How extirpations, colonizations and introductions of bird species typically alter the regional diversity, distinctiveness, and body size distribution of regional bird biota

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Abstract

Much research in recent decades has been dedicated to investigating the effects of the anthropogenically-driven factors on the Earth's biodiversity, evaluating which taxa are most at risk, and researching how to mitigate these effects. Species assemblages are shifting in response to human activities, with large-bodied species historically most at risk due to human overexploitation as well as intrinsic life history traits.

To investigate how avian communities are changing because of the Anthropocene, I analyzed the data of 10820 avian species in 105 regions from 1815 to 2015. I measured median body mass on a regional scale both as an indication of faunal assemblage change and as a way of determining if large-bodied species are still predominantly at risk. I found that regions are becoming more diverse within themselves, and more similar between themselves, with no change in median body mass, and a less diverse distribution of body masses. Although extirpations were predominantly larger-bodied species, arriving (introduced and colonizing) species were also significantly larger than surviving species. Through an increase in regional diversity, driven by arriving species, bird assemblages are changing in body mass distribution but not median mass despite the continuing extirpation of large-bodied species. There is still potential functional loss in assemblages as the largest species are lost and not replaced by similarly-sized species. Conservation efforts should focus on replacing lost ecosystem functionality by rewilding extirpated species or replacing with similarly-sized species if they have become globally extinct.

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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), Jonathan Hiley (JH), and Jonathan Hiley's RSPB supervisor, Richard Bradbury (RB).

The thesis is currently in preparation for submission as:

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

1 Introduction

Human activities are indisputably changing the world we live in (Barnosky et al., 2012; Bennett, 2016; Lenton et al., 2008; Rockström et al., 2009). In what has been defined as the Anthropocene, or the era in which humans are the greatest driving force of environmental and ecological change (Crutzen, 2002), biotas on both land and sea are shifting in response to these activities at an unprecedented scale (Collen et al., 2009; Costello, 2015; González-Suárez & Revilla, 2013; Halpern et al., 2008; Huang, Pang, Yang, Zhang, & Guo, 2011; McCauley et al., 2015; Mieszkowska, Sugden, Firth, & Hawkins, 2014; Parmesan & Yohe, 2003; Vitousek, Mooney, Lubchenco, & Melillo, 2008; Wong & Candolin, 2015). The current debate in biodiversity is moving from a loss-only perspective to a discussion of changes in biodiversity trends, requiring us to understand patterns of loss and gain at a global scale, and eventually a more local scale. Many authors have dedicated themselves in recent times to cataloguing the changes, which are happening in a multitude of directions and magnitudes (Ceballos et al., 2015; Ceballos, Ehrlich, & Dirzo, 2017; Craigie et al., 2010; Dornelas et al., 2014; Ellis, McWhorter, & Maron, 2012; Gray et al., 2016; Hiley, Bradbury, Holling, & Thomas, 2013; Jenkins, Pimm, & Joppa, 2013; McGill, Dornelas, Gotelli, & Magurran, 2015; Newbold et al., 2015; Sax & Gaines, 2003; Sax, Gaines, & Brown, 2002; Tassin, Thompson, Carroll, & Thomas, 2017; Vellend et al., 2013, 2017). Most of these changes are typically viewed unfavourably (Roy et al., 2014; Simberloff & Von Holle, 1999; Tassin et al., 2017). For example, many of the newly arriving species are perceived as damaging invasive species, while many of the local extirpated species' ecological functions are lost. However, there is a lot of variation around the perception of biodiversity trends depending on the chosen metric of biodiversity change. For instance, which assemblage is preferred to use as a baseline comparison, one from 200 or 2000 years ago, varies from author to author. Preferences between newly-arrived or longer established species can differ as well (Davis et al., 2011; Russell & Blackburn, 2017; Tassin et al., 2017). Therefore, some authors underline the potential harm caused by invasive species and emphasize the potential loss of function and beta diversity, whereas others show that distribution changes increase regional diversity and offer a way to track response to climate change, as species move to cope with changing climates and habitats

(Tassin et al., 2017). In this thesis, I discuss and analyze the changes caused by the Anthropocene to avian species specifically in 105 regions (any geographically and faunally distinct area of land), looking at regional faunal similarity on a global scale as a measure of beta diversity, and regional diversity as a measure of alpha diversity. I analyze these factors that might affect avian species in those regions, separated both into island and mainland regions as well as analyzing together. I use body mass as a metric by which to measure assemblage change, and to determine if larger-bodied species are being threatened in the present day as they have been in the past.

The Anthropocene is causing a range of both losses (Dirzo et al., 2014)and gains in species richness in various directions and magnitudes across the world (Dornelas et al., 2014). While results vary within and between taxa, the common factor is that there are negative and positive results across the board (Dornelas et al., 2014; Johnson et al., 2017; McGill et al., 2015) from global to granular levels. Much of the focus of research has been on how human impacts are quickly outstripping the balance of natural selection, causing a disruption to the diverse faunal assemblage (Brook & Bowman, 2005). Understanding the different factors driving extinction risk for different taxa is crucial to conservation efforts (Brown, 2007). Direct threats such as overexploitation (Sandom, Faurby, Sandel, & Svenning, 2014) as well as indirect threats such as habitat loss and climate change (Stork, 2010) have been demonstrated to cause what has been termed a global 'defaunation', a wave of species extinction comparable to past mass extinction events (Dirzo et al., 2014). However, species are not unimodal in their response to anthropogenic disturbance (Lees & Peres, 2008). For example, many types of habitat are destroyed to provide space for farmland or urban landscape, forcing the species present to adapt, move, or die out (Ogutu, Owen-Smith, Piepho, & Said, 2011). As human activities cause alterations in type of habitat, habitat diversity increases while species are forced to leave or go extinct (Sumasgutner, Schulze, Krenn, & Gamauf, 2014). However, this process helps natural colonists, such as the cattle egret (*Bubulcus ibis*) (Blaker, 1971) and the Eurasian collared dove (*Streptopelia decaocto*) (Hudson, 1972) as they have been demonstrated to show a preference for modified habitat. Climate change, which causes disruptions and habitat loss for many species, can also be an agent of beneficial change for species which benefit from an increase in rainfall and temperate (Walther et al., 2009). All in all, anthropogenic disturbance obviously has detrimental effects on faunal assemblages, but also provides opportunities for colonization (Hiley et al., 2013). Even as species are irreplaceably lost causing global decreases in diversity (Jenkins et al., 2013), new species movement drives regional increases in species diversity – this holds true for diverse taxa (Jackson & Sax, 2010; Vellend et al., 2013). My findings indicate no shift in global biodiversity, as global species extinctions are countered by increases on a regional scale. Many different regions may be experiencing the arrival of the same small group of species which benefit from human activity, resulting in regions becoming more faunally similar as they become more diverse within themselves. This constant fluctuation requires understanding the nuances between arrivals and disappearances or species rather than simply net loss or gain (Dornelas et al., 2014).

While the Anthropocene affects species of all sizes (Dirzo et al., 2014), there is certainly a non-random pattern to the losses and gains. Just as with mammals and other vertebrate taxa such as amphibians (McCallum, 2007), avian species have experienced a size-specific extinction event resulting in a selection of fauna being most affected. Small geographic range size, large body size, large home range size, and low reproductive rates are all linked to a higher extinction risk in most taxa (Dirzo et al., 2014). Extinction risk incurred through persecution and introduced predators is associated with large body size (Owens & Bennett, 2000). Larger-bodied species, many with some or all these life-history traits, are disproportionately affected, in addition to being affected by environmental factors like smaller bodied species (Cardillo, 2003, 2005; Cardillo & Bromham, 2001; Forero-Medina, Vieira, Grelle, & Almeida, 2009; Gaston & Blackburn, 1995; Purvis, Gittleman, Cowlishaw, & Mace, 2000). This trend is similar across many different taxa, but the most well-studied are avian and mammalian species. For example, it has been demonstrated that the threat of extinction for mammals rises sharply at 3kg threshold, and that declining species are an order of magnitude heavier than those which are stable, on average (Cardillo, 2005). Threatened bird species have been demonstrated to be larger on average than non-threatened species (Gaston & Blackburn, 1995). On a more individual species level, many of the more famous examples of the effects of human activity on large-bodied animals are negative: one has only to think of the dodo (*Raphus cucullatus)*, now extinct (Roberts & Solow, 2003)or the black rhinoceros (*Diceros bicornis*), threatened with extinction, (Mason, Bulte, & Horan, 2012). However, the circumstances facing certain species, especially large-bodied species, are no longer the same which caused many species' populations to fall into decline or extinction. Public perception has changed; there have been legislation changes in favour of protecting larger animals (Gompper, Belant, & Kays, 2015; Linnell, Swenson, & Andersen, 2001) and there has been an increase in protected areas (R. Hill, Miller, Newell, Dunlop, & Gordon, 2015). Larger species are often more charismatic and benefit from being singled out for specific attention (Cardillo, 2005). Paired with an increase in conservation investment, which is demonstrated to be linked with a diminishing rate of biodiversity loss with a tangible and scalable effect (Waldron et al., 2013), many parts of the world are finding that previously threatened large-bodied species are experiencing stable and even increasing populations. These changes mean that the positive correlation between body size and extinction risk (Henle, Davies, Kleyer, Margules, & Settele, 2004) can be offset to some extent at least by management (Barnes et al., 2016). Large carnivorous mammals, for instance, have enjoyed dramatic changes in public perception and an increase of protected areas, resulting in the recovery of some of these species (Schaufeli & VanYperen, 1992). Even though large carnivorous mammals historically are a very controversial taxon and need a large area to thrive, they are recovering outside protected areas, even in areas of high human density (Chapron et al., 2014). For example, in India, which banned hunting wildlife for sport or consumption, large carnivores such as leopards and hyaenas are experiencing growing populations even in human- and carnivore-dense population areas (Athreya, Odden, Linnell, Krishnaswamy, & Karanth, 2013). The United States is experiencing a similar trend, where an increase in cultural acceptance combined with favourable legislation are acting to support the recovery of large mammalian carnivores. The recovery in the United states is a more a result of the legacy of large protected areas, low risk of carnivore hunting, and public acceptance (Gompper et al., 2015). Even in mainland Europe large carnivores are making a comeback in 1/3 of the region, with many individuals and even populations persisting outside of protected areas (Linnell et al., 2001). In several African countries, there were large regional differences in responses to conservation efforts (Craigie et al., 2010), with larger species remaining more at risk than smaller species, but with some successes. Some protected areas in Africa showed large-bodied species making gains in their population numbers through active management, with birds having more positive results than mammals (Barnes et al., 2016). Large-bodied birds show strong increases in populations, compared to smaller counterparts (Leung, Greenberg, & Green, 2017). In short, there is evidence that large-bodied animals can overcome their inherent inclination to human-driven extinction through active management, despite past extinction patterns.

Aside from the recovery of many previously-failing populations, there are other important factors to consider when discussing shifts in regional biotas. The characteristics of countries, for example GDP, imports, or land use change, may cause more newly arriving species. Along with climate change driving movement of many species (Crick, 2004), the barriers put in place to stop introduced species have changed. This is important to keep in mind when considering recently introduced species (Abellán, Tella, Carrete, Cardador, & Anadón, 2017). As a result, the current situation is favourable to colonizing and introduced species, which are arriving in large numbers across the world (Roy et al., 2014). Broadly speaking, avian species tend to be grouped in two general types of introductions: the game birds and the cage birds (Lockwood, 2017). In the past, game birds were transported specifically to new regions to augment local hunting opportunities and enhance the aesthetics of the local avifauna. The release of caged birds is the reason behind the more recent wave of avian introductions as exotic pets become more commonplace. By nature of the reason for introduction, many of these species are larger-bodied compared to the native fauna, for example geese, grouse or parrots (Lockwood, 2017). It has been demonstrated that birds with a greater body mass were more likely to become established when introduced (Kolar & Lodge, 2001). Consequently, although the disproportionate loss of larger-bodied birds is continuing to the present day, many groups of newly arriving avian species are larger than species already present (Cassey, 2001; Cassey & Blackburn, 2004).

What has yet to be more firmly established is how the arrival and removal of species, both on a worldwide and regional scale, are affecting ecosystem functionality. For example, until recently it was not fully understood the process by which frugivores exerted strong selection pressure on several ecosystems. It was demonstrated that overhunting of large frugivorous mammals was directly linked to a decrease in fruit size across the Indo-Malay Archipelago (Brodie, 2017), underlining the fact that megafaunal species shape the environment around them in both obvious and subtle ways. One conservation practice which is becoming more popular is to introduce extant animals to replace extinct megafaunal functions (Seddon, Griffiths, Soorae, & Armstrong, 2014; Svenning et al., 2016). For example, the giant tortoises (*Testudinidae* family) which were once prolific on all continents bar Antarctica, are a species which control the distribution and abundance of other species' populations through cascading effects, like many other megafauna (Kuijper et al., 2016). They have been put forth as a potential tool to restore especially island ecosystems, for example the repatriation of the Galapagos tortoise (*Chelonoides hoodensis*) (Seddon et al., 2014). There have been documented cases where, aside from native species, introduced species and colonizing species, re-introductions have also been used successfully as a tool to reverse defaunation, with a distinct bias toward large-bodied mammals and birds (Del Monte-Luna & Lluch-Belda, 2003; Seddon et al., 2014). Many introduced and naturally colonizing birds are larger-bodied than those present already, though not as large as those which have gone extinct. It has been theorized that with the arrival of these newer larger-bodied species, some of the previously lost ecological function is recovered (Buckley & Catford, 2016). In many cases, introduced or colonizing species might be *re*-colonizing areas in which they were once driven extinct, beyond our records or knowledge, and it remains to be discovered whether they are replacing previously lost ecosystem functionality. The result of both the recovering megafaunal populations as well as the effect of larger-bodied species arriving to new areas is that regional body mass is not changing, despite the continued loss of some of the largest species, according to my results. This means some ecosystem functionality is being lost, but with the potential of being regained.

