Effects of land use on local biodiversity on islands and mainlands worldwide

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Copyright declaration

Declaration of originality

I certify that this thesis is the product of my own work, unless mentioned here or in the text. I did not collect any of the ecological field data analysed in this thesis; all data was extracted from the PREDICTS database (unless otherwise stated). The database was designed by Lawrence Hudson and Igor Lysenko and the data has been collated and curated by current and past members of the PREDICTS project, including myself. Igor Lysenko classified sites in the database as island or mainland sites. All chapters were commented on by my supervisor, Andy Purvis; Chapter 2 was also commented on by Jason Tylianakis, who was part of my Progress Review Panel and provided significant advice for the compositional similarity modelling. For analyses in Chapters 3 and 4, I used the '*roquefort*' and '*yarg*' R packages (unpublished), which were designed by Tim Newbold to process the diversity data in the PREDICTS database, gather functions needed for statistical modelling and to plot models. I developed the new implementation of the Biodiversity Intactness Index (BII) – discussed through this thesis – in collaboration with others in the PREDICTS team. In particular, BII maps were generated using a set of python libraries developed by Ricardo Gonzalez, specifically for spatial projections of PREDICTS-derived models. Alien/native classifications in Chapter 4 were performed in collaboration with Kara Taylor, who worked in the PREDICTS project as a Masters student and under my (and other PREDICTS members') supervision collated and formatted the data to classify species and wrote the R code to integrate this data to the PREDICTS database. A combination of different sections from Chapters 2, 3 and 5 has been published as a preprint in bioRxiv, with me as the first author and with the same title as Chapter 3. Results from Chapter 5 contributed to the publication of a correspondence piece by Newbold et al. (2019); Figure 5.3 is included in that publication.

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Abstract

Land-use change is a major driver of biodiversity change; while it increases many species' extinction risk and often causes a loss of local diversity, it also promotes the establishment of novel alien and native species. All these processes change the species composition of assemblages. Global syntheses rarely compare the effects of land-use change across different ecological systems, limiting our ability to identify which systems are most affected. Islands and mainlands often face different human pressures and harbour very different species assemblages. Importantly, many islands harbour native species that are particularly sensitive to human pressures and they tend to be more vulnerable than mainlands to invasions by alien species. In this thesis, I model a global collation of site-level biodiversity data from sites facing different land uses and related pressures to answer three questions. Does the change in species composition caused by land-use change differ between islands and mainlands? Have land-use change and related pressures decreased biodiversity integrity more on islands than on mainlands? How do land use and related pressures affect the diversity of alien and native species on islands? My results highlight particular cases where land-use change causes a greater change in local species assemblages on islands than on mainlands. Based on the Biodiversity Intactness Index (BII), I also show that, on average, land-use change and related pressures have reduced biotic integrity more on islands than on mainlands, mainly because island species are more sensitive to human pressures. The chapters underpinning these findings represent the first global analyses to include a wide range of taxa while comparing biodiversity responses on islands and mainlands to land-use change. Additionally, through analyses focusing exclusively on islands, I show that land-use change reduces both local richness and total abundance of island native species but increases both the number and abundance of alien species. My results highlight the sensitivity of island natives to human pressures and attest to the establishment of alien species on islands, particularly in disturbed habitats and on more isolated islands. They support calls for stronger efforts to protect islands' unique biodiversity. This thesis also contributes to the development of a new implementation of BII, improving on the statistical modelling approach used recently to estimate BII globally. In a final analysis integrating results from the different chapters, I show that this improved approach yields estimates that reflect the intactness of native biodiversity more accurately than previous estimates. Most of this improvement is attributable to the use of a more stringent definition for sites whose biota is assumed to have been minimally impacted by people, which was facilitated by a more efficient use of the underlying assemblage data.

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CHAPTER 1

General introduction

The functioning of ecosystems and their capacity to provide services to humanity depend on the state of local, rather than global biodiversity (Cardinale et al., 2012; Hautier et al., 2018). Although biodiversity is critical for the provision of ecosystem services – benefits from nature that underpin human wellbeing (Mace et al., 2012) – human-caused pressures are reducing biodiversity worldwide. This thesis is about how one particular pressure, land-use change, affects local biodiversity globally.

Land-use change is one of the main drivers of biodiversity loss (Sala et al., 2000; Maxwell et al., 2016); it increases the risk of global extinction for many species (Brummitt et al., 2015; Maxwell et al., 2016), can sharply reduce local species richness and abundance (Murphy & Romanuk, 2014; Newbold et al., 2015) and alters species composition of ecological assemblages (Socolar, 2016; Newbold et al., 2016b), e.g., by promoting the establishment of alien species and favouring a subset of tolerant or widespread species (Catford et al., 2012; Socolar et al., 2016; Newbold et al., 2018). However, the effects of land-use change vary across geographic regions (Lenzen et al., 2009; De Palma et al., 2016) and taxonomic groups (Flynn et al., 2009; Stork et al., 2009), because exposure to habitat modification and related human pressures differ across regions (Cincotta et al., 2000; Ramankutty et al., 2008), and because species' responses and vulnerability can vary according to their ecological and life history traits (Cardillo, 2003; Barbaro & van Halder, 2009; De Palma et al., 2015). This thesis focuses on how land-use change affects local ecological communities in two different ecological arenas: mainlands and islands (focusing exclusively on marine or 'true' islands – i.e., landmasses completely surrounded by ocean).

Island and mainland settings differ markedly in terms of environmental conditions, species assemblages and human pressures (Whittaker & Fernández-Palacios, 2007; Kier et al., 2009). Specifically, islands are expected to be more vulnerable to human disturbance as a consequence of their small size, isolation, and the rarity of their endemic species (Paulay, 1994; Whittaker & Fernández-Palacios, 2007; Fordham & Brook, 2010; Keppel et al., 2014), among other factors (see below). However, to date, no global analyses of a wide range of taxa have examined island-mainland differences in how biodiversity responds to land-use change and related pressures. This comparison is often not possible since data on biodiversity in disturbed landscapes are often biased towards geographic regions which are usually mainlands; e.g., mainland Europe and America (Trimble & van Aarde, 2012). For example, Newbold et al. (2016a) recently published a global map of the estimated state of an indicator of local biodiversity, the Biodiversity Intactness Index (BII: Scholes & Biggs, 2005); this map is based on global statistical models which, because of data limitations, could not allow island and mainland assemblages to respond differently to human pressures. Therefore, if island responses differ from mainlands, then Newbold et al.'s (2016a) estimates of biodiversity intactness of island assemblages may be systematically biased. In particular, if island biotas tend to be more sensitive, the published BII estimates may be overoptimistic. This thesis refines Newbold et al.'s (2016a) modelling approach to generate improved estimates of BII for the world's islands and mainlands.

The loss of island biodiversity is particularly worrying since islands harbor many unique species (i.e., endemics) and a large proportion of Earth's biodiversity (Whittaker & Fernández-Palacios, 2007; Delgado et al., 2017). For example, even though islands only constitute around 3% of Earth's land area, they contribute around 20% of terrestrial species (Whittaker et al., 2017) – "a disproportionately high biodiversity relative to their area" (Delgado et al., 2017). Importantly, nine of the 25 biodiversity hotspots – areas high in species endemism but facing a strong habitat loss (Myers, 1988) – are entirely or mostly made up of islands (Myers et al., 2000). Furthermore, some of these 'island-rich' hotspots (i.e., the Caribbean, Madagascar, Phillipines and Sundaland hotspots) are among the "most depleted habitats" (Myers et al., 2000), retaining only 10% or less of their primary vegetation, highlighting the need to prioritise these systems for conservation interventions.

In this introductory chapter, I review some of the factors that may contribute to different responses of island and mainland assemblages to human pressures, focusing on factors that drive vulnerability of island assemblages. I also discuss patterns of land-use change and additional human pressures (e.g., introduction of species) on islands and mainlands, as different levels of exposure are likely to contribute to island/mainland differences in biodiversity loss. Finally, I include a thesis overview, highlighting the main questions addressed in each chapter and the methods and approaches used.

1.1 ISLAND ASSEMBLAGES AND VULNERABILITY TO HUMAN PRESSURES

Islands are unique systems with distinctive environmental conditions (e.g., limited area, geographic isolation and lower elevational heterogeneity and seasonality than mainlands –

Weigelt et al., 2013), which shape communities in a very particular way. Previous studies have suggested that the extinction risk of island species is highly sensitive to habitat loss (Simberloff, 1995b; Brooks et al., 2002) and the literature on factors that define islands' uniqueness and vulnerability is extensive. In this section, I review how island size (area) and isolation play an essential role in shaping island species assemblages and their responses to human pressures.

1.1.1 Island species richness

Island isolation and size are the attributes that underpin the equilibrium theory of island biogeography (ETIB – MacArthur & Wilson, 1963; 1967), a model for prediction of patterns of species diversity on islands. Although other models have been developed to explain the variation in island species richness (e.g., the species-energy theory – Wright, 1983; the small-island effect – Whitehead & Jones, 1969; Triantis et al., 2006), ETIB has been widely used as a conceptual foundation for community ecology, even providing insights to community assembly in other systems (Warren et al., 2015). ETIB focuses on the species-distance and species-area relationships and bases its predictions on the balance between immigration and extinction rates. The theory assumes that as the number of species on an island increases, the rates of immigration decrease but rates of extinction increase; this implies that the number of species will reach an equilibrium point, at which the loss of species caused by extinction is balanced by the species added through immigration (MacArthur & Wilson, 1963). ETIB also hypothesises that large islands have lower extinction rates than small islands and that islands that are closer to the colonisation source (e.g. a continent or another island) have higher immigration rates (Warren et al., 2015). Based on these assumptions, ETIB makes two principal predictions: small islands have fewer species than large islands; and distant – or more isolated – islands have less species than near islands (MacArthur & Wilson, 1963).

The island species-area relationship (ISAR) varies across systems (MacArthur & Wilson, 1963; Matthews et al., 2019); for example, ISAR is expected to vary across biogeographical regions and taxa, since these factors determine the overall biotic richness of the system or source-pool region (Whittaker & Fernández-Palacios, 2007). Additionally, MacArthur and Wilson (1967) predicted that, with increasing geographic isolation, ISAR becomes steeper; for example, in minimally isolated systems a shallow ISAR slope with a high intercept (i.e., number of species on small islands) would be expected since extinction events can be rapidly reversed by recolonization (i.e. 'rescue effect' – Brown & Kodric-Brown, 1977), which can maintain a relatively high species richness on small islands (Whittaker et al., 2017). On the other hand, in a remote system, small islands have a markedly low species richness as a consequence of their low rates of immigration and restricted resources, which "cannot sustain marginal populations of small size or permit the origin and persistence of newly formed endemics" (Whittaker et al., 2017); therefore, in these systems, a steep ISAR slope with a low intercept is expected. Under these assumptions, it has been long stated that, as a consequence of their isolation, islands usually encompass fewer species than same-sized areas in mainlands (MacArthur & Wilson, 1967), and islands are considered to be undersaturated with species (Whittaker & Fernández-Palacios, 2007).

Based on ETIB, on further developments for this ecological model and adding theory on island evolution, multiple studies have examined how island size and isolation contribute to other characteristics of island assemblages and their vulnerability to human pressures:

1.1.2 Effects of island isolation on island assemblages

Island isolation acts as a barrier and filter for species colonisation (Whittaker & Fernández-Palacios, 2007). In the case of 'true islands', water represents a non-colonisable area, which enhances isolation compared to other insular systems such as montane sky islands, fragmented landscapes and caves (Warren et al., 2015), which are also present on mainlands. These other island-like systems can have changing surrounding matrices which at some point can present favourable conditions for colonisation (Warren et al., 2015). In contrast, under natural conditions, the more severe isolation of islands mainly allows the arrival of species with strong dispersal abilities (Paulay, 1994; Gillespie et al., 2008) suitable to cross the surrounding water (Whittaker & Fernández-Palacios, 2007). As a consequence, restricted immigration not only has a negative effect on island species richness, but it also creates a 'taxonomic disharmony', since taxonomic representation on islands is often biased towards groups that are good dispersers (Gillespie et al., 2008). This is mainly the case for oceanic islands that have never been connected to continents and "receive their biotas solely through dispersal" (Paulay, 1994); in contrast, a variety of taxonomic groups are often well represented on continental islands, since many of these were connected to mainlands until relatively recently, when they separated due to tectonics or postglacial sea-level rise (Whittaker & Fernández-Palacios, 2007). More groups from mainlands are also more likely to colonise continental than oceanic islands since the former are generally closer to continents (Whittaker & Fernández-Palacios, 2007).

The isolation of islands can enhance the vulnerability of their assemblages through different processes. First, because in situ diversification has played a more important role than colonization in generating the biodiversity of more isolated islands (Gillespie et al., 2008; Losos & Ricklefs, 2009), such islands often have very high levels of local endemism – since biotas of remote islands show evolutionary trajectories that are not influenced by evolutionary processes happening elsewhere (Losos & Ricklefs, 2009). Islands endemics usually evolve with lower pressures from predators, competitors and pathogens than do mainland species (Paulay, 1994; Denslow, 2003; Whittaker & Fernández-Palacios, 2007); therefore, they often show poor competitive abilities (Denslow, 2003), lack of defence strategies (Bowen & Van Vuren, 1997), loss of dispersal abilities (Cody & Overton, 1996; Gillespie et al., 2008) and reduced reproductive output (Adler & Levins, 1994; Siliceo & Diaz, 2010), all of which lower species' potential to face changes in their habitat and recover after disturbances. Furthermore, some island endemics have adapted to very particular ecological niches (i.e., through adaptive radiation – Paulay, 1994; Sakai et al., 2002; Gillespie, 2005) and can be highly specialized; such species are less likely to cope with the abiotic changes caused by habitat modification or to exploit human-dominated habitats. Although higher endemism is particularly associated with more isolated islands (Mayr, 1965; Gillespie, 2007), islands as a whole show higher average endemism than mainlands (Kier et al., 2009), which might contribute to a global pattern of higher vulnerability of island assemblages.

A second reason why isolation can enhance the islands' vulnerability to human pressures is that it prevents the rescue of declining populations, as more isolated islands are unlikely to be recolonized quickly from sites that have not been affected by human pressures (Simberloff, 1995b). Mainland settings have bigger native 'species pools' – i.e. the set of species whose propagules can reach a target community in reasonable time and establish there (Zobel, 1997; Gillespie et al., 2008) – than islands (Herben, 2005), since more sources of dispersing species are available, which reduces species extinction risk (Brown & Kodric-Brown, 1977).

Considering that remote islands (e.g., oceanic islands) have lower immigration rates (MacArthur & Wilson, 1963) and higher levels of endemism (Mayr, 1965; Gillespie, 2007), their assemblages are expected to be particularly vulnerable to habitat modification (e.g., Paulay, 1994; Keppel et al., 2014) compared to assemblages of continental or less isolated islands.

1.1.3 Effects of island area on island assemblages

Islands are geographically discrete landmasses with areas ranging from few hectares to large landmasses; but most are small (Weigelt et al., 2013; Delgado et al., 2017). One consequence of this size spectrum is that many island populations are small (Paulay, 1994; Wright, 1983). A small population size is known to increase species' sensitivity to habitat modification (Henle et al., 2004; Brook et al., 2008); for example, it leads to populations with more uniform genetic composition which usually cannot adapt to environmental changes (Mayr, 1965), increasing the likelihood of populations extinction (Lande, 1999).

Islands' restricted size also contributes to island species typically having more restricted geographic ranges than mainland species. Although some island natives might have a relatively broad distribution across several archipelagos or even mainland regions (e.g., if an island is very close to a continent or if a species manages to persist in both settings) (Whittaker & Fernández-Palacios, 2007), many are restricted to a single archipelago or island (i.e., single island endemics; e.g., Sakai et al., 2002; Paulay, 1994) with a small total land area. Moreover, island endemics can be restricted to very small areas within an island (e.g., a single volcano or areas smaller than 1 km^2 – Paulay, 1994; Gillespie et al., 2008), which has in part been attributed to these species losing dispersal ability (Gillespie et al., 2008) as an adaptation to reduce the likelihood being blown out to sea (Darwin, 1859; Carlquist, 1966; Cody & Overton, 1996). However, the narrow distribution of some species is interpretable in terms of habitat requirements and competition (Whittaker & Fernández-Palacios, 2007). For example, the 'taxon cycle' model (Wilson, 1961; Ricklefs & Cox, 1978) hypothesises that, after an island colonisation (e.g., by a widespread continental species), immigrant species tend to move from marginal habitats towards more central island habitats, partly driven by competitive interactions with later arrivals (Whittaker & Fernández-Palacios, 2007). As time passes, these species become increasingly specialized in their habitat requirements; this process therefore, limits the possibility for range expansion among island endemics (Webb & Gaston, 2000). A highly restricted habitat distribution also contributes to the small population sizes of some island natives (Brown, 1984; Gaston et al., 1997).

Regardless of its cause, the narrow geographic range of some island species increases their extinction risk (Purvis et al., 2000; Collen et al., 2016; Chen et al., 2019) from human activities. The underlying explanation is that human disturbances are more likely to affect the whole distribution of species with very narrow geographic ranges, and therefore affect all the species' populations (Charrette et al., 2006). Accordingly, it has been suggested that the reason why island species tend to be at greater risk of extinction from localized pressures is their highly restricted range rather than an inherent vulnerability (Simberloff, 1995b).

1.2 HUMAN PRESSURES ON ISLANDS AND MAINLANDS

Islands and mainlands not only have different ecological assemblages; they are also likely to experience different human pressures. The length of time since human colonisation can be one of the factors driving these differences; islands have been more recently colonized by humans compared to mainland settings (Keegan & Diamond, 1987), so at least some human pressures might have expanded and intensified more on mainlands (but see Kier et al., 2009), where humans have had more time to settle and exploit resources. Moreover, if islands have been experiencing human disturbances for a relatively short time, assemblages' responses might be in an earlier stage than on mainlands. For example, islands might still harbour species that are highly sensitive to human pressures (e.g., Spatz et al., 2017) – which are likely to be suffering strong declines where disturbances are taking place – whereas such species might have already disappeared on mainland settings as a result of a longer history of human settlement (Keegan & Diamond, 1987). Hence, on mainlands, only the more resilient species might have persisted through the 'extinction filter' (Balmford, 1996).

Pressures such as overexploitation, pollution and climate change have been pointed out as major drivers of biodiversity decline at a global scale (Maxwell et al., 2016). For islands, historical causes of species loss include predation by humans and the spread of diseases (Whittaker & Fernández-Palacios, 2007). However, across many systems (including islands: Paulay, 1994; Whittaker & Fernández-Palacios, 2007), land-use change and the introduction of species are currently the most – or among the most – important drivers of biodiversity loss (Sala et al., 2000; Brummit et al., 2015; Maxwell et al., 2016); therefore, here I focus on discussing patterns for these two pressures on islands and mainlands.

1.2.1 Land-use change and related pressures

Contrary to the expectations based on time since human colonization, in a global assessment, Kier et al. (2009) suggested that islands and mainlands have suffered an equal amount of habitat loss to date; these results were based on the percentage of total land area classified as cultivated or managed for the year 2000 (Bartholome & Belward, 2005). However, they found that the 'Human Impact Index' (Sanderson et al., 2002) – a composite measure quantifying human influence, based on global data on agricultural land, urban extent, population density, roads and navigable rivers (Kier et al., 2009) – was significantly higher for islands than for mainlands, and they predicted a future acceleration of habitat loss driven by land-use change for islands. As an explanation for the two latter findings, they suggested that islands' small size and high degree of infrastructure makes them more vulnerable to habitat loss or modification because access to pristine sites can be easier than on mainlands (Kier et al., 2009).

Kier et al.'s (2009) results might reflect global trends; however, rates of habitat modification can vary greatly across islands or within mainland regions. Particular islands, geographic regions or countries can be suffering an extensive habitat conversion; for example, Ramankutty et al.'s (2008) global maps of agricultural lands (for the year 2000), which combined agricultural inventory data and satellite data, showed that Southeast Asia and the Pacific are among the island-rich regions having a high percentage of croplands and pastures, respectively. For mainlands, the regions with the highest proportion of croplands are South Asia, Europe, and the United States, while regions with the highest proportion of pastures are some parts of South and Central America, Tropical Africa, China and the United States. Notably, from Ramankutty et al. ‘s (2008) results for 14 geographic regions, it seems that the proportion of land area with agricultural lands tends to be particularly high in some mainland regions.

Such geographic variation in the degree of habitat modification can be driven by multiple factors such as economic development and human population density (Meyer & Turner, 1992; Lambin et al., 2001; Liping et al., 2018). It is normally assumed that habitat conversion has occurred more rapidly in developed regions (Meyer & Turner, 1992); however, some studies suggest that high rates of land-use change and human population growth are taking place in regions with developing economies (Cohen, 2003; Laurance et al., 2014). A large proportion of islands (particularly small islands) belong to developing countries (Turvey, 2007), which might be an important factor defining global patterns of island land-use change. In particular, the rates of land-use change on islands can also vary according to different island characteristics. Island size, age, altitude, topographical complexity and isolation can determine space and resource availability, habitability for humans, and therefore patterns of human occupation (Delgado et al., 2017). The extraction of natural resources is likely to be more intense on larger islands than on smaller islands, since they provide a greater amount and diversity of resources (Delgado et al., 2017); moreover, larger islands are more likely to have permanent human populations and therefore greater land-use change (Trevino et al., 2007; Didham et al., 2005).

While human population growth is related to land-use intensification (e.g., expansion of agriculture and urban areas – Grimm et al., 2008; Laurance et al., 2014), human populations are also the source of additional pressures that can affect more natural habitats, such as the development of roads or hunter-gathering practices (Cincotta, 2011). Cincotta et al. (2000) estimated that, in 1995, 20% of the world population were living within biodiversity hotspots; they highlighted three hotspots “with the most elevated risks, as assessed by high human population density” (Cincotta et al., 2000), all of which are entirely or mostly made up of islands (i.e., the Caribbean, Western Ghats/Sri Lanka and Philippines hotspots). More recently, Williams (2013) reported high human population densities in the Sundaland and Wallacea hotspots and high population growth rates in the Philippines, Madagascar (and the Indian Ocean islands) and Pacific Islands region. These results are alarming because the spatial constriction of islands brings a higher human population density close to natural habitats with vulnerable biota (Delgado et al., 2017).

In summary, whether the extent and intensity of land use and related pressures differs systematically between islands and mainlands remains unclear. Habitat loss has been a major driver of species extinctions in many ecological systems (Brooks et al., 2002; Brook et al., 2003; Sodhi et al., 2009), and some studies have pointed out extreme cases of loss of forest cover or habitat transformation on islands, which have driven the extinction of many island species (Paulay, 1994; Myers et al., 2000; Whittaker & Fernández-Palacios, 2007; Delgado et al., 2017; Johnson et al., 2017). However, there has not yet been a multi-taxon synthesis of the impacts of land-use change on island ecological assemblages at the local scale.

1.2.2 Introduction of species

International trade is a primary source of introduction of alien species (Levine et al., 2003; Early et al., 2016). The number of species introduced to a defined location (i.e., colonisation pressure – Lockwood et al., 2009) increases with economic development – e.g., with increasing GDP per capita (Dyer et al., 2017a), and regions with high economic development tend to have more alien species (Hulme, 2009; Capinha et al., 2017). These patterns have been mainly attributed to the high trade volumes and high levels of pet trade in high-income countries (Early et al., 2016; Dyer et al., 2017a), which increase the chances of introducing of species as stowaways (Helmus et al., 2014) and lead to the of escape of imported species into the wild (Reichard & White, 2001; Hulme et al., 2008), respectively. Additionally, alien species can be intentionally introduced in a particular location for other economic purposes, such as forestry or agriculture (Pyšek et al., 2010; Monroe et al., 2017) or for cultural reasons – for example, many species were introduced by European settlers on some islands as an attempt to recreate their home environments (Atkinson & Cameron, 1993).

As well as the factors determining the introduction of alien species to a particular location, a further range of factors contribute to their establishment success. Higher establishment success of alien species has been related to event-level processes (Redding et al., 2019) such as a high propagule pressure (i.e, number of released individuals – Lockwood et al., 2005) (Forsyth & Duncan, 2001; Britton & Gozlan, 2013; Redding et al., 2019), but also to specific characteristics of the recipient location such as climatic suitability for the alien species and anthropogenic factors such as the presence of human disturbances, extinctions of natives or the presence of other alien species (Blackburn & Duncan, 2001; Sax et al., 2002; Jeschke et al., 2012; Duncan et al., 2014; Redding et al., 2019). In particular, previous studies have highlighted how the establishment of alien species is strongly related to habitat modification (e.g.; Lozon & MacIsaac, 1997; Didham et al., 2007) and that disturbance or land-use change often drives an increase in richness or abundance of alien species (Lonsdale, 1999; Borges et al., 2006; Meijer et al., 2011). Establishment success can also be related to traits of alien species, for example their adaptive history (Redding et al., 2019) which can make them "competitively superior to natives" (Sax et al., 2002) and particularly successful in disturbed environments (Sax & Brown, 2000).

Many studies have highlighted that islands are particularly invasible (Simberloff, 1995a; Denslow, 2003; Whittaker and Fernandez-Palacios, 2007; Dalmazzone & Giaccaria, 2014), and recently, islands have been pointed out as hotspots for alien species richness (Capinha et al., 2017; Dawson et al., 2017). This pattern has mainly been discussed in terms of the characteristics of island assemblages (a location-level factor– see Redding et al., 2019) that make islands more vulnerable to invasions than mainlands (Sax & Brown, 2000; Denslow, 2003; Pyšek & Richardson, 2006). For example, islands' species poverty and ecological undersaturation can make them less resistant against invaders (i.e., 'biotic resistance' theory, Elton, 1958; but see Lonsdale, 1999), and the reduced competitive ability of natives can favour the establishment of alien species (Denslow, 2003). Alternatively, it has been suggested that islands are more invasible than mainlands simply because of their smaller pool of native species (Herben, 2005; Gillespie et al., 2008), which leads to a low species richness per unit area and a restricted sample from a set of potential species that can establish in different habitat conditions (Herben, 2005). Given that alien species are often good dispersers (Sakai et al., 2001; Cadotte et al., 2006; Ordonez et al., 2010) and they tolerate a broad range of conditions (Sakai et al., 2001), on islands, aliens are more likely to colonize open ecological spaces (e.g., disturbed sites) than are natives (Gillespie et al., 2008).

In terms of the rates of introduction of alien species, the low economic development of many islands (Turvey, 2007) may imply low levels of international trade and thus little colonization pressure. However, previous studies have discussed how on islands – particularly remote islands (Blackburn et al., 2008) – intentional releases of alien species can be very common, perhaps because the low diversity of native species means that more species need to be introduced for economic purposes; e.g., for species trade, farming or as sources of fuel (Denslow, 2003; Blackburn et al., 2008; Dalmazzone & Giaccaria, 2014). Unintentional introductions might also be very common on some islands that have been "important provisional stations for transoceanic shipping traffic" (Denslow, 2003) or that rely on tourism (see Anderson et al., 2015); such islands are exposed to the introduction of species from many different sources (Denslow, 2003). These studies highlight that, as a consequence of anthropogenic factors, islands are no longer 'sea-isolated entities' (Delgado et al., 2017) which follow the expected species-isolation relationship (Helmus et al., 2014). Currently, island biogeography can be mainly dominated by anthropogenic factors and the introduction of species might be obscuring natural processes (Blackburn et al., 2008; Helmus et al., 2014; Nakamura et al., 2015).

Many extinctions of island species have been related to the introduction of alien species (Paulay, 1994; Sax et al., 2002; Blackburn et al., 2004; Clavero et al., 2009; McCreless et al., 2016), mainly as a consequence of predation or competition (Sax & Gaines, 2008; Whittaker & Fernández-Palacios, 2007). Alien species can be the main driver of extinctions for some taxa on islands (Clavero et al., 2009; Bellard et al., 2016). Additionally, the displacement of a native keystone species on islands can produce severe shifts in a whole ecosystem, affecting several trophic levels and reconfiguring species interactions (O'Dowd et al., 2003) – e.g., as a result of islands' low functional equivalence (Denslow, 2003) and simple food webs (Pimm, 1991).

Considering the human pressures that islands face and the sensitivity of their assemblages, it is not surprising that a recent study highlighted that almost half of the world's highly threatened terrestrial vertebrates occur on islands (Spatz et al., 2017). Higher extinction rates have also been reported on islands than on mainlands (Humphreys et al., 2019), with most known historical extinctions (e. g., over the last 500 years – Whittaker & Fernández-Palacios, 2007; Sax & Gaines, 2008) having happened on islands. Endemism has been suggested as the main factor determining extinction on islands, obscuring the effect of intensity of human pressures (Sadler, 1999). However, both the intensity of human pressures on islands and unique traits of their assemblages are likely to determine the severity of changes that island assemblages are suffering. Importantly, the combination of these two factors may combine to cause a more severe biodiversity loss on islands than on mainlands.

1.3 THESIS OVERVIEW

This thesis represents the first global analysis, including a wide range of taxonomic groups, comparing the effects of land-use change and related human pressures on local biodiversity on islands and mainlands. My analyses aim to assess the effects of land-use change on multiple aspects of island and mainland biodiversity, so involve statistical models for a range of biodiversity measures. Furthermore, the thesis includes an analysis of how land-use change affects the local diversity of alien and native species on islands. The modelling approaches used and developed throughout the thesis have also contributed to a new implementation for the Biodiversity Intactness Index (BII) (Scholes & Biggs, 2005) (see details below); in the last chapter, I demonstrate that this new implementation is an improvement on that of Newbold et al. (2016a).

All statistical modelling in this thesis uses data on species abundance and occurrence extracted from the PREDICTS (Projecting Responses of Ecological Diversity in Changing Terrestrial Systems) database (Hudson et al., 2017) in October 2016. The PREDICTS database has collated data from published research (or unpublished theses where field sampling had used published methods) that compared local biodiversity across sites facing different land uses and related pressures. In compiling the database, efforts prioritised under-represented taxa and biomes, in order to make the database – and therefore models fitted to its data – reasonably representative of terrestrial biodiversity (Hudson et al., 2017). The database is structured hierarchically into Data Sources (publications), Studies (different sampling methods within a source), Blocks (spatial blocks, if present in the study) and Sites (Hudson et al., 2014; Hudson et al., 2017). The sites in the database are classified into 10 land-use categories and three land-use intensities (Minimal, Light and Intense) within each land use; these land-use and use-intensity categories are defined in Table A.1 and in Hudson et al. (2014). The dataset extracted in October 2016 included data for 49,511 species (Figure 1.1) from 540 Data Sources, 747 Studies and 31,248 sites in 97 countries across all 14 terrestrial biomes (Figure 1.2). More detailed description for island and mainland data is provided in the following chapters.

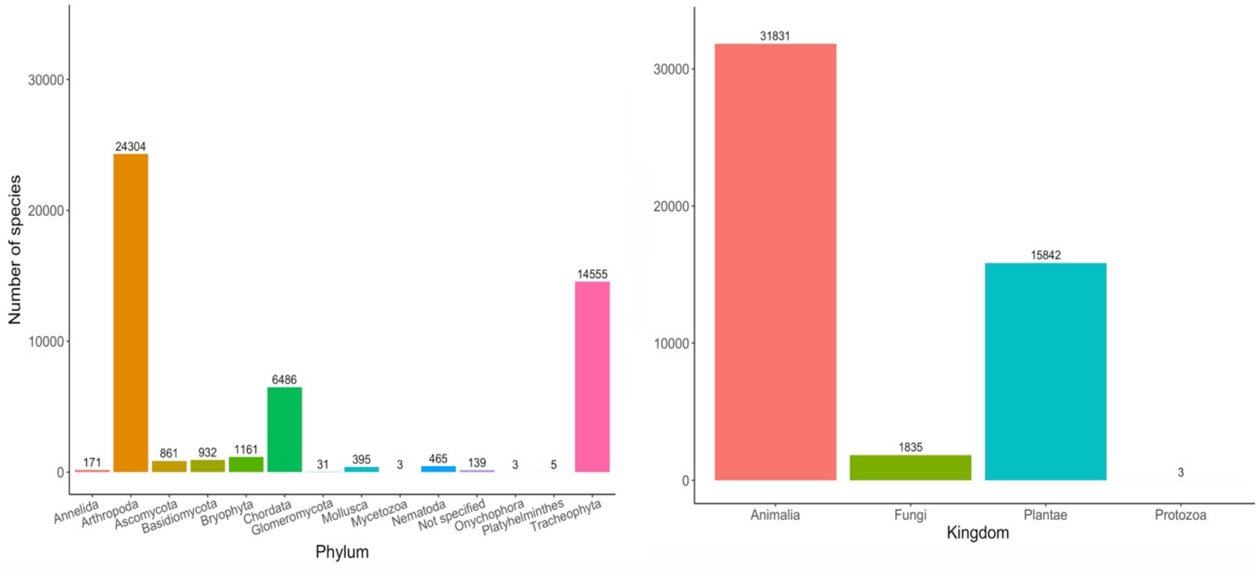


Figure 1.1. Number of species (per Phylum and Kingdom) included in the dataset extracted from the PREDICTS database in October 2016.

