The importance of Protected Areas for species undergoing distributional changes

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Doctor of Philosophy

University of York

Biology

September 2017

Abstract

The value of Protected Areas for wildlife will diminish if the species for which they were originally designated are pushed out of their boundaries by changing temperatures, or if they are infiltrated by invasive species that are harmful to native species. Here, I assess the performance of Protected Areas against this background of distributional change.

I found that Protected Areas have facilitated the range expansions of the six wetland bird species that have recently colonised the UK, both as sites at which breeding first occurs and as locations where substantial populations can establish before spreading to unprotected land. In contrast, non-native species did not initially ‘invade’ Protected Areas, but subsequently colonised them as their populations grew.

I complemented this analysis with a field research project in a Mexican Biosphere Reserve. Here, Strictly Protected Areas were resistant to non-native species (as in the UK), and important for species undergoing global population declines. However, partially-protected locations with habitat modification provided opportunities for both non-natives and native generalists. Consequently, modified areas were characterised by higher local-alpha diversity than relatively natural areas, although they contained relatively similar suites of species across different biogeographical zones. Thus, evaluating the impact of Protected Areas depended on the metric of biodiversity change considered, and on the level of protection.

Similar patterns were revealed on a global scale (considering 118 countries). Range expansions (colonisations and introductions) have outpaced countrywide extirpations over the last two centuries, resulting in a c.4% average net increase in national breeding bird avifaunas, even though gamma- and beta-diversity have decreased. Protected Areas may have promoted ‘beneficial’ change in this context; there were more colonisations and fewer extirpations in countries with more protected land.

Protected Areas will remain crucial as a part of future conservation strategies to protect biodiversity in an era of increasing distributional dynamism.

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Acknowledgements

I would like to thank the following people:

- Chris Thomas (University of York) and Richard Bradbury (RSPB), my supervisors, for providing limitless input, inspiration, patience and support. I would have given up on this project if it was not for Chris's ability to motivate, and provide clarity and direction.
- Jane Hill and Calvin Dytham (University of York), members of my Thesis Advisory Panel, for assisting with research advice, and providing help with the practical side of studying part-time.
- James Reynolds and Graham Martin (University of Birmingham), for guiding me through my MSc and making this next step possible.
- Denise Gilby and the directors of VICTORIA school, for granting me the flexibility to study whilst working full-time initially as a class-teacher, and eventually as a head-teacher.
- Patrick Clarke and Ricky Kanabar, my friends, for providing practical and moral support during my time at York.
- JP Murphy, Juan Manuel García and Valentina Magaña, for making the completion of the field-work possible.
- My family, and particularly my Dad, for endless encouragement during each long-distance phone call for six years, and for providing financial support without question.

Several others have played a part in this project, and I extend my thanks to all.

Declaration

I declare that this thesis is a presentation of original work and I am the sole author. This work has not previously been presented for an award at this, or any other, University. All sources are acknowledged as References.

The thesis involved collaboration with Chris Thomas (CT), Richard Bradbury (RB) and Mark Holling (MH).

Chapter 2 has been published as:

Hiley, J.R., Bradbury, R., Holling, M. & Thomas, C.D. (2013) Protected Areas act as establishment centres for species colonizing the UK. *Proceedings of the Royal Academy of Sciences B: Biological Sciences*, **280**, 20122310.

This chapter is reproduced in full, apart from minor formatting alterations. JRH wrote the text with input from CT and RB. RB and MH helped facilitate the collection of data. CT supervised the study.

Chapter 3 has been published as:

Hiley, J.R., Bradbury, R. & Thomas, C.D. (2014) Introduced and natural colonists show contrasting patterns of protected area association. *Diversity and Distributions*, **20**, 943-951.

This chapter is reproduced in full, apart from minor formatting alterations. JRH wrote the text with input from CT and RB. CT supervised the study.

Chapter 4 has been published as:

Hiley, J.R., Bradbury, R.B. & Thomas, C.D. (2016) Impacts of habitat change and protected areas on alpha and beta diversity of Mexican birds. *Diversity and Distributions*, **22**, 1245-1254.

This chapter is reproduced in full, apart from minor formatting alterations. JRH wrote the text with input from CT and RB. CT and RB helped with the study design and supervised the study.

Chapter 5 is currently in preparation for submission as:

Hiley, J.R., Bradbury, R. & Thomas, C.D. The changing geography of bird species richness and community composition; the roles of extirpations, introductions and colonisations. In prep.

The draft manuscript is reproduced in full, apart from minor formatting alterations. JRH wrote the text with input from CT and RB. CT and RB supervised the study.

Chapter 1: Introduction

1.1 Aims and Justification

Protected Areas are a fundamental conservation measure employed to protect biodiversity from a suite of threats headed by over-exploitation and direct persecution, habitat loss and degradation, pollution (including indirect impacts, particularly climate-change) and invasive non-native species (INNS) (Wilson, 2002). The above factors are all considered ‘main threats’ by the Convention on Biological Diversity, and attempts to either remove or mitigate against them form the core of the AICHI Biodiversity targets (CBD, 2010) and an important part of the United Nation’s Sustainable Development Goals (SDGs) (United Nations, 2015).

Protected Area designation commonly results from the *existing* presence of either a species or selection of species (including particular biological ‘communities’), or the high abundances of certain species. However, the geographic ranges of species are liable to change, and many of the threats to biodiversity are particularly associated with distributional and community dynamism. For example, the rapid spread and potential subsequent devastation of INNS is well understood (Sakai *et al.*, 2001), as, increasingly, are the latitudinal and altitudinal range shifts that have been caused by recent climatic warming (Parmesan & Yohe, 2003).

The role of Protected Areas in the context of these drivers of change has, until recently, been poorly understood. Protected Areas could potentially be devalued if, as a result of climate change or other factors, they are no longer occupied by the species for which they were originally designated (Araújo *et al*., 2004; Hannah *et al*., 2007). On the other hand, species colonising new areas will need suitable habitat in which to establish populations, and Protected Areas might provide such habitat. For Protected Areas to be effective at all, their ability to resist the spread of INNS and maintain natural habitats with minimal human modification is also important. This role has become increasingly difficult as pressures associated with biological invasions (e.g. Seebens *et al*., 2017) and land-development increase.

This thesis addresses these matters through a series of original articles, to increase our understanding of the past, current and future roles of Protected Area networks as the distributions of species change in response to a variety of environmental drivers. I assess the role played by Protected Areas for species which have expanded their distribution under their own volition (natural colonists - Chapter 2) and via human release and transportation (introductions - Chapter 3). At a local (Chapter 4) and then global scale (Chapter 5), I assess the relationships between Protected Areas, land-use change and the alpha and beta-diversity of bird species, against a backdrop of expansions (introductions and colonisations) and reductions (extirpations and extinctions) in distributional extent.

1.2 Protected Areas

1.2.1 Coverage, types and designation of Protected Areas

A Protected Area (hereon PA) is defined by the International Union for the Conservation of Nature (IUCN) as “A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values” (Dudley, 2008). PAs constitute a cornerstone of global conservation efforts.

Increased and improved coverage of PAs has been a key aim of both recent and current global biodiversity action plans. Both Sustainable Development Goal #15 (United Nations, 2015) and AICHI Target #11 (CBD, 2010) refer to the safeguarding of key biodiversity areas and AICHI #11 specifies a target of 17% PA area coverage for terrestrial systems, and 10% for marine, to be achieved by 2020. These are the latest steps towards increased protection over an extended period. Consequently, the number of PAs has risen sharply over the last six decades. In 1962, approximately 1000 sites were protected globally (Chape *et al.*, 2003), whereas Europe alone currently has over 120,000 designated sites (EEA, 2012). Over 15% of land area is now protected globally (Eklund & Cabeza, 2017), which represents significant progress towards the 17% target. This figure, however, varies strongly by region and by country. Coverage of PAs diverges from as much as 30% (e.g. Germany) to less than 1% (e.g. Iraq) (World Bank, 2017) and many of the 193 parties that adopted the AICHI guidelines have set their individual targets below the 17% level (Butchart *et al.*, 2015).

The term ‘Protected Area’ encompasses a broad variety of designations and associated management regimes, varying under IUCN designation (Table 1.1) from strict protection with limited visitor pressures, to areas which encourage sustainable, low-level use of natural resources. Thus, whilst overall PA coverage is increasing, discrepancies in the level of protection exist within countries, to add to the differences in percentage coverage in each country. Recently, there has been an increasing designation of sites (Naughton-Treves *et al.*, 2005) which allow local, and sustainable, resource use (IUCN Category VI, Table 1.1), particularly in tropical areas. The ‘ecological effectiveness’ of such sites, however, might differ significantly from more strictly protected locations (see below; Beresford *et al.,* 2013; Chapter 4).

Acquisition of PA status, whether for strict or low-level protection regimes, does not necessarily imply that conservation management is implemented successfully. Many PAs are considered by some parties to be ‘Paper Parks’, which are designated as protected but where conservation measures are not fully implemented (Watson *et al*., 2014; Blackman *et al*., 2015). Such PAs often ‘fail’ because of inadequate resources as well as lack of political will or planning (García-Frapolli *et al*., 2009). The Paper Park label has been particularly, but not uniquely, associated with marine reserves (e.g. Rife *et al*., 2013), and with PAs in emerging economies, for example in Mexico (see Chapter 4; García-Frapolli *et al*., 2009; Blackman *et al*., 2015). The designation of other land as a PA might not make much direct contribution to conservation if the PAs are located in remote or unproductive land areas where threats to habitats and biodiversity were initially low, and hence they would not have been harmed anyway.

These differences in regional coverage, categories of protection, and efficacy of policy implementation are reasons that reports of PA effectiveness (see below) are variable. These factors are taken into consideration in the analyses of PA performance which follow in the rest of this thesis.

Variation in PA performance might also stem from the reason for designation. Whereas some PAs are gazetted for reasons such as cultural diversity, the majority of PAs are designated for the presence within their borders of existing biological features (Table 1.2). For birds, typical criteria include regions which are used by a large percentage of national breeding or non-breeding populations, for example Sites of Special Scientific Interest (SSSIs) and RAMSAR sites in the UK. Key Biodiversity Areas (KBAs; Eken *et al.*, 2004) and Important Bird and Biodiversity Areas (IBAs), which are not PAs *per se*, but identify priority sites for future designations, again are sites that *at present* include vital habitat for threatened species (birdlife.org). To be effective under projections of distributional change, however, some researchers suggest that future PA networks must be more dynamic (Alagador *et al*., 2014), or be designated considering projected, rather than current, distributions (Hannah *et al*., 2007).

Table 1.1 IUCN categories of protection (iucn.org)

IUCN Category of Protection	**Overview/Activities Permitted**
Ia Strict Nature Reserve	-Strictly Protected Areas -Human visitation strictly controlled
Ib Wilderness Area	-Large unmodified or slightly modified areas -Managed to preserve natural condition
II National Park	-Large natural or near natural areas -Managed to protect large-scale ecological processes
III Natural Monument or Feature	-A particular natural monument and its surroundings -Generally small with high visitor value
IV Habitat/Species Management Area	-Protect particular species or habitats -Require regular interventions
V Protected Landscape/Seascape	-Focus on landscape/seascapes created by interactions between people and nature
VI Protected area with sustainable use of natural resources	-Large areas, mostly in natural conditions, where a proportion is used for sustainable natural resource management

Table 1.2 Examples of international and national (UK) Protected Areas and reasons for designation

Type of PA	Quantity in the UK	Focus	Designated For	Source
International				
RAMSAR sites	149	Wetlands of international importance	Presence of rare wetland types, or internationally important abundancy/variety of species or communities	www.ramsar.org
Biosphere Reserves	6	Terrestrial, marine and coastal ecosystems	Cultural *and* biological diversity. Sites which encourage sustainable development	www.unesco.org
World Heritage Sites (natural)	27	Sites of 'outstanding universal value'	Presence of 'superlative natural phenomena'. Presence of significant natural habitats for in-situ conservation of biodiversity	www.unesco.org
Special Protection Areas (SPAs)	272	Threatened species	Classified for rare and vulnerable birds (Annex I; Directive 2009/147/EC), and for regularly occurring migratory species	Jncc.defra.gov
Special Areas of Conservation (SACs)	625	Threatened habitats and species	Presence of Annex I habitats and Annex II species	Jncc.defra.gov
National (UK)				
Sites of Special Scientific interest (SSSIs)	c.7000	Sits of biological and archaeological importance	Varies by habitat and taxa. E.G. Presence of >1% of the total breeding or non-breeding population in Britain (birds)	Jnccc.defra.gov
Marine Nature Reserves (MNR)	3	Areas of sea and seabed	Presence of species or habitats of national or international importance	www.ukmpas.org
National Nature Reserve (NNR)	224	Habitats	Presence of 'good' examples of particular habitat types	www.gov.uk
Local Nature Reserve (LNR)	c.1400	Wildlife and geological features	Presence of wildlife and geological features of special interest locally	
Ares of Outstanding Natural Beauty (AONBs)	46	Sustainable development	Presence of natural beauty including flora, fauna, geological, landscape, archaeological and architectural features.	landscapesforlife.org.uk

1.2.2 PA Effectiveness (Habitat Representation and Land Use Change)

Increases in PA coverage theoretically mean that important habitats are receiving more protection, although the efficacy of this protection may vary geographically, as suggested above. The majority of parks in tropical regions successfully prevent land clearing (Bruner *et al*., 2001). Across 22 countries, PAs had lower rates of clearing compared to nearby unprotected land (Nagendra, 2008) and in a global analysis, 62 out of 76 studies indicated that PAs make a positive impact on reducing habitat loss (Geldmann *et al*., 2013). The ratio of ‘positive’ to ‘negative’ impact does vary from region to region however; in Africa seven out of 18 studies found no impact, or worse performance in relation to nearby land (Geldmann *et al*., 2013), although Beresford *et al*. (2017) suggest that natural land cover typically persists twice as long in protected sites in Africa.

Globally, the amount of land protected is increasing towards the AICHI target of 17%, but many researchers believe that a protection target of 50% is necessary for more comprehensive conservation of biodiversity (e.g. Locke, 2014; Dinerstein *et al*., 2017). Several of the world’s ecological regions still fall below the 10% conservation target set for 2010 (CBD, 2010) and thus well below the ‘Nature Needs Half’ suggestion. The World Wide Fund for Nature identify over 800 ecoregions (wwf.org) of which 13% have no strict protection (Jenkins & Joppa, 2009) and 45% are ‘imperiled’ (Dinerstein *et al*., 2017). Although biomes such as mangroves (26%) are reasonably well protected, others such as temperate grasslands (4%) and deserts and xeric shrublands (6%) suffer from a lack of protection (Dinerstein *et al*., 2017). For some biomes, such as tropical and subtropical moist broadleaf forests, achieving 50% protection of the initial area covered will not be possible even if the political will exists, given that more than half of the natural habitat has already been lost.

1.2.3 PA Effectiveness (Trends in Biodiversity)

The ‘effectiveness’, or ‘performance’ of PA networks, or ‘portfolios’ (network usually implies connectivity between different reserves - Gaston *et al*., 2008) for biodiversity can be measured in different ways. As designation is often based on the presence of species or features (Table 1.2), many PAs perform well in terms of the range of species found within their boundaries, although in some instances reserve networks perform little better than randomly selected areas in terms of representation (Deguise & Kerr, 2006). As of 2004, 95% of all mammal species occurred in PAs, as did 80% of threatened bird species (Rodrigues *et al*., 2004a).

Individually, some PAs hold massive species numbers: Madidi National Park in Bolivia reportedly has 156 mammal and 867 bird species (ParksWatch.org), representing almost 50% of the mammal species (Anderson, 1997) and 60% of the bird species (Remsen *et al*., 2016) regularly found in the country.

At first glance, these numbers appear to indicate that Protected Areas perform well in terms of species representation. However, there remain large numbers of 'gap' species (not covered by a PA portfolio). According to the Rodrigues *et al*. (2004a) study, 12% of all species, and 20% of bird species are considered to be gap species. In Brazil's Atlantic forest, a biodiversity hotspot, as of 2004, 59 endemic species had ranges completely without protection (Rodrigues *et al*., 2004b). Furthermore, for non-gap species, PA coverage might only apply to a small portion of their range. For example, a further 136 endemic species in Brazil's Atlantic Forest had less than 5% of their range protected (Rodrigues *et al*., 2004b) and only 14% (on average) of the potentially suitable habitat of threatened terrestrial bird species in Africa is protected (Beresford *et al.*, 2011). Species with higher representations might not persist if the PAs are not of sufficient size; rates of extinction of large African mammals are more prevalent in smaller national parks than larger ones, for example (Newmark, 1996). Furthermore, climate change and other anthropogenic factors are affecting the distributions of species (see below), and so the percentages above are not fixed. Also, the absence of protection in even a small part of the range of migratory species can have detrimental effects at the population level. Several important feeding areas of the endangered Spoon-billed Sandpiper *Calidris pygmaea* in Chinese wetlands are currently unprotected and face threats such as hunting, land-reclamation and pollution (Xia *et al*., 2017; Yang *et al*., 2017), thus potentially reducing overall population size.

Even if we assume that PAs are effective in terms of species coverage, the conservation measures in place might not be effective for achieving their biodiversity targets, and will certainly vary depending on the degree and type of protection offered (Porter-Bolland *et al*., 2012; Dudley *et al.*, 2016; Reddy *et al.*, 2016; Eklund & Cabeza, 2017). In general, PAs *do* appear to have higher species abundance and species diversity than nearby land (Coetzee *et al*., 2014). Effect sizes in this study, however, varied by taxon (plants were not significantly better-off in PAs), efficacy of protection (effects were not significant in each level of IUCN category) and by the IUCN red list status of species. PAs are not, therefore, universally 'successful'. African PAs have failed to adequately protect large mammal species (Craigie *et al.*, 2010), reptiles and amphibians have declined in protected old-growth rainforest in Costa

Rica (Whitfield *et al.*, 2007), and mammal abundancies have fallen in an Australian PA (Woinarski *et al.*, 2001).

Examples of PA successes, of which there are many (see Gaston *et al*., 2008), must also be interpreted carefully. PAs are often designated on sites which *a priori* are more biodiverse or favourable to biodiversity than nearby unprotected land. Therefore, even without effective conservation, abundances and diversity would be expected to be greater within PA boundaries. As a result, comparisons of measures of species trends within and outside of PAs might be considered a more appropriate measure of effectiveness. In the above examples, declines of populations in PAs might still be a relative success if the *rate* of decline has been reduced on protected land. More positive population trends of bird species targeted by the European Union Birds Directive (Annex I species) than non-target species evidences the effectiveness of conservation measures (Donald *et al*., 2007; Sanderson *et al*., 2016) although these differences were not present in long-distance migratory birds, which highlights the potential problem of non-protection in parts of the ranges of mobile species (see above). Population trends were also more positive for waterbirds in RAMSAR sites as opposed to in unprotected wetlands (Kleijn *et al*., 2014), and on Royal Society for the Protection of Birds (RSPB) wetlands as opposed to Environmentally Sensitive Areas for breeding waders (Ausden & Hirons, 2002). On the other hand, for Australian birds, woodland PAs appeared ineffective when compared to unprotected land at maintaining target specialised and threatened assemblages (Rayner *et al*., 2014), and there was no difference in trends of parrot species between protected and unprotected areas (Barnes *et al.*, 2015).

Gaps in our knowledge about the efficacy of PAs remain, particularly when it comes to the success of different levels of protection (Gaston *et al*., 2008). One of the aims of this thesis (Chapter 4) is to help address these gaps by investigating how effective varying levels of protection are at preventing habitat modification, and how biodiversity is in turn affected by different levels of protection and habitat modification, with a focus on those species undergoing range expansions and contractions.

1.3 Distributional Changes

1.3.1 Climate-driven Changes – Effects on Biodiversity

Recent climatic change has influenced physical and biological systems (IPCC, 2014). It has impacted the phenology of species, population dynamics and the composition of ecological communities (Walther *et al*., 2002; IPCC, 2014). Spring migration and breeding of Northern Hemisphere bird species has advanced, for example, as a result of warmer weather earlier in the year (Crick & Sparks, 1999; Walther *et al*., 2002; Cotton, 2003; Dunn & Moller, 2014; McDermott & DeGroote, 2016), and threats to populations of Rockhopper Penguins *Eudyptes chrysocome*, Sooty Shearwaters *Puffinus griseus* and Kittiwakes *Rissa tridactyla* have been associated with increased sea-surface temperatures and, at least for Kittiwakes, changes in ocean stratification (Cunningham & Moors, 1994; Veit *et al*., 1996; Crick, 2004; Carroll, 2015). Future climatic changes might affect migration routes (e.g. La Sorte & Fink, 2017) and patterns of vagrancy (e.g. Jiguet & Barbet-Massin, 2012) of bird species.

Perhaps the most visible effect of climate change, however, has been the distributional shifts exhibited by many species. Poleward shifts in the ranges of species have now been widely reported. Northward shifts have been found in the ranges of both winter (La Sorte & Thompson III, 2007; Maclean *et al.*, 2008) and breeding distributions of Northern Hemisphere bird species (Thomas & Lennon, 1999; Zuckerberg *et al*., 2009; Gillings *et al.,* 2015). 63% of sedentary European butterflies underwent a northward shift in distribution in the 20th century (compared with 3% to the south; Parmesan *et al*., 1999), as have most British dragonflies and damselflies (Hickling *et al.*, 2005) and fish species with range margins in the North Sea (Perry *et al.*, 2005). Studies across broad ranges of taxonomical groups have observed mean poleward shifts ranging between 6.1km (Parmesan & Yohe, 2003), 16.9km (Chen *et al*., 2011) and 23km per decade (Mason *et al.*, 2015). Within Britain, 84% of 329 species (of 75% of 16 taxonomic groups) have demonstrated northward shifts in distribution (Hickling *et al*., 2006) over 25 years. Although the general pattern of poleward shifts is clearly demonstrated, many species-specific shifts are multi-directional (VanDerWal *et al.*, 2013) and outpace the average speeds mentioned above (measuring unidirectional, i.e. northward, shifts underestimates the true rate of distribution change (Gillings *et al.*, 2015)).

Increasing mean global temperatures have precipitated elevational, as well as latitudinal, distributional shifts. 69% of the species in the Hickling *et al*. (2006) study had shifted to higher altitudes, compared to 31% moving to lower elevations. This result from Britain matches expectations from other studies; butterflies in Spain (Wilson *et al*., 2005) and the Czech Republic (Konvicka *et al*., 2003), moths in Malaysia (Chen *et al.*, 2011a), Spanish tree species (Peñuelas & Boada, 2003) and European dung beetles (Menéndez *et al.*, 2014).

Species Distribution Models (SDMs) use the relationships between the observed distributions of species and associated environmental, climatic and geographic information to explain species' ecological requirements (Elith & Graham, 2009). They can therefore be employed to predict future patterns of occurrence under different climatic scenarios (Thomas *et al.*, 2004; Huntley *et al*., 2007). Across many studies of different taxonomic groups, SDMs demonstrate that recent shifts in range are likely to continue under a variety of different climatic scenarios. For the ranges of 431 European breeding birds, for example, Huntley *et al*. (2007) predict a northerly range shift (in range centroids) of between 258 and 882km by the end of the century.

The effects of climate-change driven distributional shifts are likely to vary, as do estimates of extinction vulnerability (Thomas *et al*., 2004; Bellard *et al.*, 2012) although overall, medium-level scenarios could result in 7.9% of all species becoming extinct (Urban, 2015). Birds might be heavily affected (Jetz *et al*., 2007), with up to 30% threatened with extinction by 2100 (Şekercioğlu *et al*., 2008); although factors such as range size and dispersal ability will determine variations in impacts between different taxa. Species with limited geographical ranges will be most impacted, as well as those which are geographically isolated and those with limited dispersal capacities (La Sorte & Jetz, 2010). Whilst many species are shifting their distributions (see above), changes may lag behind rates of climate warming (Devictor *et al.,* 2008, 2012; Lindström *et al.*, 2013, although see Chen *et al*., 2011). As well as precipitating extinctions, climate-change might have a negative-impact on beta-diversity. Biotic homogenisation will result if habitat generalists adapt to changing temperatures faster than specialists (Davey *et al.*, 2012).

High altitude (i.e. mountain-top) species are likely to suffer under climate change. Extinctions could happen if the preferred climates of species cease to exist on mountain ranges or they face new competition from lowland species whose distributions have shifted uphill (Colwell *et al*., 2008; Raxworthy *et al.,* 2008; Harris *et al*., 2011). Rock Ptarmigans *Lagopus muta*, Eurasian Dotterels *Charadrius morinellus* and Snow Buntings *Plectrophenex nivalis* are bird species with breeding ranges which, within the UK, are currently restricted to Scottish mountaintops. Suitable climatic conditions are projected to be lost by the end of the century under most current projections (Morecroft & Speakman, 2013). Without higher, or more northerly, mountains to disperse to, therefore, such species might become extinct as breeders in the UK, although they may well survive in colder parts of Eurasia.

Tropical species have also been a recent focus of attention. The tropics are the most species-rich region in the World and simultaneously the region undergoing the most dramatic habitat loss (Sodhi *et al*., 2006). In such instances (which are not unique to the tropics), species face a combined threat from climate change in conjunction with other threats (see Mantyka-Pringle *et al*., 2012). Most tropical species are relatively sedentary and many are endemics with small ranges containing specific types of habitat (Şekercioğlu *et al*., 2012), making adaptation to climatic changes more difficult. Mexico's Horned Guan *Oreophasis derbianus*, a specialised cloud-forest endemic, is likely to suffer dramatic range losses under projected changes in climatic conditions (Townsend-Peterson *et al*., 2001). Tropical species have also been victims of the few extinctions which have already taken place that have been linked to climate-change (the Bramble Cay Melomys *Melomys rubicola* (Gynther *et al.*, 2016) and various Costa Rican amphibians including the Golden Toad *Bufo periglenes* (Pounds *et al.,* 2006, although see Anchukaitis & Evans, 2010).

Approaches to understanding climate risk based entirely on SDMs and climate-envelope modelling should be treated with care, however. SDMs rely on a number of assumptions (e.g. see Araújo & Guisan, 2006; Austin, 2007). Current distributions of species reflect their interaction with other species and the availability of suitable habitat, as well as their climatic tolerances (Davis *et al*., 1998; Ockendon *et al.*, 2014). The ability of species to shift distributions, therefore, also depends on future interactions with new resources, competitors, and natural enemies. Dispersal ability is also a key factor. Assuming universal dispersal capacity, distributions of some species might expand under climate-change (Townsend-Peterson *et al*., 2001), in contrast to an assumption of no dispersal capacity. Nevertheless, SDMs can be validated with a 'retrodicting' approach - strong correlations between observed and predicted changes of distribution/population trend based on historical data have indicated their accuracy (Green *et al*., 2008; Illán *et al.*, 2014) and factors such as natal-dispersal are increasingly accounted for in SDMs to improve model performance (e.g. Jiguet *et al*., 2012; Willis *et al*., 2015) and enhance their use for conservation purposes (Thomas *et al*., 2011; Pearce-Higgins *et al*., 2017).

Although the potential for climate change to precipitate extirpations is widely appreciated, climate-driven distribution shifts also provide regions with a large potential source of colonists. As many native species have been gained (as colonists) in the UK as have been lost since 1900 (Gurney, 2015) and, over the next few decades, Ausden *et al*. (2015) suggest that 15 bird species from continental Europe have a high probability of colonising or recolonising the UK (and several more with a medium/low probability), while 19 species (including those mentioned above) are at high risk of extirpation, as breeding populations. Assessments of the role of PAs as a potential means of minimising the negative effects of climate-driven shifts in distribution should therefore be considered in terms of their use by both those species undergoing range-reductions and those colonising new areas.

1.3.2 Climate-driven Changes - Role of Protected Areas

PAs are static in their location, whereas the climate and the distributions of species (see above) are dynamic. Concerns about changing species' distributions and fixed protected area boundaries are not new (Peters & Lovejoy, 1992; Hannah, 2008), but it is only relatively recently that these concerns have been quantified. Loarie *et al*. (2009) predict that 92% of Protected Areas will become climatically 'unsuitable' within a century; in the sense that the climatic conditions they currently cover will have crossed over the boundaries of the PA. Thus, as distributions of species change with the climate, their representation in PAs clearly might reduce (Heller & Zavaleta, 2009).

This does not necessarily make PAs redundant. Firstly, even if some species lose representation in reserves, PAs are unlikely to lose all of their designation species (Hole *et al.*, 2009) because not all species have the same climatic envelope, and they may also remain legally relevant if they accommodate a different variety of species, or greater abundances of different species – particularly for multi-species networks (Johnston *et al.*, 2013). Secondly, greater losses of target habitat outside than inside protected land increases the effectiveness of PAs even if, overall, habitat quality decreases (Ausden & Hirons, 2002), or suitable habitat is completely lost (Regos *et al*., 2016). Thirdly, species communities with high proportional representation in PAs might be better equipped to adjust to temperature changes than those with lower representation (Gaüzére *et al*., 2016). Fourthly, adoption of certain management techniques in existing PAs or creation of new ones can increase their effectiveness under climate-change. Flexible strategies might include selection of redundant reserves (to exchange for additional ones of higher value), increased habitat connectivity, larger reserves, use of buffer-zones (Halpin 1997; Chapter 4), protected areas that vary in space and time (Hannah, 2008; Rayfield *et al*., 2008) or the design of climatic-resilient protected areas (West & Salm, 2003). As the distributions of certain species reduce in extent, PAs may also remain of conservation benefit by, for example: delaying or reducing distribution losses at the trailing edges (i.e. the southern range edge for species shifting northwards in the northern hemisphere) of species' ranges (e.g. Gillingham *et al.*, 2015) or being prime sites for incidences of assisted colonisation (Willis *et al*., 2009).

The importance of existing PAs for species naturally colonising new areas, however, has received little attention until recently. PAs were disproportionately used by invertebrate groups colonising new areas in the UK (Thomas *et al*., 2012) and they also appear beneficial to range-expanding butterflies and odonates (Gillingham *et al*., 2014). PAs have been shown to accommodate the shifting wintering distribution of the Smew *Mergellus albellus* in Europe (Pavón-Jordán *et al*., 2015). Thus, PAs could be crucial for colonists (although the patterns of PA use described here might not be universal (see Bates *et al*., 2014)).

Even though climate-driven shifts of distribution might cause PAs to fail from the perspective of the entities for which they were originally set up to protect (Mascia & Pailler, 2011; Thomas & Gillingham, 2015) they are likely to offer a range of other benefits, which may include accommodating species undergoing said shifts (Hole *et al.*, 2009; Johnston *et al.*, 2013). This issue is further explored in Chapters 2, 3 and 5.

1.3.3 Non-native Species – Patterns of distribution

The abundance of, spread and associated threats of introduced, or non-native species (the use of the term ‘invasive’ implies that they have a negative effect on the environment (CBD, 2010), which might not always be the case (see below)) have been well documented. Pimentel *et al*. (2005) estimate that there are 50,000 non-native species in the USA, with huge economic consequences. The Global Alien Invasions Atlas (GAVIA), which provides a comprehensive catalogue of invasion records, has over 27,000 distribution records (including c.1000 records of introduction of bird species (Blackburn *et al*., 2015). Rates of non-native species spread show no sign of stopping (Seebens *et al*., 2017). There has been an increase in the number of non-native species present in Europe in recent decades (Hulme *et al*., 2009), and climatic warming has presented opportunities for non-native species to colonise new areas, as previously unsuitable regions become habitable (Walther *et al.*, 2009).

Non-native species are established across the planet, spanning over 200 countries (Turbelin *et al*., 2017), but their *relative* abundance has been linked with a variety of factors including but not limited to (1) Colonisation Pressure – there is a clear relationship between the number of individuals and number of species introduced to a location and the likelihood that they will become established (Lockwood *et al*., 2009)), (2) Imperial History – former British colonies, for example New Zealand, tend to have greater numbers of non-native species (Dyer *et al*., 2017), (3) Economic Factors – invasions have been linked with trade – non-native species are transported by humans, and so trade routes represent pathways for species to establish in new regions (Westphal, 2008; Hulme, 2009), and (4) Human Population Density – non-native species are more likely to occur where there are more humans in concentrated spaces, which may be linked to trade again, and to habitat change (e.g. Spear *et al*., 2013).

Geographically, islands are hotspots of non-native species (often for the reasons mentioned above). New Zealand, Hawaii and the Lesser Sunda Islands of Indonesia (Dawson *et al*., 2017) are prime examples. Fewer incidences of invasive species have been reported in Africa. This could be because of the absence of, for example, intense economic activity, high human colonisation pressure or human population density. Alternatively, observer intensity (see below) is lower in much of Africa, and so non-native species might be under-reported.

Different drivers affect the distributions of non-native species in different taxonomic groups, although most groups have high richness correlations – non-native species from different taxa are often found in the same place (Dawson *et al*., 2017). Mean annual temperature had a large effect on species richness of introduced ants and reptiles, whereas human population density was more important for plants and spiders, for example (Dawson *et al*., 2017).

1.3.4 Non-native Species – Effects on biodiversity

Non-native species have regularly been cited as a leading cause of extinctions globally (e.g. Blackburn *et al*., 2004; Clavero & Garcia-Berthou, 2005; although see Gurevitch & Padilla, 2004), responsible for from 27% (plants) to 62% (vertebrates) of extinctions of different taxa (Bellard *et al*., 2016). They have been the predominant reason for recent bird extinctions at both species (58.2%) and subspecies (50.7%) levels (Szabo *et al*. 2012) and the identification and removal of priority invasive species is covered by AICHI Target 9; "identification of pathways, and control or eradication of priority species" (CBD, 2010) and SDG #15.6; "prevent the introduction and significantly reduce the impact of invasive alien species on land and water" (United Nations, 2015). Non-native species can cause extinctions directly or indirectly. Well-documented examples include the arboreal Brown Tree Snake *Boiga irregularis*, which has wiped out many forest birds on the island of Guam and the fast-growing Water Hyacinth *Eichhornia crassipes*, which reduces diversity of native aquatic plants (Lowe *et al*., 2000)**.** A summary of the effects of some non-native bird species in the UK and Mexico (focus areas in this thesis) is shown below in Table 1.3.

Table 1.3 Non-native species in the United Kingdom and Mexico and their effects on biodiversity (Lever 2005, unless stated)

Species Name	**Introduced to (native range)**	**Effects on biodiversity**
Canada Goose *Branta canadensis*	UK (North America)	Aggressive. Attacks other waterfowl during breeding season. Eutrophication of water bodies.
Mandarin Duck *Aix galerictula*	UK (East Asia)	Potential competition for nest-sites with native Common Goldeneye *Bucephala clangula* (Lever, 2013).
Rose-ringed Parakeet *Psittacula krameri*	UK (South Asia)	Competes for foraging resources with native species (Peck *et al*., 2014). Non-significant competition for nest-sites (Newson *et al*., 2011).
Common Pheasant *Phasianus colchicus*	UK, Mexico (Central Asia)	Little ecological impact has been reported.
Rock Pigeon *Columba livia*	Mexico (Eurasia)	Little ecological impact due to habitat preferences (TIS, 2014).
Collared Dove *Streptopelia decaocto*	Mexico (Eurasia)	Abundance of other dove species increases with presence of *S. decaocto* (Bonter *et al*., 2009).
House Sparrow *Passer domesticus*	Mexico (Eurasia)	Competition with native Eastern Bluebirds *Sialia sialis* (Gowaty, 1984, though see Thomas, 2017).
European Starling *Sturnus vulgaris*	Mexico (Eurasia)	Competition with cavity-nesters in the USA, but see Koenig (2003).

Table 1.3 provides some evidence that for birds at least, the effects of non-native species are not always detrimental to native wildlife. Although some of the United Kingdom's non-native species might negatively affect their native counterparts, none of them have been implicated in the extinctions of UK bird species (i.e. humans rather than other invasive species extinguished Great Auks *Pinguinus impennis*, and human-pressure on coastal habitats, drainage of wetlands and land-use change were associated with the loss of Kentish Plovers *Charadrius alexandrius*, Black Terns *Childonias niger* and Wrynecks *Jynx torquilla* respectively

as breeding species (e.g. Parslow, 2010)). Globally this pattern might exist because non-native bird species show a preference for urban habitats (Chace & Walsh, 2006), where they are unlikely to overlap with species at risk of local or global extinction. Due to the presence of non-native species (Table 1.3), the UK's breeding bird avifauna is probably richer than at any point in its recent history, representing an increase in alpha (~national) diversity. Similar patterns, which contrast with conventional assumptions that non-native species typically result in a net-decrease in local alpha diversity, have been increasingly reported (Sax & Gaines, 2003; Thomas & Palmer, 2015). Globally, local-scale plant diversity has remained steady over the last century (Vellend *et al*., 2013). On islands, the number of naturalised species of land-birds equates with those that have been lost through extinction, and the number of naturalised plant species is far greater than those that have been lost (Sax *et al*., 2002).

Non-native species can affect the beta-diversity as well as the alpha-diversity of different locations. Non-native species often establish in multiple host countries. For example, feral Rock Pigeons *Columba livia* have become naturalised in more than a hundred countries on six continents (BirdLife International, 2016) and House Sparrows *Passer domesticus* have been similarly successful. Non-native species are often characterised by their broad ecological tolerance (Stigall, 2012). The net result of both of these factors is a biotic homogenisation of communities between locations; i.e. more similarity or a reduction in beta-diversity. European plant species already show increased taxonomic and phylogenetic similarity as a result of introductions (Winter *et al*., 2009) and the process will probably continue apace due to further human modification of natural environments (McKinney & Lockwood, 1999; McKinney, 2006) and because 'specialist' native species might be less likely to survive invasions than their generalist counterparts (Coetzee & Chown, 2016).

Interestingly, some introduced species, for example the Yellow-crested Cockatoos *Cacatua sulphurea* (introduced to Hong Kong) and Reeve's Pheasant *Syrmaticus reevesii* (introduced to continental Europe), are now threatened in their natural ranges (Yellow-crested Cockatoo from the pet trade, and Reeve's Pheasant from habitat loss), whilst others, including House Sparrows and European Starlings *Sturnus vulgaris* are in decline (Inger *et al*., 2014). Flourishing introduced populations could be key in preventing the future global extinctions of species and re-stocking wild populations (Gibson & Yong, 2017).

1.3.5 Non-native Species – Role of Protected Areas

Non-native species are present in PAs in at least 106 countries around the World (GISP, 2007; Iacona *et al*., 2014), and this is likely to be true for most other countries. Despite this statistic, one of the benefits of PA networks might be their relative resistance to non-natives. For example, South Africa's Kruger National Park 'filtered' out invasive plant species (Foxcroft *et al*., 2011), and marine protected areas near Pacific Islands were less vulnerable to invasive species than nearby areas of seabed (Ardura *et al*., 2016).

This might be because many PAs are in remote locations, such as 'core zones' in Biosphere Reserves (see Table 1.1, Chapter 4), and are thus inaccessible to humans and introduction pressures. In PAs which are accessible (National Parks in the US), non-native plant richness was correlated with number of visitors (Allen *et al*., 2008), suggesting that increased tourist pressure in PAs can make them vulnerable to invasions. Similarly, in South African PAs, presence of non-native species was correlated with nearby human population density (Spear *et al*., 2013).

Alternatively, the ability of PAs to resist invasions might stem from their initial levels of biodiversity. Areas with high diversity are often thought to be more resistant (e.g. Teo *et al*., 2003) to non-native species (biotic resistance hypothesis), although contrastingly, on larger spatial scales, high diversity can be correlated with increased establishment rate of invasive species (biotic acceptance hypothesis; Stohlgren *et al*., 2006). PAs established for longer appear to be more resistant than those established later (e.g. Pysek *et al*., 2003).

Another factor might be that non-native species are more likely to initially occupy modified areas in their introduced range than in their natural range (perhaps because they are more likely to be released in human-dominated regions) (Gonzáles-Moreno *et al.*, 2014). In birds, for example, the habitats of wild (peatland) and feral (suburban parks) Greylag Geese *Anser anser* in Britain are very different (Owen & Salmon, 1988). The result might be a time-lag between initial invasion and spread into natural, protected areas (see Chapter 3).

1.3.6 Other causes of distributional change

Not all distributional changes have been caused by warming temperatures and human transportation, and future distributions of species will depend on many other factors (all of which will need to be taken into account in PA management). Issues such as habitat-loss and hunting in current or predicted future ranges are likely to reduce distributions of many species, although on the flipside they provide opportunities for others. Recent changes in the UK's breeding bird avifauna highlight this. Urban environments, which represent 'natural habitat loss' have been adapted to by Peregrine Falcons *Falco peregrinus* and Black Redstarts *Phoenicurus ochruros* (Hinchliffe & Whatmore, 2006). The digging of gravel pits for the construction industry resulted in a spread of Great-crested Grebes *Podiceps cristatus* and Little Ringed Plovers *Charadrius dubius* (Simmons, 1974; Parrinder, 1989), and changes in persecution regimes (a reduction in the popularity of egg-collecting) have helped Ospreys *Pandion haliaetus* colonise Scotland.

Other potential colonisations might be attributable to chance. Vagrancy-driven breeders in the UK (included a pair of Spotted Sandpiper *Actitis macularis* in Scotland in 1975 (Wilson, 1976) and several pairs of Pallas's Sandgrouse *Syrrhaptes paradoxus* after a large influx in 1888-89 (Brown & Grice, 2005)) did not successfully establish populations, but the range expansion/population growth of other species, such as several American passerines have been correlated with rates of vagrancy (Veit, 2000).