There is a lack of knowledge behind this discussion, which is only becoming more evident over time. We have yet to fully understand how regional biotas are being altered. Is faunal similarity between regions is changing on a global level? How are arriving species (colonizing and introduced) affecting functional structure of biological assemblages? How many taxa other than plants are causing regional enrichment? What features of countries promote or demote the arrival of species? The first step to understanding these changes and addressing them effectively is research. Documenting the impacts of arriving species on species assemblages' composition and body mass distributions is critical to effectively identifying and addressing declining populations. Replacing lost ecological function needs to be a conservation priority (Ripple et al., 2014). Some methods have proven to have measured success. Rewilding has been demonstrated to be a positive method of restoring ecosystem functionality in many cases, such as the tortoise as mentioned above. For species which have gone extinct, using species of a similar size may replace functionality. For example, in some cases such as that of the aurochs, selective breeding is underway to create a modern-day substitute for these keystone species (Stokstad, 2015). Other options include using ancient DNA to reproduce these lost species (Edwards et al., 2004). Legislation, combined with changes in perception, are already demonstrated to help alleviate the pressures on some populations of larger-bodied species. Protected areas and increases in conservation spending can help with larger species, which as ecosystem engineers and a threatened group should be a conservation priority.

To discover how biotas are changing in the Anthropocene, detect the most at-risk taxa, and effectively prevent their extinction, it is necessary to understand how species' movement has changed in the recent past and to determine which species experience greater or lesser amounts of movement. It is also vital to understand how the various characteristics of countries are correlated with extirpation, survival, introduction or colonization. I found that between 1815 and 2015, avian species that went extinct are still disproportionately larger-bodied than those which survived, but larger-bodied species were also driving a large part of species turnover in regions. Arriving species were significantly larger-bodied than species already present. Overall, the median mass of avian body mass per region did not significantly change, suggesting that as larger species went extinct, species which were not as large but more numerous replaced them. What effect this has on ecological function is yet unknown – the range of body masses per region decreased significantly, suggesting species replacing extinct species were not as diverse in terms of body mass, perhaps reflecting biodiversity levels. I also found that beta diversity decreased over time, suggesting that many arrivals in new regions were driven by a similar group of species lowering overall diversity. My results show that it is important to address many different scales of research. Global results may differ from local or regional results, as they are driven by different factors. In conclusion, the patterns of biodiversity in the Anthropocene reflect change, as both losses and gains.

I test the hypotheses that:

(i) the number of species is increasing in most regions of the world,

(ii) regional faunas are becoming increasingly like one another (beta diversity is declining between regions),

(iii) the overall mean body mass of species in each region is no longer declining (if arriving species are now as heavy as those extirpated), but that

(iv) the range of body sizes might still be declining as the very largest species are still disproportionately at risk from persecution and habitat degradation.

I also evaluate the extent to which changes are linked to different indicators of environmental change, human development and conservation efforts.

This general introduction to my thesis will be similar to the more abridged version of the introduction below, which is more appropriate for a journal article. The intention when drafting the main body of this work was to prepare it for submission to a general interest journal and thus we decided it best to append a more general introduction and conclusion, to demonstrate the breadth of considered ideas for the thesis, whilst retaining a shortened manuscript for the main body, which would be more appropriate for a journal submission.

2 How extirpations, colonizations and introductions of bird species typically alter the regional diversity, distinctiveness, and body size distribution of regional bird biota

The number of species has been increasing in many regions of the world (i.e., countries, provinces or island groups which are geographically and faunally distinct), defined by the arrival of 'new' species which exceed the regional extirpation or global extinction of the 'original' species (Ellis et al., 2012; Hiley et al., 2013; McGill et al., 2015; Sax & Gaines, 2003; Sax et al., 2002; S. E. Smith, Gregory, Anderson, & Thomas, 2013; Tassin et al., 2017; Vellend et al., 2017). Regional enrichment of the flora, and perhaps also of the fauna, is taking place even though diversity is relatively stable or declining at smaller spatial scales (Dornelas et al., 2014; McGill et al., 2015; Newbold et al., 2015; Vellend et al., 2013, 2017), and declining at a global level (Clavero & García-Berthou, 2005; Diamond, Ashmole, & Purves, 1989; Pimm et al., 2014). These regional increases are expected to be accompanied by the erosion of beta diversity (reductions in the biological differences between regions) if the species that arrive are geographically more widespread than those that disappear. It is also commonly suggested that new arrivals are weedy or invasive, and fail to fulfil the same ecosystem functions as those that were extirpated (Russell & Blackburn, 2017; Simberloff & Von Holle, 1999). Thus, human attitudes towards these changes depend on individual preferences for one or another metric of regional biodiversity change (total number of species or regional distinctiveness), whether one prefers newly-arrived (via colonization or introduction) or longer-established species, and whether people prefer the new versus historical composition of biological assemblages (Davis et al., 2011; Russell & Blackburn, 2017; Tassin et al., 2017). Hence, some authors emphasize the risks of biological invasions and the erosion of functional and beta diversity, while others emphasize that distribution changes enable species to track climate change and increase regional diversity (Thomas, 2017).

This increasingly acrimonious debate is fueled by a lack of knowledge: how regional biotas are changing throughout the world, whether regional faunal similarity is indeed increasing at a global-scale, whether colonizing and introduced species might contribute to the functional structure of biological assemblages, and the extent to which regional enrichment is a feature of taxa other than plants. While there is good evidence that the number of plant species is increasing in many regions of the world, the global situation for vertebrates is less clear (Ellis et al., 2012; Sax & Gaines, 2003; Sax et al., 2002). For birds, it has been suggested that species introductions and extirpations may be closer to parity, i.e., one species in, one species out; (Sax & Gaines, 2003; Sax et al., 2002). Inventories of regional diversity change need to take 'natural' colorizations, which are often of species establishing in human-altered environments, into consideration, as well as human-assisted introductions (Hiley et al., 2013). Improved knowledge is required to establish the net change in regional bird diversity for a wider set of regions around the world, as well as an evaluation of its consequences for beta diversity.

As with mammals and other vertebrate groups, large-bodied species of bird have been disproportionately susceptible to extinction (Dirzo et al., 2014), especially when they are also island endemics (Cupper & Duncan, 2006). Removal of the largest bodied carnivores, herbivores, and seed dispersers could have major functional consequences for ecosystems. However, most megafaunal extinctions seem to take place within a few centuries to millennia after 'first contact' (Cupper & Duncan, 2006). Since New Zealand, the last major land mass to be colonized, and most of Polynesia were colonized over 700 years ago (Wilmshurst, Hunt, Lipo, & Anderson, 2011), the most 'susceptible' large bodied species may already be extinct, and hence it is not inevitable that the overall distribution of body masses will have continued to shift towards lighter-bodied species in recent centuries. Nonetheless, the more recent arrival of additional introduced predators in the last 200 years, and a growing human population combined with improved hunting technologies (especially guns) may still be driving body sizes down (Owens & Bennett, 2000). Conversely, conservation efforts disproportionately focus on charismatic, large bodied species (Seddon et al., 2014), which may thereby experience improved prospects as has been demonstrated for mammals in Europe, North America and in protected areas in Africa (Barnes et al., 2016; Chapron et al., 2014; Gompper et al., 2015). It is also possible that introduced and naturally-colonizing species which include many game and water birds (Hiley et al., 2013), are disproportionately large bodied, although not necessarily quite as large as some of those that are lost. Assessing the net change in the body mass distribution of biotas depends on comparing the masses of extirpated species with those of introduced and colonizing species. I am not aware of any such comparisons at a global scale.

Here, I examine the diversity and body size distributions of birds in 105 regions of the world, where 'region' represents any country, or geographically and faunally distinct area (such as an island group), for which my information was complete. I consider changes associated with extirpations and human-assisted introductions between 1815 and 2015, and unassisted colorizations between 1945 and 2015 (see below for explanation, and implications, of the date difference). I test the hypotheses that:

(i) the number of species is increasing in a majority of regions of the world,

(ii) regional faunas are becoming increasingly similar to one another (beta diversity is declining between regions),

(iii) the overall mean body mass of species in each region is no longer declining (if arriving species are now as heavy as those extirpated), but that

(iv) the range of body sizes (as measured by regional body size IQR) might still be declining as the very largest species are still disproportionately at risk from persecution and habitat degradation.

I also evaluate the extent to which changes are linked to different indicators of environmental change, human development and conservation efforts.

3 Methods

For each region, I compared baseline numbers of species, median body mass, and interquartile range (IQR) of breeding bird species in 1815 with equivalent numbers in 2015 after considering the extirpation of breeding species and the addition of both introduced species and natural colonists. I analyzed changed in faunal similarity between regions over time. I examined how bird species appeared and disappeared from regions globally, relative to body size and controlling for phylogenetic relatedness.

3.1 Definitions

For as many geographical 'regions' as Jonathan Hiley had collected absence/presence data for (see Appendix 1), I collected and analyzed data on bird species that were considered to be either extirpated, introduced or recently colonized (for definitions, Table 3.1). In most cases, the regions 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 regions. This occurred with the following regions: Canary Islands, Azores, Madeira, Hawaiian Islands, Galapagos Islands, Western Sahara, Peninsular and Bornean Malaysia and Taiwan. I considered introductions and extirpations since 1815, but could only consider natural colonizations since 1945. Several less well-observed regions had no information on natural colonizations, which are often less apparent to bird recorders. Many well-observed countries had little data on colonizations pre-1945, hence this cut-off date. The implications of the shorter time-frame for colonizations are considered in the interpretation of the results.

Table 3.1 Definitions of extirpation, colonization and introduction

Category	Criteria for inclusion in any given region
Extirpation	a) Natural breeding range (1815) did include that region b) It bred continuously (at least 10 pairs for a period of 10 years or greater) in a wild state in that region prior to its extirpation c) It no longer breeds in a wild state in that region (no confirmed breeding records for the 10-year period 2005-2015)
Introduction	a) Its occurrence in a region is a result of introduction (either direct introductions/escapes, is treated as 'introduced' to all New World countries). b) Its historical (1815) breeding range does not include that region c) It has bred continuously (at least 10 pairs for a period of 10 years or greater) in a wild state in that region d) It is still regarded as present (2006-2015) as a breeding species
Natural Colonization	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 region since 1945 c) Its arrival in that region did not occur as a result of introduction (see above) d) It is still regarded as present (2006-2015) as a breeding species

3.2 Database construction

I compiled current breeding bird lists for each region using data on breeding bird species and incidences of extirpations, introductions and colonizations using literature and input of local experts, collated by Jonathan Hiley (unpublished doctorate thesis, 2017) (Table 3.2). The date of 1815 was chosen as this would make is a two-hundred-year study. The baseline (1815) avifauna was estimated by taking the current breeding bird lists, removing introduced species and natural colonists, and adding extirpated species (according to the criteria in Table 3.1). 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).

As the study comprises only 200 years, I do not consider the possibility of hybridization or generation of new species. Furthermore, because the fauna for each region in 1815 are assumed to be the present fauna, including any subsequent splits and other than documented extinctions, introductions and colonizations, the possibility of species splitting over time into several species through re-categorization of species is not possible.

I chose body mass as the best assessor of body size in birds (Freeman & Jackson, 1990). Avian body mass was collected using the CRC Handbook of avian body masses and literature searches where data was missing (Dunning Jr., 2008). I used the most recent, unpublished spreadsheet of body masses, acquired via email correspondence with John Dunning (Braga, 2016).

Due to the right skew of body mass data, I log-transformed the body mass of each bird. Where body mass data for a species was missing, I conducted a search in the literature, primarily using the Handbook of Birds of the World (Christie, Juana, del Hoyo, Elliott, & Sargatal, 2014). If it was not found, I used the data of phylogenetically closest species as a substitute. Because many species' data were divided by sex in the CRC, I calculated if there was a significant difference overall, finding no significant difference. There were 990 species for which no mass data was present. Due to concerns over non-randomly missing data (Butchart & Bird, 2010), I analyzed the relationship between genus size and proportion of unavailable species data, but no relationship was found (See Appendix 2) for a graphical visualization of the analysis). The data for remaining species were not available on the time scale of the

Masters. Because many species' data had multiple samples of varying sample sizes, with different mass measurements, I calculated the mean three ways to ensure that the mass would be a valid measurement regardless of sample size for a particular measurement, or how many samples there were for a species (Table 3.3). For example, there would be multiple mass measurements if the species had been measured more than once in different locations, or if there were any subspecies. These measurements would be from groups of varying sizes, e.g. measurement A would be from a sample size of 10 birds, measurement B would be from a sample size of 10000 birds, and measurement C would be taken from a sample of 1 bird. By calculating the mean by including N (number of individuals per group) I effectively pooled all the individuals into one big group and took the mean across that group. By also using the square root of N, I ensured that group size did not play too large a role in calculating the mean, for example if there was one measurement for a group of 10000 individuals, and a measurement for a group of 10 individuals. Had I not found there to be no difference between the different methods of species mass calculation, I would have considered a different method of calculation, using the measurement with the greatest group size for instance.