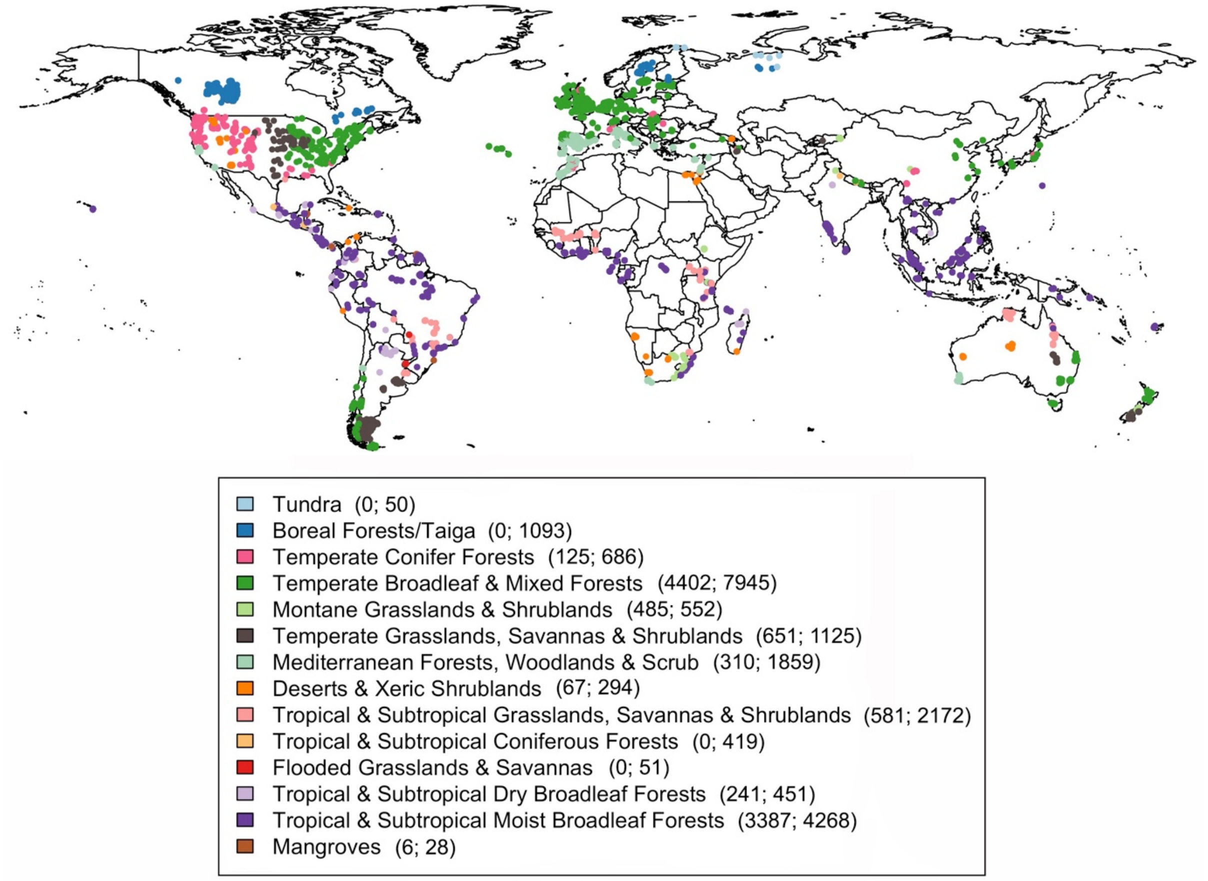


Figure 1.2. Locations of sites included in the dataset extracted from the PREDICTS database in October 2016. Sites are coloured according to the biome where they are located. Numbers in brackets show the number of island and mainland sites per biome (first value: island sites, second value: mainland sites).

The core of this thesis is the Biodiversity Intactness Index (BII), "an indicator of the average abundance of a large and diverse set of organisms in a given geographical area, relative to their reference populations" (Scholes & Biggs, 2005). BII was proposed as a suitable interim metric for assessing biotic integrity in the Planetary Boundaries framework (Steffen et al., 2015), despite at that time only having been estimated using expert judgement (Scholes & Biggs, 2005). In order to provide a scientifically robust indicator of the state of biodiversity (e.g., for any given area and using data across multiple taxa), the PREDICTS project developed a BII implementation based on the modelling of its global collation of site-level biodiversity data (Newbold et al., 2016a; Purvis et al., 2018; Chapter 3). PREDICTS' implementation of BII has become a high-profile biodiversity indicator: it has been adopted by the Convention on Biological Diversity (CBD), the Intergovernmental Science-Policy Platform for Biodiversity and Ecosystem Services (IPBES) and the Biodiversity Indicators Partnership (BIP) as an indicator for tracking progress towards biodiversity targets such as the Sustainable Development Goals and the Aichi 2020 Targets. It has attracted criticism, however; for example, Martin et al. (2019) pointed out that BII estimates from Newbold et al. (2016a) were unexpectedly high for some regions that have suffered widespread habitat loss.

Although all chapters in this thesis are related to the development, testing and refinement of BII, each of them addresses different questions about the effects of land-use change on aspects of island and mainland biodiversity. Chapter 2 asks whether the change in species composition caused by land-use change differs quantitatively between islands and mainlands. Chapter 3 combines statistical modelling with projections from those models to ask whether land use and related pressures have compromised biotic integrity – as estimated by BII – more severely on islands than on mainlands. Chapter 4 focuses exclusively on island assemblages, separating their species into natives and aliens to ask how does land use and related pressures affect diversity (species-richness, total abundance and species composition) of alien and native species on islands. The final chapter synthesises how the earlier chapters have refined the implementation of BII, asking which methodological change has the greatest effect and whether the changes are improvements. The thesis concludes with a brief general discussion.

The statistical analyses of all chapters are based on generalized mixed-effect models (GLMMs: Bolker et al., 2009). These models are needed in order to deal with the methodological heterogeneity among the studies' methods, taxonomic focus and location (e.g., differences in sampling method and effort, sampled taxa and broad-scale biogeographic differences); they are also able to accommodate differences among spatial blocks within the studies that have blocked or split-plot designs. GLMMs provide a robust approach for quantifying the variation in the response variable among studies and blocks (random-effects) without needing to estimate coefficients for each study and block (Bolker et al., 2009).

Chapters 2 and 3 respectively focus on comparing the effects of land use on the composition of local species assemblages and local biotic integrity (BII) on islands and mainlands. In order to do so, the analyses of these chapters are based on models that include interactions between the sites' Island/Mainland status and the human pressures included as explanatory variables in the models. The models in Chapter 3 are also used to project high-resolution (~1km^2) global maps of BII for the year 2005, which account for different responses between island and mainland assemblages. In contrast, Chapter 4 focuses exclusively on islands, to evaluate whether alien and native species respond differently to land-use change and related pressures, considering that island native species can be particularly vulnerable to human disturbances and that islands are at higher risk of invasions. Hence, these models for local species richness, total abundance and composition of local species assemblages include interactions between the species' alien/native status and various human pressures. In Chapter 4 I also fit models to test whether island traits (e.g., island area and isolation) and indices of economic connectance (e.g., GDP per capita) predict local richness and total abundance of alien species on islands.

Finally, in Chapter 5 I assess my implementation of BII (developed in Chapter 3) which not only allows pressure effects to differ between islands and mainlands but also includes improvements on the methods previously used to estimate BII globally (Newbold et al., 2016a). I compare my island and mainland BII estimates against global estimates in Newbold et al. (2016a) and, using estimates generated in Chapter 4 of how native species on islands respond to human pressures, I project additional high-resolution global maps of the status of island native biodiversity for year 2005. These maps, which estimate BII for islands without the need for some of the assumptions and caveats that Newbold et al. (2016a) required, are compared against island BII maps from Chapter 3 to test how well they reflect the intactness of native biodiversity. This chapter represents the first test of the validity of PREDICTS' implementation of BII.

CHAPTER 2

Differences in species assemblages among and within land uses on islands and mainlands

2.1 ABSTRACT

The transformation of natural habitat into human-dominated land uses not only causes a decline of narrow-ranged native species but also favours many widespread species that can tolerate disturbed conditions. Such processes change the species composition of assemblages of natural habitats and contribute to biotic homogenization. Global syntheses of how land-use change affects compositional similarity among assemblages are scarce and seldom consider whether these effects differ among geographic regions or ecological systems, such as islands and mainlands – two systems with very different species assemblages, environmental conditions and human pressures. In this chapter, I test whether island assemblages are more susceptible to compositional changes than mainland assemblages, as expected from the vulnerability of their endemic species to human pressures and susceptibility of their assemblages to the establishment of alien species. I estimate assemblage turnover caused by land-use change on islands and mainlands, test for biotic homogenization in human-dominated land uses on both systems, and explore whether island isolation and size can explain the differences seen between island and mainland responses. In models including all taxa, the compositional difference between minimally-disturbed primary vegetation and most human dominated land uses is greater on mainlands than on islands. Island size and isolation do not seem to have a strong effect on compositional similarity between sites on the same island; however, the greater compositional changes on mainlands could be the result of mainland sites facing more intense land use, and having bigger species pools (which provide more synanthropic species that can be assembled in disturbed sites) than island sites. In contrast, when running separate models for plant/fungal and animal assemblages, I found some cases (masked in models including all taxa), where land-use change causes greater compositional changes in island assemblages, mainly because of novel species becoming abundant. I suggest that such cases result from islands' natural species poverty and vulnerability of native species, which can ease the establishment of novel species in disturbed sites. Finally, on both islands and mainlands, most land uses mainly reduce spatial beta diversity of plant/fungal assemblages. The different responses of island and mainland

assemblages to land use should be incorporated into global biodiversity models to avoid systematic mis-estimations of the effects of human pressures on island biodiversity.

2.2 INTRODUCTION

Conversion of natural habitat to human use is a major driver of species' global extinction risk (Brummitt et al., 2015; Maxwell et al., 2016), and also drives net reductions in local-scale species richness (Gibson et al., 2011; Murphy & Romanuk, 2014; Newbold et al., 2015) and population sizes (WWF, 2016). Here I focus on an intermediate spatial scale, analysing the effects of land-use change on the compositional similarity between local assemblages.

The transformation of primary vegetation into human-dominated land uses tends to favour species that are able to thrive under disturbed conditions (McKinney, 2006; McCune & Vellend, 2013). Such species are often widespread or invasive (Newbold et al., 2018), often introduced by humans (McKinney & Lockwood, 1999), tend to tolerate a broad range of conditions (Sakai et al., 2001), and often have strong reproductive and dispersal abilities (Hamilton et al., 2005; Cadotte et al., 2006; McKinney, 2006). At the same time, the transformation causes a decline of native and narrow-ranged species in human-dominated land uses (McKinney & Lockwood, 1999; Scholes & Biggs, 2005; Newbold et al., 2018). Both these processes contribute to biotic homogenization (Socolar et al., 2016; Newbold et al., 2018); i.e., they result in species composition tending to be more similar between sites in human-dominated land uses than among undisturbed habitats (Socolar et al., 2016).

To date, despite convincing case studies (e.g., Gossner et al., 2016), few global syntheses have assessed how land-use change affects compositional similarity among terrestrial assemblages. One reason for the shortage is that estimating compositional similarity requires the site-by-species data matrix (which is often not presented in source papers), whereas meta-analyses can estimate the effects of land use on species richness from statistical summaries (which source papers nearly always do present) (Purvis et al., 2018). Another is that compositional similarity between assemblages is expected to decline with increasing geographical and/or environmental distance between them – a relationship known as the distance-decay curve (Nekola & White, 1999) – meaning that the locations of sites must also be known. The most recent global synthesis (Newbold et al., 2016b) showed that land use strongly reshapes local assemblages, with those in human-dominated land uses or an early successional stage of recovery being very dissimilar from those in primary vegetation, especially in the tropics; but that (distance-corrected) similarity of assemblages in the same land use did not differ strongly among land uses.

Newbold et al. (2016b) did not consider whether effects of land use on compositional similarity differed between islands and mainlands, even though there are several reasons why island biotas are likely to be particularly susceptible to biotic homogenization. Islands' small size makes them more vulnerable to habitat destruction because access to pristine sites can be easier and faster than in mainlands (Kier et al., 2009). Low rates of natural immigration to isolated islands can prevent the recovery of declining populations (Lomolino, 1986). Endemic species can lack the potential to face changes in their habitat if evolutionary isolation has led to the loss of traits that ease populations' recovery after disturbances; for example, loss of dispersal abilities (Gillespie et al., 2008) and reduced reproductive output (Adler & Levins, 1994). Endemic species might be particularly vulnerable on small, remote islands which often shelter more rare and fragile species and ecosystems (Delgado et al., 2017) and which have more limited resources (Whittaker and Fernandez-Palacios 2007; Delgado et al., 2017). Moreover, islands are also more susceptible than mainlands to the establishment of alien species (Simberloff, 1995a; Sax & Brown, 2000; Denslow, 2003; Dalmazzone & Giaccaria, 2014), perhaps because their species poverty (caused by their isolation and low colonisation rates – Whittaker & Fernández-Palacios, 2007) means that newcomers may find vacant niches, reduced competition from native species (Roderick & Vernon, 2009; but see Lonsdale, 1999) and more available resources (Denslow, 2003). It has also been suggested that the small pool of native species on islands (Herben, 2005) – i.e. the set of native species whose propagules can reach a target community in reasonable time and establish in the given habitat (Zobel, 1997; Gillespie et al., 2008) – increases the chances for alien species to colonize open ecological spaces, especially if the aliens have a higher propagule pressure than do island natives (Gillespie et al., 2008). Recent studies have pointed out islands as hotspots of alien species (e.g., Capinha et al., 2017; Dawson et al., 2017; Dyer et al., 2017a), and shown that geographic isolation may now be less important than economic isolation as a barrier to the arrival of alien species (Helmus et al., 2014).

If land-use changes do indeed cause greater compositional changes on islands than on mainlands, this would be concerning, given the unique biodiversity that many islands harbour (for example, the Wallacea biodiversity hotspot is entirely made up of islands: Myers et al. 2000). However, previous global models of how land-use change affects biodiversity (e.g., Newbold et al., 2016b; Alkemade et al., 2009) have so far not assessed the possibility, implicitly assuming that island and mainland biotas respond the same way to land-use change. There is therefore a risk that current models may be providing overoptimistic pictures of the state of island biodiversity (and correspondingly pessimistic estimates of the state of biodiversity on mainlands). Conversely, if a given land use tends to be less damaging on islands (e.g., due to factors such as low economic development – Turvey, 2007, or more recent human colonization than on mainlands – Keegan & Diamond, 1987), then models not incorporating land-use intensity may have overestimated the impacts on islands.

My study aims to resolve these issues by answering three main questions: 1) Does the change in species composition caused by land-use change differ significantly among islands and mainlands? I address this question by comparing compositional similarity between sites in minimally-disturbed primary vegetation with matched sites in other land use/use intensity combinations, on both islands and mainlands. 2) Does average compositional similarity between matched sites that have the same land use differ between islands and mainlands? This question is tackled by comparing compositional similarity of sites within the same land use on islands and mainlands, to test whether biotic homogenization in human-dominated land uses is more pronounced on islands. 3) Do island isolation and size explain how island assemblages respond? In interpreting the results, I also explore whether taxonomic differences between island and mainland data sets could explain any differences, given that species' responses and vulnerability can differ greatly according to their ecological and life history traits (Cardillo et al., 2005; Barbaro & van Halderand, 2009; Newbold et al., 2013; De Palma et al., 2015).

2.3 METHODS

2.3.1 Data assemblage

All data on species' abundance and presence/absence at sites were extracted from the PREDICTS database (Hudson et al., 2017 and described in detail in Chapter 1) in October 2016. Each site was classified as an island or mainland site by matching the coordinates with a global layer of land polygons taken from OpenStreetMap (OpenStreetMap Contributors, 2015). I define islands as land masses completely surrounded by ocean and smaller than continents, but here treated Australia as an island for two reasons. First, many of its characteristics are more island-like than continental: e.g., complete isolation from other continents by ocean, long isolation history (complete isolation ~ 33 Mya - Wilford & Brown, 1994) and relatively small size. Second, treating Australia as an island helped to improve the balance between island and mainland sites in my analyses. Repeating my analyses with Australia classed as a mainland did not change results qualitatively (Table B.6). The name of the island where each site was located was determined by matching the site coordinates with the Global Island Database, ver. 2.1 (UNEP-WCMC, 2015).

Sites had previously been classified into ten land-use categories and three land-use intensities (Minimal, Light and Intense) within each land use (Table A.1; Hudson et al., 2014). To obtain reasonable sample sizes (at least 100 sites) within each land-use category for both islands and mainlands, the ten land-use categories and three use intensities were collapsed into seven final land use/intensity classes: 1) Primary vegetation (Primary forest + Primary non-forest) with minimal use, 2) Primary vegetation (light and intense use combined), 3) Secondary vegetation (young + intermediate + mature + indeterminate secondary vegetation), 4) Plantation forest, 5) Cropland, 6) Pasture and 7) Urban (last five categories include all use intensities). Primary vegetation with minimal use (henceforth PriMin) was selected as a baseline for analyses, representing minimally disturbed sites. Even these sites with the most natural conditions will often have experienced human influence (e.g. Watson et al., 2016); to the extent that such influence has made the biota of such sites more similar to that in other land-use classes, my analyses will underestimate the effects of land use (Purvis et al., 2018).

Other site variables extracted from the database and used in analysis were sampling effort, diversity metric type (e.g., species richness and abundance), coordinates and maximum linear extent sampled (metres; this refers to the length of the maximum distance between multiple sampling points within a site, e.g., the extent of a single quadrat, transect or the extent that multiple traps cover within a site). Studies that did not report abundance data, that sampled only a single species, or where sampling effort varied among sites were excluded from analysis, as were any sites with unknown land use/intensity.

2.3.2 Statistical modelling

All calculations and statistical modelling used R Version 3.2.3 (R Core Team, 2017). My strategy for estimating the assemblage turnover caused by land-use change on islands and mainlands was to model two measures of compositional similarity (one abundance-based and one species-based) between pairs of sites as a function of the sites' land uses and the geographic and environmental distance between them. Pairwise comparisons were therefore excluded if the environmental distance could not be calculated due to missing data or if the estimated geographic distance equalled zero (due to lack of coordinate precision).

Newbold et al. (2016a; 2016b) chose pairs of sites to compare in such a way as to avoid any nonindependence among comparisons, limiting the complexity of the statistical models they were able to consider. Here, I use a different strategy, making all possible pairwise comparisons between sites, using matrix regression – explained in more detail below – to fit models (which can be as complex as required) to these non-independent comparisons, and using carefully-structured randomisation tests to assess term significance.

2.3.2.1 Compositional similarity

I calculated two measures of compositional similarity between sites i and j: the richness-based asymmetric Jaccard Index, J_R (= S_{ij} / S_j, where S_{ij} is the number of species common to both sites and S_j is the number of species in site j – Newbold et al., 2016a), and the abundance-based asymmetric Jaccard index, J_A (= A_{ij} / A_j, where A_{ij} is the summed abundance at site j of all species common to both sites and A_j is the summed abundance of all species at site j – Chao et al., 2004). Asymmetric measures were chosen to reflect the possibility of one site's assemblage being largely nested within another (Baselga, 2010). To see the relevance for this asymmetric metric, consider a hypothetical land use in which the assemblages have 50% of the species found in primary vegetation and no additional species. Any organisms found in these sites are bound to belong to species also found in primary vegetation, so should contribute towards compositional similarity; a symmetric measure of compositional similarity would fail to recognise this nestedness. Both measures are zero if two sites share no taxa in common, one if all taxa at site j are also present at site i, and undefined (and hence dropped from analysis) if neither site had any organisms sampled.

These asymmetric metrics, J_R and J_A, are affected by changes in richness or abundance of species in site i but are more strongly shaped by the presence and abundance of unique species in site j (i.e., species reported from site j but not from site i). Low J_R or J_A values are mainly the result of a high number or high abundance of novel species in site j increasing the denominators in the calculations. Many metrics of compositional similarity are available (Koleff et al., 2003; Tuomisto, 2010; Newbold et al., 2016b). These were chosen because they are used to estimate the Biodiversity Intactness Index (Newbold et al., 2016a; Purvis et al., 2018), so significant island/mainland differences in their responses to land use will feed directly into this indicator being systematically mis-estimated.

I made both forward and reverse comparisons between every pair of sites within each study (i.e., sampling method within a data source in the PREDICTS database – Hudson et al., 2014); comparing sites from different studies would be inappropriate due to their methodological differences. Four studies included sites in different islands, meaning that just under 1% of comparisons (13,480 out of 1,469,538) of island sites were between rather than within islands; dropping these comparisons did not change any models qualitatively.

2.3.2.2 Explanatory variables

Statistical models included four explanatory variables as follows. (1) Geographic distance between sites i and j (to account for distance-decay), calculated from the sites' coordinates using the '*distHaversine*' function in the '*geosphere*' package ver. 1.5-7 (Hijmans, 2017). (2)

The environmental distance between the sites (to account for decay of similarity with environmental distance), estimated as the Gower (1971) dissimilarity between sites based on site-level data for altitude and four bioclimatic variables (maximum and minimum temperature and precipitation of wettest and driest month) at 1-km spatial resolution (Hijmans et al., 2005); I used the '*gower_dist*' function in the '*gower*' package ver. 0.1.2 (van der Loo, 2017). (3) Land-use contrast (a 49-level factor indicating the land uses/intensities of sites *i* and *j*:, e.g. PriMin-Cropland). All 49 levels had sample sizes > 3000 on both islands and mainlands, except for PriMin-Urban on islands (Table B.1). Only two island studies in the PREDICTS database sampled in both PriMin and urban sites; I address this issue in the next section (Modelling). (4) Whether the pair of sites was on an Island or a Mainland; all studies in the PREDICTS database are either on a mainland or one or more islands, so no island site was ever compared with a mainland site.

Although all data were used in fitting models, I focus on only two sets of land-use contrasts in my results and discussion. The set of seven contrasts in which site *i* was PriMin allows estimation of how the species composition of minimally-disturbed sites is affected by change to each other land use. The set of seven contrasts where both sites are in the same land-use/intensity class allow estimation of how similar communities are among sites facing similar pressures. Hence, I discuss the effects of 13 land-use contrasts (Table B.1; PriMin-PriMin is in both sets) on compositional similarity on islands and mainlands. Results for all land-use contrasts are reported in Table B.5.

2.3.2.3 Models of land-use effects on island vs. mainland assemblages

Richness-based (J_R) and abundance-based (J_A) compositional similarity were modelled separately as linear mixed-effect models (Zuur et al., 2009) using the '*lme4*' package ver. 1.1-15 (Bates et al., 2017), to deal with the great methodological heterogeneity among studies (see Chapter 1) which might affect comparisons but whose effects are not themselves of interest.

The four explanatory variables listed in the previous section were treated as fixed effects, with two-way interactions between an Island/Mainland term and the other three fitted to test for different effects on islands and mainlands. Study was included as a random intercept. The PriMin-PriMin contrast was used as the intercept level in the models, since this contrast reflects the natural spatial turnover of species, making it a natural baseline against which to compare the other land-use contrasts.

Compositional similarity estimates were logit-transformed prior to analysis, which has advantages in power and interpretability over other transformations of proportional data

(Warton & Hui, 2011). I used an adjustment of 0.01 to avoid values of -∞ and ∞ that arise from logit transformation of 0 and 1 (Warton & Hui, 2011). Previous analyses of the PREDICTS database have used log-transformation for compositional similarity estimates, which produced well-behaved residuals (Newbold et al., 2016a; 2016b); however, such transformation does not account for the possible range of compositional similarity estimates.

Environmental and geographic distances were transformed, because both included extreme values (Zuur et al., 2007). I chose for each variable the transformation that most closely approached a normal distribution. Environmental distance was transformed using cube root. Geographic distance was first rescaled by dividing it by the median of sites' maximum linear extents, and then log-transformed; as a result, a transformed geographic distance of zero corresponds to sites separated by their median linear dimension, i.e., adjacent sites. This contrasts with previous methods in Newbold et al. (2016a, 2016b), where geographic distance was log-transformed, meaning that sites were implicitly separated by 1 m (because distances were measured in meters and log 1 = 0), an arbitrary distance. These transformations improved model fit, as judged by the Akaike Information Criterion (AIC; see Table B.4), and model diagnostics suggest that data treatment was adequate (Figure B.5).

These matrix regression models – using all pairwise comparisons – inevitably have extensive pseudo-replication, because pairwise comparisons that involve the same site are not independent. The non-independence means that standard statistical approaches cannot be used to simplify the fixed effects of the models. I therefore used permutation tests to determine whether fixed-effects of the models could be simplified without losing explanatory power. My permutation tests are conceptually identical to the treatment of non-independence in multiple regression on distance matrices (MRM) (Lichstein, 2007), an extension of partial Mantel analysis (Smouse et al., 1986).

To perform backwards stepwise model simplification, I first performed normal likelihood ratio tests for my full model against the reduced model. As a second step, I permuted the model dataset (using the '*permute'* package ver. 0.9-4: Simpson, 2013) by randomly shuffling the compositional similarity data within studies (i.e., rows of the response variable within each study) while holding all explanatory variables constant. I then fitted the full and reduced models with the permuted dataset and performed a likelihood ratio test. I repeated this permutation process 199 times to generate null distributions for the likelihood ratios. This number of permutations was enough to get distributions approaching normality. The p-values were calculated by performing a "greater" hypothesis test, where I compared the likelihood ratio from my models (observed value) against the distribution of the null likelihood ratios (comparison of 200 values: observed value + 199 null likelihood ratios), using the '*as.randtest'* function from the '*ade4'* package ver. 1.7-10 (Dray et al., 2007). This test analysed whether the likelihood ratio of my models was higher than expected based on a model comparison with the same difference in degrees of freedom but no real loss of explanatory power. In most cases (see exceptions below), the test was required only for the three interaction effects in my models since model simplification was not possible; i.e., all interaction effects showed significant p-values (0.005 in most cases, meaning that the observed effect always exceeded every permutation trial). The statistical significance of interactions between island/mainland and the other explanatory variables was tested in the same way, except that comparisons between model coefficients and the coefficients obtained from the permutation trials were two-tailed. Interaction coefficients that do not differ from the null distributions indicate no real difference between the effects of the different variables for islands and mainlands.

The overall model intercepts estimate (logit-transformed) J_R and J_A, for PriMin-PriMin contrasts on islands when (transformed) environmental and geographic distances were zero. Estimates for (logit-transformed) compositional similarity of each land-use contrast on islands were obtained by adding the model intercept to the contrast coefficients for islands; comparable values for mainlands were obtained by adding the model intercept and the PriMin-PriMin mainland coefficient to the contrast coefficients for mainlands plus each of the same island contrast coefficient. Calculating the inverse logit for these final island and mainland values converted them back to the original scale from 0 to 1.

Only two of the island studies included the PriMin-Urban contrast, which is too few for random effects to be estimated reliably (Bolker et al., 2009). Therefore, I also estimated this coefficient indirectly, as the product of estimated PriMin-Secondary and Secondary-Urban compositional similarities (in a 0 to 1 scale) – as coefficients for these contrasts could be estimated from 38 and 10 island studies, respectively (enough for reliable estimation: Bolker et al., 2009). The indirect estimates were logit-transformed and the respective model's intercept (PriMin-PriMin island contrast) was subtracted to transform these values into model coefficients (Table B.5). Good agreement between the two estimates of the PriMin-Urban compositional similarity on islands would have suggested that the original estimate was reasonable; but there was a strong disagreement (Table B.5) indicating the need for caution in interpreting it. Although based on more data, this second estimate makes the additional assumption that assemblages in secondary vegetation are directly between assemblages in primary minimal and urban sites on a straight line through multidimensional compositional space; this assumption means that this second approach is likely to underestimate the true similarity between PriMin and Urban to some degree. Given the uncertainty around the original estimate, I have tentatively used the indirect estimate.

Finally, I modelled J_R and J_A, in animal and plant/fungal assemblages separately (i.e., four additional models) to obtain a more detailed view of how species composition changes on islands and mainlands; further taxonomic subdivision was not feasible. These taxon-specific models were fitted as above. The plant/fungal data included mainly vascular plants but also additional taxa of sessile species; i.e., mosses, fungi and slime moulds. Two mainland studies in my final data that sampled both animal and plant species were excluded from these models since pairs of sites could not be classified as animal or plant data (i.e., data for all species was combined within the sites). Numbers of pairs of sites were reasonable for each land-use contrast category within animal and plant/fungal data when islands and mainlands are separated (Table B.7). Nevertheless, in the case of the plant/fungal dataset, data for some land-use contrasts including PriMin as baseline came from only two or three studies; I point out this issue in my results section. In the plant/fungal dataset, there was also no data for the PriMin-Urban and Urban-Urban contrasts on islands (Table B.7); therefore, I excluded all contrasts including Urban sites from the plant/fungal data before running the models. My final models for plant/fungal and animal assemblages fulfilled homogeneity and normality assumptions (Figure B.6).

2.3.2.4 Models including island area and isolation

As a final step, I tested whether J_R or J_A, between island sites was predicted by island area (km^2) and two measures of island isolation (from Weigelt et al., 2013): distance to the nearest mainland (distance in km from the island's centroid to the mainland coast) and a metric of surrounding landmass around the island perimeter (sum of the proportions of landmass within buffer distances of 100, 1,000 and 10,000 km). Using only the within-island comparisons from the data set described above, I averaged J_R and J_A, for each land-use contrast within each study. This approach removes the widespread pseudoreplication that using all pairs of sites would have caused, and has no cost because all the pseudoreplicated comparisons would have the same area and isolation values.

Two studies in my datasets (conducted in New Zealand and the Azores Islands) included within-island comparisons but across several islands; therefore, in these cases, I chose to only include data for the island that included most comparisons. This led to the exclusion of five islands (out of 37 – Table B.9) from the datasets. Studies conducted in Australia were also excluded from these models since Weigelt et al., 2013 did not include data for Australia (as it is usually not considered as an island).

I modelled the average J_R and J_A of each land-use contrast within each study as a function of the land-use contrast class, island area and each of the two isolation metrics in turn, including the interaction in each of the six models to test whether the land-use effect varied with island area and isolation. Island area and distance to the nearest mainland were square-root transformed, which normalized the distributions better than log-transformation. The datasets included all land-use contrasts, but I only focus on results of the same land-use contrasts as previously. Average J_R and J_A, values were weighted by the number of pairs of sites from which they were estimated, with weights rescaled within each study so that the study's maximum weight was 1; this approach greatly improved model fit. Models that included study as random intercept were preferred over models with both study and island as random intercepts, as judged by Akaike's Information Criterion (AIC) for models with the full fixed-effects structure (Zuur et al., 2009). The fixed-effects structure of the models was assessed using backwards stepwise model simplification based on likelihood ratio tests. I used post hoc analysis (using the package '*phia*' ver. 0.2-1 – De Rosario-Martinez, 2015) to test whether the coefficients of the interaction between the land-use contrasts of interest and the area and isolation metrics were significantly non-zero. The diagnostic plots showed that the models fulfilled homogeneity and normality assumptions (e.g., Figure B.12). There were insufficient data to repeat the isolation analyses using the plant/fungal and animal subsets.

2.4 RESULTS

The final data for modelling included a total of 490 studies – 339 from mainlands (14,922 sites; 25,312 species) and 151 from islands (7,157 sites; 11,793 species) (Table B.2). The island studies came from 37 different islands (Table B.9), of which 34 were in 18 different archipelagos. For both islands and mainlands, various tropical and temperate forest biomes were best represented in my data, though my final dataset included mainland studies from all 14 terrestrial biomes and island studies from 10 (Table B.3). Classifying Australia as a mainland did not qualitatively change the results when modelling all taxa (see Table B.6); I therefore present the results from the (more balanced) models in which Australia was classified as an island.

2.4.1 Effects of distance and land use on island vs. mainland assemblages

In the models that included all taxa, all highest-order interactions were statistically significant. For both richness-based and abundance-based compositional similarity (J_R and J_A, respectively) between sites, similarity decreased as geographic and environmental distance increased, but the decline with environmental distance was steeper on islands whereas the decline with geographic distance was steeper on mainlands (Figure B.2; Table B.5).

When these effects of distance are controlled for, sites in minimally-disturbed primary vegetation (i.e., PriMin sites) were more compositionally similar to each other than to sites in other land uses (especially the human-dominated land uses – plantations, croplands, pastures and urban), on both islands and mainlands (Figure 2.1). Relative to the baseline similarity between PriMin sites, land use had a greater impact on J_A (Figure B.3) than on J_R.

The significance for differences between island and mainland changes (e.g., whether the difference between similarity of PriMin-PriMin and PriMin-Cropland contrasts is bigger on islands than mainlands) was calculated based on values on a logit scale (i.e., model coefficients). However, I present compositional similarity of land-use contrasts in a 0 to 1 scale to ease understanding (e.g. Figure 2.1). Because the relationship between logit and back-transformed values for compositional similarity is not linear, the changes on a logit scale might have unexpected effects on back-transformed values (because the effect of a given change in the logit depends on the starting value), which led to non-equivalent results for magnitude of change on islands and mainlands in a few cases.

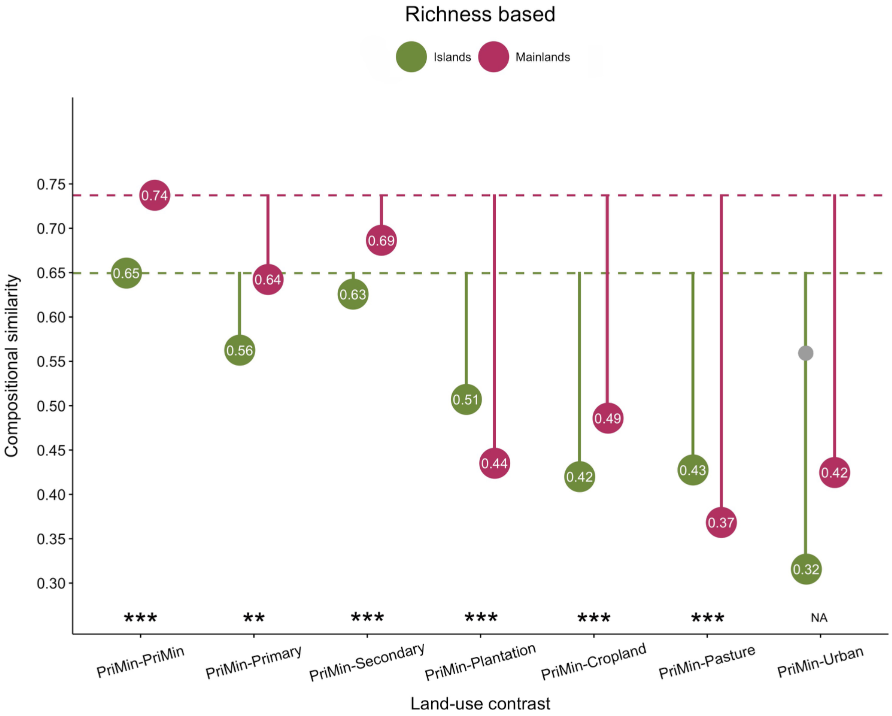


Figure 2.1. J_R estimates for land-use contrasts where site *i* is in PriMin. Solid lines show the magnitude of change in J_R driven by change to different land uses; the baseline is compositional similarity between PriMin sites on islands and mainlands respectively (dashed lines). The grey circle in the PriMin-Urban contrast for islands shows the original estimate from the model (0.56), while the displayed value corresponds to the estimate that was calculated indirectly. Significance (indicated by stars) is shown for island/mainland differences for J_R changes from PriMin-PriMin on a logit scale. Significance for PriMin-Urban is not shown since it could not be estimated using island coefficients that were caculated indirectly. When using the original coefficients, islands and mainlands showed significant differences for PriMin-Urban. Significance codes: ** $p < 0.05$, *** $p= 0.005$.

Importantly, in most cases land use reduces compositional similarity to PriMin significantly more on mainlands than on islands, especially for J_R (Figure 2.1, Figure B.3). This difference is most evident in pastures and plantations, for both J_R and J_A. Only croplands and primary vegetation reduce compositional similarity to PriMin significantly more on islands than on mainlands for J_A (Figure B.3). Although my models suggested that the similarity of urban assemblages to PriMin assemblages was very different between islands and mainlands, this result is not robust as only two studies in my dataset directly compared urban and PriMin sites on islands; indirect estimates of this comparison for islands (see Methods) were closer to the model estimates for mainlands (Figure 2.1, Figure B.3).

