
Gruiformes	Turnicidae	Turnix varius	Painted Buttonquail	6
Passeriformes	Sturnidae	Aplonis panayensis	Asian Glossy Starling	6
Struthioniformes	Rheidae	Rhea pennata	Lesser Rhea	6
Passeriformes	Paridae	Parus caeruleus	Blue Tit	6
Anseriformes	Anatidae	Branta sandvicensis	Hawaiian Goose	6
Anseriformes	Anatidae	Dendrocygna arborea	West Indian Whistling-duck	6
Psittaciformes	Psittacidae	Tanygnathus megalorynchos	Great-billed Parrot	6
Charadriiformes	Charadriidae	Vanellus vanellus	Northern Lapwing	6
Psittaciformes	Psittacidae	Cacatua sanguinea	Little Corella	6
Falconiformes	Accipitridae	Buteogallus urubitinga	Great Black-hawk	6
Psittaciformes	Psittacidae	Diopsittaca nobilis	Red-shouldered Macaw	6
Psittaciformes	Psittacidae	Aratinga finschi	Crimson-fronted Parakeet	6
Passeriformes	Timaliidae	Paradoxornis webbianus	Vinous-throated Parrotbill	6
Anseriformes	Anatidae	Cygnus buccinator	Trumpeter Swan	6
Passeriformes	Timaliidae	Minla cyanouroptera	Blue-winged Minla	6
Anseriformes	Anatidae	Anas poecilorhyncha	Spot-billed Duck	6
Galliformes	Phasianidae	Lophophorus impejanus	Himalayan Monal	6
Passeriformes	Passeridae	Sporopipes squamifrons	Scaly Weaver	6
Passeriformes	Estrildidae	Uraeginthus cyanocephalus	Blue-capped Cordonbleu	6
Passeriformes	Ploceidae	Ploceus melanocephalus	Black-headed Weaver	5
Falconiformes	Accipitridae	Accipiter gentilis	Northern Goshawk	5
Piciformes	Ramphastidae	Ramphastos vitellinus	Channel-billed Toucan	5
Passeriformes	Sturnidae	Lamprotornis purpureus	Purple Glossy-starling	5
Falconiformes	Cathartidae	Sarcoramphus papa	King Vulture	5
Passeriformes	Thraupidae	Ramphocelus bresilius	Brazilian Tanager	5
Psittaciformes	Psittacidae	Probosciger aterrimus	Palm Cockatoo	5
Galliformes	Phasianidae	Bonasa bonasia	Hazel Grouse	5
Gruiformes	Rallidae	Gallirallus philippensis	Buff-banded Rail	5

Passeriformes	Ploceidae	Ploceus galbula	Rueppell's Weaver	5
Ciconiiformes	Threskiornithidae	Platalea alba	African Spoonbill	5
Passeriformes	Sylviidae	Bowdleria punctata	New Zealand Fernbird	5
Anseriformes	Anatidae	Neochen jubata	Orinoco Goose	5
Passeriformes	Fringillidae	Serinus atrogularis	Black-throated Seedeater	5
Psittaciformes	Psittacidae	Amazona pretrei	Red-spectacled Amazon	5
Gruiformes	Gruidae	Grus virgo	Demoiselle Crane	5
Passeriformes	Passeridae	Passer luteus	Sudan Golden Sparrow	5
Piciformes	Ramphastidae	Ramphastos sulfuratus	Keel-billed Toucan	5
Passeriformes	Timaliidae	Garrulax perspicillatus	Masked Laughingthrush	5
Charadriiformes	Charadriidae	Pluvialis squatarola	Grey Plover	5
Tinamiformes	Tinamidae	Nothura maculosa	Spotted Nothura	5
Passeriformes	Sturnidae	Sturnus roseus	Rosy Starling	5
Passeriformes	Thraupidae	Tachyphonus rufus	White-lined Tanager	5
Galliformes	Phasianidae	Francolinus adspersus	Red-billed Francolin	5
Passeriformes	Ploceidae	Euplectes hordeaceus	Black-winged Bishop	5
Passeriformes	Timaliidae	Stachyris ruficeps	Rufous-capped Babbler	5
Cuculiformes	Musophagidae	Musophaga violacea	Violet Turaco	5
Coraciiformes	Bucerotidae	Anthracoceros malayanus	Black Hornbill	5
Anseriformes	Anatidae	Anas formosa	Baikal Teal	5
Galliformes	Phasianidae	Francolinus capensis	Cape Francolin	5
Strigiformes	Strigidae	Bubo virginianus	Great Horned Owl	5
Passeriformes	Ploceidae	Euplectes ardens	Red-collared Widowbird	5
Anseriformes	Anatidae	Aythya nyroca	Ferruginous Duck	5
Anseriformes	Anatidae	Chenonetta jubata	Maned Duck	5
Passeriformes	Corvidae	Cyanocorax caeruleus	Azure Jay	5
Passeriformes	Estrildidae	Pytilia melba	Green-winged Pytilia	5
Columbiformes	Columbidae	Turtur tympanistria	Tambourine Dove	5
Passeriformes	Estrildidae	Neochmia ruficauda	Star Finch	5
Galliformes	Phasianidae	Ammoperdix heyi	Sand Partridge	5
Passeriformes	Estrildidae	Amandava formosa	Green Avadavat	5
Columbiformes	Columbidae	Streptopelia capicola	Ring-necked Dove	5
Psittaciformes	Psittacidae	Cacatua leadbeateri	Major Mitchell's Cockatoo	5
Anseriformes	Anatidae	Anas sibilatrix	Chiloe Wigeon	5
Passeriformes	Ploceidae	Euplectes progne	Long-tailed Widowbird	5
Passeriformes	Ploceidae	Foudia sechellarum	Seychelles Fody	5
Columbiformes	Columbidae	Starnoenas cyanocephala	Blue-headed Quail-dove	5
Passeriformes	Maluridae	Malurus cyaneus	Superb Fairywren	5
Passeriformes	Callaeatidae	Callaeas cinereus	Kokako	5
Passeriformes	Viduidae	Vidua chalybeata	Village Indigobird	5
Anseriformes	Anatidae	Tadorna cana	South African Shelduck	5
Psittaciformes	Psittacidae	Anodorhynchus hyacinthinus	Hyacinth Macaw	5
Galliformes	Phasianidae	Lagopus muta	Rock Ptarmigan	5
Struthioniformes	Apterygidae	Apteryx australis	Southern Brown Kiwi	5
Struthioniformes	Casuariidae	Casuarius casuarius	Southern Cassowary	5
Passeriformes	Estrildidae	Erythrura prasina	Pin-tailed Parrotfinch	5
Psittaciformes	Psittacidae	Poicephalus meyeri	Meyer's Parrot	5
Passeriformes	Fringillidae	Eophona migratoria	Yellow-billed Grosbeak	4