Table 3.2 Sources of information

County/ Country Avifaunas	County or country avifaunas summarize 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	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	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

Table 3.3 Calculations to determine best single mass measurement for sources with multiple data points

Calculation	Definition
$\frac{\sum_{i=i\ldots n} \bar{x}_i}{n}$	Simple: the arithmetic mean across the groups, or the mean of means.
$\frac{\sum_{i=i\ldots n} N_i \bar{x}_i}{\sum_{i=i\ldots n} N_i}$	Weighted by N: the mean weighted by sample size, i.e. the number of individuals per sample.
$\frac{\sum_{i=i\ldots n} N_i \bar{x}_i}{\sum_{i=i\ldots n} \sqrt{N_i}}$	Weighted by $\sqrt{\boldsymbol{N}}$: the mean weighted by the square root of the number of individuals per group.

No significant difference between means was found, so I used the arithmetic mean of all data available as each species' data point.

In order to synchronize the body mass data with the presence data and the phylogenetic tree, it was necessary to list all species under a single species name. This proved challenging as many different records listed the same species under a different species name. I used R ('tidyr' package) to combine all the records for body mass, presence/absence data and phylogenetic location into one spreadsheet for analysis. Where species names did not match up between the phylogeny and the data, I searched for a matching Latin name synonym using the database acquired from Philip Downing (Philip Downing, 2017); if no match was found from synonyms, I searched for matching common names. If no match was found, a manual online search was conducted. In the case of species which had gone globally extinct since 1815, and hence were not present in the tree, I used Dr. Katie Davis' software to add the tips into the tree into phylogenetically suitable locations (J. Hill & Davis, 2014). In the case of newly split sister species or newly discovered species since the Jetz phylogeny or the CRC was published, I used BirdLife to corroborate the split (birdlife.org) and used the 'saplings' package to add the sister species and new species into phylogenetically suitable locations.

3.3 Analyzing change within and between communities

All regions were analyzed together, and again after being divided into 'mainland' and 'island' regions. The rationale for this was partly the known susceptibility of island birds to introduced mammalian carnivores (Courchamp, Chapuis, & Pascal, 2003), so islands were defined as offshore islands / island groups only if they lacked non-volant native terrestrial mammals. Madagascar, for instance, would not qualify as an 'island' as it has native non-volant predators which could have an effect on bird body size. Additionally, newly colonizing species might be better able to establish populations with no native mammalian predators.

In total, 91 continental and 14 island regions were analyzed. Data were not normally distributed (Shapiro-Wilk) and so the differences were analyzed using Wilcoxon Matched Pairs tests for analyzing change over time, and Wilcoxon Signed Rank tests for analyzing differences between mainland and island regions. The differences in the change in diversity between islands and continental regions were analyzed using Mann-Whitney tests. While non-parametric tests are more conservative, they are also most robust, given that the transformed data may not be normal either. The conclusions will still be robust based on these analyses. Exploring potential transformations to normalize data would be valuable however in future research.

Changes in faunal similarity were analyzed by calculating the β-sim value (smaller values indicating increases in similarity) for each pair of regions in 1815 and 2015. I analyzed pairwise comparisons separated by type of region, divided into island-island, mainland-island, and mainland-mainland comparisons.

3.4 Analyzing change in species distributional change

The changes in species distributional change were analyzed by comparing the category of distributional change as defined below (Table 3.4) and the log of the body mass of each species using a Generalized Linear Model. A global distributional change category was assigned to each species, considered to experience 'Gains', 'Losses', 'Partial Losses', 'Some gains and losses,' or 'No change' (for definitions see Table 3.4). The assumptions of this analysis were that the data points are independent and that the residuals were normally distributed, the variance were homogenous across the fitted values of the model and that the response variable was linearly related to the predictor.

Once all species were suitably placed within a phylogenetic framework and I had synchronized presence/absence data and mass data, I also conducted a phylogenetic generalized least-squares analysis to find the relationship between mass and distribution change defined in Table 3.4, while controlling for phylogenetic relatedness using the Jetz phylogeny with Ericson backbone. I tested both the Ericson and Hackett backbone and found no difference in results (https://birdtree.org/). This control for relatedness was chosen to ensure that any patterns I found in the data were as closely related to mass as possible, rather than for any other characteristic inherent in species families (Symonds & Blomberg, 2014). Both the GLM and PGLS were to see how the likelihood of a bird species either appearing in any new region or disappearing from one it had originally been present in, changed as mass increased.

Finally, I categorized each species' size on the logarithmic scale as 0-10g, 10-100g, 100-1,000g, 1,000-10,000g and 10,000g or more. Then I plotted how many of each distributional change category fell within each mass bin, to examine how distributional status changed as mass increased. I performed a logistic regression with the glm() command in R to determine if there was a significant different in whether or not a species experienced turnover, defined as a distributional change status which was no 'No Change', as the species became larger.

Table 3.4 Definitions of gains, losses, partial losses, some gains and losses, and no change

Category	Criteria for inclusion in any category
No change	a) It did not arrive in any region between 1815 and 2015 b) It was not extirpated in any region between 1815 and 2015
Loss	a) It did not survive in any region between 1815 and 2015 b) It was extirpated in all regions between 1815 and 2015 c) It did not arrive in any new regions between 1815 and 2015
Some losses	a) It survived in at least one region between 1815 and 2015 b) It was extirpated in at least one region between 1815 and 2015 c) It did not arrive in any region between 1815 and 2015
Some gains & some loss	a) It survived in at least one region between 1815 and 2015 b) It was extirpated in at least one region between 1815 and 2015 c) It arrived in at least one region between 1815 and 2015

Gains	a) It successfully arrived in at least one region between 1815 and 2015 b) It was not extirpated in any regions between 1815 and 2015

3.5 Drivers of species turnover

I used Generalized Linear Models (GLMs) to analyze the factors which have been associated with extirpations, introductions and colonizations over the last 200 years. As dependent variables, I specified the following: percent change in regional diversity, net change in regional median mass, and net change in regional body mass IQR. My list of predictor variables, which I sourced from Jonathan Hiley (unpublished doctorate thesis, 2017) 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 (Hiley, 2017)(Appendix 3).

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; (Stohlgren, Jarnevich, Chong, & Evangelista, 2006)

Governance and protection

2. Government Effectiveness (source - Worldwide Governance Indicators (Kaufmann, Kraay, & Mastruzzi, 2013). 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 (Holland, Peterson, & Gonzalez, 2009; Mikkelson, Gonzalez, & Peterson, 2007) and level of political corruption (R. J. Smith, Muir, Walpole, Balmford, & Leader-Williams, 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 (Hiley et al., 2013) or withstanding invasive species (Foxcroft, Jarošík, Pyšek, Richardson, & Rouget, 2011; Teo, Tan, Corlett, Wong, & Lum, 2003).

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 (Wiedmann 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, Bradbury, & Thomas, 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). It is important to note that this data is not available from before this date, and could have implications on the results, which are discussed below.

10. Log potential connectivity 200km (Hiley, 2017) (ArcGIS – see Appendix 4)

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, Baillie, Sutherland, & Gregory, 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.

I used GLMs to analyze changes in global bird distributions, investigating the relationship between body mass and likelihood of experiencing turnover (experiencing at least one loss and/or one gain in a new region between 1815 and 2015).

3.6 Model selection

For the regional GLMs, correlations among all predictor variables were calculated. 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 more strongly correlated with each of my dependent 'turnover' variables, so Log GDP 2015 was excluded as a predictor.

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, to find which regional characteristics were most highly correlated with the response variables: regional diversity, the change in median body mass between 1815 and 2015, and the change in the IQR of the distribution of body masses between 1815 and 2015. I considered models within AIC≤2 of the best fit model as equivalent and confirmed that the null model did not fall within AIC≤2 of the best fit model.

To account for differences in observer intensity between countries, I repeated the analyses for a subset of 'well-observed' regions. These were the 41 regions in my analysis 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 (See Table 3.x). The values of the predictor variables for this set of countries were compared to the equivalent values for the less well-observed countries to assess potential impacts of observer intensity (Hiley, 2017) (Appendix 5).

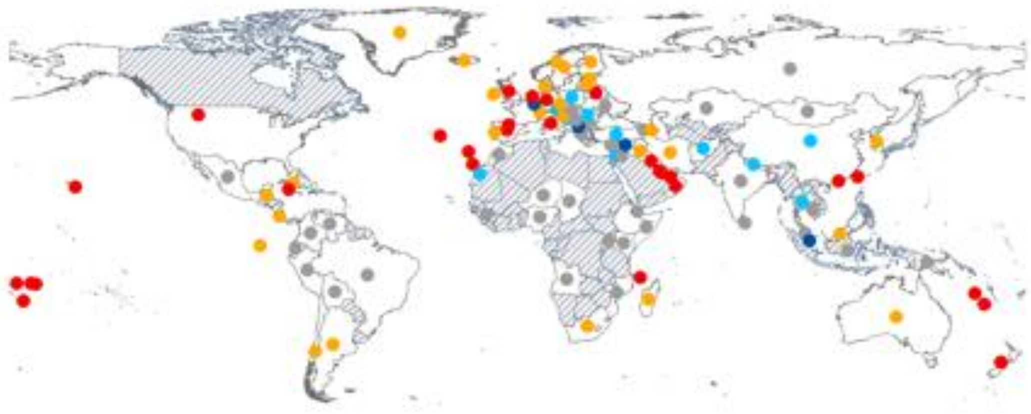
4 Results

4.1 Regional diversity change

The 105 geographic regions showed a variety of changes in number of species between 1815 and 2015, ranging from a net loss (after extirpations, introductions and colonizations) of 30 species from Singapore to a net gain of 43 species in the continental US. Overall, the percent changes ranged from a 15% decrease to a 45% increase (Fig 4.1a, Fig 4.2a). Despite this variation, there was a median increase of 4 breeding species per region, which corresponded to a median percentage increase of 1.28% in regional diversity. Thus, national diversity was significantly higher in 2015 than in 1815 (Wilcoxon: $z_{105}=4.973$, $P<0.001$).

Figure 4.1 Percent changes in 1a) species richness, 1b) median body mass and 1c) interquartile range (IQR) of body mass distributions for each region between 1815 and 2015. Hatched lines indicate no data for that region.