In comparisons of sites within the same land use, pairs of sites within most human-dominated land uses tend to have assemblages that are less similar than pairs of PriMin sites, both on islands and – especially – on mainlands (Figure 2.2 and Figure B.4), contrary to the expectation that these land uses reduce spatial beta diversity. The exceptions were land uses with forest cover (i.e., primary, secondary and plantation) on islands and urban sites on mainlands. Most but not all of these within-land-use similarities differed significantly between islands and mainlands (Figure B.4).

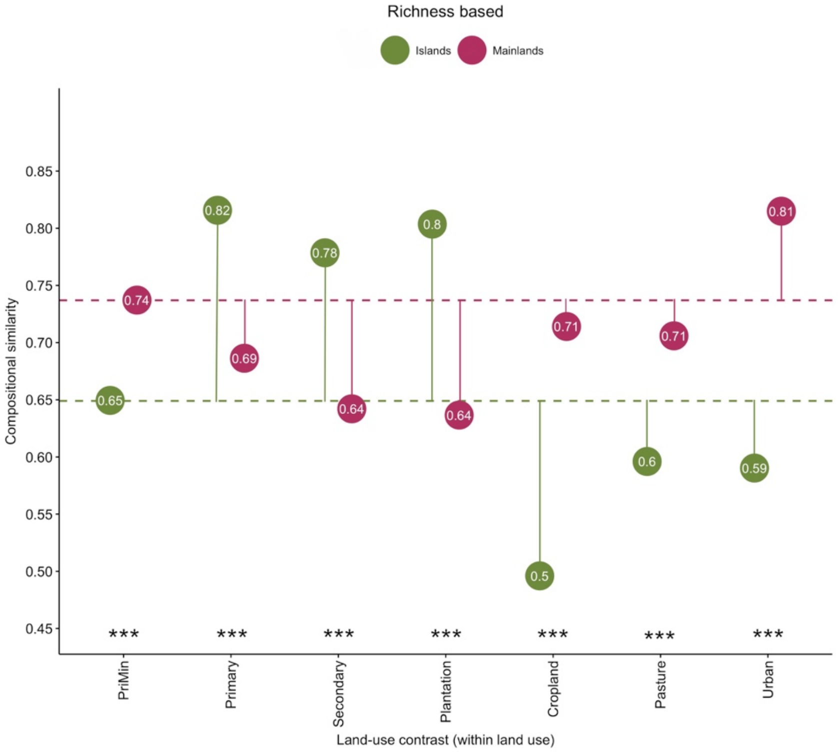


Figure 2.2. J_R estimates for sites within the same land use on islands and mainlands. Each category corresponds to a land-use contrast (i.e., Cropland= Cropland-Cropland). Solid lines show the magnitude of change in J_R for islands and mainlands, using compositional similarity between PriMin sites as baseline (dashed lines). Significance connotation and codes as in Figure 2.1.

2.4.1.1 Effects of distance and land use on plant/fungal vs animal assemblages

The plant/fungal models differed markedly from the all-taxa models (Figures 2.3 and 2.5). Environmental distance did not interact significantly with the Island/Mainland term (Table B.8), and had a relatively shallow pooled slope (-0.18 for J_R and -0.11 for J_A; Figure B.7b). Both J_R and J_A for plant/fungal assemblages decayed with geographic distance about 50% more rapidly on islands than on mainlands (Figure B.7b). Controlling for these distance effects, effects of land use differed significantly between islands and mainlands, with secondary vegetation and plantations showing a significantly greater change in both J_R and J_A on islands (Figure 2.3 and Figure B.8). Although the other land uses also showed marked differences between islands and mainlands, their estimates for islands or mainlands came from three or fewer studies (Table B.7) so should not be viewed as robust.

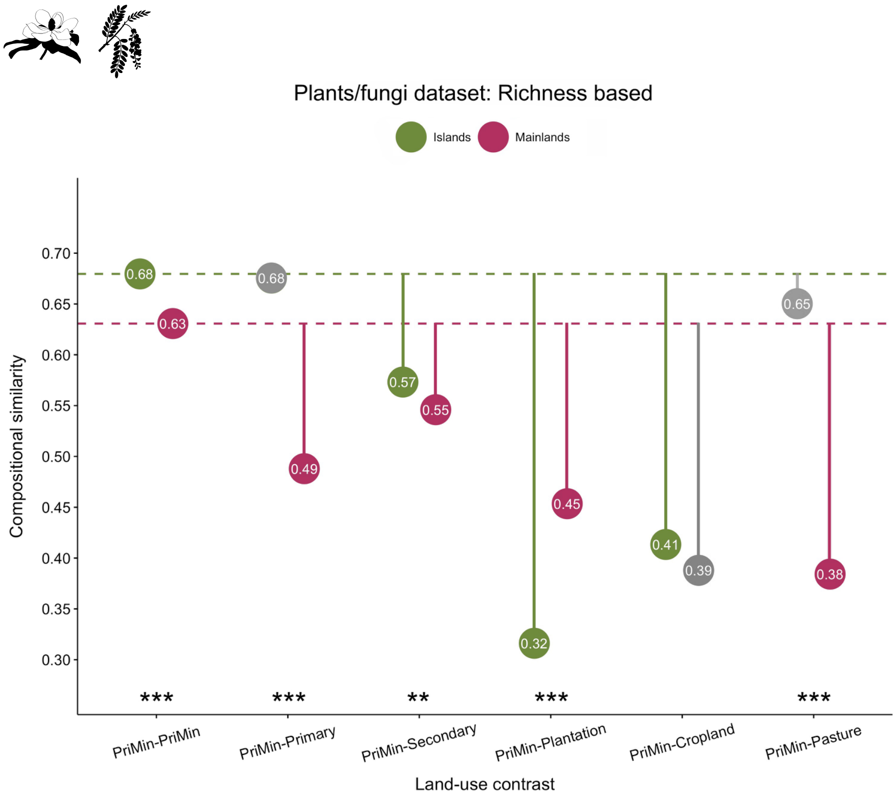


Figure 2.3. J_R estimates for plant/fungal assemblages in land-use contrasts where site *i* is in PriMin. Solid lines show the magnitude of change in J_R on islands and mainlands driven by change to different land uses. Circles in grey indicate contrasts with limited data (i.e., from three or less studies). PriMin-Urban results are not shown since no plant/fungal data was available for this contrast for islands. Significance connotation and codes as in Figure 2.1.

The models for the animal data could not be simplified, and were similar to the all-taxa models (Figures 2.4 and B.9). Compositional similarity decays more rapidly with environmental distance on islands than on mainlands, whether based on J_R (slopes of -1.2 against -0.8) or J_A (slopes of -1.5 against -0.8); but decays more rapidly with geographic distance on mainlands than on islands (J_R -0.07 against -0.04; J_A -0.08 against -0.05) (Figure B.7a). As with plants/fungi, compositional similarity of animal assemblages (to PriMin) is affected differently by land use on islands and mainlands. Plantations and pastures showed a significantly greater change in J_R on mainlands (but the effects of the other land uses on J_R did not differ significantly between islands and mainlands – Figure B.9); however, islands showed significantly larger changes in J_A than mainlands in primary and secondary vegetation, croplands and pastures (Figure 2.4). When comparing sites within the same land use, only urban sites on mainlands and land uses with forest cover on islands showed evidence of reduced beta diversity (Figure B.10).

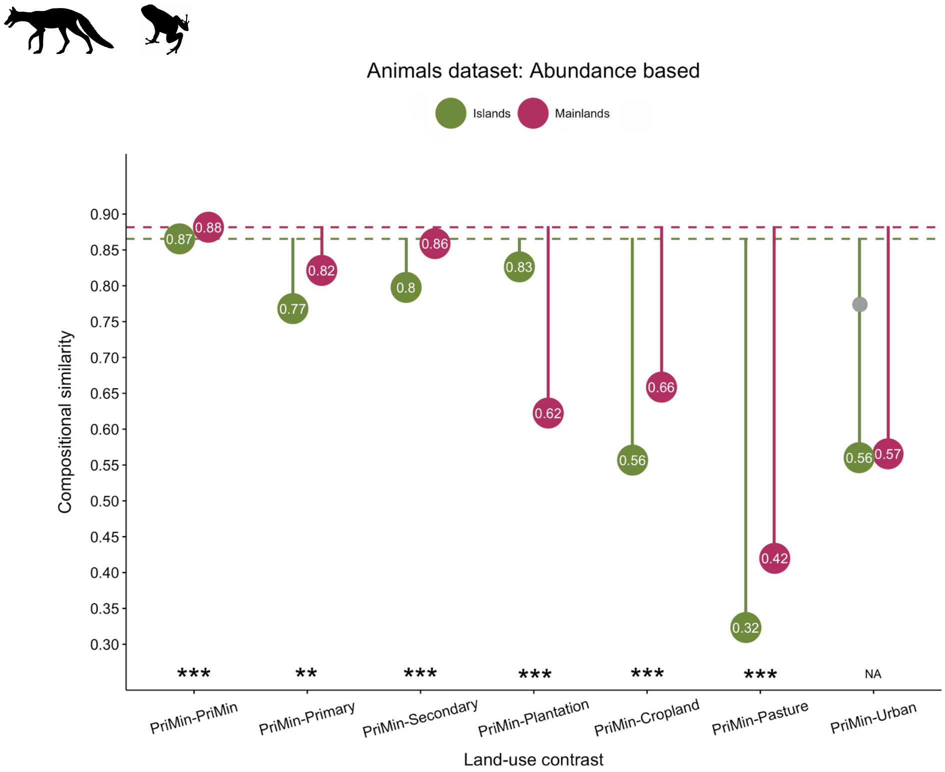


Figure 2.4. J_A estimates for animal assemblages in land-use contrasts where site *i* is in PriMin. Solid lines show the magnitude of change in J_A on islands and mainlands driven by change to different land uses. The grey circle in the PriMin-Urban island contrast shows the original estimate from the model (0.77), while the displayed value corresponds to the estimate that was calculated indirectly. When using the original coefficients, islands and mainlands showed significant differences for PriMin-Urban. Significance connotation and codes as in Figure 2.1.

These models suggest that land use might reduce spatial beta diversity (i.e., drive biotic homogenisation) more in plant/fungal than in animal assemblages. In the plant/fungal models, most land uses on both mainlands and islands showed higher average (distance-controlled) pairwise J_R and J_A than did PriMin sites (Figure 2.5 and Figure B.11), the exceptions being secondary vegetation and croplands on islands. The effect is strongest in primary vegetation, plantations and pastures on islands, especially for J_R (Figure 2.5).

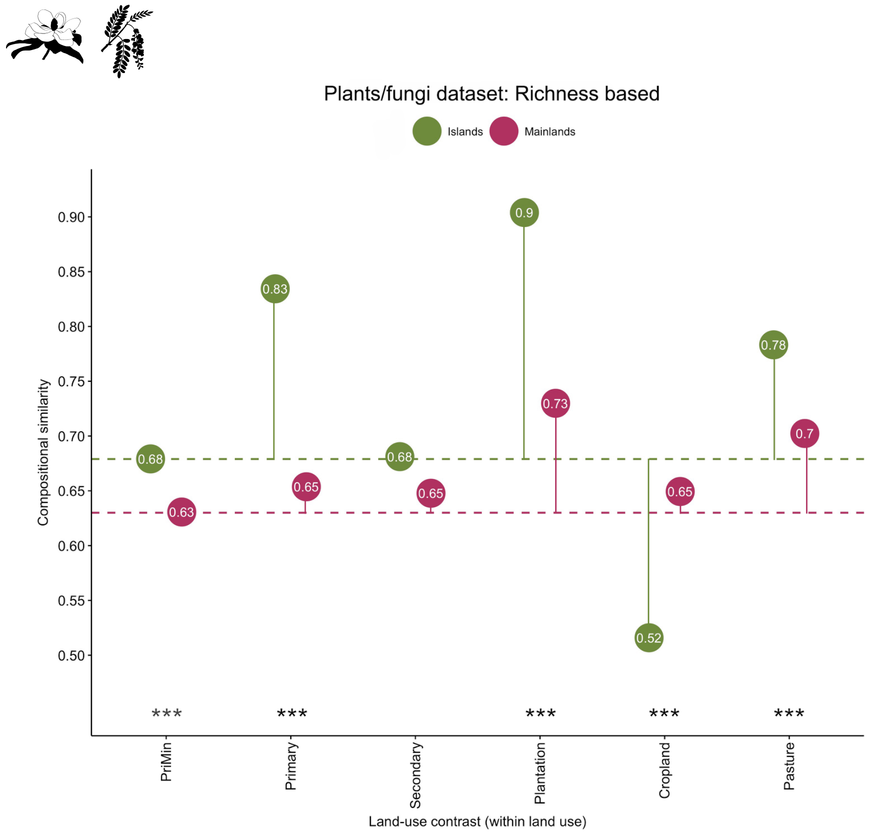


Figure 2.5. J_R estimates for plant/fungal assemblages of sites within the same land use on islands and mainlands. Solid lines show the magnitude of change in J_R for islands and mainlands using compositional similarity between PriMin sites as baseline (dashed lines). Urban-Urban results are not shown since no plant/fungal data was available for this contrast for islands. Significance connotation and codes as in Figure 2.1.

2.4.2 Influence of island area and isolation on land-use effects

Isolation metrics seldom correlated significantly with compositional similarity between island sites (Tables B.10 and B.11). The only exception was that surrounding landmass interacted significantly with land-use contrast in the model of abundance-based similarity (P= 0.02, d.f.= 48, Type II Wald Chi Square test) although it was not significant as a main effect (P > 0.1, d.f.= 1, Type II Wald Chi Square test). Only one contrast had an interaction coefficient differing significantly from zero: compositional similarity between croplands and PriMin decreases as the surrounding landmass around the island perimeter increases (Figure B.13).

Island area only had a significant effect on J_R between island sites (Tables B.10 and B.11), interacting significantly with land-use contrast (P= 0.04, d.f.= 48 , Type II Wald Chi Square test) without being significant as a main effect (P > 0.1, d.f.= 1 , Type II Wald Chi Square test). However, none of the land-use contrasts of interest had interaction coefficients that differed significantly from zero in post-hoc tests.

2.5 DISCUSSION

Previous studies established that human-dominated land uses support drastically different assemblages from minimally disturbed-primary vegetation (Hawes et al., 2009; De Lima et al., 2013; Newbold et al., 2016b). My analyses add that land use affect community composition differently on islands and mainlands. Differences between human pressure effects on islands and mainlands should therefore be accounted for in global models aiming to develop biodiversity projections under different land-use change scenarios. Such an approach would lead to less biased estimates of the geographic pattern in the intactness of local ecological assemblages.

According to the all-taxa models, there are greater compositional differences between minimally-disturbed primary vegetation and most human-dominated land uses (especially pastures and plantations) on mainlands than on islands, contrary to the hypothesis that island assemblages would be more susceptible to change (Simberloff, 2000; Denslow, 2003; Pyšek & Richardson, 2006). There are two possible – and non-exclusive – explanations for these results.

First, agriculture and plantation forest might tend to be more intensive on mainlands than on islands. For example, Ramankutty et al. (2008) calculated that the percentage of land area with pastures or croplands tends to be especially high in some mainland regions such as North America, Europe and Asia. Less intense land use might mainly characterise islands with low economic development or remote islands with a more recent human colonization – other islands, such as the UK, are farmed very intensively. Although data limitations means that use intensity could not be incorporated as an explanatory variable, inspection of the use intensity recorded in the PREDICTS database partly supports this suggestion, with mainland sites being more likely to have higher use intensity within many land uses (Figure B.1). A lower use intensity on islands might enable land uses such as pastures and plantation forests to retain more natural conditions (e.g., patches of natural vegetation and canopy cover) and to harbour more native species, which could limit the establishment of novel species (Kennedy et al., 2002). Particularly, the low intensity of island pastures in my dataset (Figure B.1) might be caused by the prevalence of rangelands (i.e., land where native vegetation consists mainly of grasses and shrubs and therefore is used for grazing– Lund, 2007; Allen et al., 2011) on some islands that are well represented in my data; e.g., Australia, Tierra del Fuego and South Island-New Zealand (Ellis & Ramankutty, 2008). Around 60% of pasture sites included in island comparisons of PriMin vs pastures are in these islands, where grasslands, savannas and shrublands are naturally widespread (Olson et al., 2001). Rangelands can develop in these ecosystems since the natural vegetation can tolerate grazing (Allen et al., 2011); therefore, the production of grazing livestock in these regions usually does not involve high impacts from land use (Ellis & Ramankutty, 2008).

The second explanation is that mainland settings are more likely than islands to provide larger numbers of synanthropic species, as a result of their bigger native species pools (Herben, 2005) increasing the chances of finding species that are adapted to disturbed conditions (Lepš et al., 2001). Such synanthropic species might be missing from natural sites but can be assembled into novel human-dominated ecosystems (Šilc, 2010), resulting in communities that are less nested within natural assemblages. Compared to mainland assemblages, there are two reasons why island assemblages may be invaded less often by synanthropes, even if they are more intrinsically invasible (Denslow, 2003): the small pool of native species on islands (Herben, 2005) may not include many that are successful in disturbed sites, and invasions by alien species are less likely on islands than on mainlands (assuming a species–isolation relationship – MacArthur & Wilson, 1963). Considering that islands have been pointed out as hotspots of alien species (e.g., Capinha et al., 2017; Dawson et al., 2017; Dyer et al., 2017a) and that it is unlikely that many island natives are able to colonise disturbed sites, it is likely that novel species in human-dominated land uses on islands are mainly introduced species, while on mainlands assemblages of these sites could be composed by both alien and native synanthropic species. Larger and less isolated islands would be expected to show more similar patterns to those in mainlands, providing larger numbers of synanthropic species. Against this, my models including island area and isolation do not support the hypotheses that bigger islands harbour larger numbers of synanthropic species (Chown et al., 1998) or that less isolated islands are invaded more often by these species. However, my island dataset may be too biased (mainly including data for bigger and less isolated islands such as Australia and Great Britain) or too small for powerful tests of these hypotheses. Alternatively, economic isolation of islands – not considered here – could be a more relevant measure, as a result of anthropogenic processes obscuring the the species–isolation relationship (Helmus et al., 2014).

The plant/fungal and animal models revealed effects of human-dominated land uses on island assemblages that were masked in the models including all taxa. Plant/fungal assemblages in secondary vegetation and plantations (J_R and J_A) and animal assemblages in croplands, pastures and primary and secondary vegetation (J_A) showed greater compositional changes on islands than on mainlands. These abundance-based results for animal assemblages suggest that in some cases, even if fewer novel species invade disturbed sites on islands than on mainlands, these few species may reach higher abundances than on mainlands perhaps due to islands' species poverty and reduced competition from native species (Sax & Brown, 2000; Roderick & Vernon, 2009). Unfortunately, my plant/fungal data is very limited for some land-use contrasts, which impedes drawing strong conclusions about whether plant/fungal assemblages could change more drastically due to land-use change on islands than on mainlands. However, previous studies have found cases where alien plants have become extremely successful on islands (e.g., Sax et al., 2002; Lugo & Helmer, 2004), especially in severely disturbed sites (Rodgers & Parker, 2003).

Three linked limitations of the data make it difficult to estimate the importance of species introductions. First, I use spatial comparisons of sites in different land uses to estimate the temporal effect of land-use change, because true before-vs-after comparisons are much less common in the literature (De Palma et al., 2018b; Purvis et al., 2018). Consequently, the composition of assemblages in present-day minimally-impacted primary vegetation can differ from the original composition of assemblages at sites where land use has changed. Second, even assemblages in minimally-used primary vegetation are likely to have experienced, in the past and/or currently, some human impact (e.g. Watson et al., 2016) that could change community composition. Lastly, these analyses have not separated native from alien species in the island or mainland studies. Although sufficiently complete and detailed distributional data are available for some taxonomic groups, and a few of my data sources provide this information, it is not in general possible to test the assumption that species inhabiting minimally-impacted primary vegetation on islands or mainlands are natives, or to estimate what fraction of species found in human-dominated land uses, but not at natural sites, are aliens. An analysis focusing on studies where species can be separated in this way would help to clarify the importance of introduced species in driving the effects seen here. Such an analysis will require collation of distributional information from many sources, though databases of alien species occurrences are increasingly becoming available (e.g., Dyer et al., 2017b; Threatened Island Biodiversity Database Partners, 2017; van Kleunen et al., 2019). These limitations may have combined to bias my inferences of the impacts of land use on ecological assemblages. In particular, widespread invasive species may have become established even in more natural habitats on many islands, reducing the inferred effect of land use.

The pattern of similarity between sites in the same land use differs strongly between mainlands and islands: mainlands show more self-similarity within cropland, pasture and urban land uses; whereas islands show more in forested land uses. I found little evidence of homogenization at the scale of sites within studies in models including all taxa (which mainly reflected responses of animal assemblages); however, forested land uses on islands and urban sites on mainlands were exceptions, where pairs of sites have assemblages that are more similar than pairs of PriMin sites. This combination of results is hard to explain without speculation. A possible explanation for the apparent lack of homogenization of animal assemblages within most human-dominated land uses is that the addition of novel species does not always increase compositional similarity among human-altered sites (Socolar et al., 2016). Heterogeneity of animal assemblages across disturbed sites – within most land uses on islands and mainlands – might be caused by the invasion of a variety of alien species or native synanthropic species, which do not become ubiquitous (Socolar et al., 2016); for example, some alien arthropods can be habitat specialists that form heterogeneous communities in disturbed sites (Florencio et al., 2015). Animal assemblages within some human-dominated land uses might also be more heterogeneous than assemblages in minimally-disturbed sites if formerly ubiquitous species characteristic of communities in natural habitats disappear from all or some of the disturbed sites (Socolar et al., 2016).

The homogenization in urban sites on mainlands agrees with previous studies that have suggested that urbanization is one of the strongest factors driving homogenization of species assemblages (McKinney, 2006; Newbold et al., 2018), considering that only a few species can thrive in such disturbed conditions. On the other hand, a possible explanation for the homogenization of animal assemblages within forested land uses on islands draws on the 'taxon cycle' hypothesis (a model of evolutionary change on islands – Wilson, 1961; Ricklefs & Cox, 1972; Ricklefs & Bermingham, 2002). I suggest that forested land uses on islands are likely to harbour fewer novel species than are more marginal or significantly disturbed habitats. More species in the source pool might be able to colonise the most disturbed sites where competition is reduced (Wilson & Tilman, 1993) –or very limited in the case of islands (Denslow, 2003)–; successively, fewer novel species would be expected towards more intact and more competitive habitats. These fewer species in forested land uses, could become widespread if natives are replaced, creating homogenous communities. Alternatively, assemblages within forested land uses on islands might become homogeneous if rare and sensitive species disappear or decline across sites within these land uses (while ubiquitous species persist) (Socolar et al., 2016).

Plant/fungal assemblages showed evidence of homogenization across most land uses on both islands and mainlands; i.e., sites within the majority of the land uses have plant/fungal assemblages that are more similar than assemblages within PriMin sites. My plant/fungal data is limited; however, these results might be driven by responses of highly invasive plant species such as grasses and weeds, which are very successful colonizers and spread widely across disturbed habitats (Westbrooks, 1998). A few of these invasive species could displace a wide set of species and become highly abundant across disturbed sites within most land uses.

I assessed homogenization within land uses based on the reduction in spatial turnover (beta diversity) of species assemblages. Alternative approaches have also been used: in a global analysis, Newbold et al. (2018), concluded that land-use change homogenizes assemblage composition across space since assemblages in disturbed habitats have more widespread species on average. My approach has limitations since the effects of habitat conversion on composition of assemblages can be scale-dependent (McGill et al., 2015); e.g., the partial conversion of natural habitat might cause an increase in beta diversity of assemblages at a local scale but a decrease at larger scales (Newbold et al., 2018). However, interpreting results from analyses of species ranges is also not straightforward if range completeness (i.e., the extent to which the recorded occurrences of a species fill its geographic distribution: Meyer et al., 2015) differs between islands and mainlands or between animals and plants, which is not unlikely.

My compositional similarity estimates showed a much wider range than estimates from the most recent global analysis of assemblage turnover caused by land use change (Newbold et al., 2016a). Although my data set is slightly expanded, the difference is more likely to be driven by methodological differences. For example, Newbold et al. (2016a) used logarithmic transformation for compositional similarity data; this approach is commonly adopted and yielded well-behaved residuals; however, it does not reflect the boundedness of the response variable. I opted for logit transformation which captures this boundedness. The baseline representing natural habitats also differs between the studies; whereas I used minimally-disturbed primary vegetation, Newbold et al. (2016a) included all use intensities of primary vegetation as baseline sites for comparisons. In Chapter 5, I discuss in detail these two methodological differences and assess their relative effects.

My analyses provide the first global evidence that land use, geographic distance and environmental distance together shape the compositional turnover of ecological assemblages in ways that differ systematically between islands and mainlands. I suggest that the difference between compositional changes of island and mainland assemblages results mainly from a) differences in land-use intensity which determines the severity of native species declines and the opportunities for the establishment of novel species; and b) differences in species pools, determining the number of available synanthropic species on islands and mainlands that can assemble in disturbed sites. I highlight particular cases where land-use change causes larger compositional changes in island than mainland assemblages, and suggest that they result from islands' species poverty and vulnerability of native species, since both factors ease the establishment of novel species. Despite their ongoing importance in studies of ecology, evolution and conservation, islands have not previously been contrasted with mainlands in global biodiversity models. My results suggest that this omission risks systematically mis-estimating the status of island biodiversity.

CHAPTER 3

Land use and related pressures have reduced biotic integrity more on islands than on mainlands

3.1 ABSTRACT

Tracking progress towards biodiversity targets requires indicators that are sensitive to changes at policy-relevant scales, can easily be expressed at any spatial scale and are simple to understand. The Biodiversity Intactness Index (BII), which estimates the average abundance of a diverse set of organisms in a given area relative to their reference populations, was proposed in 2005 in response to this need. A new implementation of BII was developed as part of the PREDICTS project in 2016 and has been adopted by GEO BON, IPBES, Biodiversity Indicators Partnership and CBD. The previous global models used in estimating BII could not accommodate pressures having different effects in different settings. Islands are a setting of particular interest: many are home to a disproportionate number of endemic species; oceanic islands may have relatively low overall species diversity because of their isolation; and the pattern and timing of human pressures can be very different from that seen on mainlands. Here, I test whether land use and related pressures have compromised biotic integrity – as estimated by BII – more severely on islands than mainlands. I refine the methods previously used to estimate BII globally (Newbold et al., 2016a) to allow pressure effects to differ between islands and mainlands, while also implementing some other recent improvements in modelling. I estimate BII for islands and mainlands by combining global models of how two aspects of biodiversity – overall abundance, and compositional similarity to minimally-impacted sites – have been affected by human pressures. I use these models to project high-resolution (~1km^2) global maps of BII for the year 2005. I calculate average BII for island and mainland biomes, countries, IPBES regions and biodiversity hotspots; and repeat my analyses using a richness-based variant of BII. BII on both islands and mainlands has fallen below the values proposed as safe limits across most regions, biomes and biodiversity hotspots. Average BII does not differ strongly between islands and mainlands, but richness-based BII has fallen by more on islands. It appears that native species are more negatively affected by rising human population density and road development on islands than mainlands. My results highlight the parlous state of biodiversity native to islands.

3.2 INTRODUCTION

Biodiversity is continuing to decline and the pressures driving the declines are not easing (Butchart et al., 2010; Tittensor et al., 2014). The loss of biodiversity from ecosystems can compromise their functioning (Hooper et al., 2012) and therefore their capacity to contribute to human wellbeing (Díaz et al., 2018). Ongoing debates have tried to identify a set of suitable indicators to inform about the state of biodiversity and progress towards biodiversity targets such as the Aichi 2020 Targets. The Convention on Biological Diversity (CBD) established a set of criteria that indicators of biodiversity change should satisfy; for example, indicators should be sensitive to changes at policy-relevant spatial and temporal scales, be easily aggregated and disaggregated to any spatial scale, allow comparisons with a baseline situation and be affordable and simple to understand (UNEP, 2003; Scholes & Biggs, 2005).

The Biodiversity Intactness Index (BII) was proposed by Scholes & Biggs (2005) with these criteria in mind, defining it as "the average abundance of a large and diverse set of organisms in a given geographical area, relative to their reference populations". The index estimates biodiversity loss as a result of human pressures by focusing on the status of originally present species relative to a reference condition, which is represented by minimally-disturbed sites (since historical data are very rare: Scholes & Biggs, 2005). Decreases in an ecosystem's BII – i.e., the loss or population decline of originally present species – may imply decreases in its resilience and ability to continue to meet societal needs: e.g., when facing disturbances, a high diversity ensures the persistence of at least a few species which might continue delivering ecosystem services – Biggs et al., 2012). BII initially only incorporated the effects of land use – among the main drivers of biodiversity loss (Maxwell et al., 2016; Brummitt et al., 2015) – without taking into account other related pressures such as human population growth.

BII has been proposed as a metric for assessing biotic integrity in the Planetary Boundaries framework (Steffen et al., 2015), which aims to define a safe operating space for humanity (Rockström et al., 2009; Steffen et al., 2015). This framework places a precautionary safe limit at 10% reduction of BII, but acknowledges this limit to be highly uncertain: a less conservative estimate lies at 70% reduction (Steffen et al., 2015). The proposed safe limit is intended to reflect the biotic integrity needed to ensure the long-term maintenance of large-scale ecosystem function (Mace et al., 2014; Steffen et al., 2015).

BII began as an index that relied on carefully-pooled expert opinion and focused on specific geographical areas instead of global analyses, because suitable empirical data were lacking (Scholes & Biggs, 2005). The PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project has recently implemented BII (Purvis et al., 2018) by modelling a global collation of site-level biodiversity in sites facing different land uses and related pressures. This implementation leads to the estimation of local BII, which can be averaged for any larger spatial scale (e.g., globally, by countries, biodiversity hotspots or biomes). This approach also permits the exploration of temporal changes in BII under observed recent (De Palma et al., 2018a) or projected future changes in land use and other pressures (Hill et al., 2018) to inform policy. Local BII estimates are therefore relevant for global biodiversity assessments such as those developed by the Group on Earth Observations Biodiversity Observation Network (GEO BON) and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES).

PREDICTS' first global estimate of BII (Newbold et al., 2016a) estimated that land use and related pressures have reduced local biodiversity intactness below the planetary boundary across at least 58% of the world's land surface. Newbold et al. (2016a) noted that data limitations precluded biome- or clade-specific models, so made no attempt to accommodate possible different responses to pressures in different ecological systems, such as islands and mainlands.

Island and mainland systems can differ greatly in species assemblages and human pressures, with the result that islands might be suffering a greater decline of native species than mainlands – but that this will be missed by BII as currently implemented. Islands' small size can facilitate access to undisturbed areas, promoting a fast acceleration of habitat loss (Kier et al., 2009), and islands' isolation can prevent the recovery of declining populations through natural immigration (Lomolino, 1986). Moreover, island endemic species usually lack the potential to face disturbances in their habitat since evolutionary isolation often leads to the loss of traits that ease populations' recovery after disturbances; for example, many island species present low reproductive output (Adler & Levins, 1994; Meiri et al., 2012) and poor dispersal abilities (Gillespie et al., 2008). Islands are also more vulnerable to the establishment of alien species than mainlands (Sax & Brown, 2000, Whittaker & Fernández-Palacios, 2007), perhaps related to their species poverty (a result of island isolation and low colonisation rates: Whittaker & Fernández-Palacios, 2007) or high resource availability (Denslow, 2003). The introduction of alien species has led to extreme declines of island native populations (Whittaker & Fernández-Palacios, 2007). Any decline of biotic integrity on islands is especially alarming since it might involve the loss of a large number of endemic species with unique evolutionary histories (Whittaker & Fernández-Palacios, 2007).

Here I refine and improve the BII estimates from Newbold et al. (2016a), allowing island and mainland assemblages to respond differently to drivers. I test whether biodiversity intactness has decreased more severely on islands than mainlands, as a result of larger decreases of local diversity and larger changes in species composition in human-dominated land uses. I also compare the intensity of land use and related pressures on islands and mainlands to determine whether this factor contributes to island/mainland differences in BII.

I estimate BII for islands and mainlands by combining models of how land use, human population density and distance to roads affect local biodiversity with models of how land use affects the similarity of species assemblages to assemblages in minimally-disturbed sites. I use estimates based on abundance and richness data and generate fine-scale (~1km^2) global maps for BII estimates that address some previous criticisms of BII (see Rouget et al., 2006 and Faith et al., 2007). I also implement other methodological improvements that allow more efficient use of data and a more principled error structure than in Newbold et al. (2016a).

3.3 METHODS

All the models used data on species abundance and occurrence extracted in October 2016 from the PREDICTS database (Hudson et al., 2017 and described in Chapter 1). I classified each site in the database as a mainland or island site (see Chapter 2 for details); Australia and all smaller land polygons were classified as islands. Treating Australia as an island helped to improve the balance between island and mainland sites in my analyses (though I also assessed the influence of this decision on my findings; see below).

3.3.1 Statistical modelling

Biodiversity Intactness Index

PREDICTS' approach for estimating BII requires combining two statistical models (detailed below): a model of how land use and related pressures affect overall abundance or species richness at a site, and a model of how land use affects compositional similarity of assemblages to baseline assemblages (minimally-disturbed primary vegetation experiencing minimal values of any other pressures incorporated in the model). Scholes & Biggs (2005) explicitly excluded alien species from the calculation of BII; since it is usually difficult to classify species (except for vertebrates) into natives and aliens, models of compositional similarity are instead used to correct for the species that are not present in minimally-disturbed primary vegetation (here referred as novel species).

Following Scholes & Biggs (2005), I estimated BII based on species abundance. However, I also calculated a species-richness-based variant of BII to address the criticism that abundance-based BII might overlook species losses and calculate overoptimistic estimates if the abundance of the remaining species in disturbed sites increases (Faith et al., 2007). Using abundance-based and richness-based estimates also provides information about different consequences of BII decline for ecosystem functions and services. For example, abundance-based metrics give more weight to common species; therefore, the use of total abundance might be more appropriate when analysing the amount of ecosystem service provision (Winfree et al., 2015). However, richness-based metrics give equal weight to rare and common species, which might be more relevant for stability of ecosystem service provision (Hautier et al., 2015; Dee et al., 2019).

All statistical analyses were performed using R Version 3.2.3 (R Core Team, 2017). The analyses are based on Generalized mixed-effect models (GLMMs), which were fitted using the '*lme4'* package ver. 1.1-15 (Bates et al., 2017). I use GLMMs to deal with the methodological heterogeneity among studies (i.e., sampling method within a data source – Hudson et al., 2014) in the PREDICTS database (see Chapter 1) and with biotic differences among spatial blocks. GLMMs allow to quantify the variation among studies (random-effects) without directly considering their effect in the analysis (Bolker et al., 2009). The detailed account of the modelling (below) emphasises where I improved the approach compared to that of Newbold et al. (2016a). The improvements are fully discussed in Chapter 5, where I also analyse their contribution to differences between my BII estimates and those of Newbold et al. (2016a).