1.4 Data and Methods

1.4.1 Data availability

In this thesis, I use a variety of sources of data to tackle a series of related questions about the abilities of species that are shifting their distributions to make use of PAs, and the consequences for diversity change. This required compilation of existing online data, searching literature sources (including the 'grey' literature), and carrying out new fieldwork. This mixed strategy enabled me to include specifically designed (and thereby relatively robust) research, but inevitably of limited geographic scope, as well as a global compilation of data, from which any conclusions are more circumstantial but provide an international perspective. Chapter 4 reports the results of the field work that I carried out in the Sierra Gorda Biosphere Reserve, a Mexican PA. This work involved many challenges, including long hours, inaccessible locations and difficult terrain. Planned field studies allow data to be collected in a controlled (as far as possible), scientific manner. Due to lack of resources, and manpower, however, they can be limited in scale. On the other hand, studies which aim to look for ecological patterns over larger geographical areas (from regional to global) or longer timeframes face different challenges.

Thus, Chapter 4 represents a novel field study of the associations of species with different levels of habitat protection, Chapters 2 and 3 report detailed patterns of the arrivals and departures of species in one well-recorded region (the UK), and Chapter 5 is based on a global-scale collation of information (developed from a global network of informants which was generated from scratch). Table 1.4 summarises the sources of information used in this thesis.

1.4.2 Issues of data reliability

Most of the sources of data listed in Table 1.4 result from incidental records submitted by members of the public, as opposed to scientifically-designed surveys. The potential of citizen science – in which volunteers collect data to be utilised in scientific studies – is now well-recognised (Silvertown, 2009), although there are clearly drawbacks as well as benefits to using such data (provided by birdwatchers as "a network of avian biological sensors" (Sullivan *et al*., 2009)). Over the course of the last century, organisations such as the National Audubon Society in the USA and the British Trust for Ornithology in the UK have collected millions of records of thousands of species thanks to the efforts of amateur naturalists. Advances in technology have made submission, collation and presentation of large quantities of data easier, thus allowing researchers to see and analyse ecological patterns over a large scale.

Such recording schemes are vulnerable to various sources of bias which include, but are not limited to, (1) observer skill-level (variations can result in misidentification of birds when submitting checklists (Sullivan *et al*., 2009) or misjudgement of distance when estimating species density (e.g. Buchanan *et al*., 2006), although checks can limit the prevalence of this problem), (2) spatial variation both within regions (ornithologists devote more recording time close to regions of high human population density; e.g. Ferrer *et al*., 2006) and between regions (biological recording is more popular in more developed countries; several 'global' studies have blank spaces over much of Africa, for example, due to lack of observer effort), and (3) species preference (certain species or groups of species such as migrants or birds considered rare in a region might be over-recorded whilst other others are under-recorded (Ferrer *et al*., 2006)). These matters notwithstanding, these data-sets have been widely used for generating and reporting national trends (e.g. Christmas Bird Count (Audubon.org) and Garden Bird Watch (bto.org)).

These and other potential biases are considered carefully in the study-designs and interpretation of the results that I present in this thesis. By way of examples - in Chapter 2, I analyse population and observation trends in a group of comparator species to assess the robustness of the results presented for colonising species, and in Chapter 5, results for all countries are compared with results for a smaller subset of 'well-observed' entities.

Table 1.4 Sources of information (other than own data)

Source	Chapter	Description
Rare Breeding Bird Panel UK (RBBP)	2,3	The RBBP collate breeding records of bird species considered "rare or scarce" in the UK and publish an annual report (e.g. Holling, 2009). Breeding sites are sensitive, and so specific sites are not mentioned in the reports – although the RBBP do hold this information.
County Bird Recorders/ Reports	2,3	In the UK each county has a bird recorder who is responsible for collating records submitted by bird-watchers within that county. Each county publishes a report annually, which usually documents breeding records of all species, and other noteworthy records throughout the year.
Nest-box Record cards	2	I used these for breeding Common Goldeneyes in the Scottish Highlands. Nest-boxes are erected to encourage breeding. These are regularly checked by volunteers and the progress of breeding pairs is monitored. Information such as location, size of clutch etc is recorded.
County/ Country Avifaunas	2,3,5	County (e.g. Mather, 1986) or country (e.g. Brown & Grice, 2005) avifaunas summarise historical bird records within a region. They usually indicate where and when species first bred, as well as other notable records/patterns. Avifaunas also indicate species which formerly bred in that region (extirpations) and species which have been introduced. Information is collated from incidental records, bird reports, and scientific surveys.
Local Experts	5	I consider local experts to be individuals with specialist knowledge of a region's bird-life. These might be bird recorders (see above), or authors who have published work on a region.
eBird	5	eBird (ebird.org) is an online portal to which casual bird-watchers submit checklists of birds seen at a specific location. Over 300,000,000 records of bird species have been submitted to the eBird platform and its data has been used in more than 150 peer-reviewed articles

1.5 Outline of Thesis

The remainder of this thesis is divided into articles which explore the importance of PAs in the face of the distributional changes outlined above. In Chapter 2, I analyse patterns of breeding occurrence of wetland bird species that have colonised (many as a result of climatic changes) the United Kingdom recently to explore whether PAs were used as points from which these species established populations in their new ranges. I carry out similar analyses in Chapter 3 to compare and contrast the use of PAs by non-native species and natural colonists as they have arrived, and become established in, different counties across the UK.

In Chapter 4, I report results from a fieldwork study which examines how the alpha and beta-diversity of locations in a Mexican PA are affected by different levels of protection, and different levels of human habitat modification. This study also considers the degree to which PAs are important for species undergoing global declines in population, and for non-native species which have become established in the study area.

Chapter 5 considers these changes on a global scale. I consider species turnover in countries throughout the World – analysing the extent to which introductions of non-native species, and natural colonisations have countered the declines in alpha diversity caused by extirpations of species from countries, and whether these changes have contributed to a biotic homogenisation of the areas under question. This analysis also considers the importance of PAs in the context of these changes in communities – their potential roles in preventing extirpations and introductions, whilst simultaneously facilitating colonisations.

Chapter 2: Protected Areas act as establishment centres for species colonising the United Kingdom

2.1 Abstract

Protected Area (PA) networks will remain valuable for conservation, as the global environment changes, if they facilitate the colonisation of new regions by species that are shifting their geographical ranges. We tested the extent to which wetland bird species colonising the UK since 1960 have exploited PAs. Colonisation commenced in a PA for all six species that established permanent (greater than 10 years) breeding populations in the UK during this period. Subsequently, birds started to breed outside as well as inside PAs: the colonising species showing declining fractions of breeding within PAs over time, a trend not seen in already-resident species. PAs were valuable as 'landing pads' for range-shifting species first arriving in a new region, and then as 'establishment centres' from which viable populations spread. Given future projections of range change across a broad range of taxonomic groups, this role for PAs can be expected to become increasingly important.

2.2 Introduction

The population size and long-term conservation status of species needing to shift their geographic ranges, for example in response to climate change, will depend not only on their persistence in the regions where they currently occur, but also on their capacity to colonise new areas (Thomas *et al.,* 2004; Williams *et al.*, 2005). Facilitating range expansion, therefore, has the potential to become one of the most effective conservation strategies that can be deployed to minimise climatic and other risks to species (Heller & Zavaleta, 2009; Pearce-Higgins *et al.*, 2011). However, such strategies still lack robust empirical underpinning: there is limited evidence of the effectiveness of static protected areas (PAs) to protect species *per se* (Gaston *et al.*, 2006, 2008; Fuller *et al.*, 2010, but see Donald *et al.*, 2007), l*et al*one if species distributions become more dynamic (Dockerty *et al.*, 2003; Araújo *et al.*, 2004, 2011; Hannah *et al.*, 2005, 2007).

While PAs may lose species that were previously present, and indeed those for which the sites were designated, they could conceivably gain others if they safeguard habitats that are colonised by species spreading beyond their former geographic ranges. There is some modelling support for the continuing value of PAs under climate change (Hole *et al.*, 2009) on the assumption that PAs will contain the most suitable habitats for colonists. There is also empirical evidence that species disproportionately colonise PAs in areas where they have not previously been recorded (Thomas *et al.*, 2012). However, we still lack information on (1) the extent that PAs act as 'landing pads' for species, enabling them to breed and establish for the first time in new regions, and (2) how their dependency on PAs varies over time. The latter relates to whether PAs act as 'establishment centres' from which viable populations can subsequently spread within the region being colonised.

We address these issues by analysing the PA associations of those wetland bird species that have colonised the UK naturally since 1960. Wetland birds account for six of the eight bird species which have established continuous breeding populations in the UK in this period (see below). They are especially suitable for study because of the intensive scrutiny they receive from ornithologists, as well as from formal surveys (e.g. Sharrock, 1976; Gibbons *et al.*, 1994). The breeding distributions of many birds have shifted polewards in recent decades (Thomas & Lennon, 1999; Brommer, 2004; Hitch & LeBerg, 2007; Maclean *et al.*, 2008) and are projected to continue to do so (Huntley *et al.*, 2007). In the UK, this phenomenon has already been linked with the recent arrival of Cetti's Warblers *Cettia cetti* (Bonham & Robertson, 1975) and Little Egrets *Egretta garzetta* (Lock & Cook, 1998), two of our focal species. Expansions in other species have been linked with anthropogenic factors such as reduced persecution (e.g. Whooper Swan *Cygnus cygnus* (Boiko & Kampe-Persson, 2010) or habitat creation (e.g. Great Bittern *Botaurus stellaris* (Gilbert *et al.*, 2010)). However, most species are likely to have been affected by a combination of climatic and non-climatic changes to the environment.

We identify the PA status of the first breeding locations for all 18 wetland bird species that bred for the first time in the UK since 1960 (Table 2.1). For the six species that then established apparently permanent populations, we also evaluate how the percentage of the population breeding in PAs changed over time after initial breeding. We hypothesised that the proportion of the population breeding in PAs would decline over time, as populations grow in PAs (potentially becoming saturated), resulting in birds starting to breed outside of PAs. In contrast, we predicted that such trends would not be present for a 'control' group of long-term resident wetland species that have bred continuously in Britain throughout the same period.

2.3 Materials and Methods

2.3.1 Criteria for selecting species

We considered UK wetland bird species (habitat classification based on Gibbons *et al.* (1994)). We identified the first breeding locations for species that first bred in the UK after 1960 (from British Trust for Ornithology; blx1.bto.org/birdfacts), within the 1949 (first designated of Sites of Special Scientific Interest (SSSIs)) to 2012 period. We analysed temporal trends in PA use for the six 'successful colonists', defined as breeding in at least ten successive years up until 2012. We analysed 31 'comparator species' to help control for observer effort on and off PAs. Comparators were native wetland bird species which bred throughout 1900-2009 and which had $\geq$30 geo-referenced records (from 'county bird reports', Appendix 1A). These included species breeding in 'lowland wetland' and 'upland lakes and streams' habitats (Gibbons *et al.*, 1994), 'coastal' species that regularly breed inland (Common Shelduck *Tadorna tadorna*, Common Ringed Plover *Charadrius hiaticula*, Great Cormorant *Phalacrocorax carbo*) and 'unclassified' but primarily wetland species (Black-headed Gull *Chroicocephalus ridibundus*, Common Tern *Sterna hirundo* and Sand Martin *Riparia riparia*).

2.3.2 Obtaining Data

For colonisers, data on breeding locations since 1973 were obtained from the Rare Breeding Birds Panel (RBBP: see 'Species List'; http://www.rbbp.org.uk/rbbp-species-list-full.htm). For pre-1973 data, and instances when RBBP referred only to county totals, we obtained site data from the relevant 'county bird reports', which are annual compilations of UK bird records by region. When county bird reports lacked sufficient detail, we consulted county bird recorders, who hold historical records of birds submitted within each region. For Common Goldeneye, we searched the nest-box record cards (in this case held by the Royal Society for the Protection of Birds, RSPB), which contain locations of erected nest boxes and records of breeding attempts in each box. For comparator species, breeding locations were obtained from county bird reports (1964-2009) of ten counties (Appendix 1A). Counties were selected based on the availability of county bird reports for each year, whilst maximising their latitudinal and longitudinal spread.

2.3.3 Determining PA status of records

The PAs considered are UK SSSIs (Areas of Special Scientific Interest (ASSIs) in Northern Ireland), which correspond to IUCN level IV of protection (Dudley, 2008). Breeding records were cross-referenced against PA location using the interactive mapping software provided by Natural England (NE) (http://www.natureonthemap.naturalengland.org.uk), the Countryside Council for Wales (CCW) (http://www.ccw.gov.uk/landscape--wildlife/protecting-our-landscape/protected-sites-map.aspx), Scottish Natural Heritage (SNH) (http://gateway.snh.gov.uk/sitelink/searchmap.jsp) and the Northern Ireland Environment Agency (NIEA) (http://maps.ehsni.gov.uk/NIEAProtectedAreas/Default.aspx#). Records with grid references were assigned PA status if the entire grid cell (normally 100 x 100 m resolution) was within the boundary of a PA. Records without grid references were assigned PA status only if associated with site/reserve names for which PA status was unambiguous. County bird recorders were consulted for clarification when grid references partially overlapped PAs or location names were vague; if still ambiguous, the records were omitted.

We obtained PA notification dates from SSSI/ASSI citation documents from NE (www.naturalengland.org.uk), CCW (www.ccw.gov.uk), SNH (www.snh.gov.uk) and NIEA (maps.ehsni.gov.uk)). To avoid instances of a PA being designated because of the arrival of a colonist, we identified sites which were designated after a colonist had begun breeding there.

This situation applied only to Cetti's Warbler and Whooper Swan, for which 20 out of 843 (2.37%) and 1 out of 21 (4.76%) sites respectively were designated after their arrival. Records from these sites were excluded if a breeding population of the relevant colonist was cited as a principal reason for notification. This was only the case for two Cetti's Warbler sites. Excluding all records from sites which were designated after arrival did not change the conclusions for either species (Appendix 1B).

2.3.4 Calculating Protected Area associations

For each colonising species, we calculated the percentage of 'confirmed' breeding population (pairs) in PAs each year and the percentage of localities in PAs for colonial breeders (Svensson, 2009). 'Confirmed breeding' pairs follows the European Bird Census Council definition (Hagemeijer & Blair, 1997) for each species, apart from the elusive Cetti's Warbler, for which we used the number of singing males (as reported by the RBBP (e.g. Holling, 2009)).

For each comparator species, we estimated the percentage breeding in PAs in every fifth year between 1964 and 2009. Breeding is rarely 'confirmed' for established species, so we used 'probable breeding' (Hagemeijer & Blair, 1997) records for each species, apart from the elusive Reed Warbler *Acrocephalus scirpaceus* and Sedge Warbler *Acrocephalus schoenobaenus* for which we used numbers of singing males. For each species, we estimated the percentage of breeding pairs present on PA land in a given year, provided that at least 10 breeding pairs were recorded. If fewer pairs were recorded, the interval was binned with the following available year until $\geq$10 breeding pairs was achieved. Ambiguous reports of exact numbers (e.g. 'several', or 'breeding was recorded') at a given location were analysed as 'two pairs'. This uncertainty only really affected seven of the 31 comparator species (for which >5% of records were ambiguous). Nonetheless, we carried out a complementary analysis of the percentage of *sites* from which breeding was reported for all 31 comparator species and obtained similar results (Appendix 1C).

We also analysed Cetti's Warbler in two separate counties which were colonised in different years to distinguish the effects of year-since-colonisation from year-*per-se* on PA use. Cetti's Warbler was selected because it is by far the most numerous and widespread colonist, and the counties were chosen as they provided the most complete continuous set of records for this species: Norfolk between the initial establishment of a population (10 singing males) in

1975 and a temporary population crash in 1991, and Hampshire between initial establishment in 1980 and 2008.

For each colonising and comparator species, we calculated Spearman Rank values for the correlation between year and percentage breeding in PAs to determine the temporal trend. Mean 'PA usage' for each species was estimated as the average percentage of population breeding in PAs at each time interval.

2.4 Results

2.4.1 Coverage

Six wetland bird species have established persistent (>10 years) breeding populations in the UK since 1960. For four of these, Whooper Swan, Little Egret, Common Crane *Grus grus* and Mediterranean Gull *Larus melanocephalus*, we were able to categorise over 95% of all recognised UK records (based on RBBP data) as in/out of a PA. For Cetti's Warblers, the proportion of the population that we could designate as in/out of PA was >90% for the first ten years, but declined as the population increased. Records were incomplete for Common Goldeneye, and varied year-to-year (see Discussion).

2.4.2 First breeding records of colonising species

The first breeding record of each of the six successful colonists was in a PA (Table 2.1). Including species breeding but not (yet) established for $\geq$10 years, 18 of 20 species first bred in PAs in the UK (Table 1).

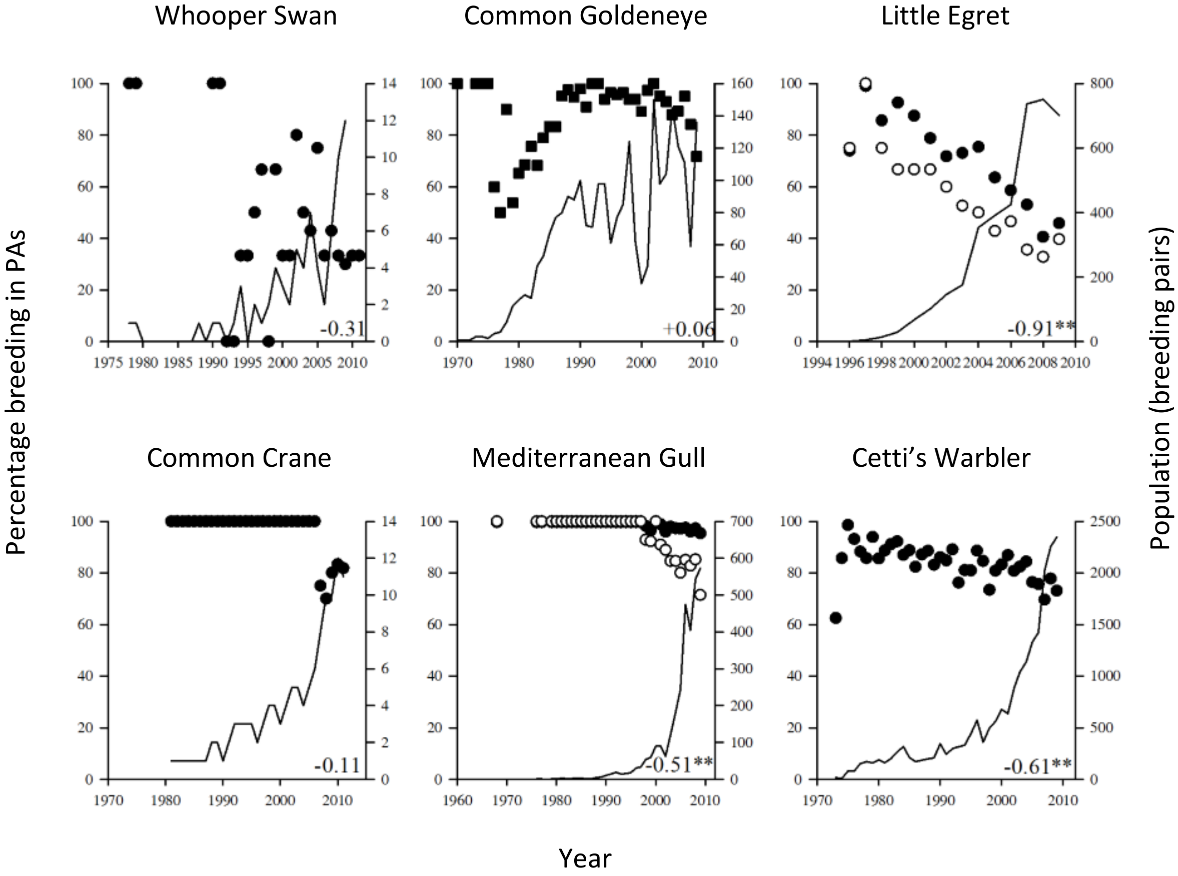
2.4.3 Trends in breeding in PAs

Five of the six colonising species showed a similar pattern, with most early breeding records in PAs, but the percentage of the population breeding in PAs declining over time (Figure 2.1). This trend was significant for the three species (Spearman's rank correlations: Little Egrets n=14, r_s=-0.91, P=0.001; Mediterranean Gulls n= 34, r_s=-0.51, P=0.0034; Cetti's Warbler n=37, r_s=-0.61, P=0.0002; all less than critical P=0.0083 after Bonferroni correction for six tests) that (1) currently have the largest established breeding populations and (2) are 'southerly' species, whose range expansions have been associated with climatic change (Appendix 1D). The sixth species, Common Goldeneye, showed an idiosyncratic pattern (Figure 2.1), apparently driven by the availability of nest boxes and frequency with which they were checked and reported (Appendix 1D).

Table 2.1 Wetland bird species that first bred in the UK after 1960 (during the period 1949 to 2012). Those that have not bred for at least ten consecutive years, prior to 2012, are underlined. For Pectoral Sandpiper, the asterisk indicates ‘presumed’ breeding. Population estimates are derived from the RBBP 2010 report unless otherwise stated. For Cetti’s Warbler, the double asterisk indicates ‘singing males’.

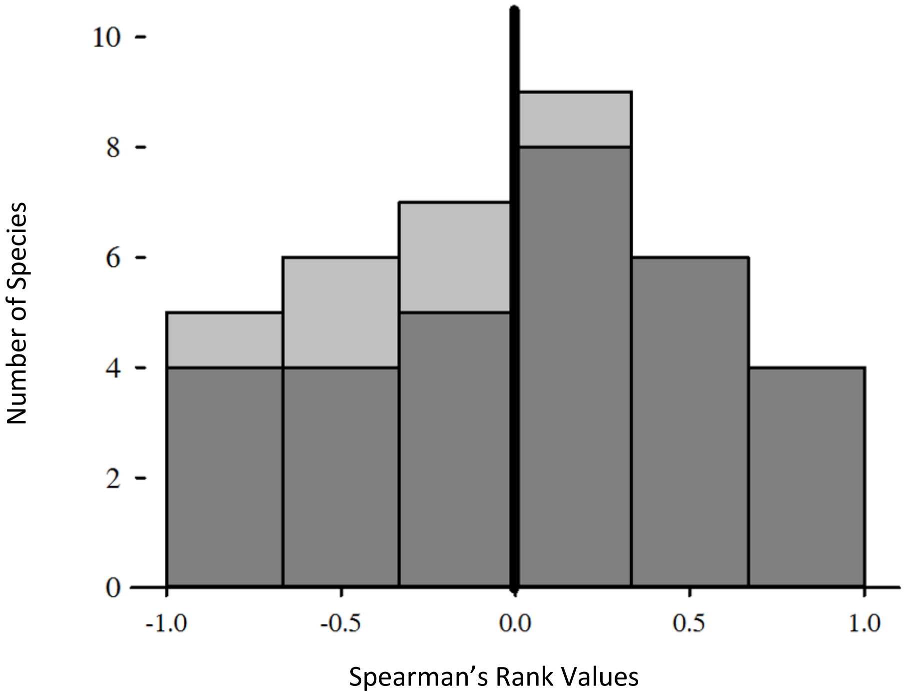
Species	**Year first recorded breeding**	**Site first recorded breeding**	**Status of site**	**Current population estimate (breeding pairs)**
Little Egret *Egretta garzetta*	1996	Brownsea Island, Dorset	SSSI	718
Common Crane *Grus grus*	1981	Horsey Mere, Norfolk	SSSI	13
Whooper Swan *Cygnus cygnus*	1978	An Fhaodhail, Tiree	SSSI	14
Cetti’s Warbler *Cettia cetti*	1973	Stodmarsh, Kent	SSSI	1907
Common Goldeneye *Bucephala clangula*	1970	Loch an Eilein, Highlands	SSSI	196
Mediterranean Gull *Larus melanocephalus*	1968	Needs Oar, Hampshire	SSSI	1016
Great White Egret *Ardea alba*	2012	Shapwick Heath, Somerset	SSSI	2 – in 2012
Purple Heron *Ardea purpurea*	2010	Dungeness, Kent	SSSI	1
Cattle Egret *Bubulcus ibis*	2008	Undisc., Somerset	SSSI	0
Pectoral Sandpiper* *Calidris melanotus*	2004	Loch of Strathbeg, Highland	SSSI	0
Spoonbill *Platalea leucorodia*	1998	Orford Ness, Suffolk	SSSI	8 – in 2011
Red-necked Grebe *Podiceps grisegena*	1988	Undisc., Cambs	Non-SSSI	0
Little Bittern *Ixobyrchus minutus*	1984	Potteric Carr, Yorkshire	SSSI	1
Black-winged Stilt *Himantopus*	1983	Nene Washes, Cambs	SSSI	0
Spotted Sandpiper *Actitis macularius*	1975	Uig, Skye	Non-SSSI	0
Little Gull *Larus minutus*	1975	Ouse Washes, Cambs/Norfolk	SSSI	0
Bluethroat Luscinia svecica	1968	Insh Marshes, Highlands	SSSI	0
Black Tern *Childonius niger*	1966	Ouse Washes, Cambs/Norfolk	SSSI	0
Ruff *Philomachus pugnax*	1963	Ouse Washes, Cambs/Norfolk	SSSI	0
Savi’s Warbler *Locustella luscinioides*	1960	Stodmarsh, Kent	SSSI	0

Figure 2.1 The percentage of breeding pairs (or singing males for Cetti's Warbler) of each colonising species in PAs each year since colonisation (closed circles). For colonial species, the percentage of breeding localities (open circles) within PAs each year is also shown. The squares for Common Goldeneye denote that some data are known to be missing. Lines represent population estimates based on RBBP reports (Appendix 1A). Spearman's Rank values (lower right of each panel) describe correlations between year since arrival and percentage breeding in PAs (* $P<0.05$, ** $P<0.01$).



For comparator species, 13 out of 31 species showed declining temporal trends for percentage breeding within PAs, but 18 species showed positive trends (Appendix 1E, Figure 2.2), indicating no overall pattern of increasing or decreasing association with PAs (Binomial Test: $P=0.47$). Nonetheless, five of the 13 negative trends (Mallard $n=10$, $r_s=-0.77$, $P=0.009$; Eurasian Teal $n=10$, $r_s=-0.74$, $P=0.014$; Grey Heron $n=10$, $r_s=-0.75$, $P=0.013$; Black-headed Gull $n=10$, $r_s=-0.68$, $P=0.029$; Common Tern $n=10$, $r_s=-0.66$, $P=0.038$), and two of the 18 positive trends (Little Grebe $n=8$, $r_s=0.76$, $P=0.028$; Moorhen $n=10$, $r_s=0.90$, $P=0.002$) reached nominal significance at $P=0.05$. These would not attain individual significance after Bonferroni correction for 31 tests (critical *P*=0.0016), but the probability of obtaining 7 or more individually significant trends at ≤P=0.05, out of 31, is itself unlikely (Binomial Test: *P*=0.0008), suggesting that some of the trends are real.

Figure 2.2 Spearman's Rank correlation value describing relationships between year since arrival and percentage breeding in PAs for colonisers (light grey) and comparator species (dark grey).

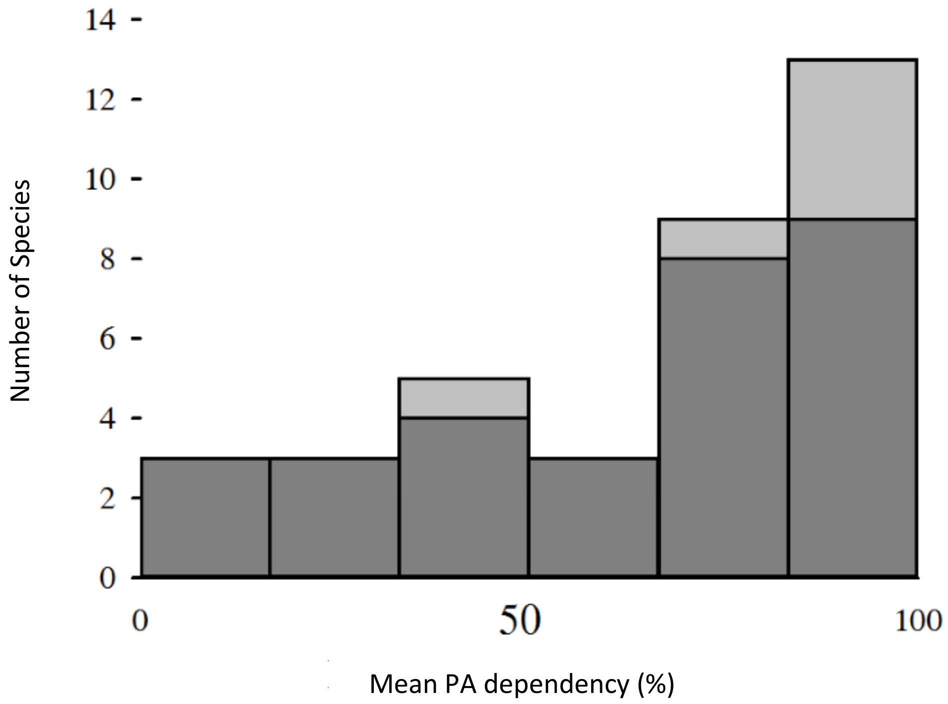


Spearman's rank correlation values for the colonisers were significantly more negative than for the comparators (Figure 2.2; Mann-Whitney, $z_{6,31}$=-2, two-tailed *P*=0.046; Appendix 1E), indicating that colonists showed declining patterns of association with PAs over time, compared to the long-term resident comparator species.

2.4.4 Overall PA dependence

PA dependence varied among species for both the colonists and the comparators (Figure 2.3), with riparian birds such as Grey Wagtails *Motacilla cinerea* and Dippers *Cinclus cinclus* breeding infrequently in PAs, and reed bed specialists such as Bearded Tits *Panarus biarmicus* breeding almost exclusively within PAs (Appendix 1E). Although the colonists were clustered at the top end of PA dependency (Figure 2.3), there was no significant difference between the overall PA dependency of colonists and comparator species (Mann-Whitney, $z_{6,31}$=1.59, *P*=0.112, two-tailed).

Figure 2.3 Mean overall PA dependency for colonisers (light grey) and comparator species (dark grey).

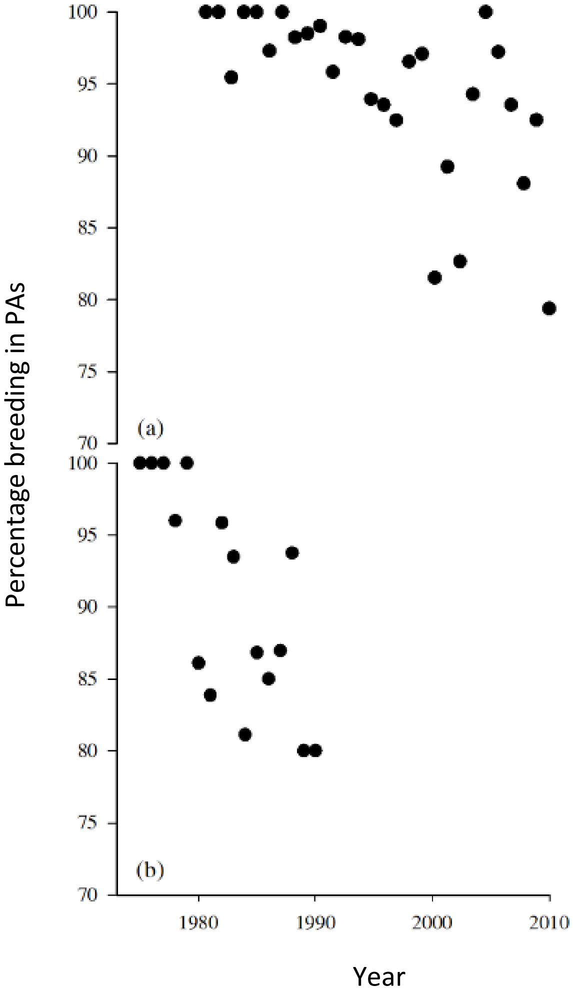


2.4.5 Trends at different times

Different species initiated their declining association with PAs at different times (Figure 1.1). Percentages of Cetti's Warblers breeding in PAs have been declining since 1975; Whooper Swans since the early 1990s; Mediterranean Gull and Little Egret since the mid-1990s, and Common Cranes between 2006 and 2008.

Percentages of Cetti's Warblers breeding in PAs started to decline earlier in Hampshire (which was colonised earlier) than in Norfolk. The pattern in Norfolk then followed that in Hampshire (Figure 2.4).

Figure 2.4 The percentages of Cetti's Warblers breeding in PAs each year in (a) Norfolk and (b) Hampshire.



2.5 Discussion

The conservation value of Protected Areas will be maintained and in some cases enhanced if they can facilitate the colonisation of new regions by species whose geographic ranges are expanding. Our results suggest that a PA network can be effective in this context.

Although avian colonisations of new areas are not unique to recent years (Von Haartman, 1973) an apparently increasing number of wetland birds have arrived in the UK over the last half-century and began to breed. This appears to have happened for a variety of reasons, but primarily as a result of climatic factors and reductions in persecution (Appendix 1D). Each 'successful' colonisation started off in a PA, but, as populations became more established, breeding spread into additional sites, not all of which were PAs (Figure 2.1). PAs provided suitable habitat for wetland birds, initially as 'landing pads' where they first bred upon arrival, and as ‘establishment centres’, from which populations subsequently spread to other locations in the same region. The Common Goldeneye was a partial exception, perhaps because some of the early data were incomplete or unavailable for this species, and its colonisation was affected by the widespread erection of nest boxes outside as well as inside PAs (Appendix 1D). Nonetheless, even this species was concentrated in PAs during its initial establishment (Figure 2.1).

Most wetland bird species which have not yet established in the UK also bred for the first time in PAs (Table 2.1), as did the two non-wetland bird species which met our criteria of ‘successful colonists’ since 1960 (Firecrests *Regulus incapillus* on a SSSI in Hampshire (Batten 1973); Yellow-legged Gulls *Larus michahellis* on a SSSI in Dorset; RBBP data). The geographical ranges of birds are expected to continue to change (Huntley *et al.*, 2007), and thus the trend of wetland birds colonising the UK could continue. Evidence already exists to show that wetland birds might experience stronger range margin shifts than birds associated with other habitats (Brommer, 2008). Our findings corroborate this by showing that most recent colonisers were wetland birds. A future area of study might address whether this high proportion of wetland birds is a function of PAs being particularly attractive to this group, or whether they are intrinsically more prone to range change and then subsequently use PAs.

Whichever the reason, our results suggest that future breeding populations of these birds in the UK will most probably be centred on protected sites, before expanding into additional undesignated locations. This is concordant with studies which have suggested that PAs will remain important for conservation under climate change (Hole *et al.*, 2009; Thomas *et al.*, 2012) and provides a contrast to the conclusions of research on alien invasive species, whose colonising distributions are typically associated with landscapes affected by human activity (Westphal *et al.*, 2008).

The records that we use here to determine the percentages of birds breeding in PAs are a product of casual observations as opposed to systematic surveys, and we are aware that a bias in observer effort towards PAs could lead to a bias in the proportion of records that come from PAs. Resultantly, we took a number of steps to evaluate the robustness of our findings in this context. (1) There was no systematic declining trend in the percentage of comparator species being reported from PAs (Figure 2.2) implying that there was no general shift away from PAs in terms of observer coverage of wetland birds during this period. (2) Individual colonists showed declining trends at different points in time (Figure 2.1) and (3) the association of one colonist species with PAs declined at different times in different British counties (Figure 2.4), both implying that there was no ‘general’ temporal shift in observer effort. Further, (4), five of the colonising species are large-bodied, conspicuous birds (the sixth has a loud and characteristic song) which, given the high density of bird-watchers in the UK and novelty of their occurrence in Britain, would be extremely unlikely to be overlooked and not reported regardless of the designation of any particular site. We are confident, therefore, that the results are robust, and are not artefacts of changes in the historical distribution of observer effort.

In conclusion, Protected Areas have represented ‘establishment centres’ for wetland bird species colonising the UK since 1960, breeding in these sites for the first time, establishing populations, and then expanding into additional unprotected sites. Hence, PAs enable species to establish in new regions in addition to their benefits to species already established within them.

2.6 Acknowledgements

We are grateful to all of the numerous volunteer bird recorders and those involved in the production of county bird reports. We give thanks to Natural England, Scottish Natural Heritage, the Countryside Council for Wales and the Northern Ireland Environment Agency for the use of their online software, and particular thanks to the following individuals for help with the provision of data: Andrew Henderson (Kent Ornithological Society), Keith Betton (Hampshire Ornithological Society), and Pete Moore and Andrew Stanbury (Royal Society for the Protection of Birds). We thank Malcolm Ausden for his support at each stage of the research, and the Royal Society for the Protection of Birds for financial support.

Chapter 3: Introduced and natural colonists show opposite patterns of Protected Area association in UK wetlands

3.1 Abstract

Aim Protected wildlife habitats provide valuable stepping stones for species that shift their distributions in response to climatic and other environmental changes, but they might also aid the spread of invasive alien species. Here, we quantify the use of Protected Areas (PAs) by both introduced and natural wetland colonists in the UK to analyse patterns of colonisation and examine the propensity of invaders to use PAs.

Location United Kingdom

Methods We calculate PA associations for six species of wetland birds deliberately introduced to the UK and compare these with eight others that have recently colonised the UK naturally. We assess PA associations at three different stages of establishment – first breeding in each county, early establishment of a population (4-6 years after initial breeding), and subsequent consolidation (14-16 after initial breeding) – and analyse changes in PA association over time.

Results Introduced wetland bird species were less associated with PAs than natural colonists at each stage of establishment. During the later stages of colonisation, the PA association of introduced species tended to increase. In contrast, natural colonists usually colonised PAs first, and their established populations subsequently spread into non-PA sites.

Main Conclusions The United Kingdom PA network did not facilitate the invasion of introduced species during the initial stages of their colonisation, but was vulnerable to colonisation as populations established. This is in contrast to natural colonists, which are more reliant on PAs during initial colonisation but become less dependent as they establish. During a period of rapid environmental change, PAs have facilitated expansions of natural colonists, without acting as the prime sites for invasion by introduced species.

3.2 Introduction

Numbers of introduced species are rapidly increasing around the world (Strubbe & Matthysen, 2007), and their negative impacts on native species (e.g. Williamson, 1996; Stein *et al*., 2000), ecosystems and ecosystem services are well recognised (e.g. Sakai *et al*., 2001; Gurevitch & Padilla, 2004; de Lange & van Wilgen, 2010). The global-scale costs of controlling them may run into billions of dollars annually (Pimentel *et al*., 2005), making it increasingly important to understand their patterns of spread. This is particularly relevant during a period of rapid environmental change, when native (to a broad geographic region) as well as introduced species are in the process of shifting their geographic ranges. Conservation strategies are increasingly being devised to enable species to track predicted changes in the distributions of suitable climates, and these might also unintentionally facilitate the spread of introduced and potentially invasive species.

In regions with a long history of habitat loss and fragmentation, species colonising regions by natural means show a strong reliance on Protected Area (PA) networks (Thomas *et al*., 2012; Hiley *et al*., 2013). The same PAs might also be susceptible to colonisation by introduced species; invasive alien species are a threat to PAs in over 106 countries (GISP, 2007) and Usher (1988) suggested that all nature reserves, apart from some in Antarctica, contained at least some introduced species. Reserves, therefore, offer opportunities for invaders as well as native species (Burfeind *et al*., 2013), and human visits to reserves could increase their exposure (MacDonald *et al*., 1989; Allen *et al*., 2009). However, the fact that introduced species often disproportionately colonise human-disturbed landscapes (Chuan Lim *et al*., 2003), and their distributions are associated with international trade and human population density (McKinney, 2006; Westphal *et al*., 2008), might suggest the reverse – that they would be less associated with PAs than with the surrounding landscape. PAs may be more resistant to 'invasions' than unprotected land as a result of harbouring greater biodiversity, giving native communities a competitive advantage over invaders (e.g. Tansley, 1939; Elton, 1958). These conflicting possibilities indicate that research is needed to assess directly whether introduced and natural colonists differ in their reliance on PAs. This is relevant to the design of PA networks and to any PA management aiming to protect native from introduced species (e.g. Tu, 2009).

Wetland birds naturally colonising the United Kingdom are appropriate for study with regard to range expansion, principally because of the number of potential study species and high levels of observer effort in the UK (e.g. Sharrock, 1976; Gibbons *et al*., 1994; Hiley *et al*., 2013). They can also be used to analyse range expansion patterns of introduced species. Seven wetland birds (Table 3.1) have become naturalised in the UK (i.e. they currently have persistent breeding populations resulting from escaped/introduced individuals). A further 13 species (see Appendix 2A) have bred in the wild in the UK having escaped/been introduced. As has been demonstrated with other introduced birds (e.g. Temple, 1992), several of these introduced species have caused ecological and societal conflicts (Lever, 2005).

Here, we investigate the use of PAs since 1960 by those introduced wetland bird species which have been expanding their range within the UK since that time. Records from county bird reports and the Rare Breeding Birds Panel (RBBP (www.rbbp.org.uk)) are used to assess how frequently introduced species use PAs as 'landing-pads' when they colonise new UK counties, and also whether the association of introduced species with PAs changed as populations become more established and consolidated within each county. These are compared directly with natural colonists, for which it has been shown that PA usage declines with time (Hiley *et al*., 2013). We hypothesised that introduced species would show less association with PAs than natural colonists either at the initial stage of their colonisation or as their populations became more established.

3.3 Methods

3.3.1 Species Selection

Introduced species were defined as wetland birds (habitat classification from Gibbons *et al*. 1995) with native breeding ranges (ranges ascertained from BirdLife International http://www.birdlife.org/datazone) that do not include the UK or adjacent parts of continental Europe, but which have established persistent breeding populations (≥10 pairs for at least 5 years to 2012, according to RBBP data) deriving from individuals that were either deliberately released or which accidentally escaped from captivity (see Table 3.1, Appendix 2B).

Table 3.1 Introduced wetland birds with persistent breeding populations in the UK. Population estimates from Henderson (2006) (for Ruddy Duck), Musgrove *et al*. (2013), and the Rare Breeding Birds Panel (for Black Swan). Red-crested Pochard was not included for analysis as it breeds naturally in continental Europe.