Columbiformes	Columbidae	Streptopelia semitorquata	Red-eyed Dove	4
Strigiformes	Strigidae	Pulsatrix perspicillata	Spectacled Owl	4
Passeriformes	Icteridae	Psarocolius montezuma	Montezuma Oropendola	4
Passeriformes	Icteridae	Quiscalus mexicanus	Great-tailed Grackle	4
Passeriformes	Thraupidae	Tangara arthus	Golden Tanager	4
Gruiformes	Gruidae	Grus americana	Whooping Crane	4
Psittaciformes	Psittacidae	Rhynchopsitta terrisi	Maroon-fronted Parrot	4
Psittaciformes	Psittacidae	Brotogeris sanctithomae	Tui Parakeet	4
Columbiformes	Columbidae	Columba palumbus	Common Wood-pigeon	4
Psittaciformes	Psittacidae	Primolius auricollis	Yellow-collared Macaw	4
Psittaciformes	Psittacidae	Coracopsis nigra	Black Parrot	4
Psittaciformes	Psittacidae	Poicephalus rueppellii	Rueppell's Parrot	4
Passeriformes	Thraupidae	Ramphocelus carbo	Silver-beaked Tanager	4
Columbiformes	Columbidae	Leptotila jamaicensis	Caribbean Dove	4
Passeriformes	Emberizidae	Zonotrichia capensis	Rufous-collared Sparrow	4
Passeriformes	Cardinalidae	Piranga rubra	Summer Tanager	4
Psittaciformes	Psittacidae	Cyanoramphus unicolor	Antipodes Parakeet	4
Passeriformes	Emberizidae	Gubernatrix cristata	Yellow Cardinal	4
Psittaciformes	Psittacidae	Amazona festiva	Festive Amazon	4
Columbiformes	Columbidae	Geotrygon montana	Ruddy Quail-dove	4
Columbiformes	Columbidae	Leptotila verreauxi	White-tipped Dove	4
Psittaciformes	Psittacidae	Aratinga jandaya	Jandaya Parakeet	4
Gruiformes	Rallidae	Fulica americana	American Coot	4
Psittaciformes	Psittacidae	Pionus senilis	White-crowned Parrot	4
Passeriformes	Estrildidae	Lonchura nana	Madagascar Munia	4
Galliformes	Odontophoridae	Callipepla douglasii	Elegant Quail	4
Passeriformes	Viduidae	Vidua regia	Queen Whydah	4
Ciconiiformes	Ciconiidae	Mycteria ibis	Yellow-billed Stork	4
Ciconiiformes	Ciconiidae	Mycteria leucocephala	Painted Stork	4
Passeriformes	Sturnidae	Sturnus malabaricus	Chestnut-tailed Starling	4
Passeriformes	Sturnidae	Fregilupus varius	Reunion Starling	4
Passeriformes	Corvidae	Corvus macrorhynchos	Large-billed Crow	4
Passeriformes	Sturnidae	Coccycolius iris	Emerald Starling	4
Anseriformes	Anatidae	Anas discors	Blue-winged Teal	4
Ciconiiformes	Ciconiidae	Ephippiorhynchus asiaticus	Black-necked Stork	4
Passeriformes	Acanthisittidae	Xenicus longipes	Bush Wren	4
Passeriformes	Pittidae	Pitta guajana	Banded Pitta	4
Pelecaniformes	Pelecanidae	Pelecanus erythrorhynchos	American White Pelican	4
Passeriformes	Estrildidae	Lonchura ferruginosa	White-capped Munia	4
Passeriformes	Ploceidae	Ploceus benghalensis	Black-breasted Weaver	4
Passeriformes	Irenidae	Irena puella	Asian Fairy-bluebird	4
Passeriformes	Estrildidae	Erythrura cyaneovirens	Red-headed Parrotfinch	4
Anseriformes	Anatidae	Anas capensis	Cape Teal	4
Passeriformes	Estrildidae	Erythrura trichroa	Blue-faced Parrotfinch	4
Anseriformes	Anatidae	Anas penelope	Eurasian Wigeon	4
Passeriformes	Estrildidae	Poephila acuticauda	Long-tailed Finch	4
Passeriformes	Turdidae	Sialia mexicana	Western Bluebird	4
Passeriformes	Estrildidae	Uraeginthus granatinus	Common Grenadier	4

Passeriformes	Estrildidae	Neochmia modesta	Plum-headed Finch	4
Passeriformes	Corvidae	Corvus moneduloides	New Caledonian Crow	4
Passeriformes	Estrildidae	Estrilda perreini	Black-tailed Waxbill	4
Passeriformes	Estrildidae	Estrilda melanotis	Swee Waxbill	4
Galliformes	Phasianidae	Pavo muticus	Green Peafowl	4
Passeriformes	Estrildidae	Lonchura hunsteini	Mottled Munia	4
Passeriformes	Pycnonotidae	Hypsipetes borbonicus	Olivaceous Bulbul	4
Psittaciformes	Psittacidae	Trichoglossus ornatus	Ornate Lorikeet	4
Passeriformes	Sturnidae	Aplonis metallica	Metallic Starling	4
Anseriformes	Anatidae	Dendrocygna arcuata	Wandering Whistling-duck	4
Passeriformes	Timaliidae	Babax lanceolatus	Chinese Babax	4
Galliformes	Phasianidae	Lophura ignita	Crested Fireback	4
Falconiformes	Falconidae	Falco rusticolus	Gyr Falcon	4
Anseriformes	Anatidae	Anser erythropus	Lesser White-fronted Goose	4
Passeriformes	Timaliidae	Panurus biarmicus	Bearded Parrotbill	4
Galliformes	Phasianidae	Catreus wallichi	Cheer Pheasant	4
Ciconiiformes	Threskiornithidae	Platalea leucorodia	Eurasian Spoonbill	4
Anseriformes	Anatidae	Branta bernicla	Brent Goose	4
Passeriformes	Timaliidae	Garrulax cineraceus	Moustached Laughingthrush	4
Anseriformes	Anatidae	Coscoroba coscoroba	Coscoroba Swan	4
Pelecaniformes	Pelecanidae	Pelecanus onocrotalus	Great White Pelican	4
Cuculiformes	Cuculidae	Eudynamys scolopaceus	Asian Koel	4
Passeriformes	Sylviidae	Sylvia communis	Common Whitethroat	4
Passeriformes	Pycnonotidae	Pycnonotus sinensis	Light-vented Bulbul	3
Passeriformes	Estrildidae	Lagonosticta rubricata	African Firefinch	3
Passeriformes	Estrildidae	Estrilda erythronotos	Black-cheeked Waxbill	3
Strigiformes	Strigidae	Strix aluco	Tawny Owl	3
Passeriformes	Turdidae	Turdus tephronotus	Bare-eyed Thrush	3
Psittaciformes	Psittacidae	Loriculus vernalis	Vernal Hanging-parrot	3
Passeriformes	Pycnonotidae	Pycnonotus xanthopygos	White-spectacled Bulbul	3
Columbiformes	Columbidae	Columba guinea	Speckled Pigeon	3
Psittaciformes	Psittacidae	Rhynchopsitta pachyrhyncha	Thick-billed Parrot	3
Columbiformes	Columbidae	Patagioenas squamosa	Scaly-naped Pigeon	3
Passeriformes	Cinclidae	Cinclus cinclus	White-throated Dipper	3
Anseriformes	Anatidae	Anas undulata	Yellow-billed Duck	3
Passeriformes	Paridae	Parus palustris		3
Psittaciformes	Psittacidae	Aratinga nana	Olive-throated Parakeet	3
Anseriformes	Anatidae	Oxyura maccoa	Maccoa Duck	3
Passeriformes	Timaliidae	Alcippe morrisonia	Grey-cheeked Fulvetta	3
Anseriformes	Anatidae	Anas flavirostris		3
Anseriformes	Anatidae	Dendrocygna javanica	Lesser Whistling-duck	3
Passeriformes	Ploceidae	Ploceus capensis	Cape Weaver	3
Passeriformes	Ploceidae	Ploceus vitellinus	Vitelline Masked-weaver	3
Passeriformes	Sturnidae	Sturnus erythropygius	White-headed Starling	3
Ciconiiformes	Ardeidae	Egretta garzetta	Little Egret	3
Passeriformes	Aegithalidae	Aegithalos caudatus	Long-tailed Tit	3
Passeriformes	Aegithalidae	Aegithalos concinnus	Black-throated Tit	3
Passeriformes	Muscicapidae	Cinclidium leucurum	White-tailed Robin	3