3.3.1.1 Modelling total abundance and species richness

As site-level measures of biodiversity, I calculated each site's total abundance (sum of abundances of all present taxa) and species richness (number of unique present taxa). Where the sampling effort varied among sites in one study, total abundance was divided by the sampling effort to make data comparable among the study's sites.

Sites in the database had previously been classified into 10 land-use categories and three land-use intensities (Minimal, Light and Intense) within each land use (details on all categories in Hudson et al., 2017). The ten land-use categories were collapsed into six final classes (primary vegetation, secondary vegetation, plantation forest, cropland, pasture and urban) to give reasonable sample sizes for both islands and mainlands. I created an additional site variable by combining land use and use intensity of each site (LUI), giving 18 categories (Table C.1). Primary vegetation with minimal use (henceforth PriMin) was used as the baseline in modelling.

I obtained site-level data for human population density (HPD) and distance to the nearest road (DistRd). HPD (for the year 2000) was obtained from the Global Rural-Urban Mapping Project, Version 1 (GRUMPv1): Population Density (CIESIN, 2011), whereas DistRd was extracted from the Global Roads Open Access Data Set, Version 1 (gROADSv1) (CIESIN, 2013). Sites missing data for any of the human pressure variables were excluded from these models.

To model the responses of overall abundance on islands and mainlands, I fitted an initial maximal model where total abundance was analysed as a function of site-level land use and intensity category (LUI), human population density, distance to the nearest road and Island/Mainland classification (fixed-effects). I included two-way interactions between the Island/mainland term and the three human pressures, plus three-way interactions between the Island/Mainland term, land use and either HPD or DistRd. Not all abundance data were counts of individuals, meaning they could not be analysed with discrete error distributions such as Poisson. Given that, prior to analysis I rescaled total abundance to a 0-1 scale within each study, reducing the variance among studies caused by differences in the taxonomic focus and sampling effort. The rescaled total abundance was then square-root transformed (as this gave a better residual distribution than log transformation: Figure C.1) and modelled using a Gaussian error structure. My transformation for total abundance differs from that in Newbold et al. (2016a), where no rescaling was performed and abundance only was log-transformed. HPD and DistRd were log transformed and then rescaled to a zero-to-one scale to reduce the effects of extreme values and to reduce collinearity. HPD and DistRd were fitted as quadratic orthogonal polynomials in the models.

Akaike's Information Criterion (AIC) was used to determine the best random-effects structure for the maximal model fitted using Restricted Maximum Likelihood (REML) (Zuur et al., 2009). All three random-effects structures considered included random intercepts of study (to account for methodological differences among studies) and block within study (to account for spatial structure of sites within many studies). The three models that were compared additionally included either: (i) random slopes for land uses within study, (ii) random slopes for land uses + use intensity within study, or (iii) no random slopes. The random slopes account for the variation among studies in the relationships of sampled biodiversity with land use and land-use intensity. The fixed-effects structure of the final model was determined using backwards stepwise model simplification with the model fitted using Maximum Likelihood (Zuur et al., 2009).

Species richness, which was always a count, was not rescaled within studies. I modelled it in the same way as abundance except that I used a Poisson error structure with a log link and used Maximum Likelihood (ML). I tested for overdispersion in the richness model using the '*dispersion_glmer*' function in the '*blmeco*' package ver. 1.2 (Korner-Nievergelt et al., 2018), which indicated that overdispersion was not present.

For both abundance and richness models, prior to modelling, I assessed multicollinearity for all explanatory variables using Generalized Variance Inflation Factors (GVIFs) (Zuur et al., 2009). All values for both models were below 3, indicating that there was no strong collinearity within the sets of explanatory variables (Zuur et al., 2009). Model diagnostics for the final abundance and richness models showed that both models fulfilled homogeneity and normality assumptions (Figures C.1b and C.2).

3.3.1.2 Modelling abundance- and richness-based compositional similarity

I used the models fitted in Chapter 2 to extract estimates of compositional similarity between assemblages in different land uses and those in minimally-disturbed primary vegetation on islands and mainlands. I used the abundance-based and richness-based models including all taxa, which modelled compositional similarities between pairs of sites as a function of the land use where both sites were located (i.e., land-use contrast), the geographic distance between them, the environmental differences between them, and the Island/Mainland location of the pair of sites.

To calculate BII, I exclusively used the model estimates for compositional similarity between minimally-disturbed primary vegetation and seven land uses (Table C.8). Only these estimates are needed to correct the estimates of the richness and abundance models by excluding the proportion of species or total abundance (respectively) that correspond to species that are not present in minimally-disturbed primary vegetation. Because only studies that include PriMin sites can contribute, data limitations meant that I was not able to use LUI categories for the land-use contrasts.

Table C.8 shows the backtransformed values (on a scale from 0 to 1) for compositional similarity of island and mainland land-use contrasts, which in this case were rescaled so that the contrast of PriMin against itself had a value of 1 on both islands and mainlands; this was done to avoid conflating natural spatial turnover with the effects of land use (Newbold et al., 2016a). In the case of the PriMin-Urban contrast for islands, Table C.8 also shows the estimates that were calculated indirectly (product of estimated PriMin-Secondary and Secondary-Urban compositional similarities; Chapter 2).

The biggest conceptual changes to how BII is estimated are to be found in these compositional similarity models. Newbold et al. (2016a) constructed sets of independent pairs of sites within studies and averaged the coefficients of 100 models fitted with 100 different sets of randomly-chosen pairwise comparisons. This random selection meant that land uses found in relatively few sites could be contrasted with the baseline land use (representing natural habitats) even more rarely, leading to small sample sizes and greatly restricting the complexity of models that could be fitted. My approach (Chapter 2), using all possible pairwise comparisons within studies and performing permutation tests to overcome the resulting nonindependence, allows the use of all available data in a single model. This more efficient use of data enabled another conceptual improvement. Whereas Newbold et al. (2016a) had to combine all primary vegetation sites as their baseline condition (taken to represent the natural habitat), I was able to use only the sites with minimally-disturbed primary vegetation (PriMin) as a more stringent baseline for the contrasts. A third change to the compositional similarity models is how data were transformed. Newbold et al. (2016a) log transformed all variables, including compositional similarity data which is bounded between 0 and 1. I transformed explanatory variables to optimise their distributions and logit-transformed the compositional similarity estimates, in line with their possible range (Chapter 2).

3.3.1.3 Calculation of BII and spatial projections

To project BII and estimate global values, I first separately map the modelled responses of overall abundance, species richness and compositional similarity (abundance-based and richness based). I used global pressure data at a resolution of 30 arc sec (~1 km^2) for each of the human pressure variables. I used the land use maps from Newbold et al. (2016a), which were generated by downscaling (Hoskins et al., 2016) the harmonized land-use dataset for 2005 (Hurtt et al., 2011). No map was available for plantation forests since global land-use layers rarely distinguish this land use from other forests. Therefore, following Newbold et al. (2016a), I modelled biodiversity responses to plantation forest but I omitted this effect when performing the global projections and therefore from BII calculation. Land-use intensity maps were generated using the statistical models in Newbold et al. (2015). Under this approach, the Global Land Systems dataset (van Asselen & Verburg, 2013) is reclassified into land-use and use-intensity combinations and models are fitted to estimate how the proportion of each 0.5 degree grid cell under each land use-intensity combination depends on the proportion of the grid cell under a particular land use, human population density and United Nations sub-region.

The gridded map for human population density (for the year 2000) and a vector map of the world’s roads were obtained from NASA’S Socioeconomic Data and Applications Centre (CIESIN, 2011 and CIESIN, 2013). Following Newbold et al. (2016a), I computed the gridded map of distance to nearest road using a Python code written for the *arcpy* module of ArcMap Version 10.3 (ESRI, 2011). The vector map was first projected onto an equal-area (Behrmann) projection to then calculate the average distance to the nearest road within each 782-m grid cell using the ‘*Euclidean Distance*’ function. Finally, the map was reprojected back to a WGS 1984 projection at 30 arc sec resolution.

The resulting global maps of human pressures were separated into island and mainland maps, by clipping to island and mainland shapefiles derived from OpenStreetMap (OpenStreetMap Contributors, 2015). These maps were used to separately drive the four statistical models of how island and mainland biodiversity respond to pressures. For projections of the abundance and richness models, I constrained the maps of HPD and DistRd to not exceed the maximum values in the modelled datasets to avoid extrapolations beyond my data. The HPD and DistRd maps were log-transformed and rescaled as in the models. For projections of total abundance and species richness, the values were back-transformed and expressed relative to minimally-disturbed primary vegetation with zero human population and at a distance to the nearest road equal to the maximum value in the final data used in the models (195.3 km). For compositional similarity projections (abundance-based and richness-based), I used models that included the indirect (rather than the direct – Table B.5) estimate for the PriMin-Urban contrast on islands (given the uncertainty around the original estimate – Chapter 2). Compositional similarity values were back-transformed and expressed relative to compositional similarity among minimally-disturbed primary vegetation sites with zero environmental distance and a geographic distance equal to the median sampling extent in the dataset (i.e., adjacent sites – see Chapter 2). Abundance- and richness-based BII were calculated for islands and mainlands by multiplying these spatial projections; e.g., island abundance-based BII is the product of island projections for responses of overall abundance and abundance-based compositional similarity. I present my BII estimates in a 0 to 1 scale where 1 = 100% intactness.

I calculated average BII values separately for island and mainland areas within each biome (Olson et al., 2001), IPBES region (Brooks et al., 2016), country and Conservation International biodiversity hotspot (Myers et al., 2000). I also calculated average BII values for each island listed in the Global Island Database, ver. 2.1 (UNEP-WCMC, 2015). Values were calculated by averaging modelled BII values across all cells intersecting the corresponding region shapefiles after reprojecting the BII maps and the shapefiles to a Behrmann equal-area projection. The intersection of the maps was performed using the separated island/mainland BII maps and separated island/mainland maps for countries and biomes (the global shapefiles were clipped using island and mainland shapefiles). This step was necessary because 23,460 cells (around 0.1% of the island cells) intersected with both island and mainland shapefiles (see Figure C.9) and so were in both BII maps; the different models for islands and mainlands mean that BII estimated for these cells will differ between island and mainland maps, even though the pressure data will be the same. I used the global shapefiles for IPBES regions and hotspots for the intersection with the island and mainland BII maps since these regions are very broad. In the case of the shapefile from the Global Island Database, I added Australia as an additional polygon before intersecting it with the island BII maps. I calculated average BII for islands using the unique island ID code (id_gid) in the Global Island Database; averages for Australia were calculated using an exclusive code for the polygon. The standard deviation for BII averages was calculated as a measure of spatial heterogeneity.

Using the projected BII maps (Behrmann equal-area projection), I calculated the percentage of land surface on islands and mainlands that is below the recommended safe limit for reduction of biodiversity intactness: beyond 10% decrease – i.e., below 0.9 on my 0 to 1 scale – for abundance based BII (according to the proposed planetary boundary – Steffen et al., 2015) and beyond 20% decrease – below 0.8 in my scale – for richness-based BII (according to the limit used in Newbold et al., 2016a, based on Hooper et al., 2012). I also calculated the percentage of land surface under each land-use and use-intensity combination on islands and on mainlands, to enable exploration of reasons behind any island-mainland differences. I likewise compared the distributions of HPD and DistRd on island and mainland maps. For these calculations I used projected (Behrmann equal-area) land-use intensity, HPD and DistRd maps for islands and mainlands, including only those cells that had a defined value in the final BII maps.

Since the classification of Australia as an island is debatable, as a sensitivity analysis, I calculated island average BII values and the percentage of land surface under the safe limits using BII island maps where Australia (only the landmass considered as mainland Australia) was excluded. Considering that a high percentage of land surface in my original island maps corresponded to Australia, I also recalculated the percentage of land surface under each land-use and use-intensity combination using island use-intensity maps excluding Australia.

3.4 RESULTS

The final data for models of total abundance and species richness are described in Tables C.1-C.3; the data for models of compositional similarity are described in Chapter 2.

All models showed significant differences between island and mainland responses to human pressures. The abundance model could be simplified since DistRd, though significant as a main effect, did not interact significantly with any other variable (Figure C.4). No other interactions could be dropped (Table C.5). The richness model retained all terms (Table C.7). For both models, the best random-effects structure included land use and use intensity as random slopes, as well as random intercepts of study and block within study (Tables C.4 and C.6). However, due to convergence issues, in the final richness model I did not include use intensity as random slope. For some LUI (Figures C.3 and C.6) and particular combinations of human pressures (Figures C.5, C.7 and C.8), the models suggested a steeper decline of total abundance and species richness on islands than on mainlands, but this trend was not universal. Confidence intervals were sometimes very wide (e.g., Figure C.3).

Based on the rescaled compositional similarity estimates (Table C.8), similarity of assemblages in human-dominated land uses to those in minimally-disturbed sites was not always lower on islands than on mainlands: compared to mainlands, islands showed lower abundance-based compositional similarity to PriMin assemblages only in primary vegetation, secondary vegetation and croplands; whereas islands' richness-based compositional similarity to PriMin assemblages was lower only primary vegetation, croplands and urban sites.

When projected globally, BII is lower, and slightly less spatially heterogeneous, for islands than for mainlands based on both total abundance and species richness (Figure 3.1). The difference is slight for abundance-based BII (0.71 (s.d. = 0.13) for islands compared with 0.73 (s.d. = 0.19) for mainlands) but greater for richness-based BII (0.62 (s.d.= 0.16) for islands compared with 0.71 (s.d.= 0.19) for mainlands).

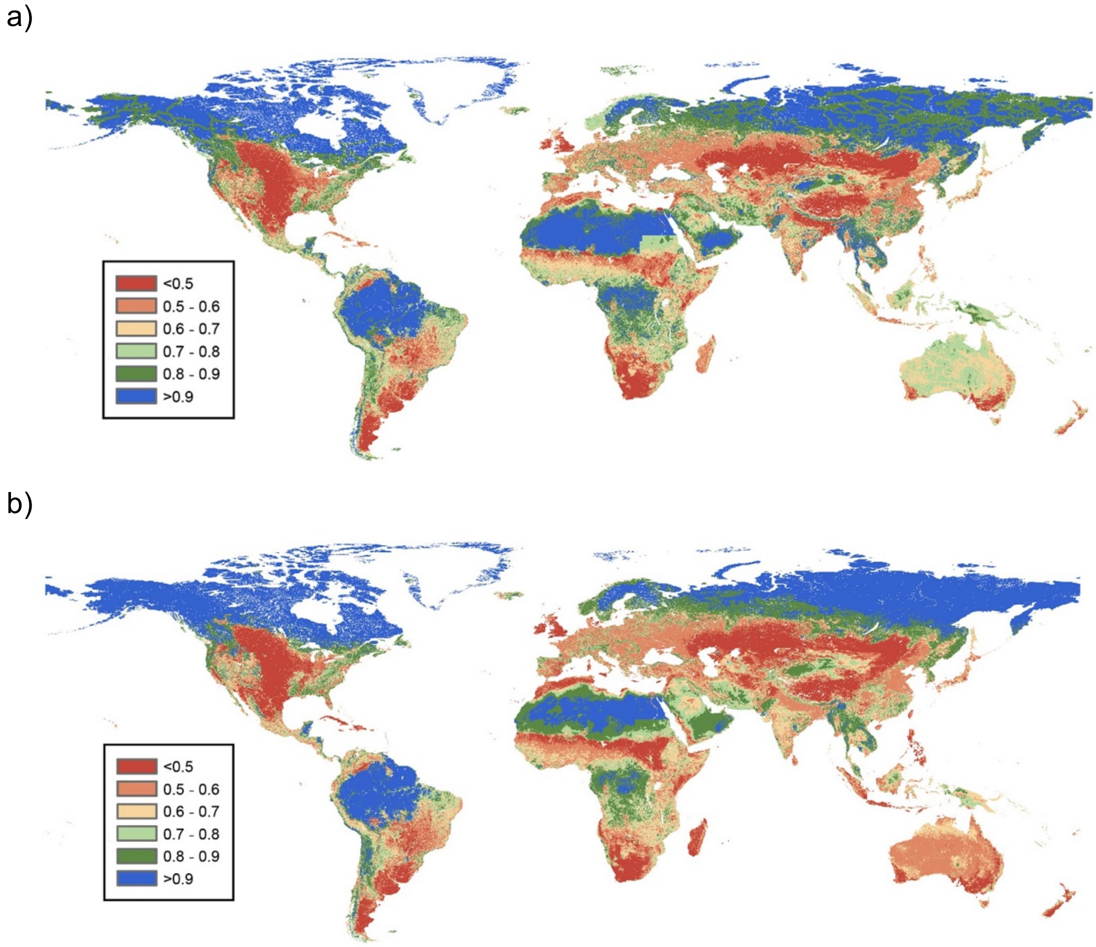


Figure 3.1. Global maps of biodiversity intactness. a) Abundance-based BII. b) Richness-based BII. BII values are shown in a 0 to 1 scale (1= 100% intactness).

On both islands and mainlands, the average local abundance and species richness of originally present species have fallen below the values proposed as safe limits (0.9 for abundance and 0.8 for richness: Steffen et al., 2015; Newbold et al., 2016a). Around 88.6% of the island area is below the recommended abundance-based safe limit, and 85.9% transgresses the richness-based safe limit. On mainlands, 76.5% of the land is below the abundance-based boundary and 59.7% below the richness-based limit.

Comparing the land-use intensity maps for islands and mainlands, islands have a higher proportion of minimally-used primary vegetation than do mainlands (~38% vs 28%) (Table 3.1). On the other hand, a higher fraction of island than mainland is given over to pasture or urban use (most use intensities – Table C.11). Mainlands showed a higher percentage of land surface with secondary vegetation and croplands (all use intensities) than islands (Table 3.1). Islands tended to have more low values of HPD and high values for DistRd (Figure C.10, Table C.12) when compared to mainlands.

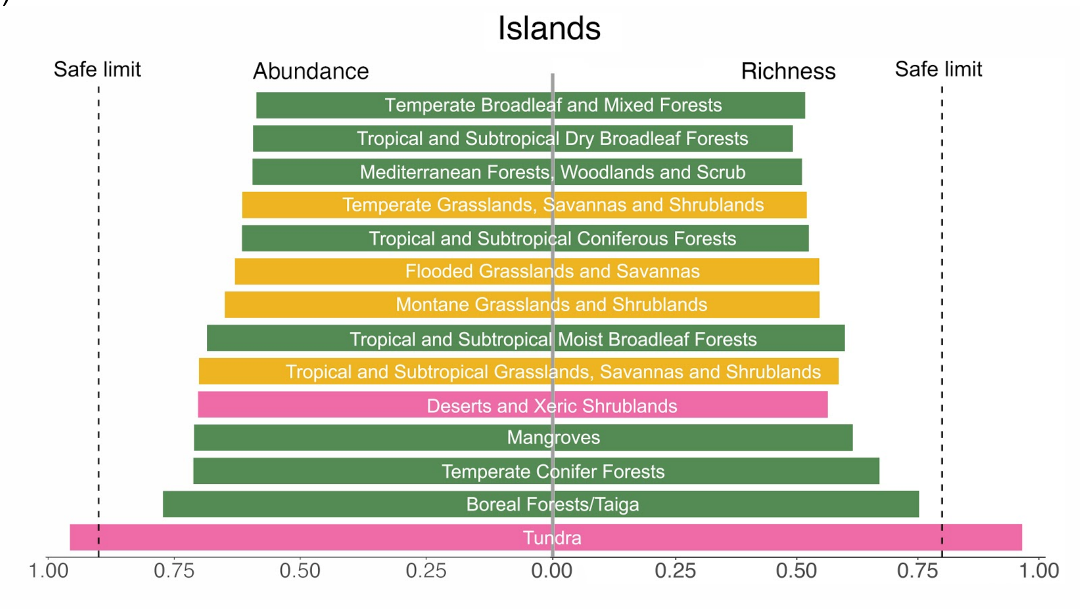
Excluding Australia from the island maps changed some the island percentages markedly; in particular, minimally-used primary vegetation (increasing to ~45%), primary vegetation (from ~9% to ~16% –Table 3.1) and pastures (e.g., light-use pasture decreased from ~30% to ~10% – Table C.11). Excluding Australia from the island BII maps slightly increased estimated BII (abundance-based BII to 0.73 and richness-based BII to 0.67) and decreased the percentage of island area below proposed safe limits (to 77.1% for abundance-based BII and 71.8% for richness-based BII; these percentages were still higher than those found for mainlands). Distribution of DistRd did not change markedly when Australia was excluded from the island map; however, HPD data was less skewed towards low values and land with low HPD (values between 0 and 0.3 on a 0 to 1 scale) constituted a higher fraction of mainland (77%) than island area (70%) (Figure C.10, Table C.12).

Table 3.1. Percentage of land surface under different land-use and use-intensity combinations (LUI) in the island and mainland BII maps. LUI classes are collapsed as in the compositional similarity models (see Chapter 2). Percentages for all LUI classes (each land use with different use intensities) are shown in Table C.11.

LUI	Percentage on islands	Percentage on mainlands	Percentage on islands excluding Australia
Primary Vegetation Minimal use	38.45	28.48	45.21
Primary Vegetation	9.38	9.73	16.47
Secondary Vegetation	10.30	24.42	13.27
Cropland	8.98	12.29	11.77
Pasture	32.38	24.68	12.46
Urban	0.49	0.39	0.84

Figure 3.2 shows how average BII varies among biomes on islands and mainlands. On mainlands, grassland biomes tend to have the lowest values, whereas various forest biomes show the lowest island values. Tundra and boreal forests are the least affected on both islands and mainlands. Tundra is the only biome within safe limits for average BII (both abundance-based and richness-based) on both islands and mainlands; boreal forests on mainlands also have average BII above the safe limits.

a)



b)

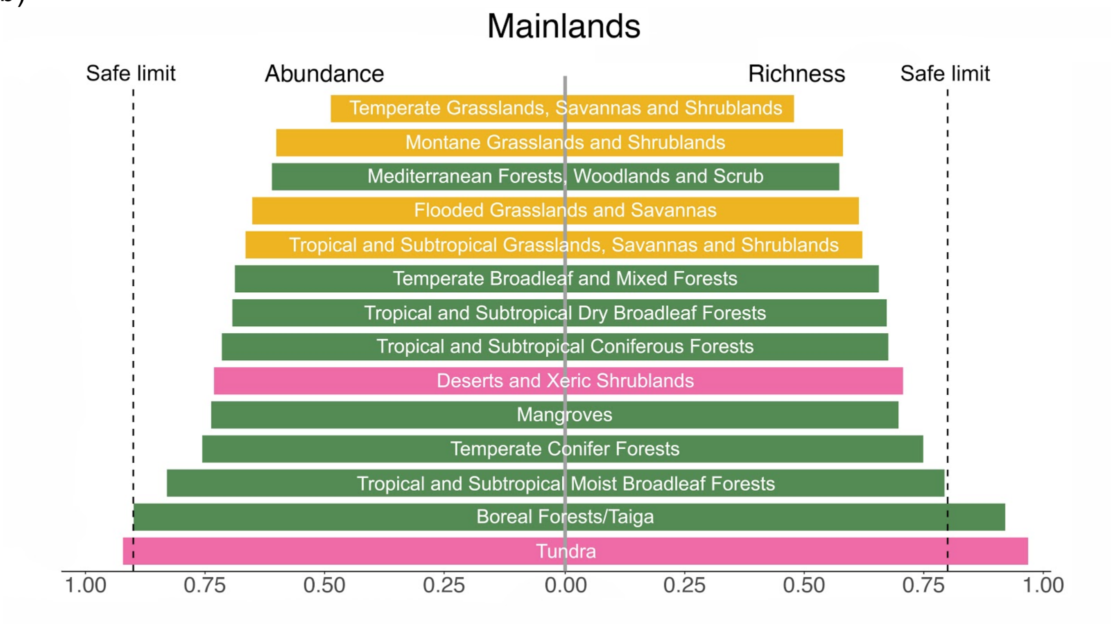


Figure 3.2. BII averages (abundance-based and richness-based) for biomes on a) islands and b) mainlands. The figures are replicas of those in Newbold et al. (2016a) to ease comparisons. Colours indicate major biome type (green: forests, yellow: grasslands, pink: other).

Average BII also varies among biodiversity hotspots on islands and mainlands. For islands, the Mediterranean Basin has the lowest BII average, followed closely mainly by tropical hotspots (e.g., Coastal Forests of Eastern Africa, Caribbean Islands and Madagascar and the Indian Ocean Islands), with the Tumbes-Chocó-Magdalena hotspot being least impacted (Figure 3.3a). On mainlands, temperate hotspots are the worst impacted, with the Succulent Karoo having the lowest average BII while Indo-Burma and Sundaland are the least affected (Figure 3.3b). For both islands and mainlands, abundance- and richness-based BII averages for all hotspots were below their respective safe limits.

Figure 3.4 shows the variation in average BII among countries; across regions, European countries have the lowest median values, for both islands and mainlands. For islands, countries in Oceania (abundance-based) and Asia (richness-based) have the highest median values. For mainlands, the highest median value for average BII was for American countries. Within each region, median country-level BII was lower on islands than on mainlands (Figure 3.4). In the case of IPBES regions, island average BII values are lowest for Africa and highest for the Americas, while mainland values are lower for the Asia-Pacific region than for the other three regions (Table 3.2).

Table 3.2. Average BII (abundance-based and richness-based) for IPBES regions on islands and mainlands. s.d. are shown within parenthesis. Results for Areas Beyond National Jurisdiction (ABNJ) are not shown. Results here differ from those in Figure 3.4, since these values correspond to averages for regions while Figure 3.4 uses averages for countries that are grouped into UN geographic regions and highlights the median values.

IPBES region	Average BII (abundance-based)		Average BII (richness-based)	
	Islands	Mainlands	Islands	Mainlands
Africa	0.58 (0.06)	0.75 (0.18)	0.49 (0.05)	0.70 (0.17)
Americas	0.88 (0.14)	0.75 (0.20)	0.86 (0.18)	0.74 (0.20)
Asia-Pacific	0.68 (0.09)	0.67 (0.17)	0.57 (0.08)	0.64 (0.15)
Europe-Central Asia	0.75 (0.21)	0.75 (0.18)	0.72 (0.24)	0.75 (0.20)

Estimated average BII for the 3,602 islands for which pressure data was available and whose name was listed in the Global Island Database plus Australia are publicly available at: https://doi.org/10.1101/576546. Roosevelt Island (U.S.A.) has the lowest BII average (~0.2 for both abundance-based and richness-based BII). The islands with the highest BII averages (~0.98) are mainly located in Greenland, Canada and Russia.

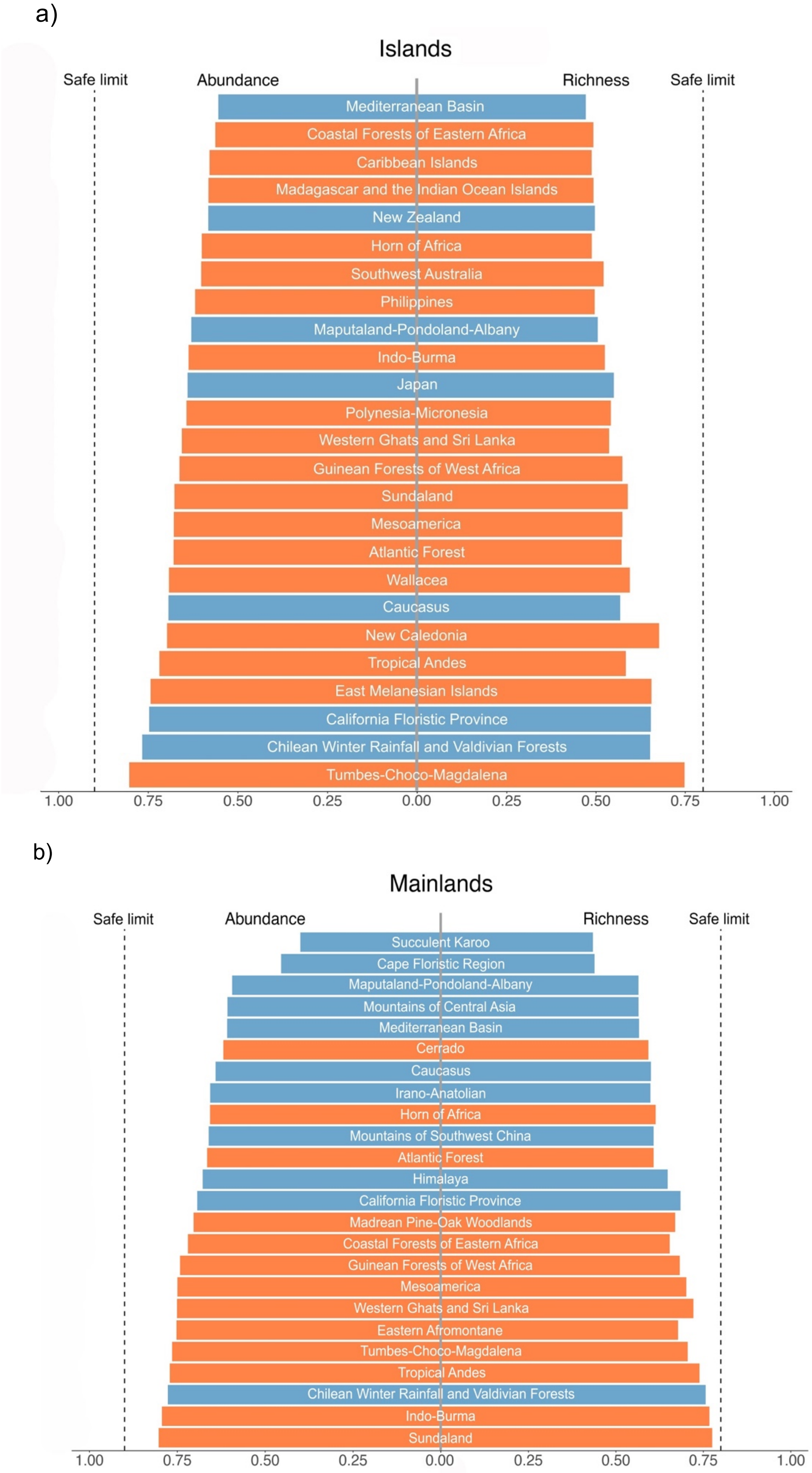


Figure 3.3. BII averages (abundance-based and richness-based) for biodiversity hotspots on a) islands and b) mainlands. Colours indicate whether hotspots are in the tropical (orange) or temperate (blue) realms.

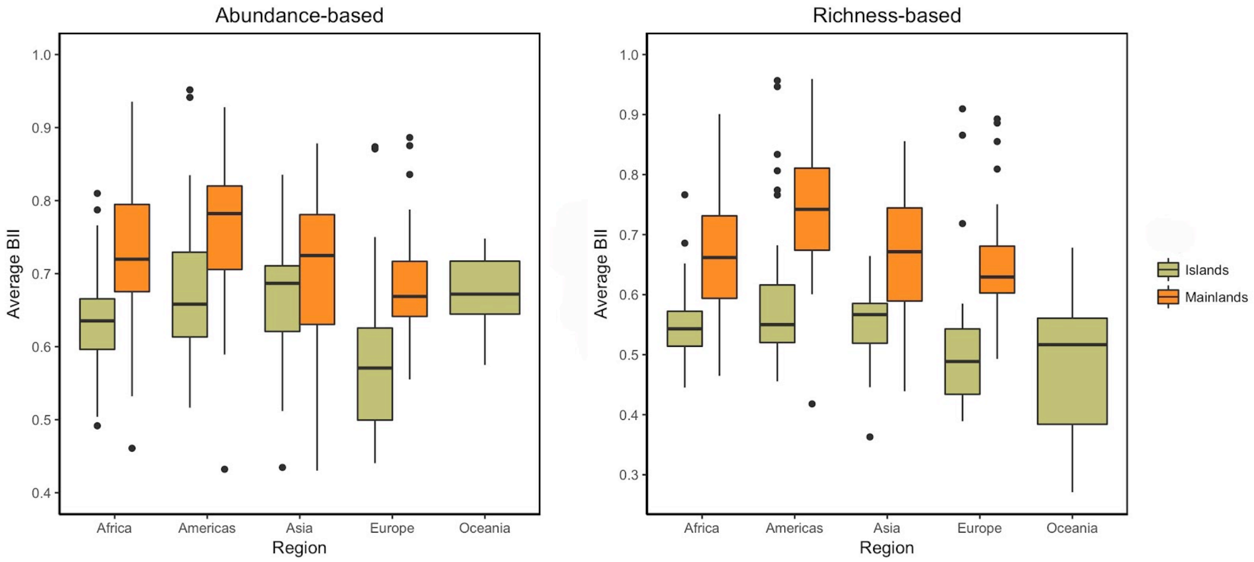


Figure 3.4. Average BII (abundance-based and richness-based) at the country level across different regions (UN geographic regions) on islands and mainlands. Lines within boxes show the median value, boxes show data within the 25th to 75th percentiles, whiskers show points that are up to 1.5 times the interquartile range of the data and points show countries that fall outside of these limits.

3.5 DISCUSSION

Although the Biodiversity Intactness Index (BII) was originally proposed nearly 15 years ago (Scholes & Biggs 2005), it has become a more prominent indicator in recent years because of two developments. First, the Planetary Boundaries framework (Steffen et al., 2015) proposed its use as a provisional metric to assess whether loss of biotic integrity exceeds safe limits. Second, as a result of the first development, the PREDICTS project has implemented BII based on global (Newbold et al., 2016a; Hill et al., 2018) or biome-specific (De Palma et al., 2018a) statistical models fitted using a large global database (Hudson et al., 2017). These models have not so far allowed different ecological systems to respond differently to human pressures, relying instead on the underpinning data being reasonably representative across higher taxa and major biomes (Hudson et al., 2017; Purvis et al., 2018). However, islands can be very distinct from mainlands, both ecologically (Whittaker & Fernández-Palacios, 2007; Gillespie et al., 2008; Delgado et al., 2017) and socioeconomically (e.g., Turvey, 2007), meaning that comparing BII between islands and mainlands is likely to be invalid. This chapter presents comparisons based on statistical models that, for the first time, allow island and mainland assemblages to have different distance-decay relationships of compositional similarity and to respond differently to human drivers.

I estimate the global average BII to be lower on islands than on mainlands, both for abundance-based (0.71 vs 0.73) and richness-based BII (0.62 vs 0.71, though the island value rises to

0.67 if Australia is excluded). The BII averages within countries and IPBES regions are also consistently lower for islands than mainlands in most regions (Figure 3.4; Table 3.2); though the Americas (IPBES region) are an exception (Table 3.2).