Species Name	**First bred in the wild in the UK**	**Current Population Estimate (pairs)**
Canada Goose *Branta canadensis*	Pre-1800	62,000
Egyptian Goose *Alopochen aegyptiacus*	Pre-1900	1100
Black Swan *Cygnus atratus*	1902	25
Mandarin Duck *Aix galericulata*	1932	2300
Barnacle Goose *Branta leucopsis*	c. 1960	900
Ruddy Duck *Oxyura jamaicensis*	1960	3000 (peak)
Red-crested Pochard *Netta rufina*	1937	10-21

Natural colonists were wetland birds which have recently colonised the UK, defined as having first bred in the UK (dates obtained from the BTO http://www.bto.org/about-birds/birdfacts) after 1940, and that maintain a persistent breeding population currently (as for introduced species, see above). Also included were wetland birds that were absent from the UK (defined as no confirmed breeders for at least two consecutive years according to RBBP data) before re-colonising (Table 3.2). This applied to three species (Black-tailed Godwit *Limosa limosa,* Avocet *Recurvirostra avosetta,* and Great Bittern *Botaurus stellaris*). Although no confirmed Great Bittern nests were found for two consecutive years, a very small remaining population may have continued to breed during this period. For Whooper Swan *Cygnus cygnus*, breeding in the UK has involved both feral and 'wild' birds. RBBP records, however, distinguish between the two states (based on geography) and thus records were included in the appropriate category.

Table 3.2 Naturally occurring wetland birds with currently persistent breeding populations that first bred in the UK after 1940. Population estimates from Musgrove *et al*. (2013). Osprey and Common Crane could not be analysed due to sensitivity over breeding locations.

Species Name	**First bred in the wild in the UK**	**Current Population Estimate (pairs)**
Avocet *Avosetta recurvirostra*	1941 (after extinction in 1883)	1500
Black-tailed Godwit *Limosa limosa*	1946 (after extinction in 1885)	54-57
Mediterranean Gull *Larus melanocephalus*	1968	600-630
Common Goldeneye *Bucephala clangula*	1970	200
Cetti's Warbler *Cettia cetti*	1973	2000
Whooper Swan *Cygnus cygnus*	1978	9-14
Great Bittern *Botarus stellaris*	1987 (after extinction in 1985)*	80
Little Egret *Egretta garzetta*	1996	660-740
Osprey *Pandion haliaetus*	1954 (after extinction in 1916)	200-250
Common Crane *Grus grus*	1984	9-14

*See note in text about whether this was an absolute extinction

3.3.2 Obtaining Data

Data were obtained from county avifaunas, which contain historical information on each bird species that has been observed in that county. Breeding data at later stages of colonisation were obtained from county bird reports, which are annual compilations of bird sightings, and the RBBP, who hold detailed accounts of breeding for species considered 'rare breeding birds' (see 'species list'; http://www.rbbp.org.uk/rbbp-species-list-full.htm). For Black Swan *Cygnus atratus*, which has largely been ignored by county recorders, all breeding data were obtained from the RBBP.

3.3.3 Determining PA status

The PAs considered are UK Sites of Special Scientific Interest (SSSIs), which are considered to meet the IUCN level IV of protection. Breeding records were cross-referenced against PA location using the interactive mapping software provided by Natural England (NE) (http://www.natureonthemap.naturalengland.org.uk), the Countryside Council for Wales (CCW) (http://www.ccw.gov.uk/landscape--wildlife/protecting-our-landscape/protected-sites-map.aspx), and Scottish Natural Heritage (SNH) (http://gateway.snh.gov.uk/sitelink/searchmap.jsp). Records with grid references were assigned PA status if the entire grid cell (normally 100 x 100 m resolution) was within the boundary of a PA. Records without grid references were assigned PA status only if associated with site/reserve names for which PA status was unambiguous. County bird recorders were consulted for clarification when grid references partially overlapped PAs or location names were vague; if still ambiguous, the records were omitted (Hiley *et al.,* 2013).

3.3.4 Calculating PA Associations

For each species, we considered each UK county that was colonised by one of our sample species after 1960 (pre-1960 bird reports are limited in terms of data-quality). For each of these ‘county colonisation events’, we considered the first breeding location, and then all breeding in two different time periods. Period 1 was in years 4-6 after initial breeding, which we consider the *establishment* phase. Period 2 was in years 14-16 after initial breeding, which we consider the *consolidation* phase. During each period, we considered all records of confirmed breeding for natural colonists, and both confirmed and probable breeding (see RBBP for definitions) for Great Bittern and Cetti’s Warbler (which both nest in dense, inaccessible vegetation, but which sing loudly), and the introduced species (counts are normally given in pairs as opposed to confirmed breeding). From these data, we were able to calculate PA associations for each species upon arrival (percentage of the first county breeding locations that were in PAs), and in Period 1 and Period 2 (percentage of all breeding records associated with PAs for both periods). If there were fewer than five records of a species available in any particular period, it was not considered for analysis in that period. This occurred with Little Egret (a recent colonisation) and Black Swan (recently established) in Period 2.

To test the robustness of our results, we carried out complementary analyses based on the number of *sites* (breeding locations) where breeding took place, as opposed to the number of pairs that bred.

3.3.5 Additional species

The strict species selection criteria were adopted to ensure directly comparable data and full, sustained establishment for introduced and naturally colonising species. However, data relevant to our biological questions were also available for a selection of additional species. Therefore, we extended the scope of the study by carrying out supplementary analyses on (1) introduced wetland bird species that had become established in the UK, but had died out again by 2012, (2) non-wetland introduced and native bird species that have become established in the UK and (3) introduced wetland bird species that are not in the family *Anatidae* (which were over-represented among introduced species) that are currently established in continental Europe (Appendices 2C, 2D).

3.3.6 Statistical tests

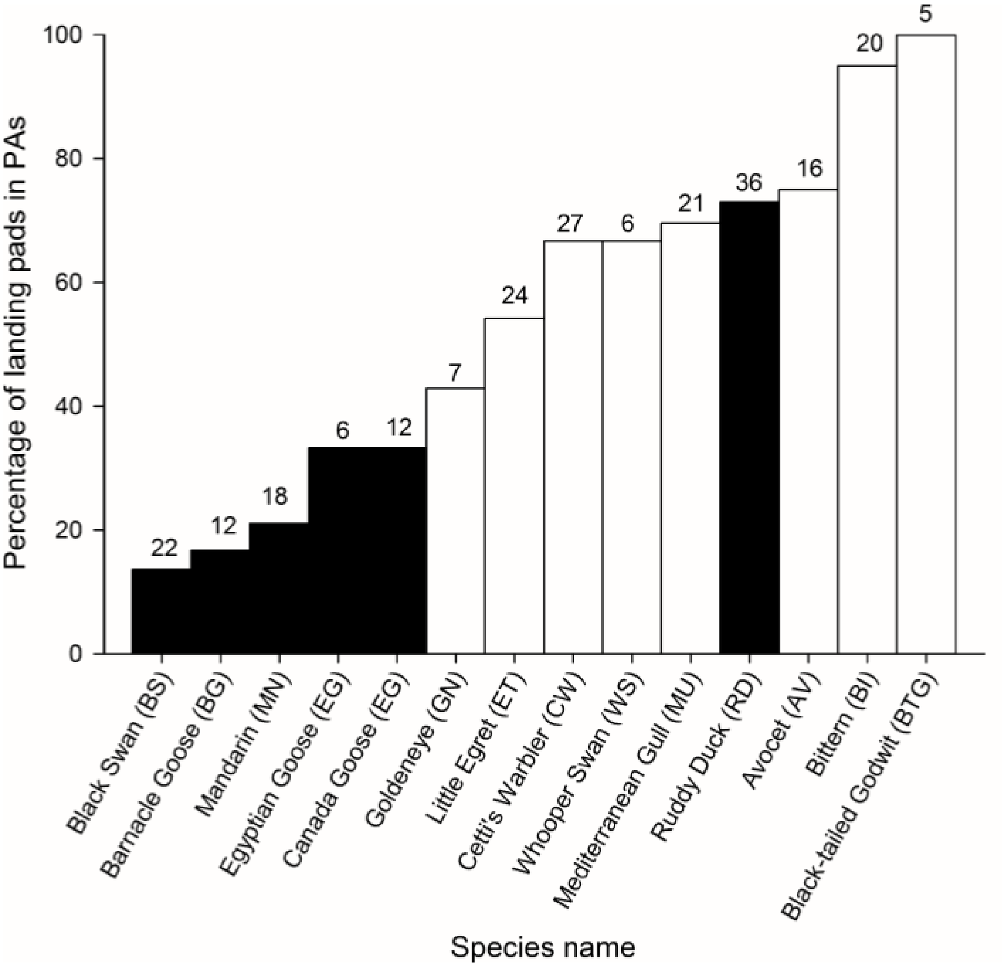
Mann-Whitney U tests were used throughout to compare PA associations of introduced species and colonists at different stages of colonisation (sample sizes were insufficient to test for normality robustly). When comparing changes in PA association between Periods 1 and 2 between introduced and natural colonists, the data could be tested for normality (Shapiro-Wilk, w_{12}, P=0.316) and we then used a 2-sample t-test. A supplementary analysis was also carried out excluding Great Bittern from the list of natural colonisers (due to doubts over whether they did disappear as breeding birds in the UK during the study period, see above, Appendix 2E). All probabilities reported are two-tailed.

3.4 Results

3.4.1 First breeding records of colonising species

Introduced species were less likely to use PAs as landing pads than natural colonisers (Figure 3.1, Mann-Whitney, $z_{6,8}$=2.39, P=0.0168, Medians: 33% (introduced species), 67% (natural colonisers)).

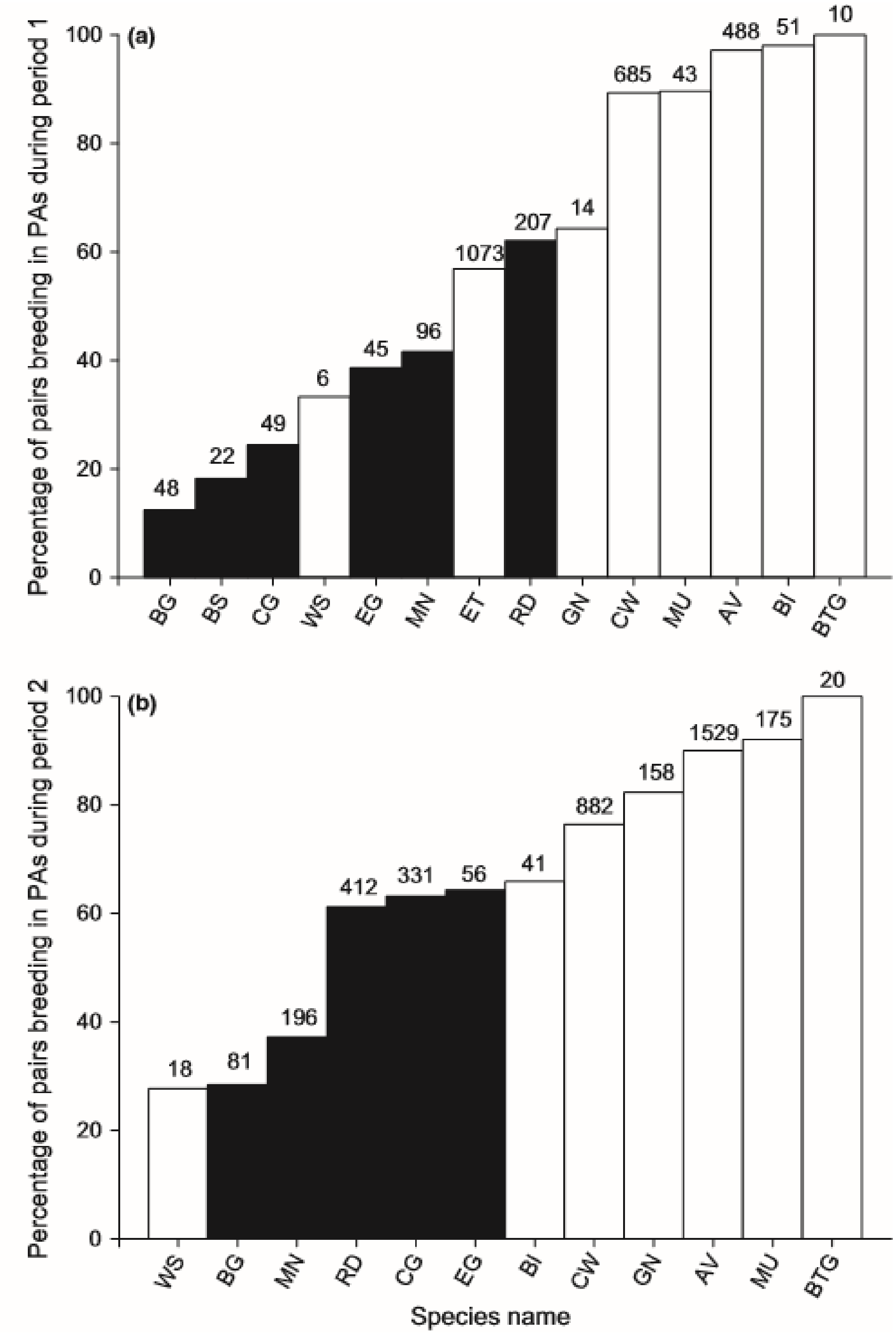
Figure 3.1 Comparison of use of PAs as landing pads in newly colonised counties between introduced species (black) and natural colonists (whites). Shown are the percentage of sites that were in PAs out of all the 'first' breeding locations in counties colonised after 1960. Numbers above the columns represent the sample size (numbers of counties).



3.4.2 PA Association of Colonising Species in Period 1 (establishment phase)

The percentage of breeding attempts of the introduced species that was in PAs was much lower than that of natural colonisers during Period 1 (Figure 3.2(a), Mann-Whitney, $z_{6,8}$=-2.64, P=0.0117, Medians: 31% (introduced), 89% (natural)); 4-6 years after the initial colonisation of counties. There was also a significant difference between introduced and natural colonists when analysing the data in terms of the number of sites colonised (Mann-Whitney, $z_{6,8}$=-2.9, P=0.0037), rather than the number of pairs.

Figure 3.2 PA Association of introduced species (black) and natural colonists (white) during Periods 1 (*establishment*: 4-6 years after initial breeding in county, panel a) and 2 (*consolidation*: 14-16 years after initial breeding in county, panel b). The percentages shown derive from the total number of pairs breeding in PAs in all newly colonised counties during the period relative to all breeding pairs (in PAs and non-PAs) in that period. The numbers represent the total number of pairs analysed in each period. The abbreviations for species names are shown in Figure 3.1.



3.4.3 PA Association of Colonising Species in Period 2 (consolidation phase)

In Period 2 (14-16 years after initial colonisation of counties), the percentage of breeding attempts of introduced species that was in PAs was lower than that for natural colonists, but the difference was not significant (Figure 3.2(b), Mann-Whitney, $z_{5,7}$=-1.95, P=0.0512, Medians: 62% (introduced), 82% (natural)). The difference was significant in the site-based analysis (Mann-Whitney, $z_{5,7}$=-2.27, P=0.0232).

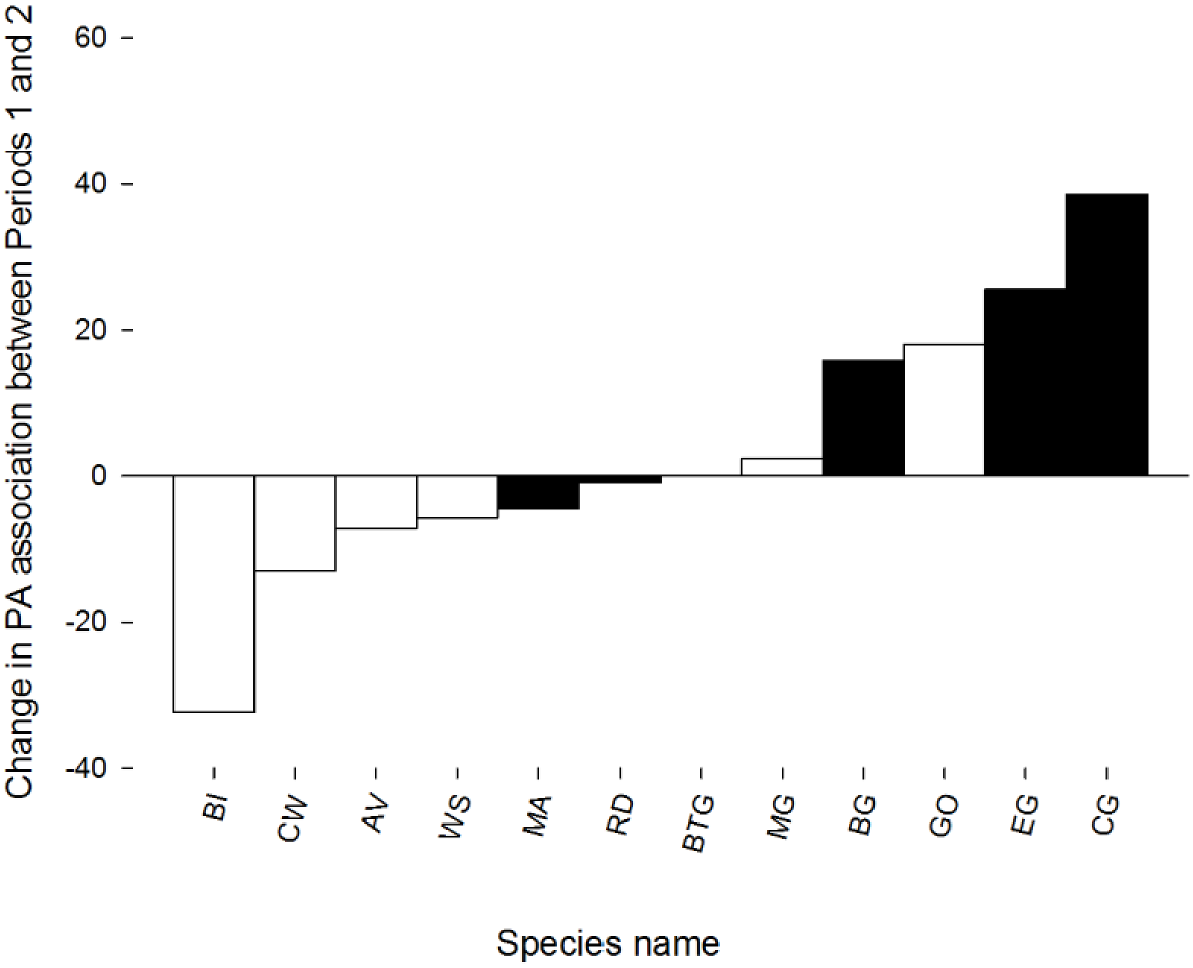
3.4.4 Comparison of PA Association of Colonising Species between Periods

Changes in PA associations between Periods 1 and 2 suggest that several introduced species may have showed increasing associations with PAs over time (Figure 3.3). However, the possible difference in temporal trends in PA association between introduced and natural colonists was not significant (t-test, $t_{7,5}$=-2.045, P=0.076).

3.4.5 Additional species

One additional (outside *Anatidae*) introduced wetland bird species became established in the UK after 1940 (Black-crowned Night Heron *Nycticorax nycticorax*) but died out again as a breeding species in 2003. All sites occupied by *N. nycticorax* during Landing Pad, consolidation and establishment phases were outside PA land. Hence, inclusion of this species in the analyses resulted in increased significance of the differences between introduced species and natural colonists at all stages of arrival and establishment (Appendix 2F). We extended the analysis to include three non-wetland species, which were the Firecrest *Regulus ignicapillus*, Collared Dove *Streptopelia decaocto* (both natural colonists), and Rose-ringed Parakeet *Psittacula krameri* (introduced). The results remained significant with these species included, even though *S. decaocta* is closely associated with non-PA land (Appendix 2F, Discussion).

Figure 3.3 The difference in PA association (measured in percentage points) between Periods 1 and 2 for introduced species (black) and natural colonists (white). The abbreviations for species names are shown in Figure 3.1.



3.5 Discussion

Introduced species can have negative environmental and economic impacts, particularly within PA networks, which might harbour protected native species. Although the vulnerability of PAs to colonisation by introduced species is theoretically low (e.g. Tansley, 1939), empirical evidence suggests that invasions of reserves are common (e.g. Usher, 1988; McDonald *et al.*, 1989; GISP, 2007; Allen *et al.*, 2009; Burfeind *et al.*, 2013). Nonetheless, we hypothesised that introduced wetland birds in the UK would show weaker PA associations than natural colonists; they have different habitat requirements, and are more likely to be released away from reserves.

When colonising a new county, bird species can first breed on either protected or unprotected land; protected land attracts colonising species (Hiley *et al.*, 2013), whereas the majority of first breeding events by introduced species were outside PAs (Figure 3.1). The benchmark for associations with protected areas – for these wetland-associated species – is the percentage of wetland under protection (Appendices 2G, 2H), which is around 30% (compared to 12% of the total land area (jncc.defra.gov.uk)). Using coarse metrics of the availability of protected and unprotected wetland in each county, introduced species colonised PAs and non-PA land approximately in proportion to their availability, whereas natural colonists still favoured them (Appendix 2I). Further data are required to test this conclusion more robustly because the land cover data for this analysis were too coarse to accurately calculate species-specific levels of protected and unprotected habitat availability (i.e. land cover layers did not adequately describe species-specific associations with open water, reed, grazing marsh, freshwater/saline conditions).

Given the different habitat requirements of the two groups, this result is expected. Many PA management actions are specifically targeted at habitat improvement for some of the subject species (reedbed maintenance for Great Bittern and water level control for Avocet *Recurvirostra avosetta*). On the other hand, management would not be directed towards the requirements of the introduced wetland birds, such as *Anatidae*, which are often successful 'invaders' (Lever, 2005). The Canada Goose *Branta canadensis*, for example, breeds on manicured lawns, such as those found in parks, airports and golf courses, in both their natural and introduced ranges (Cabot, 2009). The invasive species which showed the highest association with PAs, Ruddy Duck *Oxyura jamaicensis* (Figure 3.1), was also the species whose habitat-requirements most closely match British PA priority habitats.

In this study, the group of introduced species was unavoidably taxonomically narrower than the natural colonists. We do not believe, however, that this affects either the conclusions or the implications of this study because invaders frequently belong to a non-random subset of potential taxa that could be introduced (e.g. Schmidt & Drake, 2011). Furthermore, our introduced species are representative of introduced wetland bird species in general. For example, of the 31 introduced wetland bird species that have become established in Africa and Eurasia, 27 (87%) are from the family *Anatidae* (Banks *et al.*, 2008).

Nevertheless, we carried out three further analyses to test the robustness of our findings. Other introduced wetland species (outside *Anatidae*), both in continental Europe and historically in the UK, appear to follow patterns in PA use similar to the Anatidae (Appendices

2F, 2J). The inclusion of those non-wetland bird species (both introduced and natural colonists) that have recently colonised the UK also validated our results (Appendix 2F), although the Collared Dove, which is an invasive species in North America (e.g. Hengeveld, 1993) but a natural colonist to the UK, was an interesting exception.

Whereas most natural colonists showed a declining association with PAs as they became established (Hiley *et al*., 2013), there is a trend for introduced species to show the opposite pattern (Figure 3.3). Although the difference in temporal trends between natural colonists and introduced species was not statistically significant using species as replicates, we did observe that there was an increase in the total percentage of pairs of introduced species that were in PAs: only about a third (38%) of 'first breeding' events was in PAs (Figure 3.1), whereas over a half (55%) of all pairs was in PAs 14-16 years after their first arrival (Figure 3.2). Such a pattern might reflect either a natural process of introduced species moving away from points of release in non-PAs and into the nearest available habitat or, alternatively, a growing preference for a PA network which can potentially offer invaders, as well as natural colonists, high quality habitat in which to breed, and a safe haven from potential threats. Whatever the reason, large numbers of individuals of non-native species now regularly appear on reserves. Increasing incidences of invasions are being noted across a broad range of groups (e.g. Huang *et al*., 2011), potentially leading to an increased need for control measures (one of our subject species, Ruddy Duck, has subsequently been reduced by an eradication programme to help prevent global extinction, by hybridisation, of the European native White-headed Duck *Oxyura leucocephalus*).

This study used data from county bird reports, which provide an important historical record of bird sightings on a regional scale in the UK. Such a dataset, which relies on contributions from casual observers, is particularly important when analysing distribution patterns of rare birds, or 'new' birds within a county, which attract more interest from bird watchers and recorders (e.g. Pithon & Dytham, 2002). Although sightings data in general may show a bias towards protected areas, it has been previously demonstrated, for a wide range of wetland bird species, that there was no systematic trend in observer effort either towards or away from PAs (Hiley *et al.*, 2013). Thus, the differing trends in PA use presented here appear robust.

Wetland bird species that have been introduced to the UK in the past have been significantly less associated with PAs than natural colonists during the initial stages of their colonisation. However, with time, their propensity to use PAs increases. Whilst not specifically favoured for initial colonisation, PAs might unintentionally subsequently facilitate the establishment of persistent populations. The patterns of first arrival, establishment and consolidation observed for these bird species suggest that PAs are more effective at facilitating the range expansion of naturally colonising species from nearby regions than they are at assisting the establishment of introduced species from other parts of the world.

3.6 Acknowledgements

We are grateful to all of those involved in the collation of records for, and the production of, county bird reports. We give thanks to Natural England, Scottish Natural Heritage and the Countryside Council for Wales for the use of their online software and particular thanks to the Rare Breeding Birds Panel for their continued support throughout this work.

Chapter 4: Impacts of habitat change and protected areas on the alpha and beta diversity of Mexican birds

4.1 Abstract

Aims To investigate how habitat change and different levels of protection interact to determine variation in the (alpha and beta) diversity of bird communities in three bioclimatic zones, considering the impacts of non-native species, and the contribution of these effects to global (gamma) diversity.

Location Sierra Gorda Biosphere Reserve, central Mexico

Methods We carried out bird surveys in a number of locations which varied according to their underlying vegetation-type, their level of protection, and the degree to which they had undergone modification by humans. We conducted a range of analyses to determine the impacts of protection and modification on the richness and mean global population trends of the species found in each location. We compared community composition in order to assess the homogenisation effect of habitat modification.

Results Human-modified environments in each of three bioclimatic zones held significantly greater numbers of species (alpha diversity) than unmodified habitats. Human-mediated changes to local bird communities altered patterns of beta diversity in opposite directions; communities across bioclimatic zones were more similar to one another in modified areas than in unmodified areas but, on a local scale, modification of vegetation increased community dissimilarity. The changes are likely to contribute to a decline in global (gamma) diversity, given that globally vulnerable (declining) birds were mostly associated with unmodified, strictly protected areas.

Main Conclusions We highlight that assessment of human impacts and conservation need depends on the metric of biodiversity used and scale considered: small-scale habitat change increased local and regional avian diversity but strictly protected areas are still required to protect globally vulnerable species.

4.2 Introduction

Human modification of natural areas typically has a negative effect on biodiversity (e.g. Newbold *et al.*, 2014), often as a result of habitat loss (Brooks *et al*., 2002) and the introduction of invasive species (e.g. Clavero & Garcia-Berthou, 2005; although see Thomas & Palmer, 2015). However, although Newbold *et al.* (2014) report widespread losses in biodiversity as a result of human alterations to vegetation, impacts are context dependent, and vary according to type and intensity of change (e.g. MacGregor-Fors & Schondube, 2011), spatial scale, and the metric of diversity measured (McGill *et al*., 2015). For example, reductions in local alpha-diversity might be particularly severe in tropical regions undergoing fundamental land-use change (Murphy & Romanuk, 2014), but subsistence farmland (e.g. Mulwa *et al.,* 2012), or low-intensity agricultural mosaics can hold similar numbers, or even more species than nearby natural habitat (regardless of their value for vulnerable species; Milder *et al*., 2010). On a regional scale, human modification of habitat might increase alpha-diversity through the introductions of non-native species, but decrease beta-diversity as a result of homogenisation of habitats (McGill *et al*., 2015). Empirical studies that consider different biodiversity metrics at different spatial scales are therefore clearly necessary.

The designation of Protected Areas (PAs) remains the most common conservation measure employed to protect rare or specialised species from threats such as exploitation and habitat loss, and thereby to minimise biodiversity losses. PAs cover approximately 13% of the world's land surface (Venter *et al*., 2014), yet their effectiveness in terms of maintaining species richness, adequacy of coverage and reducing threats is debated (Gaston *et al*., 2008; Cabeza, 2013). Increased bird diversity inside PAs is common (e.g. Devictor *et al*., 2007; Greve *et al*., 2011), but not universal (Rayner *et al*., 2014), and depends as much on the richness of locations before they were designated as on the efficacy of the protection after the PAs were established. Population trends of species, however, do appear to respond positively to protective measures, at least in Europe (Donald *et al*., 2007; Sanderson *et al*., 2016). PAs, as safe-havens from threats such as deforestation and hunting, should conserve habitats, and, globally, PAs appear to offer good protection to forest habitats (Beresford *et al*., 2013; Geldmann *et al*., 2013).

However, many PAs might be 'paper parks', particularly in developing and transitional countries – designated as protected but short of the resources needed to be effective against all external pressures (Watson *et al*., 2014; Blackman *et al*., 2015). Almost half of Mexico's protected area network, for example, has been regarded as weak or non-effective at preventing land cover change (Figueroa & Sánchez-Cordero, 2008; Figueroa *et al.*, 2011). Uncertainty about the efficacy of PAs may also stem from the consideration of different metrics of diversity and focal taxa in different studies, and whether non-native species are included within species counts. Non-natives are often initially associated with human activity (e.g. population density; McKinney, 2006) and trade patterns (Westphal *et al.*, 2008), that typically occur in unprotected land, and hence this could increase measured diversity outside PAs, or decrease diversity if invasive species pose a threat to native species (GISP, 2007).

Habitat change, legal protection and invasion act together, and hence it is unclear how – in combination – they affect different measures of biodiversity. Here, we investigate how legal protection and habitat modification interact to affect different measures of biodiversity at different scales, encompassing: the species richness of local communities sampled in different bioclimatic zones (alpha diversity), differences between the bird communities in different locations (beta diversity), and the representation of globally declining species in bird communities (a regional contribution to global, or gamma, diversity). Specifically, we assess the impacts of human-driven habitat change on bird diversity in unprotected, protected and strictly protected areas in three major bioclimatic zones (each represented by a different major vegetation type) in central Mexico. Assuming that our study area was not a so-called 'paper park', we hypothesised that avian species richness would be higher in regions unmodified by humans and in areas that were protected. We also predicted that non-native species would be more prevalent in modified areas, contributing to a more homogenous community composition across areas affected by habitat conversion.

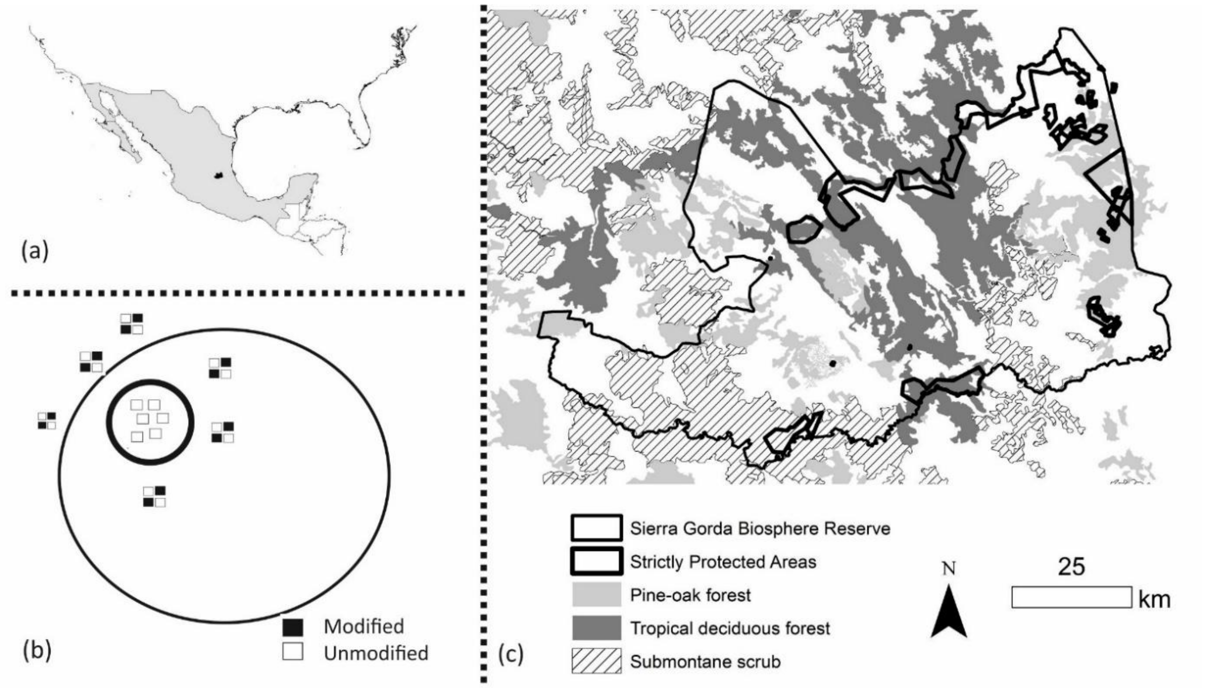
4.3 Methods

4.3.1 Study Area

The study was carried out in and around the Sierra Gorda Biosphere Reserve (SGBR) in Querétaro, Central Mexico (Figure 4.1(a); Appendix 3A) which covers 383,567 hectares and ranges from 300 m to 3160 m in elevation. It is an area has received little previous ornithological attention (Hernandez-Diaz *et al.*, 2015). We focused on three of the key bioclimatic zones protected within the SGBR, each naturally associated with a different predominant vegetation type: pine-oak forest, submontane scrub and tropical deciduous forest (for descriptions, see Appendix 3B). The SGBR contains 11 'nucleus zones' and a number of privately managed nature reserves (corresponding to International Union for

Conservation of Nature, hereafter IUCN, Category Ia – strict protected areas, see Appendix 3C) surrounded by a 'buffer zone' (IUCN Category VI), in which human activity is permitted, with some restrictions in place (Appendix 3C). We also considered locations around the SGBR that fell within the same bioclimatic and vegetation zones, but for which there was no legal protection (hereafter 'unprotected'). The combination of three bioclimatic (vegetation) zones that we considered (permitting replication across zones), three different levels of protection (unprotected, protected, strictly protected), and the contrast between disturbed and undisturbed locations that were available in and around the SGBR made it a particularly suitable region to tease apart the impacts of protection and disturbance on bird diversity patterns.

Figure 4.1 Location of (a) the study area within Mexico, (b) a schematic of the study design for each bioclimatic zone indicating modified and unmodified squares in unprotected, buffer and strictly protected areas, and (c) an outline of the SGBR showing strictly protected areas and different bioclimatic zones.



4.3.2 Study Design

We surveyed the birds associated with natural habitats versus habitats which have been modified as a result of small-scale human habitation and agricultural development (see Appendix 3D). Modified and unmodified squares were compared in three bioclimatic zones, and for three different levels of protection within each bioclimatic zone. This allowed us to separate impacts of habitat change from legal protection (with the underlying bioclimatic zones as replicates), and to consider the interactions. However, human-modified habitats were not available within the strictly-protected zones (by definition; for IUCN 1a classification). Hence, our sampling and analysis has two 'designs' (Appendix 3E). Design 1 considers human-modified and relatively natural habitats (two levels of habitat modification) within each bioclimatic zone (three levels), and two different protection zones (unprotected, buffer). Design 2 considers only the relatively natural habitats (one level), measuring the effects of bioclimatic zone (three levels) and protection (three levels; unprotected, buffer, strict). Six one-kilometre squares (see below) were surveyed for birds and associated environmental data for each combination of habitat modification / bioclimatic zone / protection (excluding modified habitat in areas with strict protection, which does not exist). 89 sample squares were surveyed in total (only 5 squares were surveyed within a tropical deciduous forest nucleus zone, see below).

Each one-kilometre sample square (of a given type) was located to be as independent as possible, within the constraints that the distribution of different bioclimatic zones are associated with elevation and climatic gradients, and levels of protection come as blocks of land (particularly for the strict protection areas) (Appendix 3C)). Designation of land into protection level (buffer, strict) was based on the official SGBR boundaries (Figure 4.1(c)), with all unprotected squares being selected within 20km of the SGBR boundary. The three bioclimatic zones are linked to variation in precipitation and temperature, and were based on maps of the three target vegetation types; pine-oak forest, submontane scrub and tropical deciduous forest from INEGI (2013).

Habitat modification by humans was defined as unmodified (less than 10% of the square affected by signs of human modification on land cover maps (INEGI, 2013) and satellite imagery – see Appendix 3D), or modified (more than 50% of the square affected by human modification, and within 3km of an unmodified square). For a given bioclimatic zone, each square was: (1) in the same elevation band (600 – 1200m for tropical deciduous forest; 1600 – 2200m for submontane scrub; and 1850 – 2450m for pine-oak forest), (2) on a flat or non-north facing slope, (3) within 2km of a road, for access, and (4) at least 1km away from other squares in the same class. Within each protection class, squares were arranged in three ‘clusters’, for logistical purposes – each containing two unmodified and two modified squares and located at least 4km away from other clusters (Figure 4.1(b)). All squares were designated as belonging to a specific type (combination of habitat modification / bioclimatic zone / protection level) from literature and from remotely obtained data and images prior to the field visits.

Point counts were undertaken at the four corners of a 500m square centred in the middle of each one-kilometre square, with data from the four points combined to generate a single measure of each variable for each one-kilometre square. These points were defined prior to the field visit, but were moved during the field visit if a point fell: (1) within modified habitat in an ‘unmodified’ square (see above), (2) within the unmodified part of a ‘modified’ square, (3) on private property where no access could be negotiated, or (4) on inaccessible land due to steep slopes/impenetrable vegetation. Under these circumstances, the point was then moved to the nearest accessible/permitted location within the ‘correct’ (modified/unmodified) habitat designation. Points could be moved up to a maximum of 300 metres, whilst ensuring that the new point remained a minimum of 200 metres away from all other points within the square. If this was not possible, squares were discarded from the study and pre-determined, randomly selected alternatives were used.

The 500m-cell point count design was not feasible in the strictly protected areas, which have restricted access, and are characterised by their inaccessibility, remoteness, high vegetation density and steepness. In these squares, point counts were taken at 200m intervals along transects across squares which matched the criteria outlined above. If the length of transect determined that a square had more than four point counts taken in it, four were chosen randomly from all of the counts taken. Again, data from the four points were combined to generate a single measure of each variable for each one-kilometre square. Six squares were surveyed in pine-oak and submontane scrub nucleus zones and five in a tropical deciduous forest nucleus zone.

4.3.3 Surveys

All 356 points were surveyed during the non-breeding season, between 5 October 2014 and 10 March 2015 inclusive, sampling resident and wintering species for the entirety of the study period (based on typical arrival/departure dates www.ebird.org). A 10-min point count was conducted at each survey point, during which all birds seen or heard within a 100m radius were recorded (hence the minimum 200m between sample points). Distances to each individual were estimated to the nearest 10m, and overflying birds were recorded if they were flying within 50m of the ground. All point counts were conducted before 13.30 h and in conditions with good visibility (minimum 300m) and without rain or strong wind (Beaufort 5 or above). All squares within the same cluster were surveyed within two weeks of each other for logistical purposes. The order of surveys completed was randomised to ensure no temporal bias of bioclimatic zone, habitat modification level or protection level.

In addition to bird counts, we measured micro-disturbances observed in each square (see Appendix 3D), and we estimated the vegetation density at each point (measured as the number of stems with circumference greater than 20cm at knee height or bushes with girth of 1m or greater at knee height in tropical deciduous forest and submontane scrub, and the number of stems with circumference greater than 20cm at chest height in pine-oak forest) to account for its potential effect on bird detectability.

4.3.4 Analysis

For all birds recorded at any point in a square, we entered the distance estimated (from the observation point to the bird) into the software Distance (Thomas *et al*., 2010), which uses the drop off in frequencies of observation with distance from an observer to calculate an Effective Detection Radius (EDR) for each sample point. EDR was tested for significance in our models and also specified as a dependent variable in a separate Generalised Linear Model (GLM) to see if it was significantly affected by bioclimatic zone, habitat modification, protection, vegetation stem density or any interaction effect that would influence interpretation of the results.

Species richness (absolute number of species observed) and the mean global population trend (species were ranked +1 if their populations are increasing at a global level, 0 if stable and -1 if decreasing: www.birdlife.org/datazone) of species observed in each square were normally distributed (Shapiro-Wilk test) and were specified as dependent variables in separate Generalised Linear Mixed Models (GLMMs) using the software SPSS (IBM Corp, Armonk, NY, USA). As fixed factors (see Appendix 3F), we tested the effects of bioclimatic zone (pine-oak, submontane scrub or tropical deciduous forest), protection level (unprotected, buffer or strict), modification level (unmodified or modified), microdisturbance (see Methods, Appendix 3D), julian day since start of study, julian day squared, time of day (mean time of day of the four point counts, in minutes after sunrise), time of day squared, elevation, vegetation stem density (see above) and EDR. Clusters, which were groups of four squares in the same protection class situated geographically close together (see study design), were included as a random categorical factor in the GLMMs, to account for non-independence of species richness in nearby squares. Design 1 models consider modified and unmodified habitats at two levels of protection (unprotected, buffer), and design 2 models consider only the unmodified habitats, but at three levels of protection (unprotected, buffer, strict). Note that the differing spatial arrangement for sampling used for the strictly protected squares (see above) could affect species richness (summed over the four sample points, see results), but not analyses based on those species' population trends.