c) Species Richness



b) Median Body Mass

a) Regional Body Mass IQR

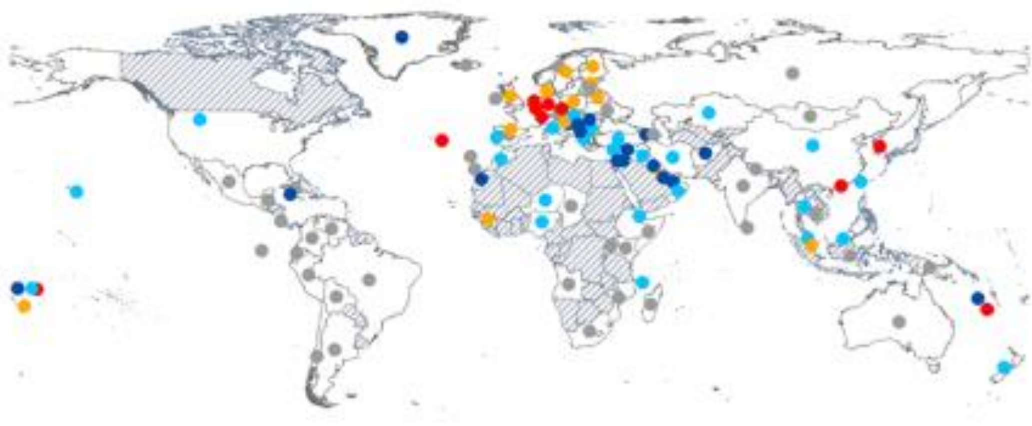
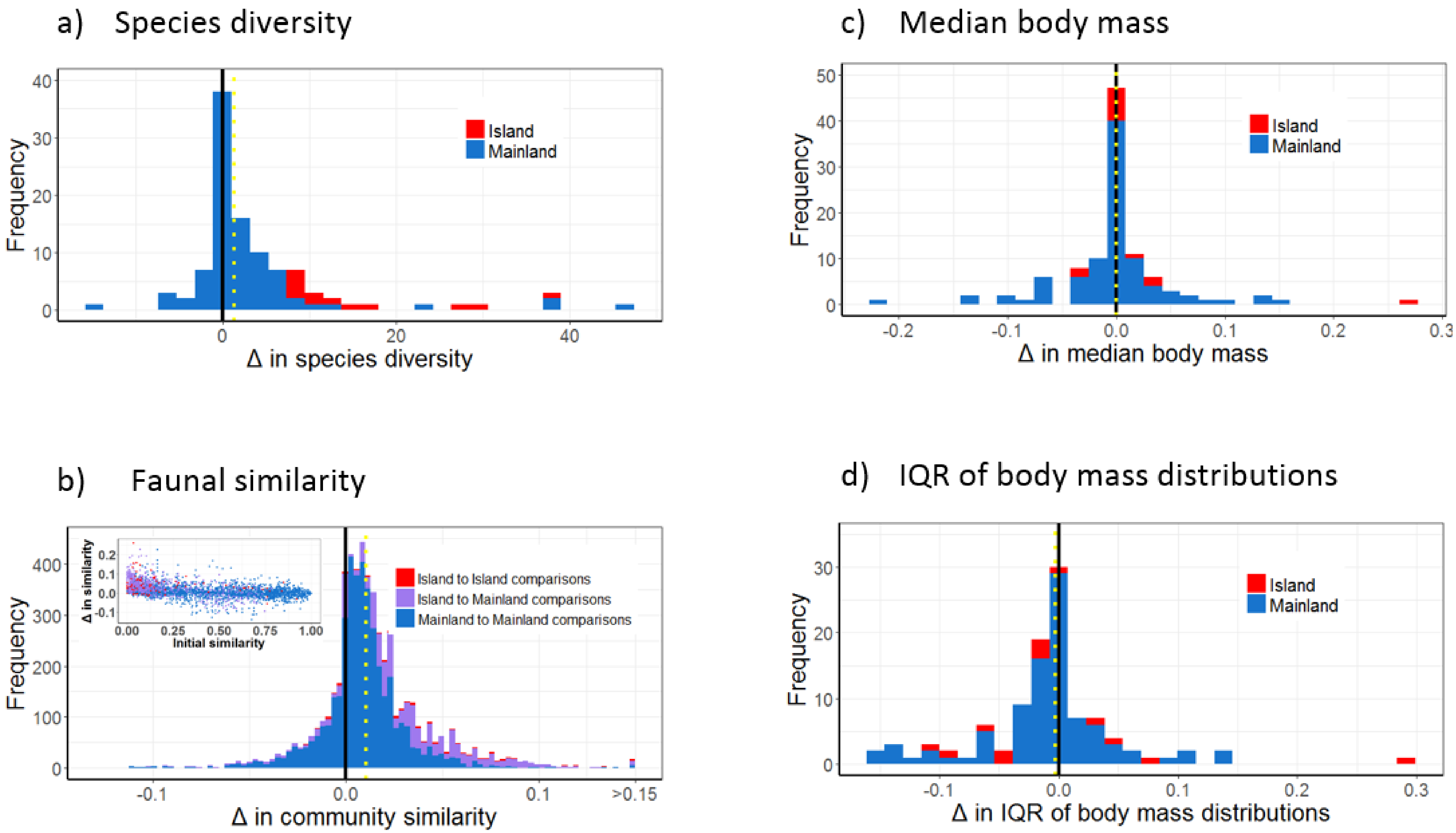
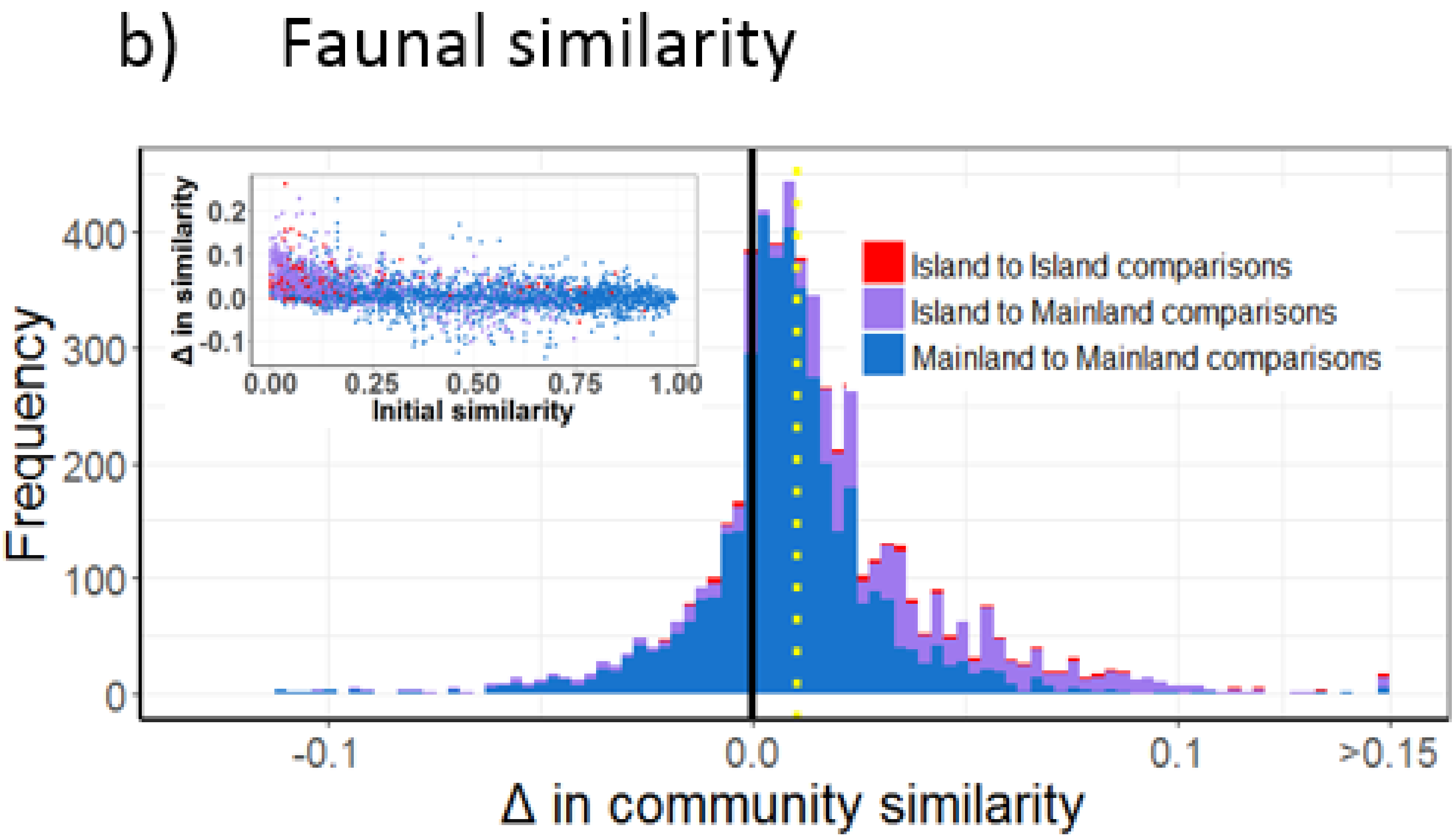


Figure 4.2 Changes in a) regional diversity, b) faunal diversity, c) median body mass, and d) interquartile range of body mass distributions between 1815 and 2015. Figures 2a), 2c) and 2d) show change over time for alpha diversity, log median mass and log IQR respectively against frequency of number of regions. The vertical lines are x = 0, the yellow dashed lines indicate the median for that set of data. Figure 2b) shows change in faunal similarity (measured as β-sim values) for each pairwise comparison over time, divided into island-to-island, island-to-mainland, and mainland-to-mainland comparisons. The inset panel in 2b) illustrates the relationship between initial faunal similarity with change in faunal similarity over time, again divided into island-island, island-mainland, and mainland-mainland pairwise comparisons. A larger version of 4.2b is provided further below.


a) Species diversity
Frequency
40
30
20
10
0
0
20
40
Δ in species diversity
Island
Mainland
b) Faunal similarity
Frequency
400
300
200
100
0
-0.1
0.0
0.1
>0.15
Δ in community similarity
Δ in similarity
0.2
0.1
0.0
-0.1
0.00
0.25
0.50
0.75
1.00
Initial similarity
Island to Island comparisons
Island to Mainland comparisons
Mainland to Mainland comparisons
c) Median body mass
Frequency
50
40
30
20
10
0
-0.2
-0.1
0.0
0.1
0.2
0.3
Δ in median body mass
Island
Mainland
d) IQR of body mass distributions
Frequency
30
20
10
0
-0.1
0.0
0.1
0.2
0.3
Δ in IQR of body mass distributions
Island
Mainland


b)
Faunal similarity
Frequency
400
300
200
100
0
-0.1
0.0
0.1
>0.15
Δ in community similarity
Δ in similarity
0.2
0.1
0.0
-0.1
0.00
0.25
0.50
0.75
1.00
Initial similarity
Island to Island comparisons
Island to Mainland comparisons
Mainland to Mainland comparisons

4.2 Faunal similarity

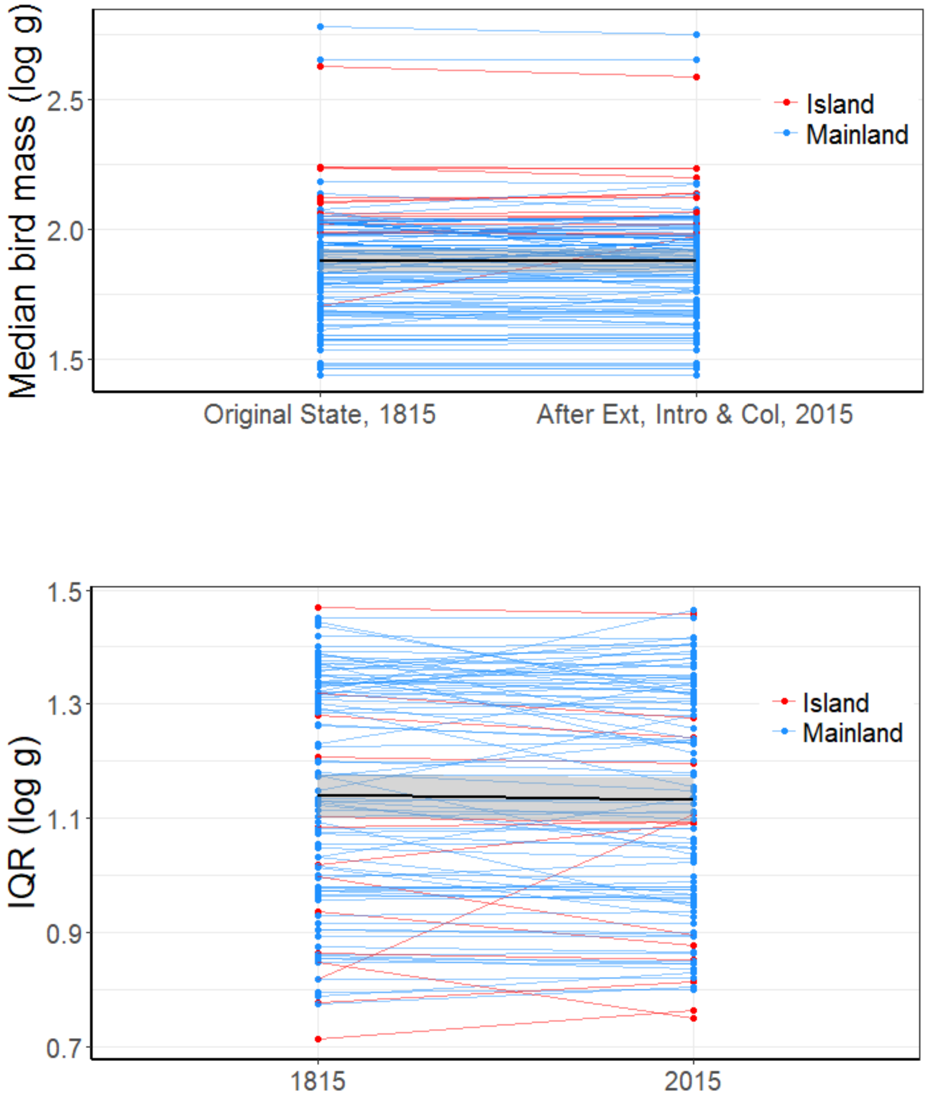
Overall, regions became significantly more similar to each other over time (Wilcoxon: $n = 105$, $V = 1167000$, $p < 0.001$), measured as β-sim, but there was a great deal of variation. The change in faunal similarity between pairs of regions ranged from a decrease of -0.13 to an increase of 0.263 (Fig 4.2b), with the median value of a 0.0106 increase. To place these numbers in context: the median represents an increase in similarity between Sri Lanka and the Republic of Ireland of two species, because of two colonizations; the 5% quantile (-0.0261) represents a decrease in similarity between Russia and Portugal because of three extinctions; and the 95th quantile (0.0671) represents an increase in similarity between Argentina and Hawaii, which shared four species in 1815 and 13 in 2015 (29 species originally present in only one of the pair were extirpated, six species were introduced to or colonized both regions, and five species were introduced to or colonized one region, having previously been present in the other). The overall increase in similarity was most strongly affected by distant regions, which initially shared few if any species, but which showed increasing faunal similarity by 2015 (Mantel test of similarity change versus geographic distance between regions, $n = 105$ regions, $r = 0.327$, $p < 0.001$, Fig 4.2b inset).