Passeriformes	Timaliidae	Yuhina diademata	White-collared Yuhina	3
Passeriformes	Turdidae	Turdus rufopalliatus	Rufous-backed Robin	3
Passeriformes	Turdidae	Turdus migratorius	American Robin	3
Anseriformes	Anatidae	Tadorna variegata	Paradise Shelduck	3
Apodiformes	Apodidae	Collocalia vanikorensis	Uniform Swiftlet	3
Passeriformes	Ploceidae	Foudia rubra	Mauritius Fody	3
Passeriformes	Ploceidae	Euplectes nigroventris	Zanzibar Bishop	3
Anseriformes	Anatidae	Tadorna radjah	Radjah Shelduck	3
Passeriformes	Pycnonotidae	Spizixos semitorques	Collared Finchbill	3
Cuculiformes	Musophagidae	Tauraco schalowi	Schalow's Turaco	3
Anseriformes	Anatidae	Sarkidiornis melanotos	Comb Duck	3
Passeriformes	Muscicapidae	Chaimarrornis leucocephalus	White-capped Water-redstart	3
Passeriformes	Thraupidae	Tangara larvata	Golden-hooded Tanager	3
Ciconiiformes	Ciconiidae	Ciconia ciconia	White Stork	3
Passeriformes	Emberizidae	Emberiza cioides	Meadow Bunting	3
Cuculiformes	Cuculidae	Crotophaga sulcirostris	Groove-billed Ani	3
Charadriiformes	Laridae	Larus occidentalis	Western Gull	3
Falconiformes	Falconidae	Falco tinnunculus	Common Kestrel	3
Piciformes	Ramphastidae	Ramphastos toco	Toco Toucan	3
Sphenisciformes	Spheniscidae	Aptenodytes patagonicus	King Penguin	3
Falconiformes	Falconidae	Falco columbarius	Merlin	3
Psittaciformes	Psittacidae	Agapornis pullarius	Red-headed Lovebird	3
Coraciiformes	Bucerotidae	Buceros bicornis	Great Hornbill	3
Columbiformes	Columbidae	Ducula whartoni	Christmas Imperial-pigeon	3
Passeriformes	Cracticidae	Strepera versicolor	Grey Currawong	3
Psittaciformes	Psittacidae	Prosopeia splendens	Crimson Shining-parrot	3
Coraciiformes	Bucorvidae	Bucorvus abyssinicus	Abyssinian Ground-hornbill	3
Charadriiformes	Charadriidae	Pluvialis apricaria	Eurasian Golden Plover	3
Psittaciformes	Psittacidae	Aprosmictus erythropterus	Red-winged Parrot	3
Ciconiiformes	Ardeidae	Nycticorax caledonicus	Rufous Night-heron	3
Passeriformes	Fringillidae	Serinus dorsostriatus	White-bellied Canary	3
Psittaciformes	Psittacidae	Psephotus haematonotus	Red-rumped Parrot	3
Gruiformes	Rallidae	Gallinula chloropus	Common Moorhen	3
Psittaciformes	Psittacidae	Poicephalus crassus	Niam-niam Parrot	3
Falconiformes	Accipitridae	Geranospiza caerulescens	Crane Hawk	3
Passeriformes	Emberizidae	Passerina amoena	Lazuli Bunting	3
Passeriformes	Fringillidae	Eophona personata	Japanese Grosbeak	3
Passeriformes	Emberizidae	Loxigilla violacea	Greater Antillean Bullfinch	3
Columbiformes	Columbidae	Goura cristata	Western Crowned-pigeon	3
Anseriformes	Anatidae	Anas castanea	Chestnut Teal	3
Columbiformes	Columbidae	Gallicolumba stairi	Shy Ground-dove	3
Passeriformes	Fringillidae	Coccothraustes coccothraustes	Hawfinch	3
Falconiformes	Accipitridae	Milvus milvus	Red Kite	3
Passeriformes	Emberizidae	Melopyrrha nigra	Cuban Bullfinch	3

Galliformes	Phasianidae	Alectoris melanocephala	Arabian Partridge	3
Galliformes	Phasianidae	Francolinus leucoscepus	Yellow-necked Spurfowl	3
Passeriformes	Acanthizidae	Mohoua albicilla	Whitehead	3
Columbiformes	Columbidae	Columbina passerina	Common Ground-dove	3
Anseriformes	Anatidae	Anas cyanoptera	Cinnamon Teal	3
Passeriformes	Fringillidae	Carduelis psaltria	Lesser Goldfinch	3
Falconiformes	Accipitridae	Buteo jamaicensis	Red-tailed Hawk	3
Anseriformes	Anatidae	Lophodytes cucullatus	Hooded Merganser	3
Anseriformes	Anatidae	Anas georgica	Yellow-billed Pintail	3
Struthioniformes	Apterygidae	Apteryx haastii	Great Spotted Kiwi	2
Psittaciformes	Psittacidae	Polytelis swainsonii	Superb Parrot	2
Galliformes	Phasianidae	Lophura swinhoii	Swinhoe's Pheasant	2
Anseriformes	Anatidae	Oxyura australis	Blue-billed Duck	2
Galliformes	Phasianidae	Rollulus rouloul	Crested Partridge	2
Psittaciformes	Psittacidae	Glossopsitta concinna	Musk Lorikeet	2
Anseriformes	Anatidae	Oxyura leucocephala	White-headed Duck	2
Psittaciformes	Psittacidae	Pseudeos fuscata	Dusky Lory	2
Galliformes	Cracidae	Pipile cumanensis	Blue-throated Piping-guan	2
Cuculiformes	Cuculidae	Phaenicophaeus tristis	Green-billed Malkoha	2
Galliformes	Phasianidae	Francolinus clappertoni	Clapperton's Francolin	2
Anseriformes	Anatidae	Anas erythrorhyncha	Red-billed Duck	2
Galliformes	Phasianidae	Francolinus hildebrandti	Hildebrandt's Francolin	2
Anseriformes	Anatidae	Anas versicolor	Silver Teal	2
Anseriformes	Anatidae	Aythya americana	Redhead	2
Galliformes	Megapodiidae	Leipoa ocellata	Malleefowl	2
Anseriformes	Anatidae	Plectropterus gambensis	Spur-winged Goose	2
Piciformes	Picidae	Dendrocopos major	Great Spotted Woodpecker	2
Coraciiformes	Bucerotidae	Aceros undulatus	Wreathed Hornbill	2
Anseriformes	Anatidae	Tadorna tadornoides	Australian Shelduck	2
Cuculiformes	Cuculidae	Chrysococcyx maculatus	Asian Emerald Cuckoo	2
Galliformes	Cracidae	Penelope purpurascens	Crested Guan	2
Galliformes	Cracidae	Ortalis cinereiceps	Grey-headed Chachalaca	2
Anseriformes	Anatidae	Anas clypeata	Northern Shoveler	2
Coraciiformes	Bucerotidae	Bycanistes brevis	Silvery-cheeked Hornbill	2
Galliformes	Phasianidae	Meleagris ocellata	Ocellated Turkey	2
Psittaciformes	Psittacidae	Coracopsis vasa	Vasa Parrot	2
Coraciiformes	Alcedinidae	Halcyon leucocephala	Grey-headed Kingfisher	2
Psittaciformes	Psittacidae	Ara chloropterus	Red-and-green Macaw	2
Anseriformes	Anseranatidae	Anseranas semipalmata	Magpie Goose	2
Piciformes	Ramphastidae	Megalaima asiatica	Blue-throated Barbet	2
Passeriformes	Sittidae	Sitta europaea	Wood Nuthatch	2
Passeriformes	Turdidae	Turdus iliacus	Redwing	2
Passeriformes	Turdidae	Turdus plumbeus	Red-legged Thrush	2
Passeriformes	Muscicapidae	Niltava vivida	Vivid Niltava	2
Passeriformes	Muscicapidae	Phoenicurus frontalis	Blue-fronted Redstart	2
Passeriformes	Muscicapidae	Saxicola caprata	Pied Bushchat	2