Models containing bioclimatic zone, habitat modification, protection and all combinations of variables (including two-way interactions) were run, both with and without the interaction terms. The final models cited are those which had the lowest AIC_c values. Models with AIC_c values within two of the best-fit model were considered equivalent and are provided in Appendix 3G.

To check whether our conclusions might have been affected by the detectability of species and local population densities, we used the software SPADE (Chao & Shen 2010) to calculate estimates of actual species richness, based on six different models: Chao1, Chao1bc, ACE, ACE1, Jackknife1 and Jackknife2 (See http://chao.stat.nthu.edu.tw/wordpress/wp-content/uploads/software/SPADE_UserGuide.pdf for full descriptions of models). Each of these estimates was tested as the dependent variable in a separate GLMM to check the robustness of the results reported for observed species richness in design 1 (low species counts in strictly protected locations meant that these models didn't consistently function for design 2).

We also made pairwise comparisons of the bird species observed in different squares to allow us to test for differences in community composition between modified and unmodified squares, both within- and between-bioclimatic zones. Unprotected and buffer squares within each bioclimatic zone/modification level were not distinguished for this analysis (Appendix 3H) and strict squares were omitted. When comparing between bioclimatic zones, we calculated coefficients of similarity (Jaccard) within modified locations and also within unmodified locations (testing whether different bioclimatic zones have more similar bird communities where the original vegetation has been modified), and we also made comparison between modification levels. We made pairwise calculations, avoiding non-independence of pairwise comparisons. For the within-modification level comparisons, each square was randomly labelled 1-12, and paired using a 'round-robin' generator in Microsoft Excel. The process was repeated for 11 'rounds', which is the maximum number of permutations possible whilst ensuring that no pairs of numbers are repeated. For the across-modification level comparisons, unmodified squares were paired with the equivalent modified squares (1 vs 1, 2 vs 2 etc). This process was repeated 12 times with each unmodified square (in ascending order) paired with the next 'available' modified square whilst ensuring that no pair of numbers was repeated (2nd permutation: 1 vs 2, 2 vs 3, …, 12 vs 1. 3rd permutation: 1 vs 3, 2 vs 4…etc). The mean coefficients were then calculated for each permutation for both the within- and the across-modification level tests, and these coefficients were compared with a one-way Analysis of Variance (ANOVA) test.

For each between-bioclimatic zone comparison (three levels: pine-oak versus submontane scrub, pine-oak versus tropical deciduous and submontane scrub versus tropical deciduous), we compared similarity within unmodified squares and within modified squares (within modification level). For both modification levels, each square was paired with one from the other bioclimatic zone. Means for each permutation were calculated as above and compared using t-tests.

Although there were some differences in similarity between buffer and unprotected squares for each bioclimatic zone (Appendix 3H), there were no significant differences (out of six tests) in comparisons of within protection level similarity (combined for buffer and unprotected) and between-protection level similarity for either modification level in any of the three bioclimatic zones. This suggests that protection level didn't have an overarching effect on community similarity, and thus we didn't distinguish unprotected and buffer zone squares for the above analysis.

To see whether introduced species were more associated with a particular protection or modification level, we used a chi-squared test of association to analyse which squares did, and did not, contain introduced species.

4.4 Results

We recorded 3164 birds from 168 species (see Appendix 3I). 363 species have been reported in total from the SGBR (INECC, 1999), although this total includes summer visitors outside the study period, vagrants and species from habitats and bioclimatic zones not included in this study, such as wetlands and cloud forest. Estimated actual species richness varied from 183.5 to 200 based on different models, and thus our species-level coverage was approximately 90%. Of all the species recorded, 44 were from populations of species classified by BirdLife International as in global decline.

Effective detection radius (detectability) was not significantly affected by bioclimatic zone, protection level, habitat modification, vegetation density or any interaction effects (see Appendix 3G). Incorporating EDR into our models did not improve them or alter the main conclusions, suggesting that the results presented below using the raw data are robust to sampling error associated with any potential variation in the visibility of species in different environments (see Appendix 3G for models not shown in the main body of text).

4.4.1 Species Richness (alpha diversity)

For unprotected and buffer zone locations (design 1), the lowest AICc model (Table 4.1) showed that local species richness (number of species counted per 1km square) was significantly higher (on average by 42%) in human-modified than in unmodified habitats (Figure 4.2, Appendix 3J). Local richness was also affected by interactions between bioclimatic zones and habitat modification (the greatest effect of habitat modification was in submontane scrub (Figure 4.2)) and between bioclimatic zone and protection level (protection was positively associated with species richness in pine-oak forest and submontane scrub, but not in tropical deciduous forest). Species richness also increased in modified habitat in models with interaction terms removed (Appendix 3G).

Figure 4.2 Mean observed species richness in each bioclimatic zone for unprotected and buffer squares (design 1). Bars represent Standard Errors. Tables of means are shown in Appendix 3J.

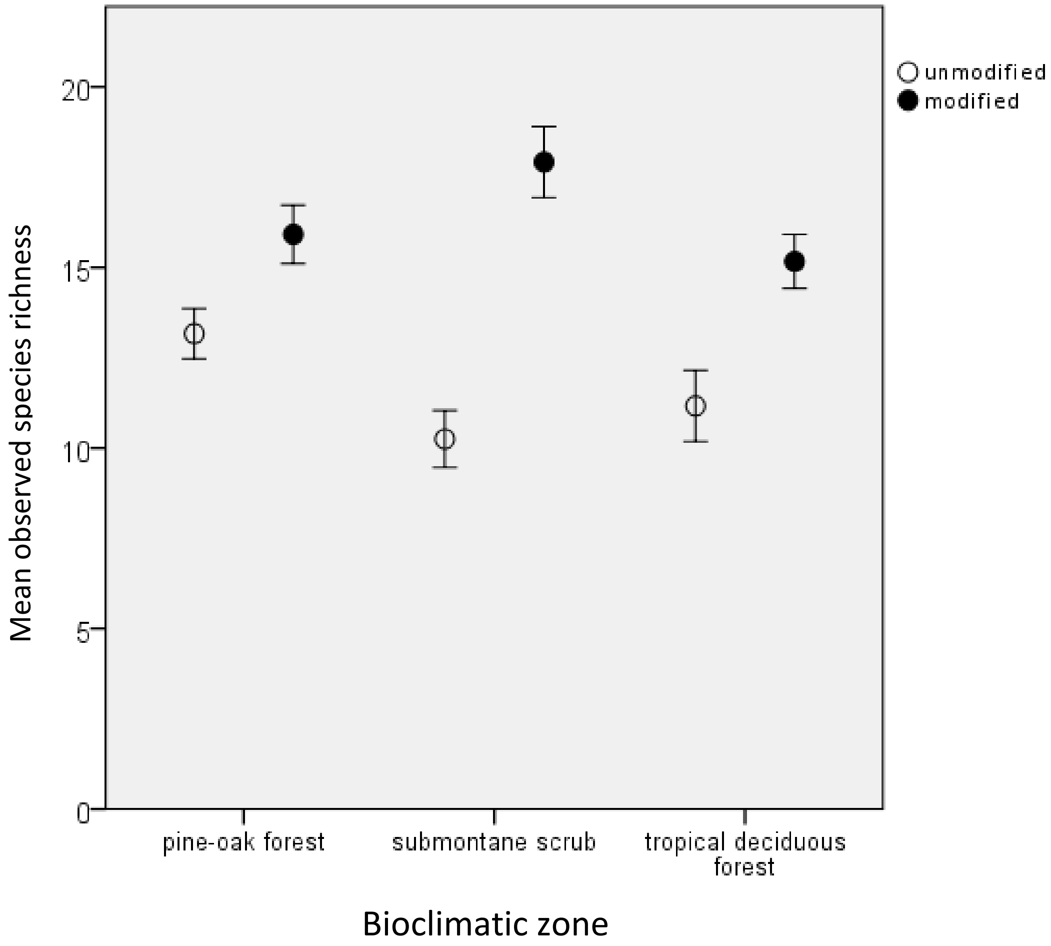


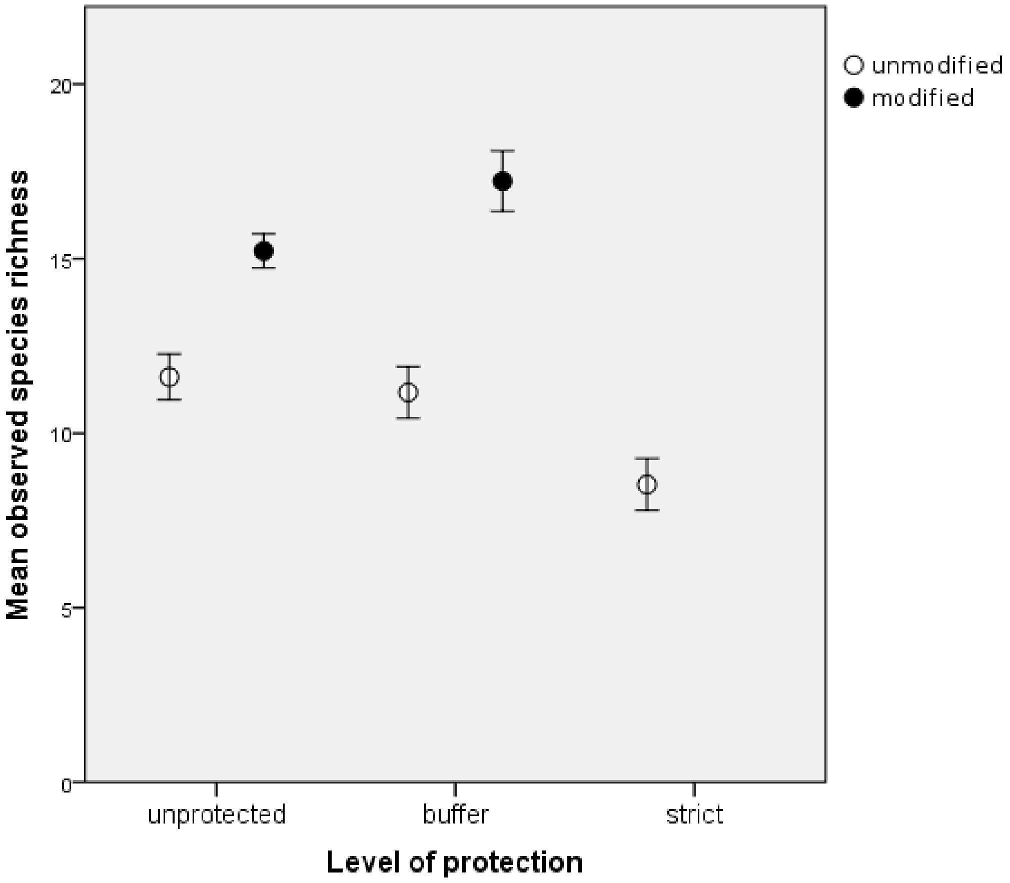
Table 4.1 Fixed and random effects of GLMMs predicting species richness (upper) and representation of globally declining species (lower) in unprotected and buffer zone environments (design 1) and in all unmodified environments (design 2)

	F	df1,2	Sig.
Species Richness			
Design 1: Corrected Model	9.559	9,62	<0.001
Fixed Factors			
Bioclimatic zone	1.460	2,62	0.240
Protection level	1.657	1,62	0.203
Habitat modification	58.287	1,62	<0.001
Bioclimatic zone * Protection level	4.119	2,62	0.021
Bioclimatic zone * Modification	5.494	2,62	0.006
Protection level * Modification	3.944	1,62	0.051
Random Factor			
Cluster			0.797
Design 2: Corrected Model[1]	3.229	8,44	0.006
Fixed factors			
Bioclimatic zone	4.326	2,44	0.019
Protection level	6.114	2,44	0.005
Bioclimatic zone * Protection level	1.211	4,44	0.320
Representation of Globally Declining Species			
Design 1: Corrected Model	5.991	4,67	<0.001
Fixed Factors			
Bioclimatic zone	7.224	2,67	0.001
Protection level	.356	1,67	0.553
Habitat Modification	9.160	1,67	0.004
Random Factor			
Cluster			0.110
Design 2: Corrected Model	4.252	4,48	0.005
Fixed factors			
Bioclimatic zone	4.152	2,48	0.022
Protection level	4.138	2,48	0.022
Random factor			
Cluster			0.688

[1] Cluster was removed as a random factor in this model as it explained no variance.

Modification was also strongly associated with greater diversity for all six models that analysed different estimates of (instead of observed) species richness (Appendix 3K), although the strength and significance of the interaction terms varied, and two models showed a marginal direct effect of protection. Analyses including only unmodified areas and three levels of protection (design 2), found that species richness was strongly affected by the level of protection and by bioclimatic zone (Table 4.1); measured richness was lower in strictly protected locations than elsewhere (Figure 4.3), and lowest in submontane scrub. The design of data collection (points along a transect, rather than a square) was necessarily different in strictly protected locations (see Methods), so interpretation should be cautious. Nonetheless, the same result was obtained when using species per point as a dependent variable (with square as a random factor) rather than the summed number of species seen at each point in a square (Appendix 3G). There is no reason why the number of species per point would be affected by the arrangement of points.

Figure 4.3 Mean observed species richness in each protection level in modified (filled) and across all bioclimatic zones. Bars represent Standard Errors. Tables of means are shown in Appendix 3J.



4.4.2 Analysis of globally-declining species (regional effects on global or gamma diversity)

This analysis considered the global population trends of species found in each location (as opposed to their population trends within the sample area itself), and so assessed the contribution of different bioclimatic zones, habitat modification and protection levels to supporting globally declining species. For unprotected and buffer zone locations (design 1), the global population trends of species varied significantly by bioclimatic zone (positive-trend species were most prevalent in the community of the tropical deciduous forest), and species with stable or declining global population trends were more strongly represented in the communities of unmodified habitats (Table 4.1, Appendix 3L).

Within unmodified areas (design 2), both protection and bioclimatic zone (Table 4.1) were significant predictors of the ratio of globally increasing/stable to declining species in the community. Stable/declining species featured more prominently in strictly protected locations, although there was little difference between unprotected areas and areas in the buffer zone (Appendix 3L). Tropical deciduous forest contained a higher proportion of globally increasing species than the other two bioclimatic zones.

4.4.3 Community composition differences within and between modification levels (beta diversity)

Beta diversity was higher when comparing unmodified and modified sample squares (lower similarities for ‘unmodified versus modified’ rows in Table 4.2) than when comparing one unmodified square with another unmodified square, or comparing one modified square with another (higher similarities for rows one and two for each bioclimatic zone in Table 4.2); although the significance varied for the different bioclimatic zones (Table 4.2). Five out of six post-hoc comparisons (involving 1 versus 3 and 2 versus. 3) were significant and the sixth had a non-significant trend in the same direction, indicating that the modification of squares within a bioclimatic zone increased local beta-diversity, provided that unmodified habitat was also retained.

The three bioclimatic zones shared 20 species within modified areas, but only six in the unmodified areas. Thus, bird communities from different bioclimatic zones typically shared only 4% of species (very low similarities for unmodified habitats; Table 4.2), except where habitats had been modified, in which case an average of 11% of species were in common; similarities in modified habitats were significantly higher than for unmodified habitats (Table 4.2). Hence, beta diversity was higher within unmodified habitats than within modified habitats, although still 89% dissimilar in faunal composition in modified habitats.

Table 4.2 – Mean similarity (Jaccard) of community composition of pairs of squares within, and between bioclimatic zones.

	Mean	***N***
Within Bioclimatic zone		
Pine-Oak		
1. Unmodified	0.243	11
2. Modified	0.222	11
3. Unmodified versus Modified	0.151	12
ANOVA $F=35.334$ $p<0.001$		
post-hoc 1 v 2 $p=0.210$		
1 v 3 $p<0.001$		
2 v 3 $p<.001$		
Submontane Scrub		
1. Unmodified	0.207	11
2. Modified	0.286	11
3. Unmodified versus Modified	0.176	12
ANOVA $F=69.611$ $p<0.001$		
post-hoc 1 v 2 $p<0.001$		
1 v 3 $p=0.007$		
2 v 3 $p<.001$		
Tropical Deciduous		
1. Unmodified	0.211	11
2. Modified	0.299	11
3. Unmodified versus Modified	0.202	12
ANOVA $F=58.523$ $p<0.001$		
post-hoc 1 v 2 $p<0.001$		
1 v 3 $p=0.631$		
2 v 3 $p<.0.001$		
Between Bioclimatic Zones		
Pine-Oak versus Submontane Scrub		
1. Unmodified	0.025	12
2. Modified	0.121	12
t-test $t_{22}=-19.553$, $p<0.001$		
Pine-Oak versus Tropical Deciduous		
1. Unmodified	0.034	12
2. Modified	0.064	12
t-test $t_{22}=-8.388$, $p<0.001$		
Submontane Scrub versus Tropical Deciduous		
1. Unmodified	0.071	12
2. Modified	0.135	12
t-test $t_{22}=-15.850$, $p<0.001$		

4.4.4 Introduced Species

Four (Collared Dove, Rock Pigeon, House Sparrow, European Starling) of the seven established introduced species (avibase.com) in Mexico were observed in the study, as well as Great-tailed Grackle *Quiscalus mexicanus*, which was probably introduced to the Mexican plateau in the 1500s (Haemig, 2014). We recorded these five introduced species (including Great-tailed Grackle) in 18 squares, each of which was modified. A chi-squared test showed that this association was significant (χ^2_1=21.14, p<0.001). Only six of those squares were protected (buffer). No introduced species were recorded in strictly protected areas.

4.5 Discussion

The loss of natural habitat can have a severe impact on biodiversity (e.g. Newbold *et al*., 2014). We expected this effect to be amplified in Mexico, where the effectiveness of the existing PA network has been questioned (e.g. Blackman *et al*., 2015), and where deforestation rates are high (195,000 hectares of forest per year were lost between 2000 and 2010 (FAO, 2011)). We found, however, that human modification of natural habitats can increase local species richness, and it can also increase beta diversity (provided that some natural vegetation remains) because additional species are present in modified habitats that are not present in the unmodified vegetation. In each of the three bioclimatic zones we studied, human habitat alteration ensured that species were recorded that would otherwise not be present. This included each of the non-native species (see above), as well as farmland-associated birds such as Brown-headed Cowbird *Molothrus ater* and White-winged Dove *Zenaida asiatica*, which exploit opportunities created by habitat modification. Alongside these species, many birds associated with natural habitats persisted in the modified environment, consistent with other research that has stressed the importance of subsistence agriculture (e.g. Mulwa *et al*., 2012), and particularly of agricultural mosaics in the neotropics (e.g. Şekercioğlu *et al*., 2007; Milder *et al*., 2010) for avian diversity.

It is important to note, however, that the increased species richness that we observed here in modified locations, and the persistence of species in agricultural frameworks, might not equate to increased densities of individual species, which may decrease under 'land-sharing' arrangements (e.g. Phalan *et al*., 2011; Hulme *et al*., 2013). The 'positive' effect of habitat modification in this study appeared to be related to the underlying diversity of the bioclimatic zone that had been modified; the effect was greatest in the zone which, in its natural state, was least species rich (Submontane Scrub – Figure 4.2) and least in the relatively species-rich pine-oak forest.

While these increases in local richness in modified habitats result in increased average per-unit area (per km^2 in the present study) richness across the study region, their net impact on the overall richness of the region is less strong. Beta diversity either declines or increases with human modification, depending on the comparison made. Communities in modified locations were relatively similar to one another (compared with communities in unmodified locations), eroding the original differences between bioclimatic zones; these results confirm the potential negative effects on beta-diversity of habitat modification (e.g. Devictor *et al*., 2007). Conversely, habitat modification also increased beta-diversity within each bioclimatic zone because modified and unmodified environments share relatively few species. Which of these tendencies predominates depends on the scale considered. Our results demonstrate, therefore, that future considerations of human impact on biodiversity must carefully consider spatial scale (McGill *et al*., 2015).

Protected area designation indicates that habitats are conserved and thus have the potential to support more diverse communities, although this is dependent on parks being well-resourced, and well-managed compared to unprotected land, which might not always be the case in many developing (and developed) countries (e.g. Watson *et al*., 2014). In our study area, in keeping with previous reports of limited, or even negative effects of protection on reported biodiversity (e.g. Gaston, 2008; Barnes *et al*., 2015), similar micro-disturbance pressures were present in buffer and unprotected environments (Appendix 3M), and buffer protection had little effect on either the number of species present (Figure 4.3), or the representation of globally declining species (Table 4.1).

Within Mexico, several bird species (e.g. the Imperial Woodpecker *Campephilus imperialis* and Slender-billed Grackle *Quiscalus palustris*) have been lost within the last century, and many more are critically endangered (Townsend Peterson & Navarro-Sigüenza, 2016). Protected areas can be of conservation value if they protect such vulnerable species, or species undergoing population declines or expansions under climate change (e.g. Hiley *et al*., 2013). Here, we have demonstrated the importance of strictly protected areas for globally declining species. The SGBR's strictly protected areas were isolated from human habitation, pro-actively managed, and had fewer disturbance pressures than either buffer or unprotected areas (Appendix 3M). Although overall species richness was lower in strictly protected areas (they contained specialist species, but lacked habitat generalists (Table 4.1) and introduced birds) – they held much higher proportions of species that were in global decline. In addition to those observed in this study (Appendix 3I), the SGBR's strictly protected areas are also the only parts of the reserve where vulnerable (IUCN Red List) and highly sensitive (particularly to hunting) species such as Great Curassows *Crax rubra*, Bearded Wood-partridges *Dendrortyx barbatus* and Military Macaws *Ara militaris* nest. Our results were mirrored elsewhere in Mexico, in both the Lacandona rainforest of Chiapas and the cloud forest of Veracruz, where larger, undisturbed stretches of forest were valuable for specialists (Carrara *et al*., 2015) and threatened (Rueda-Hernandez *et al*., 2015) bird species, whereas habitat generalists benefited from more fragmented landscapes.

Non-native species were recorded exclusively in modified environments, and most regularly in unprotected areas. They were absent from strictly protected areas, suggesting that PAs can be resistant to invasions. However, given that new non-native species are appearing in Querétaro (Hernandez-Diaz *et al*., 2015), and existing ones are undergoing range and population expansions (e.g. European Starling and Collared Dove; Howell & Webb, 1995), numbers of non-native species in the SGBR are likely to increase. As PAs can be vulnerable to invasions as bird populations establish (Hiley *et al*., 2014), such an effect would likely strengthen the observations we make here; higher local species richness in modified buffer environments, and further homogenisation of community composition between modified areas.

By considering the interacting effects of habitat modification and legal protection on different measures of avian diversity across different bioclimatic zones and at different spatial scales, this study of a Mexican PA and surrounding land demonstrates that (1) small-scale modification of natural areas can consistently (across bioclimatic zones) have a positive effect on local species-richness (alpha-diversity), (2) modification can increase local beta-diversity between modified and unmodified areas within bioclimatic zones, but results in more similar community composition across bioclimatic zones, and (3) strictly protected areas are more favourable for globally declining species and thus are important for maintaining global – gamma – diversity. Our results confirm that further studies of the effects of human pressures on biodiversity must consider different metrics of diversity and different spatial scales, and clarify the role of protection in regions where natural habitats are increasingly threatened by such land-use pressures.

4.6 Acknowledgements

We thank the following organisations and individuals for facilitating the collection of data: the Grupo Ecológico Sierra Gorda I.A.P., the Royal Society for the Protection of Birds, J.M. Garcia and R. Pedraza Ruiz.

Chapter 5: The changing geography of bird species richness and community composition; the roles of extirpations, introductions and colonisations

5.1 Abstract

Aims To investigate how alpha and beta diversity have been affected by extirpations, introductions and natural colonisations of bird species over the last 200 years, and to understand the factors which have driven each of these facets of species turnover.

Location Global, incorporating 118 geographic 'entities' (regions, mostly defined as countries).

Methods We collected data on breeding bird species and incidences of extirpations, introductions and colonisations using literature and the input of local experts, and used it to analyse changes in both alpha (change in the number of breeding bird species) and beta (difference in number of shared species) diversity from 1815-2015. We used Generalised Linear Models to evaluate the drivers associated with extirpations, introductions and colonisations.

Results The number of bird species breeding per entity has increased on average by four percent over the last two hundred years. The biggest increases have been on islands (14% increase) and in the western hemisphere. As a result of these changes, entities have more similar breeding bird avifaunas than previously. As well as governance and economic factors, more land use change and a greater amount of protected land were associated with more colonisations, although land use change also resulted in more extirpations. More isolated entities had fewer colonisations and more introductions.

Main Conclusions Anthropogenically-driven factors such as land-use change and introductions have facilitated opportunities for some bird species to expand their distributions whilst others undergo extirpations. The net result is entity-scale increased alpha diversity, reduced between-entity beta diversity, and overall global losses in breeding bird diversity (reduced gamma diversity). Protected Area networks might be beneficial to diversity by simultaneously reducing incidences of extirpation and enabling colonisations of new species.

5.2 Introduction

Understanding the impact of species turnover on biodiversity metrics, and the factors that drive species turnover, is of critical importance as pressures such as climatic changes, introductions and habitat change lead to increasingly dynamic distributions of species. These dynamics require us to consider the spatial and temporal scales of conservation priorities, given that species will not necessarily stay where they were first observed, and that overall biodiversity patterns are also changing. This provides challenges for the conservation of biodiversity. International conservation efforts, as articulated by the Convention on Biological Diversity, are commonly directed towards halting the 'loss of biodiversity', yet different metrics of diversity may be changing at different rates, and even in different directions (McGill *et al.*, 2015). Understanding the patterns and causes of different metrics of change may help us identify and restrict drivers that are associated with 'negative' change, without resisting the factors that are associated with 'acceptable' change.

Globally, biodiversity has declined as factors such as habitat destruction and the introduction of non-native species act to reduce the number of species on the planet (Diamond, 1989; Clavero & Garcia-Berthou, 2005). On smaller scales, however, there are instances of local- and regional-scale alpha-diversity remaining stable or even increasing (Sax *et al.,* 2002; Sax & Gaines, 2003; Vellend *et al.*, 2013; Dornelas *et al.*, 2014). Changes in alpha-diversity can be determined by relating initial biodiversity to subsequent levels having accounted for immigration, extinction, speciation and emigration (Blackburn *et al.*, 2016). Considering relatively short-term changes (here, the last 200-years), most diversity change is likely to be associated with extinction (extirpation) from the region under consideration and immigration, whereas speciation is generally a slower-acting process. Emigration, as in the wholesale departure of all individuals, is likely to be relatively rare (major distribution changes are usually achieved by extirpation from some regions, but colonisation of others). Both immigration and extirpation are affected by humans. For example, anthropogenic climatic and habitat changes create opportunities for species to expand their distributions, just as they threaten others (Thomas, 2017). The balance of new immigrants that establish populations and extirpations of species that were previously present will determine whether this results in a net increase or decrease in local diversity. Here we assess the levels of immigration and extirpation for 118 geographic regions, which in most cases correspond to UN nations, but in some instances are distinct biogeographical regions that are not countries (e.g., the Hawaiian Islands). We refer to these regions as 'entities'.

Rates of ‘invasions’ (immigration) of bird species have been linked to a variety of factors – including, but not limited to, the economic and social history of a location. There are more alien bird species in areas with high trade (Westphal *et al.*, 2008), high human population density (McKinney, 2006), and in regions with an imperial history – distributions of many aliens were driven by European colonialism (Dyer *et al.*, 2017). Incidences of natural colonisations, on the other hand, are less widely reported, and the factors driving them are less well understood. Protected Area (PA) networks, which can potentially be resistant to invasions (e.g. Foxcroft *et al.*, 2011; Teo *et al.*, 2013; Hiley *et al.*, 2016), are important for species naturally colonising new areas, by acting as ‘landing pads’ (sites of first breeding) or ‘establishment centres’ (sites of population increase) (Thomas *et al.*, 2012; Hiley *et al.*, 2013; Gillingham *et al.*, 2015). In contrast, the range expansions of several well-recognised avian colonists (e.g. Collared Doves in Europe (Hudson, 1972), and Cattle Egrets *Bubulcus ibis* (Blaker, 1971) and Shiny Cowbirds *Molothrus bonariensis* in the Americas (Post & Wiley, 1977)) have been linked to their associations with disturbed habitats and novel ecosystems. In terms of facilitating colonisations, therefore, both land-use change and protected areas (which seek to limit land-use change) may be important factors, benefitting different species.

Loss of relatively unmodified land cover or changes in land-use and management have been implicated in past losses (e.g. Chamberlain & Fuller, 2000) and future predictions of extinctions (e.g. Pimm & Askins, 1995; Jetz *et al.*, 2007). Reducing the rate of loss of ‘natural’ land cover, therefore, remains a key conservation priority globally (AICHI target 5 (CBD, 2010)). Invasive alien species and hunting have also been identified as key factors influencing the extinction of bird species, especially on islands where mammalian predators and/or continental pathogens were previously absent (Szabo *et al.*, 2012), although in some instances thriving non-native populations may be key to the survival of species which are under threat in their historical ranges (Gibson & Yong, 2017). By limiting or reducing the prevalence of land-use change (Joppa *et al.*, 2008), hunting and some invasive species, PAs might be important by slowing extinction risk (Butchart *et al.*, 2012), particularly of globally declining species (Hiley *et al.*, 2016), although this depends on PA performance – many PAs are ‘paper parks’ and fail to meet conservation targets (see Pimm *et al.*, 2014).

If the immigration of species to new areas does exceed the level of extirpation, regional diversity will increase, but this may be at the expense of reductions in global, or gamma diversity (Sax & Gaines, 2003). Extinctions (global loss) as opposed to extirpations (local loss) reduce the total number of species on the planet. Beta-diversity may also decline

(Smart *et al.*, 2006; Winter *et al.*, 2009), when regions are ‘invaded’ by the same species. This process of global-scale biotic homogenisation (e.g. Wilkinson, 2004) is likely to be strongest if invasions also contribute to the loss of unique endemic species. Furthermore, native ‘generalist’ species are more likely to persist through invasions than specialists (Stigall, 2012), also potentially contributing to a reduction in beta-diversity between locations

Here, we look at how bird extirpations since 1815, as well as introductions and colonisations, have individually, and together, affected the alpha diversity of regions and the beta diversity between regions. We also assess the key factors which may have driven rates of species turnover. Given the results of recent studies (e.g. Sax *et al.*, 2002), we hypothesized that introductions and colonisations would compensate for extirpations of species in most of these geographical entities, but that the net effect would be more similar breeding bird avifaunas. We predicted that overall species turnover would be driven by a combination of factors relating to the economy, physical and human geography, land-use change and habitat protection of a given location.

5.3 Methods

For each entity, we compared baseline numbers of breeding bird species (1815), with equivalent numbers in 2015 after considering the extirpation of breeding species, and the addition of both introduced species and natural colonists. Further details follow.

5.3.1 Definitions

For as many geographical ‘entities’ as possible, we collected and analysed data on bird species that we considered to be either extirpated, introduced or recently colonised (for definitions, Table 5.1). In the majority of cases, the entities considered were whole countries, because bird data is usually collated and presented on a national scale. In instances where countries incorporate offshore island groups or geographically distinct areas which were treated by country recorders as separate avifaunal units, these were included as separate entities. This occurred with the following entities: Canary Islands, Azores, Madeira, Hawaiian Islands, Galapagos Islands, Western Sahara, Peninsular and Bornean Malaysia, Taiwan. We considered introductions and extirpations since 1815, but could only consider natural colonisations since 1945. Several less well-observed entities (see below) had no information on natural colonisations, which are often less apparent to bird recorders. Many well-observed countries had little data on colonisations pre-1945, hence this cut-off date. The implications of the shorter time-frame for colonisations are considered in the interpretation of the results.

Table 5.1 Definitions of extirpation, colonisation and introduction.

Category	**Criteria for inclusion in any given entity**
Extirpation	a) Natural breeding range (1815) did include that entity b) It bred continuously (at least 10 pairs for a period of 10 years or greater) in a wild state in that entity prior to its extirpation c) It no longer breeds in a wild state in that entity (no confirmed breeding records for the 10-year period 2005-2015)
Introduction	a) Its occurrence in an entity is a result of introduction (either direct introductions/escapes, or spread from locations where it was introduced e.g. House Sparrow *Passer domesticus* is treated as 'introduced' to all New World countries) b) Its historical (1815) breeding range does not include that entity c) It has bred continuously (at least 10 pairs for a period of 10 years or greater) in a wild state in that entity d) It is still regarded as present (2006-2015) as a breeding species
Natural Colonisation	a) The first recorded breeding of that the species happened after 1945 b) It has bred continuously (at least 10 pairs for a period of 10 years or greater) in that entity since 1945 c) Its arrival in that entity did not occur as a result of introduction (see above) d) It is still regarded as present (2006-2015) as a breeding species

5.3.2 Data on Bird Species

Current breeding bird lists for each entity were compiled using regional sources (principally the European Bird Census Council Atlas, Hagemeijer & Blair, 1997; the South American Classification Committee, Remsen *et al.*, 2016; the African Bird Club, www.africanbirdclub.org), or seasonal country data extracted from Bird Life species data maps, where regional sources were not available (see Appendix 4A).

Data on extirpations, introductions and colonisations was initially compiled from a wide variety of secondary literature (Appendix 4B). Data for each category was then sent to an expert within each entity, who was responsible for checking the lists and suggesting amendments. Experts were identified as individuals with specialist knowledge on a particular country's avifauna (Appendix 4B). In 13 entities, data on natural colonisations were not available. This included seven entities for which no expert was consulted but where the literature consulted (Appendix 4B) was recent (post 2015) and categorised introductions and extirpations in accordance with our definitions (Table 5.1).

We estimated the baseline (1815) avifauna by taking the current breeding bird lists, removing introduced species and natural colonists, and adding extirpated species (according to the criteria in Table 5.1). This means that any natural colonisations prior to 1945 will be incorporated within the baseline avifauna. Baseline species lists were compared with lists (a) 'After Extirpation' (by removing extirpated species), (b) 'After Extirpation and Introduction' (removing extirpated species and adding introduced species), (c) 'After Extirpation and Colonisation' (removing extirpated species and adding natural colonists), and (d) 'Present' (removing extirpated species and adding both introduced species and natural colonists).

5.3.3 Changes in Diversity

All entities were analysed together, and also after being split into 'continental' and 'island' entities. The rationale for this was partly the known susceptibility of island birds to introduced mammalian carnivores, so islands were defined as offshore islands / island groups only if they lacked non-volant native terrestrial mammals (e.g., New Zealand was placed in the 'island' category, and New Guinea was 'continental'). 101 continental entities were analysed in total, and 17 island entities.

The number of documented breeding bird species present in each entity in 1815 was compared with the 2015 equivalent, having accounted for the effects of extirpations, introductions and colonisations. Data were not normally distributed (Shapiro-Wilk) and so the difference was analysed using a Wilcoxon Matched Pairs test. The differences in the change in diversity between islands and continental entities were analysed using Mann-Whitney tests.

Changes in beta diversity were analysed by comparing the number of species (and the percentage of species) shared between the entities studied (increased similarity indicating decreased beta diversity). The mean number and mean percentage of shared species between all pairs of entities in 1815 were compared with the 2015 equivalent considering extirpations only, extirpations and introductions, extirpations and colonisations, and extirpations, introduction and colonisations together. These analyses only included those entities (n=105) for which full data on extirpations, introductions and colonisations was available. For 1815, for example, the similarity was calculated between the avifauna of country *x* and each of the other 104 countries, in turn, and the mean calculated (a larger value indicating more species in common with other countries, on average). The differences between mean number of shared species (and percentages) in 1815 and 2015 (considering effects of extirpations, introductions and colonisations separately) were analysed using Wilcoxon Matched Pairs tests (pairs being the value of similarity for country x before and after a given element of change was included).

5.3.4 Drivers of Species Turnover

We used Generalised Linear Models (GLMs) to analyse the factors which have been associated with extirpations, introductions and colonisations over the last 200 years. As dependent variables, we specified the following: the number of species extirpated from the entity since 1815, the number introduced since 1815, the number of colonisations since 1945 (each as log-linear models with Poisson distributions), and the net gain/loss of species (as normal distribution). Our list of predictor variables (with sources and justification) was as follows below. In some instances, predictor variable information was missing for some entities. When this happened, alternative sources of information were used, entities were ascribed the scores of the parent country (e.g. Canary Islands assigned those of Spain) where appropriate and unless a separate value was available, or the entity was excluded from the analysis (Appendix 4C).

Ecological

1. Original Number of Species (source – see above)

Areas with high initial diversity (the number of species per entity) may be more resistant to invasive species (biotic resistance hypothesis), although, contrastingly, at larger spatial scales, high diversity can be correlated with an increased establishment rate of invasive species (biotic acceptance hypothesis; Stöhlgren *et al*., 2006).

Governance and protection

2. Government Effectiveness (source - Worldwide Governance Indicators (WGI, 2017). Countries are ranked from -2.5 to 2.5, approximately normally distributed)

Government Effectiveness considers, amongst other thing, the quality of policy formulation and implementation. We considered it relevant as conservation measures, including effectiveness of Protected Area networks, depend on government funding and enforcement, to avoid being ‘paper parks’. Other aspects of governance such as the level of economic inequality (e.g. Mikkelson *et al.*, 2007; Holland *et al.*, 2009) and level of political corruption (Smith *et al.*, 2003) have also been associated with biodiversity change.

3. PA% (Source: The World Bank, World Development Indicators 2017)

Percentage of the land designated as Protected Area (PA as % of total land area) may be important in terms of attracting new colonists (e.g. Hiley *et al.*, 2013) or withstanding invasive species (biotic resistance – e.g. Foxcroft *et al.*, 2011; Teo *et al.*, 2013; Hiley *et al.*, 2016).

4. Log Total absolute Protected Area (calculated as Land Area [from 9] multiplied by PA% [from 3])

Economic

5. Log GDP 2015 (The World Bank, World Development Indicators 2017)

Higher rates of GDP (measured in Log_{10} US$) may equate to more pressure on the land for resources, although there is evidence that the environmental impacts of economic activities that fuel wealthy countries are felt in less-developed countries (e.g. Wieldmann *et al.*, 2015). Higher GDP might also be associated with an altered tendency to keep exotic pets, and a greater awareness and care for conservation issues amongst the population (for example more bird-watching takes place in developed countries). Thus, GDP may be linked to extinction, the generation of novel habitats, and the direct importation of species.

6. Log Value of Imports 2015 (The World Bank, World Development Indicators 2017)

Imports (measured as Log 2015 goods and services import value, in US$) indicate the potential for invasive species to enter a country, and has previously been associated with the presence of non-native species (Westphal *et al*., 2008). It is also a general measure of economic activity within an entity (see above).

Human and physical geography

7. Log Population 2015 (The World Bank, World Development Indicators (2017)

Increased population puts more pressure on land, and might also increases the potential for non-native species to be present given the human transportation of non-native species, although this trait might also be associated with other population traits such as colonial history (Dyer *et al.*, 2017).

8. Land Use Change 1965 – 2015 (The World Bank, World Development Indicators 2017)

This was calculated as the difference between the percentage of land in agricultural use in 1965 from the equivalent figure in 2015. Land use change has been associated with providing opportunities for invasives (Hiley *et al.*, 2016), as well as increasing rates of extinction.

9. Log Land Area (The World Bank, World Development Indicators 2017)

Land Area (measured as Log_{10} km^2) could have varying implications for different aspects of species turnover. Regions with larger areas typically host higher native and introduced biodiversity (Jeschke & Genovesi, 2011).

10. Log potential connectivity 200km (ArcGIS – see Appendix 4D)

This metric measured the total amount of land area located within 200km of the boundaries of each entity, so it is the inverse of the degree of isolation of the entity from potential sources of colonists. This buffer is greater than a range of typical breeding and natal dispersal distances (Paradis *et al.*, 1998). Less isolated countries have a greater potential for colonisation over the period considered, and perhaps also more potential for species introduced to neighbouring countries to colonise.

5.3.5 Model Selection

Correlations among all predictor variables were calculated (Appendix 4E). High collinearity was found between Log GDP 2015 and Log Imports 2015 (Pearson r = 0.841, d.f. = 117, p<0.001). Log Imports was the more strongly correlated with each of our dependent 'turnover' variables, so Log GDP 2015 was excluded as a predictor.

The univariate relationships betweens between each dependent variable and each predictor variable are shown in Figure 5.1. For each dependent variable, the 'best fit' set of predictor variables was found using the glmulti package in the software R. This procedure tests all combinations of specified predictor variables and returns the models with the lowest AIC values. We considered models within AIC≤2 of the best fit model as equivalent.

To account for differences in observer intensity between countries, we repeated the analysis for a subset of 'well-observed' entities. These were the 45 entities in our study from which observers have submitted the most 'checklists' to the eBird portal (as of March 2017 www.ebird.org) and thus reflects countries in which there is a relatively high level of observer intensity. The values of the predictor variables for this set of countries were compared (see Appendix 4F) to the equivalent values for the less well-observed countries in order to assess potential impacts of observer intensity.

5.4 Results

5.4.1 Changes in Alpha Diversity

Across the 105 entities (countries and other geographic areas) for which information was complete, the median number of breeding species per entity (after extirpations, introductions and colonisations) increased by 4 between 1815 and 2015, which corresponded to a mean percentage increase of 4.28% (Figures 5.2, 5.3; Table 5.2). Thus, national diversity was significantly higher in 2015 than in 1815 (Wilcoxon: z_{105}=4.973, P<0.001).

Islands have undergone significantly larger increases in alpha diversity than continental entities in terms of species numbers and percentage increases (median change (+6 (islands), +4 (continental)), Mann-Whitney U-tests: species, $z_{15,90}$=2.52, P=0.012, percentages: $z_{15,90}$=5.09, P<0.001).

Figure 5.1 Univariate relationships between the predictor variables tested in our models, and the total number of extirpations (upper panels), introductions (middle panels) and colonisations (lower panels) in the entities studied. Each panel shows raw data (dots) as well as the mean relationship between the two variables, and 95% confidence bands. Full descriptions of units for the axes titles are shown above in section 5.3.4.