The island-mainland differences, though not large, suggest that island assemblages may be more sensitive and/or more exposed to human pressures than are mainland assemblages. In terms of sensitivity, increasing human population density from very low values and decreasing distance to roads both reduce species richness steeply in primary vegetation on islands but not on mainlands (Figures C.7 and C.8); and human population density also affects overall abundance in much the same fashion (Figure C.5). Habitats with primary vegetation would be likely to be the last refuges of any native species that are highly sensitive to human pressures, and it may be that such species still persist on islands whereas mainlands do not have them, either because they never did (i.e., mainland species have broader tolerances than island species: Delgado et al., 2017; Whittaker & Fernández-Palacios, 2007) or because such species have already been lost from the whole system (e.g., due to mainlands' longer history of human settlement: Keegan & Diamond, 1987) with only the more resilient species having persisted through the 'extinction filter' (Balmford,1996). Other coefficients in the models tend to be similar between islands and mainlands (Figures C.3-C.8; Table C.8).

Island-mainland differences in exposure are complex, with the sign of many differences changing if Australia is excluded. For example, around 37% of mainland area is cropland, pasture or urban; for islands, the corresponding figure is 42% if Australia is included but only 25% if it is excluded (Table 3.1). If Australia is excluded, the fractions that are cropland, urban or intensely used (the classes usually associated with lowest abundance and species richness in my models) are similar between islands and mainlands. Additionally, the fraction of 'people-free' land (e.g., low human population density) on islands decreases from 84% to 70% and as a result, mainlands show a higher fraction of area (77%) with low human population density than islands. However, minimally-used primary vegetation constitute a higher fraction of island than mainland area (however Australia is treated: Table 3.1); remote high-latitude islands are likely to contribute largely to the fraction of island area that is minimally disturbed and underpin the high average BII estimated for islands in the Americas region. Previous reports of strong human pressures on islands have highlighted how islands' small size can facilitate access to remaining primary vegetation (Kier et al., 2009) and brings a higher human population density in close proximity to natural habitats (Delgado et al., 2017). Ramankutty et al. (2008) suggested that some island-rich regions, such as Southeast Asia and the Pacific, have a high percentage of croplands and pastures (among the land uses with the most severe changes from natural habitats: Foley et al., 2005; McKinney, 2006; Chapter 2). Kier et al., (2009) reported that islands tended to have higher values of the Human Impact Index (Sanderson et al., 2002) than did mainlands. Some island-native species may have greater need than mainland species of 'people-free space'; but there is little indication from my data on pressures that they get it.

On both islands and mainlands, average BII is below the proposed 'safe limits' (Steffen et al., 2015; Newbold et al., 2016a), globally, for every IPBES region (apart from islands in the Americas using richness-based BII), for every biome except for tundra and boreal forest, and for every biodiversity hotspot. These results are much less optimistic than those of Newbold et al. (2016a), who estimated that only 9 of the 14 terrestrial biomes and 22 of the 34 terrestrial biodiversity hotspots have on average transgressed the safe limits for BII. Especially for islands, my BII estimates are much lower than those from Newbold et al. (2016a), where global averages were ~0.85 and ~0.77 for abundance-based and richness-based BII, respectively. I analyse the causes of these differences in Chapter 5.

My modelling approach still has some of the limitations of other implementations of BII discussed previously (Newbold et al., 2016a; Purvis et al., 2018; De Palma et al., 2018a). I might still be overestimating BII by 1) ignoring lagged responses; 2) not considering the effects of climate change or any other drivers with a different spatial pattern than the human pressures in my models; 3) the likely presence of human pressures on many sites in the reference class (assumed as minimally-disturbed); and 4) shortcomings in pressure data for some regions (most obviously, the lack of plantation forests in land-use maps, and bias and incompleteness in currently available road maps such as gROADS – Meijer et al., 2018). Effects of roads on islands might be underestimated if island roads are less likely to be recorded than those on mainlands. A further limitation more specific to this study is that many more studies are available for mainlands than islands (Table C.1), particularly within some biomes (Table C.2). Less confidence can also be placed in results for biomes that are relatively poorly represented in my data such as taiga, tropical and subtropical coniferous forests in islands; and tundra, mangroves and flooded grassland and savanna in both islands and mainlands (Table C.2).

I chose to perform my analyses based only on human pressure data from 2005 so that I could also focus on comparing my BII estimates for islands and mainlands with those of Newbold et al. (2016a) (see Chapter 5), who used the same pressure data. More recently, De Palma et al. (2018a) estimated annual change in BII for tropical forest biomes between 2001 and 2012, and Hill et al. (2018) predicted possible future impacts to biodiversity intactness at a global scale. Both studies implemented the modelling improvements that I use here – and discuss in Chapter 5 – but have gone further in making projections using time-varying pressure data. Additionally, De Palma et al. (2018a) included human population density and roads in their models of compositional similarity, increasing their ability to account for the effect of habitat degradation; and Hill et al. (2018) used refined land use classes (Land-Use Harmonization 2 – Hurtt et al., in prep.) which differentiate rangelands from pastures; this can lead to higher levels of BII across regions where rangelands are common such as Australia.

Despite its limitations, my study marks an important technical improvement in the estimation of BII, and shows that biotic integrity worldwide has been much more seriously diminished – especially on islands – than previously estimated (Newbold et al., 2016a). Some species native to islands appear much less able than mainland species to persist in the face of rising human population density and road development. My results highlight the need for stronger efforts to arrest the loss of native island biodiversity in order to achieve biodiversity targets, especially in the endemic-rich and heavily impacted island-based biodiversity hotspots (Myers et al., 2000).

CHAPTER 4

Effects of land-use change and related pressures on alien and native subsets of island communities

4.1 ABSTRACT

Studies assessing the different effects of human pressures on native and alien assemblages on islands are scarce, despite many suggestions that island species and habitats are particularly vulnerable to human disturbances, and accumulating evidence that anthropogenic changes are overwriting natural biogeographic patterns seen among islands. In this chapter, I model how land-use change and related pressures affect diversity (species-richness and summed abundance) of alien and native species on islands. I also test whether richness and abundance of alien species is predicted by island size and isolation – as has often been shown for native species – and GDP per capita as a proxy for the intensity of trade-mediated species introductions. Finally, fitting models of compositional similarity, I evaluate the turnover among natives and aliens caused by land-use change on islands and estimate how homogeneous native and alien communities are among sites within the same land use. My results suggest that, on islands, land use and – to a lesser extent – human population density and proximity to roads reduce both richness and abundance of natives, whereas the number and abundance of alien species are high in sites on human-dominated land uses. Moreover, more isolated islands have a higher number of alien species across most land uses than less isolated islands. Finally, alien species have a major role in the turnover and homogenization in island assemblages. The declines of native assemblages of islands in the face of human pressures, and the proneness to invasions of even the more remote islands, highlight the importance of stronger efforts to lower the intensity of human pressures on islands and to prevent the establishment of alien species for island biodiversity conservation.

4.2 INTRODUCTION

Previous chapters have shown that land use and related pressures strongly shape the diversity within and turnover between local ecological assemblages, in ways that differ significantly between islands and mainlands. This chapter focuses on island sites, and models how these pressures affect two subsets of the ecological assemblages: natives and aliens. Studying alien and native responses to human pressures on islands is important for two main reasons. First, many species native to islands have characteristics – e.g., narrow-range endemism, small population size – that make them both particularly vulnerable to human disturbances and irreplaceable (Paulay, 1994; Simberloff, 2000; Sakai et al., 2002; Chapter 1). Second, islands have been highlighted as hotspots of alien species (Capinha et al., 2017; Dyer et al., 2017a) and as systems at higher risk of invasions (Simberloff, 1995a; Sax & Brown, 2000; Denslow, 2003; Dalmazzone & Giaccaria, 2014).

Natural and anthropogenic factors combine to make island, and their site-level communities, prone to invasion. Islands – especially remote islands – may have a relatively small source pool of native species (Herben, 2005) from which their communities are assembled, resulting in low species richness for their area (Whittaker et al., 2017), which is hypothesised to result in more available resources (Sax & Brown, 2000), low pressures from predators or pathogens, and disharmonic communities (Denslow, 2003; Gillespie et al., 2008). Additionally, native species often have low competitive ability (Denslow, 2003), and have evolved reduced dispersal abilities (Gillespie et al., 2008) and reproductive output (Adler & Levins, 1994; Siliceo & Diaz, 2010; Meiri et al., 2012). These natural factors combine to facilitate establishment by alien colonists, especially in disturbed sites (e.g; Borges et al., 2006; Meijer et al., 2011; Marini et al., 2012). Many land uses involve site-level disturbance, favouring the establishment of alien species (often good dispersers that reproduce rapidly and tolerate to a broad range of conditions: Sakai et al., 2001; Hamilton et al., 2005; Cadotte et al., 2006) over natives. Crucially, humans have directly introduced many alien species to islands, with propagule pressure (i.e., number of released individuals – Lockwood et al., 2005) and the presence of other groups of introduced species (Redding et al., 2019) both influencing the probability of establishment. In contrast, disturbed habitats can represent novel environments for some native species, to which they are not adapted (Sax & Brown, 2000). Hence, natives often cannot tolerate the effects of habitat modification, particularly species with traits related to a high extinction risk, such as large size (Cardillo et al., 2005; Ripple et al., 2017), low fecundity, limited dispersal abilities, stenotopy (McKinney & Lockwood 1999) and small range-size (Collen et al., 2016; Ripple et al., 2017).

Importantly, although some studies have addressed how alien invasions change the composition of island communities (Sobral et al., 2016; Florencio et al., 2013), the question of whether compositional changes (e.g., assemblage turnover and homogenization) are mainly driven by the presence of alien species in disturbed sites or the turnover of native species (e.g., disturbance favouring more resilient or widespread natives) has not been broadly explored. This question is important on mainlands as well as on islands, but a practical reason dictates that it is easier to address on islands: classifying species as native or alien tends to be easier for island than mainland sites.

Classifications of species on mainlands are usually based on species distribution at a country level and uncertainty in native vs non-native status is often unclear. Even though using political boundaries to determine the status of a species might not be ideal (since they do not reflect biological or ecological barriers: Richardson et al., 2000; Pyšek et al., 2004), more precise data are rarely available, especially for large sets of species, and working at a country level provides the opportunity of obtaining defined environmental and economic parameters (Pyšek et al., 2004). Efforts to identify alien and invasive species on islands have intensified in recent years due to programs focusing on the eradication of invasive species on islands to benefit endemic threatened species (e.g., Holmes et al., 2019). Such sources can provide data on species status that are less biased towards particular taxonomic groups than is the case for mainlands; e.g., global data for native vs non-native status is mainly available for a restricted set of taxa such as birds and plants (see for example The Global Avian Invasions Atlas and The Global Naturalized Alien Flora – Dyer et al., 2017b; van Kleunen et al., 2019).

If alien species follow the natural patterns of island biogeography, large islands would be expected to have more alien species than small islands, and isolated islands less alien species than islands that are closer to continents or other islands (MacArthur & Wilson, 1967). However, recent studies have suggested that anthropogenic processes have particularly changed the species–isolation relationship (e.g., Blackburn et al., 2008; Helmus et al., 2014). Currently, anthropogenic factors such as colonisation pressure (i.e., number of species introduced to a defined location – Lockwood et al., 2009; Dyer et al., 2017a) or economic isolation of islands (Helmus et al., 2014) may be more important than geographic isolation.

While metrics such as shipping traffic among islands and mainlands (or among islands themselves) have been used as direct measurements of islands' economic isolation (Helmus et al., 2014) related to the arrival of alien species, these are not available for all islands globally. Other indicators of islands' socio-economic development may be more useful in global or multi-regional analyses aiming to predict alien species diversity. Measures of economic activity are related to propagule pressure (e.g., trade volumes), ecological disturbances (Westphal et al., 2008) and infrastructure development (Hulme, 2009) (e.g., roads, railways), all of which ease the arrival and establishment of alien species (Westphal et al., 2008; Hulme, 2009). For example, Dyer et al. (2017a) found that at a global scale, the number of alien introductions to a country was positively correlated with its per capita GDP, while Capinha et al. (2017) found that regional numbers of established alien amphibian and reptile species were positively associated with per capita GDP. These patterns have been mainly associated with high levels of species trade (e.g., plants and pet trade) and higher trade volumes in high-income countries (Early et al., 2016; Dyer et al., 2017a). International trade has been pointed out as a primary source of introduction of alien species (Levine & D'antonio, 2003; Early et al., 2016) since it leads to the escape or release of imported species into the wild (Reichard & White, 2001; Hulme et al., 2008) and the introduction of further alien species as stowaways (Helmus et al., 2014) or contaminants of goods (e.g., pest and pathogens – Hulme et al., 2008). Notably, based on data from Dalmazzone (2000), Hulme (2009) pointed out that the positive relationship between alien richness and GDP was stronger for island estates than for continents, which reflects the greater proportion of imported products that contribute to their GDP.

In this chapter, I model the effects of land-use change and related pressures on native and alien communities of islands. This study is the first global analysis of its kind to include a wide range of taxa while focusing specifically on islands. Based on models of local total abundance and species richness, I show that native and alien species on islands are affected differently by three human pressures (land use, human population density and distance to the nearest road). Additionally, I test whether richness and abundance of alien species is predicted by island size, geographic isolation and – as an index of economic connectance – GDP per capita. To evaluate the turnover of native and alien assemblages caused by land-use change on islands, I estimate how species composition of alien and native communities in minimally-disturbed sites is affected by land use change. Finally, I estimate how homogeneous communities of native and alien species are among sites within the same land use.

4.3 METHODS

4.3.1 Data assemblage

All the models used data on species abundance and occurrence extracted from the PREDICTS database (Hudson et al., 2017) in October 2016; the database is described in detail in Chapter 1. For this study, I only used data for island sites in the PREDICTS database (i.e., sites in Australia and all land polygons with a smaller area). The name of the island where each site was located was determined by matching the site coordinates with the Global Island Database, ver. 2.1 (UNEP-WCMC, 2015). All data processing and statistical analyses were performed using R Version 3.3.3 (R Core Team, 2017).

Data for island sites in the PREDICTS database includes 17,776 species and 1,339,339 biodiversity records (each one being a single diversity record of a species within a site within a study). I only attempted to classify species having a curated taxonomic name (i.e., a Latin binomial) in the PREDICTS database. 42 of the data sources in the PREDICTS database (including 51 studies) had already classified the sampled species as aliens or natives at the sites sampled.

To greatly extend the available data, I collated data from external sources to classify species based on the island (when possible) or country where they were sampled. I first used three global databases that could provide island-specific (rather than country-level) species classifications: the Global Naturalized Alien Flora database (GloNAF; van Kleunen et al., 2019); the Global Inventory of Floras and Traits (GIFT; Weigelt et al., 2017), a global set of regional plant checklists; and the Threatened Island Biodiversity database (TIB; Threatened Island Biodiversity Database Partners, 2017), which also reports on native and invasive species on islands. The matching of PREDICTS species names against species in GloNAF and GIFT databases used the original taxon names in the two databases or taxon names after correction or standardization using The Plant List database Version 1.1 (http://www.theplantlist.org/). I identified all matching species-island combinations between the three databases and PREDICTS island data to classify as many species as possible based on their distribution at an island level.

To further extend the data set, I used additional databases for species status at a country level which could provide downloadable datasets (six databases – Table D.1) or access to data through an application programming interface (API). For the latter case, I accessed data from the IUCN Red List (IUCN, 2017), the Global Invasive Species Database (GISD; Invasive Species Specialist Group ISSG, 2015) and Flora Europaea (Euro+Med, 2006) using the R packages '*rredlist*' ver. 0.5.0 (Chamberlain, 2018) (function '*rl_occ_country*') and '*originr*' ver. 0.2.0 (Chamberlain & Bartomeus, 2016) (functions '*gisd*' and '*is_native*'), respectively. I also used a dataset previously shared by the GLONAF team with the PREDICTS team, which gave the status of plant species found in both PREDICTS and GLONAF databases for all countries or regions included in GLONAF database. All matching species-country combinations in these sources and the PREDICTS island data were used to classify records for species whose status could not be defined at an island level. Most of these external sources provided a direct indication of the species status in different locations (e.g. alien, invasive, naturalized, native, endemic). When databases provided geographic ranges for species (e.g., Red List, AntMaps), I first extracted the status for the matching species-country combinations, but also classified species according to the geographic ranges provided by these sources. In particular, if a species was found in these sources, and the sampling location in my dataset was not included in the native range of the species, I classified it as alien (i.e., even if the source did not specifically list the species as alien in that country); where possible, I confirmed such designations of alien status using additional sources. In a final step, I searched for data sources that could help classifying specific species or taxa that were very common in my dataset (i.e., with many records in island data) but had remained unclassified to this point (mainly arthropods); these additional sources included taxonomic experts from different institutions, publications and databases for specific taxa and countries (Table D.1). In total, 27 external sources were used to classify species as aliens or natives (Table D.1).

4.3.2 Statistical modelling

4.3.2.1 Models of total abundance and species richness

Using only records where species were classified as aliens or natives, I calculated each site's total abundance (sum of abundances of all present taxa) and species richness (number of unique present taxa) for alien and native species (i.e., site-level biodiversity measures were calculated separately for aliens and natives). When sampling effort varied among sites within a study, total abundance was divided by the sampling effort to make data comparable among the study's sites.

To model the responses of alien and native species to human pressures, I fitted models for total abundance and species richness following the methods for the models that were used to estimate the Biodiversity Intactness Index (BII) (Scholes & Biggs, 2005; Newbold et al., 2016a) in Chapter 3 (generalized mixed-effect models – GLMMs; '*lme4'* package ver. 1.1-15– Bates et al., 2017). Total abundance was rescaled to a zero-to-one scale within each study to reduce the variance among studies, square-root transformed and modelled using a Gaussian error structure. Species richness was modelled using a Poisson error structure and log link. As fixed-effects, the two initial models included two-way interactions between each of three human pressures at a site-level (land use, human population density (HPD) and distance to nearest road (DistRd)) and the species status (alien/native) plus three-way interactions between species status, land use and HPD or DistRd. HPD and DistRd were log transformed and rescaled to a zero-to-one scale prior to modelling to deal with extreme values and to reduce collinearity. Generalized Variance Inflation Factors (GVIFs) (Zuur et al., 2009) did not indicate strong collinearity among the explanatory variables. For these models, the 10 land-use categories and three land-use intensities within each land use in the PREDICTS database (Hudson et al., 2017) were collapsed into seven final land use/use intensity classes: 1) Primary vegetation with minimal use (henceforth PriMin and considered as a baseline representing minimally disturbed sites), 2) Primary vegetation (light and intense use combined), 3) Secondary vegetation, 4) Plantation forest, 5) Cropland, 6) Pasture and 7) Urban (last five classes including all use intensities). These collapsed classes gave reasonable sample sizes (at least 100 sites) within each land-use class for both alien and native data (Table D.5). The best random-effects structure was identified using the Akaike's Information Criterion (AIC), with the initial models fitted using Restricted Maximum Likelihood (REML) for total abundance and Maximum Likelihood (ML) for species richness. I assessed two possible random-effects structures: (i) random slopes for land uses within study + random intercepts of study and block within study and (ii) random intercepts of study and block within study. The richness model was not overdispersed, so did not need an observation-level random effect (Harrison, 2014). Finally, I tried to simplify the fixed-effects structure of the models using backwards stepwise model simplification and likelihood ratio tests with models fitted using Maximum Likelihood. Model diagnostics showed that the final abundance and richness models fulfilled homogeneity and normality assumptions (Figure D.1).

4.3.2.2 Models including island traits as predictors

Using only the data for alien species, I fitted GLMMs to test whether island area, isolation and (two estimates of) GDP per capita predicted total abundance and richness of aliens. Island area (in km^2) was calculated using a global layer of land polygons taken from OpenStreetMap (OpenStreetMap Contributors, 2015) in cylindrical equal area projection. To estimate island isolation, I used Weigelt et al.'s (2013) values for the sum of the proportions of landmass within buffer distances of 100, 1,000 and 10,000 km around the island (henceforth, surrounding landmass). This metric has previously shown to be the isolation metric that best explains diversity of certain taxa (e.g., plants – Weigelt & Kreft, 2013) on islands at a global scale. Data for three Japanese islands and Australia (Table D.9) were missing from Weigelt et al. (2013), so these four islands were not included in these models. I used two estimates of GDP per capita (in current US dollars for the year 2005, World Data Bank). Country-level GDP per capita (henceforth, country GDP) was taken from World Data Bank. To estimate island-level GDP per capita (henceforth, island GDP), I divided the product of the island area and country GDP by the country's land area (World Data Bank). Although this metric might not be completely accurate to reflect islands' socio-economic development, it is a proxy that could be estimated using reliable data available for all countries and islands in my dataset. Where a single island represented almost the total territory of a country (i.e., Australia, Puerto Rico, Sri Lanka and Madagascar – Table D.9), I used the country's GDP per capita as the estimate for the island. When an island was politically divided among several countries (i.e., Ireland, Borneo, New Guinea, Tierra del Fuego), I used the GDP per capita and area of the country with the biggest percentage of territory in the island. For example, Borneo GDP per capita was calculated based on Indonesia.

I fitted a total of eight models – four of total abundance of aliens and four of alien species richness – using the same modelling approach as in the previous section except as follows.

As fixed effects, each initial model included one two-way interaction between land use and one of the four island traits (i.e., island area, surrounding landmass, country GDP and island GDP). Because island area, country GDP and island GDP included extreme values, I transformed them (Zuur et al., 2007), choosing the transformation that most closely approached a normal distribution and that yielded well-behaved residuals (Figures D.7 and D.9). Island area was square-root transformed, while both country and island GDP per capita were log-transformed. Surrounding landmass did not require transformation. I considered two possible random-effects structures for the models: (i) random intercepts of study (ii) random intercepts of study and island. I performed post hoc analysis (package '*phia*' ver. 0.2-1 – De Rosario-Martinez, 2015) to test whether the coefficients of the interaction between the land uses and the metrics for the island traits were significantly non-zero.

4.3.2.3 Models of compositional similarity

I adapted the methods used in Chapter 2 to model how land-use change on islands affected the turnover of native and alien assemblages. Compositional similarity was calculated, separately for alien and native data, for all possible pairwise comparisons between sites within each study using the abundance-based (J_A) and richness-based (J_R) asymmetric Jaccard Index. I then used linear mixed-effect models to model both J_A and J_R as a function of the sites' land uses (referred to as the land-use contrast; e.g, PriMin-Pasture), the geographic and environmental distance between the sites and the species status (native or alien). Land-use contrast was a 49-level factor; however, as in Chapter 2, I only focus on results for 13 land-use contrasts grouped in two sets (Table D.14): a) the set of contrasts with site *i* in PriMin, estimating how the composition of native and alien species of minimally-disturbed sites is affected by change to each other land use, and b) the set of contrasts with both sites in the same land use, estimating how similar communities are among sites facing similar pressures. For both alien and native data, most of the land-use contrasts of interest had sample sizes >1900 and included data from five or more studies (Table D.14); the only exception was PriMin-Urban, for which sample sizes were <60 (Table D.14) and data only came from one study for aliens and two studies for natives. I do not report results for this contrast since the estimates are unreliable; however, model coefficients for all land-use contrasts are shown in Table D.16. Unlike in Chapter 2, I did not attempt to perform an indirect calculation for compositional similarity estimates of PriMin-Urban, because sample sizes for the Secondary-Urban contrasts were also small (2 studies for aliens and 5 studies for natives).

As fixed effects, the models included two-way interactions between species status (alien/native) and each of the other three explanatory variables (geographic and environmental distances between sites and land-use contrast). I included study identity as a random intercept.

As in Chapter 2, I used the PriMin-PriMin contrast as the intercept level in the models, since it is an indicator of the natural spatial turnover of species and therefore, a baseline against which to compare the other land-use contrasts. Data transformations are as in Chapter 2: compositional similarity was logit-transformed, while environmental distance was transformed using cube root, and geographic distance was divided by the median maximum linear extents of the sites in the dataset and then log-transformed. Permutation tests were used to assess significance of terms during backwards stepwise model simplification and statistical significance of interactions between alien/native status and the other explanatory variables, again as in Chapter 2. The final models for J_A and J_R fulfilled homogeneity and normality assumptions (Figure D.11).

4.4 RESULTS

4.4.1 Species status

Of the 17,776 species recorded from island sites in the PREDICTS database, 3,059 were already classified as native or aliens at particular sites, these data coming from 42 data sources. This number includes 1,503 species without a curated Latin binomial; 5,217 other species similarly without a binomial could not be checked against other databases. For species having a curated Latin binomial in the PREDICTS database, there were 13,060 unique combinations of species and island, of which 1,109 (for 1,039 species) could be classified using the island-specific databases (i.e., GLONAF, GIFT and TIB); and 10,968 unique combinations of species and country, of which 2,160 (for 1,866 species) could be classified using the country-level external sources.

This matching process produced a dataset with 799 alien species (Table D.2) (from 4,799 sites in 99 studies, 38 islands and 21 countries) and 5,522 native species (Table D.2) (from 7,354 sites, in 157 studies, 79 islands and 29 countries). In total, I was able to classify ~52% of the island biodiversity records in the PREDICTS database as native or alien (Table D.3), with more coming from the PREDICTS database than from other sources (Table D.4). The dataset retained ~70% of the island studies and ~75% of island sites in the PREDICTS database.

4.4.2 Effects of human pressures on native and alien species

The best random-effects structure for the abundance and richness models (judged by AIC) included random slopes for land uses within study and random intercepts of study and block within study (Table D.6); however, I used a richness model without random slopes due to convergence issues. For both overall abundance (Table D.7) and species richness (Table D.8), aliens and natives responded very differently to human pressures.

On average, ~17% of the species and total abundance in sites in minimally-disturbed primary vegetation corresponded to alien species (and ~83% to native species) (Figures D.5. and D.6). Relative to this baseline of primary vegetation with minimal use, three land uses had significant negative impacts on overall abundance of natives: pastures (-33%), plantation forests (-24%) and secondary vegetation (-13%) (Figure 4.1). By contrast, relative to the same baseline, all land uses increase the overall abundance of aliens (Figure 4.1), by more than 100% in secondary vegetation, and by even more in human-dominated land uses (~260% increase in croplands, ~420% in plantations, ~430% in pastures and ~650% in urban sites). The effects of DistRd on total abundance of natives and aliens were weaker and less clear (and in this case the three-way interaction between species status, land use and DistRd was not significant – Table D.7); however, total abundance of native species tended to increase with DistRd (Figure D.2). In the case of HPD, native species showed a decline in total abundance as HPD increased mainly in human-dominated land uses (Figure 4.2). The effects of HPD on natives' total abundance was less clear in less disturbed or forested land uses (Figure 4.2). Total abundance of alien species increases with HPD mainly in pastures; effects were less clear across the rest of the land uses (Figure D.3).

Numbers of native species were lower in most human-dominated land uses than in the PriMin baseline, with particularly severe reductions in croplands (-45%), pastures (-29%) and plantation forests (-25%) (Figure 4.3). In contrast, the numbers of alien species are significantly higher in pastures (~270%), urban sites (~130%), plantation forests (~90%) and croplands (~80%) (Figure 4.3). HPD has only weak effects on numbers of native (Figure 4.4) and alien (Figure D.4) species within most land uses, but the number of native species tends to decline across some land uses as HPD increases (Figure 4.4). The number of alien species tends to decrease slightly as DistRd increases (with the main exception of urban sites –Figure 4.5); whereas numbers of native species tends to increase with DistRd in human-dominated land uses (i.e., plantation forests, pastures, croplands and urban sites –Figure 4.5).

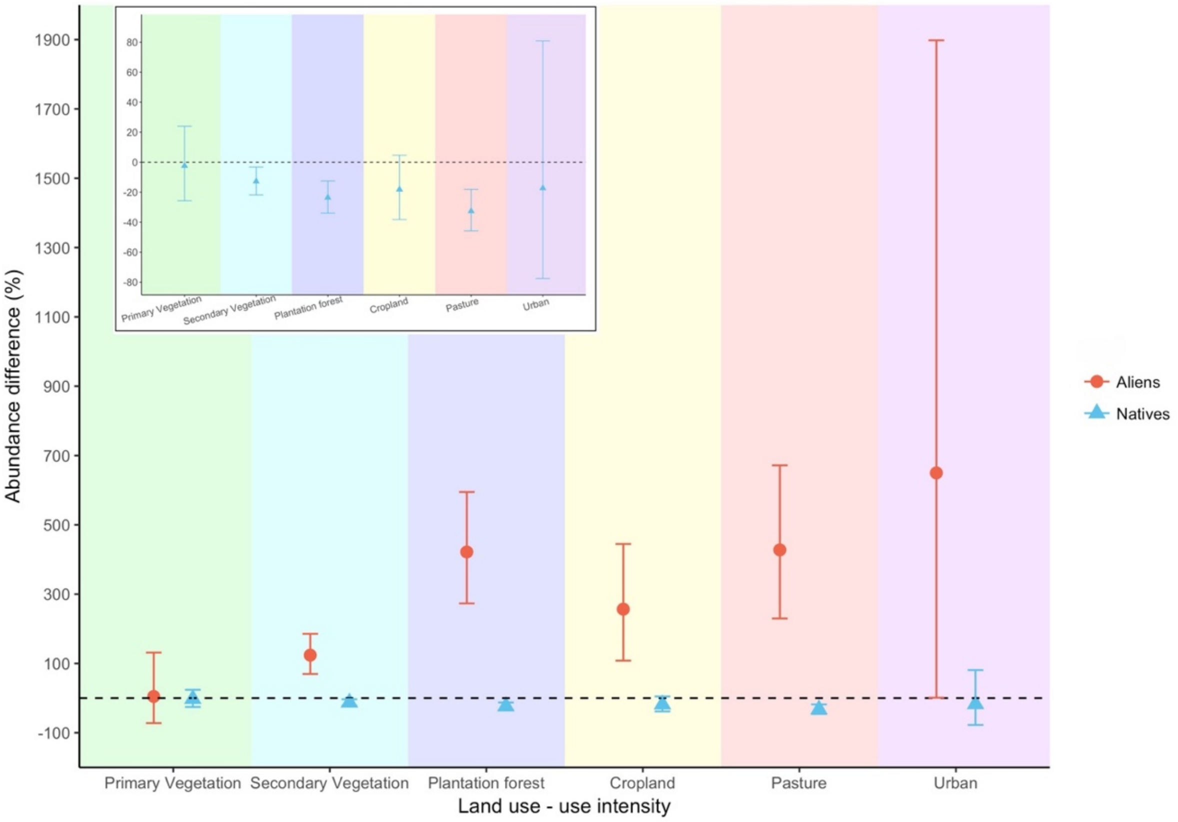


Figure 4.1. Response of total abundance of aliens and natives to land use. Values indicate decrease or increase in percentage of total abundance using minimally-used primary vegetation as baseline (dashed line). Bars indicate 95% confidence intervals. The inset shows results for natives, which are not clearly visible in the main plot.

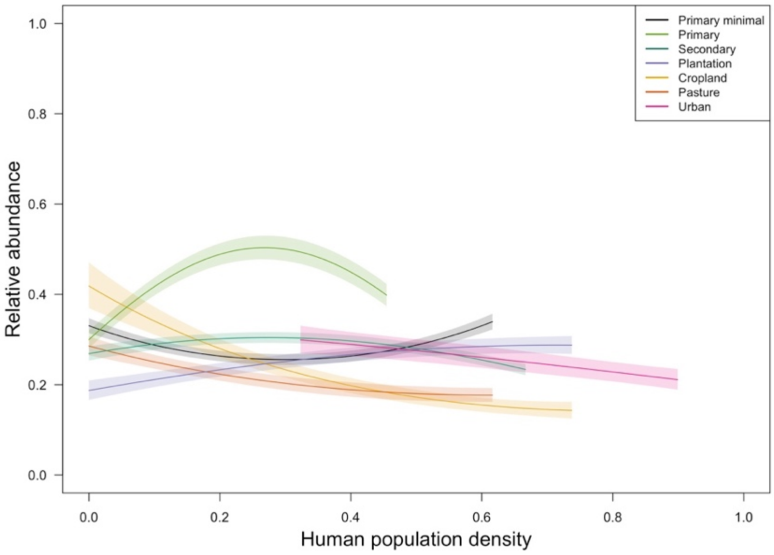


Figure 4.2. Response of total abundance of natives to human population density (HPD) across land uses. The x limits of each coloured line indicate the 2.5th and 97.5th percentiles for the values of HPD represented in each land use in the model dataset. For clarity, the error bars show half the standard error. HPD values are shown on a rescaled axis (as fitted in the models). Abundance is shown on a zero-to-one scale (as fitted in the models; i.e., abundance rescaled within studies).

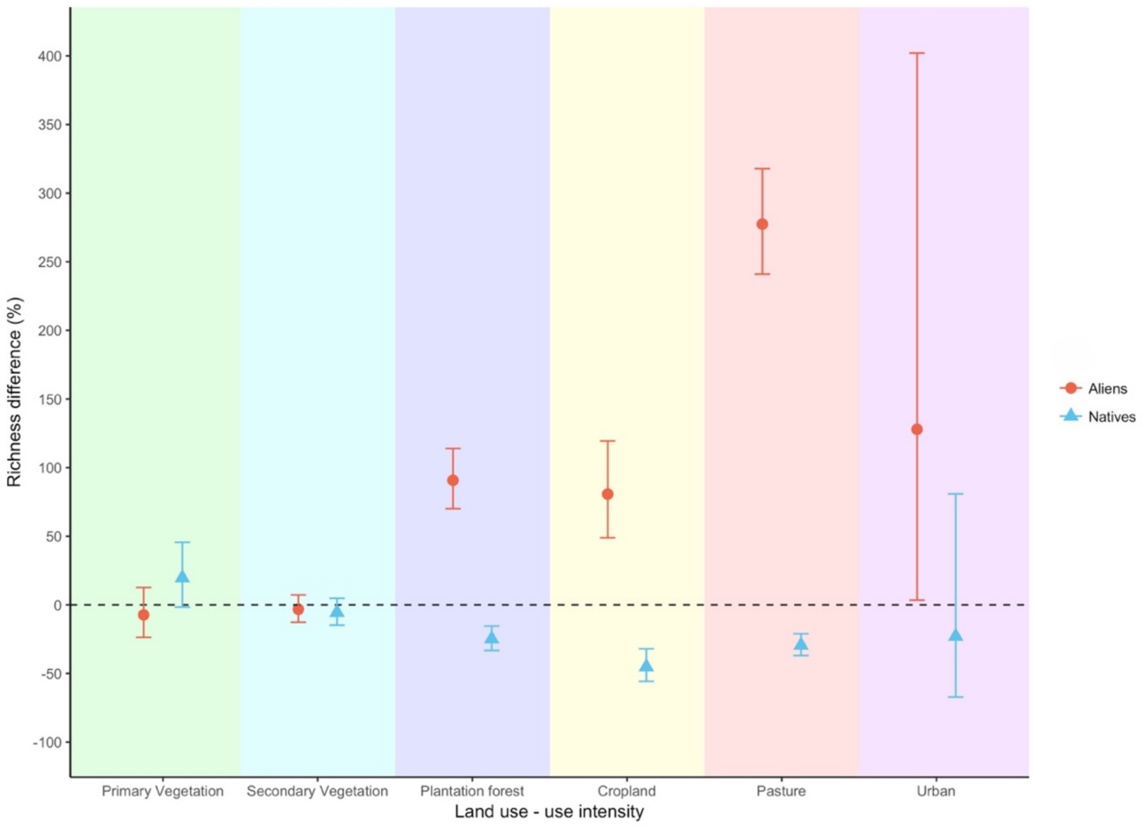


Figure 4.3. Response of richness of aliens and natives to land use. Values indicate decrease or increase in percentage of species richness using minimally-used primary vegetation as baseline (dashed line). Bars indicate 95% confidence intervals.