Passeriformes	Sturnidae	Lamprotornis purpuroptera	Rueppell's Glossy-starling	2
Passeriformes	Timaliidae	Timalia pileata	Chestnut-capped Babbler	2
Passeriformes	Sturnidae	Sturnus philippensis	Chestnut-cheeked Starling	2
Passeriformes	Oriolidae	Oriolus xanthornus	Black-hooded Oriole	2
Passeriformes	Paridae	Parus monticolus	Green-backed Tit	2
Passeriformes	Pycnonotidae	Pycnonotus xanthorrhous	Brown-breasted Bulbul	2
Passeriformes	Pycnonotidae	Pycnonotus leucotis	White-eared Bulbul	2
Passeriformes	Timaliidae	Garrulax elliotii	Elliot's Laughingthrush	2
Passeriformes	Timaliidae	Garrulax milnei	Red-tailed Laughingthrush	2
Falconiformes	Falconidae	Falco peregrinus	Peregrine Falcon	2
Passeriformes	Sturnidae	Sturnus sturninus	Purple-backed Starling	2
Passeriformes	Petroicidae	Petroica traversi	Black Robin	2
Pelecaniformes	Phalacrocoracidae	Phalacrocorax bougainvillii	Guanay Cormorant	2
Ciconiiformes	Threskiornithidae	Plegadis falcinellus	Glossy Ibis	2
Ciconiiformes	Threskiornithidae	Geronticus eremita	Northern Bald Ibis	2
Ciconiiformes	Threskiornithidae	Threskiornis melanocephalus	Black-headed Ibis	2
Ciconiiformes	Ciconiidae	Ciconia episcopus	Woolly-necked Stork	2
Sphenisciformes	Spheniscidae	Spheniscus magellanicus	Magellanic Penguin	2
Passeriformes	Bombycillidae	Bombycilla garrulus	Bohemian Waxwing	2
Passeriformes	Meliphagidae	Entomyzon cyanotis	Blue-faced Honeyeater	2
Passeriformes	Rhipiduridae	Rhipidura albicollis	White-throated Fantail	2
Passeriformes	Laniidae	Lanius collurioides	Burmese Shrike	2
Passeriformes	Acanthizidae	Mohoua ochrocephala	Yellowhead	2
Passeriformes	Corvidae	Cyanocorax dickeyi	Tufted Jay	2
Passeriformes	Corvidae	Urocissa caerulea	Taiwan Magpie	2
Passeriformes	Corvidae	Corvus corax	Common Raven	2
Passeriformes	Oriolidae	Oriolus chinensis	Black-naped Oriole	2
Passeriformes	Timaliidae	Chrysomma sinense	Yellow-eyed Babbler	2
Passeriformes	Ptilonorhynchidae	Ptilonorhynchus violaceus	Satin Bowerbird	2
Passeriformes	Emberizidae	Loxigilla noctis	Lesser Antillean Bullfinch	2
Passeriformes	Emberizidae	Sporophila torqueola	White-collared Seedeater	2
Passeriformes	Emberizidae	Passerina caerulea	Blue Grosbeak	2
Passeriformes	Icteridae	Gnorimopsar chopi	Chopi Blackbird	2
Passeriformes	Icteridae	Quiscalus niger	Greater Antillean Grackle	2
Strigiformes	Strigidae	Ninox novaeseelandiae	Southern Boobook	2
Passeriformes	Chloropseidae	Chloropsis cochinchinensis	Blue-winged Leafbird	2
Passeriformes	Timaliidae	Liocichla phoenicea	Red-faced Liocichla	2
Passeriformes	Chloropseidae	Chloropsis aurifrons	Golden-fronted Leafbird	2
Passeriformes	Emberizidae	Emberiza leucocephalos	Pine Bunting	2
Passeriformes	Timaliidae	Garrulax poecilorhynchus	Rusty Laughingthrush	2
Passeriformes	Timaliidae	Paradoxornis gularis	Grey-headed Parrotbill	2
Gruiformes	Rallidae	Gallinula nesiotis		2
Passeriformes	Paridae	Parus ater		2
Passeriformes	Muscicapidae	Cyornis banyumas		2

Strigiformes	Tytonidae	Tyto javanica		2
Galliformes	Megapodiidae	Megapodius reinwardt	Orange-footed Megapode	2
Passeriformes	Ploceidae	Ploceus hypoxanthus	Asian Golden Weaver	2
Passeriformes	Timaliidae	Minla ignotincta	Red-tailed Minla	2
Passeriformes	Alaudidae	Mirafra javanica	Australasian Lark	2
Passeriformes	Alaudidae	Galerida cristata	Crested Lark	2
Passeriformes	Alaudidae	Eremophila alpestris	Horned Lark	2
Passeriformes	Nectariniidae	Aethopyga gouldiae	Gould's Sunbird	2
Passeriformes	Nectariniidae	Aethopyga saturata	Black-throated Sunbird	2
Passeriformes	Emberizidae	Emberiza bruniceps	Red-headed Bunting	2
Passeriformes	Ploceidae	Ploceus aurantius	Orange Weaver	2
Passeriformes	Emberizidae	Emberiza cia	Rock Bunting	2
Passeriformes	Ploceidae	Quelea erythrops	Red-headed Quelea	2
Passeriformes	Estrildidae	Estrilda rhodopyga	Crimson-rumped Waxbill	2
Passeriformes	Fringillidae	Serinus alario	Black-headed Canary	2
Passeriformes	Fringillidae	Carduelis yarrellii	Yellow-faced Siskin	2
Passeriformes	Fringillidae	Carpodacus roseus	Pallas's Rosefinch	2
Passeriformes	Fringillidae	Loxia pytyopsittacus	Parrot Crossbill	2
Passeriformes	Muscicapidae	Niltava macgrigoriae	Small Niltava	2
Passeriformes	Passeridae	Passer euchlorus	Arabian Golden Sparrow	2
Falconiformes	Accipitridae	Butastur teesa	White-eyed Buzzard	2
Gruiformes	Rallidae	Porphyrio alleni	Allen's Gallinule	2
Gruiformes	Rallidae	Gallinula mortierii	Tasmanian Native-hen	2
Charadriiformes	Laridae	Larus novaehollandiae	Silver Gull	2
Columbiformes	Columbidae	Goura victoria	Victoria Crowned-pigeon	2
Falconiformes	Accipitridae	Aegypius monachus	Cinereous Vulture	2
Psittaciformes	Psittacidae	Pionites melanocephalus	Black-headed Parrot	2
Strigiformes	Strigidae	Strix leptogrammica	Brown Wood-owl	2
Falconiformes	Accipitridae	Haliaeetus albicilla	White-tailed Eagle	2
Gruiformes	Rallidae	Gallinula comeri	Gough Moorhen	2
Falconiformes	Falconidae	Falco cherrug	Saker Falcon	2
Strigiformes	Strigidae	Strix varia	Barred Owl	2
Falconiformes	Accipitridae	Haliastur indus	Brahminy Kite	2
Gruiformes	Rallidae	Crex crex	Corncrake	2
Psittaciformes	Psittacidae	Brotogeris pyrrhoptera	Grey-cheeked Parakeet	2
Psittaciformes	Psittacidae	Brotogeris tirica	Plain Parakeet	2
Gruiformes	Gruidae	Grus rubicunda	Brolga	2
Psittaciformes	Psittacidae	Agapornis nigrigenis	Black-cheeked Lovebird	1
Galliformes	Phasianidae	Polyplectron napoleonis	Palawan Peacock-pheasant	1
Passeriformes	Estrildidae	Lonchura bicolor	Black-and-white Munia	1
Passeriformes	Estrildidae	Lonchura leucosticta	White-spotted Munia	1
Passeriformes	Viduidae	Vidua fischeri	Straw-tailed Whydah	1
Passeriformes	Fringillidae	Serinus pusillus	Fire-fronted Serin	1
Passeriformes	Fringillidae	Serinus serinus	European Serin	1
Galliformes	Phasianidae	Syrmaticus ellioti	Elliot's Pheasant	1
Passeriformes	Fringillidae	Serinus sulphuratus	Brimstone Canary	1
Galliformes	Phasianidae	Crossoptilon auritum	Blue Eared-pheasant	1
Caprimulgiformes	Podargidae	Podargus strigoides	Tawny Frogmouth	1
Passeriformes	Ploceidae	Euplectes macroura	Yellow-shouldered	1