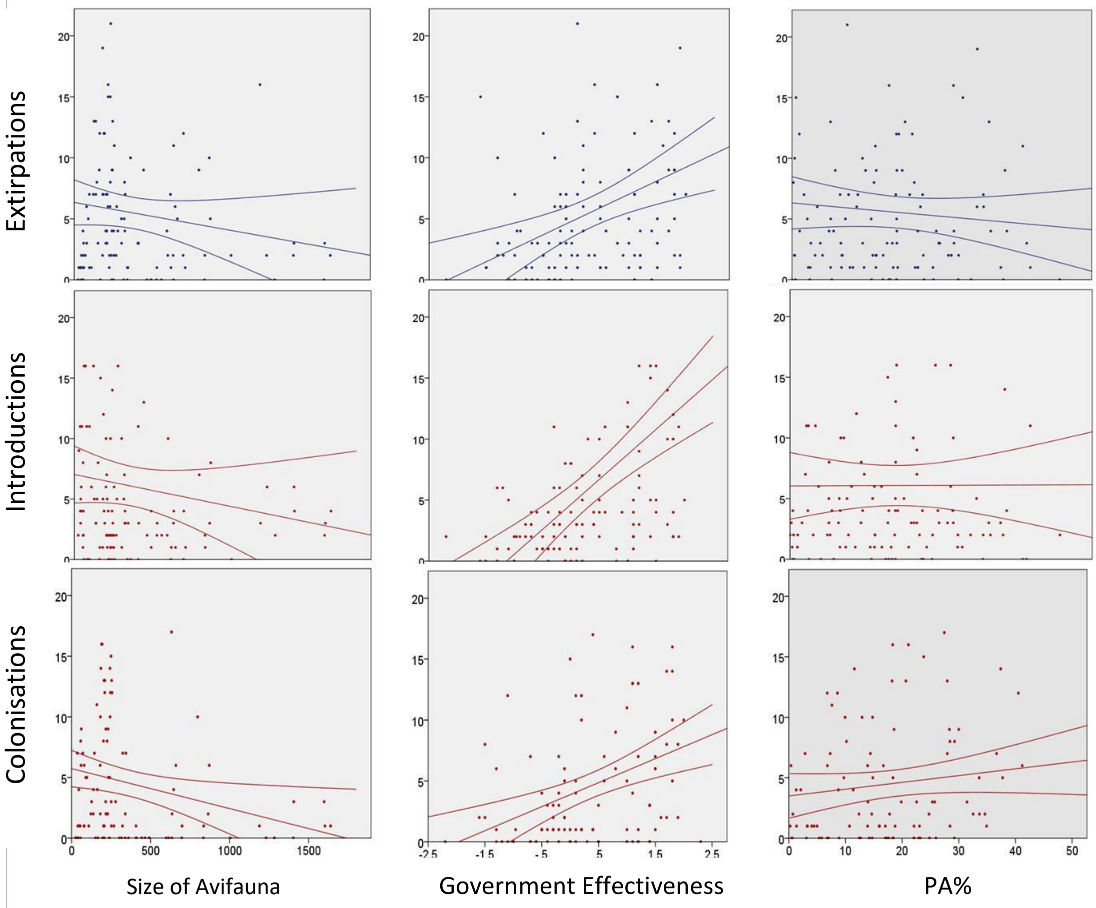


Figure 5.1 (cont)

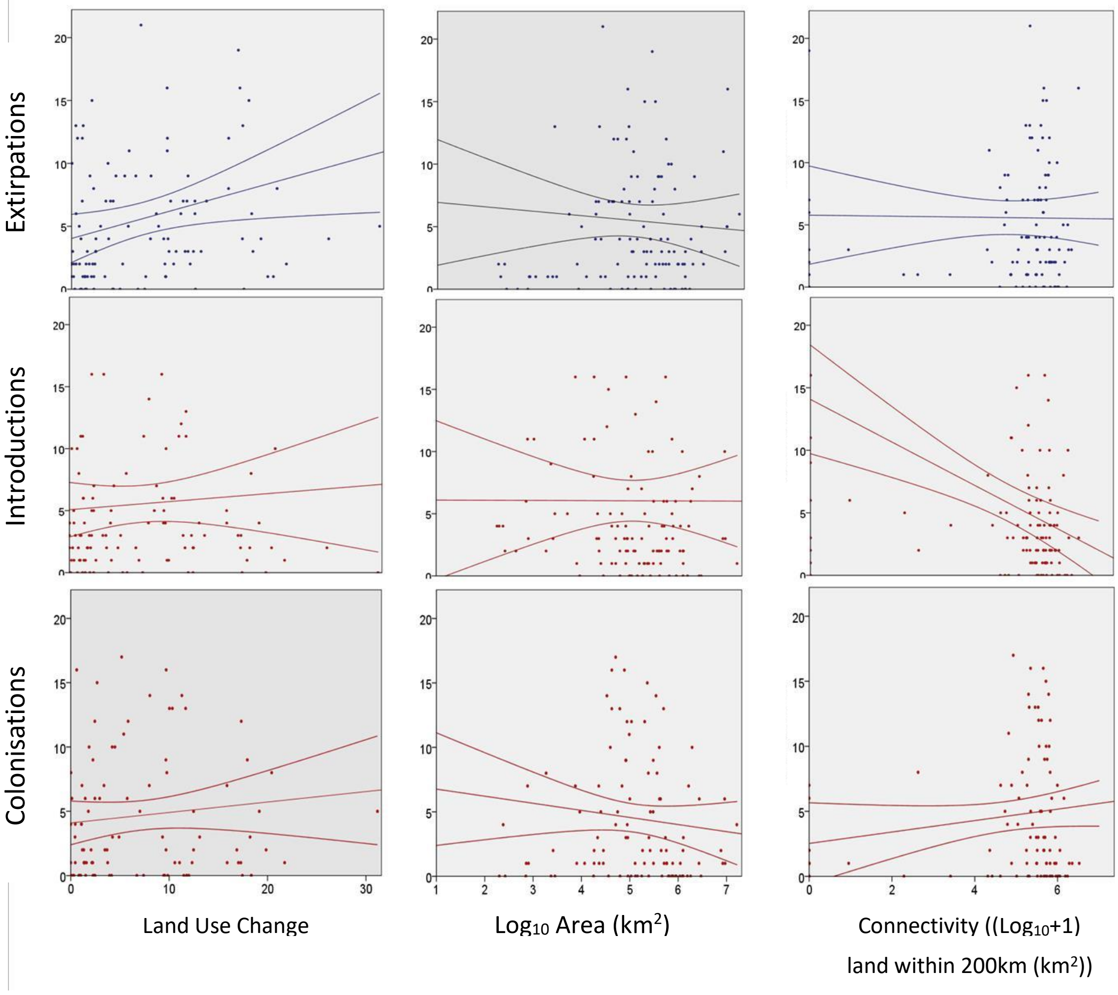
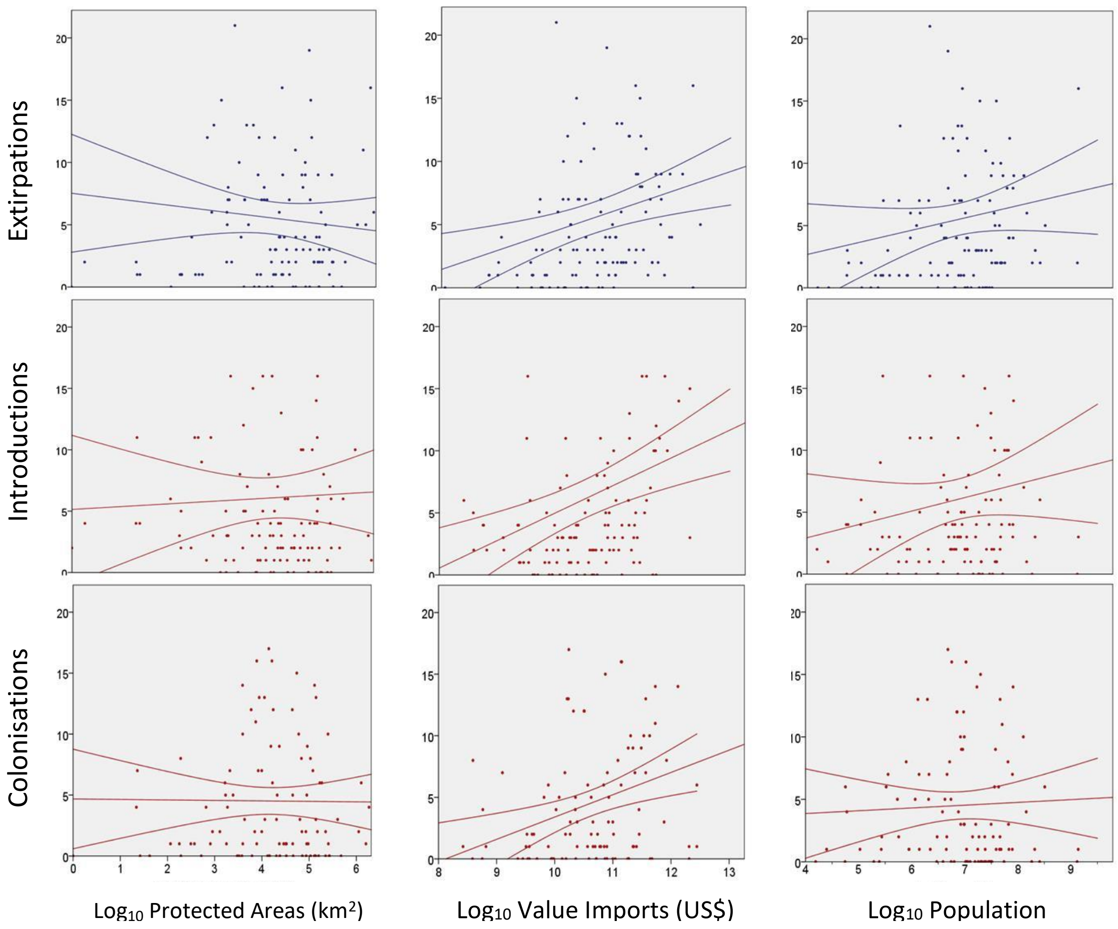


Fig 5.1 (cont)


Extirpations
Introductions
Colonisations
0
5
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15
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4
5
6
7
8
9
Log$_{10}$ Protected Areas (km^2)
Log$_{10}$ Value Imports (US$)
Log$_{10}$ Population

Figure 5.2 Changes in national diversity from 1815-2015 attributed to extirpations, introductions, colonisations (upper three panels) and net change (bottom panel).

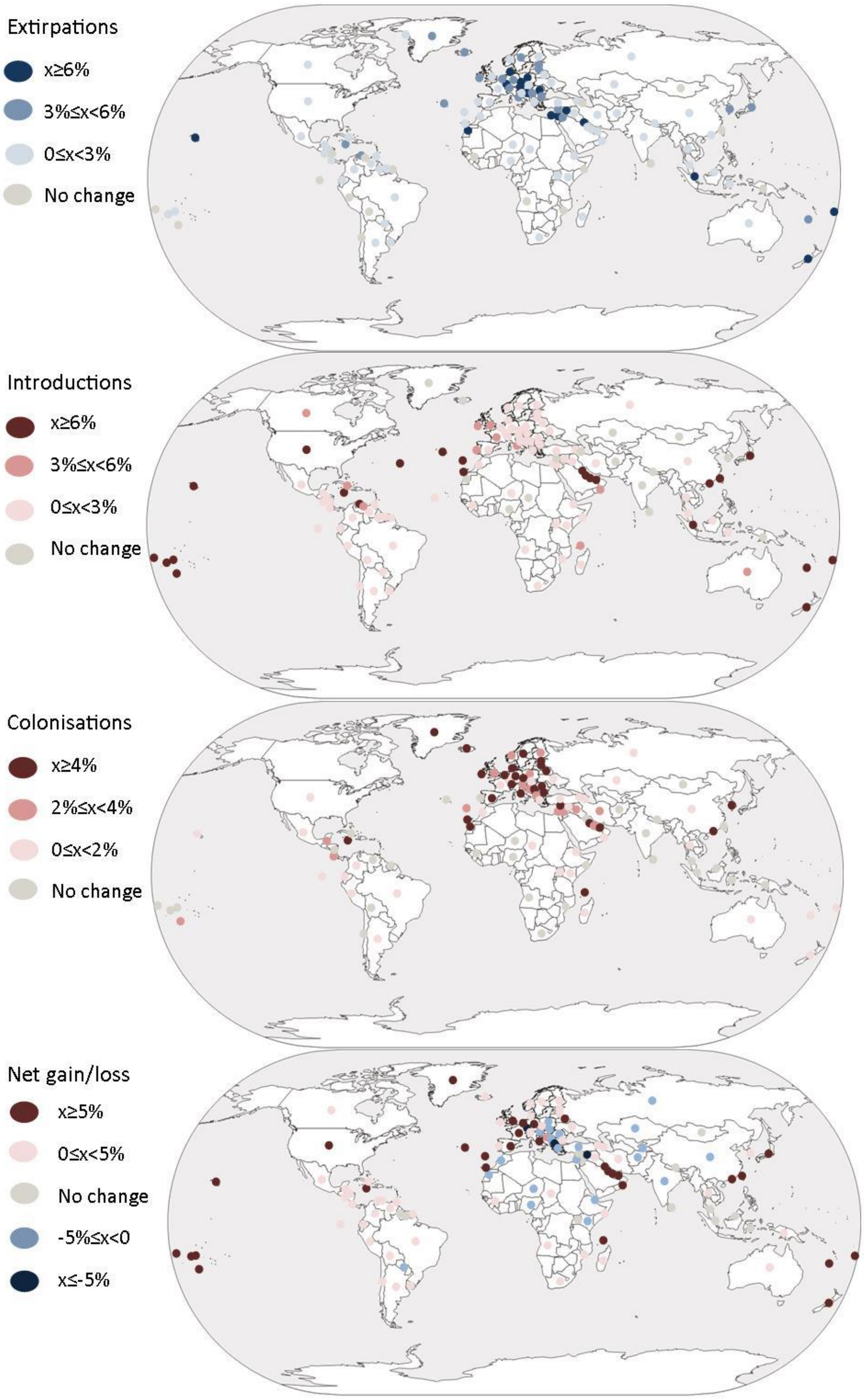
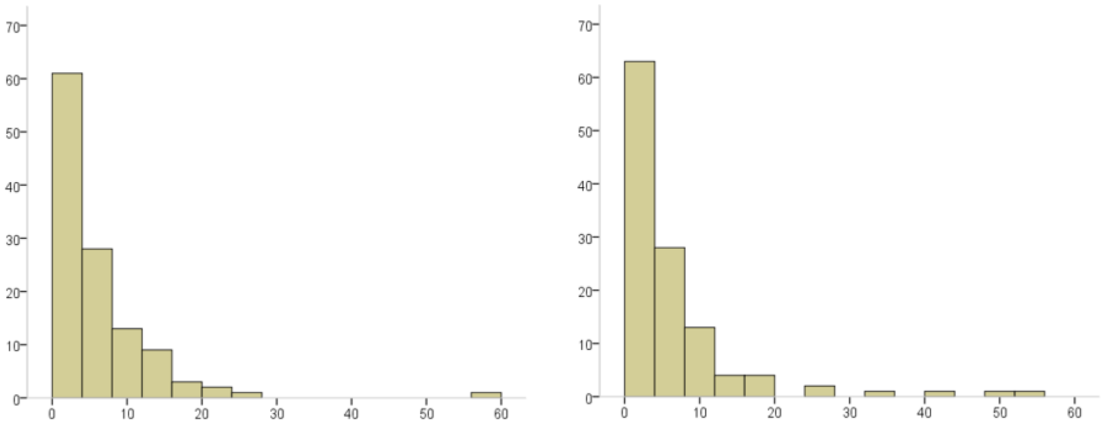
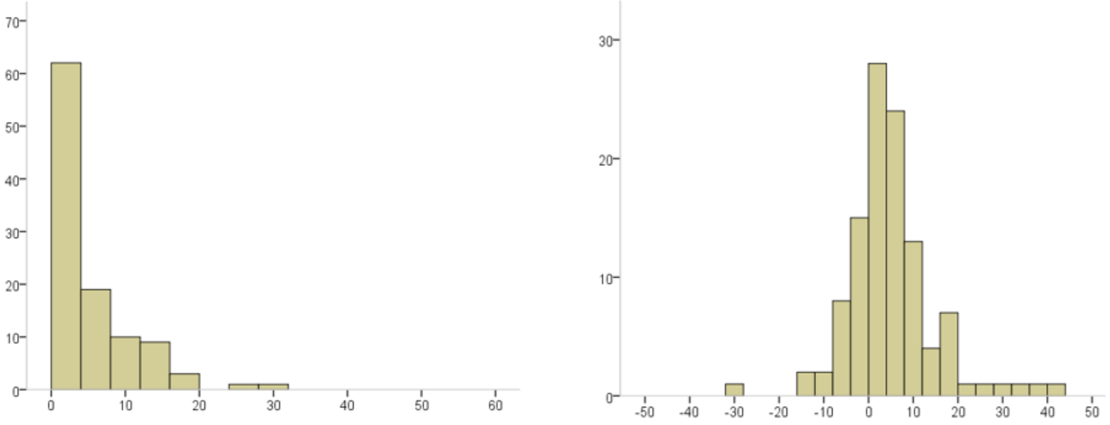


Figure 5.3 Histograms showing the number of extirpations, colonisations, introductions and absolute change across all entities.



Extirpations

Introductions



Colonisations

Net gain/loss

Table 5.2 Changes in the alpha-diversity of all entities, and separately for continental and island entities.

Factor of Composition Change (number of entities)	Median species change (range)	Mean percentage change (range)
All (Initial Avifauna 372.49 species)		
Extirpations (118)	-3 (0 to -57)	-2.84% (0% to -28.93%)
Introductions (118)	+3 (0 to +55)	+4.37% (0% to +68.75%)
Colonisations (105)	+2 (0 to +28)	+2.76% (0% to +28.87%)
Net (105)	+4 (-30 to +43)	+4.28% (-15.23% to +45.95%)
Islands (Initial 72.12)		
Extirpations (17)	-1 (0 to -24)	-4.62% (0% to 30%)
Introductions (17)	+5 (+1 to +55)	+14.58% (+1.82% to 68.75%)
Colonisations (15)	+1 (0 to +8)	+2.83% (0% to 13.79%)
Net (15)	+6 (+2 to +32)	+13.88% (+1.98% to 38.75%)
Continental (Initial 423.05)		
Extirpations (101)	-4 (0 to -57)	-2.54% (0% to -28.93%)
Introductions (101)	+3 (0 to +48)	+2.66% (0% to 29.73%)
Colonisations (90)	+3 (0 to +28)	+2.48% (0% to 28.87%)
Net (90)	+3 (-30 to +43)	+2.78% (-15.23% to 45.95%)

5.4.2 Changes in Beta Diversity

The countries studied initially (in 1815) shared an average of 45.62 species with each other country (range 2.78 to 112.03 species). In terms of individual pairs of countries, the number of shared species ranged from 0 (several pairs) to 1235 (Ecuador and Colombia). By 2015, the average number of shared species was lower after considering only extirpations ($\bar{x}$=44.01 species (2.75 to 108.40)) but higher when also considering introductions ($\bar{x}$=46.55 species (3.73 to 112.38)) or colonisations ($\bar{x}$=46.11 species (3.04 to 111.16)). The combined effect of considering extirpations, introductions and colonisations together was a significant increase (Wilcoxon: z_{105}=8.762, P<0.001)) in the number of shared species to $\bar{x}$=48.69 (3.76 to 115.04).

This corresponded to average percentages of shared species (out of total species numbers in pairs of countries) of: $\bar{x}$=10.90% (range 1.05% to 25.52%) in 1815, $\bar{x}$=10.73% (1.11% to 25.21%) after extirpations, $\bar{x}$=11.04% (1.32% to 25.20%) after extirpations and introductions, $\bar{x}$=11.09% (1.28% to 25.76%) after extirpations and colonisations, and $\bar{x}$=11.40% (1.52% to 25.74%) considering extirpations, introductions and colonisations together. Thus as a result of extirpations, introductions and colonisations, countries shared a significantly larger percentage of species in 2015 than in 1815 (Wilcoxon: z_{105}=8.515, P<0.001), although the net change is only an average 0.50% increase in sharing of species between countries.

In 1815, pairs of island entities shared an average of $\bar{x}$=8.27 species (9.03%) and pairs of continental entities shared $\bar{x}$=58.95 species (13.60%). By 2015, having accounted for extirpations, introductions and colonisations combined, island entities shared $\bar{x}$=11.42 species (10.25%) and continental countries shared $\bar{x}$=61.95 species (14.01%). Thus, beta diversity decreased across all entities, but more so in island (increase in sharing of species by 1.22%) than continental entities (increase by 0.41%).

5.4.3 Drivers of Species Turnover

Different predictor variables were driving the three facets of species turnover (Figure 5.3; Tables 5.3, 5.4, 5.5).

5.4.3.1 *Extirpations*

Considering all 118 entities (Tables 5.3, 5.4, 5.5), extirpations were significantly more likely to take place in entities which had undergone more land use change, and where protected areas were limited in size. Extirpations were also more likely to take place in larger entities (by area) and those which have higher levels of imports and more effective governments.

When just considering the 45 well-observed entities (Table 5.4), extirpations were again more likely to take place in larger entities, entities where protected areas were limited in size, those which had undergone more land-use change, and in entities with more effective governments. However, imports ceased to be a significant predictor.

5.4.3.2 *Introductions*

Considering all 118 entities (Tables 5.3, 5.4, 5.5), introductions were more likely to take place in entities which were geographically isolated, and in entities with more effective governments and higher human populations. Introductions were less likely to take place in entities with more protected land.

For well-observed entities (Table 5.4, 5.5), introductions remained more likely in geographically isolated entities, and those with large human populations. There were also more introductions to smaller entities, those with smaller initial avifaunas, and those with higher levels of imports.

5.4.3.3 *Colonisations*

Considering the 105 entities for which information on natural colonisations was available (Tables 5.3, 5.4, 5.5), colonisations were more likely to take place where: there were smaller initial avifaunas, for smaller and less geographically isolated entities, for those with higher levels of imports, and where a greater area is protected.

When just considering well-observed entities (Table 5.4, 5.5), the relationships remained as described above. However, in addition, entities which had undergone more land-use change had gained more natural colonists.

Table 5.3 Results of 'best-fit' Generalised Linear Models for each dependent variable, for changes in species number.

Dependent Variable	Parameter	Estimate	Standard Error	Z-value	P
Number of Extirpations	(Intercept)	-3.673	0.717	-5.121	<0.001
	Govt. Effect.	0.183	0.072	2.528	0.011
	Area	0.403	0.116	3.453	<0.001
	Protected Areas (absolute)	-0.578	0.093	-6.242	<0.001
	Land Use Change	0.04	0.006	7.120	<0.001
	Connectivity	-0.009	0.038	-0.249	0.803
	Imports	0.503	0.083	6.038	<0.001
Number of Introductions	(Intercept)	-1.326	0.402	-3.303	<0.001
	Govt. Effect.	0.604	0.046	13.134	<0.001
	Protected Areas (absolute)	-0.128	0.050	-2.567	0.010
	Land Use Change	0.004	0.007	0.726	0.468
	Population	0.627	0.080	7.843	<0.001
	Connectivity	-0.263	0.023	-9.249	<0.001
Number of Colonisations	(Intercept)	-3.133	0.901	-3.479	<0.001
	Size of Avifauna	-0.001	0.000	-5.390	<0.001
	Govt. Effect.	0.008	0.087	0.092	0.926
	Area	-0.683	0.156	-4.386	<0.001
	Protected Areas (absolute)	0.492	0.134	3.666	<0.001
	Land Use Change	0.012	0.007	1.762	0.078
	Connectivity	0.183	0.054	3.384	<0.001
	Imports	0.506	0.098	5.163	<0.001
Net gain/loss	(Intercept)	-4.180	7.235	-0.578	0.565
	PA %	0.143	0.078	1.825	0.071
	Govt. Effect.	2.607	0.891	2.924	0.004
	Land Use Change	-0.126	0.129	-0.976	0.331
	Population	1.860	1.166	1.595	0.114
	Connectivity	1.418	0.728	-1.949	0.054

Table 5.4 Predictor variables included in models within AIC≤2 of the 'best-fit' models shown for all countries (upper panel) and for just 'well-observed' countries (lower panel). Shown are the total number of models found for each dependent variable (in column 1) and the number of those models in which each predictor variable was included, as well as the percentage (of the total number of models) in which each predictor variable was significant ($p<0.05$).

	Size of Avifauna	PA%	Government Effectiveness	Land Area	Protected Areas (absolute)	Land Use Change	Population	Connectivity	Imports
Extirpations (4)	1	1	**4**	**4**	**4**	**4**	1	4	**4**
	0%	0%	**100%**	**100%**	**100%**	**100%**	0%	0%	**100%**
Introductions (6)	1	2	**6**	2	5	6	**6**	**6**	1
	0%	0%	**100%**	0%	50%	0%	**100%**	**100%**	0%
Colonisations (4)	**4**	1	3	**4**	**4**	4	1	**4**	**4**
	100%	0%	0%	**100%**	**75%**	0%	0%	**100%**	**100%**
Net gain/loss (12)	2	5	**12**	2	4	12	3	12	1
	0%	7%	**83%**	0%	0%	0%	0%	0%	0%
Extirpations (5)	0	1	**5**	5	5	**5**	1	5	**1**
	0%	0%	**100%**	**100%**	**100%**	**100%**	0%	0%	0%
Introductions (2)	**2**	2	1	**2**	**2**	2	**2**	**2**	**2**
	100%	0%	0%	**100%**	**100%**	0%	**100%**	**100%**	**100%**
Colonisations (10)	2	5	3	**9**	6	**10**	8	**10**	**8**
	0%	20%	20%	**70%**	10%	**100%**	50%	**80%**	**80%**
Net gain/loss (7)	1	2	1	**7**	5	7	1	1	**7**
	0%	0%	0%	**57%**	0%	0%	0%	0%	**100%**

5.4.3.4 *Net gain/loss after extirpations, introductions and colonisations*

Considering all entities, government effectiveness was a consistently significant predictor of net change (Tables 5.3, 5.4, 5.5), with more effective governments experiencing a greater net gain in bird species.

However, government effectiveness ceased to be significant in well-observed entities (Tables 5.4, 5.5), for which smaller entities and those with higher levels of imports experienced more positive change.

5.5 Discussion

Despite the fact that extirpations have significantly affected the number of bird species breeding in geographical entities over the last 200 years, the combined effects of extirpations in conjunction with introductions and natural colonisations have, on average, increased the number of breeding species per country (or equivalent geographic entity). At this scale, the alpha-diversity of breeding bird species has increased. This phenomenon has been particularly strong in island groups (e.g. Hawaiian Islands +39%, Canary Islands +30%) and in the Western Hemisphere (Figure 5.2). On the contrary, beta-diversity has decreased as a result of the combined effects of extirpations, introductions and colonisations, albeit only, on average by a 0.5% increase in shared breeding species. Many of the introduced species (e.g. House Sparrow *Passer domesticus* and Rock Pigeon) and some natural colonists (e.g. White-faced Heron *Egretta novaehollondiae*) now breed in several 'new' countries, thus making the avifauna of those countries more similar (a decrease in Beta-diversity). Global (gamma) diversity has also declined since 1815 because several of the extirpations, for example Ivory-billed Woodpecker *Campephilus principalis* in the USA and Mexico and Great Auk in the UK and Iceland, are genuine extinctions. Since 1815, 96 species have gone extinct, a further 22 are considered possibly extinct and five are considered extinct in the wild (IUCN Red List, 2017). Thus, globally the number of breeding bird species has declined by approximately 1% during this period.

Our results robustly demonstrate the association of land-use change with extirpations. Such an association has been previously demonstrated (e.g. Chamberlain & Fuller, 2000), and modelling studies predict large losses in biodiversity as land-use change intensifies (e.g. Jetz *et al.*, 2007). It is less well documented that changes in land use also provide opportunities for natural colonisations. The preference of some well-known natural colonists such as Cattle Egret *Bubulcus ibis* (Blaker, 1971) and Collared Dove (e.g. Hudson, 1972) for 'modified' habitats has been acknowledged. Our results, particularly in well-observed entities, demonstrate that this might be a more general phenomenon. Land-use change creates novel environments which have facilitated species' range expansions. Such expansions are dependent on dispersal capabilities of nearby species, however. Geographically isolated entities (with less surrounding land and therefore fewer potential colonisers) have had fewer natural colonists. In contrast, isolated entities typically have more introduced species, resulting in net increases in diversity. This may be due to increased probabilities of establishment of escapees in isolated locations, especially on oceanic islands, rather than because of increased rates of release.

There were more colonisations and fewer extirpations and introductions in entities with greater amounts of protected land, supporting the idea that PAs can act as establishment centres for species undergoing range expansions (Hiley *et al.*, 2013), potentially resist invasions and remain of importance to species undergoing range retractions. The effectiveness of PA networks globally is difficult to generalise however, due to the presence of 'paper parks' (Watson *et al.*, 2014), the varying efficacy of different levels of protection (e.g. Hiley *et al.*, 2016) and the variety of reasons for which a PA might be designated. In our analysis, protected areas were less consistently associated with colonisations when considering well-observed entities (which may on average have better protection for birds outside PAs).

5.5.1 *Constraints and caveats*

These conclusions must be carefully interpreted within the context of the study. Clearly the scale at which diversity is considered is important (McGill *et al.*, 2015). Species which have undergone widespread local extirpations within a country but which still 'hang on' at a few sites were considered present as breeding bird species in our analysis, while some newly-arrived species (both colonisations and introductions) are widespread and others are localised. Studies based on smaller spatial scales (local community alpha, beta diversity between locations within a country, and country total as the equivalent of gamma diversity) might, therefore, yield different results.

Our data on extirpations, introductions and colonisations rely largely on records submitted by bird-watchers, the results of bird surveys, and local knowledge. The gaps in our data (for example in much of Africa, Figure 5.2) reflect regions with limited data availability.

Our results should also therefore be interpreted against this background of a wide variety in observer intensity between entities. Each extirpation, introduction and colonisation is more likely to be recorded in entities with lots of bird-watchers – a pastime most typically followed in more economically developed countries (which correspond with those with higher imports and Government Effectiveness, Appendix 4F). We believe that the patterns of increased diversity reported here are robust, however, because (1) our results broadly demonstrated the same patterns when just considering 'well observed' entities (average increase +6.94%, Table 5.4), (2) the criteria that we used for qualification as extirpation, introduction or colonisation (≥10 pairs for ≥10 years) ensured a certain degree of visibility and reduced the chance of bias due to observer intensity, and (3) although reported incidences of extirpation and colonisation may rise in well observed countries, there is no reason why either one would be 'favoured' over the other, in terms of reporting. Our report of diversity increases might even be an under-estimate, given that pre-1945 natural colonists were not considered (they would count as though they were extant throughout the period).

Several of the drivers of species turnover that we focus on here (e.g. connectivity, land-use change and protection) do not appear to be correlated (see Appendix 4F) with observer intensity, and indeed connectivity and protection act in different directions for different aspects of species turnover. We conclude therefore that the importance of these factors, and the general increase in diversity reported, are genuine as opposed to artefacts of a variety in observer intensity. Economic and governance factors such as levels of imports and population are also clearly important for different aspects of species turnover (Table 5.5). Level of imports was significantly related to each aspect of species turnover, and our analysis also highlighted the particular significance of human population size for introductions, and government effectiveness for extirpations and introductions. Further interpretation of these factors, however, must be handled carefully because of the observer effort issue.

5.5.2 *Conclusion*

Our results indicate increasing average country-level diversity (number of species) by 4.28%, an increase in the sharing of species between regions by 0.5%, and a 1% decline in global diversity. Various drivers of change are affecting the different elements of species turnover (Table 5.5) but, in terms of net turnover, the effects of these drivers seem effectively to 'cancel each other out'. For example, there are more extirpations and colonisations in entities which have undergone a lot of land-use change, and there are more colonisations but fewer introductions in geographically isolated countries. Neither of these two factors therefore significantly affected the net turnover of bird species. The main exception is that (originally) mammal-free islands have gained the most species, despite losing a number of endemic species after the arrival of terrestrial carnivores. Many of these islands may initially have experienced ‘prehistoric’ reductions in diversity following the first arrival of humans and associated mammals (Duncan *et al.*, 2013), but these same locations have gained the most species in the last 200 years.

Table 5.5 Effects of predictor variables on dependent variables. Arrows indicate the direction of the effects for predictor variables which were significant in more than half of all accepted GLMs (within AIC≤2 of the best fit model) for each dependent variable. Bracketed arrows represent the results for the subset of 45 well-observed entities.

	Extirpations	Introductions	Colonisations	Net turnover
Size of avifauna		(⇩)	⇩	
PA %				
Government Effectiveness	⇧ (⇧)	⇧		⇧
Land area	⇧ (⇧)	(⇩)	⇩ (⇩)	(⇩)
Protected Areas (absolute)	⇩ (⇩)	⇩ (⇩)	⇧	
Land Use Change	⇧ (⇧)		(⇧)	
Population		⇧ (⇧)	(⇩)	
Connectivity		⇩ (⇩)	⇧ (⇧)	
Imports	⇧	(⇧)	⇧ (⇧)	(⇧)

Given the relationships that we demonstrate here between anthropogenic factors and extirpations, colonisations and introductions, continued human-pressure on natural resources is likely to further increase rates of species turnover globally. Assuming that current trends continue, the result will be more breeding bird species within countries, but less heterogeneity between countries, and fewer breeding species globally. Land-use change accelerates this process by provoking extirpations and increasing colonisations. As a conservation measure, protecting habitats can potentially generate two benefits, by reducing extirpations and simultaneously facilitating colonisations.

5.6 Acknowledgements

We thank the experts in each country (Appendix 4B) for their contributions to this research. Each expert took the time and effort to review lists and suggest amendments. We also thank BirdLife International and the Royal Society for the Protection of Birds for helping us to identify valuable sources of information.

Chapter 6: General Discussion

The aim of this thesis was to explore and analyse the importance of Protected Areas (PAs) against a backdrop of widespread distributional changes in species' ranges. This is important because the role of PAs – a crucial element of global conservation practice - has been questioned, because the species for which they were originally designated might no longer occupy them under future climatic scenarios (Araújo *et al*., 2004, 2011; Hannah *et al*., 2007).

6.1 Summary of results

Protected Areas remain and will continue to remain a cornerstone of conservation efforts into the future.

The distributions of species *are* changing as a result of climatic and other factors (Hickling *et al*., 2006; Huntley *et al*., 2007; Maclean *et al*., 2008; Lenoir & Svenning, 2015; Stephens *et al*., 2016). This might push some species out of reserves, but as species colonise new areas, they will need 'landing pads' (sites on which to first breed) and 'establishment centres' (sites from which populations can develop before spreading more widely; Thomas *et al*., 2012; Gillingham *et al*., 2014). PAs provided both of these functions for colonising wetland bird species in the UK, at a national scale (Chapter 2) and at a local (county) scale (Chapter 3). As well as providing havens for 'acceptable' species (so-called natural colonists are welcomed by conservationists), PAs also appeared to be initially resistant to the six non-native wetland bird species that have established in the UK (Chapter 3), although PAs were increasingly likely to be colonised by these species during the later stages of establishment.

PA performance is variable, however, and depends on the efficacy of protection as well as the political commitment to enforce conservation rules. Buffer zone areas of a Biosphere Reserve in Mexico offered negligible benefits to biodiversity in comparison to unprotected land, but they do shelter core zone areas, which are crucial for globally declining species (Chapter 4). The core zones, whether via a process of biotic resistance or their geographical remoteness, were free from non-native species, further supporting the idea that PAs can resist invasions. One of the aims of protection is to prevent modification of natural habitats. Where modification does occur, however, local diversity can be higher than in relatively natural areas – partly due to the presence of the non-native species and habitat generalists, which strictly protected areas resist.

On a global scale, non-native species introductions and natural colonists have compensated for the losses of species (extirpations) from individual countries, resulting in national scale avian diversity increases of about 4% (Chapter 5), although the net result of the three facets of species turnover (extirpations, introductions and colonisations) has been global-scale species declines (a reduction in gamma diversity) and a global-scale decline in beta-diversity – a process of biotic homogenisation. Land-use change (effectively habitat modification) contributes to species loss but also creates opportunities for colonists. This global analysis suggests that PAs can potentially delay species loss and resist the spread of non-native species, and simultaneously facilitate the establishment of natural colonists, in line with the results for Britain and Mexico.

6.2 Wetland birds, and developments since publication

In Chapter 2, I demonstrated the association of wetland bird colonists in the UK with PAs as sites of first breeding (‘landing pads’) and sites from which populations can grow and spread (‘establishment centres’). Since this publication, wetland bird species (predominantly the Herons *Ardeidae*) have continued to colonise the UK from continental Europe. Table 2.1 identified six species that had established breeding populations (bred for at least ten consecutive years) by 2012 and a further suite of species that had bred for the first time in the UK after 1960 but had not by then become established, by my definitions. Table 6.1 demonstrates that many of the latter have experienced further population growth and that the association of colonising wetland birds with PAs has continued.

However, wetland birds might not be ‘typical’ of colonising species. Historically, the distributions of wetland birds retreated as a result of a combination of severe habitat depletion (Stewart, 2004) and exploitation for food and feathers (Shrubb, 2013). The speed of the recent range expansions of such species probably therefore reflects a recovery from historic persecution as well as a response to climate change.

There are other reasons why a focus on wetland bird species might exaggerate the importance of PAs for colonisers. Within the UK at least, wetlands typically receive more protection than other habitats (c.30%; Appendix 2G). Non-wetland species might consequently show lower PA associations during colonisation. Although Firecrests have established in PAs, the spread of Collared Doves has clearly been facilitated by human-modified habitats (Chapter 3; Hudson, 1965) and three of the four recent breeding attempts by burrow-nesting European Bee-eaters *Merops apiaster* in the UK have been in non-PA quarries (Durham in 2002, Cumbria in 2015 and Nottinghamshire in 2017; rspb.org).

Table 6.1 Population status of large wading birds that first bred in the UK after 1960, but which had not established breeding populations (bred for at least consecutive years) prior to 2012.

Species	Year first recorded breeding in the UK	Breeding Population 2017*	% of breeding pairs in SSSIs
Black-crowned Night Heron *Nycticorax nycticorax*	2017	1	100%
Great White Egret *Ardea alba*	2012	11 pairs	100%
Purple Heron *Ardea purpurea*	2010	0	Na
Cattle Egret *Bubulcus Ibis*	2008	7 pairs	100%
Spoonbill *Platalea leucorodia*	1998	>10 pairs	100%
Little Bittern *Ixobrychus minutus*	1984	1 confirmed and 3 singing males	100%

*Personal Communication (RSPB and Rare Breeding Birds Panel)

Nevertheless, given that (1) many of the species that have a high likelihood of colonising the UK in the near future, for example Whiskered Tern *Childonias hyridus*, Baillon's Crake *Porzana pusilla* and Great Reed Warbler *Acrocephalus arundinaceus* (Ausden *et al.*, 2015), are wetland bird species, and (2) globally many species colonising new countries (or equivalent entities) are wetland birds (for example, 10 out of 11 in the Republic of Korea, 5 out of 6 in Greenland and 12 out of 14 in Germany; data from Chapter 5), the fact that PAs 'cater' for wetland species is highly important irrespective of the preferences of non-wetland species. Furthermore, PAs are likely to provide higher quality habitat for potential non-wetland bird species (apart from those that are associated with human-modified areas), and can therefore be expected to continue to be of value to a wide spectrum of colonising species.

Wetland bird species probably account for a lower proportion of all non-native species globally than they do for natural colonists; escaped cage birds such as Parrot *Psitaccidae sp*. account for most non-natives in many parts of the World (Gibson & Yong, 2017), although not in the UK. Table 3.1 shows the introduced wetland birds with *persistent* breeding populations in the UK. Since 1996, however, a further 33 non-native species have bred in a wild state in the UK, of which 16 (48%) have been waterbirds (Holling *et al*., 2014). These additional species retain the potential to establish persistent populations in the UK. The role of UK PAs in terms of resisting the spread of non-native wetland species (as described in Chapter 3) and non-wetland species (as described in Chapters 4 and 5) is thus of continuing relevance.

6.3 How representative are birds?

The research in this thesis focuses on the importance of PAs for *bird* species undergoing distributional changes. Other taxa are also widely established in new areas of the world over the last several centuries, and hence the issues considered here (i.e., natural colonisation, accidental introduction, deliberate introduction) are more widely relevant. Several of the findings that I report here do match expectations from studies of other taxonomic groups.

The association of wetland birds with PAs during early stages of colonisation of new regions within the UK, which I reported in Chapter 2, has also been demonstrated for butterflies and odonates (Gillingham *et al*., 2014), as well as other invertebrates (Thomas *et al*., 2012). I recognise that colonisations and disproportionate colonisations of PAs might be limited to visible species with high observer effort (hence the above groups), but these instances do provide clear evidence of the relevance of PAs for species other than those for which they were originally designated.

As well as attracting colonists, the ability of PAs to resist the spread of non-native species has also been explored. Here, I demonstrated that non-native Mexican (Chapter 4) and UK wetland bird species (Chapter 3) were less likely to be present in PAs. PAs have also resisted the spread of non-native plant species (Foxcroft *et al*., 2011) although some marine PAs have enhanced populations of non-native marine life (Burfeind *et al*., 2013, although see Ardura *et al*., 2016), and Argentinian PAs have not filtered out invasive mammals (Merino *et al*., 2009; Gantchoff *et al*., 2013). The presence or absence of non-native species in PAs across a range of taxonomic groups might be related to the human pressure on those locations. In the Sierra Gorda Biosphere Reserve, non-native species were present in and around modified habitats. Further afield, non-native plants are found most frequently on protected land which is close to human settlements (Iacona *et al*., 2014) or affected by tourist pressure (Anderson *et al*., 2015), and non-native plants (Dimitrakopoulos *et al*., 2017) and mammals (Gantchoff *et al.,* 2013) are found close to roads.