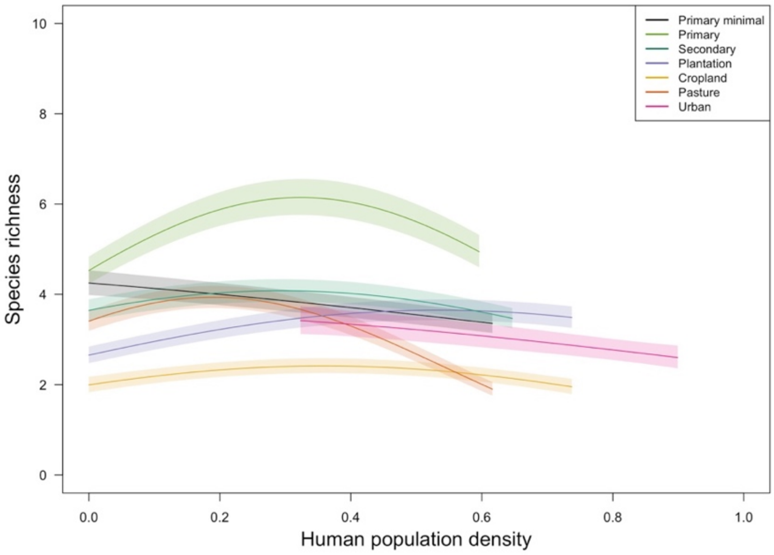


Figure 4.4. Response of richness of natives to human population density across land uses. Values of human population density are shown on a rescaled axis (as fitted in the models).

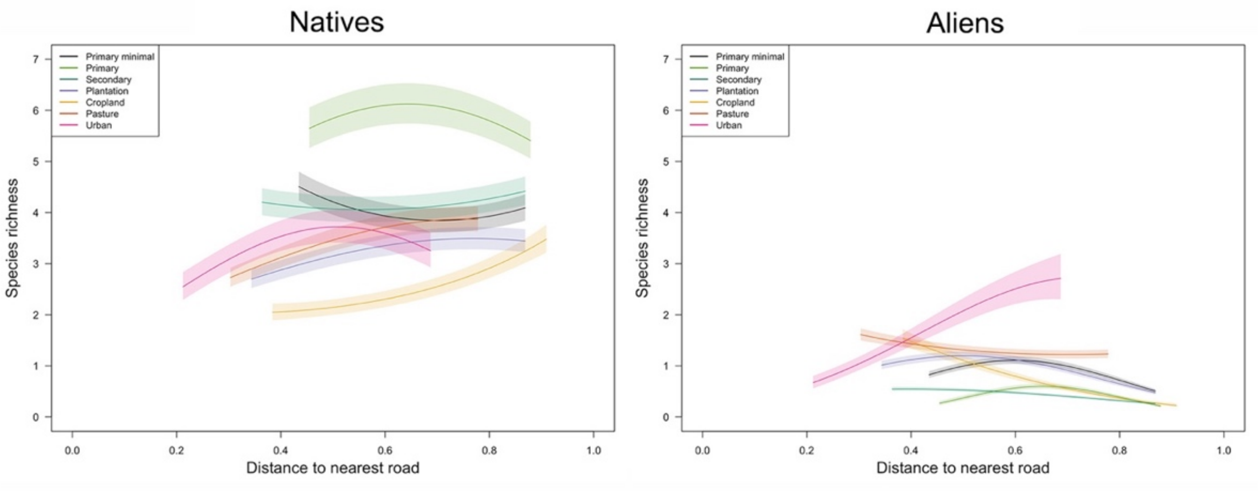


Figure 4.5. Response of richness of aliens and natives to distance to the nearest road. Distance to road values are shown on a rescaled axis (as fitted in the models).

4.4.3 Island traits as predictors of alien abundance and richness

The abundance models for alien species which included island area or GDP per capita metrics used data from 85 studies in 30 islands, whereas the corresponding species-richness models used data from 99 studies and 39 islands. Analyses involving surrounding landmass were based on fewer data: 65 studies from 26 islands in the model of abundance, and 76 studies from 35 islands in the richness model (Table D.9). Most of these models used more data than the previous abundance and richness models, as I only excluded data for sites without a defined land use or where data were not available for the surrounding landmass from Weigelt et al. (2013).

For all eight models, the best random-effects structure (judged by AIC) included random intercepts of study and island (Tables D.10 and D.12). None of the models could be simplified, because land use interacted significantly with each island characteristic (Tables D.11 and D.13). However, only a few land uses had significant interaction coefficients (Figures D.8 and D.10), especially in the richness models, so few clear patterns could be discerned. The clearest pattern was seen in the effects of surrounding land mass on site-level species richness (Figure 4.6): as the surrounding landmass increases, the number of alien species decreases significantly within most land uses (but not pastures or plantation forests), especially in primary vegetation and urban sites.

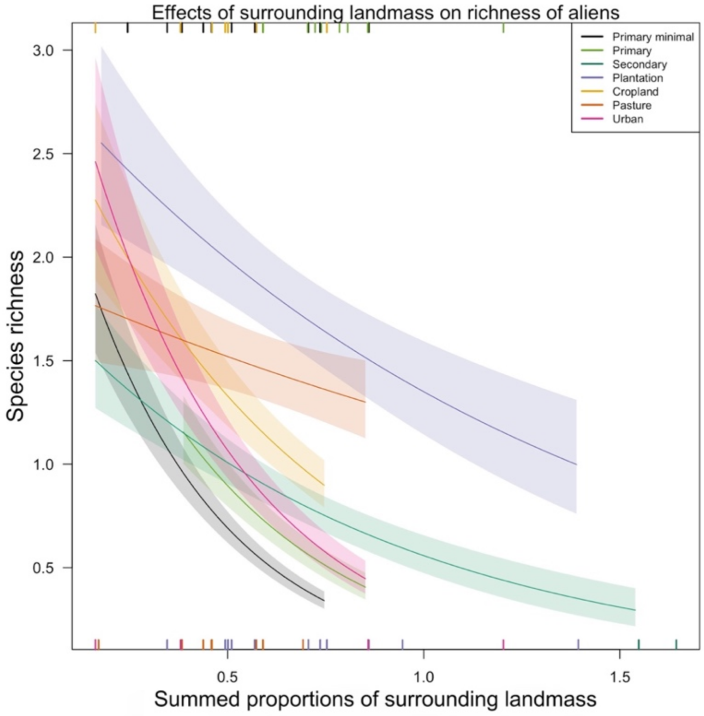


Figure 4.6. Effects of surrounding landmass on richness of alien species across land uses. For clarity, the error bars show half the standard error. Slopes that are significantly different from zero: Primary minimal (-2.875, P= <0.001), Primary vegetation (-2.254, P= <0.01), Secondary vegetation (-1.182, P=0.05), Cropland (-1.594, P= <0.05) and Urban (-2.479, P= <0.001). Rugs along the horizontal margins show the values of surrounding landmass represented (across land uses) in the model data set (rugs for minimally-used primary vegetation, primary vegetation and croplands in the top margin and the rest of the land uses in the bottom margin). Rugs for land uses can overlap, therefore some data is not visible.

4.4.4 Effects of land use on native vs alien assemblages

The final data for models of compositional similarity included 91 studies: 60 including data for alien species (2,780 sites; 597 species) and 90 including data for native species (4,293 sites; 3,199 species). Data for alien species came from 25 different islands and data for natives from 32 islands. All interactions in the two models were significant (Table D.15). For both J_A and J_R, the decline in similarity with geographic distance is significantly steeper for alien species than for native, whereas the reverse is true for the decline in similarity with environmental distance (Table D.16 and Figure D.12).

Once distance-decay effects are controlled for, land use affects compositional similarity to PriMin (i.e., the presence and abundance of novel species in land uses other than PriMin) significantly more in alien assemblages than in native assemblages, for both J_A and J_R (Figures 4.7 and D.13). Alien assemblages of sites within PriMin were more compositionally similar to each other than to assemblages of sites in other land uses (particularly croplands, plantations and pastures). In contrast, native assemblages of PriMin sites were slightly less similar to each other than to assemblages of sites in most other land uses. Only primary vegetation and pastures seemed to reduce compositional similarity to PriMin for native assemblages .

Moving to compositional similarity within a land use, pairs of sites within most land uses tend to have assemblages that are more similar than are pairs of PriMin sites, for both alien and native assemblages and for both J_A and J_R (Figures 4.8 and D.14). The only exceptions to this pattern are urban sites and croplands. Most of these within-land-use similarities differed significantly between alien and native assemblages; the reduction of spatial beta diversity (when compared to similarity between PriMin sites) is stronger for alien assemblages, particularly in primary vegetation and plantation forests, but also, for J_R, in pastures and urban sites. Native assemblages only showed a slightly stronger reduction of spatial beta diversity than alien assemblages in models for J_A in secondary vegetation and pastures (Figure D.14).

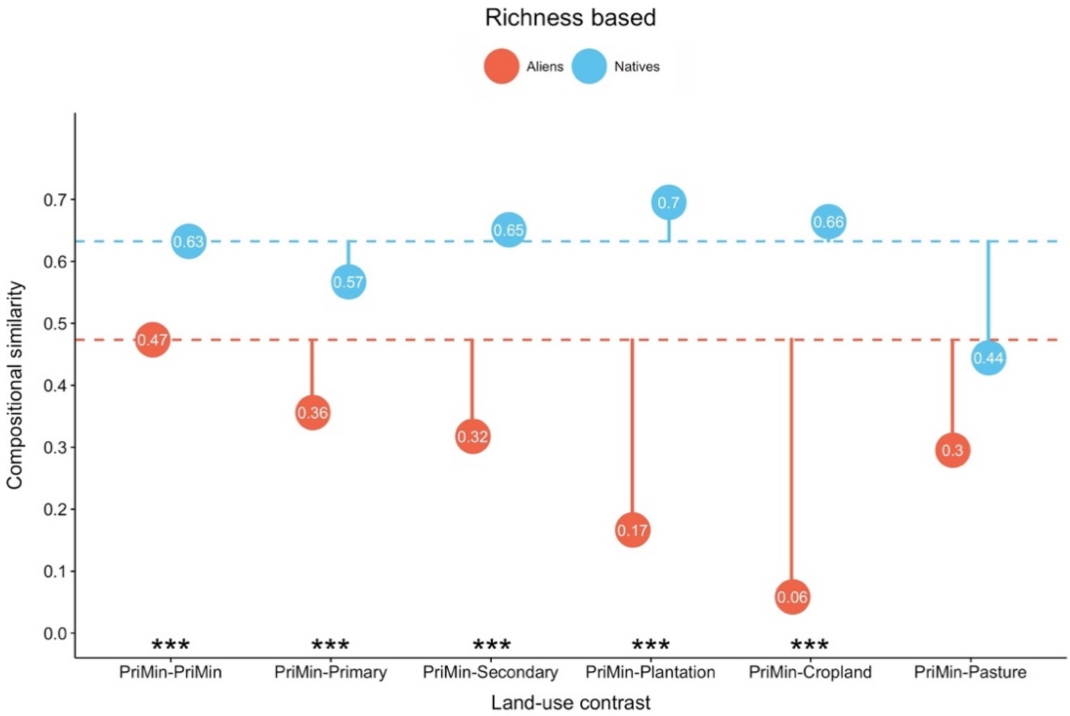


Figure 4.7. J_R estimates for land-use contrasts where site *i* is in PriMin. Solid lines show the magnitude of change in J_R driven by change to different land uses; the baseline is compositional similarity between PriMin sites for alien and native assemblages respectively (dashed lines). Significance (indicated by stars) is shown for alien/native differences for J_R changes from PriMin-PriMin on a logit scale (results from permutation tests and two-tailed tests comparing the coefficients for interaction between alien/native and land-use contrast to null distributions). Results for the PriMin-Urban contrast are not shown because sample sizes for this contrast were very small (but see the coefficients in Table D.16) Significance code: 0.005***

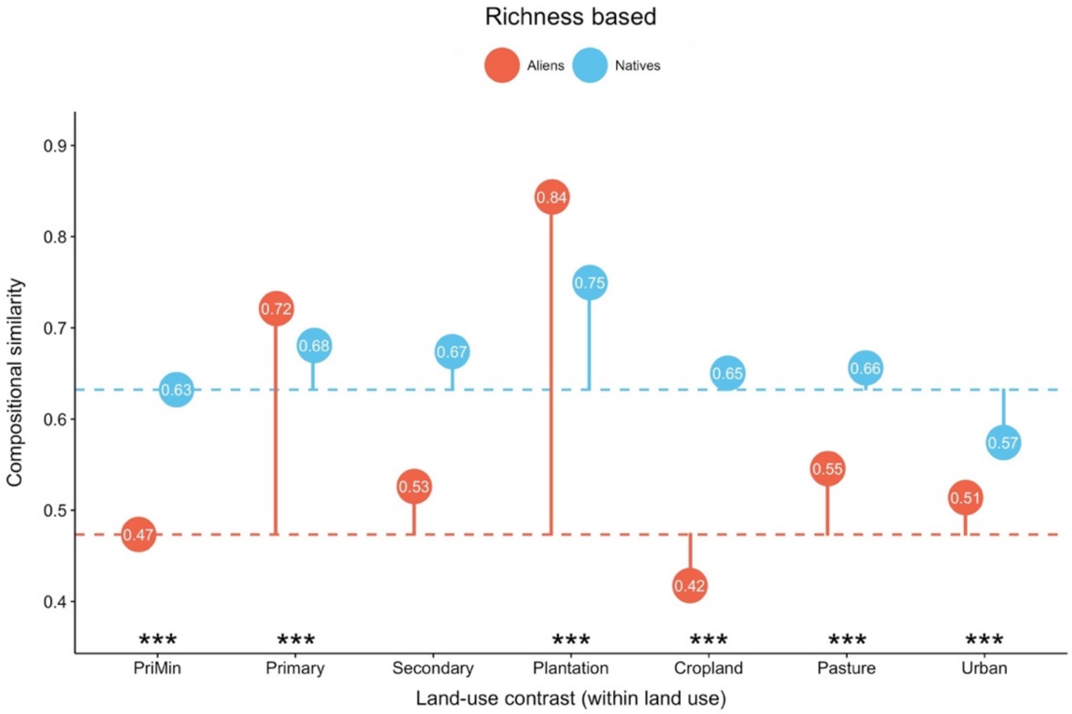


Figure 4.8. J_R estimates for alien and native assemblages in sites within the same land use. Each category corresponds to a land-use contrast (i.e., Cropland= Cropland-Cropland). Solid lines show the magnitude of change in J_R using PriMin-PriMin compositional similarity as baseline (dashed lines). Significance connotation and codes as in Figure 4.7.

4.5 DISCUSSION

Human-dominated land uses markedly decrease the total abundance and richness of native species on islands while dramatically increasing the abundance and richness of alien species. These findings are in line with previous suggestions that habitat modification tends to have negative impacts on natives (McKinney & Lockwood 1999; Scholes & Biggs, 2005) or narrow-range species (Newbold et al., 2018), and with the hypothesis that alien species can be very successful in disturbed habitats (Sax & Brown, 2000; Catford et al., 2012; Lembrechts et al., 2016). My results also agree with the global pattern that agriculture is among the main causes of biodiversity loss (Maxwell et al., 2016; Brummitt et al., 2015): croplands and pastures showed the strongest declines in numbers of native species; and pastures also showed the strongest decline in their abundance. The lack of a strong decline in overall abundance of natives in croplands was more surprising, but such a pattern is common in initial phases of habitat modification (Gonzalez & Chaneton, 2002), when the species being lost tend to be those at low initial abundance with more resilient native species persisting and even increasing in abundance.

Most sites in minimally-disturbed primary vegetation have very few alien species with a low total abundance of aliens (although there are exceptions – Figures D.5 and D.6); such a low baseline contributes to the extreme percentage increases seen in human-dominated land uses. In my final dataset, fewer than 10% of the species and total abundance in most minimally-disturbed sites corresponded to alien species (mean percentage across all these sites was ~17%). Absolute (rather than relative) values for total abundance and species richness are shown in the plots of the effects of human population density and distance to road (e.g., Figures 4.2 and 4.5)

Alien species are much more common on human-dominated land uses than on more natural land uses (especially minimally-used primary vegetation), which was expected given their tolerance to disturbed conditions and the fact that introduced species are expected to colonise sites that are altered by human activities instead of minimally-disturbed sites where they would need to displace native species (Sax & Brown, 2000). Alien species seem to be particularly successful in pastures and urban sites, although estimates for the latter are highly uncertain because of small sample size (Figures 4.1 and 4.3). Previous studies have highlighted that aliens can be very common or abundant in pastures (Meijer et al., 2011; Pouteau et al., 2015) and especially in cities (Pyšek, 1998; McIntyre, 2000; McKinney, 2002), where they have often been intentionally introduced (e.g., for livestock forage –Monroe et al., 2017 – or trade in cities – Kowarik, 2011). Moreover, once introduced, aliens can become very successful if they can tolerate the extreme conditions of these drastically altered habitats (McKinney, 2006). Overall, the positive effects of land-use change on aliens' diversity was stronger for total abundance, suggesting that the number of alien species arriving and establishing in disturbed sites might not be particularly high, but those species can be very successful in these sites and reach relatively high abundances (Pyšek & Richardson, 2007), perhaps reflecting the lack of competition by native species in human-dominated land uses (Sax & Brown, 2000), particularly on islands (Denslow, 2003).

Human population density, which can be related to land-use intensity (Lambin et al., 2001), has negative effects on natives (although this effect is not very strong) but no clear effects on aliens. Although my models suggest that in some cases aliens might particularly thrive where the human population is high (McKinney, 2001; Marini et al., 2012) (see especially the case of pastures – Figures D.3 and D.4), in other cases, richness or abundance of aliens was higher where human population density was intermediate or low (Figures D.3 and D.4). Island natives seem to have a greater need of 'people-free land' (Cincotta, 2011; McKee et al., 2013; McCreless et al., 2016). While in most human-dominated land uses, the increase in human population density seems to worsen the decline in native diversity, this negative effect was also seen in minimally-used primary vegetation. Cincotta (2011) suggested that, even without considering the relationship between human populations and habitat modification or invasive species, human populations in natural ecosystems represent a threat to native species, especially considering the negative effects of hunter-gathering (Cincotta, 2011; Maxwell et al., 2016). However, the effect of human populations in natural habitats is less severe than expected based on the results from Chapter 3, for reasons that are unclear. One possibility is that the difference arises from the exclusion of many species that could not be classified as aliens or natives.

The number of alien species tends to increase with proximity to the nearest road decreases across most land uses, while the richness of island natives tends to show the opposite trend within human-dominated land uses. These effects, though not particularly strong, were as expected; the development of roads or other infrastructure involves a direct traffic of vehicles and goods as well as severe modification of natural habitats (Spellerberg, 1998; Trombulak & Frisell, 2000; Hulme, 2009), all of which can promote the arrival and establishment of alien species (Trombulak & Frisell, 2000; Westphal et al., 2008; Hulme, 2009). Additionally, the development of roads can worsen the conditions of sites that have seen land conversion, can fragment habitats (Andrews, 1990) and can lead to collisions with vehicles, all of which increase mortality (Spellerberg, 1998; Trombulak & Frisell, 2000) so can lead to the loss of vulnerable native species.

The only island characteristic significantly associated with alien diversity was surrounding land mass: more isolated islands have higher numbers of alien species across most land uses. This pattern was also found for abundance of aliens but only in primary vegetation (Figure D.8). These results agree with previous studies suggesting that island biogeography of exotic species is not defined by the natural species–isolation relationship (Blackburn et al., 2008; Helmus et al., 2014). They also support a recent suggestion that island remoteness promotes invasions by alien species worldwide (Moser et al., 2018). This pattern can be in part attributed to location-level factors driving the success of establishment, such as features of communities of the recipient location; for example, Redding et al. (2019) recently found that the presence of other groups of introduced species (but also climatic suitability) at the introduction location is one of the main determinants of successful establishment. In this case, the reduced diversity of remote islands (MacArthur & Wilson, 1967), can also make them more invasible (Roderick & Vernon 2009; Helmus et al., 2014; but see Lonsdale, 1999), e.g., due to their high resource availability, missing functional groups and/or low pressures from competitors, pathogens or predators (Denslow, 2003; Gillespie & Baldwin, 2010). A particularly relevant result in this context was the rapid decrease of alien richness and abundance in minimally-disturbed primary vegetation as surrounding landmass (and hence the source pool of natural colonists) increases, suggesting that intact assemblages of native species are able to stem the influx of aliens (Kennedy et al., 2002). Isolated islands are expected to have particularly small species pools as a result of a restricted immigration (MacArthur & Wilson, 1967), leading to lower species richness per unit area and smaller samples from the set of potential species that can survive in different conditions (Herben, 2005). Through its influence on the size of the species pool, isolation may tip the balance between natives and aliens in terms of which species colonise disturbed sites.

In addition to factors affecting establishment, factors related to the initial arrival or introduction of alien species also need to be taken into account. Anthropogenic factors might be more important drivers of the pattern for remote islands; alien introductions by humans have gained importance by breaking geographical barriers and are now masking the natural negative species-isolation relationship (Helmus et al., 2014). In particular, propagule and/or colonisation pressure – positively related to the establishment of aliens (Dyer et al., 2017a; Redding et al., 2019) – might be higher in remote islands (Blackburn et al., 2008), where there can be more intentional releases of alien species and high levels of imports (Dalmazzone & Giaccaria, 2014), because isolated islands often harbour a low diversity of native species that can be used for farming, hunting, as sources of fuel and fibre or for other economic purposes (Denslow, 2003; Blackburn et al., 2008). This argument is consistent with the observed higher number of alien species in human-dominated land uses of isolated islands.

Composition of alien assemblages on islands is more dramatically changed than that of natives by conversion of land from minimally-used primary vegetation to other land uses. This is because the low number and abundance of alien species in natural habitats (Figures D.5 and D.6) means that other land uses are less likely to have alien species in common with minimally-disturbed sites. These results again suggest that alien species are more likely to establish in disturbed sites (Sax & Brown, 2000; Rodgers & Parker, 2003), especially those with more extreme conditions (Catford et al., 2012), such as croplands (Figure 4.7). Novel species in most land uses did not cause such marked changes in native assemblages when compared with communities in minimally-disturbed sites. In disturbed sites on islands, native assemblages are likely to be nested subsets of undisturbed communities (Baselga, 2010), given the small source pool of potential native colonisers, their lack of adaptation to disturbed sites, and their poor competitiveness (Denslow, 2003; Herben, 2005; Whittaker and Fernandez-Palacios 2007). Pastures seem to be an important exception: my results suggest the presence of native novel species in this land use. Most pasture sites compared in the PriMin-Pasture land-use contrast have either minimal or light use intensity (133 of 141 sites); these pastures might be mainly rangelands (i.e., ecosystems where the native vegetation has the potential to be grazed – Allen et al., 2011), since many of the sites are in areas where rangeland is common, such as the South Island of New Zealand, Australia, Madagascar and

Tierra del Fuego (Ellis & Ramankutty, 2008). Resilient species among the natives may be able to establish in such rangelands and other low-intensity grazed sites.

My results suggest that most land uses reduce spatial beta diversity for both alien and native assemblages, relative to the beta diversity between minimally-disturbed sites. The effect is stronger for alien assemblages, which agrees with previous studies focusing on particular human-dominated land uses (La Sorte et al., 2014) and suggests that the gain of alien species in disturbed sites might be the main cause of assemblage homogenization on islands (McKinney, 2004; La Sorte et al., 2014). Addition of alien species drives homogenization if the same species become widespread in more disturbed sites but are absent from natural habitats (Socolar et al., 2016). Although my results suggest this process may be in force in forested land uses (i.e., plantations and primary vegetation with light or intense use), alien assemblages in croplands are more heterogeneous than assemblages within minimally-disturbed sites. This means that the new alien species in this land use are not ubiquitous across sites (Florencio et al., 2015; Socolar et al., 2016), perhaps due to a higher diversity of alien species being introduced (e.g., different aliens with different crops) and establishing across sites this particular land use. The relatively weak homogenization pattern for native assemblages across land uses might be the result of a subtractive homogenization, caused by the loss or decline of different species from different sites (Socolar et al., 2016) and the persistence of common species; the exception seems to be urban sites, where perhaps even formerly common species are lost, resulting in subsets of native assemblages that remain distinct across sites (La Sorte et al., 2014).

Although I was able to include around half of the island biodiversity records in the PREDICTS database and most of the island sites and studies, the restricted data in the sources that I used to classify species as alien or natives mean that the dataset used in this chapter is much more limited than the island datasets used in previous chapters (Table D.2). This limitation may at least partly underlie one of the ambiguous results discussed above (e.g., effects of human population density or roads). Expanding the dataset to more islands with more different characteristics would increase the power of the models using island characteristics as explanatory variables. However, it is also possible that the characteristics used in these models truly do not have an important effect on alien diversity: e.g., any effect of island area on the number of abundance of alien species might simply be outweighed by anthropogenic factors such as colonisation pressure. Island and country per capita GDP were expected to be stronger predictors of alien diversity, since a high economic activity is usually expected to ease the arrival and establishment of alien species (Dalmazzone, 2000; Capinha et al., 2017; Dyer et al., 2017a); however, country-level values may not reflect island attributes well, while my estimates of island GDP are crude.

Despite data limitations, my results support previous suggestions that natives can be replaced by alien or invasive species in degraded habitats (Irwin et al., 2010; Catford et al., 2012) and that, on islands, species turnover caused by land-use change might be driven mainly by novel alien species rather than novel native species. These results could provide an explanation for the patterns seen in Chapter 2 (which did not separate natives from aliens), where mainland assemblages showed greater compositional differences between minimally-used primary vegetation and most human dominated land uses (when including all taxa in the models) than island assemblages. Of the hypothesis Chapter 2 proposed to explain the island/mainland differences, the one best supported by this chapter is that mainland settings tend to provide more species that could establish in disturbed sites than do islands. Among these species are resilient natives (i.e., mainlands' larger species pools mean higher probabilities of finding more competitive or more adapted species – Herben, 2005). Hence, the big changes that were found for mainland assemblages might be driven by both alien and native synanthropic species missing from natural habitats but assembling into novel human-dominated ecosystems; on islands, changes in assemblages could be smaller if they are driven only by the presence of aliens in disturbed sites.

A question that remains is whether land use change is the main driver of native species decline or if its effects interact with the presence of alien species (Didham et al., 2007). I did not account for the effects of alien richness or abundance on native communities, but previous studies have pointed out habitat modification as the main driver of biodiversity decline, outcompeting other drivers such as invasive species or climate change (Maxwell et al., 2016). However, some studies have highlighted that alien species are important drivers of native extinctions, particularly on islands (Gurevitch & Padilla, 2004; McCreless, 2016). More comprehensive analyses (e.g., evaluating interactions between environmental variables and different human pressures) are needed to disentangle the importance of different threats in driving losses of island biodiversity.

CHAPTER 5

Testing and refining the Biodiversity Intactness Index

5.1 ABSTRACT

How best to estimate the Biodiversity Intactness Index (BII) has recently become a subject of debate due to its adoption as a core indicator for biodiversity global assessments. In Chapter 3, I improved on the methods previously used to estimate BII globally (Newbold et al., 2016a), while also allowing pressure effects to differ between islands and mainlands. My BII estimates are lower globally and within all biodiversity hotspots and most biomes than those in Newbold et al. (2016a). Detailed analysis of these differences shows that they arise mostly from a combination of improvements to the modelling framework, especially from more sensitive modelling of compositional similarity. To assess my implementation of BII, I use estimates of responses of island native species to human pressures generated in Chapter 4 and project new high-resolution global maps of the status of island native biodiversity for the year 2005. These new maps (abundance- and richness-based) were compared to island BII maps from Chapter 3 and Newbold et al. (2016a). The global average for abundance-based intactness of island natives (0.6), was more similar to the BII average for islands calculated in Chapter 3 (~0.1 higher) than to the average calculated from Newbold et al.'s (2016a) maps (~0.2 higher). Average richness-based intactness of island natives was very similar to the BII richness-average for islands from Newbold et al. (2016a) and slightly higher (~0.1) than the average from Chapter 3. I discuss the factors that might drive the differences between biodiversity intactness estimates from the three different implementations. Importantly, island BII maps from Chapter 3 correlate more strongly with maps for island natives. After comparing three different ways of calculating biodiversity intactness, my results suggest that BII estimates calculated with the new modelling approach (Chapter 3) are not far from reflecting the intactness of native biodiversity.

5.2 INTRODUCTION

The Biodiversity Intactness Index (BII) (Scholes & Biggs, 2005; Newbold et al., 2016a) became prominent conceptually since it was proposed as a metric for assessing biotic integrity in the Planetary Boundaries framework (Steffen et al., 2015). The index – initially relying on carefully-pooled expert opinion (Scholes & Biggs, 2005) – offered a promising approach for the assessment of the status of different ecosystems, and for identifying regions that have crossed the ‘safe limit’ (Steffen et al., 2015) for loss of biotic integrity. As a response for the need of a robust, and scientifically based approach (Steffen et al., 2015), the PREDICTS project implemented BII based on a global collation of site-level biodiversity (Purvis et al., 2018). Such implementation –transparent, data-based, spatially and temporally resolved and scientifically credible – has been adopted as a core indicator for biodiversity global assessments such as the one recently developed by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2019).

To date, PREDICTS’ implementation of BII (Newbold et al., 2016a; Purvis et al., 2018) is the only framework that allows the estimation of effects of land-use change and related pressures on biodiversity intactness at a global scale, but based on local data and including a wide range of taxa (Newbold et al., 2019). Limitations of PREDICTS’ implementation that can cause an overestimation of BII have been previously acknowledged (Newbold et al., 2016a; Purvis et al., 2018; De Palma et al., 2018a; Chapter 3). Since the publication of the first global BII estimates in Newbold et al. (2016a), the modelling framework for BII calculation has been under a continuous assessment by the PREDICTS research group. This has led to the identification of additional limitations of the models used for BII calculation and the development of new framework (Chapter 3; De Palma et al., 2018a; Hill et al., 2018). The new implementation of BII has allowed more refined projections of biodiversity intactness for specific systems, such as islands and mainlands (Chapter 3) and specific biomes such as tropical and subtropical forests (De Palma et al., 2018a), which had not been possible previously. The improvements in the modelling approach were in part possible due to the expansion of PREDICTS database in recent years (Hudson et al., 2017), allowing the development of models that could not have been fitted previously. However, the refinement of BII projections has also been made possible by changes in various modelling steps for BII calculation, as a result of a thorough re-evaluation of the framework. These methodological improvements allow more efficient use of data and a more principled error structure than in Newbold et al. (2016a), creating an approach that can be used with smaller datasets, enabling future analyses of BII for particular biomes or clades.

Given the current high profile of BII, different concerns about PREDICTS’ implementation have been recently discussed. In particular, Martin et al. (2019) argued that Newbold et al.’s (2016a) BII estimates were overoptimistic for many geographic regions and particularly for biodiversity hotspots. As a response, Newbold et al. (2019) briefly discussed some details about the new implementation of BII that have led to estimates that begin to address previous limitations. However, to date, there has been no detailed analyses on the contribution of the different improvements to differences between results in Newbold et al. (2016a) and the more recent –

generally lower – BII estimates (Chapter 3; De Palma et al., 2018a). Such an analysis is needed to clarify whether previous limitations have been overcome and to direct the continuing improvement of the modelling framework. Additionally, the most recent BII estimates need to be evaluated to examine whether they address the current concerns and criticisms.

All PREDICTS' implementations estimate BII by combining models of abundance or richness and abundance- or richness-based compositional similarity, but the validity of this strategy has not been tested directly. The strategy carries two assumptions. First, a species' response to land-use change is assumed to be independent of its initial abundance. This assumption is called into question by Newbold et al.'s (2018) finding that naturally-widespread species tend to increase in abundance in human-dominated land uses whereas narrow-ranged endemic species tend to decrease; but the magnitude of any effect on BII estimates is not known. The second assumption is that all species present in sites in the land-use class representing natural habitats (e.g., minimally-used primary vegetation) are species that were originally present in the area under consideration. However, such sets of species might not represent accurately native assemblages, especially if such sites have already suffered human impacts and harbour non-native species. Classifying species as natives or aliens is often difficult since available data is usually limited for many taxonomic groups and regions (Chapter 4), and uncertainty in classifications is often unclear – for example, if classifications are based on political boundaries (Pyšek et al., 2004) or on species distributions that already have been altered by human transportation. Islands – with their sharply defined geographical and ecological boundaries – can offer a higher certainty for alien and native classifications, so can be used to test this second assumption specifically as well as enabling more accurate comparisons between BII as estimated indirectly through combining two models (as in the rest of this thesis) and more directly, through modelling the abundance of native species on islands.

In this chapter, for each modelling step needed to calculate BII, I summarize the changes made to methods in Newbold et al. (2016a), which were implemented in Chapter 3. To understand the sources of the difference between BII estimates (i.e. higher values in Newbold et al. (2016a)), I use a series of model comparisons to quantify the contributions of more data, more sensitive modelling of compositional similarity, and permitting different responses on islands and mainlands. Finally, I perform global projections for intactness of island native communities and test whether BII projections from Chapter 3 and Newbold et al. (2016a) show similar patterns to those found by projecting models fitted to data for native species only.

5.3 METHODS

5.3.1 Quantifying the effects of changes in how BII is modelled

As explained fully in Chapter 3, PREDICTS' approach for estimating BII combines a model of how land use and related pressures affect overall abundance or species richness at a site level, and a model of how land use affects compositional similarity of assemblages to baseline assemblages in natural habitats. Compositional similarity models are used to correct the estimates of the richness or abundance models by excluding the proportion of species or total abundance (respectively) that correspond to species that are not present in natural habitats (Purvis et al., 2018); this is done as an alternative to specifically excluding alien species from BII calculation as originally performed by Scholes & Biggs (2005).