			Widowbird	
Passeriformes	Fringillidae	Bucanetes githagineus	Trumpeter Finch	1
Passeriformes	Fringillidae	Rhodopechys obsoletus	Desert Finch	1
Strigiformes	Strigidae	Strix uralensis	Ural Owl	1
Galliformes	Phasianidae	Gallus sonneratii	Grey Junglefowl	1
Psittaciformes	Psittacidae	Loriculus galgulus	Blue-crowned Hanging-parrot	1
Passeriformes	Fringillidae	Pyrrhula erythaca	Grey-headed Bullfinch	1
Passeriformes	Fringillidae	Telespiza ultima	Nihoa Finch	1
Galliformes	Phasianidae	Arborophila crudigularis	Taiwan Partridge	1
Galliformes	Phasianidae	Crossoptilon mantchuricum	Brown Eared-pheasant	1
Galliformes	Phasianidae	Tympanuchus pallidicinctus	Lesser Prairie-chicken	1
Passeriformes	Alaudidae	Melanocorypha leucoptera	White-winged Lark	1
Passeriformes	Alaudidae	Eremalauda dunni	Dunn's Lark	1
Gruiformes	Psophiidae	Psophia leucoptera	Pale-winged Trumpeter	1
Galliformes	Odontophoridae	Cyrtonyx montezumae	Montezuma Quail	1
Gruiformes	Gruidae	Grus grus	Common Crane	1
Passeriformes	Nectariniidae	Nectarinia jugularis	Olive-backed Sunbird	1
Columbiformes	Columbidae	Ducula rosacea	Pink-headed Imperial-pigeon	1
Passeriformes	Motacillidae	Anthus novaeseelandiae	Australasian Pipit	1
Passeriformes	Passeridae	Pseudonigrita arnaudi	Grey-headed Social-weaver	1
Passeriformes	Estrildidae	Pytilia phoenicoptera	Red-winged Pytilia	1
Columbiformes	Columbidae	Treron waalia	Bruce's Green-pigeon	1
Passeriformes	Estrildidae	Emblema pictum	Painted Firetail	1
Passeriformes	Ploceidae	Ploceus castaneiceps	Taveta Golden Weaver	1
Passeriformes	Ploceidae	Ploceus nigerrimus	Vieillot's Black Weaver	1
Passeriformes	Ploceidae	Ploceus rubiginosus	Chestnut Weaver	1
Columbiformes	Columbidae	Geopelia placida	Peaceful Dove	1
Columbiformes	Columbidae	Geopelia maugeus	Barred Dove	1
Passeriformes	Ploceidae	Euplectes capensis	Yellow Bishop	1
Passeriformes	Ploceidae	Euplectes axillaris	Fan-tailed Widowbird	1
Strigiformes	Strigidae	Bubo scandiaca	Snowy Owl	1
Passeriformes	Ploceidae	Euplectes jacksoni	Jackson's Widowbird	1
Columbiformes	Columbidae	Macropygia unchall	Barred Cuckoo-dove	1
Passeriformes	Ploceidae	Ploceus subaureus	African Golden Weaver	1
Passeriformes	Reguliidae	Regulus ignicapilla	Firecrest	1
Passeriformes	Emberizidae	Emberiza aureola	Yellow-breasted Bunting	1
Psittaciformes	Psittacidae	Pyrrhura leucotis	Maroon-faced Parakeet	1
Pelecaniformes	Pelecanidae	Pelecanus occidentalis	Brown Pelican	1
Galliformes	Megapodiidae	Megapodius nicobariensis	Nicobar Megapode	1
Passeriformes	Icteridae	Icterus cayanensis	Epaulet Oriole	1
Psittaciformes	Psittacidae	Amazona xantholora	Yellow-lored Amazon	1
Galliformes	Cracidae	Crax blumenbachii	Red-billed Curassow	1
Psittaciformes	Psittacidae	Amazona leucocephala	Cuban Amazon	1
Psittaciformes	Psittacidae	Pionus maximiliani	Scaly-headed Parrot	1
Galliformes	Cracidae	Pipile pipile	Trinidad Piping-guan	1

Psittaciformes	Psittacidae	Ara rubrogenys	Red-fronted Macaw	1
Psittaciformes	Psittacidae	Amazona guildingii	St Vincent Amazon	1
Galliformes	Cracidae	Ortalis garrula	Chestnut-winged Chachalaca	1
Galliformes	Cracidae	Ortalis guttata	Speckled Chachalaca	1
Passeriformes	Emberizidae	Junco hyemalis	Dark-eyed Junco	1
Tinamiformes	Tinamidae	Eudromia elegans	Elegant Crested-tinamou	1
Psittaciformes	Psittacidae	Pionus menstruus	Blue-headed Parrot	1
Tinamiformes	Tinamidae	Crypturellus soui	Little Tinamou	1
Tinamiformes	Tinamidae	Tinamus major	Great Tinamou	1
Passeriformes	Icteridae	Sturnella magna	Eastern Meadowlark	1
Falconiformes	Accipitridae	Buteo polyosoma	Red-backed Hawk	1
Psittaciformes	Psittacidae	Touit batavicus	Lilac-tailed Parrotlet	1
Psittaciformes	Psittacidae	Nannopsittaca panychlora	Tepui Parrotlet	1
Struthioniformes	Casuariidae	Casuarius bennetti	Dwarf Cassowary	1
Passeriformes	Turdidae	Turdus nudigenis		1
Passeriformes	Sylviidae	Hippolais pallida	Eastern Olivaceous Warbler	1
Passeriformes	Emberizidae	Sporophila albogularis	White-throated Seedeater	1
Passeriformes	Emberizidae	Emberiza caesia	Cretzschmar's Bunting	1
Passeriformes	Alaudidae	Melanocorypha bimaculata	Bimaculated Lark	1
Galliformes	Phasianidae	Coturnix coromandelica	Rain Quail	1
Anseriformes	Anatidae	Oxyura vittata	Lake Duck	1
Passeriformes	Emberizidae	Zonotrichia albicollis	White-throated Sparrow	1
Passeriformes	Cardinalidae	Piranga olivacea	Scarlet Tanager	1
Passeriformes	Thraupidae	Thraupis palmarum	Palm Tanager	1
Passeriformes	Thraupidae	Euphonia trinitatis	Trinidad Euphonia	1
Passeriformes	Thraupidae	Tangara fastuosa	Seven-coloured Tanager	1
Passeriformes	Thraupidae	Tangara nigrocincta	Masked Tanager	1
Passeriformes	Thraupidae	Cyanerpes caeruleus	Purple Honeycreeper	1
Gruiformes	Otididae	Chlamydotis macqueenii		1
Apodiformes	Trochilidae	Chaetocercus jourdanii	Rufous-shafted Woodstar	1
Galliformes	Phasianidae	Perdicula erythrorhyncha	Painted Bush-quail	1
Passeriformes	Emberizidae	Loxigilla portoricensis	Puerto Rican Bullfinch	1
Galliformes	Phasianidae	Francolinus icterorhynchus	Heuglin's Francolin	1
Passeriformes	Cardinalidae	Pheucticus melanocephalus	Black-headed Grosbeak	1
Psittaciformes	Psittacidae	Psittacula columboides	Malabar Parakeet	1
Passeriformes	Icteridae	Icterus wagleri	Black-vented Oriole	1
Passeriformes	Icteridae	Chrysomus icterocephalus	Yellow-hooded Blackbird	1
Apodiformes	Trochilidae	Florisuga mellivora	White-necked Jacobin	1
Apodiformes	Apodidae	Collocalia fuciphaga	Edible-nest Swiftlet	1
Passeriformes	Icteridae	Dolichonyx oryzivorus	Bobolink	1
Psittaciformes	Psittacidae	Cacatua ophthalmica	Blue-eyed Cockatoo	1
Anseriformes	Anatidae	Anas crecca	Common Teal	1
Passeriformes	Thraupidae	Tersina viridis	Swallow Tanager	1
Passeriformes	Corvidae	Cyanocorax chrysops	Plush-crested Jay	1