The arrival of new species, as well as the extirpation of some of those that used to be present, inevitably alters patterns of diversity. Chapter 4 demonstrated increases in *local* alpha-diversity as a result of habitat modification. Similar results have been reported in other studies of avian (e.g. Milder *et al.*, 2010; Mulwa *et al*., 2012; Chapter 4) and plant species richness (Flynn *et al*., 2009), often because of the presence of non-native species (Thomas & Palmer, 2015). However, the same pattern might not be true for all taxonomic groups (Flynn *et al.*, 2009), particularly mammals (e.g. Ramesh & Downs, 2015).

Increased, or similar, levels of *regional* scale alpha diversity as a result of the opposite effects of extirpations and introductions (as reported here in Chapter 5) has also been observed in plants (Sax *et al.*, 2002; Sax & Gaines, 2003; Thomas & Palmer, 2015), freshwater fish (Sax *et al*., 2002) and in mammals, reptiles and amphibians in California (Hobbs & Mooney, 1998), as have the corresponding reductions in global-scale beta-diversity (e.g. Winter *et al*., 2009).

Even if species diversity is increased by non-natives and widespread generalists in modified habitats, populations of individual species might decline – as has been demonstrated with insects (e.g. Benton *et al*., 2002) and plants (Aebischer, 1991). My results in Chapter 4 indicate that the effects of habitat modification on measures of diversity (alpha and beta) are likely to be dependent on the degree of modification, and they varied with the initial biodiversity of the bioclimatic zone that has been modified. The effects of modification on local alpha diversity were most positive in the bioclimatic zone that had the lowest level of initial species richness (submontane scrub). The extent to which this pattern can be generalised over a wider geographical and taxonomic scale would be an interesting area for further research.

Birds have experienced slightly higher past rates of extinction, compared to other taxonomic groups (1.40% compared to 1.00% all species), but future threats may be relatively reduced: the percentage of species considered threatened by the IUCN is about half of that for other taxa (13.13% for birds versus 28.28% for all species), and the projected risk of extinction from climate change is also reduced (5 – 8% for birds versus 7.9% (all species; Thomas *et al*., 2004; Urban, 2015); Table 6.2). For the UK at least, the rates of unaided colonisation of birds since 1900 (5.24% of all current species) fall within the range of other taxonomic groups; i.e. between land molluscs and herptiles (both 0%), and shieldbugs and odonata (8.06% and 9.09% respectively; Gurney, 2015).

Birds do, however, have some unique characteristics. They are mobile and most species are capable of flying long distances. Thus they have higher dispersal abilities than groups such as flightless invertebrates and therefore a higher likelihood of finding extra-limital habitats to colonise (Walther *et al*.. 2002). Birds are also associated with a higher level of observer effort than other taxonomic groups, meaning that patterns in distribution are often based on more sightings than in other taxa, where new discoveries may be more likely to be ascribed to unknown previous residents, rather than recognised as colonists.

Table 6.2 Rates of extinction and threatened species in different taxonomic groups (data adapted from IUCN, 2015) and projected extinction risks from climate change (Urban, 2015).

Taxonomic Group	Total Species	% Extinct	% Threatened	Projected Extinction from climate change*
Birds	11121	1.40%	13.13%	6.3%
Mammals	5560	1.49%	21.47%	8.6%
Reptiles	5473	0.51%	19.92%	9.0%
Amphibians	6533	0.51%	31.64%	12.9%
Bony Fish	14931	0.42%	14.42%	7.6%
Insects	6912	0.84%	18.78%	
Gastropods	6033	4.39%	29.73%	
Plants	22326	0.52%	52.29%	7.3%
All species	86265	1.00%	28.28%	6.9%
All Species Except Birds	75144	0.94%	30.52%	7.0%

Clearly, variations exist between different taxonomic groups in terms of percentages at risk of extirpation/extinction (Table 6.2), rates of colonisation (Hickling *et al*., 2006; Gurney, 2015), and likelihood of introductions. This is inevitable given the differences in dispersal capability (Lester *et al*., 2007), rates of endemism (Begon *et al*., 1990), and the vulnerability to persecution, land-use change and invasive species that exist between taxa. Nevertheless, we can learn some interesting things from studying birds about the way these different forces combine to affect overall species turnover and diversity patterns.

6.4 How representative are the study areas?

Chapters 2, 3 and 4 in this thesis focus on single region studies – the UK in Chapters 2 and 3, and a large biosphere reserve in Mexico in Chapter 4. The findings from these case studies, however, clearly have implications beyond the shores of the UK and the borders of the SGBR in Mexico.

Levels of protection, governance and the numbers of extirpations, introductions and colonisations in both the UK and Mexico are similar to the averages for Europe and the Americas respectively (Table 6.3), indicating that the distributional changes in both countries could be typical for their region, although, like all countries, their avifaunas have unique features. For example, the UK's geographical position makes it well placed to receive vagrant birds (Lees & Gilroy, 2009), its high allocation of resources for conservation projects have allowed for the re-introduction of native bird species such as the Western Capercaillie *Tetrao urogallus* and the White-tailed Eagle *Haliaeetus albicilla*, thus 'reversing' previous extirpations, and the era of colonialism and historical desire of British landowners to keep ornamental waterbirds on their ponds has resulted in a high number of introductions (e.g. Sutherland & Allport, 1999). In Mexico, the majority of the established non-native species are present having spread southwards from populations introduced into the USA by European settlers. Despite these individualities, however, a number of the patterns are likely to apply elsewhere.

I consider it likely that the patterns of PA association shown by colonising species in the UK can be extrapolated to other countries. Positive trends of species targeted by conservation measures across Europe (Donald *et al*., 2007; Sanderson *et al*., 2016) and North Africa (Kleijn *et al*., 2014) demonstrate the effective performance of PA networks (including in the UK) *per se*, and I found colonisation to be positively correlated with the amount of protected land in geographic 'entities' in the global analysis (Table 5.5). These results suggest that such networks are important for species expanding their range across the World; although the relative importance of PAs for species expanding their distributions might be related to the degree to which wildlife faces pressures (e.g. persecution, farming intensification) in non-protected land. It may also be related to the policing and management of PA networks. Strong associations between colonisers and PAs has been demonstrated in the UK, which has one of the highest-intensity farming regimes in Europe (Donald *et al*., 2001) combined with a relatively large amount of protected land (Table 6.3).

Table 6.3 Measures of protection, quality of governance and rates of species turnover in the UK and Mexico and the averages for their respective continents. Regional data (for Europe, Americas and World) is calculated as the average across the countries which were included in the Chapter 5 study.

			Numbers from 1815-2015 (colonisations from 1945)		
Country/Region	**PA%**	**Governance**	**Extirpations**	**Introductions**	**Colonisations**
UK	28.43	1.7	4	10	8
Mexico	12.92	0.2	9	7	10
Europe	20.31	0.85	7.24	4.13	7.89
Americas	20.61	0.12	3.64	7.81	4.30
World	18.84	0.32	5.49	6.04	4.51

Distributional patterns of range-expanding non-native species are also informative beyond the UK. The spread of non-native populations of Sacred Ibis *Threskiornis aethopicus*, Purple Swamphen *Porphyrio porphyrio* and Chilean Flamingo *Phoenicopterus chilensis* has been associated with unprotected land in continental Europe (Appendix 2J) and on a broader scale there appear to be fewer introductions in regions with higher amounts of protected land (Table 5.5).

Globally, there are 669 Biosphere Reserves in 120 countries (unesco.org), providing a model of protection based on core area(s) surrounded by a buffer zone. Thus the findings of Chapter 5 are clearly of wider importance. Although the buffer zones themselves, which correspond to IUCN Category VI (Table 1.1), might not necessarily contain greater species richness than nearby unprotected, or transition land, they serve a purpose in sheltering core zones, which I have shown are important for species undergoing global declines. Core zones within other Biosphere Reserves in Mexico contain threatened bird species such as Great Curassows *Crax rubra* (Sian Ka'an Biosphere Reserve) and Horned Guans (El Triunfo Biosphere Reserve), and species from other taxonomic groups such as Jaguars *Panthera onca* (Sierra de Santa Marta Biosphere Reserve; CONABIO, 1995) and Monarch butterflies *Danaus plexippus* (Monarch Butterfly Biosphere Reserve). Beyond Mexico, Biosphere Reserves and their core zones harbour globally endangered species such as Spanish Imperial Eagles *Aquila adalberti* (Castro Verde Biosphere Reserve), Snow Leopards *Panthera uncia* (Khangchendzonga Biosphere Reserve, India; cpreec.org), Giant Pandas *Ailuropoda melaleuca* (Baishuijiang National Nature Reserve) and important species assemblages – the Savegre Biosphere Reserve in Costa Rica hosts 54% of the country's mammals and 59% of its birds (nationalgeographic.com). Broad research on whether these species are found disproportionately in core zones is missing, although it appears true at least for Military Macaws, Horned Guans (González-García & Abundis, 2005) and Monarchs (Vidal & Rendón-Salinas, 2014). In most cases, core zones undergo less land clearing and are affected by less human disturbance than nearby buffer zones (Walker & Solecki, 1999; Chowdhury, 2006; Vester *et al*., 2007; Xu *et al*., 2016), which supports the hypothesis that they are important for species which are threatened by human activity.

As PAs which promote sustainable development (Price, 2002) and the interaction of biological and cultural diversity (Bridgewater, 2002), however, the importance of Biosphere Reserves goes beyond measures of species richness or the presence of important individual species. Biosphere Reserves, rather than being protected from people, actively depend on the people living within them playing participatory roles in the management of the reserve (Price, 2002). Stakeholder participation was identified as the most important aspect influencing the 'success' (as measured by expert opinion) of the Biosphere Reserve network (Van Cuong *et al*., 2017). Mexico is one of many emerging economies where competition for resources is high, and allocation of resources for conservation is relatively low. PAs within Mexico (Blackman *et al*., 2015), in neighbouring countries (e.g. Guatemala - Bonham *et al*., 2008) and globally (fewer than 25% of PAs in developing countries are adequately managed (Dudley & Stolton, 1999)) can become ‘paper parks’ (see Introduction). In such areas, community engagement, participation and understanding might be as appropriate as measures of PA success as purely biological metrics.

6.5 Drivers, and different metrics, of diversity change

Much of the content of this thesis has focused on climate and human-transportation as key drivers of past, present and future changes in the distributions of species. Climate-change has affected distributions of a wide range of taxonomic groups (e.g. Hickling *et al*., 2006) and will continue to do so (e.g. Huntley *et al*., 2007). Similarly, the spread of non-native species has been well documented (e.g. Dyer *et al*., 2017). However, it is clear that changes in the species composition of regions are also being driven by several other factors. This can be seen by examining the reasons for species turnover that were analysed in Chapter 5. I identified 22 incidences of species turnover (extirpations, introductions and colonisations) for the UK in the past 200-years. Including pre-1945 colonisations (for example Black-necked Grebe *Podiceps nigricollis*, Slavonian Grebe *Podiceps auritus*) and species which either ‘re-colonised’ (e.g. Osprey *Pandion haliaetus*, Avocet *Recurvirostra avosetta*) or were ‘re-introduced’ (e.g. White-tailed Eagle *Haliaeetus albicilla*, Western Capercaillie *Tetrao urogallus*) would add several more to this list. A crude analysis would show that introductions are associated with 13 of these incidences, and climate can only confidently be associated with 6 incidences (colonisations of the UK by populations spreading northwards). Land-use change and changes in persecution regimes (increases in the persecution of some species have caused extirpations, and reductions in persecution of others have allowed recolonisation) have also been major factors affecting the changing composition of species richness in both the UK and Mexico

These factors are major sources of extinction risk for birds in general (Owens & Bennett, 2000) and have driven past species turnover in other locations; my results from Chapter 5 (Table 5.5) provide more agreement that land use change is an important global driver of extirpations and colonisations, as are protected areas (which may resist persecution). However, the particular balance of these factors will vary in different parts of the World. For example, introduced species will have a greater impact in isolated countries (e.g. Island entities), both as threats to natives (and therefore causes of extirpations) and as established non-native species components of biological communities. The importance of different factors can also vary through time. The more recent incidences of species turnover in the UK have been climate-associated, whereas historical ones were more frequently related to persecution. Thus, sweeping statements about the drivers of diversity change should be treated with caution.

Sweeping statements about the directionality of diversity change should also be treated with care. As well as the geographic context, the scale at which biodiversity changes are measured is important, and differences in scale can lead to different conclusions. Globally, the number of species is declining to such an extent that some ecologists talk in terms of a sixth mass extinction (Barnosky *et al*., 2011). McGill *et al*. (2015) suggest however, that in terms of the variety of species in any given location (alpha-diversity), this global trend (negative) contrasts with regional (positive) and local (flat or sometimes positive) trends. My results support this. On a national scale, species extirpations have been outnumbered by inflows from introductions and colonisations since 1815: the UK (6.93%), Mexico (1.00%), and other countries across the world (average 4.28%) all currently (2015) contain more breeding bird species. However, species and population declines often happen at more local scales, and thus are not considered in national or regional scale metrics of extirpation; for example, formerly widespread birds such as Corncrakes *Crex crex* and Aplomado Falcons *Falco femoralis* have declined without being lost completely as breeding birds from the UK and Mexico respectively. Local increases are also not considered in national scale metrics of species turnover either; since its initial colonisation, the Collared Dove has gone from an initially localised distribution in the UK to a near-universal distribution in areas with human habitation. In Mexico's SGBR, the spread of non-native species and those with an apparent preference for human-altered environments into recently modified habitats more than compensated (numerically) for the loss of those species which had retreated into core zones. At a local scale, alpha-diversity was about 42% higher in modified locations than in relatively undisturbed areas. Although I did not measure local changes in alpha diversity in the UK, I did observe the spread of colonising and non-native wetland bird species across several counties, demonstrating that the widely reported losses of groups such as farmland birds, has, to some extent, been balanced out at the aggregate scale of UK bird diversity.

My findings also indicate that beta-diversity (as measured by the difference in species composition between places), has been affected by changes in the distribution of bird species. At a local scale in the SGBR, habitat modification and subsequent presence of non-natives resulted in less similarity (an increase in beta-diversity) within bioclimatic zones, but more similarity (a decrease in beta-diversity) between bioclimatic zones, as habitat generalists and non-natives established in each zone. The avifaunas of different countries were more similar in 2015 than in 1815 (again, a decrease in beta-diversity), mainly because several non-native and colonising species established in multiple new countries. This process of biotic homogenisation is further increased by the extinctions of endemic species, such as the Guadalupe Storm Petrel *Oceanodrama macrodactyla* and the Guadalupe Caracara *Caracara lutosa* from Mexico.

6.6 Conservation Issues

6.6.1 The role of Protected Areas

This thesis has demonstrated that, as species have undergone distributional changes, PAs can (1) facilitate colonisations, (2) resist non-native species, and (3) provide appropriate environments for species in global decline. As such, they contribute to AICHI Target #9 (by preventing the spread of non-natives within a country, if not necessarily preventing initial introduction), AICHI Target #12 (preventing the extinction of known threatened species) and parts of UN Sustainable Development Goal #15 (protect and prevent the extinction of threatened species). PAs (see Introduction) are most likely to be designated for the presence of a species, species assemblage, or high numbers of individuals. When PAs do contain threatened species (e.g. the SGBR's core protected areas), they remain of *current* relevance for those species for which they have been designated. In this context, however, the *future* relevance of PAs has been questioned, given that the distribution of species are shifting as a result of climate change and other factors. If the climatic requirements of Military Macaws and Bearded Wood Partridges soon fall outside of the SGBR's core protected areas, their value will have been reduced. The challenge here is that PAs may cease to meet some of the original reasons for their designation, even if they facilitate colonisations of new species and resist non-natives. These colonisations demonstrate that PAs will continue to be important as the distributions of species shift in response to climatic and other drivers. In this respect, the intention to increase the coverage of PAs to 17% (AICHI Target #11) or beyond (e.g. Dinerstein *et al.*, 2017) is an important conservation goal. However, designations will need to be sufficiently flexible to accommodate changes in the composition of the biota in any specific PA.

Increased coverage of PAs, however, may be difficult to achieve due to competition for land resources, which have historically biased PA land towards relatively unproductive ecosystems. Further, where PAs are designated, their presence alone does not then guarantee continued achievement of conservation targets. More than 50% of Mexico's land is part of an ejido – communal agricultural land which has been typically characterised by unsustainable resource use, high poverty, and restrictions on land transfer (World Bank, 2001). As such, acquisition of land for PAs is difficult, especially given the competition for available land provided by economically more attractive alternatives such as the development of the tourism industry. In the south-east of Mexico, tourism is now the most important economic activity in Quintana Roo (Barsimantov *et al*., 2009), and in the north-west it is the major contributor to the local economy of many parts of Baja California (Angeles *et al*., 2009). Whilst tourism development and protection for conservation might come into conflict (Saarinen, 2016), the growth of nature- and eco-tourism activities such as whale-watching (Brenner *et al*., 2016) provide an environmentally more-stable, and increasingly economically viable alternative to competing economic activities like gillnet fishing (associated with the decline of the Vaquita *Phoecena sinus*; D'Agrosa *et al*., 2000).

When land is designated as a PA, the level of protection and the degree to which the protection is enforced will determine its 'effectiveness'. In the SGBR, the levels of micro-disturbance that I observed were similar in areas with buffer protection (IUCN Category VI) and unprotected areas. The core protected areas that I visited were largely free from macro and micro-disturbance, although this should be considered in context as well. The core zones that I censused were in remote, inaccessible locations, and were regularly patrolled by rangers. This is not the case with *all* of the core protected areas in biosphere reserves across Mexico (Roberto Pedraza pers. comm), some of which are affected by illegal logging and hunting. The authorities which run the reserves do not have enough resources to comprehensively patrol the boundaries of each of the core areas. When this happens, the value of PAs may be reduced by a lack of conservation enforcement. In such cases, their ecological effectiveness, particularly in terms of protecting vulnerable species, might be reduced. Nevertheless, in a global analysis which included many countries that have been associated with 'paper parks', PA coverage was still associated (Tables 5.3, 5.4, 5.5) with reduced extirpations and increased colonisations.

6.6.2 Non-native Species

Non-native species are those which have taken advantage of human 'assistance' to colonise novel regions. The drivers of non-native species richness (trade, human population density;

Table 5.5) are unlikely to disappear soon, and so the growth of non-natives will continue. Comprehensive culls of non-native species may be effective, on occasion, depending on population size and other factors. For example, because of fears of hybridisation with endangered White-headed Ducks, the Ruddy Duck population of Europe has been controlled (Henderson, 2010) and they have now largely been eradicated from the UK (Holling *et al.*, 2014). PAs might act as another measure in resisting the spread of non-native species. In the UK, non-native wetland birds were initially absent from PAs in recently colonised counties. In Mexico, core protected areas were free of non-natives, and globally, countries with more protected land had fewer introduced species. Yet the reasons for this resistance might vary between regions and between species. UK PAs were increasingly vulnerable as the populations of non-native wetland birds grew, perhaps because the 'release point' of non-natives has tended to be in human-modified environments. Mexican core PAs might have been free of non-natives because of their geographic isolation from 'establishment centres' of non-natives in Mexico (although for those species spreading from the USA, core PAs are equally as remote as disturbed parts of the landscape). Alternatively, the lack of disturbance in core zones meant that there were fewer opportunities for non-natives species, which in the SGBR were largely found in human-modified environments. Attempts to control the spread of non-native species must, therefore, be context dependent.

The default conservation position on non-native species should also be considered. Non-native bird species in the UK, Mexico and across most of the world rarely pose direct threats to other bird species (Table 1.3). The case of the Ruddy Duck is apparently an exception, rather than the rule. In contrast, non-natives add to the alpha-diversity of the regions which they occupy, and in this respect are a positive component of distributional change (the presence of non-native birds has numerically compensated for the loss of native species in most countries across the World, resulting in a typical increase in national alpha diversity of about 1.5%). The range of species found on British wetlands and disturbed Mexican forest and scrub is higher as a result of non-natives. The spread of species such as Black Swans into British wetlands is welcomed with considerably less enthusiasm than, for example, the Great Egrets which have recently colonised the south of the country. Yet, just as House Sparrows (now a protected and much-loved 'native' species in many European countries) did 5,000 to 10,000 years ago (Thomas, 2017) and Collared Doves did 60 years ago, both species are opportunists taking advantage of human-induced actions. In these examples, the species took advantage of human-modified habitats, whereas others have benefitted from their ability to escape from bird collections or to respond to changed climates. To add another layer of moral confusion, whilst many parties are preoccupied with the removal of non-native species, the population of Common Pheasants (native to Asia) and other game species is artificially augmented each year in the UK and many parts of the World to provide sport for hunters. Game management is not universally positive, of course, but such effects (for example, predator management) are not restricted to non-native gamebirds.

Although their status and life histories differ, each of the above species have made the British breeding bird avifauna richer than it was before their arrival, and perhaps should not be viewed through a lens which is, by default, negative.

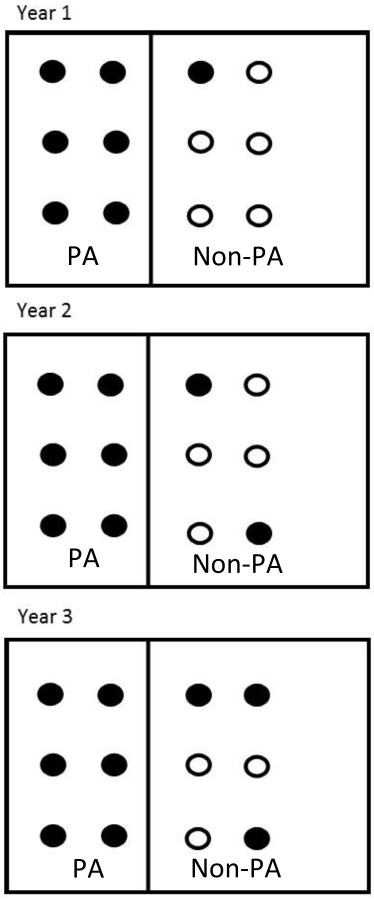
6.7 Observer Effort and measures of Beta-diversity

Issues related to spatial and temporal variation in observer effort were a recurring theme throughout this work, and the results reported in each of the data chapters should be interpreted carefully against this backdrop.

The association of colonising species with PAs as both sites of first reported breeding (Table 2.1) and sites where populations establish (Fig 2.1) could potentially be explained by the differences that exist between protected and unprotected land in terms of (1) intensity of observer effort (in this case bird-watching time) and (2) the probability of incidences of breeding being reported to the relevant bodies. Given that bird-watchers are more attracted to protected areas (Ferrer *et al*., 2016) and therefore focus attention in PAs, and that wardens within PAs are perhaps more likely to confirm breeding than casual observers outside of PAs, it is plausible that the *true* percentage of ‘landing pads’ (sites of first reported breeding for colonising species) that have occurred in PAs is lower than the figures that we report in Chapters 2 and 3.

Furthermore, the declining association of colonising species with PAs over time could also be counfounded by this observer effort issue. Firstly, it could be argued that observers within PAs are more likely to identify ‘new’ species. As public awareness of colonising species grows, observers outside of PAs become better equipped to identify, and then report incidences of breeding. Secondly, under the assumptions that observer intensity is higher in PAs and that colonising species breed at the same site year-after-year, a declining trend of association with PAs would be reported even if it was not happening in reality, as incidents of breeding in unprotected land are gradually discovered. Figure 6.1 illustrates this issue under the assumption of 100% observer coverage in PAs, and imperfect coverage in unprotected land.

Figure 6.1 Potential influence of variation in observer effort on reported association of colonising species with PAs over time. Open circles are breeding pairs which have not been reported, closed circles are breeding pairs which have been reported. This model assumes 100% observer coverage in PAs, and imperfect detection in unprotected land.



Number of breeding pairs: 12

Reported breeding pairs: 7

True percentage in PA: 50%

Reported percentage in PA: 86%

Number of breeding pairs: 12

Reported breeding pairs: 8

True percentage in PA: 50%

Reported percentage in PA: 75%

Number of breeding pairs: 12

Reported breeding pairs: 9

True percentage in PA: 50%

Reported percentage in PA: 67%

Figure 6.1, while illustrative of the potential issues presented by variation in observer effort, is an extreme scenario, and is unlikely to reflect reality for many species. This is because (1) the discrepancy in observer coverage is unlikely to be as high as shown in Fig 6.1 (in the UK at least the popularity of ‘patch’ birding ensures coverage in unprotected land), (2) for some species, PAs contain a large proportion of the suitable breeding habitat within the wider landscape and so by default, percentages breeding in PA *must* be high, and (3) many of the colonising species that we focus on e.g. Little Egret and, more recently, Spoonbill, are large-bodied, conspicuous species and thus highly visible and likely to be reported whether or not the breeding event is in a PA. Furthermore, we present contrasting trends for colonising non-native species in Chapter 3, indicating that a declining association in PAs is not a 'given' for species undergoing range-expansions.

Analysis of the spatial distribution of bird records submitted to online portals such as BirdTrack (UK), or eBird (globally) could allow researchers to quantify the true extent of the difference in observer intensity between PAs and unprotected land, and would be a worthwhile avenue of future study. The use of null models based on estimates of observer effort in/out of PAs and probabilities of detection of species would allow trends in PA use over time to be verified.

In Chapter 4, we used four ten-minute point counts for the bird surveys in each square. This time limit was used for logistical reasons, but it might have influenced the reported species richness of different locations on the basis that rates of species accumulation potentially vary between bioclimatic zones, modification categories and levels of protection. Longer counts increase the probability of detection of inconspicuous species, and also the likelihood of detecting mobile species which have moved into the study area during the point count (Fuller & Langslow, 1984). Analysis of species accumulation curves in different bioclimatic zones/modification categories/protection levels would allow us to set an objective time limit in order to take representative samples of true local species richness at each site.

Issues related to observer effort are further discussed in sections 1.4.2, 2.5, 3.5 and 5.5.1

At least 24 presence-absence measures of beta-diversity have been employed by researchers (Koleff *et al.*, 2003), as well as several more which use species abundance data (Barwell *et al*. 2015). The relative performance of these metrics can be evaluated in different ways, including independence from alpha-diversity and sensitivity to sample size. The $\beta_{Jaccard}$ measure, which was used in Chapters 4 and 5 to measure pairwise similarity of squares and entities, performs well for several measures, including independence from alpha-diversity when the pairs of assemblages compared are equal in size, and independence from differences in abundance. When comparing assemblages which vary in species richness, however, the β_{sim} metric may be favoured as it is less sensitive to nestedness (Barwell *et al.*, 2015). Thus attempts to compare similarity of assemblages should consider the structure and underlying assumptions of the data before deciding on the most appropriate metrics. Although the use of different metrics of beta-diversity in this thesis might have affected the size of any reported change, both the patterns observed here (the presence of habitat generalists in modified areas in *several* different vegetation zones in Chapter 4, and the presence of non-native/naturally colonising species in *several* 'new' entities), and the implications of these issues for conservationists, remain relevant.

6.8 Further research

This thesis has provided a thorough contribution to our knowledge regarding the importance of PAs for species undergoing distributional changes. As with every time- and resource-limited study, however, there are areas that have not been covered.

The work on wetland birds in Chapters 1 and 2 could be repeated in different geographical regions and for different taxa, although the choice of locations is tempered by the availability of data. Few countries have the kind of detailed and accessible historical breeding records of recent colonists or other bird species that would allow the type of analysis demonstrated in Figure 2.1 and Appendix 1E.

Many countries were unable to provide dates of extirpation, introduction or colonisation of the species which were analysed in Chapter 5, highlighting one aspect of the variety in observer intensity between countries. Furthermore, natural colonisations could only be identified relatively recently, for most countries. If these data were available, changes in alpha- and beta- diversity could be tracked through time, giving us a more detailed picture of how the geographic composition of species richness has changed, and perhaps allowing predictions of future changes to be expected.

The breadth of research in Chapter 4 was limited by man-power and time (this research required an entire winter of sampling effort to cover just three bioclimatic zones in one reserve). It would have benefited from repetition in different bioclimatic zones in order to further explore the relationship between the effect of habitat modification on species richness and the underlying primary productivity of the bioclimatic zone. I predicted that habitat modification would have the most positive effect on species richness in the least productive habitats. This relationship could also be explored with a meta-analysis of the studies which have explored the effects of land use change on species richness. This chapter highlighted the varying effects of different levels of protection – something which should be taken into consideration into all future studies considering the 'effectiveness' of PAs.

6.9 Conclusion

The distributions of species have always been dynamic. Humans have accelerated this process, particularly as transporters of non-native species (i.e. increasing long-distance colonisation rates) and as emitters of the pollution that has caused climatic warming. Protected Areas are designed to protect biodiversity from these pressures, as well as others such as persecution and land-use change, although nowhere is completely protected from human modification. Where enforcement has worked and detrimental human impacts are limited, I conclude that Protected Areas remain important, even if the identities of the species that are present changes over time. Several researchers fear that Protected Areas will become redundant as the distributions of those species for which they were designated undergo latitudinal or elevational shifts. Here, however, I demonstrate that the ecological effectiveness of Protected Areas is not just relevant to the species which initially occupy them. As distributions do change, the importance of Protected Areas is enhanced by their ability to shelter declining species, facilitate the range expansions of colonising species, and at least temporarily withstand the spread of non-natives.

List of Appendices

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Appendix 1 – Supporting Information for Chapter 2

Appendix 1A Sources consulted during the collation of breeding records of colonisers and comparator species.

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Lancashire and Cheshire Fauna Society (1964, 1969, 1974, 1979, 1984, 1989, 1994, 1999, 2004, 2009) *Lancashire Bird Report.*

Norfolk and Norwich Naturalists' Society (1964, 1969, 1974, 1979, 1984, 1989, 1994, 1999, 2004, 2009) *Norfolk Bird and Mammal Report.*

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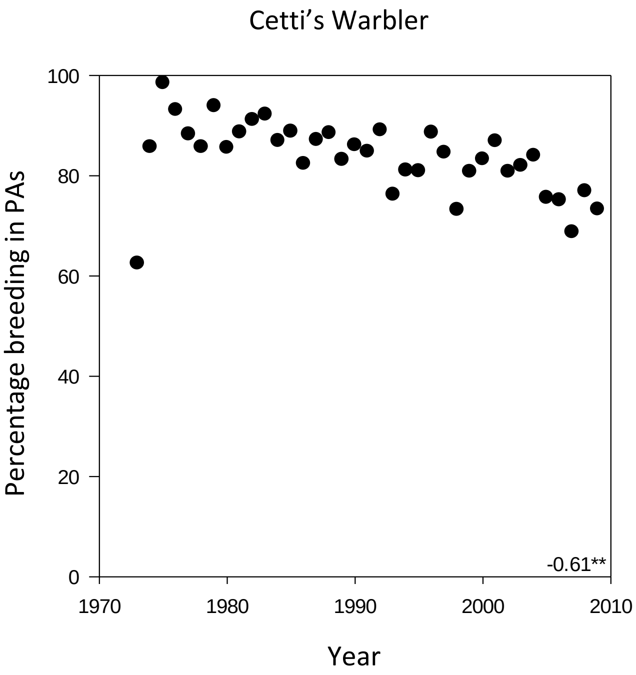
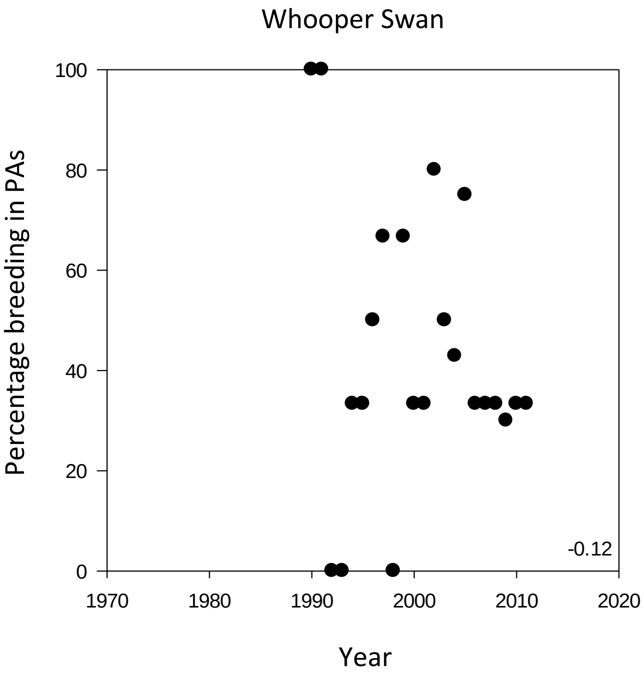
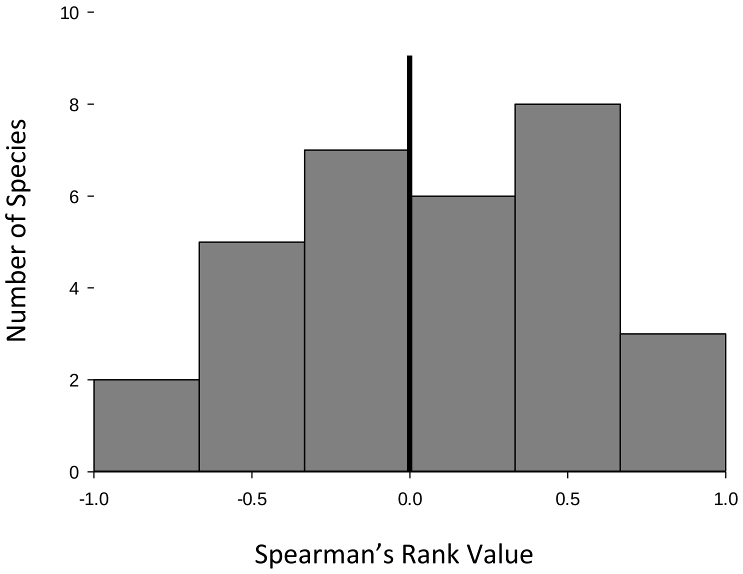
Appendix 1B The percentages of the Cetti's Warbler and Whooper Swan population breeding in PAs each year, after excluding all sites which were designated as PAs after the species started to breed there.





Appendix 1C Trends of Comparator Species 1964-2009 based on percentage of total sites during each time interval which were in PAs, as opposed to the percentage of total number of breeding pairs that were in PAs (shown in Appendix 1E).



Appendix 1D Species accounts of the colonists, highlighting range, population, characteristics, nesting habitat and the driver of distributional change for each species.

Species name	World breeding range (Robinson, 2005)	European population (pairs)(Bird life, 2004)	Characteristics and nesting habitat	Driver of distributional change
Little Egret *Egretta garzetta*	S & C Europe, Asia, Africa, Australasia	61,000-84,000	Little Egrets are white, large-bodied colonial breeding herons, which nest in tall trees such as willows or tamarisks near marshy lakes, rivers or coastal lagoons (Kazantzidis *et al*., 1997; Cramp & Simmons, 1983).	Milder winters and warmer summers in previously unsuitable areas have allowed Little Egrets to advance their range northwards through Europe (Lock & Cook, 1998), although long-term reductions in persecution (e.g. (Cocker & Mabey, 2005)) might also be a factor. Colonisation of the UK was preceded by large influxes of Little Egrets appearing in the autumn, and staying to breed the following spring.
Common Crane *Grus grus*	N & E Europe, N & C Asia	49,000 – 70,000	Common Cranes are Europe's tallest birds (Cocker & Mabey, 2005). They require an undisturbed, inaccessible nest site, typically in flat areas adjacent to water, such as bogs, swampy clearings, or reedy wetlands (Cramp & Simmons, 1983).	Common Cranes bred in the UK in the 17th century but habitat loss and over-exploitation caused them to die out (Cocker & Mabey, 2005). The recent increase in breeding numbers in continental Europe has been attributed to enhanced legal protection and the restoration of wetlands (Meine & Archibald, 1996). Breeding productivity in the UK has been increased through specific conservation measures in PAs, for example protection from human disturbance and predator control (Stanbury, 2011).
Whooper Swan *Cygnus cygnus*	Northern Europe (Iceland, Scandinavia)	c. 40,000	Whooper Swans are huge, white waterfowl (Svensson, 2009), which occupy shallow lakes with a maximum depth of 1m to allow underwater grazing (Cramp & Simmons, 1983). They typically require an undisturbed, well-vegetated nesting area, but may be becoming 'less shy' in their habits (Svensson, 2009).	Whooper Swans were hunted to extremely low levels in Northern Europe until the 1950s (Boiko & Kampe-Persson, 2010). However, having received enhanced legal protection since then (Boiko & Kampe-Persson, 2010). They have experienced a southern spread throughout their breeding range (Poysa & Sojornen, 2000).
Common Goldeneye *Bucephala clangula*	N. Europe, N.Asia, N.America	290,000-380,000	Common Goldeneyes are small, hole-nesting diving ducks, which require tall forest growth close to productive lake, pool or river (Cramp & Simmons, 1983). In Scandinavia, they typically nest in old Black Woodpecker *Dryocopus martius* holes, but will also readily take to nestboxes (Cramp & Simmons, 1983; Johnsson *et al*., 1993). They are easily monitored at nest boxes and when ducklings are taken out onto open water.	The provision of nestboxes is known to increase local breeding populations of Common Goldeneyes (Eriksson, 1982; Dow & Fredga. 1985). This management action may be responsible for allowing over-summering birds to start breeding in Scotland (Dennis & Dow, 1984). A series of 'Scandinavian' springs in Scotland may have been initially responsible for the appearance of summering birds (Dennis & Dow, 1984). Throughout most of their range, however, there is little evidence of significant expansion (Hagemeijer & Blair, 1997).
Cetti's Warbler *Cettia cetti*	S & C Europe, S. Asia, Middle East	600,000 – 1,600,000	Cetti's Warblers are small, inconspicuous, insectivorous, birds which are rarely seen (Cocker & Mabey, 2005). Their noisy, distinct call, however, gives away their presence. They require dense, tall and well delimited vegetation, preferably near but not in water, such as swamps and reedbeds (Cramp & Simmons, 1983).	The northward spread of Cetti's Warblers through Europe has been linked to a reduction in the incidence of cold winters (Bonham & Robertson, 1975) which cause high rates of mortality in this non-migratory bird.
Mediterranean Gull *Larus melanocephalus*	coastal Europe	117,000-310,000	In the United Kingdom, Mediterranean Gulls usually breed in Black-headed Gull colonies. These are always found near water, for example, at coasts, deltas, estuaries, lagoons, marshes or large inland waters (Cramp & Simmons 1983).	Mediterranean Gulls were restricted in range to the Black Sea until the 1960s (Zielinska *et al*., 1997) before expanding into western and central Europe (Meininger & Flamant, 1998). This species may be benefiting from climate change (RSPB, 2011), although the extent to which climate change is driving this range change in relation to other factors is unclear.

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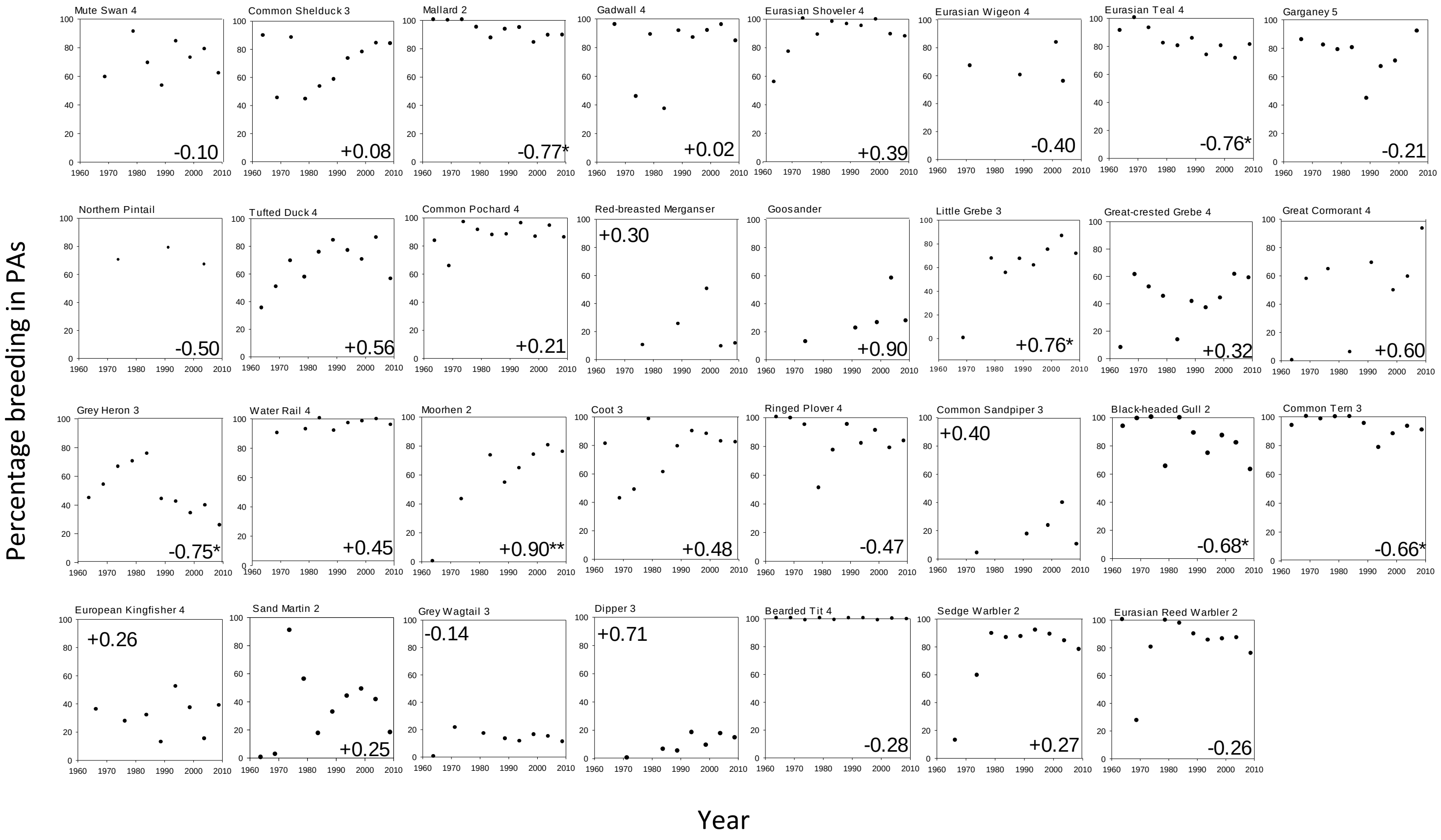
Appendix 1E Scatter plots showing the percentage of the population of each established wetland species breeding in PAs at 5-yearly intervals between 1964 and 2009. Spearman's Rank values (mostly lower right of each panel) describe correlations between year since arrival and percentage breeding in PAs. (* P<0.05 **P<0.01). Numbers by species' names indicate level of breeding abundance in the UK (1=very abundant, 2=abundant, 3=fairly abundant, 4=scarce or local, 5=rare (Svensson, 2009)).