In this section, I compare models and results for islands and mainlands (Chapters 2 and 3) against Newbold et al.'s (2016a) results for each of the three steps involved in BII calculation: 1) abundance and richness modelling, 2) compositional similarity modelling, 3) projections and calculation of BII.

5.3.1.1 Comparing abundance and richness models

I first compared models of total abundance and species richness (Chapter 3). The main differences between my models and those in Newbold et al. are the inclusion of an island/mainland term to test for different responses from island and mainland assemblages, the use of bigger datasets and – as a result – more land-use classes in my models, plus the random-effect structures that were used (Table 5.1). The abundance models had bigger differences since they used different data transformations for total abundance (i.e., my transformation – Table 5.1 – aiming to reduce the variance among studies caused by methodological and taxonomic differences) and Newbold et al.'s minimum-adequate model (MAM) did not include distance to the nearest road (Table 5.1), since this variable was dropped during model simplification.

To compare my results against those in Newbold et al. (2016a), I focused on the coefficients for responses of total abundance and species richness to the different land use and use intensity categories (LUI). By plotting my island and mainland coefficients against the corresponding global coefficients from Newbold et al. (2016a) and calculating the correlation (Pearson's *r*) between them, I assessed whether previous global estimates were more similar to the island or mainland coefficients.

Table 5.1. Comparison of the models for total abundance and species richness (minimum adequate models) fitted in Newbold et al. (2016a), Chapter 3 (islands vs mainlands) and Chapter 4 (natives vs aliens on islands). All models were used for calculation of biodiversity intactness using different approaches. All abundance models were fitted using a Gaussian error structure (identity link) and Restricted Maximum Likelihood and richness models using a Poisson error structure (log link) and Maximum Likelihood. LandUse, LU and LUI refer to land use/use intensity combinations but they all include different classes (i.e., according to the way land-use and use-intensity classes were collapsed); the classes for each one of these variables are listed under the table. HPD= human population density; DistRd= distance to the nearest road; SS= study within data source; SSB= block within study; SSBS= site.

	Abundance models			Richness models		
	Newbold et al.	Islands/mainlands	Island natives/aliens	Newbold et al.	Islands/mainlands	Island natives/aliens
Data	18,659 sites	23,385 sites (7,786 island sites)	6,636 sites (6,246 sites with data for island natives)	18,659 sites	26,755 sites (8,628 island sites)	7,609 sites (7,232 sites with data for island natives)
Land-use classes	16 classes= All combinations between six land uses and three use intensities (LUI), excluding Secondary vegetation- intense use and Urban- light use	18 classes = All combinations between six land uses and three use intensities (LUI).	7 classes = Collapsed land uses (LU); use intensity only used for defining PriMin.	16 classes (as in abundance model)	18 classes (as in abundance model)	7 classes (as in abundance model)
Model terms (Fixed-effects) in minimum-adequate model	LUI HPD HPD × LandUse	LUI Island/Mainland HPD DistRd LUI × Island/Mainland HPD × Island/Mainland HPD × LandUse HPD × LandUse × Island/Mainland	LU Alien/Native HPD DistRd LU × Alien/Native HPD × Alien/Native HPD × LU HPD × LU × Alien/Native DistRd × Alien/Native DistRd × LU	LUI HPD DistRd HPD × LandUse DistRd × LandUse	LUI Island/Mainland HPD DistRd LUI × Island/Mainland HPD × Island/Mainland HPD × LandUse HPD × LandUse × Island/Mainland DistRd × Island/Mainland DistRd × LandUse DistRd × LandUse × Island/Mainland	LU Alien/Native HPD DistRd LU × Alien/Native HPD × Alien/Native HPD × LU HPD × LU × Alien/Native DistRd × Alien/Native DistRd × LU DistRd × LU × Alien/Native
Random effects	(1+LandUse|SS) + (1|SSB)	(1+LandUse+UseIntensity|SS) + (1|SSB)	(1+LU|SS) + (1|SSB)	(1+LandUse|SS) + (1|SSB) + (1|SSBS)	(1+LandUse|SS) + (1|SSB)	(1|SS) + (1|SSB)
Transformation for response variable	Log-transformation	Rescaled to a 0-1 scale within study + square-root transformation	Rescaled to a 0-1 scale within study + square-root transformation	--	--	--
Transformation for HPD and DistRd	Log-transformation and rescaled to a 0-1 scale	As in Newbold et al.	As in Newbold et al.	Log-transformation and rescaled to a 0-1 scale	As in Newbold et al.	As in Newbold et al.

LandUse= Primary vegetation, Secondary vegetation, Plantation forest, Cropland, Pasture, Urban
LU= Primary vegetation- minimal use, Primary vegetation, Secondary vegetation, Plantation forest, Cropland, Pasture, Urban
LUI= Primary vegetation- minimal use, Primary vegetation- light use, Primary vegetation- intense use, and three levels with the three use intensities for Secondary vegetation, Plantation forest, Cropland, Pasture, Urban (18 classes). Newbold et al. (2016) collapsed Secondary vegetation with intense use and light use (referred as Secondary-light use) and Urban with light use and minimal use (referred as Urban-minimal use).

Table 5.2. Comparisons of the compositional similarity models fitted in Newbold et al. (2016a) and in Chapter 2 (islands vs mainlands). The conditions were used for both abundance-based and richness-based models. Under both approaches, as response variable, similarity between sites was calculated using the same asymmetric version of the Jaccard Index (Chapter 2). EnvDist= Environmental distance between pairs of sites; GeogDist= Geographic distance between sites; SS= study within data source

	Compositional similarity models	
	Newbold et al.	Islands/mainlands
Dataset	Independent pairs of sites within studies (randomly-chosen)	All possible pairwise comparisons within studies
Modelling approach	Averaging coefficients of 100 models fitted with 100 different sets of randomly-chosen pairwise comparisons	Fitting a single model and performing permutation tests to address the dataset's pseudo-replication
Baseline in land-use contrasts	Primary vegetation	Primary vegetation- minimal use
Model terms (Fixed-effects) in minimum-adequate model	Land-use contrast EnvDist GeogDist	Land-use contrast EnvDist GeogDist Island/Mainland Land-use contrast × Island/Mainland EnvDist × Island/Mainland GeogDist × Island/Mainland
Random effects	(1|SS)	(1|SS)
Transformation for response variable	Log-transformation	Logit transformation
Transformation for EnvDist and GeogDist	Log-transformation	EnvDist: Cube-root transformation GeogDist: Divided by the median maximum linear extent of sites + log-transformation

5.3.1.2 Comparing compositional similarity models

The biggest change to how BII is estimated is the modelling of compositional similarity (Chapter 2, Table 5.2). Newbold et al.’s (2016a) approach was to average the coefficients from 100 models using different sets of randomly-chosen pairwise comparisons (sets of independent pairs of sites within studies), combine all primary vegetation sites as their baseline condition and log transform all variables in the models (Table 5.2). In my models (Chapter 2), all possible pairwise comparisons within studies were used and permutation tests were performed to overcome the resulting nonindependence; since data was used more efficiently, minimally-disturbed primary vegetation (henceforth PriMin) could be used as baseline for the contrasts. Additionally, I transformed explanatory variables to optimise their distributions (Table 5.2) and logit-transformed the compositional similarity data, which better reflects the bounded nature of the compositional similarity estimates (Warton & Hui, 2011) than does the log-transformation used by Newbold et al. (2016a).

Using the abundance-based model (Chapter 2), I assessed how using the new baseline and different data transformations (focusing on logit transformation for compositional similarity data) affected compositional similarity estimates. For this assessment I used a subset of 30% of the pairwise comparisons of my abundance-based compositional similarity data (randomly sampling 30% of comparisons within each study); this percentage was enough to replicate my results while facilitating tests by reducing the time and computational power needed to run the models. To assess the effects of logit transformation and the baseline on compositional similarity estimates, I re-fitted my model using different combinations of baselines and data transformations. I first fitted my model log-transforming all the variables but without changing the land-use contrasts to extract estimates of contrasts using PriMin as baseline (Table E.1). In a second test, before running the model, I collapsed land-use contrasts using PriMin and Primary vegetation (since my dataset included all possible land-use contrasts) to replicate Newbold et al.’s (2016a) baseline. I then ran a model using my data transformations and a second one using Newbold et al.’s (2016a) (Table E.2). Using the mainland coefficients from each of these models, I calculated the average compositional similarity for the land-use contrasts of interest within each model (Tables E.1 and E.2: contrasts using either PriMin or primary vegetation as baseline, according to the model). The averages were calculated using back-transformed similarity values (0 to 1 scale), rescaled so that the contrast of PriMin against itself (or Primary against itself) had a value of 1 (Tables E.1 and E.2). I also calculated this average for my original abundance-based model from Chapter 2 to first evaluate the magnitude of difference between this average and the one from the model replicating the conditions of models in Newbold et al. (2016a). Finally, based on averages from models with intermediate conditions (i.e. model with PriMin baseline + log transformation and model with Primary baseline + logit transformation) I defined whether the new baseline or the logit transformation was the main factor driving differences between my estimates and estimates generated by following methods from Newbold et al. (i.e., which model average was more similar to the average from my original model) (Table 5.3).

5.3.1.3 Comparing BII averages

Using the BII projections from Chapter 3 and Newbold et al. (2016a), I examined differences between my BII estimates for islands and mainlands and the global BII estimates from Newbold et al. (2016a). I first mapped the differences between the estimates by subtracting my abundance and richness global BII maps (joining island and mainland maps – Figure 5.1) from Newbold et al.'s (2016a) corresponding global maps. With these maps I aimed to identify areas were BII estimates from Newbold et al. were lower, higher or very similar to mine. I also separated Newbold et al.'s (2016a) global BII maps into island and mainland maps, enabling me to compare their average BII estimates for islands and mainlands with my averages. Finally, I compared my average BII values for biomes and biodiversity hotspots for islands and mainlands against the biomes and hotspots global averages.

5.3.2 Testing BII: comparisons with intactness of native species

In order to test whether BII estimates (using the two different implementations) are comparable to estimates of intactness of native communities, I used island BII maps from Chapter 3 and Newbold et al. (2016a) to examine their similarity to new maps projected from models that specifically evaluated responses of island native species to human pressures.

I used the models for alien and native species richness and total abundance from Chapter 4 to extract the estimates for responses of island native species to land-use change and related pressures. These models differ from those in Chapter 3 and in Newbold et al. (2016a) mainly in terms of their complexity (Table 5.1). Models for alien/native species needed to be simpler due to data limitations (i.e., the many species that could not be classified as alien or natives were excluded from these models), so they had simpler land-use classes and random-effect structures (Table 5.1).

Using the estimates for responses of island natives to human pressures, I projected high-resolution global maps of the status of island native biodiversity for the year 2005. The projections were performed following the same methods in Chapter 3, except that I only projected the responses of overall abundance and species richness of island natives; there was no need to use compositional similarity models, because results from the models correspond exclusively to responses of native communities and so provide a more direct estimate of BII than has been possible previously. I compared these maps of island native community intactness (abundance-based and richness-based) with the maps of island BII from Chapter 3 and the island part of Newbold et al.'s (2016a) global BII maps. I mapped the differences between the estimates from the different maps by pairing them and subtracting one map's values from the other (Figure 5.5). Additionally, I calculated the correlation (Pearson's *r*) between estimates from the different maps and compared the averages for islands' biodiversity intactness calculated from the three maps.

5.4 RESULTS

5.4.1 Effects of changes in BII modelling

Each of the statistical models that I fitted in Chapter 3 for BII calculation produced some marked differences from Newbold et al.'s (2016a) models. In the models of how LUI affects total abundance and species richness, several of Newbold et al.'s (2016a) global coefficients are very similar to my corresponding coefficients for mainlands but less similar to my island coefficients (Figures E.1 and E.2). Newbold et al.'s (2016a) abundance-model coefficients were less well correlated with island (r= 0.54, P= 0.03) than with mainland-abundance coefficients (r= 0.63, P= 0.01); their richness-model coefficients correlated strongly with both of these two (r= 0.89, P= <0.001 with island-richness coefficients and r=0.86, P=<0.001 with mainland coefficients). My abundance-model coefficients tended to be more different from (and usually lower than) Newbold et al.'s (2016a) than did the coefficients in my richness models.

My estimates for compositional similarity of assemblages in different land uses to those in natural habitats (see Table C.8) were much lower (for both islands and mainlands) – and showed a wider range – than those in Newbold et al. (2016a) (available at: https://doi.org/10.5519/0073893). These differences are driven by both the logit- (rather than log-) transformation of compositional similarity data and the use of minimally-disturbed primary vegetation (rather than all primary vegetation) as the baseline representing undisturbed habitats. When fitting models of abundance-based compositional similarity with different conditions, I found that the highest compositional similarity values (i.e., final rescaled values) came from models that use a baseline of collapsed primary vegetation (Tables E.1 and E.2). Of the two conditions that were tested, the use of minimally-disturbed primary vegetation as baseline appears to be more important, driving almost the entire difference from Newbold et al.'s (2016a) models (i.e., a model using log transformation but only Primary- Minimal sites as a baseline gives an average for land-use contrasts ten times as near to my original model – Chapter 2– than to a model with the structure of Newbold et al. (2016a): Table 5.3).

Table 5.3. Average compositional similarity for the land-use contrasts of interest in models using different baselines and data transformations. The cell on the left extreme shows the average for estimates from the abundance-based model from Chapter 2 (using PriMin as baseline for land-use contrasts and logit transformation for compositional similarity). The cell on the right extreme shows the average for estimates from the model where the baseline was collapsed primary vegetation (all use intensities) and compositional similarity was log-transformed (as in Newbold et al., 2016a). Cells in between show the averages for estimates from models with intermediate conditions. For the models where PriMin was used as baseline for land-use contrasts, I did not include the estimate for PriMin-Primary vegetation to calculate the averages in order to have the same number of land-use contrasts (i.e, six contrasts) across all models.

PriMin + Logit	PriMin + Log	Primary + Logit	Primary + Log
0.770	0.776	0.825	0.836

My average BII values for islands (0.71 and 0.62 for abundance-based and richness-based BII, respectively) and mainlands (0.73 and 0.71 respectively) calculated in Chapter 3, were lower than the averages obtained by splitting Newbold et al.'s (2016a) map into islands (for which the corresponding values are 0.79 and 0.76) and mainlands (values are 0.85 and 0.77).

Mapping the differences between Newbold et al.'s (2016a) BII estimates and mine (Figure 5.1) shows that my estimates are lower in most regions, with the main exceptions being Australia (abundance-based), the Scandinavian peninsula, Russia (richness-based) and the Sahara desert (abundance-based and richness-based). Differences are more pronounced on islands, in North America and in South Africa. My abundance-based BII estimates were particularly lower than those of Newbold et al. (2016a), with much of Europe, Africa and Asia showing big differences.

My average BII estimates for both islands and mainlands were lower than Newbold et al.'s (2016a) global averages within most biomes (Figures 5.2 and E.3) and in all hotspots (Figures 5.3 and E.4). Mainland averages for biomes and hotspots were more similar to the global averages (especially in the case of richness-based BII – Figure E.3 and E.4).

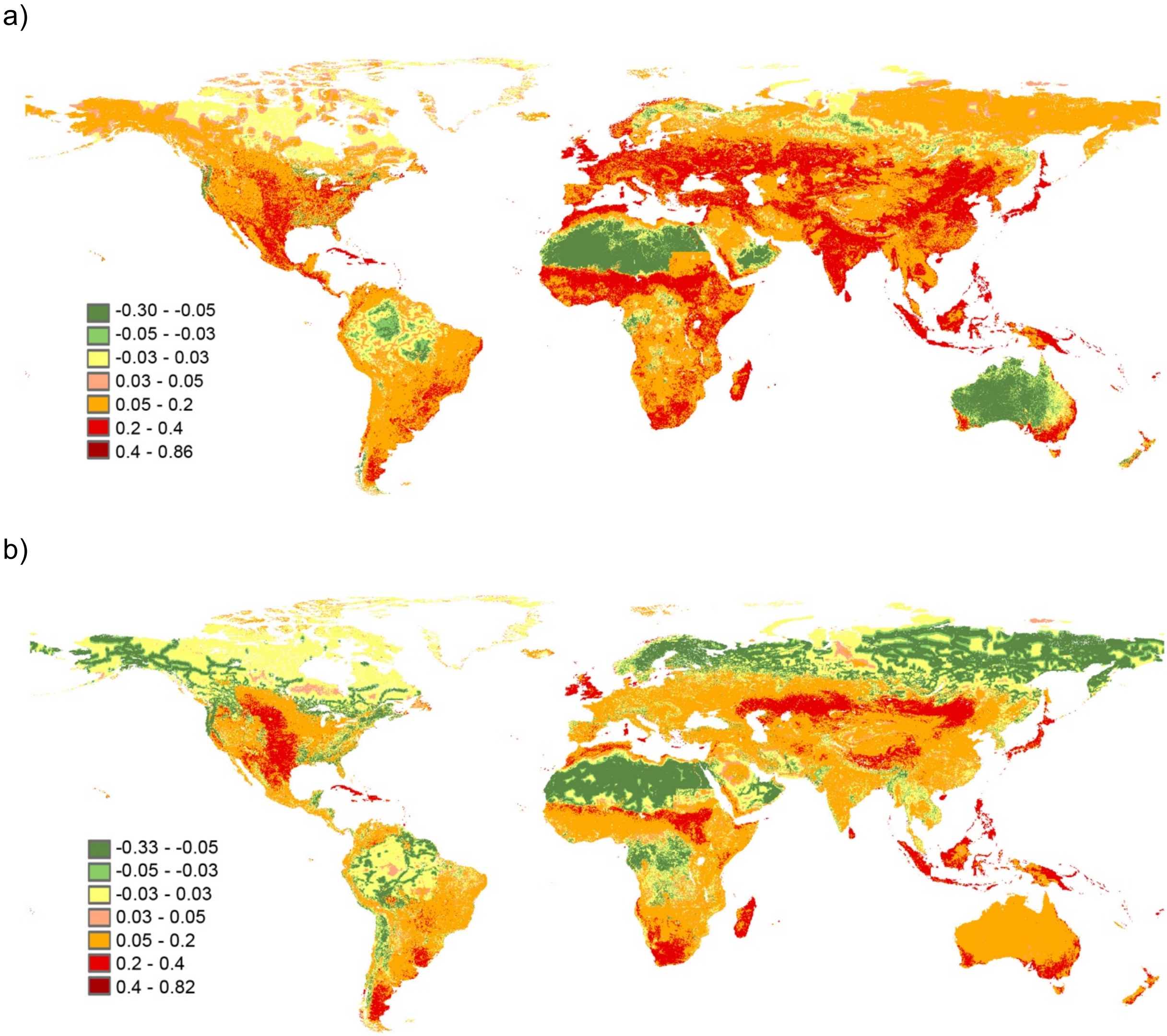


Figure 5.1. Mapped differences between BII estimates from Newbold et al. (2016a) and Chapter 3. a) Abundance-based BII, b) Richness-based BII. Maps were produced by subtracting my global BII maps (island + mainland maps) from the global maps from Newbold et al. The maps that were used included BII estimates in a 0 to 1 scale where 1 = 100% intactness. Positive values (shown in red and orange) indicate cases where my estimates are lower than those in Newbold et al. Negative values (shown in green) indicate cases where my estimates are higher than previously. The yellow areas show cases where estimates from both studies differ minimally (maximum by 0.03).

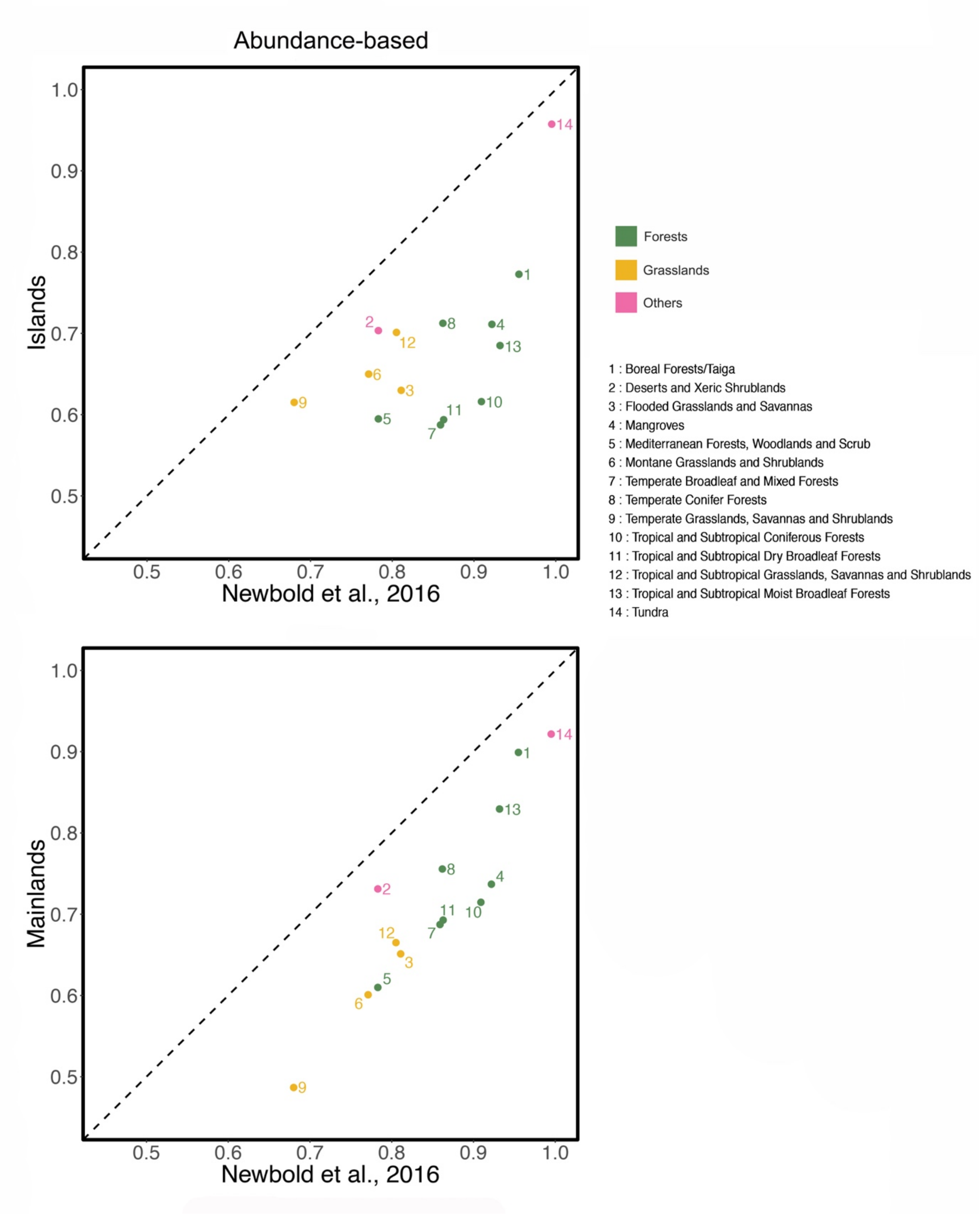


Figure 5.2. BII estimates (abundance-based) for biomes on islands and mainlands compared with global estimates from Newbold et al. (2016a). Colours indicate major biome type. Values from 0 to 1 correspond to BII (1= 100% intactness).

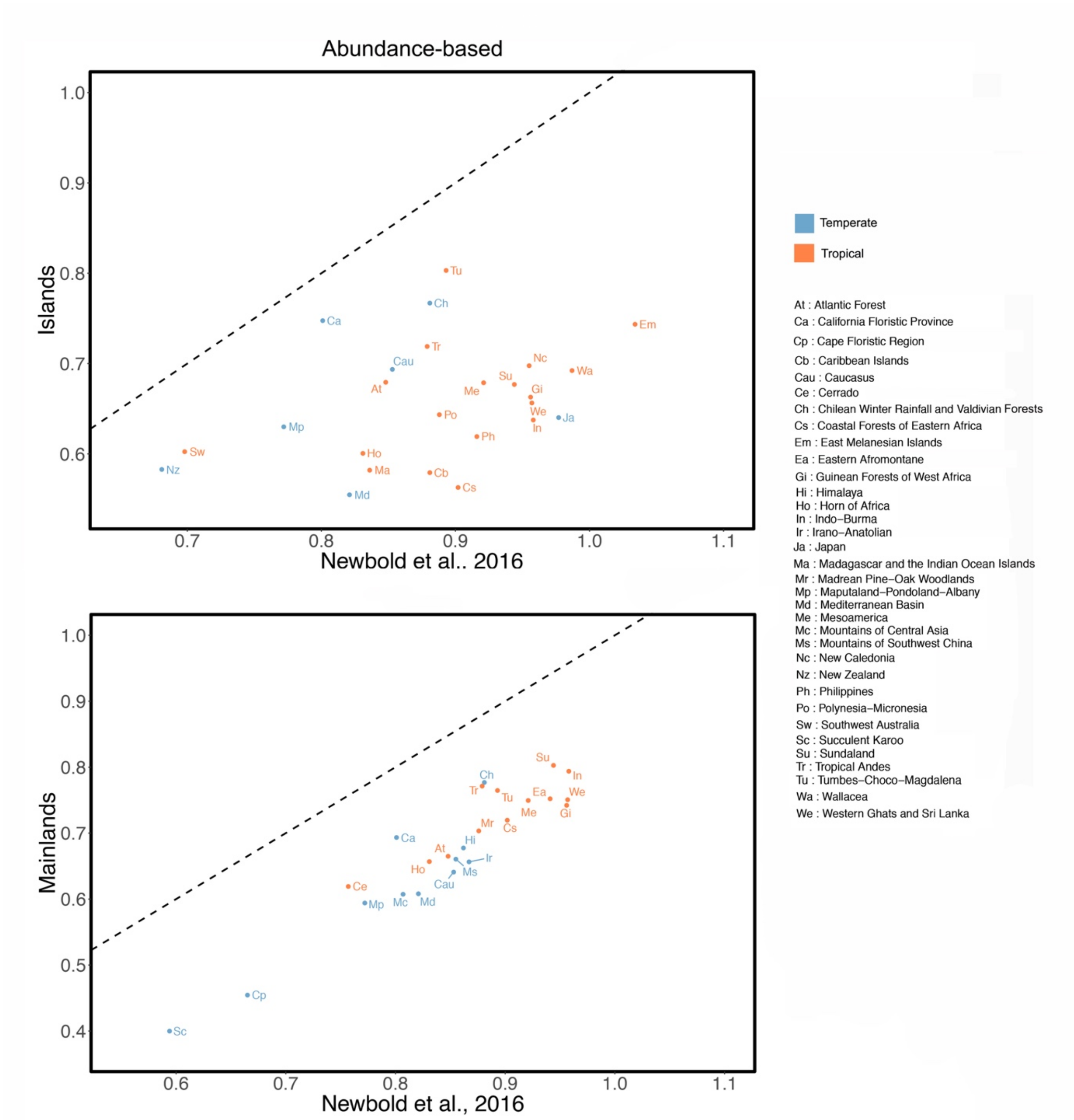


Figure 5.3. BII estimates (abundance-based) for biodiversity hotspots on islands and mainlands compared with global estimates from Newbold et al. (2016a). Some hotspots are exclusively located on islands or mainlands. Colours indicate whether hotspots are in the tropical or temperate realms. Values from 0 to 1 correspond to BII (1= 100% intactness).

5.4.2 BII vs intactness of native biodiversity on islands

My maps of intactness of native biodiversity on islands are shown in Figure 5.4. The abundance-based average of 0.6 (s.d.= 0.13) is about 0.1 lower than the abundance-based BII average for islands calculated in Chapter 3 and about 0.2 lower than Newbold et al.'s (2016a) maps. The richness-based average intactness of 0.75 (s.d.= 0.1) is very similar to the richness-based BII average calculated from Newbold et al.'s maps (0.76), but about 0.1 higher than the average calculated in Chapter 3.

The intactness maps from Figure 5.4 are compared with corresponding BII estimates in Figure 5.5, which maps the pairwise differences between estimates. In terms of abundance-based BII, the natives model estimates correlate strongly with BII estimates from Chapter 3 but are generally lower; Newbold et al.'s (2016a) BII estimates do not correlate strongly with either of these two and are generally higher. The three estimates of richness-based intactness correlate strongly – although correlation between the natives model estimates and Newbold et al.'s (2016a) is slightly weaker. The richness-based estimates for natives were generally higher than BII estimates from Chapter 3 but still lower than those from Newbold et al. (2016a), except for parts of Australia and Madagascar – (Figure 5.5).

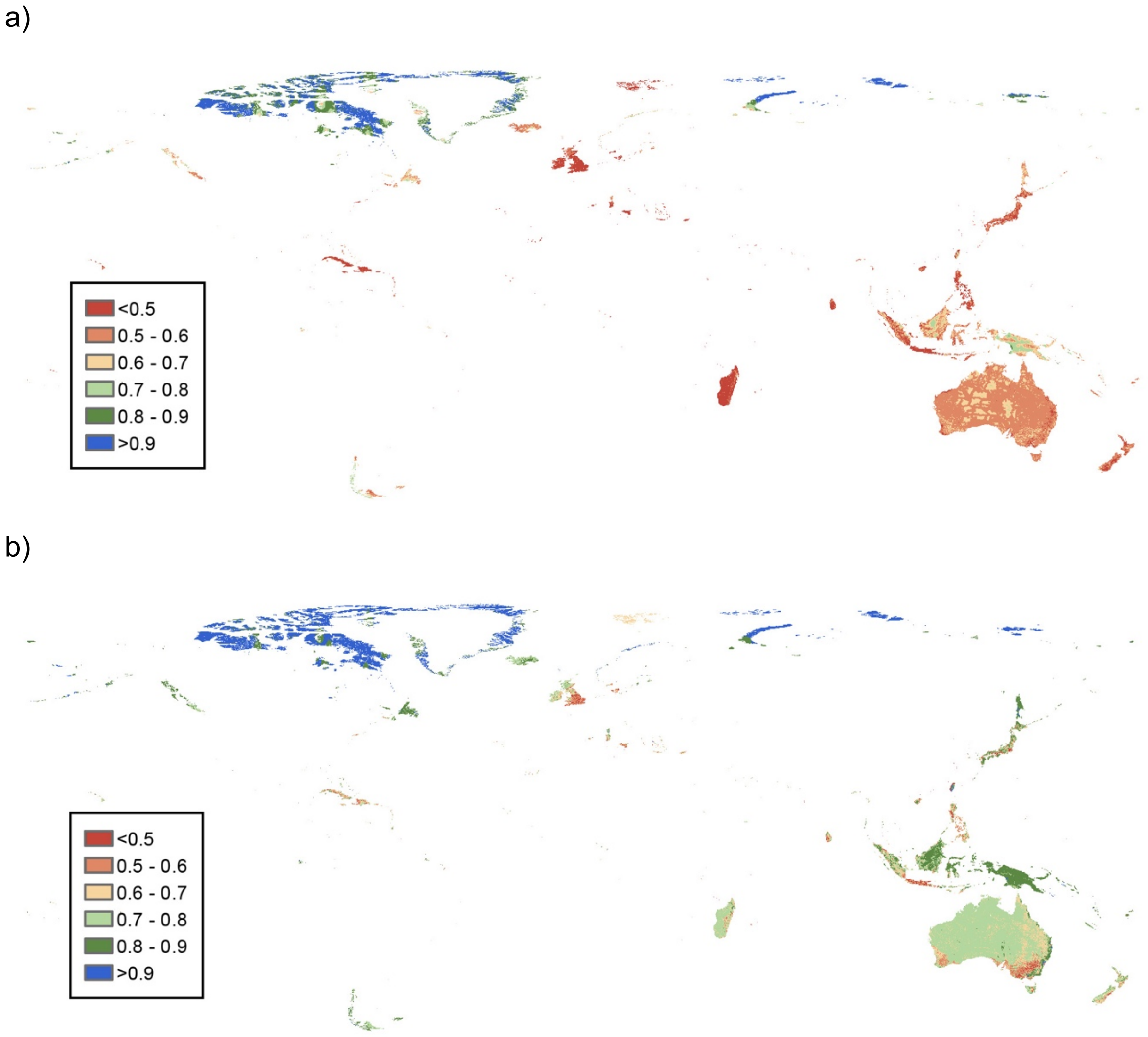
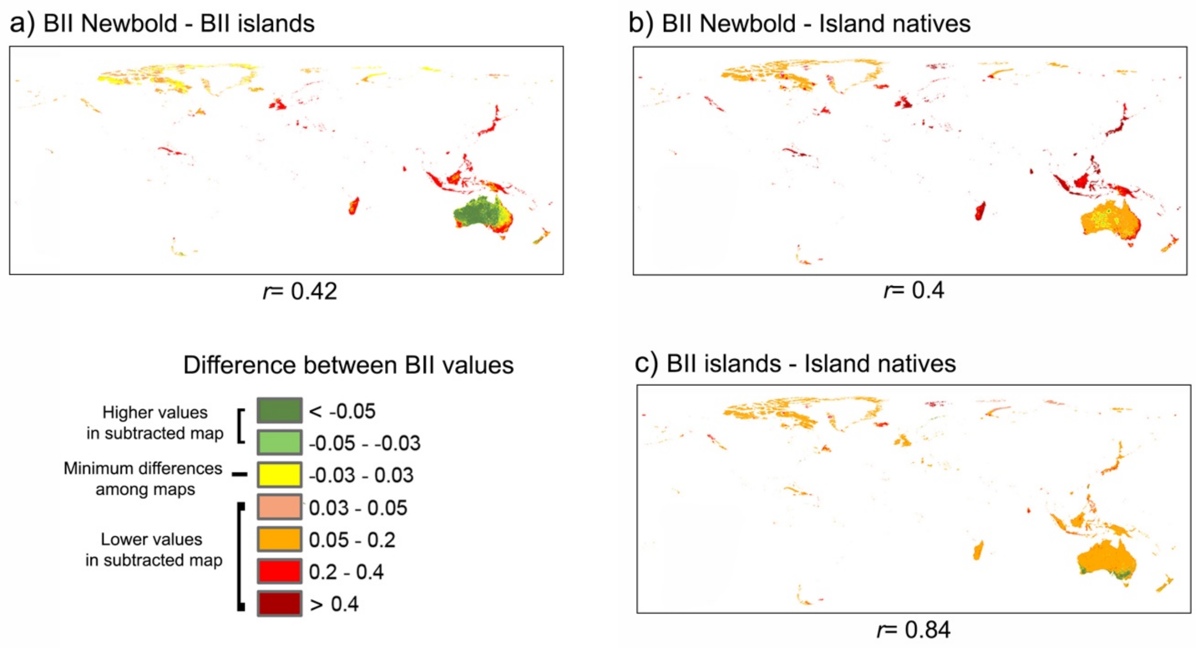


Figure 5.4. Global maps of intactness of island native biodiversity. a) Abundance-based intactness. b) Richness-based intactness. Values are shown in a 0 to 1 scale (1= 100% intactness).