Passeriformes	Tyrannidae	Tyrannus savana	Fork-tailed Flycatcher	1
Anseriformes	Anatidae	Mergus merganser	Common Merganser	1
Falconiformes	Accipitridae	Haliaeetus pelagicus	Steller's Sea-eagle	1
Anseriformes	Anatidae	Bucephala islandica	Barrow's Goldeneye	1
Anseriformes	Anatidae	Aythya novaeseelandiae	New Zealand Scaup	1
Passeriformes	Chloropseidae	Chloropsis hardwickii	Orange-bellied Leafbird	1
Falconiformes	Accipitridae	Elanoides forficatus	American Swallow-tailed Kite	1
Passeriformes	Laniidae	Lanius tephronotus	Grey-backed Shrike	1
Passeriformes	Laniidae	Lanius collaris	Common Fiscal	1
Passeriformes	Cinclosomatidae	Cinclosoma ajax	Painted Quail-thrush	1
Gruiformes	Rallidae	Porzana porzana	Spotted Crake	1
Passeriformes	Corvidae	Cyanocitta cristata	Blue Jay	1
Passeriformes	Pittidae	Pitta moluccensis	Blue-winged Pitta	1
Charadriiformes	Laridae	Larus cirrocephalus	Grey-headed Gull	1
Passeriformes	Corvidae	Cissa chinensis	Green Magpie	1
Passeriformes	Corvidae	Dendrocitta vagabunda	Rufous Treepie	1
Passeriformes	Corvidae	Pyrrhocorax pyrrhocorax	Red-billed Chough	1
Passeriformes	Corvidae	Corvus corone	Carrion Crow	1
Passeriformes	Corvidae	Corvus ruficollis	Brown-necked Raven	1
Charadriiformes	Laridae	Larus dominicanus	Kelp Gull	1
Anseriformes	Anatidae	Anas rhynchotis	Australasian Shoveler	1
Anseriformes	Anatidae	Anas platalea	Red Shoveler	1
Passeriformes	Cracticidae	Strepera graculina	Pied Currawong	1
Charadriiformes	Glareolidae	Glareola ocularis	Madagascar Pratincole	1
Falconiformes	Accipitridae	Chondrohierax uncinatus	Hook-billed Kite	1
Ciconiiformes	Ciconiidae	Mycteria cinerea	Milky Stork	1
Falconiformes	Falconidae	Falco biarmicus	Lanner Falcon	1
Podicipediformes	Podicipedidae	Podiceps auritus	Horned Grebe	1
Psittaciformes	Psittacidae	Vini ultramarina	Ultramarine Lorikeet	1
Ciconiiformes	Ardeidae	Egretta gularis	Western Reef-egret	1
Ciconiiformes	Ardeidae	Ardea goliath	Goliath Heron	1
Ciconiiformes	Ardeidae	Nyctanassa violacea	Yellow-crowned Night-heron	1
Psittaciformes	Psittacidae	Chalcopsitta atra	Black Lory	1
Falconiformes	Falconidae	Falco sparverius	American Kestrel	1
Ciconiiformes	Threskiornithidae	Bostrychia hagedash	Hadada Ibis	1
Falconiformes	Falconidae	Milvago chimachima	Yellow-headed Caracara	1
Pelecaniformes	Pelecanidae	Pelecanus philippensis	Spot-billed Pelican	1
Passeriformes	Pittidae	Pitta versicolor	Noisy Pitta	1
Falconiformes	Cathartidae	Gymnogyps californianus	California Condor	1
Piciformes	Picidae	Melanerpes carolinus	Red-bellied Woodpecker	1
Coraciiformes	Coraciidae	Coracias cyanogaster	Blue-bellied Roller	1
Ciconiiformes	Ciconiidae	Ciconia nigra	Black Stork	1
Ciconiiformes	Ciconiidae	Ciconia abdimii	Abdim's Stork	1
Falconiformes	Accipitridae	Accipiter badius	Shikra	1
Ciconiiformes	Ciconiidae	Ciconia boyciana	Oriental Stork	1
Ciconiiformes	Ciconiidae	Leptoptilos crumeniferus	Marabou Stork	1
Coraciiformes	Bucerotidae	Tockus nasutus	African Grey Hornbill	1
Sphenisciformes	Spheniscidae	Spheniscus demersus	African Penguin	1

Procellariiformes	Pelecanoididae	Pelecanoides urinatrix	Common Diving-petrel	1
Piciformes	Ramphastidae	Megalaima lineata	Lineated Barbet	1
Anseriformes	Anatidae	Anas luzonica	Philippine Duck	1
Coraciiformes	Alcedinidae	Megaceryle torquata	Ringed Kingfisher	1
Passeriformes	Zosteropidae	Zosterops modestus	Seychelles White-eye	1
Charadriiformes	Charadriidae	Vanellus spinosus	Spur-winged Lapwing	1
Passeriformes	Mimidae	Cinclocerthia ruficauda	Brown Trembler	1
Psittaciformes	Psittacidae	Platycercus icterotis	Western Rosella	1
Passeriformes	Paridae	Parus afer	Grey Tit	1
Psittaciformes	Psittacidae	Northiella haematogaster	Bluebonnet	1
Passeriformes	Pycnonotidae	Pycnonotus atriceps	Black-headed Bulbul	1
Gruiformes	Rallidae	Porphyrio flavirostris	Azure Gallinule	1
Passeriformes	Pycnonotidae	Pycnonotus bimaculatus	Orange-spotted Bulbul	1
Passeriformes	Pycnonotidae	Hypsipetes madagascariensis	Madagascar Black Bulbul	1
Passeriformes	Pycnonotidae	Hypsipetes crassirostris	Seychelles Bulbul	1
Passeriformes	Cisticolidae	Cisticola cherina	Madagascar Cisticola	1
Anseriformes	Anatidae	Cyanochen cyanoptera	Blue-winged Goose	1
Passeriformes	Zosteropidae	Zosterops pallidus	Pale White-eye	1
Passeriformes	Sturnidae	Creatophora cinerea	Wattled Starling	1
Passeriformes	Sylviidae	Cettia cetti	Cetti's Warbler	1
Passeriformes	Sylviidae	Locustella luscinioides	Savi's Warbler	1
Passeriformes	Sylviidae	Acrocephalus melanopogon	Moustached Warbler	1
Passeriformes	Sylviidae	Acrocephalus scirpaceus	Eurasian Reed-warbler	1
Passeriformes	Sylviidae	Acrocephalus arundinaceus	Great Reed-warbler	1
Passeriformes	Timaliidae	Garrulax monileger	Lesser Necklaced Laughingthrush	1
Psittaciformes	Psittacidae	Neopsephotus bourkii	Bourke's Parrot	1
Psittaciformes	Psittacidae	Lathamus discolor	Swift Parrot	1
Passeriformes	Muscicapidae	Ficedula superciliaris	Ultramarine Flycatcher	1
Gruiformes	Rallidae	Porzana parva	Little Crake	1
Gruiformes	Rallidae	Rallus aquaticus	Water Rail	1
Passeriformes	Cisticolidae	Prinia gracilis	Graceful Prinia	1
Passeriformes	Turdidae	Brachypteryx montana	White-browed Shortwing	1
Gruiformes	Rallidae	Gallirallus owstoni	Guam Rail	1
Passeriformes	Monarchidae	Pomarea dimidiata	Rarotonga Monarch	1
Charadriiformes	Charadriidae	Charadrius dubius	Little Ringed Plover	1
Anseriformes	Anatidae	Anas fulvigula	Mottled Duck	1
Passeriformes	Turdidae	Zoothera citrina	Orange-headed Thrush	1
Passeriformes	Turdidae	Sialia sialis	Eastern Bluebird	1
Passeriformes	Turdidae	Catharus guttatus	Hermit Thrush	1
Passeriformes	Turdidae	Turdus ruficollis	Dark-throated Thrush	1
Passeriformes	Turdidae	Turdus naumanni	Dusky Thrush	1
Charadriiformes	Jacanidae	Jacana jacana	Wattled Jacana	1
Charadriiformes	Scolopacidae	Limosa limosa	Black-tailed Godwit	1
Passeriformes	Sturnidae	Sturnus sinensis	White-shouldered Starling	1
Passeriformes	Turdidae	Turdus grayi	Clay-coloured Thrush	1
Charadriiformes	Charadriidae	Vanellus miles	Masked Lapwing	1

Anseriformes	Anatidae	Nettapus coromandelianus	Cotton Pygmy-goose	1
Passeriformes	Muscicapidae	Ficedula narcissina	Narcissus Flycatcher	1
Psittaciformes	Psittacidae	Forpus xanthopterygius	Blue-winged Parrotlet	1
Charadriiformes	Scolopacidae	Scolopax minor	American Woodcock	1
Ciconiiformes	Threskiornithidae	Threskiornis spinicollis	Straw-necked Ibis	1
Passeriformes	Muscicapidae	Erythropygia galactotes	Rufous-tailed Scrub-robin	1
Passeriformes	Muscicapidae	Phoenicurus ochruros	Black Redstart	1
Columbiformes	Pteroclididae	Pterocles orientalis	Black-bellied Sandgrouse	1
Psittaciformes	Psittacidae	Platycercus caledonicus	Green Rosella	1
Passeriformes	Sturnidae	Lamprotornis splendidus	Splendid Glossy-starling	1
Psittaciformes	Psittacidae	Platycercus venustus	Northern Rosella	1
Passeriformes	Turdidae	Turdus falcklandii	Austral Thrush	1

Appendix E. The full model selection tables from Chapter 5, identifying the most likely models for log alien range size at the global scale and then for each realm separately. Only models with ΔAICc < 4 are included.