4.3 Body mass

I found no significant overall change in the median bird masses of regions between 1815 and 2015 (Wilcoxon, $n = 105$, $V = 1986$, $p = 0.3367$): some regions showed net increases in median body mass over time, most showed very little or no change, while others showed decreases (Fig 4.1b, 4.2c). In contrast, there was a significant decrease in the interquartile range (IQR) of the body masses per region (Wilcoxon, $n = 105$, $V = 2008$, $p = 0.019$), indicating that the overall range of body sizes present in regions had declined. However, IQR of the range of body masses increased in some regions, decreased in others, and commonly showed little change (Fig 4.1c, 4.2d). Although this reduction in the range of body sizes was statistically significant, this should not be interpreted as a major change in the functional composition of bird assemblages over time. Median body mass in 2015 was almost the same ($R^2 =$

0.944) as median body mass in 1815, and IQR was very similar between 1815 to 2015 ($R^2 = 0.908$). The R^2 is a formal estimate of the proportion of the variation that can be explained, with the remaining variation representing the change. In other words, there was considerably more variation in body masses (and body mass range) between geographic regions than there was over time (Fig 4.3a, 4.3b).

Figure 4.3 Regional body mass change over time. Plot a) shows regional median body mass change between 1815 and 2015. B) Regional body mass IQR change between 1815 and 2015. Red lines indicate island regions; blue lines indicate mainland regions. The black line indicates the line of best fit between the two sets of points.



I also considered the relationship between body mass and the status changes of species (as opposed to regions) between 1815 and 2015. Species that experienced a change in distribution, whether by arriving in new regions, being extirpated from original regions, or some combination of both, were significantly larger-bodied than those which experienced no change (Fig 4.4, Fig 4.5, Table 4.1, Table 4.3) as seen in the results from the GLM, which examined the likelihood of a bird species not changing its distributional status . I conducted a phylogenetic generalized least squares analysis to control for relatedness and found similar results (Table 4.2), though there was no longer a significant difference in body mass between species which experienced no change in distribution and species which experienced only gains.

Figure 4.4 Distribution of the proportion of body masses across changes in distribution. N indicates total number of species within the mass bracket.

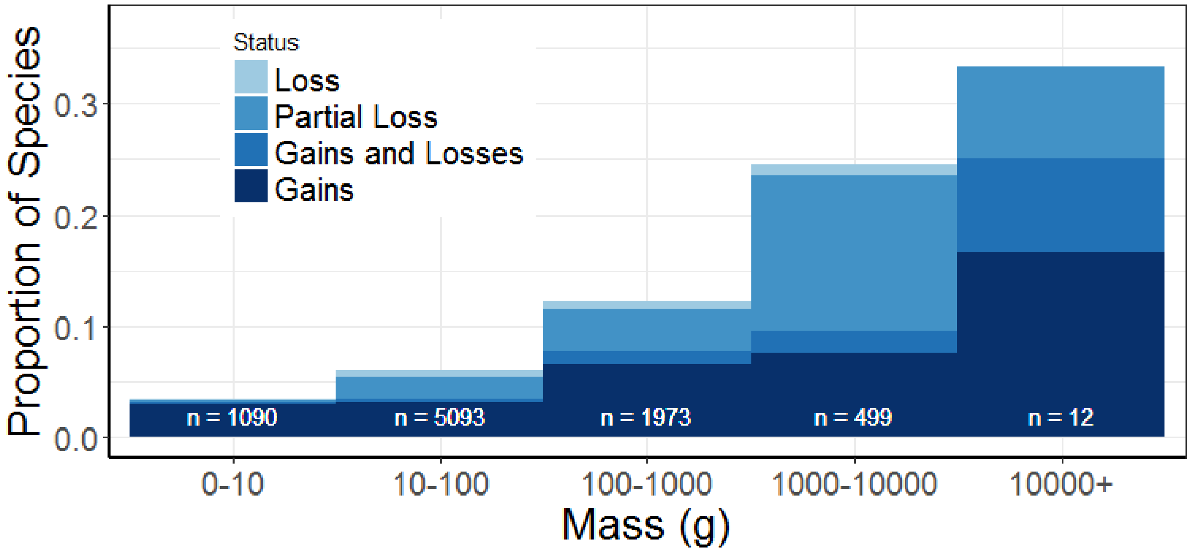


Figure 4.5 Distribution of body masses of birds in each category of distribution change between 1815 and 2015.

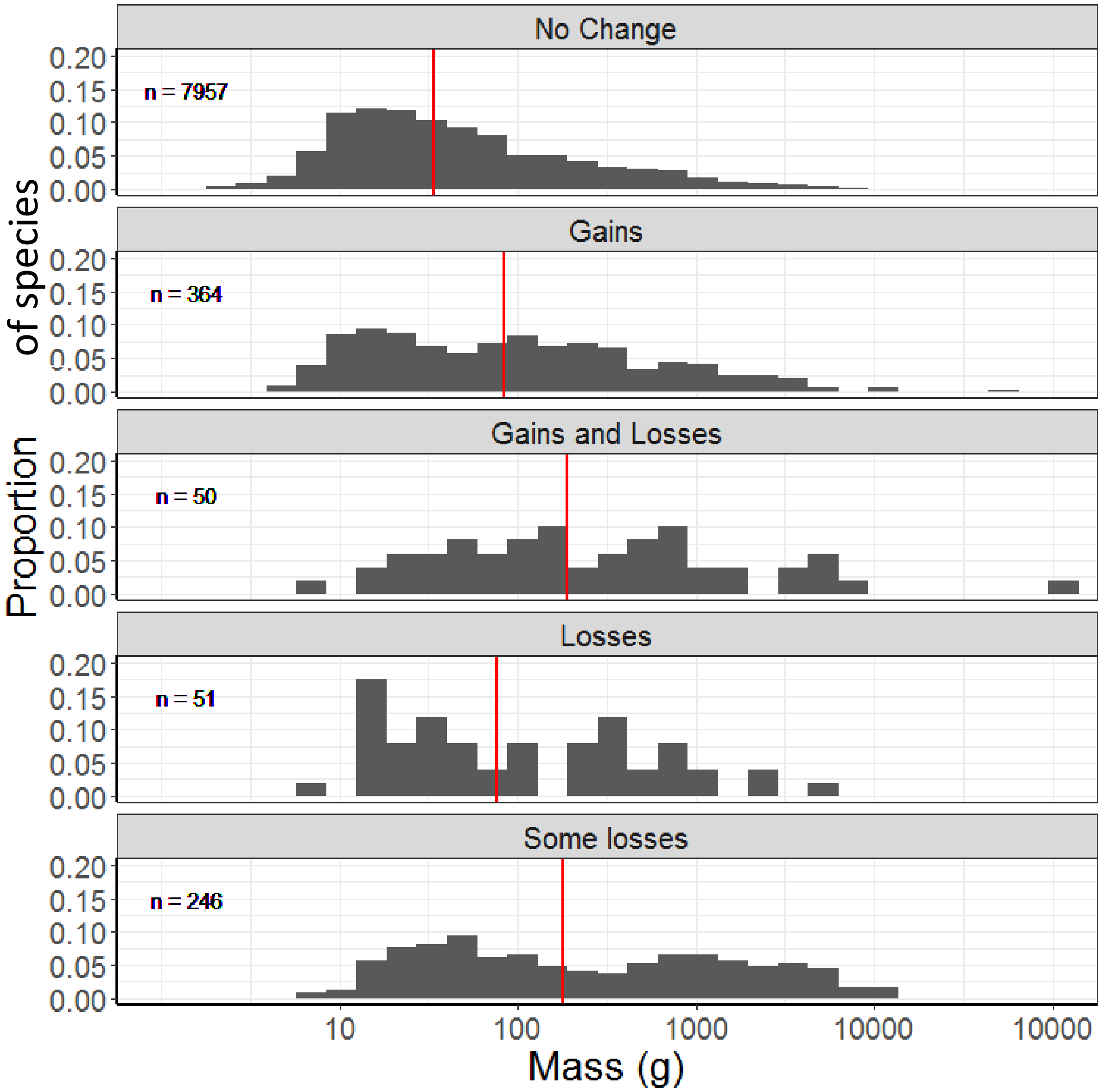


Table 4.1 Results of generalized linear model showing the relationship between change in regional distribution and body size.

Dependent Variable	**Parameter**	**Estimate**	**Standard Error**	**t-value**	**P value**
Change in distribution	(Intercept)	1.67	0.007	218.154	**<0.001**
	Gains	0.292	0.0364	8.017	**<0.001**
	Gains and Losses	0.749	0.101	7.418	**<0.001**
	Losses	0.386	0.095	4.071	**<0.001**
	Some Losses	0.699	0.044	15.793	**<0.001**

Table 4.2 Results of phylogenetic generalized least-squares model showing the relationship between change in distribution and body mass, while controlling for phylogenetic relationship.

Dependent Variable	**Parameter**	**Estimate**	**Standard Error**	**t-value**	**P value**
Change in distribution	(Intercept)	2.77	0.186	14.933	**<0.001**
	Gains	0.008	0.0081	0.9936	0.320
	Gains and Losses	0.044	0.021	2.156	**0.031**
	Losses	0.151	0.0375	4.025	**<0.001**
	Some Losses	0.035	0.011	3.197	**0.001**

Table 4.3 Results of the logistic regression analysis examining the relationship between mass and distributional change.

Dependent Variable	Parameter	Estimate	Standard Error	z-value	P value
Change in distribution	(Intercept)	-3.99211	0.11209	-35.62	**<0.001**
	Mass	0.83349	0.05049	16.51	**<0.001**

4.4 Island versus mainland comparisons

Island regions were defined as those which historically had no non-volant mammalian predators, as island birds are known to be susceptible to introduced mammalian carnivores. Hence, we also conducted separate analyses for island and mainland regions. We found that island regions increased more than mainland regions in alpha diversity in terms of both species numbers and percentage increases (Mann-Whitney U-tests: species, $z_{15,90}$=2.52, p=0.012, percentages: $z_{15,90}$=5.09, p<0.001). Island regions decreased in beta diversity (1.22% increase in shared species) more than mainland regions (0.41% increase in shared species). Although island regions had a higher median body mass than mainland regions, there was no significant difference in amount of median body mass change between island and mainland regions (Wilcoxon*,* n = 105, W = 664.5, p = 0.26), or in IQR changes between islands and mainlands (Wilcoxon*,* n = 105, W = 5745, p = 0.5942).

4.5 Drivers of change in regional diversity, median body mas, and body mass distribution

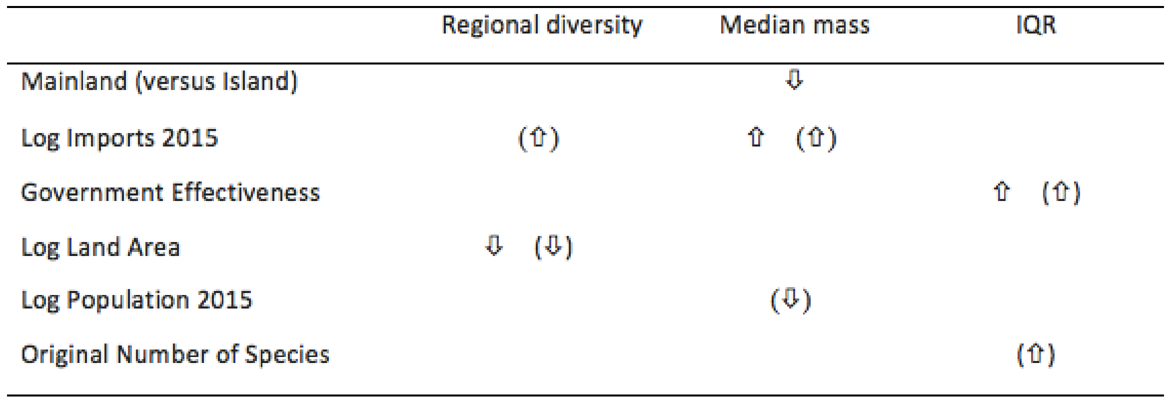
Different predictor variables were associated with the percent change in regional diversity, net change in regional median mass, and net change in regional body mass IQR (Table 4.4). For results on individual factors behind regional diversity change, i.e. number of extirpated species, introduced species, and colonizing species, see Jonathan Hiley's thesis manuscript (Hiley, 2017). Considering all 105 regions, regional diversity increased the most in larger geographic regions (greater land area). Regions with more imports (in 2015) tended to show increases in median body mass, and body mass IQRs were retained or increased in regions with greater government effectiveness. I also found that median body mass tended to decline on mainlands relative to on islands. To check that observer intensity differences between regions were not responsible for these conclusions, I repeated the analysis for a subset of 41 'intensively-observed' regions (see methods). The first three results were robust, and only the mainland versus island comparison of body mass change ceased to be significant (because the sample size of intensively-observed regions was too low for islands). The 41-region analysis identified three further effects: regional diversity increases were linked to imports, median body masses were declining in countries with greatest population size, and the IQR of body mass increased in regions with larger bird faunas.