Appendix 2 – Supporting Information for Chapter 3

Appendix 2A Non-native wetland birds that have bred on at least one occasion in the UK, but that don’t maintain persistent populations currently. *As of 2017, Black-crowned Night Heron has bred in a wild state in the UK as well.

Trumpeter Swan *Cygnus buccinator*

Snow Goose *Chen caerulescens*

Pink-footed Goose *Anser brachyrhynchus*

Bean Goose *Anser fabalis*

White-fronted Goose *Anser albifrons*

Red-breasted Goose *Branta ruficolis*

Emperor Goose *Chen canagica*

Bar-headed Goose *Anser idicus*

Ruddy Shelduck *Tadorna ferruginea*

Cape Shelduck *Tadorna cana*

Muscovy Duck *Carina moschata*

Wood Duck *Aix sponsa*

*Black-crowned Night Heron *Nycticorax nycticorax*

Appendix 2B Brief histories of wetland bird species that have been introduced to the UK.

Species	**Native Breeding Range**	**Arrival in Britain**
Barnacle Goose *Branta leucopsis*	Greenland, Spitzbergen, North Russia	This species winters in Britain (e.g. Lack, 1986), but is also a popular collection species. Current feral populations derive from escaped individuals and have bred in habitat totally different from that of their natural range (Blair *et al*., 2002).
Canada Goose *Branta canadensis*	North America	Introduced to Britain in St. James Park in the mid 17th century (http://www.bto.org/birdfacts). It did not spread away from parks until after the Second World War (Lack, 1986).
Egyptian Goose *Alopochen aegyptiaca*	Sub-Saharan Africa	Introduced in the late 18th century to East Anglia as an ornamental bird in parkland. By the mid-19th century, flocks were present on 'many private estates' (Sutherland & Allport, 1991).
Ruddy Duck *Oxyura jamaicensis*	North and Central America	First escaped from a collection in Slimbridge in 1952. Since then the population spread and grew in Britain until it was determined to be a threat to indigenous White-headed Duck *Oxyura leucocephalus* populations in Europe and was subsequently culled.
Mandarin *Aix galericulata*	East Asia	Popular with 'garden pond' collectors since first brought to Britain in 1745. Juveniles are released and form feral populations
Black Swan *Cygnus atratus*	Australia	Ornamental birds have been present since 1791, with escaped birds breeding in the wild intermittently since 1902.

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Appendix 2C Inclusion of additional introduced species established in the UK

Species Selection

We searched the relevant scientific literature (Lever, 2005; www.rbbp.org.uk; Banks *et al*., 2008) to identify introduced wetland species (not from *Anatidae*) that have been established (≥10 pairs breeding for at least five years) at any point since 1950 in the UK.

We also identified non-wetland species in both categories, following the same protocol as used in the main body of the work (see Methods).

Analysis

Species were subjected to the same analysis as outlined in Methods, except that we did not include the condition of five pairs as a minimum criteria for establishment (determining the exact breeding locations of non-wetland birds is less easy than for wetland birds, and thus there are fewer geographically specific records, see below).

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Appendix 2D Inclusion of invasive non-wetland species in Europe (non-Anatidae)

Species Selection

We identified introduced wetland birds that have become established (≥10 or more pairs breeding for at least five years) outside of their normal range as a result of deliberate or accidental releases, and which don't belong to *Anatidae* (using Banks *et al*. 2008). Species with naturally occurring populations in Europe (e.g. Greater Flamingo *Phoenicopterus roseus*) were excluded as the introduced populations could be augmented by natural vagrants. Purple Swamphen *Porphyrio porphyrio* does have a naturally occurring population in Europe, but was included as the La Selva population (see below) is recognised to have descended directly from captive individuals (Banks *et al*. 2008).

Identifying Landing Pads

For each species within this category, we identified the European countries in which it has bred, and the regions (administrative regions in France, first-level administrative divisions in Italy, metropolitan regions in Germany, autonomous communities in Spain) within those countries in which it has bred. We chose regions in order to replicate counties in the UK. The relevant scientific literature (see References in Appendix 2J below) was then used to identify the locations of first breeding by each species in each region.

Identifying Protected Area status of Landing Pads

Breeding locations were cross-referenced with the interactive mapping system available on the website of the relevant authority in each country in order to determine the status of each location (France – www.reserves-naturelles.org, Italy – www.parks.it, Germany – www.bfn.de , Spain –www.gencat.cat, www.gobiernodecanarias.org). If the site had *any* level of protection (see relevant websites), it was considered 'Protected'. If not, it was considered 'Not Protected'. If there was any ambiguity, the location was excluded from the analysis.

Appendix 2E Results with Great Bittern excluded from the analysis.

When Great Bittern was excluded from the analysis due to doubts over whether they did disappear as breeding birds in the UK during the study period, introduced species remained less likely to use PAs at the landing pad stage (Mann-Whitney, $z_{6,7}$=2.21, P=0.0271), and in Period 1 (Mann-Whitney, $z_{6,7}$=2.21, P=0.0271) but only a marginal effect in Period 2 (Mann-Whitney, $z_{5,6}$=1.73, P=0.0836).

Appendix 2F Inclusion of additional introduced species established in the UK.

Species

Black-crowned Night Heron (of the American race) is the only non-Anatidae wetland bird to have been established in the UK during this time (last bred 2003).

Although a number of introduced non-wetland bird species have become established in the UK, only Rose-ringed Parakeet *Psittacula krameri* fully met our inclusion criteria. The majority of natural colonists that have colonised the UK since 1940 have been wetland species and only the Firecrest and Collared Dove fall into the category of non-wetland natural colonists.

Note on Collared Dove

In the UK, the Collared Dove population spread and grew at an exponential rate (Hudson, 1965). Ten years after first breeding (in 1955), this species had been recorded in 62 counties across the UK with a total population estimated conservatively at over 18,000. This species, which is a non-native invasive species in many parts of its range, is almost exclusively associated with human habitation, with some pairs breeding on adjacent open farmland. Given its rapid expansion, subsequent breeding locations after initial colonisation of a county were rarely recorded in bird reports. Each of the landing pads that we identified was in non-protected land. We thus estimated the PA usage in both Period 1 and Period 2 conservatively at 0%.

First Breeding Records of Colonising Species

With Black-crowned Night Heron and the terrestrial colonists included in the analysis, introduced species remain less likley to use PAs as Landing Pads than natural colonists (Mann-Whitney, $z_{8,10}$=2.18, P=0.0293, Medians: 19% (introduced species), 67% (natural colonisers)).

PA Association of Colonising Species in Period 1 (Establishment Phase)

With Black-crowned Night Heron and the terrestrial colonists included in the analysis, the percentage of breeding attempts of the introduced species that was in PAs remains much lower than that of natural colonists during Period 1 (Mann-Whitney, $z_{8,10}$=-2.27, P=0.0232, Medians: 16% (introduced), 77% (natural)).

PA Association of Colonising Species in Period 2 (Consolidation Phase)

With Black-crowned Night Heron and the terrestrial colonists included in the analysis, the percentage of breeding attempts of the introduced species that was in PAs remains lower than that of natural colonists during Period 2, but not significantly so (Mann-Whitney, $z_{7,9}$=-1.69, P=0.091, Medians: 32.8% (introduced), 71% (natural)).

Comparison of PA Association of Colonising Species between Periods

With Black-crowned Night Heron and the terrestrial colonists included in the analysis, there was a difference in temporal trends between introduced and natural colonists, although it was not significant (t-test, $t_{7,9}$=2.032, P=0.0616).

References

Hudson, R. (1965) The Spread of the Collared Dove in Britain and Ireland, 1965-70. *British Birds*, **58**, 105-139.

Appendix 2G Areas of wetlands, as well as percentages of wetlands that are protected, in the counties whose bird reports were used in the study.

County	Total Area (km^2)	Freshwater/Estuaries Area (km^2)	All SSSI Area (km^2)	SSSI Fresh/Est Area (km^2)	% of Total Area SSSI	% of Total Fresh/Est Area SSSI
Anglesey	683.28	7.57	52.44	5.71	7.67	75.39
Angus	2109.88	8.52	74.92	3.35	3.55	39.27
Argyll	7264.41	168.84	660.15	22.75	9.09	13.48
Avon	1370.50	12.98	45.96	8.66	3.35	66.74
Ayrshire (N)	3583.62	31.73	528.48	12.39	14.75	39.03
Ayrshire (S)	7264.41	170.43	660.15	24.16	9.09	14.18
Bedfordshire	1127.57	9.71	11.27	0.30	1.00	3.07
Berkshire	1223.85	19.01	52.71	3.66	4.31	19.26
Borders	4663.93	19.18	23.44	10.12	0.50	52.76
Buckinghamshire	1570.06	8.18	25.75	0.47	1.64	5.71
Caernarvonshire	2637.83	28.27	541.05	13.30	20.51	47.03
Cambrian'	3321.11	35.84	593.49	19.00	17.87	53.01
Cambridgeshire	3061.20	29.05	76.13	9.52	2.49	32.79
Carmarthenshire	2380.08	5.22	135.16	2.61	5.68	50.05
Ceredigion	1877.11	8.04	197.02	2.20	10.50	27.34
Cheshire	2165.96	21.14	55.39	4.74	2.56	22.41
Cleveland	595.38	4.42	32.37	0.70	5.44	15.75
Cornwall	3604.87	16.07	180.60	3.17	5.01	19.74
Cumbria	6850.30	77.71	1021.43	39.64	14.91	51.01
Denbighshire	831.98	4.89	117.56	1.13	14.13	23.16
Derbyshire	2655.88	23.02	279.23	1.44	10.51	6.27
Devon	6604.08	12.97	448.21	2.59	6.79	19.99

Appendix 2C continued

Dorset	2608.61	9.97	178.01	6.16	6.82	61.76
Durham	2229.83	9.72	464.06	1.52	20.81	15.66
Essex	3414.32	28.80	148.55	16.53	4.35	57.38
Flintshire	444.94	2.63	24.85	1.32	5.59	50.08
Glamorgan	2774.87	15.96	170.15	3.90	6.13	24.46
Gloucestershire	3271.72	57.54	118.21	37.95	3.61	65.97
Gower	378.66	1.58	55.11	0.03	14.55	1.66
Greater London	1531.49	28.88	37.22	5.82	2.43	20.16
Greater Manchester	1365.33	17.06	59.27	1.38	4.34	8.11
Gwent	1228.31	9.03	99.56	5.48	8.11	60.66
Hampshire	3795.85	15.88	450.68	6.80	11.87	42.85
Hertfordshire	1633.28	10.67	22.24	2.63	1.36	24.67
Highland	26106.02	783.81	5135.02	277.21	19.67	35.37
Isle of Wight	387.59	2.64	33.94	1.53	8.76	57.83
Kent	3543.87	29.08	211.12	11.70	5.96	40.24
Lancashire	3058.48	26.27	263.69	4.36	8.62	16.60
Leicestershire	2525.52	24.24	47.77	15.51	1.89	63.97
Lincolnshire	7019.97	33.09	97.92	6.82	1.39	20.60
Lothian	1790.16	10.21	62.90	3.13	3.51	30.63
Moray	2225.12	9.32	196.85	5.05	8.85	54.14
North-east Scotland	10945.74	43.30	665.95	15.07	6.08	34.80
Norfolk	5474.20	42.11	440.65	14.23	8.05	33.79
Northamptonshire	2326.42	18.67	37.57	9.72	1.61	52.06
Northumberland	5054.63	33.68	541.65	4.86	10.72	14.43
Nottinghamshire	2154.72	21.57	33.72	3.52	1.56	16.31
Outer Hebrides	3237.81	192.82	348.43	35.61	10.76	18.47

Appendix 2C continued

Oxfordshire	2620.96	18.28	45.42	0.64	1.73	3.51
Pembrokeshire	1612.05	2.58	101.67	1.61	6.31	62.47
Perth and Kinross	5437.08	123.21	647.22	29.13	11.90	23.64
Powys	5084.94	28.26	528.60	7.09	10.40	25.09
Shetland	1454.61	32.78	169.60	6.76	11.66	20.63
Shropshire	3482.69	12.49	73.22	1.52	2.10	12.20
Somerset	4226.69	24.89	303.46	12.30	7.18	49.42
Staffordshire	2709.00	20.75	84.41	4.94	3.12	23.80
Suffolk	3751.03	20.48	269.48	11.40	7.18	55.69
Surrey	1679.92	20.25	116.10	5.23	6.91	25.85
Sussex	3758.32	19.38	213.37	5.97	5.68	30.82
Warwickshire	1964.03	12.41	11.88	0.89	0.60	7.13
West Midlands	7233.40	45.01	144.68	7.19	2.00	15.97
Wiltshire	3431.50	6.63	280.69	0.46	8.18	6.94
Worcestershire	1784.74	8.63	39.15	0.95	2.19	10.98
Yorkshire	14422.49	79.69	1548.85	19.10	10.74	23.97

Appendix 2H Calculating the percentage of habitat that is protected within each of the counties in the UK that was analysed.

Calculating Freshwater/Estuary Areas

All operations were done with the mapping software ArcGIS v9.3 (ESRI, 2009). The counties occupied at each stage of colonisation for each species were selected from the attribute table of a shapefile showing UK administrative counties and made into a new layer. Land cover information for this layer was attained by using the 'intersect' tool for this layer and the 'Land Cover Map 2007' shapefile, obtained from the Centre for Ecology and Hydrology (Morton *et al.* 2011). From this intersect, all 'Freshwater' habitats were selected (as well as 'Estuary' habitats, for those species that breed in intertidal habitats), and their area was measured using the 'Calculate Geometry' tool.

Calculating Protected Freshwater/Estuary Areas

We used the 'intersect' tool for the layer containing the relevant counties for each species in each period and a layer showing all UK SSSIs. This isolated all the SSSIs in a particular set of counties, and we created a new layer from this. We then used the 'intersect' tool for this new layer, and the layer showing all 'Freshwater' (and 'Estuary' habitats where appropriate) within those counties. This isolated all Freshwater/Estuary Areas that were in a SSSI. Their area was measured using the 'Calculate Geometry' tool.

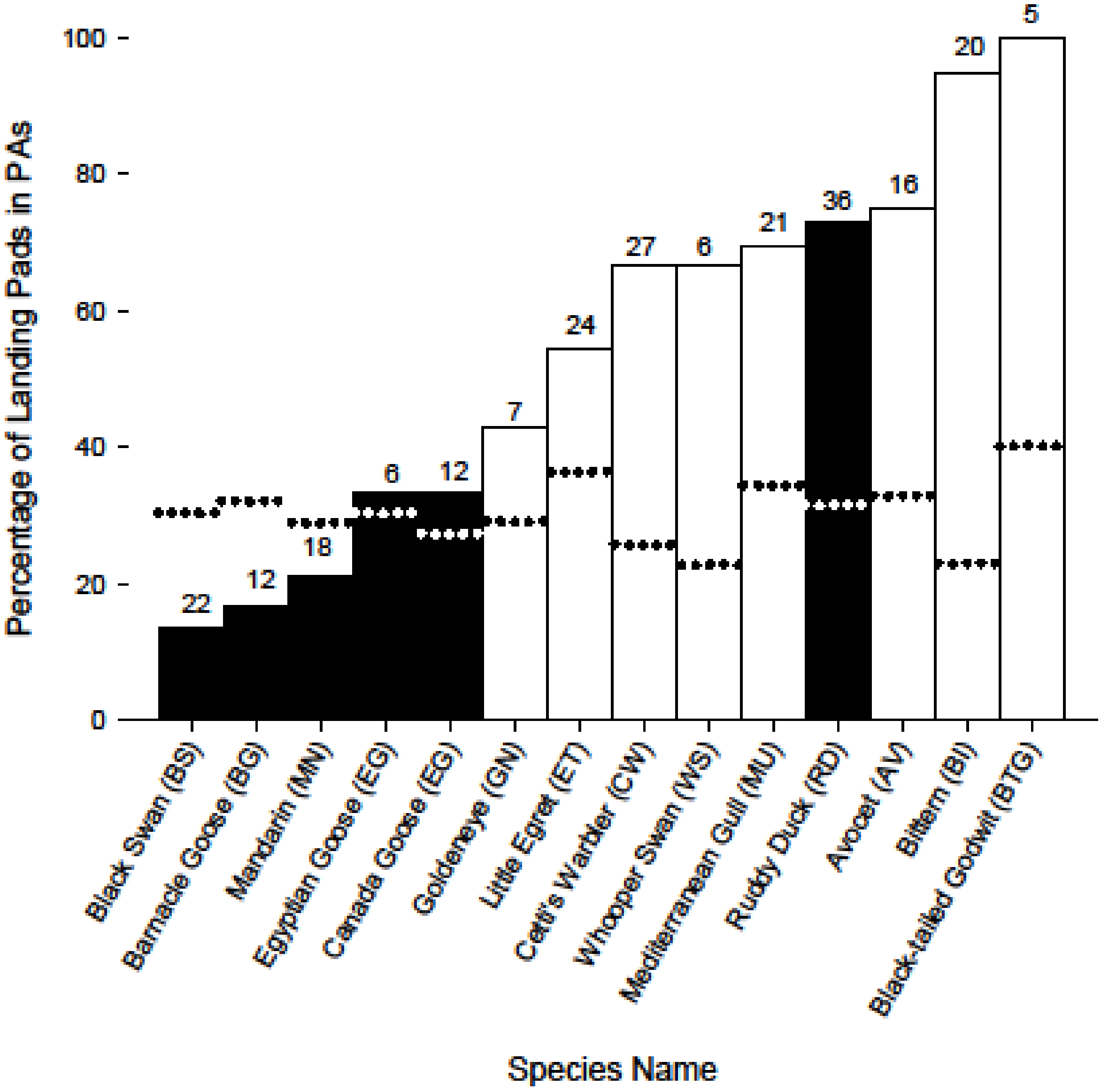
We were thus able to calculate the percentage of all freshwater/estuary areas that were protected in the counties colonised by each species in each period.

References

ESRI (Environmental Systems Resource Institute) (2009). ArcMap 9.3. ESRI, Redlands, California, USA.

Morton, D., Rowland, C., Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R. & Simpson, I.C. (2011) *Final Report for LCM2007 – the new UK Land Cover Map.* Countryside Survey Technical Report No. 11/07 NERC/Centre for Ecology and Hydrology 112pp. (CEH Project Number C03259), CEH, UK.

Appendix 2I The percentage of sites that were in PAs out of all the 'first' breeding locations in counties colonised after 1960. The dotted lines represent expected PA association (percentage of all potential breeding habitat for that species that is protected within the counties colonised by that species). Numbers above the columns represent the sample size (numbers of counties).



Appendix 2J Inclusion of introduced wetland species in Europe (non-Anatidae).

Species Name	European Countries (confirmed breeding)	Regions (confirmed breeding)	Site name	Date of first breeding	Status of Site*
Sacred Ibis *Threskiornis aethopicus*	France	Bretagne	Ile-aux-moines	1993	NOT PROTECTED
		Pays de la Loire	Lac de Grand Lieu	1993	PROTECTED
		Poitous-Charente	Marais de Brouage	c. 1980	NOT PROTECTED
		Aquitaine	Parc du Teich	1997	NOT PROTECTED
		Languedon - Rousillon	Etangs de Bages-Sigean	2000	NOT PROTECTED
	Italy	Piedmont	Vespolate	1989	NOT PROTECTED
	Spain	Catalonia	Barcelona	1974	NOT PROTECTED
		Fuertevent ura	Oasis Park	1997	NOT PROTECTED
		Lanzarote	Arrecife	1997	NOT PROTECTED
Chilean Flamingo *Phoenicopter us chilensis*	France	Hautes-Alpes	Etang du Fangassier	1987	NOT PROTECTED
	Germany	Nordrhein-Westfalen	Zwillbrocker Venn	1983	PROTECTED
Purple Swamphen *Porphyrio porphyrio*	Italy	Lazio	La Selva	c. 1980	NOT PROTECTED

*'Status of Site' refers to the actual breeding location. In some cases, other parts of the 'general site' may be protected.

References

Banks, A.N., Wright, L.J., Maclean, I.M.D., Hann. C., 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*. BTO Report. British Trust for Ornithology, UK.

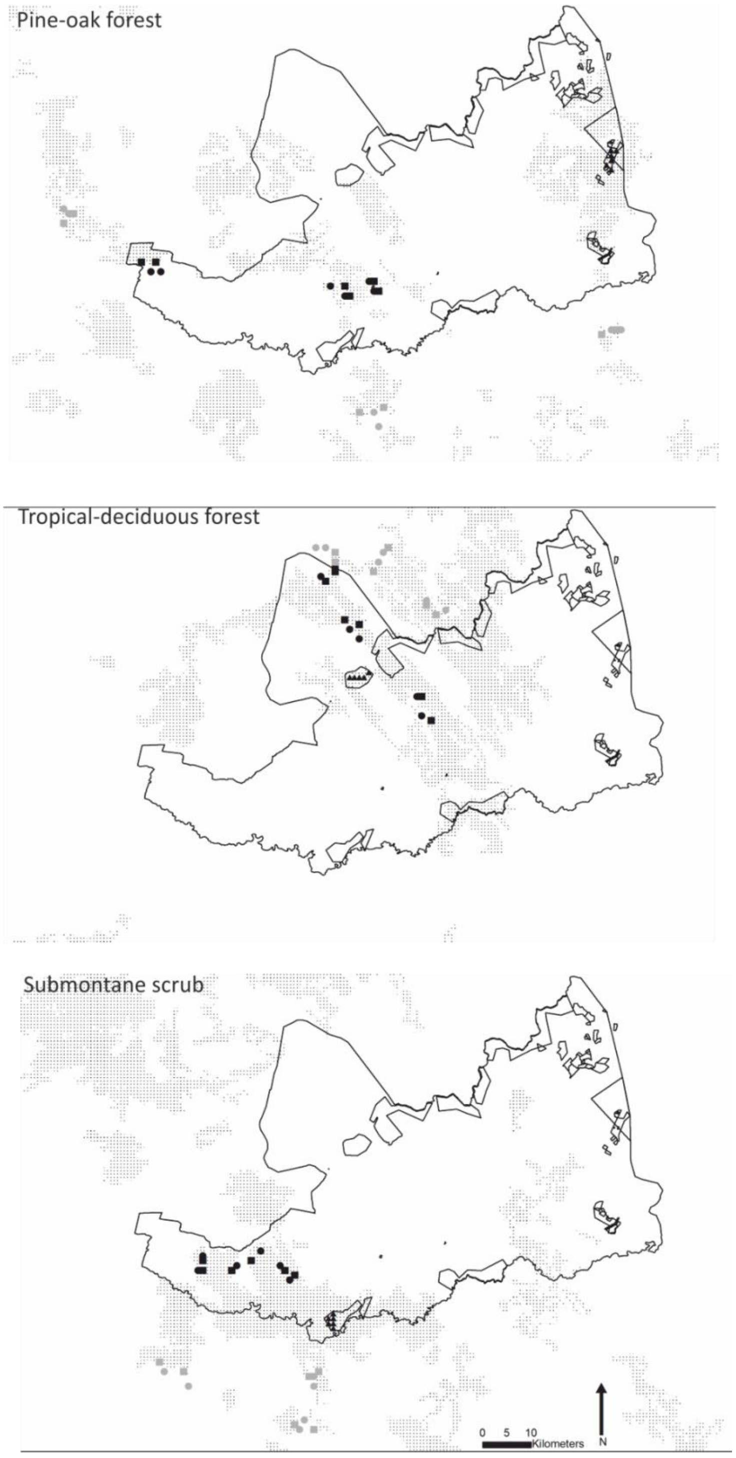
Dubois, P.J. (2007) Les oiseaux allochtones en France: statut et interactions avec les espéces indigenes. *Ornithos*, **14**, 329-364.

Palacios Palomar, C.J. (2001) Notes about reproductive biology of Cattle Egret Bubulcus ibis, in Lanzarote, Canary Islands (Aves, Ardeidae). *VIERAEA*, **29**, 97-102.

Yesou, P. & Clergeau, P. (2006) Sacred Ibis: a new invasive species for Europe. *Birding World*, **18,** 517-526.

Appendix 3 – Supporting Information for Chapter 4

Appendix 3A Study squares (squares – unmodified, circles – modified, both in and outside of the buffer zone, and triangles – strictly protected) sampled in each bioclimatic zone within the study region.



Appendix 3B Descriptions of the three bioclimatic zones studied.

Bioclimatic Zone	**Typical Annual Precipitation (mm)**	**Typical Temperature Range (°c)**	**Altitude (metres above sea level)**
Pine-oak forest	<2500	10 – 28	<3200
Submontane scrub	<900	<40	<2200
Tropical deciduous forest	<1500	18-28	<1200

Appendix 3C Summaries of Levels of Protection within the SGBR. For full details, see INECC (1999) and LGEEPRA (2015).

Strictly Protected Areas (IUCN Category 1a)

Also known as nucleus zones (Zonas Nucleo), they aim to preserve ecosystems in the medium and long-run. The only activities permitted are those which preserve the ecosystems; investigations and scientific data collection and environmental education. Nucleus zones include subzones (a – Protection) where the only activities permitted are those which monitor the environment and scientific investigations which neither extract nor relocate specimens. Nucleus zones can also include subzone b (Restricted Use), which are areas in a good state of conservation in which the aim is to maintain current conditions. In subzone b, environmental education is permitted as well as low impact eco-tourism which doesn't imply modifications of natural conditions. Construction of installations for monitoring the environment or scientific investigations are permitted in subzones b. The strictly protected areas sampled in this study were from subzone a.

Buffer Zone (IUCN Category 6)

The main function of the buffer zone (Zona de Amortiguamiento), which consists of the whole reserve apart from the nucleus zones, is to protect the nucleus zones within it and to manage land-use in a sustainable manner, whilst at the same time creating conditions necessary to benefit conservation of ecosystems in the long run. The SGBR Buffer Zone is split into different subzones, but in all of the buffer zone activities are restricted to those which benefit the communities which live within the Buffer Zone, and those which are strictly compatible with the objectives specified in the Management Program. Examples of restrictions in place across all of the buffer zone in the SGBR are as follows:

- Restoration and conservation of soils.
- Subsistence use of natural resources for the communities.
- Agriculture (livestock and crops) only permitted under controlled conditions according to certain regulations.
- Change of land-use for urban growth restricted

References

Instituto Nacional de Ecologia y Cambio Climático (INECC) (1999) Programa de manejo Reserva de la Biosfera Sierra Gorda, INECC, Mexico.

Ley General del equilibrio ecologico y la proteccion ambiental (LGEEPRA) (2015). Retrieved from: http://www.diputados.gob.mx/LeyesBiblio/pdf/148_090115.pdf.

Appendix 3D Categories of Modification.

Squares were considered unmodified if less than 10% of the square (by eye) was affected by human modification: land was considered modified if satellite imagery (Google, 2014) showed concentrated urban, agricultural, or mixed development, or if land cover maps (INEGI, 2013) indicated that land was ‘induced pasture’, ‘seasonal agriculture’ or ‘urban development’.

The following micro-disturbances were also recorded during surveys of square. Each square was assigned a score, in five categories. In four of the categories: Urban, Agriculture, Traffic and Logging, the score was assigned according to whether disturbance was considered absent, light or intense (e.g. Murphy & Romanuk, 2014). In the fifth category (Other), all extra disturbances (see below) were summed. Scores in each category were summed to give each square a total score (0 to 37).

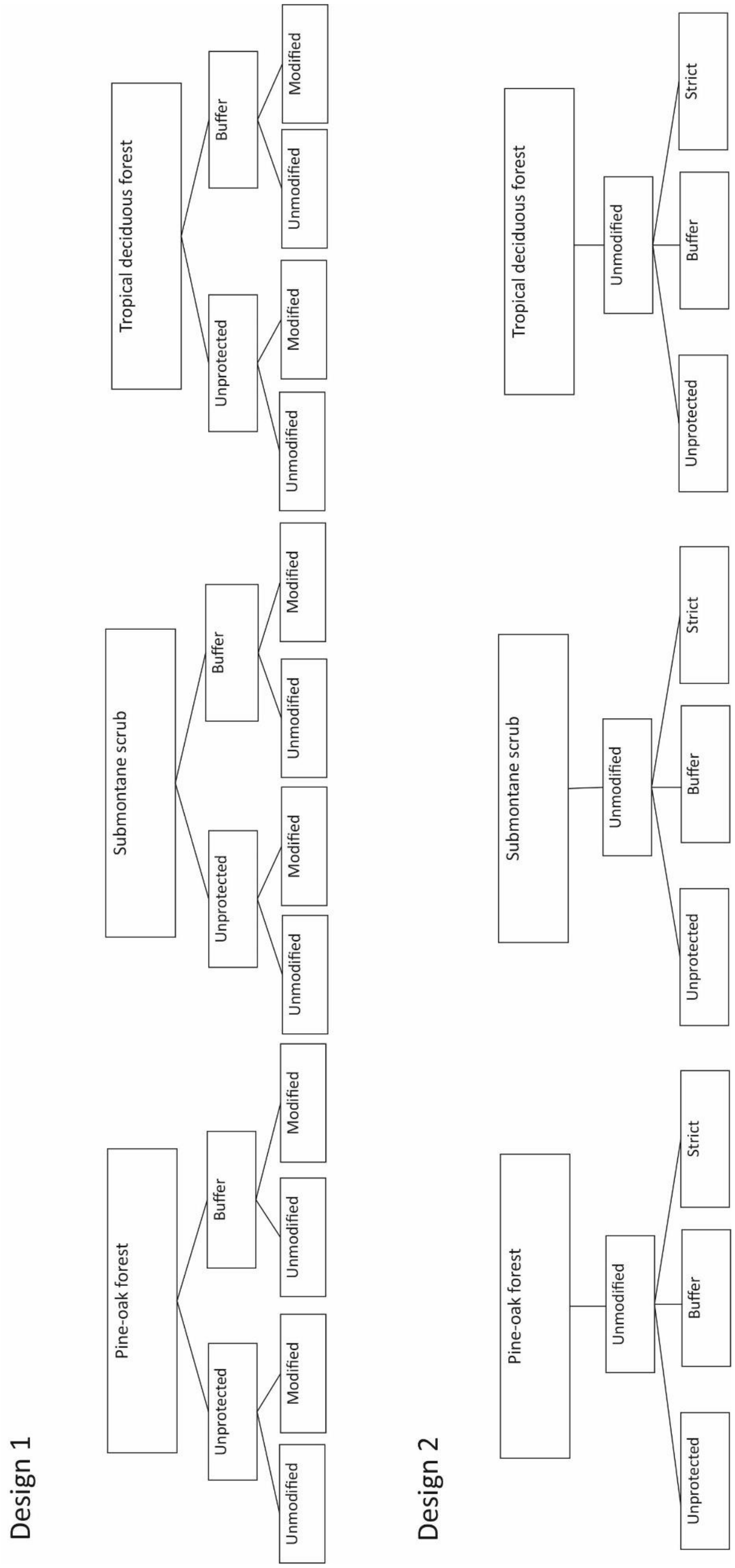
Category	Disturbances	Score Assigned
Urban	*Absent* – no evidence of buildings	0
	Light – scattered buildings	4
	Intense – concentrated buildings	8
Agriculture	*Absent* – no evidence of agricultural development	0
	Light – Some land cleared OR evidence of grazing OR scattered crop fields	4
	Intense – Concentrated crop fields OR pasture	9
Traffic	*Absent* – no roads	0
	Light – Minor Road (non paved)	2
	Intense – Major Road (paved)	4
Logging	*Absent* – no evidence of logging	0
	Light – Evidence of small scale logging/harvesting	2
	Intense – Evidence of large scale logging/harvesting	4
Other	Domestic Animals	1
	Tracks	1
	Rock Walls OR fences	1
	Pylons OR wires	1
	Litter	1
	Mining	8

References

Instituto Nacional de Estadistica y Geografia (INEGI) (2013) National Cluster of Current Land and Vegetation Use, scaled 1: 250,000, series V, INEGI. Mexico.

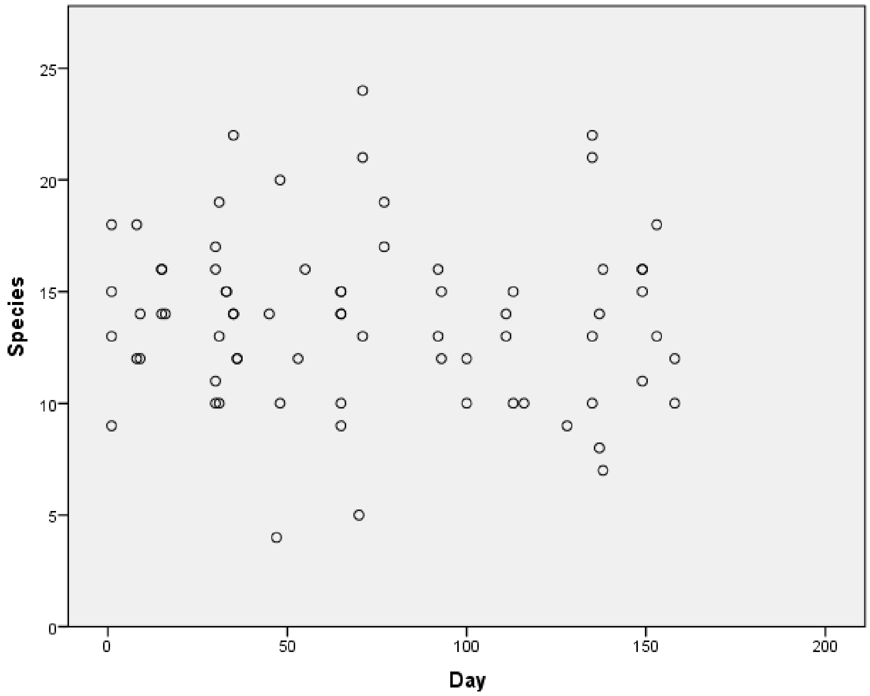
Murphy, G.E.P. & Romanuk, T.N. (2014) A meta-analysis of declines in local species richness from human disturbances. *Ecology and Evolution*, **4**, 91-103.

Appendix 3E Schematic showing the designs used for statistical analysis of data

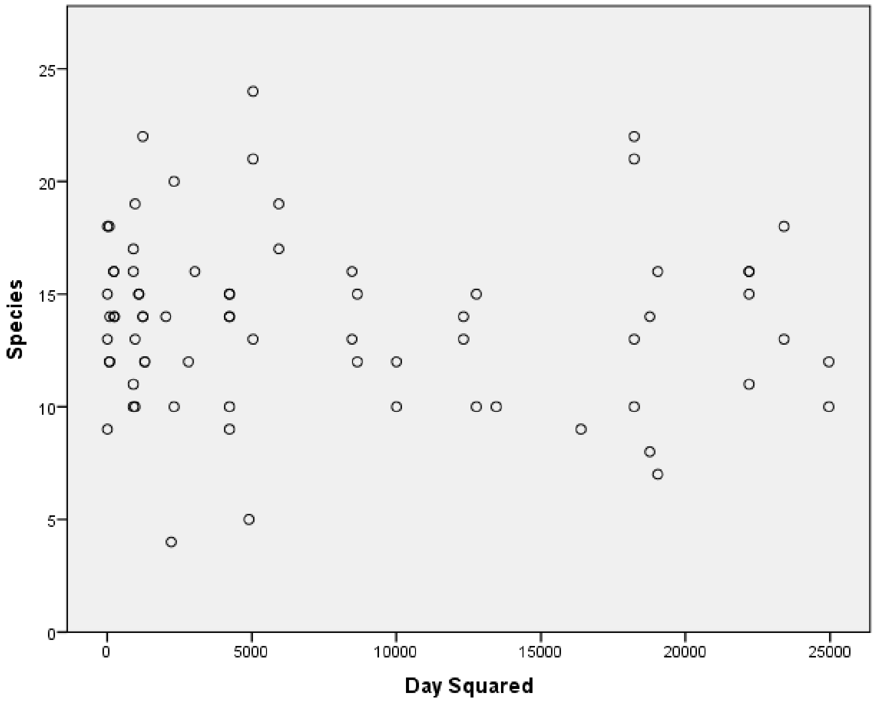


Appendix 3F Graphs showing the relationship between species richness and different predictor variables (see methods) within unprotected and buffer zone environments.