ALL GLOBAL	**(Intercept)**	**No. of Successful introductions**	**(No. of Successful introductions)^2**	**Native range size**	**Residence time**	**(Residence time)2**	**Body mass**	**Specialisation index**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
Model 31	2.76	1.21	0.09	0.31	-0.43	-	0.13	-	6	-687.82	1387.89	0.00	0.26
Model 32	2.22	1.21	0.09	0.32	-0.42	-	0.14	0.12	7	-687.61	1389.56	1.67	0.11
Model 29	2.39	1.62	-	0.32	-0.43	-	0.13	-	5	-689.81	1389.81	1.92	0.10
Model 63	2.28	1.20	0.09	0.31	-0.20	-0.03	0.13	-	7	-687.77	1389.88	1.99	0.10
Model 27	3.23	1.18	0.09	0.32	-0.40	-	-	-	5	-689.87	1389.94	2.04	0.09
Model 30	1.87	1.62	-	0.33	-0.42	-	0.14	0.12	6	-689.61	1391.49	3.60	0.04
Model 64	1.70	1.20	0.09	0.32	-0.16	-0.03	0.15	0.12	8	-687.55	1391.55	3.66	0.04
Model 61	2.71	1.62	-	0.32	-0.59	0.02	0.13	-	6	-689.79	1391.84	3.95	0.04
Model 25	2.87	1.60	-	0.33	-0.40	-	-	-	4	-691.87	1391.86	3.97	0.04

AFROTROPICAL	**(Intercept)**	**No. of Successful introductions**	**(No. of Successful introductions)^2**	**Native range size**	**Residence time**	**(Residence time)2**	**Body mass**	**Specialisation index**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
Model 10	-0.52	1.61	-	0.24	-	-	-	0.71	4	-137.40	283.46	0.00	0.13
Model 26	0.82	1.72	-	0.24	-0.30	-	-	0.63	5	-136.70	284.40	0.93	0.08
Model 9	1.92	1.56	-	0.19	-	-	-	-	3	-139.12	284.63	1.17	0.07
Model 25	3.23	1.70	-	0.20	-0.38	-	-	-	4	-138.01	284.68	1.21	0.07
Model 1	4.59	1.61	-	-	-	-	-	-	2	-140.65	285.49	2.02	0.05
Model 14	-0.41	1.36	0.06	0.24	-	-	-	0.72	5	-137.30	285.60	2.13	0.04
Model 12	-0.64	1.62	-	0.24	-	-	0.02	0.74	5	-137.40	285.79	2.33	0.04
Model 2	3.41	1.66	-	-	-	-	-	0.50	3	-139.81	286.01	2.55	0.04
Model 17	5.93	1.74	-	-	-0.32	-	-	-	3	-139.86	286.11	2.65	0.03
Model 11	2.14	1.53	-	0.20	-	-	-0.09	-	4	-138.93	286.51	3.05	0.03
Model 28	0.50	1.76	-	0.24	-0.34	-	0.08	0.70	6	-136.57	286.57	3.11	0.03
Model 58	1.83	1.71	-	0.24	-0.80	0.06	-	0.63	6	-136.61	286.64	3.17	0.03
Model 30	0.87	1.51	0.05	0.25	-0.29	-	-	0.63	6	-136.63	286.68	3.21	0.03
Model 13	2.03	1.34	0.05	0.19	-	-	-	-	4	-139.05	286.75	3.29	0.03
Model 57	4.10	1.69	-	0.20	-0.80	0.05	-	-	5	-137.95	286.89	3.43	0.02
Model 29	3.29	1.54	0.04	0.20	-0.37	-	-	-	5	-137.97	286.93	3.47	0.02
Model 27	3.24	1.69	-	0.21	-0.36	-	-0.02	-	5	-138.00	287.00	3.54	0.02
Model 18	4.70	1.75	-	-	-0.26	-	-	0.41	4	-139.30	287.25	3.79	0.02

AUSTRALASIAN	(Intercept)	No. of Successful introductions	(No. of Successful introductions)^2	Native range size	Residence time	(Residence time)2	Body mass	Specialisation index	df	logLik	AICc	ΔAICc	weight
Model 9	1.10	1.83	-	0.33	-	-	-	-	3	-176.95	360.20	0.00	0.12
Model 57	17.19	1.89	-	0.30	-7.61	0.89	-	-	5	-174.72	360.20	0.00	0.12
Model 25	3.29	2.03	-	0.33	-0.55	-	-	-	4	-176.35	361.21	1.01	0.07
Model 10	0.16	1.87	-	0.34	-	-	-	0.33	4	-176.46	361.43	1.24	0.07
Model 61	18.96	2.47	-0.14	0.30	-8.63	1.00	-	-	6	-174.21	361.51	1.31	0.06
Model 11	0.57	1.85	-	0.33	-	-	0.09	-	4	-176.57	361.65	1.45	0.06
Model 58	15.97	1.92	-	0.30	-7.41	0.87	-	0.26	6	-174.40	361.89	1.69	0.05
Model 59	15.69	1.93	-	0.30	-7.04	0.81	0.07	-	6	-174.51	362.11	1.91	0.05
Model 26	2.18	2.07	-	0.34	-0.53	-	-	0.37	5	-175.74	362.25	2.05	0.04
Model 13	0.99	1.98	-0.04	0.33	-	-	-	-	4	-176.91	362.32	2.13	0.04
Model 12	-0.87	1.91	-	0.34	-	-	0.13	0.43	5	-175.78	362.33	2.13	0.04
Model 27	1.99	2.00	-	0.34	-0.45	-	0.12	-	5	-175.95	362.66	2.47	0.04
Model 62	17.74	2.50	-0.14	0.31	-8.44	0.98	-	0.27	7	-173.88	363.23	3.03	0.03
Model 60	13.49	1.97	-	0.31	-6.55	0.75	0.10	0.34	7	-174.01	363.50	3.30	0.02
Model 14	-0.01	2.06	-0.05	0.34	-	-	-	0.34	5	-176.41	363.58	3.38	0.02
Model 29	2.29	2.24	-0.07	0.34	-0.41	-	-	-	5	-176.41	363.59	3.39	0.02
Model 28	0.51	2.05	-	0.35	-0.41	-	0.15	0.40	6	-175.26	363.60	3.41	0.02
Model 63	17.77	2.44	-0.12	0.30	-8.14	0.94	0.05	-	7	-174.12	363.71	3.52	0.02
Model 15	0.54	1.91	-0.02	0.33	-	-	0.09	-	5	-176.56	363.89	3.70	0.02

INDOMALAY	(Intercept)	No. of Successful introductions	(No. of Successful introductions)^2	Native range size	Residence time	(Residence time)2	Body mass	Specialisation index	df	logLik	AICc	ΔAICc	weight
Model 25	4.52	1.56	-	0.41	-1.05	-	-	-	4	-194.28	397.06	0.00	0.18
Model 29	4.99	0.75	0.22	0.40	-1.04	-	-	-	5	-193.22	397.17	0.12	0.17
Model 57	6.42	1.48	-	0.40	-2.04	0.14	-	-	5	-193.97	398.69	1.63	0.08
Model 27	3.98	1.58	-	0.42	-1.07	-	0.11	-	5	-194.05	398.85	1.79	0.07
Model 26	5.59	1.56	-	0.38	-1.07	-	-	-0.21	5	-194.15	399.03	1.98	0.07
Model 31	4.49	0.79	0.21	0.40	-1.05	-	0.10	-	6	-193.01	399.07	2.02	0.07
Model 61	6.01	0.78	0.20	0.39	-1.59	0.08	-	-	6	-193.12	399.30	2.24	0.06
Model 30	5.56	0.78	0.21	0.38	-1.05	-	-	-0.11	6	-193.18	399.40	2.35	0.06
Model 59	5.79	1.51	-	0.40	-1.98	0.13	0.10	-	6	-193.79	400.63	3.57	0.03
Model 58	7.01	1.49	-	0.37	-1.96	0.13	-	-0.15	6	-193.90	400.86	3.80	0.03
Model 28	4.82	1.58	-	0.39	-1.08	-	0.09	-0.15	6	-193.99	401.02	3.97	0.03