I found the log value of imports in 2015 was a significant predictor only for well-observed regions. When just considering the 41 well-observed regions, increase in median mass was again correlated with larger log imports, while median mass was negatively correlated with the log population in 2015. These were the 41 regions 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 regions in which there is a relatively high level of observer intensity. When just considering the 41 well-observed regions, government effectiveness remained a predictor for an increase in IQR, and the original number of species in a region became a significant predictor for an increase in IQR (Table 4.1, Table 4.4). For parameter estimates and model formulae, refer to attached Appendix 6.

Table 4.4 Predictor variables included in models within AIC≤2 of the best-fit models shown for all countries (upper panel) and for just ‘well-observed’ regions (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 total number of models in which each predictor variable was significant in brackets (p<0.05).

	Number of models	Island or Mainland	Government Effectiveness 2015	Log Imports 2015	Land Use Change	Log Land Area	Connectivity	Original Number	Log Population	Log Protected	Percent Protected
Regional diversity	7	1 (0)	7 (0)	6 (0)	7 (0)	**7 (6)**	7 (0)	1 (0)	1 (0)	1 (0)	1 (0)
Median mass	5	**5 (5)**	0	**5 (5)**	0	1 (0)	0	1 (0)	1 (0)	1 (0)	0
IQR of mass distribution	11	3 (2)	**9 (9)**	3 (2)	10	4 (1)	0	9 (4)	5 (1)	3 (1)	0
Regional diversity	6	0	1 (0)	**6 (6)**	6 (0)	**6 (6)**	6 (0)	1 (0)	1 (0)	1 (0)	1 (0)
Median mass	11	2 (0)	1 (0)	**10 (10)**	0 (0)	6 (4)	0	3 (0)	0	5 (3)	0
IQR of mass distribution	7	1 (0)	**6 (5)**	2 (2)	6 (0)	2 (0)	0	**7 (5)**	2 (1)	1 (0)	1 (0)

Table 4.5 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 41 well-observed regions.



	Regional diversity	Median mass	IQR
Mainland (versus Island)		⇩	
Log Imports 2015	(⇧)	⇧ (⇧)	
Government Effectiveness			⇧ (⇧)
Log Land Area	⇩ (⇩)		
Log Population 2015		(⇩)	
Original Number of Species			(⇧)

5 Discussion

Changes to bird biotas across the world are evident, generating significantly larger regional faunas, significantly increased faunal similarities between regions, unchanged median body masses, and a slightly but significantly reduced range of body sizes per region. However, it is worth appreciating that different individual regions showed a large variety of trends, varying in the direction of change for these metrics, as well as in the magnitudes of change. This corroborates what many different studies have been finding across many different metrics of biodiversity, in many different taxa (Dornelas et al., 2014; Dyer et al., 2017; McGill et al., 2015; Vellend et al., 2013, 2017). It is not clear what, if any, loss of ecological function has taken place, but it is evident that this must be a conservation priority for future study.

5.1 Changes in diversity

Regions are gaining more species over time on average, despite the continuing role of extirpations in affecting the faunal assemblage. This is due to the combined effects of introductions and natural colonizations. It is unlikely, given the 200-year period this experiment examined, that this was due to any reason other than species being introduced to or naturally colonizing new locations. Extirpations from 1815 to 2015 have been more than offset (in terms of species number) by the arrival of species that have been introduced by humans directly, introduced to nearby regions and then spread under their own volition (treated as 'introduced' here), or colonized 'naturally' from their former historic distribution. Therefore, the increases in regional diversity that have been observed in plants (Ellis et al., 2012; Sax et al., 2002; Vellend et al., 2017) are repeated in this vertebrate group, albeit with a much smaller proportional increase in species per region. Those increases have been greatest in relatively small regions and island regions (e.g. Hawaiian Islands +39%, Canary Islands +30%), suggesting that 'maximum regional increases' in faunal sizes have taken place at a spatial scale smaller than 183630 km^2 which was the median areas for the countries and island groups I considered. One area of future study could be to determine if these variables strongly correlated, that is that islands have smaller land area than the mainland, and to determine if this influences the results found. Interestingly, metrics of land use, conservation status (Protected Areas) and governance were not linked to net diversity changes, although they are clearly important to certain species. Further interpretation of these factors, however, must be handled carefully because of the observer effort issue.

Furthermore, the factors affecting the arrival of new species to new locations have changed (Abellan et al., 2017). Through the globalization process, many new introduced species may arrive in new locations. As locations become more favourable to the arrival of species, colonizing species may arrive predominantly in certain locations of the world. For example, the preference of some well-known natural colonists such as Cattle Egret (*Bubulcus ibis)* (Blaker, 1971) and Eurasian Collared Dove (*Streptopelia decaocto*) (Hudson, 1972) for 'modified' habitats have been acknowledged. Although land use change was not linked to any response variables in the results, it is possible this is because it was a shorter time frame than some other variables.

The overall consequence of extirpations and arrivals has been to increase the similarity, or reduced beta diversity, of bird faunas across the world, particularly for island groups, which have experienced continued extinctions of island endemics and the arrival of continental species. Some of these increases in similarity are driven by a relatively small cast of increasingly widespread species, such as the house sparrow, rock pigeon, and white-faced heron, but very large numbers of species are involved; one recent compilation of data estimated that 971 different bird species are now established in at least one location outside their historical distributions (Dyer et al., 2017).

5.2 Changes in body mass median and distribution

Despite the known propensity for large-bodied vertebrates to be endangered or become extinct (Dirzo et al., 2014), there was no net change in median body mass, taken across the overall bird fauna of each region. This was because newly established species are also relatively heavy, compared to the overall bird fauna of each region; species with large body masses tended to show high rates of turnover in general (higher arrival rates as well as extirpations). In Britain, for example, many of the new introduced and colonizing species are water birds, which are heavier than the mean body mass of British birds (Hiley et al., 2013; Hiley, 2017). Extirpated species have often been slightly heavier than introduced and colonizing species, but the overall change in regional diversity indicates that more species have been arriving than disappearing. Hence, the loss of some heavy birds and replacement by a larger number of slightly less heavy species has caused no overall net change in body mass. This is the overall pattern, but there are many small species of extirpated, colonizing and introduced birds.

The effect of replacing heavy species by slightly less heavy species results in the observed reduction in the interquartile range of body sizes of regions, although some regions experienced increases. Functional changes to biological communities could potentially be linked to an IQR reduction in the bird fauna. For example, one could consider the loss of top carnivores and the largest seed dispersers. However, the newly established species may partly compensate for this. Removing introduced and recently colonized species would further reduce the IQR, and it would also reduce the median body size, such that the removal of 'non-native' species could potentially impair previous ecosystem processes further. Targeted introduction of additional heavy species could even be considered. For all these changes, nearly all the variation in median body mass, and of IQR, between regions in 2015 could be accounted for by the median body masses and IQRs of the same regions in 1815, and hence it is unlikely that the major distribution and faunal changes will have compromised ecosystem functions, although local distribution and abundance changes may well have done so.

5.3 Caveats and Future Research

The data I compiled involved using existing data sources and gaining input from experts in all 105 regions considered, but the data are not complete. For example, many predictor variables of regional characteristics were not available for the 200-year time frame of this study. Land use change, for instance, has been linked to both extirpation and arrival of new species (Blaker, 1971; Hudson, 1972; Newbold et al., 2015). My analyses of 41 intensively-observed regions found additional important factors, rather than invalidating the conclusions drawn for the larger set of regions. It is important to note that no analysis was conducted to analyze the correlation between well-observed regions and for example population number or size, both of which might influence the number of checklists. For future research, this should be investigated and if found to vary considerably, an analysis to be re-run investigating how the effects of high-intensity observer regions are correlated with various regional characteristics. Furthermore, due to the incomplete nature of the available data for the colonizations, the colonization data begin only in 1945 and onwards. This must be taken into account when considering the effect of colonizations on regions.

6 Conclusions

The effects of human involvement and globalization are evident. Many species, particularly those which are largest, are still going extinct. This is like overall trends found in defaunation, i.e., that larger animals by virtue of intrinsic and extrinsic traits are more targeted than those of a smaller size. Nevertheless, other human-driven pressures may be driving species to new parts of the world.

My results indicate increasing average regional diversity and an increase in faunal similarity across regions. Various drivers of change are affecting the different elements of species turnover 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, Boyer, & Blackburn, 2013)but these same locations have gained the most species in the last 200 years.

Altogether, I found that regions lose their biggest species while gaining more species which are similar in size to their current assemblage. This causes faunal assemblages to become more similar between one another, but more diverse within themselves. Nevertheless, the loss of some of the largest species, causing a decrease in range of body masses, may reflect a loss in ecological functionality, which must be a priority for conservational efforts moving forward.

I conclude that conservational focus ought to be on the biggest species where possible to conserve the functional aspect of the ecosystem; if they are extinct and cannot be reintroduced, a possible remedy may be to introduce new species of similar body size to the extirpated species or replace with ancient DNA.

7 Concluding Remarks

It is evident that the Anthropocene (Crutzen, 2002), is driving species turnover in terms of both removals from regions in which species used to be present (Dirzo et al., 2014) and arrivals to new regions (Hiley et al., 2013)The Anthropocene has overseen positive changes, such as the introduction of protective legislation (Gompper et al., 2015; Linnell et al., 2001), the increasing number of protected areas (Athreya et al., 2013), and changing public perception about species which used to be targeted (Barnes et al., 2016). Negative changes have also been ushered in by the Anthropocene: more effective hunting techniques (Owens & Bennett, 2000), an increase in the demand of ecosystem services (Seddon et al., 2014), and a large amount of habitat loss and destruction (Dirzo et al., 2014). The overall net outcome is hard to measure, as this myriad of factors causes diverse effects depending on the timescale, location, metric, and taxon affected.

Analyzing biodiversity is only one way to discuss the effects of the Anthropocene, and even then, the scale of study is vital for contextual understanding. The results of this study demonstrate that while global biodiversity is decreasing, many regions are increasing in diversity, and that faunal assemblage similarity is increasing as more species arrive in regions than are removed. These findings represent a marked shift from a previously loss-only perspective that until recently has been prevalent among research circles. These results certainly do not diminish the incalculable impact of the loss of species both globally and regionally, nor the effect of newly arriving species on local faunal assemblages, but they do underline the importance of considering all aspects of the Anthropocene, both the potential positive and negative effects of human activity on global and local faunal assemblages. While most regions are experiencing gains in their species number, faunal assemblage similarity is increasing across the world. This suggests the same group of species which are commonly introduced or able to easily colonize might be driving the bulk of these regional increases. Perhaps because so many avian species that historically have been introduced are larger than the native faunal assemblage, the median avian body mass has experienced no significant change in the past two hundred years, despite larger-bodied avian species still being more at risk of extirpation and extinction than those which are smaller-bodied.

This turnover in faunal assemblage might mean a significant loss of ecosystem functionality. To address this loss, possible solutions include re-wilding, or if a species is globally extinct, carefully reintroducing species of a similar size as those which have been lost.

The need to understand the patterns happening using small-scale analyses to capture all the potential spatial variation is growing (Dornelas et al., 2014). Our society values biodiversity (Johnson et al., 2017), on a spatial scale ranging from global to granular. This can be due to anything from preserving ecosystem services provided by species, to intrinsic species value (S. E. Smith et al., 2013). Despite increasing pressures on ecosystem services, continual habitat fragmentation and climate change (Dirzo et al., 2014), for most regions of the world the number of avian species is increasing. Changing composition of species assemblages could be driven by many different variables such as climate change, expanding invasive species, and anthrophilic species (McGill et al., 2015). Whether due to species which are better able to colonize due to increased heterogeneity in habitats (Sumasgutner et al., 2014), accidental introductions such as through the release of caged birds, or intentional introductions such as the release of game birds (Lockwood, 2017), biodiversity is increasing on a regional level. In addition to measuring how regional biodiversity changes over time, understanding the organization of biodiversity on a global scale is crucial for measuring regional faunal similarity. Through a combination of human-caused factors, this has either increased (species composition has become more diverse), decreased, or remained the same in different parts of the world. However, the overall trend is one of increasing similarity. This is most likely because the same group of species is repeatedly being introduced or colonizing new regions, driving the overall trend which is one of increasing faunal similarity as regions become more species-rich.