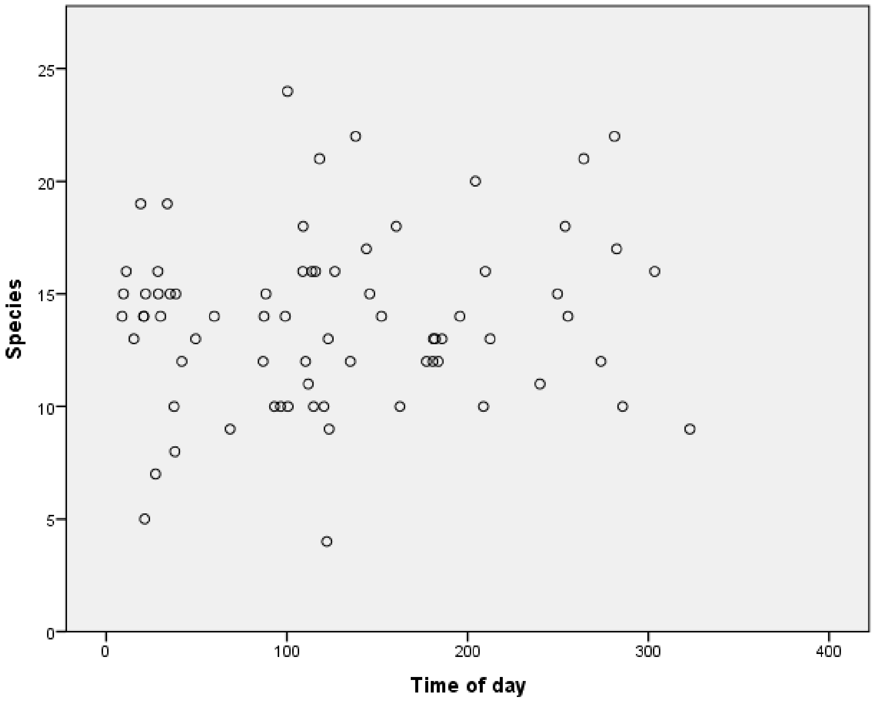
(a) Species Richness by Julian Day since start of study



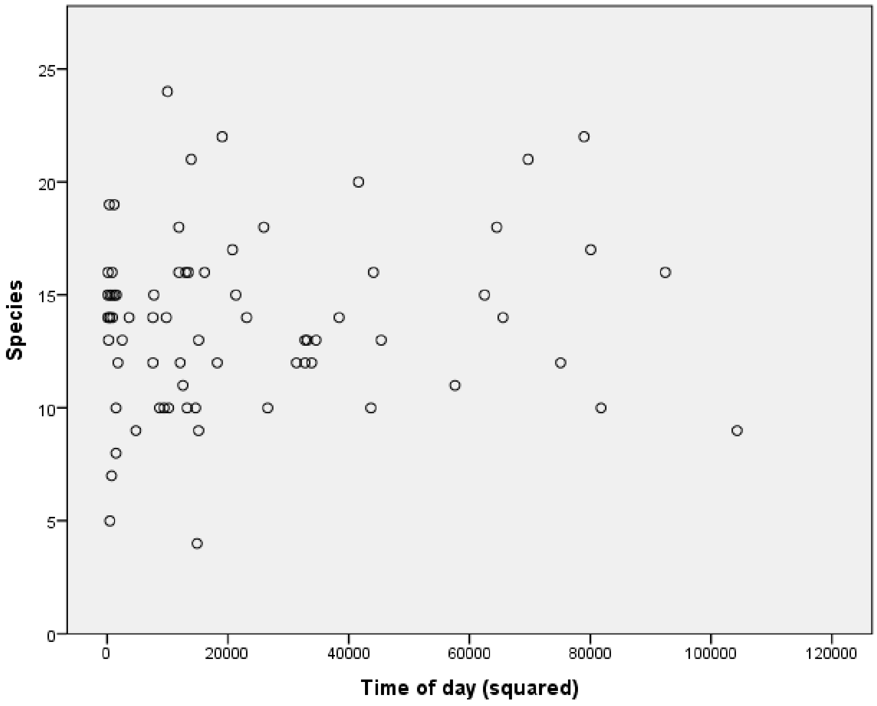
(b) Species richness against Julian Day (Squared) since start of study



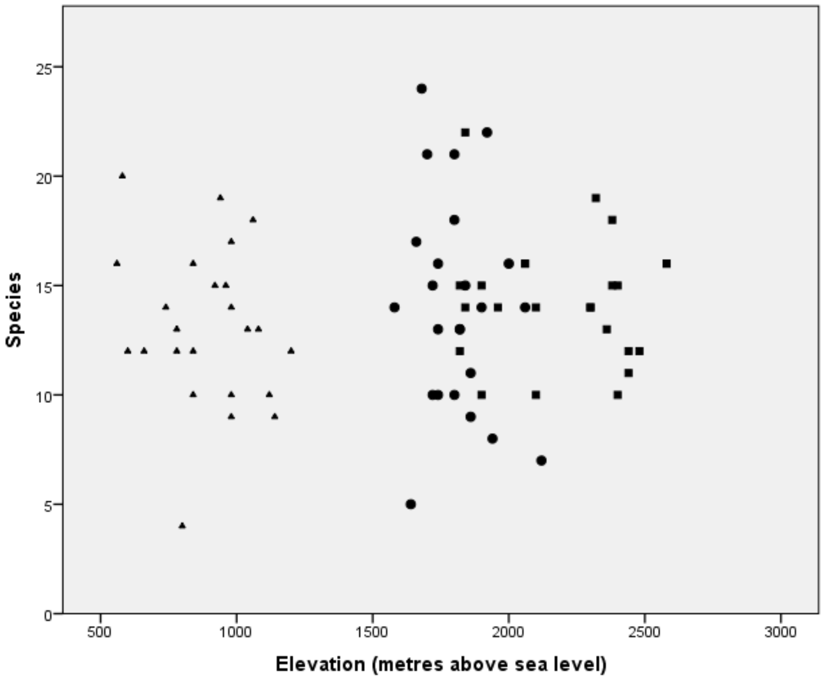
(c)Species richness against time of day (average number of minutes after sunrise of the four point counts)



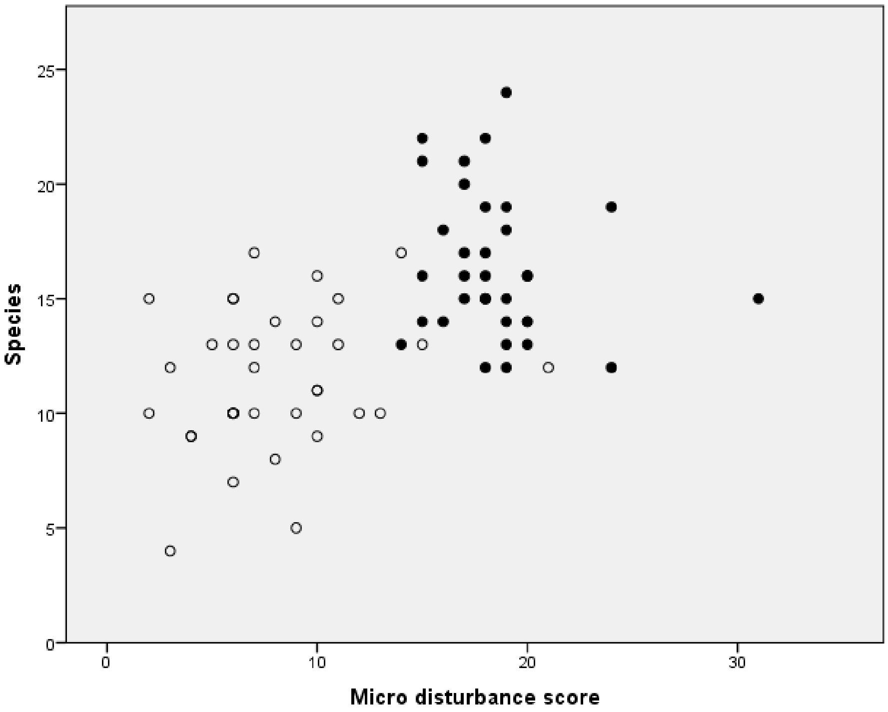
(d) Species richness against time of day (squared)



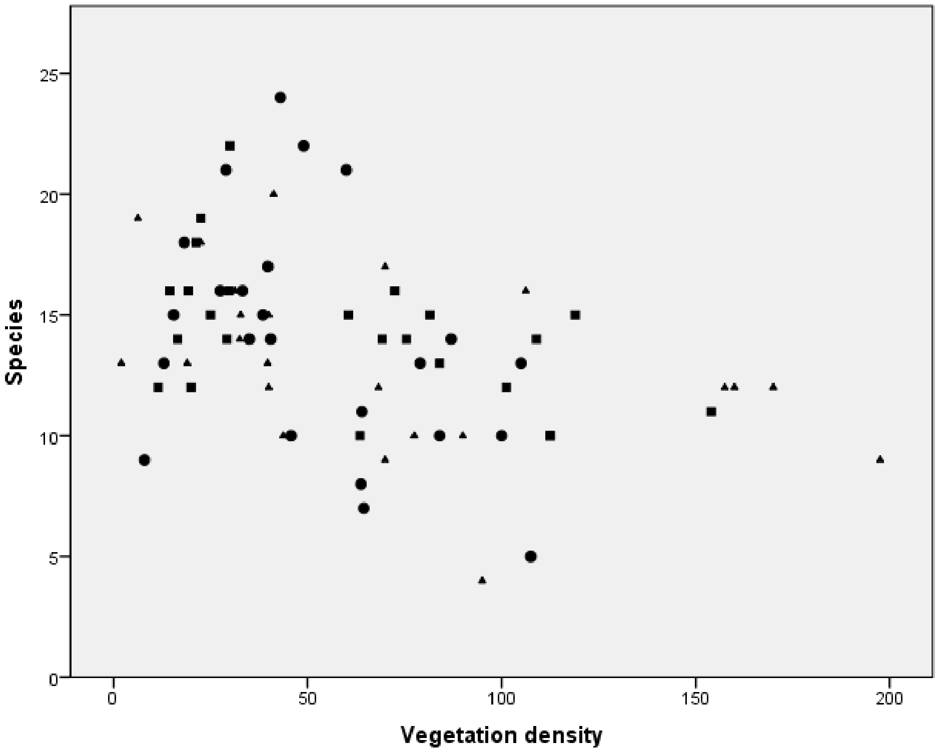
(e) Species richness against elevation in tropical deciduous forest (triangles), submontane scrub (circles) and pine-oak forest (squares).



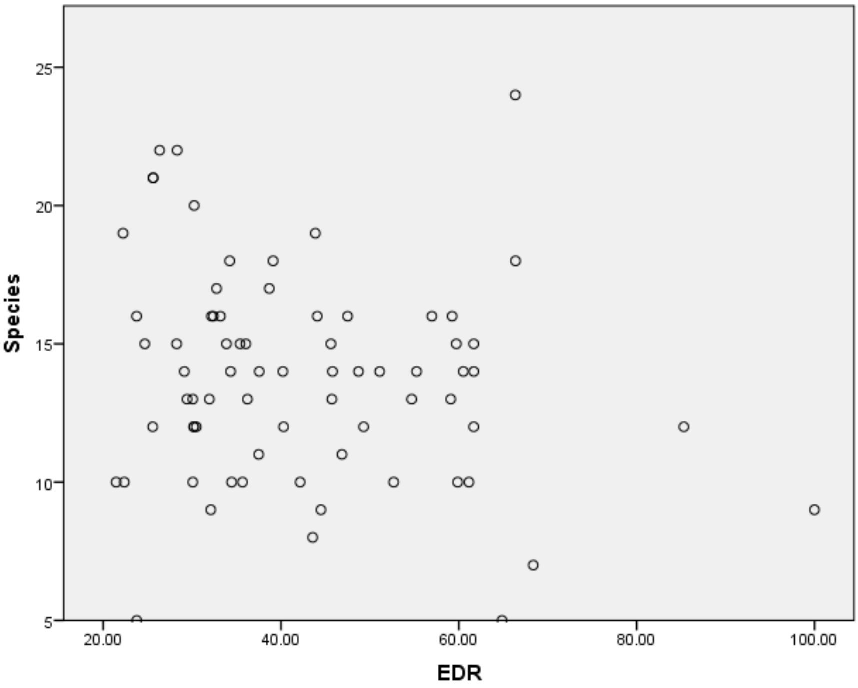
(f) Species richness against micro disturbance scores in modified (circles) and unmodified (open circles) squares.



(g) Species richness against vegetation density in tropical deciduous forest (triangles), submontane scrub (circles) and pine-oak forest (squares)



(h) Species richness against Effective Detecting Radius in all bioclimatic zones.



Appendix 3G Full results tables of models cited in the main text (excluding tables shown within the main text).

Generalised Linear Model testing the effects of bioclimatic zone, protection, disturbance and vegetation density on Effective Detection Radii for all squares. The model below had the lowest AICc value for any model combining the above factors and 2-way interactions. Other models had an AICc value within 2, but in none of them were any factors significant

	F	**df1,2**	**Sig.**
Corrected Model	1.749	8,80	.100
Fixed Factors			
Bioclimatic zone	1.227	2,80	.299
Protection level	1.186	2,80	.311
Modification	.954	1,80	.332
Bioclimatic zone*Modification	2.065	1,80	.133
Protection level*Modification	2.361	2,80	.128

Generalised Linear Mixed Model (GLMM) Classes 1-4 for observed species richness, excluding interaction terms.

	F	**df1,2**	**Sig.**
Corrected Model	13.220	4,67	<.001
Fixed factors			
Bioclimatic zone	.743	2,67	.480
Protection level	.915	1,67	.342
Habitat modification	50.479	1,67	<.001
Random factors			
Cluster			.455

GLMM (using a Poisson distribution with a log link) testing observed species per point as a dependent variable (design 2), with square as a random factor.

	F	**df1,2**	**Sig.**
Corrected Model	7.285	4,207	<.001
Fixed factors			
Bioclimatic zone	3.734	2,207	.026
Protection level	11.006	2,207	<.001
Random factor			
Square			.114

Appendix 3H Comparisons of similarity of community composition within bioclimatic zones within buffer and unprotected zones, and between buffer and unprotected zones. The non-significant results of the t-tests demonstrate that, if unprotected communities are compared with protected communities, composition is no more dissimilar than if communities within each level of protection are compared.

	Mean	*N*
Within Bioclimatic Zones (comparison of means of unique combinations of pairs)		
Pine-Oak		
Unmodified		
Within Buffer, within Unprotected	0.238	10
Between Buffer and Unprotected	0.242	6
t-test t_{14}=-0.172, *p*=0.866		
Modified		
Within Buffer, within Unprotected	0.222	10
Between Buffer and Unprotected	0.222	6
t-test t_{14}=-0.016, *p*=0.988		
Submontane Scrub		
Unmodified		
Within Buffer, within Unprotected	0.230	10
Between Buffer and Unprotected	0.182	6
t-test t_{14}=-1.058, *p*=0.308		
Modified		
Within Buffer, within Unprotected	0.311	10
Between Buffer and Unprotected	0.268	6
t-test t_{14}=-1.637, *p*=0.124		
Tropical Deciduous		
Unmodified		
Within Buffer, within Unprotected	0.215	10
Between Buffer and Unprotected	0.210	6
t-test t_{14}=0.300, *p*=0.769		
Modified		
Within Buffer, within Unprotected	0.282	10
Between Buffer and Unprotected	0.270	6
t-test t_{14}=0.701, *p*=0.495		

Appendix 3I Species observed in different bioclimatic zones and different classes of square (1 – unmodified buffer, 2 – modified buffer, 3 – unmodified unprotected, 4 – modified unprotected, 5 – nucleus zone).

Bioclimatic Zone	tropical deciduous forest					submontane-scrub					pine-oak forest				
Square Class	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Crypturellus cinnamomeus					✓										
Ortalis vetula			✓												
Callipepla squamata								✓							
Dactylortyx thoracicus															✓
Cathartes aura	✓	✓	✓	✓		✓	✓	✓		✓	✓	✓	✓	✓	
Coragyps atratus	✓	✓		✓							✓			✓	
Accipiter cooperii	✓	✓													
Buteo jamaicensis				✓			✓		✓					✓	
Columba livia									✓					✓	
Patagioenas fasciata											✓		✓		✓
Streptopelia decaocto									✓						
Columbina inca		✓		✓			✓		✓			✓			
Columbina passerina	✓					✓									
Leptotila verreauxi	✓				✓										
Zenaida macroura		✓	✓			✓			✓	✓		✓			
Zenaiada asiatica	✓	✓	✓	✓			✓	✓	✓						
Geococcux californianus										✓					
Strix virgate											✓				
Glaucidium gnoma											✓				
Athene cunicularia										✓					
Aeronautes saxatalis									✓	✓					
Cynanthus latirostris	✓	✓	✓	✓	✓	✓	✓	✓	✓						
Amazilia violiceps							✓								
Eugenes fulgens											✓	✓		✓	
Lampornis clemenciae												✓	✓	✓	
Basilinna leucotis											✓	✓	✓	✓	✓
Calothorax Lucifer	✓						✓			✓					
Archilochus colubris				✓		✓									
Trogon elegans					✓										
Trogon mexicanus											✓				✓
Momotus coeruliceps					✓										
Melanerpes formicivorus											✓	✓	✓	✓	
Melanerpes aurifrons		✓		✓			✓	✓	✓						
Sphyrapicus varius											✓				✓
Colaptes auratus					✓	✓		✓	✓			✓			
Picoides scalaris											✓				✓
Picoides villosus													✓		
Caracara cheriway		✓		✓											
Falco sparverius		✓					✓		✓			✓			
Falco rufigularis														✓	
Lepidocalaptes affinis											✓		✓		✓
Camptostoma imberbe	✓	✓	✓		✓	✓		✓							
Sayornis phoebe	✓	✓		✓											
Sayornis nigricans												✓			
Sayornis saya							✓	✓	✓						
Mitrephanes phaeocercus											✓		✓		
Contopus pertinax											✓				✓
Empidonax minimus	✓	✓	✓		✓										
Empidonax oberholseri						✓									
Empidonax affinis											✓		✓		
Pyrocephalus rubinus		✓		✓			✓	✓	✓			✓		✓	
Myiozetetes similis	✓	✓		✓											
Pitangus sulphuratus	✓	✓		✓	✓										
Megarhynchus pitangua		✓		✓	✓										
Tyrannus melancholicus		✓													
Tyrannus couchii		✓	✓	✓											
Tyrannus vociferans						✓				✓		✓		✓	
Myiarchus tuberculifer	✓		✓	✓	✓						✓				
Myiarchus cinerascens	✓		✓	✓		✓	✓	✓							
Myiarchus crinitus	✓		✓												
Myiarchus tyrannulus	✓														

Lanius ludovicianus									✓	✓					
Vireo griseus				✓											
Vireo plumbeus											✓				
Vireo cassinii							✓								
Vireo huttoni											✓			✓	
Cyanocorax luxuosus	✓	✓	✓	✓	✓								✓		
Cyanocitta stelleri															✓
Aphelocoma wollweberi											✓	✓	✓	✓	✓
Corvus imparatus		✓													
Corvus corax			✓	✓		✓	✓	✓	✓		✓	✓	✓	✓	
Ptilogonys cinereus					✓						✓		✓	✓	✓
Phainopepla nitens							✓		✓						
Baeolophus wollweberi															✓
Baeolophus atricristatus	✓	✓	✓	✓						✓					
Auriparus flaviceps			✓				✓	✓	✓						
Tachycineta thalassina								✓	✓	✓					
Stelgidopteryx serripennis			✓						✓						
Hirundo rustica								✓	✓			✓			
Psaltriparus minimus								✓			✓	✓		✓	
Regulus calendula						✓	✓				✓	✓	✓	✓	✓
Campylorhynchus gularis				✓			✓							✓	
Campylorhynchus brunneicapillus						✓	✓	✓	✓	✓					
Salpinctes obsoletus						✓	✓	✓	✓	✓					
Catherpes mexicanus	✓		✓	✓	✓	✓	✓	✓	✓	✓		✓			✓
Thryomanes bewickii						✓	✓	✓	✓	✓		✓	✓	✓	
Pheugopedius maculipectus		✓													
Troglodytes aedon	✓	✓	✓	✓			✓	✓	✓		✓	✓	✓		
Henicorhina leucophrys											✓				
Polioptila caerulea	✓	✓	✓	✓	✓	✓	✓	✓	✓		✓	✓	✓	✓	
Sitta carolinensis															✓
Certhia americana															✓
Dumetella carolinensis			✓												
Mimus polyglottos						✓	✓	✓	✓	✓					
Toxostoma longirostre			✓								✓				
Toxostoma curvirostre	✓	✓	✓			✓	✓		✓			✓		✓	
Melanotis caerulescens	✓	✓	✓	✓	✓										
Sturnus vulgaris									✓						
Sialia sialis												✓		✓	
Myadestes occidentalis					✓		✓				✓	✓	✓	✓	✓
Catharus aurantiirostris											✓				
Catharus occidentalis											✓		✓		
Catharus ustulatus											✓				
Catharus guttatus										✓	✓	✓		✓	✓
Turdus grayi		✓	✓	✓	✓										
Turdus assimilis											✓				
Turdus migratorius													✓	✓	✓
Passer domesticus				✓			✓		✓			✓		✓	
Haemorhous mexicanus				✓		✓	✓	✓	✓	✓		✓		✓	
Loxia curvirostra											✓				✓
Spinus psaltria				✓			✓	✓	✓			✓		✓	
Spinus pinus											✓				✓
Spinus notatus													✓		
Euphonia affinis	✓	✓	✓	✓											
Euphonia hirundinacea			✓												
Euphonia elegantissima				✓										✓	
Mniotilta varia	✓		✓									✓	✓		
Oreothlypis superciliosa											✓		✓		
Leiothlypis celata		✓	✓			✓	✓	✓	✓	✓			✓	✓	
Leiothlypis ruficapilla			✓		✓		✓								
Geothlypis trichas	✓	✓													
Setophaga pitiayumi					✓										
Setophaga auduboni		✓		✓		✓	✓	✓	✓	✓		✓	✓	✓	
Setophaga nigrescens							✓						✓		
Setophaga townsendi							✓				✓		✓	✓	✓
Setophaga occidentalis			✓								✓		✓	✓	✓
Basileuterus rufifrons	✓	✓	✓	✓	✓	✓	✓			✓		✓	✓	✓	
Basileuterus belli											✓		✓		✓
Cardellina pusilla	✓	✓	✓	✓	✓		✓		✓		✓	✓	✓	✓	✓
Cardellina rubrifrons															✓
Myioborus pictus											✓	✓	✓	✓	✓
Myioborus miniatus											✓			✓	✓

Icterus parisorum								✓				✓		✓	
Icterus graduacauda		✓	✓		✓							✓		✓	
Icterus gularis		✓													
Icterus bullockii											✓				
Icterus abeillei							✓					✓			
Icterus wagleri				✓			✓	✓	✓						
Icterus cucullatus	✓	✓		✓											
Molothrus aeneus		✓		✓											
Quiscalus mexicanus		✓		✓					✓					✓	
Melospiza lincolnii			✓			✓	✓		✓	✓		✓		✓	
Junco phaeonotus												✓		✓	
Spizella passerina						✓	✓		✓			✓		✓	
Spizella atrogularis							✓	✓							
Spizella pallida							✓	✓	✓	✓					
Pooecetes gramineus								✓							
Chondestes grammacus		✓		✓		✓	✓	✓	✓			✓			
Amphispiza bilineata								✓							
Aimophila ruficeps								✓		✓					
Pipilo maculatus											✓	✓	✓	✓	✓
Melozone fusca							✓	✓	✓	✓		✓		✓	
Arremonops rufivirgatus												✓			
Atlapetes pileatus											✓	✓	✓	✓	
Chlorospingus flavopectus													✓		✓
Thraupis palmarum		✓		✓											
Diglossa gloriosissima												✓			
Tirias olivaceus			✓	✓											
Piranga bidentata					✓										
Piranga hepatica											✓	✓	✓	✓	✓
Piranga rubra	✓	✓	✓		✓										
Piranga ludoviciana					✓										
Pheucticus melanocephalus				✓						✓				✓	
Cardinalis cardinalis	✓	✓	✓	✓											
Cardinalis sinuatus				✓											
Passerina caerulea							✓								
Passerina cyanea							✓								
Passerina versicolor						✓	✓								

Appendix 3J Table of means for species richness.

	n	Mean	Standard Error
All bioclimatic zones	89	12.90	0.46
Modified (all)	36	16.33	0.52
Unprotected	18	15.23	0.51
Buffer	18	17.39	0.84
Unmodified (all)	53	10.57	0.46
Unprotected	18	11.72	0.68
Buffer	18	11.33	0.78
Strict	17	8.53	0.74
Unprotected (all)	36	13.50	0.51
Buffer (all)	36	14.36	0.76
Pine-oak forest (all)	30	13.63	0.60
Modified (all)	12	15.92	0.81
Unprotected	6	14.83	0.98
Buffer	6	17.00	1.21
Unmodified (all)	18	12.11	0.63
Unprotected	6	12.33	0.95
Buffer	6	14.00	0.97
Strict	6	10.00	0.73
Unprotected (all)	12	13.58	0.75
Buffer (all)	12	15.50	0.60
Submontane scrub (all)	30	12.67	0.96
Modified (all)	12	17.92	0.98
Unprotected	6	15.50	0.76
Buffer	6	20.33	1.15
Unmodified (all)	18	9.17	0.70
Unprotected	6	10.17	1.14
Buffer	6	10.33	1.20
Strict	6	7.00	0.93
Unprotected (all)	12	12.83	1.04
Buffer (all)	12	15.33	1.70
Tropical deciduous forest (all)	30	12.38	0.76
Modified (all)	12	15.17	0.75
Unprotected	6	15.50	1.02
Buffer	6	14.83	1.17
Unmodified (all)	17	10.41	0.92
Unprotected	6	12.67	1.31
Buffer	6	9.67	1.28
Strict	5	8.60	2.01
Unprotected (all)	12	13.50	0.51
Buffer (all)	12	14.36	0.76

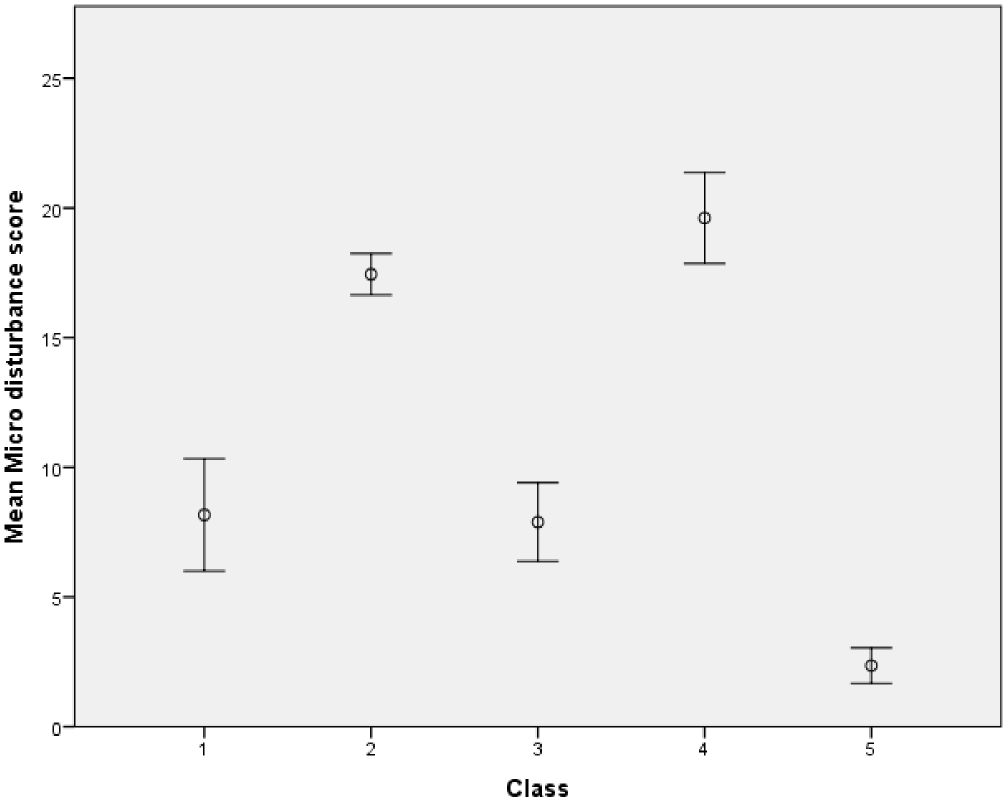
Appendix 3K Synoptic results of GLMMs (design 1) using estimated, instead of observed, species richness as a dependent variable.

Model used for estimated species richness	**Fixed factor**	**Significance Level**
Chao1	Modification	<.001
Chao1bc	Modification	<.001
ACE	Modification	<.001
ACE1	Modification	<.001
Jackknife1	Modification	<.001
Jackknife2	Modification	<.001

Appendix 3L Table showing the mean 'global population trend' of all species recorded per square. Individual species were assigned -1 (declining), 0 (stable) or +1 (increasing) and the mean of these scores calculated per square.

	N	Mean	Standard Error
All bioclimatic zones	89	0.11	0.03
Modified (all)	36	0.22	0.03
Unprotected	18	0.19	0.06
Buffer	18	0.24	0.04
Unmodified (all)	53	0.03	0.03
Unprotected	18	0.10	0.06
Buffer	18	0.11	0.04
Strict	17	-0.12	0.05
Unprotected (all)	36	0.14	0.04
Buffer (all)	36	0.18	0.03
Pine-oak forest (all)	30	0.06	0.03
Modified (all)	12	0.17	0.04
Unprotected	6	0.18	0.08
Buffer	6	0.16	0.03
Unmodified (all)	18	-0.02	0.04
Unprotected	6	0.05	0.08
Buffer	6	-0.02	0.09
Strict	6	-0.10	0.04
Unprotected (all)	12	0.12	0.06
Buffer (all)	12	0.07	0.05
Submontane scrub (all)	30	0.01	0.04
Modified (all)	12	0.07	0.05
Unprotected	6	0.02	0.10
Buffer	6	0.12	0.02
Unmodified (all)	18	-0.03	0.05
Unprotected	6	-0.03	0.11
Buffer	6	0.15	0.04
Strict	6	-0.21	0.04
Unprotected (all)	12	-0.00	0.07
Buffer (all)	12	0.14	0.02
Tropical deciduous forest (all)	30	0.26	0.05
Modified (all)	12	0.41	0.04
Unprotected	6	0.37	0.06
Buffer	6	0.45	0.05
Unmodified (all)	17	0.15	0.07
Unprotected	6	0.26	0.09
Buffer	6	0.20	0.07
Strict	5	-0.05	0.16
Unprotected (all)	12	0.31	0.05
Buffer (all)	12	0.32	0.06

Appendix 3M Levels of micro-disturbance in different classes of square (1 – unmodified buffer, 2 – modified buffer, 3 – unmodified protected, 4 – modified protected, 5 strict).



Appendix 4 – Supporting Information for Chapter 5

Appendix 4A Process for extracting breeding bird lists.

When regional sources were not available, we used distribution maps of bird species from BirdLife International (2012) in order to generate breeding bird lists for geographical entities. We used the mapping software ArcGIS version 10.4.1 (ESRI, 2015), and followed the following process:

1. Shapefiles for all extant bird species were combined using the ‘merge’ function.
2. Using the ‘select’ function, we reduced this new combined shapefile to just include areas where bird species were ‘Resident’ or present during ‘Breeding Season’.
3. Geographical outlines of particular entities were found by selecting from a shapefile of global boundaries.
4. We used the ‘identity’ function to generate the list of bird species (already selected for by seasonality) with ranges that included any particular entity.

References

BirdLife International and NatureServe (2012) *Bird species distribution maps of the world.* Version 2.0. BirdLife International, Cambridge, UK and NatureServe, Arlington, USA.

ESRI (2015) ArcVie GIS, version 3.1. Environmental Systems Research Institute Inc., Redlands, California, USA.

Appendix 4B Sources of Data for Introductions and Extirpations.

Entity	Source for Baseline Breeding Bird Lists	Literature Consulted for Introductions, Exirpations and Colonisations*	Expert
Afghanistan	Bird Life	Ayé *et al*., 2012	Raffael Ayé
American Samoa	Watling, 2016	Watling, 2004; Watling 2016	Dick Watling
Angola	Bird Life	Mills & Melo, 2013	Michael Mills
Argentina	Remsen *et al.,* 2016	Remsen *et al.*, 2016;	Juan Ignacio Areta
Armenia	EBCC	Avibase	Vasil Ananian
Aruba	Remsen *et al.,* 2016	Prins *et al.*, 2009; Remsen *et al.*, 2016	Remsen *et al*., 2016
Australia	Garnett *et al.,* 2015	Slater, 2009; Garnett *et al.*, 2015	Stephen Garnett Guy Dutson
Austria	EBCC	Ranner, 2014	Norbert Teufelbauer
Azerbaijan	EBCC	Avibase	Elchin Sultanov
Azores	Rodebrand, 2012	Rodebrand, 2012	Joel Bried
Bahrain	King, 2006	Hawar Islands, 2006	Howard King
Belarus	EBCC	Belarus Bird List, 2015	Alexandre Vintchevski
Belize	Bird Life	Howell & Webb, 1995	Lee Jones
Bolivia	Remsen *et al.,* 2016	Remsen *et al.,* 2016	Bennett Hennessey
Bosnia and Herzegovina	EBCC	Avibase	Branislav Gasic
Brazil	Remsen *et al.,* 2016	Remsen *et al.,* 2016	Pedro Develey
Bulgaria	EBCC	BUNARCO, 2009	Nikolay Petkov
Cambodia	Bird Life	Avibase	Frederic Goes
Canada	Bird Life	Sibley, 2000	Andrew Couturier
Canary Islands	EBCC	Clarke & Collins, 1996	Juan Antonio Lorenzo
Cayman Islands	Bradley & Rey-Millet, 2013	Bradley & Rey-Millet, 2013	Patricia Bradley
Chad	Dowsett *et al.,* 2016a	WABDAB, 2017	Joost Brouwer
Chile	Remsen *et al.,* 2016	Jaramillo, 2003; Remsen *et al.,* 2016	Alvaro Jaramillo
China	Bird Life	CBR, 2013	Yang Liu
Colombia	Remsen *et al.,* 2016	Remsen *et al.,* 2016	Thomas Donegan
Comoros	Bird Life	Dowsett *et al.,* 2016b	Michel Louette
Costa Rica	Garrigues *et al.,* 2015	Avibase	Jim Zook
Croatia	EBCC		Ivan Budinski
Cuba	Bird Life	Garrido *et al*., 2000	Patricia Bradley
Curaçao	Remsen *et al.,* 2016	Prins *et al.,* 2009; Remsen *et al.* 2016	Remsen *et al.* 2016
Cyprus	EBCC	Flint & Stewart, 1992	Martin Hellicar
Czech Republic	EBCC		Jiri Flousek
Denmark	EBCC	Netfugl, 2016	Knud Flensted
Djibouti	Bird Life	Dowsett *et al.,* 2016c	Houssein A. Rayaleh

Ecuador	Remsen *et al.,* 2016	Ridgeley & Greenfield, 2001; Remsen *et al.,* 2016	Juan Freile Ortiz
El Salvador	Bird Life	Howell & Webb, 1995	Oliver Komar
Estonia	EBCC	CNCEAS, 2008	Jaanus Elts
Fiji	Watling, 2016	Watling, 2004	Dick Watling
Finland	EBCC	Rassi *et al*., 2010.	Aleksi Lehikoinen
France	EBCC	UICN, 2016	Frederic Jiguet
French Guiana	Remsen *et al.,* 2016	Remsen *et al,* 2016	Remsen *et al.* 2016
Galapagos	Wiedenfeld, 2006	Wiedenfeld, 2006	Juan Freile Ortiz
Germany	EBCC	Sudbeck *et al.,* 2007; Bauer & Woog, 2008	Martin Flade
Greece	EBCC	Michalis *et al*., 2009	George Handrinos
Greenland	EBCC	Boertmann, 1984	David Boertmann
Guinea	Dowsett *et al.,* 2016d	Dowsett *et al.,* 2016d	Ron Demey
Guyana	Remsen *et al.,* 2016	Remsen *et al.,* 2016	Remsen *et al.* 2016
Hawaii	Pyle & Pyle, 2017	Pyle & Pyle, 2017	Pyle & Pyle 2017
Honduras	Bird Life	Howell & Webb, 1995	Oliver Komar
Hong Kong	HKBWS, 2015	HKBWS, 2015	Yat-tung Yu
Hungary	EBCC		Tibor Szép
Iceland	EBCC	Pétursson, 2008	Gudmundur A. Gudmundsson
India	Bird Life	OBC, 2016	Raju Kasambe
Iran	Scott & Adhami, 2006	Scott & Adhami, 2006, OSME, 2017	Derek Scott
Iraq	Bird Life	Ararat *et al.,* 2011	Richard Porter
Israel	Bird Life	Israbirding.com	Yoav Perlman
Italy	EBCC	Brichetti & Massa, 1995	Lorenzo Fornasari
Japan	Bird Life	Kantori Group, 2017	Mark Brazil
Jordan	Bird Life	OSME, 2017	Nashat Hamidan
Kazakhstan	Bird Life	Ayé *et al*., 2012	Raffael Ayé
Kenya	Bird Life	Dowsett *et al.,* 2016e,	Kairuki Ndanganga
Kuwait	Bird Life	OSME, 2017	Mike Pope
Latvia	EBCC	Avibase	Ainar Ainarsen
Luxembourg	EBCC	Bastian & Lorgé, 2014	Patric Lorgé
Macedonia	EBCC	Avibase	Metodija Velevski
Madagascar	Bird Life	Dowsett *et al.,* 2016f	Roger Sifford
Madeira		Madeira SW, 2006	Catarina Correia-Fagundes
Malaysia Bornean	MNS, 2015	MNS, 2015	Yeap Chin Aik
Malaysia Peninsular	MNS, 2015	MNS, 2015	Yeap Chin Aik
Mexico	Berlanga *et al*., 2015	Howell & Webb, 1995	Hector Gomez de Silva, Rick Erickson
Mongolia	Bird Life		Nyambyar Batbayar
Morocco	Atkinson & Caddick, 2017a	Atkinson & Caddick, 2017a, Bergier & Bergier, 2003	Imad Cherkaoui
Mozambique	Dowsett *et al.,* 2016g	Ryall, 2016; Dowsett *et al.,* 2016g	Gary Allport
Nepal	Bird Life	Baral *et al*., 2012	Ishana Thapa

Netherlands	EBCC	Van den Berg, 2016	Chris Van Turnhout
New Caledonia	Watling, 2016	Watling, 2016	Guy Dutson
New Guinea	Gregory, 2008	Gregory, 2008	Guy Dutson
New Zealand	NZBO, 2013	NZBO, 2013	Colin Miskelly
Nicaragua	Bird Life	Howell & Webb, 1995	Liliana Cahavarria-Duriaux
Niger	Dowsett *et al.*, 2016h	WABDAB, 2017; Dowsett *et al.*, 2016h	Joost Brouwer
Nigeria	Dowsett *et al.*, 2016i	Dowsett *et al.,* 2016i	Joseph Onoja
Norway	EBCC	Birding Norway, 2001	Husby Magne
Oman	Bird Life	Birds Oman, 2016; OSME 2017	Jens Eriksen
Paraguay	Remsen *et al.*, 2016	Remsen *et al.,* 2016	Rob Clay
Peru	Remsen *et al.*, 2016	Schultenberg *et* al., 2010; Remsen *et al.,* 2016	Remsen *et al.* 2016
Poland	EBCC	CLANGA, 2016	Przemyslaw Chylarecki
Portugal	EBCC	Elias, 2017	João E. Rabaça
Qatar	QBRC, 2017	QBRC, 2017	Gavin Farnell
Republic of Ireland	EBCC	IRBC, 2015	Stephen Newton
Romania	EBCC	Avibase	Sandor Attila
Russia	Bird Life	Koblik *et al*., 2006	Alexander MIschenko
Samoa	Watling, 2016	Watling, 2004	Dick Watling
Serbia	EBCC	Avibase	Milan Ruzic
Singapore	NSS, 2011	NSS, 2011	Kim Keang
Somalia	Bird Life	Dowsett *et al.,* 2016j	John Miskell
South Africa	Dowsett *et al.,* 2016k	Dowsett *et al.,* 2016k	Peter Ryan
Spain	EBCC	Paterson & Garcia, 2008; Muddeman & Villa, 2016	Ernest Garcia
Sri Lanka	Bird Life	Avibase	Rahula Perera
Suriname	Remsen *et al.,* 2016	Remsen *et al.,* 2016	Otto Ottema
Sweden	EBCC	Haas *et al.,* 2014	Åke Lindström
Switzerland	EBCC	Sattler *et al*., 2016	Hans Schmid
Syria	Bird Life	Murdoch & Betton, 2008	David Murdoch
Taiwan		Tzung-Su *et al*., 2012	Woei-horng Fang
Thailand	Bird Life	Robson, 2002	Phillip Round
Tonga	Watling, 2016	Watling, 2004	Dick Watling
Trinidad and Tobago	Remsen *et al.,* 2016	Remsen *et al.,* 2016	Remsen *et al.* 2016
Turkey	EBCC	Green & Moorhouse, 1995	Süreyya Isfendiyaroglu
Uganda	Dowsett *et al.,* 2016l	Dowsett *et al.,* 2016l	Derek Pomeroy
Ukraine	EBCC	Grischenko, 2004	Igor Gorban
United Arab Emirates	Pedersen *et al*., 2017	Pedersen *et al*., 2017	Oscar Campbell
United Kingdom	EBCC	Svensson, 2010	Mark Holling
USA	Bird Life	Sibley, 2000	Timothy Brush, Bill Pantry
Uruguay	Remsen *et al.,* 2016	Remsen *et al.,* 2016	Remsen *et al.* 2016
Venezuela	Remsen *et al.,* 2016	Remsen *et al.,* 2016	Chris Sharpe

Wallis and Futuna	Watling, 2016	Watling, 2004; Watling 2016	Dick Watling
Western Sahara	Atkinson & Caddick, 2017b	Bergier & Bergier, 2003; Atkinson & Caddick, 2017b	Imad Cherkaoui

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Appendix 4C Alternative sources of information for predictor variables and missing predictor variables.

- Information on Land Use Change was not available for the following entities: Azores, Canary Islands, French Guiana, Galapagos Islands, Hawaiian Islands, Madeira, Taiwan, Wallis and Futuna.
- For the following entities, Land Use data for 1965 was not available, and so land use change was calculated from later dates (shown in brackets): Armenia, Azerbaijan, Croatia, Bosnia-Herzegovina, Belarus, Estonia, Russia, Macedonia (all 1992), Belarus, Czech Republic (both 1993), Luxembourg (2000) and Serbia (2006).
- Alternative sources of information for GDP were used for the following entities: Cayman Islands, Bolivia, Curaçao, Wallis and Futuna, American Samoa (all CIE World Factbook – cia.gov), Hawaii, Greenland, New Guinea, Taiwan, Western Sahara, New Caledonia (all worldatlas.com), Syria, Wallis and Futuna, Aruba (Google.com), Galapagos (Ecuador equivalent), American Samoa (bea.gov).
- For Imports, PA% and Government Effectiveness, the following entities were assigned the scores of their 'parent' countries (in brackets): Canary Islands (Spain), Azores and Madeira (Portugal), Galapagos (Ecuador), Western Sahara (Morocco), Wallis and Futuna (France), Hawaii (USA), Taiwan (China).
- For Imports, 2015 information was not available for the following countries, so we used information from different years (in brackets): Comoros, Iran (both 2014), Cuba, Thailand (both 2013)
- For Peninsular and Bornean Malaysia, predictor variables for the country Malaysia were assigned to both, apart from Connectivity (not available).
- Values for Connectivity were also missing for Russia, continental USA, Aruba and Curaçao.

Appendix 4D Process for calculating connectivity of entities.

To calculate the amount of land within 200km of each entity, we used the mapping software ArcGIS version 10.4.1 (ESRI, 2015), and followed the following process:

1. Individual entities were selected from a shapefile of world boundaries.
2. The ‘buffer’ function was used with a range of 200km specified to create a 200km buffer zone around the boundary of each entity.
3. The amount of land within the buffer area was calculated.
4. The area of the entity in question was subtracted from the total amount of land within the buffer area.

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Appendix 4E Correlation matrix (Pearson's R-squared) of predictor variables.

	Size of Avifauna	PA%	Government Effectiveness	GDP	Land Area	Protected Area	Land Use Change	Population	Connectivity	Imports
Size of Avifauna	1	.039	-.339**	.319**	.585**	.544**	-.013	.534**	.388**	.148
PA %		1	.133	.041	-.061	.276**	.123	-.218*	-.052	.133
Government Effectiveness			1	.360**	-.248**	-.114	.031	-.117	-.220*	.533**
GDP				1	.568**	.573**	.008	.781**	.440**	**.840****
Land Area					1	.899**	-.059	.763**	.529**	.430**
Protected Areas						1	.049	.646**	.466**	.495**
Land Use Change							1	.048	-.040	-.012
Population								1	.540**	.617**
Connectivity									1	.244**
Imports										1

Appendix 4F Results of independent t-tests comparing values of predictor variables (see Methods) in well-observed countries and in less-well observed entities.

Imports: $t_{44,72}$=-7.26 , P<0.001

Land Use Change: $t_{41,68}$=-0.15, P=0.88

Population: $t_{44,72}$=3.72, P<0.001

Isolation: $t_{44,72}$=0.31, P=0.78

Government Effectiveness: $t_{44,71}$=5.42, P<0.001

Area: $t_{44,72}$=2.34, P=0.02

Protected Areas: $t_{44,72}$=3.02, P=0.003

PA%: $t_{44,72}$=0.77, P=0.44

Size of Avifauna: $t_{44,72}$=1.91, P=0.059

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