NEARCTIC	**(Intercept)**	**No. of Successful introductions**	**(No. of Successful introductions)^2**	**Native range size**	**Residence time**	**(Residence time)2**	**Body mass**	**Specialisation index**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
Model 7	2.53	0.09	0.60	0.28	-	-	-	-	4	-172.75	354.03	0.00	0.15
Model 8	1.77	0.07	0.61	0.24	-	-	0.26	-	5	-171.68	354.17	0.14	0.14
Model 4	5.12	-0.18	0.71	-	-	-	0.30	-	4	-172.92	354.37	0.34	0.13
Model 3	6.69	-0.21	0.71	-	-	-	-	-	3	-174.40	355.12	1.09	0.09
Model 39	1.48	0.18	0.58	0.31	-	-	-	0.22	5	-172.61	356.03	2.00	0.06
Model 40	0.57	0.18	0.59	0.28	-	-	0.26	0.25	6	-171.50	356.15	2.12	0.05
Model 15	2.81	0.13	0.60	0.29	-0.13	-	-	-	5	-172.69	356.19	2.16	0.05
Model 12	4.49	-0.21	0.70	-	0.15	-	0.31	-	5	-172.83	356.48	2.45	0.04
Model 16	1.84	0.08	0.61	0.24	-0.03	-	0.25	-	6	-171.68	356.50	2.47	0.04
Model 36	5.16	-0.18	0.71	-	-	-	0.30	-0.01	5	-172.92	356.64	2.61	0.04
Model 35	6.91	-0.23	0.71	-	-	-	-	-0.09	4	-174.38	357.29	3.26	0.03
Model 11	6.44	-0.22	0.70	-	0.06	-	-	-	4	-174.39	357.31	3.28	0.03

NEOTROPICAL	**(Intercept)**	**No. of Successful introductions**	**(No. of Successful introductions)^2**	**Native range size**	**Residence time**	**(Residence time)2**	**Body mass**	**Specialisation index**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
Model 7	2.54	0.36	0.27	0.30	-	-	-	-	4	-176.57	361.62	0.00	0.19
Model 8	2.15	0.37	0.28	0.27	-	-	0.16	-	5	-176.00	362.75	1.13	0.11
Model 15	3.37	0.51	0.26	0.30	-0.24	-	-	-	5	-176.28	363.29	1.67	0.08
Model 39	3.54	0.33	0.27	0.28	-	-	-	-0.27	5	-176.28	363.30	1.68	0.08
Model 5	1.63	1.27	-	0.34	-	-	-	-	3	-178.95	364.18	2.56	0.05
Model 16	3.13	0.55	0.27	0.29	-0.29	-	0.11	-	6	-175.90	364.85	3.23	0.04
Model 4	5.61	0.35	0.32	-	-	-	0.25	-	4	-178.18	364.85	3.23	0.04
Model 40	2.80	0.35	0.28	0.26	-	-	0.14	-0.16	6	-175.91	364.87	3.25	0.04
Model 47	4.46	0.48	0.27	0.27	-0.24	-	-	-0.29	6	-175.93	364.92	3.30	0.04
Model 31	2.87	0.50	0.27	0.30	0.02	-0.03	-	-	6	-176.24	365.53	3.91	0.03
Model 13	2.40	1.38	-	0.34	-0.22	-	-	-	4	-178.53	365.55	3.93	0.03

OCEANIC	**(Intercept)**	**No. of Successful introductions**	**(No. of Successful introductions)^2**	**Native range size**	**Residence time**	**(Residence time)2**	**Body mass**	**Specialisation index**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
Model 13	3.63	0.76	-	0.34	-0.36	-	-	-	4	-218.85	446.07	0.00	0.10
Model 7	2.52	0.19	0.15	0.33	-	-	-	-	4	-218.88	446.14	0.07	0.10
Model 6	1.79	0.68	-	0.31	-	-	0.17	-	4	-219.02	446.42	0.35	0.08
Model 15	3.92	0.27	0.16	0.34	-0.38	-	-	-	5	-217.94	446.44	0.36	0.08

Model 14	3.20	0.78	-	0.32	-0.39	-	0.19	-	5	-218.03	446.63	0.55	0.08
Model 37	1.52	0.67	-	0.35	-	-	-	0.18	4	-219.51	447.39	1.31	0.05
Model 8	2.07	0.25	0.13	0.31	-	-	0.15	-	5	-218.43	447.43	1.36	0.05
Model 16	3.53	0.34	0.14	0.32	-0.40	-	0.16	-	6	-217.38	447.55	1.48	0.05
Model 39	1.63	0.17	0.16	0.35	-	-	-	0.22	5	-218.59	447.75	1.67	0.04
Model 29	4.98	0.75	-	0.34	-1.05	0.08	-	-	5	-218.62	447.80	1.73	0.04
Model 38	0.69	0.69	-	0.34	-	-	0.20	0.25	5	-218.65	447.86	1.79	0.04
Model 45	2.96	0.76	-	0.36	-0.35	-	-	0.15	5	-218.72	448.00	1.92	0.04
Model 47	3.13	0.25	0.16	0.36	-0.36	-	-	0.18	6	-217.73	448.27	2.20	0.03
Model 46	2.17	0.78	-	0.34	-0.38	-	0.22	0.22	6	-217.74	448.28	2.21	0.03
Model 31	4.78	0.29	0.15	0.34	-0.82	0.05	-	-	6	-217.84	448.48	2.41	0.03
Model 30	4.18	0.77	-	0.32	-0.88	0.06	0.18	-	6	-217.92	448.64	2.56	0.03
Model 40	0.86	0.23	0.14	0.34	-	-	0.17	0.28	6	-217.96	448.71	2.64	0.03
Model 48	2.38	0.31	0.15	0.34	-0.38	-	0.19	0.25	7	-217.00	449.07	3.00	0.02
Model 61	4.33	0.75	-	0.36	-1.06	0.09	-	0.16	6	-218.47	449.73	3.66	0.02
Model 32	4.07	0.35	0.13	0.32	-0.67	0.03	0.16	-	7	-217.34	449.76	3.69	0.02

PALEARCTIC	**(Intercept)**	**No. of Successful introductions**	**(No. of Successful introductions)^2**	**Native range size**	**Residence time**	**(Residence time)2**	**Body mass**	**Specialisation index**	**df**	**logLik**	**AICc**	**ΔAICc**	**weight**
Model 9	4.73	1.27	-	-	0.52	-	-	-	3	-177.01	360.31	0.00	0.13
Model 11	5.31	0.73	0.12	-	0.48	-	-	-	4	-176.27	361.02	0.72	0.09
Model 13	2.85	1.29	-	0.13	0.48	-	-	-	4	-176.53	361.54	1.23	0.07
Model 10	4.92	1.27	-	-	0.56	-	-0.07	-	4	-176.81	362.11	1.80	0.05
Model 41	5.27	1.26	-	-	0.49	-	-	-0.18	4	-176.88	362.23	1.93	0.05
Model 12	5.66	0.64	0.14	-	0.53	-	-0.10	-	5	-175.88	362.48	2.18	0.04
Model 25	4.52	1.28	-	-	0.62	-0.01	-	-	4	-177.00	362.49	2.18	0.04
Model 15	3.65	0.79	0.11	0.11	0.45	-	-	-	5	-175.92	362.57	2.26	0.04
Model 43	5.88	0.71	0.13	-	0.45	-	-	-0.19	5	-176.12	362.97	2.67	0.03
Model 27	4.51	0.69	0.14	-	0.90	-0.05	-	-	5	-176.17	363.08	2.77	0.03
Model 14	3.06	1.28	-	0.13	0.52	-	-0.07	-	5	-176.34	363.41	3.11	0.03
Model 45	3.29	1.28	-	0.12	0.47	-	-	-0.10	5	-176.49	363.71	3.40	0.02
Model 29	2.64	1.29	-	0.13	0.59	-0.01	-	-	5	-176.52	363.77	3.47	0.02
Model 42	5.70	1.25	-	-	0.53	-	-0.09	-0.25	5	-176.58	363.88	3.58	0.02
Model 16	4.07	0.70	0.13	0.11	0.50	-	-0.09	-	6	-175.56	364.15	3.84	0.02
Model 44	6.59	0.60	0.15	-	0.50	-	-0.12	-0.28	6	-175.56	364.16	3.86	0.02
Model 3	7.01	0.82	0.16	-	-	-	-	-	3	-178.96	364.20	3.90	0.02