In order to understand the net change in body mass distribution, both globally and regionally, it is important to separate the different effects of introductions, colonizations, and extirpations. Just as the Anthropocene causes the reasons for species movement around the world to alter, the large-bodied taxa which were once threatened are no longer being affected by the same set of factors, and may be going extinct, becoming extirpated or newly arriving for different reasons to those 200 years ago. Stochastically, large-bodied species are more likely to go extinct, if only because they require large ranges, have small populations, and tend to be overhunted (Dirzo et al., 2014). Although large-bodied species are still more at risk than smaller-bodied species by these intrinsic life-history traits, some populations which were at risk are now stable, or even increasing for reasons which do not benefit smaller-bodied species (Barnes et al., 2016; Cardillo, 2005). Some of this may be explained by factors such as an extinction filter – all the biggest species have already gone extinct and therefore the same patterns of predominantly larger-bodied species going extinct are no longer being seen (Fritz, Bininda-Emonds, & Purvis, 2009; Turvey & Fritz, 2011). Overall however, threats which drove large-bodied avian species towards extinction in the past are no longer present in modern-day time (Bromham, Lanfear, Cassey, Gibb, & Cardillo, 2012)). Some of the recovery must be attributed to human action. While they are still subject to the same additional extinction risks smaller-bodied species face, such as climate change, they are also enjoying the benefits of actively managed populations, especially in more developed regions, causing several of the more charismatic species experiencing a slowing decline, stable, or even increasing populations in very recent times (Barnes et al., 2016). In the wealthiest regions of the planet, which for the most part no longer rely on bush meat for food and have an effective government capable of constructing more than ‘paper parks’ for protected areas and controlling the arrival of dangerous introductions (Geldmann et al., 2015), there has been significant change in how large-bodied avian species interact with humans. India, for example, has presided over the recovery of eight carnivorous mammalian species persisting in a landscape which is dominated by humans (Athreya et al., 2013). Furthermore, there is some evidence to show that larger-bodied species are arriving in more new regions than those which are smaller-bodied. As previously mentioned, game birds especially and to a lesser extent caged birds, which drive the primary waves of introduction to new regions, tend to be larger-bodied (Lockwood, 2017). As well as interspecies human preference for larger, more charismatic species, there is some evidence that climate change selects intra-specially for larger body size in avian species (Easterling et al., 2000). As there are more snap weather events, smaller-bodied individuals of a species – especially migrating species – find it more difficult to cope and are more likely to die (Goodman, Lebuhn, Seavy, Gardali, & Bluso-Demers, 2012). Effects vary across regions; factors affect large bodied avian species in diverse ways depending on where they are occurring.

The loss and gain of species on these various spatial levels have long-lasting ramifications on their respective ecosystems. It is continually being demonstrated that species have irreplaceable function in their ecosystems (Brodie, 2017). The reduction in species body mass distribution on a regional scale suggests that though large-bodied species are replacing those which are lost or move from their original habitats, functionality is still being lost. Because predominantly large-bodied species are still being lost and – only perhaps – being partially replaced, the bulk of this loss of functionality stems from this taxon. Potential solutions for replacing this lost functionality include re-wilding, which is becoming an increasingly popular option, and has been put successfully into practice in a few places (Seddon et al., 2014). The appeal is hard to deny: restructuring the faunal assemblage, economic rewards through ecotourism, stopping the decline and disappearance of some of the world's megafauna. Many communities retain a stigma against large-bodied species. For instance, raptors in North America have historically suffered from persecution from farmers poisoning, trapping and hunting them to protect livestock (Farmer, Goodrich, Inzunza, & Smith, 2008). Nevertheless, there have been some successes. Notable among them is the case of the red kite reintroduction, brought back from the very brink of extinction to a thriving population now widespread across England (Balmer, Gillings, & Caffrey, 2013). Another successful reintroduction is that of the grey wolf in Yellowstone Park. Hunted to extinction in 1926, their absence caused the elk population in the park to grow faster than was sustainable (Beschta & Ripple, 2016). While coyotes could somewhat fill the niche left empty, it was not enough to control elk populations, and furthermore had a deprecatory effect on other species, such as sheep and red foxes. After thirty years of deliberation, taking comments from and educating the public, the U.S. government could implement the plan, resulting in a cascade of effects that ultimately restored the elk population to manageable levels (Berger, Gese, & Berger, 2008). However, there are clear challenges behind this approach. For instance, due to effects of climate change which have already taken place, it is challenging to decide upon a ‘pristine’ era to which it would be desirable to revert. Not all reintroductions proposed are for species that disappeared recently enough for the ramifications to be understood enough to mitigate the risk of reintroductions causing a harmful cascade of effects on the present ecosystem. Unlike the grey wolf example, which was well-studied, documented and happened recently enough that the effects of the species’ disappearance and the probable effects of its reappearance to be catalogued, many proposed reintroductions stem from the Pleistocene era, long enough ago that it is difficult to ascertain whether species which might have once been widespread would still be a feasible option, even assuming there were a favourable public opinion of reintroducing large animals to the landscape. Conservative measures to protect biodiversity have already had a sometimes-negative impact on the communities surrounding them (Johannesen, 2007; Oldekop, Holmes, Harris, & Evans, 2016), without even considering the further issues that could be caused by a poorly-planned reintroduction. The factors that drove these species out from old habitats are not fully understood, and it could be that even if the old threats, such as overhunting or lack of readily available prey, were removed, climate change has caused the area to no longer be suitable. For example, restoring some form of equine species to North American plains has been suggested as a possible option for rewilding (Donlan et al., 2005). However, this might cause overgrazing in the new habitat where once they roamed and grazed freely. In situations where the species are globally extinct and hence cannot be re-wilded to their original habitat, conservation efforts might include species of a similar size which could potentially replace he lost functionality. Selective breeding or using ancient DNA are further avenues for future research to consider for restoring functionality to ecosystems.

In conclusion, the Anthropocene is causing unforeseen effects on every part of the planet, the ramifications of which are not yet fully understood. Some of these changes are negative, such as pervasive and harmful human-mediated invasive species (Blackburn, Delean, Pyšek, & Cassey, 2016)or overexploitation of rare species (Fritz et al., 2009). However, some are positive, such as carefully managed reintroductions (Seddon et al., 2014), the creation of protected areas (Geldmann et al., 2013), or some species becoming adapted to live in human-dense areas (Athreya et al., 2013). Many questions remain about how to identify, prioritize and address species loss and the perceptions around them (Bennett, 2016). There is no one-size-fits-all solution for conservation; it will take a nuanced, well-comprehended approach for different parts of the world to slow, halt, and eventually reverse the loss of species happening on a global level because of the diverse aspects of the Anthropocene. Conservation efforts ought to prioritize comprehending the scope of these changes, how they affect the planet on a global and regional scale, and how to include them in future conservation approaches to proactively prevent species loss, using the limited resources available (Waldron et al., 2013). Conservation focus should be placed primarily on the biggest species which, despite changing attitudes, increases in conservation spending and protected area, are still some of the most at-risk taxa. This will help conserve the functional aspect of the ecosystem.

Appendices

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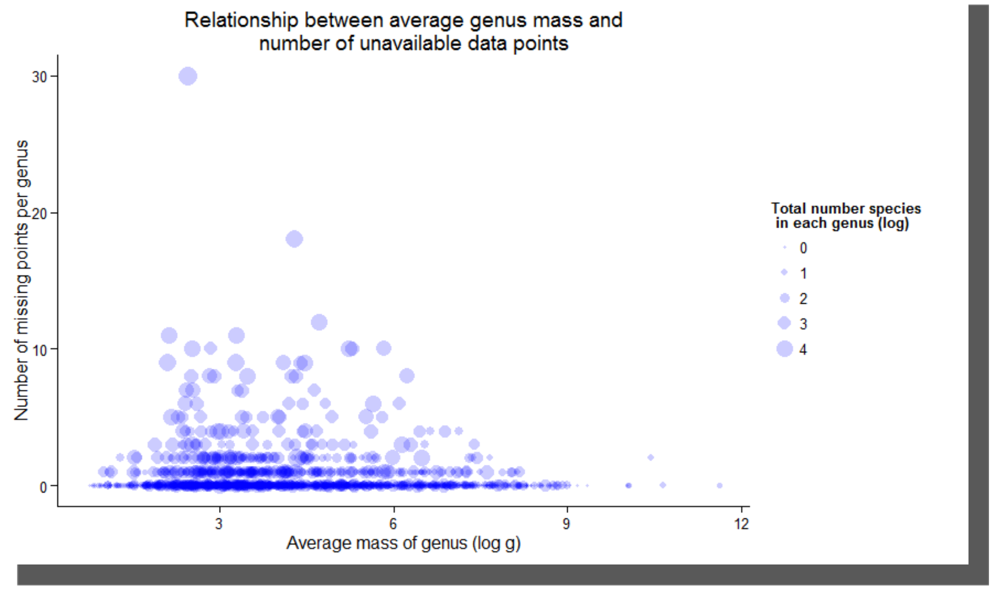
Appendix 1 Table of regions, whether they are considered and island or mainland region, and whether it came from a high-checklist region ('high') or not ('low').

Country	Island or Mainland	Quality
Afghanistan	Mainland	Low
American Samoa	Island	Low
Angola	Mainland	Low
Argentina	Mainland	High
Armenia	Mainland	Low
Australia	Mainland	High
Austria	Mainland	High
Azerbaijan	Mainland	Low
Azores	Island	High
Bahrain	Mainland	Low
Belarus	Mainland	Low
Belize	Mainland	Low
Bolivia	Mainland	Low
Bosnia and H	Mainland	Low
Brazil	Mainland	High
Bulgaria	Mainland	Low
Cambodia	Mainland	Low
Canary Islands	Island	High
Cayman Islands	Island	Low
Chad	Mainland	Low
Chile	Mainland	High
China	Mainland	Low
Colombia	Mainland	High
Comoros	Island	Low
Costa Rica	Mainland	High
Croatia	Mainland	Low
Cuba	Mainland	High
Cyprus	Mainland	Low
Czech Re	Mainland	Low
Denmark	Mainland	Low
Djibouti	Mainland	Low
Ecuador	Mainland	High
Estonia	Mainland	Low
Fiji	Island	Low
Finland	Mainland	High
France	Mainland	High
Galapagos	Island	Low
Germany	Mainland	High
Greece	Mainland	Low
Greenland	Mainland	Low
Guinea	Mainland	Low

Hawaii	Island	High
Hong Kong	Mainland	High
Hungary	Mainland	Low
Iceland	Mainland	High
India	Mainland	High
Indonesia	Mainland	Low
Iran	Mainland	Low
Iraq	Mainland	Low
Israel	Mainland	High
Italy	Mainland	High
Jordan	Mainland	Low
Kazakhstan	Mainland	Low
Kenya	Mainland	Low
Kuwait	Mainland	High
Latvia	Mainland	Low
Luxembourg	Mainland	Low
Macedonia	Mainland	Low
Madagascar	Mainland	Low
Madeira	Island	Low
Malaysia (bornean)	Mainland	High
Malaysia (peninsular)	Mainland	High
Mexico	Mainland	High
Mongolia	Mainland	Low
Morocco	Mainland	Low
Mozambique	Mainland	Low
Nepal	Mainland	Low
Netherlands	Mainland	High
New Caledonia	Island	Low
New Guinea	Mainland	Low
New Zealand	Island	High
Niger	Mainland	Low
Nigeria	Mainland	Low
Norway	Mainland	High
Oman	Mainland	Low
Peru	Mainland	High
Poland	Mainland	Low
Portugal	Mainland	High
Qatar	Mainland	Low
Republic of Ireland	Mainland	High
Republic of Korea	Mainland	Low
Romania	Mainland	Low
Russia	Mainland	Low
Samoa	Island	Low
Serbia	Mainland	High
Singapore	Mainland	Low

Somalia	Mainland	Low
South Africa	Mainland	High
Spain	Mainland	High
Sri Lanka	Mainland	Low
Sweden	Mainland	Low
Switzerland	Mainland	High
Syria	Mainland	Low
Taiwan	Mainland	High
Thailand	Mainland	High
Tonga	Island	Low
Turkey	Mainland	High
UAE	Mainland	High
Uganda	Mainland	Low
UK	Mainland	High
Ukraine	Mainland	Low
USA (continental)	Mainland	High
Venezuela	Mainland	High
Wallis and Futuna	Island	Low
Western Sahara	Mainland	Low

Appendix 2 Analysis to demonstrate there is no relationship between average genus mass and number of missing species per genus.



Appendix 3 Alternative sources of information for predictor variables and missing predictor variables (Hiley, 2017).

- 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 4 Process for calculating connectivity of entities (Hiley, 2017).
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.

References

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

Appendix 5 Results of independent t-tests comparing values of predictor variables (see Methods) in well-observed countries and in less-well observed entities (Hiley, 2017).

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

Appendix 6 Parameter estimates and model formulae

Regional Diversity Change for all regions

1	x
(Intercept)	-1.30603
Government Effectiveness 2015	-0.24491
Log Imports 2015	2.927093
Land Use Change	0.076611
Log Land Area	-3.97427
Log Isolation	-1.11852

2	x
(Intercept)	-4.67018
Island or Mainland	-4.53797
Government Effectiveness 2015	-0.34218
Log Imports 2015	3.338763
Land Use Change	0.071374
Log Land Area	-3.78286
Log Isolation	-0.68409

3	x
(Intercept)	20.39901
Government Effectiveness 2015	1.46164
Land Use Change	0.070206
Log Land Area	-2.73494
Log Isolation	-0.65299

4	x
(Intercept)	-3.29248
Government Effectiveness 2015	-0.33109
Original Number of Species	-0.00165
Log Imports 2015	3.021676
Land Use Change	0.091446
Log Land Area	-3.69987
Log Isolation	-1.07354

5	x
(Intercept)	-2.39068
Government Effectiveness 2015	-0.43201
Log Imports 2015	3.309513
Log Population 15	-0.52315
Land Use Change	0.079506
Log Land Area	-3.83562
Log Isolation	-1.11166

	x
(Intercept)	-1.2273
Government Effectiveness 2015	-0.28818
Log Total Protected Area	0.160622
Log Imports 2015	2.943561
Land Use Change	0.0758
Log Land Area	-4.14957
Log Isolation	-1.12237

	x
(Intercept)	-1.30652
Government Effectiveness 2015	-0.24542
Percent Protected Area	0.000194
Log Imports 2015	2.926945
Land Use Change	0.07661
Log Land Area	-3.97439
Log Isolation	-1.11865
Log Isolation	-3.97439
	-1.11865

Median Mass Change for all regions

	x
(Intercept)	-0.18005
Log Imports 2015	0.01689

	x
(Intercept)	-0.01619
Log Protected Area Total	0.003679

	x
(Intercept)	-0.17391
Log Imports 2015	0.022478
Log Population 15	-0.00946

	x
(Intercept)	-0.16522
LogGDP15	-0.01059
Log Imports 2015	0.026329

	x
(Intercept)	-0.17826
Log Imports 2015	0.019423
Log Land Area	-0.00563

IQR Change for all regions

	x
(Intercept)	-0.06646
Government Effectiveness 2015	0.035974

Original Number of Species	6.15E-05
Land Use Change	-0.00114
	x
(Intercept)	-0.25566
Government Effectiveness 2015	0.031315
Original Number of Species	5.52E-05
Log Imports 2015	0.017573
Land Use Change	-0.00079
	x
(Intercept)	-0.13444
Log Total Protected Area	0.012983
Log Population 15	0.018297
Land Use Change	-0.00187
Log Land Area	-0.01202
	x
(Intercept)	-0.16037
Government Effectiveness 2015	0.037813
Original Number of Species	5.86E-05
Log Population 15	0.019168
Land Use Change	-0.001
Log Land Area	-0.00861
	x
(Intercept)	-0.16481
Government Effectiveness 2015	0.036741
Original Number of Species	5.18E-05
Log Population 15	0.013954
Land Use Change	-0.00101
	x
(Intercept)	-0.06779
Government Effectiveness 2015	0.035949
Original Number of Species	6.12E-05
Land Use Change	-0.00114
Log Land Area	0.000277
	x
(Intercept)	-0.53728
Island or Mainland	-0.05904
Original Number of Species	-1.02E-05
Log Total Protected Area	0.01253
Log Imports 2015	0.049099
	x
(Intercept)	-0.20375
Government Effectiveness 2015	0.01978
Log Population 15	0.024777
Land Use Change	-0.00097
	x
(Intercept)	-0.11707
Island or Mainland	0.050737

Government Effectiveness 2015	0.036861
Original Number of Species	6.23E-05
Land Use Change	-0.00136

	x
(Intercept)	-0.24232
Government Effectiveness 2015	0.032442
Original Number of Species	5.40E-05
Log Imports 2015	0.014047
Log Population 15	0.003495
Land Use Change	-0.00083

Regional Diversity Change for High Observer Level Regions

	x
(Intercept)	-65.3061
Log Imports 2015	10.25686
Land Use Change	0.216428
Log Land Area	-5.95061
Log Isolation	-2.20954

	x
(Intercept)	-65.8272
Log Total Protected Area	3.070984
Log Imports 2015	10.42106
Land Use Change	0.24239
Log Land Area	-8.82013
Log Isolation	-2.20703

	x
(Intercept)	-66.7573
Percent Protected Area	0.103556
Log Imports 2015	10.09193
Land Use Change	0.232396
Log Land Area	-5.77417
Log Isolation	-2.17629

	x
(Intercept)	-73.0935
Log Imports 2015	12.00884
Log Population 15	-2.47172
Land Use Change	0.260859
Log Land Area	-4.96893
Log Isolation	-2.00724

	x
(Intercept)	-66.0009
Original Number of Species	0.00207
Log Imports 2015	10.65069
Land Use Change	0.202008
Log Land Area	-6.64851
Log Isolation	-2.39321

	x
(Intercept)	-67.6049

Government Effectiveness 2015	-0.79608
Log Imports 2015	10.73627
Land Use Change	0.196301
Log Land Area	-6.23165
Log Isolation	-2.3765

Median Mass Change for High Observer Level Regions

	x
(Intercept)	-0.65845
Log Imports 2015	0.082604
Log Population 15	-0.06399
Log Land Area	0.03891

	x
(Intercept)	-0.6824
Government Effectiveness 2015	-0.00556
Log Imports 2015	0.08774
Log Population 15	-0.06833
Log Land Area	0.039415

	x
(Intercept)	-0.66165
Log Total Protected Area	-0.00628
Log Imports 2015	0.082942
Log Population 15	-0.06468
Log Land Area	0.045097

	x
(Intercept)	-0.59325
Percent Protected Area	-0.00183
Log Total Protected Area	0.035492
Log Imports 2015	0.081331
Log Population 15	-0.0595

	x
(Intercept)	-0.63673
Percent Protected Area	-0.00086
Log Imports 2015	0.082979
Log Population 15	-0.06388
Log Land Area	0.037228

	x
(Intercept)	-0.61292
Original Number of Species	3.18E-05
Percent Protected Area	-0.00207
Log Total Protected Area	0.029812
Log Imports 2015	0.090711
Log Population 15	-0.0691

	x
(Intercept)	-0.67016
Original Number of Species	1.73E-05
Log Imports 2015	0.087372
Log Population 15	-0.06861

Log Land Area	0.035839

	x
(Intercept)	-0.64871
Original Number of Species	3.31E-05
Percent Protected Area	-0.00128
Log Imports 2015	0.092286
Log Population 15	-0.07267
Log Land Area	0.030543

	x
(Intercept)	-0.63643
Government Effectiveness 2015	-0.01041
Percent Protected Area	-0.00194
Log Total Protected Area	0.036911
Log Imports 2015	0.091187
Log Population 15	-0.06813

	x
(Intercept)	-0.63958
Island or Mainland	-0.01674
Log Imports 2015	0.079149
Log Population 15	-0.05843
Log Land Area	0.037922

	x
(Intercept)	-0.56941
Island or Mainland	-0.02255
Percent Protected Area	-0.00184
Log Total Protected Area	0.034644
Log Imports 2015	0.076944
Log Population 2015	-0.05263

IQR Change for High Observer Level Regions

	x
(Intercept)	-0.06646
Government Effectiveness 2015	0.035974
Original Number of Species	6.15E-05
Land Use Change	-0.00114

	x
(Intercept)	-0.25566
Government Effectiveness 2015	0.031315
Original Number of Species	5.52E-05
Log Imports 2015	0.017573
Land Use Change	-0.00079

	x
(Intercept)	-0.11707
Island or Mainland	0.050737
Government Effectiveness 2015	0.036861
Original Number of Species	6.23E-05
Land Use Change	-0.00136

	x

(Intercept)	-0.16481
Government Effectiveness 2015	0.036741
Original Number of Species	5.18E-05
Log Population 2015	0.013954
Land Use Change	-0.00101
	x
(Intercept)	-0.05272
Government Effectiveness 2015	0.036932
Original Number of Species	6.72E-05
Log Total Protected Area	-0.00372
Land Use Change	-0.00117
	x
(Intercept)	-0.64871
Original Number of Species	3.31E-05
Percent Protected Area	-0.00128
Log Imports 2015	0.092286
Log Population 2015	-0.07267
Log Land Area	0.030543
	x
(Intercept)	-0.06779
Government Effectiveness 2015	0.035949
Original Number of Species	6.12E-05
Land Use Change	-0.00114
Log Land Area	0.000277

List of Model Formulae

Regional Diversity Change for all regions
[[1]]
Regional Diversity Change ~ 1 + Government Effectiveness 2015 +
Log Imports 2015+ Land Use Change + Log Land Area+
Log Isolation

[[2]]
Regional Diversity Change ~ 1 + Island or Mainland+ Government Effectiveness 2015 +
Log Imports 2015+ Land Use Change + Log Land Area+
Log Isolation

[[3]]
Regional Diversity Change ~ 1 + Government Effectiveness 2015 +
Land Use Change + Log Land Area + Log Isolation

[[4]]
Regional Diversity Change ~ 1 + Government Effectiveness 2015 +
Original Number of Species + Log Imports 2015 + Land Use Change + Log Land Area+
Log Isolation

[[5]]
Regional Diversity Change ~ 1 + Government Effectiveness 2015 +
Log Imports 2015+ Log Population 2015+ Land Use Change + Log Land Area+
Log Isolation

[[6]]
Regional Diversity Change ~ 1 + Government Effectiveness 2015 +
Log of Total Protected Land Area+ Log Imports 2015 + Land Use Change +
Log Land Area + Log Isolation

[[7]]
Regional Diversity Change ~ 1 + Government Effectiveness 2015 +
% Protected Area + Log Imports 2015 + Land Use Change + Log Land Area +
Log Isolation

Median Mass Change for all regions
[[1]]
Change in Median Body Mass~ 1 + Island or Mainland+ Log Imports 2015

[[2]]
Change in Median Body Mass~ 1 + Island or Mainland+ Log of Total Protected Land Area+
Log Imports 2015

[[3]]
Change in Median Body Mass~ 1 + Island or Mainland+ Log Imports 2015 + Log Land Area

[[4]]

Change in Median Body Mass~ 1 + Island or Mainland+ Original Number of Species + Log Imports 2015

[[5]]
Change in Median Body Mass~ 1 + Island or Mainland+ Log Imports 2015 + Log Population 2015

IQR Change for all regions
[[1]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + Land Use Change

[[2]]
Change in Body Mass IQR~ 1 + Log of Total Protected Land Area+
Log Population 2015+ Land Use Change + Log Land Area

[[3]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + Log Population 2015+ Land Use Change + Log Land Area

[[4]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + Log Population 2015 + Land Use Change

[[5]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + Land Use Change + Log Land Area

[[6]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + % Protected Area + Land Use Change

[[7]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Log Population 2015+ Land Use Change

[[8]]
Change in Body Mass IQR~ 1 + Island or Mainland+ Government Effectiveness 2015 +
Original Number of Species + Land Use Change

[[9]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + Log Imports 2015 + Log Population 2015+ Land Use Change

[[10]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + Log of Total Protected Land Area+ Land Use Change

[[11]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + Log Imports 2015 + Land Use Change

Regional Diversity Change for high observer level regions

[[1]]
Regional Diversity Change ~ 1 + Log Imports 2015 + Land Use Change +
Log Land Area + Log Isolation

[[2]]
Regional Diversity Change ~ 1 + Log of Total Protected Land Area+
Log Imports 2015+ Land Use Change + Log Land Area+ Log Isolation

[[3]]
Regional Diversity Change ~ 1 + % Protected Area +
Log Imports 2015+ Land Use Change + Log Land Area+
Log Isolation

[[4]]
Regional Diversity Change ~ 1 + Log Imports 2015 + Log Population 2015+
Land Use Change + Log Land Area+Log Isolation

[[5]]
Regional Diversity Change ~ 1 + Original Number of Species + Log Imports 2015 + Land Use Change +
Log Land Area+Log Isolation

[[6]]
Regional Diversity Change ~ 1 + Government Effectiveness 2015 +
Log Imports 2015+ Land Use Change + Log Land Area+
Log Isolation

Median Mass Change for high observer level regions

[[1]]
Change in Median Body Mass~ 1 + Log Imports 2015 + Log Population 2015+
Log Land Area

[[2]]
Change in Median Body Mass~ 1 + % Protected Area +
Log of Total Protected Land Area+ Log Imports 2015 + Log Population 2015

[[3]]
Change in Median Body Mass~ 1 + % Protected Area +
Log Imports 2015+ Log Population 2015+ Log Land Area

[[4]]
Change in Median Body Mass~ 1 + Original Number of Species + % Protected Area +

Log of Total Protected Land Area+ Log Imports 2015 + Log Population 2015

[[5]]
Change in Median Body Mass~ 1 + Original Number of Species + Log Imports 2015 + Log Population 2015 + Log Land Area

[[6]]
Change in Median Body Mass~ 1 + Original Number of Species + % Protected Area +
Log Imports 2015+ Log Population 2015 + Log Land Area

[[7]]
Change in Median Body Mass~ 1 + Government Effectiveness 2015 +
% Protected Area + Log of Total Protected Land Area+
Log Imports 2015+ Log Population 2015

[[8]]
Change in Median Body Mass~ 1 + Island or Mainland+ Log Imports 2015 + Log Population 2015+
Log Land Area

[[9]]
Change in Median Body Mass~ 1 + Island or Mainland+ % Protected Area +
Log of Total Protected Land Area+ Log Imports 2015 + Log Population 2015

[[10]]
Change in Median Body Mass~ 1 + Government Effectiveness 2015 +
Log Imports 2015+ Log Population 2015+ Log Land Area

[[11]]
Change in Median Body Mass~ 1 + Log of Total Protected Land Area+
Log Imports 2015+ Log Population 2015+ Log Land Area

IQR Change for high observer level regions
[[1]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + Land Use Change

[[2]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + Log Imports 2015 + Land Use Change

[[3]]
Change in Body Mass IQR~ 1 + Island or Mainland+ Government Effectiveness 2015 +
Original Number of Species + Land Use Change

[[4]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + Log Population 2015+ Land Use Change

[[5]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + Log of Total Protected Land Area+ Land Use Change

[[6]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + % Protected Area + Land Use Change

[[7]]
Change in Body Mass IQR~ 1 + Government Effectiveness 2015 +
Original Number of Species + Land Use Change + Log Land Area

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