Abundance-based



Richness-based

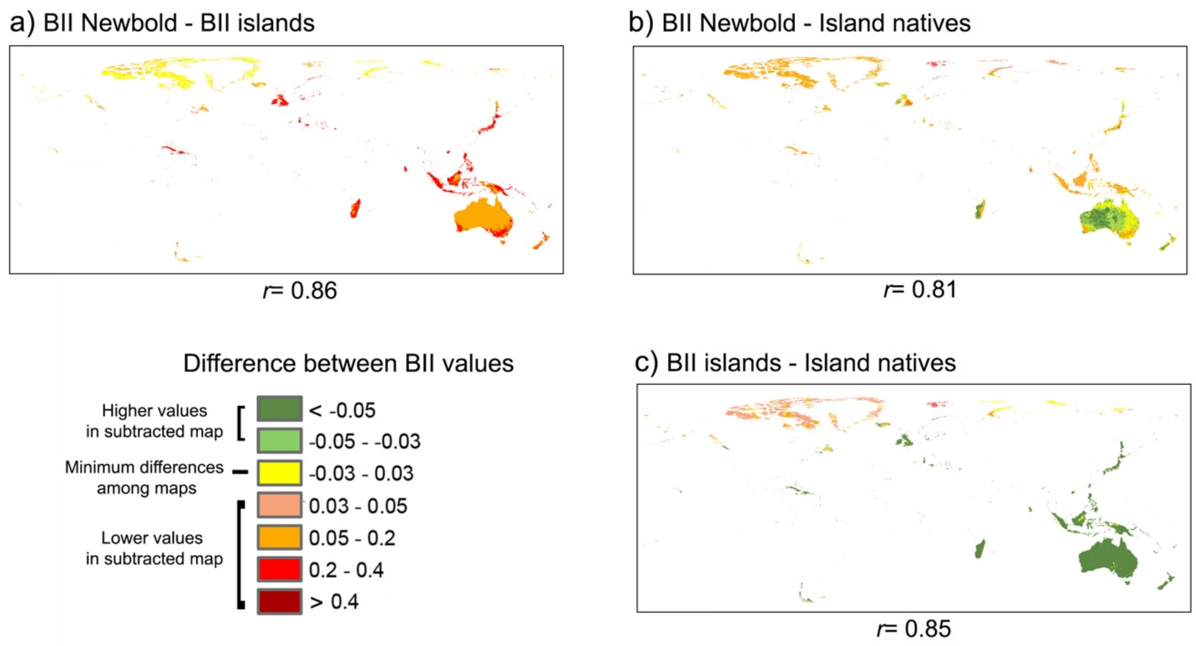


Figure 5.5. Differences between the estimates (abundance- and richness-based) from island BII maps from Newbold et al. (2016a), island BII maps from Chapter 3 (referred as BII islands) and island maps of intactness of native biodiversity (referred as island natives). The correlation (Pearson's *r*) between estimates from the different maps is also shown.

5.5 DISCUSSION

As Chapter 3 highlighted, the BII estimates calculated using the new implementation are much lower than those from Newbold et al. (2016a), especially for islands. Here, I have shown that the main reason why my BII estimates are lower is that my estimates of compositional similarity are lower. Whereas Newbold et al.'s (2016a) estimates for abundance- and richness-based similarity between other land uses and PriMin were never below 0.9, my estimates reached as low as ~0.6 for abundance-based similarity and ~0.5 for richness-based similarity, for both islands and mainlands (see Table C.8). These lower estimates of similarity seem to arise almost entirely from using minimally-disturbed primary vegetation as a baseline for sites' comparisons (whereas Newbold et al. (2016a) included all primary vegetation sites in the baseline). This suggests that when modelling assemblage turnover among land uses, using minimally-disturbed primary vegetation as the baseline accounts better for disturbance of natural habitats (Newbold et al., 2019), while using all sites in primary vegetation –experiencing different levels of degradation– means using a more 'shifted' baseline that can lead to the overestimation of similarity between assemblages in different land uses and natural habitats.

Although Newbold et al.'s (2016a) global maps also have lower average BII for islands than mainlands, islands stand out clearly on 'difference maps' that compare my BII estimates with the earlier ones (Figure 5.1), suggesting that previous global estimates may have been biased towards the mainland picture, as the PREDICTS database has many more mainland than island studies. Not allowing island assemblages to respond differently from mainland assemblages appears to have led to optimistic estimates of BII for these vulnerable but less data-rich systems, relative to the estimates for mainland assemblages.

My BII estimates are lower than those published in 2016 not only globally, but also within all biodiversity hotspots and within most biomes; island BII averages across these different regions were particularly lower than those from Newbold et al. (2016a) (Figures 5.2 and 5.3). My results address some of the recent criticisms and concerns about BII being too optimistic, especially for biodiversity hotspots (Martin et al., 2019), which have lost 70% or more of their original primary vegetation (Myers et al., 2000). Martin et al. (2019) especially pointed out how Newbold et al.'s high BII estimates for hotspots entirely or mostly made of islands such as the Madagascar, Sundaland and Philippines hotspots – ~0.9 and ~0.8 for abundance- and richness-based BII, respectively – contrast with Myers et al.'s (2000) suggestion that these hotspots have only retained around 10% or less of their primary vegetation. My island BII averages for these three hotspots are ~0.6 (abundance-based) and ~0.5 (richness-based). Although this is still markedly higher than the suggested intact area of primary vegetation, the higher value may partly reflect the fact that other land uses retain some originally-present biodiversity. It seems that both the modelling improvements and accounting for differences between island and mainland responses have led to more realistic estimates for biotic integrity across geographical regions, considering the human pressures that they have faced.

Although the new BII implementation has improved estimates for biotic integrity, my findings do not invalidate any of the major conclusions of Newbold et. al (2016a). Their study suggested that BII was already below the proposed Planetary Boundary (Steffen et al., 2015) across most of the world's land surface; moreover, they were careful to phrase their conclusions conservatively, recognising that there were several possible reasons why their estimates might be too high (Newbold et al., 2016a; Newbold et al., 2019) and highlighting that certain taxa and geographic regions were particularly underrepresented in their data, which did not allow to fit models allowing for different ecological systems to respond differently to human pressures.

Differences between estimates of intactness of native biodiversity and BII were expected considering that under these different implementations, different (though not independent) datasets (Tables 5.1, E.3 and E.4) and models (Table 5.1) are used. However, the estimates from island BII maps (abundance- and richness-based) that are based on the new implementation (Chapter 3) correlate strongly with estimates from maps of intactness of island natives; furthermore, the intactness global averages (abundance- and richness-based) calculated from these maps only differ moderately (by ~0.1). Hence, allowing island assemblages to respond differently and producing more accurate compositional similarity estimates has also led to BII estimates that reflect patterns for native diversity more accurately than previous estimates from Newbold et al. (2016a), which are generally higher and less well correlated with estimates from maps of native intactness (Figure 5.5). In general, Newbold et al.'s (2016a) BII appears underestimate the decline of native diversity caused by human pressures, mainly due to their high compositional similarity estimates, which fail to discount an accurate fraction of overall abundance or species that is made up of species not present in minimally-disturbed primary vegetation.

Determining the specific sources of the differences between biodiversity intactness estimates produced by the three different approaches (Figure 5.5) is difficult because of the multiple factors at play; however, I provide a few possible non-exclusive explanations. The abundance-based projections for intactness of native biodiversity on islands suggest a bigger decline of biotic integrity compared to BII estimates from either my (Chapter 3) or – especially – Newbold et al.'s (2016a) implementations (Figure 5.5). There are several differences in the abundance models (Table 5.1) underpinning the three different projections for biodiversity intactness that could have led to this difference. Newbold et al.'s abundance model (MAM) did not include distance to the nearest road and in the model from Chapter 3 (MAM) this variable was only significant as a main effect (Table 5.1). In contrast, in the abundance model (MAM) from Chapter 4 (aliens/natives), distance to the nearest road had stronger effects, interacting significantly (but separately) with land use and alien/native status of species (Table 5.1); i.e., suggesting that decreasing distance to the nearest road tends to affect negatively total abundance of species in particular land uses and that, in general, this pressure tends to cause a decrease in total abundance of natives (see Figure D.2). In the case of human population density, only Newbold et al.'s (2016a) model did not find negative effects of this pressure on total abundance of species (with the exception of urban sites). Not accounting for the effects of distance to the nearest road and the lack of a negative effect of human population density could have contributed to the particularly high abundance-based BII estimates in Newbold et al. (2016a) and their low correlation with estimates from the other projections (Figure 5.5). Modelling the specific responses of native species seems to have captured particular negative responses to human pressures that were lost in models including all taxa – particularly the global model in Newbold et al. (2016a) not accounting for different responses between island and mainland assemblages. This could also be evidence for island natives being particularly sensitive to some pressures compared to mainland natives, as it was suggested previously in Chapter 3 – based on results for primary vegetation, assuming that this land use could be the last refuge of any native species–.

In contrast, when compared to my BII estimates (Chapter 3), projections for richness-based intactness of native biodiversity are slightly more optimistic, perhaps because the model for native species does not have strong effects of human population density and distance to roads. In Chapter 3, I highlighted how increasing human population density and decreasing distance to roads both seem to reduce species richness steeply in primary vegetation on islands. Why does richness of island native species not show this strong pattern? One obvious possibility is the loss of data for many species (Table E.4) – i.e., all those not classified as native or non-native – across taxonomic groups, and therefore the loss of many sites (Table E.3). Although Newbold et al.'s (2016a) projections for richness-based BII were higher than my projections for native assemblages, all three different richness-based projections show strong intercorrelation (Figure 5.5). This similarity may be because all the richness models have similar structure: they all included land use, human population density and distance to the nearest road and used the same error structure (Table 5.1). However, as in the abundance model, Newbold et al. (2016a) did not find marked decreases for species richness with increased pressures of human population density and roads, perhaps because the mainland data 'swamped' the island data in the model-fitting.

Finally, an additional factor that can contribute to differences between estimates of intactness of native assemblages and BII (abundance- and richness-based) is the exclusion of use intensity in the native-only models (Table 5.1), forced by data limitations. Whereas models and projections in Newbold et al. (2016a) and Chapter 3 used land-use classes that include different levels of use intensity, those for native species only considered use intensity for identifying minimally-used primary vegetation (Table 5.1). This means that projections for intactness of native assemblages cannot account for differences in use intensity across different areas, instead using a single estimate for each land use that can over- or under-estimate abundance or richness in different areas according to their use intensity. For example, while BII projections would tend to show higher values for biodiversity intactness in areas with minimal or light use (Chapter 3; Newbold et al., 2016a), projections for native assemblages in lightly-used regions could be too low and those for intensively-used regions too high.

In this chapter, I have compared three ways for estimating biodiversity intactness. My new implementation of BII (Chapter 3), which uses the more sensitive modelling of compositional similarity (developed in Chapter 2), has allowed analyses focusing on smaller datasets (e.g., islands or particular biomes). As a consequence, I have been able to develop models that allow different systems to respond differently to human pressures, and models with a more stringent baseline for estimating compositional turnover between various land uses and natural habitats. These improvements yield BII estimates that address most of the recent criticisms towards the index (Martin et al., 2019), correlate strongly with estimates of intactness of native assemblages on islands, and produce global averages that are very similar to those for native biodiversity intactness. The new approach might still overestimate BII since even minimally-disturbed primary vegetation can represent a “shifted-baseline”; e.g., assemblages in these sites are likely to have experienced some human impact (Watson et al., 2016) and harbour alien species – as results from Chapter 4 suggested, since on average, ~17% of the species and total abundance in sites in minimally-disturbed primary vegetation corresponded to alien species –. The ideal situation would be to go beyond the two-model approach to estimate BII: if all species across more taxonomic groups could be classified as natives or non-natives, complex models could permit different responses between ecological systems and the use of more precise land-use categories. Given the ongoing Wallacean shortfall (Hortal et al., 2015), the two-model approach is likely to be required for some time. According to my results, the two-step estimation of BII that I have developed in this thesis represents a clear improvement on the previous implementation of BII (Newbold et al., 2016a) and produces a robust provisional metric to assess loss of biotic integrity.

In this last chapter, I have developed the first comprehensive test for BII; my results show the big impact of the recent improvements to methods in Newbold et al. (2016a) and contribute to the validation of this index which currently plays an important role in global biodiversity assessments and therefore can contribute to urge stronger efforts to halt biodiversity loss.

CHAPTER 6

Conclusions and general discussion

In this thesis I have used data from the PREDICTS database to (i) model how land-use change and related human pressures affect local terrestrial biodiversity on islands and mainlands (Chapter 2 and 3), (ii) model how land-use change and related pressures affect diversity of alien and native species on islands (Chapter 4) and (iii) improve previous methods to estimate the Biodiversity Intactness Index (BII) and validate this new implementation (Chapter 5). In this final chapter, I recap my main findings for these three major topics within the thesis, while highlighting what they add to previous studies. Finally, I discuss some general limitations of my analyses and possible future research.

Effects of land-use change on island and mainland biodiversity

The effects of land-use change on island and mainland biodiversity were compared in Chapters 2 and 3, based on changes in the composition of natural species assemblages and the Biodiversity Intactness Index (BII) (Scholes & Biggs, 2005; Newbold et al., 2016a), respectively. These two chapters represent the first comprehensive global analyses – including a wide range of taxa – to compare the biodiversity responses of island and mainland assemblages to land-use change. Both chapters showed that the effects of land-use change on local biodiversity differ between islands and mainlands, with island assemblages tending to suffer more severe changes when facing land-use change. Both chapters suggest that omitting the possibility of different responses of island and mainland assemblages to human pressures in global biodiversity models can lead to a mis-estimation – specifically, an overoptimistic estimation – of the status of island biodiversity.

Land-use change drives important changes in the community composition on both islands and mainlands, as a consequence of the addition of novel species (i.e., species not present in minimally-disturbed habitats) in human-dominated land uses. When plant and animal assemblages were analysed separately, I found that some land-use changes had bigger impacts on species assemblages (especially animal assemblages) on islands than on mainlands, mainly because of novel species becoming abundant in human-dominated land uses – which might be facilitated by islands' species poverty and reduced competition from native species (Chapter 1 reviews these topics). Importantly, Chapter 2 also found evidence of biotic homogenization for plant assemblages within most land uses on islands and mainlands and for island animal assemblages within forested land uses. The island-mainland differences in this chapter could not be explained unambiguously because changes in the composition of assemblages could have been caused by the presence of both novel native or alien species (not separated in these analyses) in human-dominated land uses. However, this chapter: 1) represents the first global synthesis showing the different effects of land-use change on plant and animal assemblages of islands and mainlands; 2) points out the islands' characteristics that can make them more vulnerable than mainlands to both assemblage turnover and biotic homogenization when facing human pressures (although these conclusions are mainly speculative); and 3) indirectly suggests that – though further work is needed – islands could be facing higher rates of invasions by alien species than mainlands (especially in disturbed sites), in line with the hypothesis that islands are more susceptible than mainlands to the establishment alien species (Simberloff, 1995a; Sax & Brown, 2000; Denslow, 2003; Pyšek & Richardson, 2006).

Importantly, Chapter 3 showed clear island-mainland differences in sensitivity and exposure to human pressures. I showed that on average, land-use change and related pressures have reduced biotic integrity (i.e., reducing species richness of originally present species) more on islands than on mainlands. I showed that this pattern mainly results from a higher sensitivity of island native species to rising human population density and road development (based on responses of species in primary vegetation on islands, assuming these species to be island natives). To date, this is the first global analysis including many different taxa to show that islands are suffering a more severe biodiversity loss than mainlands (a pattern that is consistent across different geographic regions), mainly as a consequence of the sensitivity of their native species to particular pressures. Such sensitivity can be driven by the restricted geographic ranges and small population sizes of island species, and traits such as poor dispersal abilities and stenotopy (Paulay, 1994; Simberloff, 2000; Sakai et al., 2002; Gillespie et al., 2008; Chapter 1) which lower their potential to disperse to undisturbed sites or recover after facing human pressures. Previous studies discussing human impacts on islands have mainly highlighted cases for specific islands or island-rich regions that have suffered a strong habitat and biodiversity loss (e.g., Paulay, 1994; Myers et al., 2000; Whittaker & Fernández-Palacios, 2007; Johnson et al., 2017). However, there are no other studies comparing island and mainland responses to specific human pressures, and the hypothesis that island natives are generally more sensitive than mainland natives (discussed in Chapter 1) has not been broadly tested with empirical data.

In terms of island and mainland exposure to human pressures, I reported the fraction of island and mainland area given over different land uses, use intensities and with low or high values of human population density and proximity to the nearest road. This goes beyond the only previous global assessment focusing on human pressures on islands and mainlands (Kier et al., 2009), which only compared the overall amount of habitat loss and the 'Human Impact Index' (Sanderson et al., 2002) on islands and mainlands; my analysis provides much more detail. Notably, Kier et al. (2009) pointed out a higher 'Human Impact Index' for islands than for mainlands, while I found that islands have a lower fraction of area with low human population density than mainlands. Results from both studies highlight islands' high exposure to different human pressures.

Effects of land-use change on native and alien communities of islands

In Chapter 4, unlike in previous chapters, I was able to separate alien from native species in many of the island studies in the PREDICTS database. By performing a global analysis focusing specifically on islands, I showed that land-use change reduces both richness and total abundance of island native species but that the number and abundance of alien species are very much higher in sites with human-dominated land uses than in minimally-disturbed primary vegetation. These results provide further – and more direct – evidence for the sensitivity of island natives to human pressures (particularly agriculture), which was suggested by results from Chapter 3 but based on data including all species. Furthermore, they show the widespread establishment of alien species on islands, particularly on disturbed habitats, suggesting that land-use change may facilitate a 'true colonization' (see Rosindell & Harmon, 2013) following the immigration of alien species to an island. The results from this chapter therefore contribute to literature and previous syntheses on island native biodiversity and its threats (e.g., Paulay, 1994; Simberloff, 2000; Whittaker & Fernández-Palacios, 2007; Gillespie et al., 2008; Delgado et al., 2017).

My findings reinforce previous studies suggesting that habitat modification has negative impacts on natives or narrow-range species (e.g., McKinney & Lockwood 1999, Scholes & Biggs, 2005; Newbold et al., 2018), and that alien species tend to be successful in disturbed habitats (Sax & Brown, 2000; Catford et al., 2012; Lembrechts et al., 2016). Previous studies focusing on particular islands found much the same patterns that I found for total abundance and richness of alien and native species in disturbed sites (e.g., Borges et al., 2006; Meijer et al., 2011); however, my results provide a new insight into the effects of land-use change on island assemblages, since I also showed that the addition of alien species on human-dominated land uses has a major role in the turnover and homogenization of island assemblages. These results resolve some of the questions left unanswered in Chapter 2, where the observed patterns for changes in composition of natural assemblages could not be attributed only to the introduction of species. I suggest that, while on mainlands these compositional changes could be caused by the presence of both alien and native synanthropic species on disturbed sites (as a result of mainlands' larger native species pool – Herben, 2005), they might be mainly or entirely driven by alien species on islands.

Importantly, Chapter 4 also showed that richness of alien species, in absolute terms, tends to be higher in sites (across different land uses) on remote islands than on less isolated islands. This finding supports previous island biogeographic studies that have highlighted how anthropogenic factors are changing natural biographic patterns of islands (e.g., Helmus et al., 2014; Nakamura et al., 2015), with even isolated islands now seeming to be highly exposed to invasions by alien species (e.g., Blackburn et al., 2008; Moser et al., 2018). I have suggested that sites in remote islands could harbour more alien species than sites in less isolated islands as a result of: 1) remote islands' reduced diversity and small species pool (i.e., a location-level factor – Redding et al., 2019) that can make them more invasible (Roderick & Vernon, 2009; Helmus et al., 2014; but see Lonsdale, 1999), and 2) a possible higher propagule and/or colonisation pressure in remote islands, where more species need to be introduced for economic purposes due to their low diversity of native species (Denslow, 2003; Blackburn et al., 2008; Dalmazzone & Giaccaria, 2014). Even though Chapter 4 did not explore whether islands are more invasible than mainlands, I have synthesised evidence of biological invasions on islands worldwide, and shown that these can be strongly driven by human pressures.

Estimation and validation of the Biodiversity Intactness Index (BII)

While developing this thesis, I was strongly involved in the assessment and refinement of the PREDICTS' modelling framework for the calculation of BII. My main contribution to the improvement of previous methods to estimate BII (Newbold et al., 2016a) is the development of a new approach to fit the compositional similarity models (Chapter 2) needed for BII calculation. This improvement allows a more efficient use of data meaning that, for the first time, PREDICTS' BII implementation can be used with smaller datasets. It has already allowed more refined projections of BII for islands and mainlands (Chapter 3) and tropical and subtropical forests (De Palma et al., 2018a), and will enable further analyses of BII for other ecological systems or particular clades. All of the chapters of this thesis have contributed to the development of the methodological improvements for BII calculation (chapters 2 and 3) and the validation of the index (chapters 4 and 5).

In Chapter 3, I calculated BII for islands and mainlands implementing the modelling improvements, but also using models accounting for differences between island and mainland responses (an approach that had not been used before). This new approach led to lower BII estimates for both islands and mainlands than those in Newbold et al. (2016a), globally and within all biodiversity hotspots and most biomes. Importantly, in Chapter 5, I showed that these differences arise mainly from the new and more sensitive modelling of compositional similarity (Chapter 2), especially as a result of using minimally-disturbed primary vegetation as a baseline for sites' comparisons (a more stringent baseline than the one used in Newbold et al. (2016a)). Chapter 5 also showed that previous global estimates were biased towards the mainland picture; it seems that previous global models, which did not allow island assemblages to respond differently from mainland assemblages, led to optimistic BII estimates for islands. Therefore, I emphasize that many other vulnerable systems might end up with overoptimistic BII estimates in global projections if global models do not allow them to respond differently to human pressures.

I have highlighted that previous methods to calculate BII (Newbold et al., 2016a) led to generally optimistic estimates of biodiversity intactness. For example, whereas I found that average BII is below the proposed 'safe limits' (Steffen et al., 2015; Newbold et al., 2016a) for all biodiversity hotspots on both islands and mainlands (Chapter 3), Newbold et al. (2016a), suggested that only 22 of the 34 terrestrial biodiversity hotspots have on average transgressed the safe limits for BII. Newbold et al.'s (2016a) high BII estimates for some biodiversity hotspots were criticised by Martin et al. (2019); I provided more realistic BII estimates for the biodiversity hotspots, considering the human pressures that they have faced (Myers et al., 2000). Therefore, my BII implementation also yields BII estimates that address some of the recent criticisms towards the index; hence, my results formed part of the reply to Martin et al.'s criticism (Newbold et al., 2019).

Importantly, based on projected biodiversity intactness for islands, I also developed the first stringent validation test of PREDICTS' BII implementation (Chapter 5). Estimates of responses of island native species to human pressures (generated in Chapter 4) allowed me to project high-resolution global maps of the status of island native biodiversity, providing an alternative way of estimating BII (for islands at least) that makes far fewer assumptions than the approach used in Chapter 3. Comparing these maps of island native community intactness against both my maps of island BII developed in Chapter 3 and the island part of Newbold et al.'s (2016a) global BII maps, revealed that my island BII maps correlate more strongly with estimates from maps of intactness of island natives. Therefore, I conclude that using models allowing island and mainland assemblages to respond differently to human pressures, and implementing the improvements for BII modelling, have led to BII estimates that reflect patterns for native diversity more accurately than estimates generated with the previous implementation of BII (Newbold et al., 2016a).

According to my new BII projections, the global average for abundance-based BII is 0.76, while the richness-based BII average is 0.73. These estimates suggest that biotic integrity (average local abundance and richness of originally present species) globally has fallen by around 25% relative to the baseline level expected in the absence of land-use change and related pressures. Even this reduction is optimistic compared with the picture from vertebrate species presented in the most recent Living Planet Report (WWF, 2018). Based on the Living Planet Index (LPI: Loh et al., 1998) – which analyses global population trends of vertebrate abundance to measure changes in the state of biodiversity through time (Loh et al., 2005) – this global assessment reported "an overall decline of 60% in species population sizes between 1970 and 2014"; i.e., an average reduction in vertebrate population size of more than half in less than 50 years (WWF, 2018). On the other hand, my BII estimates are less optimistic than results from Dornelas et al. (2014), where no net loss of α diversity (measured by 10 different metrics) was found when analysing 100 ecological assemblage time series (global data including different biomes and taxa, representing a time interval from ~1900 to ~2000). However, Dornelas et al. (2014) found changes in community composition through time; for example, based on the Jaccard similarity index they estimated that per decade there was an average change in community composition of 10% of the species. This temporal turnover evidences a loss of biotic integrity (i.e., assemblages are suffering a substitution of their species) as suggested by my results for BII.

The lack of evidence for a net loss of α diversity in Dornelas et al. (2014) has been attributed to biases in their dataset, which was "not spatially representative of species diversity or human impacts" across the planet (Gonzalez et al., 2016). In the case of LPI, it is known that the data underpinning this index (Living Planet Database – www.livingplanetindex.org) is biased towards data for birds, mammals, temperate regions (Collen et al., 2009) and threatened species of particular taxa (McRae et al., 2017); therefore, LPI estimates may be biased towards negative population trends of threatened or rare species (McRae et al., 2017). It seems that BII estimates calculated with the new PREDICTS' implementation are somewhere in between these scenarios of no net loss of local diversity and extreme species population declines.

Limitations and future perspectives

Specific limitations for the different analyses that I performed were listed in each chapter. However, a general limitation of all the analyses included in this thesis is the use of the approach known as the space-for-time substitution (De Palma et al., 2018b). All analyses based on PREDICTS data (Hudson et al., 2017) try to estimate the temporal effect of land-use change on biodiversity based on spatial comparisons of nearby sites with different land uses and related pressures (Purvis et al., 2018) (e.g., comparing minimally-disturbed primary vegetation against human-dominated land uses). The main problem with this approach is that the composition of assemblages in present-day minimally-disturbed primary vegetation can be different from the original composition of assemblages at sites where land use has changed. Therefore, this approach can result in misleading estimates of how site-level biodiversity is affected by pressures if the control site (i.e., minimally-disturbed sites) does not accurately represent the conditions of the disturbed site prior to the land-use change it underwent. Additionally, by relying on spatial comparisons rather than analysing time-series data, models based on PREDICTS data might be capturing only a glimpse of the whole process of biodiversity change (De Palma et al., 2018b), since the full effects of land-use change can sometimes take many years to unfold – i.e., biotic lag (Tilman et al., 1994; Wearn et al., 2012). However, the PREDICTS project has relied on spatial comparisons because before-vs-after comparisons for sites that have faced land-use change are much less common in the literature (De Palma et al., 2018b; Purvis et al., 2018), and the taxonomic, geographic and ecological coverage of the database would be much more restricted if the project would only aim to collate time-series data. Even where time-series data are available, they are only rarely from an experimental design that allows for unbiased estimation of the effect of land-use change (i.e., a true manipulative experiment having a Before-After-Control-Impact design: De Palma et al., 2018b).

My analyses comparing island and mainland responses to land-use change and related pressures were in part possible due to the expansion of the PREDICTS database in recent years (Hudson et al., 2017), partly through my own addition of several island-based studies. Nonetheless, many fewer studies were available for islands than mainlands, and data for some taxa and biomes was extremely limited or not available for islands (e.g., Tables C.2, and C.3). Furthermore, whereas studies on bigger islands in developed nations (e.g., Australia, Great Britain, South Island) are reasonably common in PREDICTS database, there is a shortage of data from smaller, poorer and tropical islands. This restricted island data evidences a shortfall for island studies sampling biodiversity across disturbed sites, and suggests a need for further efforts to develop biodiversity surveys across islands in less developed countries.

There are several ways in which my biodiversity models and BII projections for islands and mainlands could be refined and extended. Two relevant approaches that the PREDICTS project has already explored are the use of more refined land-use classes and the development of projections to predict possible future impacts to biodiversity intactness. Most of my models analysed the effects of six land uses (and three use intensities) on biodiversity (i.e., primary vegetation, secondary vegetation, plantation forests, croplands, pastures and urban). This set of land-use classes is based on the classes defined in the harmonized land-use data developed by Hurtt et al. (2011) (but adding plantation forests), and was chosen to facilitate global spatial and temporal projections of PREDICTS models (Purvis et al., 2018). However, Hurtt et al. (Land-Use Harmonization 2 (LUH2) – in prep) have more recently expanded the harmonized land-use data by refining their land-use classes; importantly, agricultural land is now split more finely, for example by subdividing croplands according to crop types and differentiating rangelands from managed pastures. Using these refined land-use classes could lead to more accurate estimates and projections of the state of island and mainland biodiversity. However, currently, developing models for island/mainland biodiversity including more land-use classes might not be possible, due to the restricted island data in the PREDICTS database, which would likely lead to small sample sizes (i.e., data from few sites) for several land-use classes. Provisionally, certain subcategories that are likely to cause important changes in spatial projections and biodiversity estimates could be tested; for example, by differentiating rangelands from pastures, island and mainland regions where rangelands are common would likely exhibit higher BII estimates.

Recently, Hill et al. (2018) re-curated sites in the PREDICTS database for them to be compatible with the refined land-use classes used by Hurtt et al. (in prep.). This allowed them to develop projections for possible future impacts to biodiversity intactness (estimated by BII) at a global scale under different socio-economic scenarios, incorporating for the first time the five Shared Socio-economic Pathway scenarios (SSPs: Riahi et al., 2017) that have been developed by the current round of Intergovernmental Panel on Climate Change (IPCC) reports. By following this approach, I could evaluate whether the BII island-mainland differences that I estimated for the year 2005, could be accentuated in the future; i.e., whether the possible future trajectories of BII under different scenarios would continue to show a more reduced biotic integrity on islands than mainlands.

Final remarks

Most of my chapters highlight the parlous state of island native biodiversity. For the first time, I have estimated the global reduction of local island biodiversity caused by land use and related pressures, based on empirical data spanning many taxonomic groups and regions. Based on my results, I conclude that island species assemblages might be suffering more severe changes (e.g., compositional changes and loss of originally present species) than mainland assemblages because of a combination of their great exposure to human pressures, their more sensitive native species and their greater proneness to the establishment of alien species.

The results in this thesis represent important contributions towards understanding how human pressures affect island biodiversity. By analysing the island-mainland differences in responses to human pressures, I have highlighted the unique characteristics of island assemblages and their particular responses. Even though islands have been used as model systems in ecology (Warren et al., 2015), their assemblages might not reflect biological communities in general, but instead might often exhibit exceptional ecological dynamics, especially when facing human pressures.

My work will hopefully eventually help to publicly highlight island vulnerability to human pressures. In particular, considering the current high profile of BII, my results for biodiversity intactness may help to emphasise in global biodiversity assessments the alarming state of island biodiversity, lending weight to the development of stronger efforts to lower the intensity of human pressures on islands and to prevent the establishment of alien species to protect islands' unique biodiversity.

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Appendices

APPENDIX A

Supplement for Chapter 1

Table A.1. Land use and land-use intensity definitions used to classify sites in the PREDICTS database (taken from Hudson et al., 2014; see publication for further details)

Land Use	General definition	Minimal use	Light use	Intense use
Primary Vegetation (Forest)	Native vegetation that is not known or inferred to have ever been completely destroyed, before the year in which the biodiversity was sampled, by human actions or by extreme natural events that do not normally play a role in ecosystem dynamics.	Any disturbances identified are very minor (e.g., a trail or path) or very limited in the scope of their effect (e.g., hunting of a particular species of limited ecological importance).	One or more disturbances of moderate intensity (e.g., selective logging) or breadth of impact (e.g., bushmeat extraction), which are not severe enough to markedly change the nature of the ecosystem. Primary sites in suburban settings are at least Light use.	One or more disturbances that is severe enough to markedly change the nature of the ecosystem; this includes clear-felling of part of the site too recently for much recovery to have occurred. Primary sites in fully urban settings should be classed as Intense use.
Primary Vegetation (Non-Forest)				
Mature Secondary Vegetation	Where the original primary vegetation was completely destroyed. This could be by human actions (including fire), and includes where sites are recovering to a natural state following a period of human-dominated land use (cropland, plantation forest, pasture or urban). The decision whether to classify Secondary sites as Young Secondary, Intermediate Secondary, Mature Secondary or Secondary (Indeterminate) should depend on structural complexity of the vegetation as described in the paper, with the time since the site became secondary vegetation being a reasonable proxy.			
Intermediate Secondary Vegetation				
Young Secondary Vegetation				
Secondary Vegetation (indeterminate age)				
Plantation forest	Previously cleared areas that people have planted with crop trees or crop shrubs for commercial or subsistence harvesting of wood and/or fruit. The species planted may or may not be native. Planting an area with native woody plants for habitat restoration rather than for goods does not constitute plantation forest	Extensively managed or mixed timber, fruit/coffee, oil-palm or rubber plantations in which native understorey and/or other native tree species are tolerated, which are not treated with pesticide or fertiliser, and which have not been recently (< 20 years) clear-felled.	Monoculture fruit/coffee/rubber plantations with limited pesticide input, or mixed species plantations with significant inputs. Monoculture timber plantations of mixed age with no recent (< 20 years) clear-felling. Monoculture oil-palm plantations with no recent (< 20 years) clear-felling.	Monoculture fruit/coffee/rubber plantations with significant pesticide input. Monoculture timber plantations with similarly aged trees or timber/oil-palm plantations with extensive recent (< 20 years) clear-felling.

Cropland	Land that people have planted with herbaceous crops, even if these crops will be fed to livestock once harvested. Sites described as “fields”, “arable”, “ploughed” or “tilled” all qualify as cropland.	Low-intensity farms, typically with small fields, mixed crops, crop rotation, little or no inorganic fertiliser use, little or no pesticide use, little or no ploughing, little or no irrigation, little or no mechanisation.	Medium intensity farming, typically showing some but not many of the following: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, no crop rotation, mechanisation, monoculture crop. Organic farms in developed countries often fall within this category, as may high-intensity farming in developing countries.	High-intensity monoculture farming, typically showing many of the following features: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, mechanisation, no crop rotation.
Pasture	Land where livestock is known to be grazed regularly or permanently. The plant species may be predominantly native (as in rangelands) or strongly associated with humans (as in European-style pastures).	Pasture with minimal input of fertiliser and pesticide, and with low stock density (not high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture either with significant input of fertiliser or pesticide, or with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture with significant input of fertiliser or pesticide, and with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).
Urban	Areas with human habitation and/or buildings, where the primary vegetation has been removed, and where such vegetation as is present is predominantly managed for civic or personal amenity.	Extensive managed green spaces; villages.	Suburban (e.g. gardens), or small managed or unmanaged green spaces in cities.	Fully urban with no significant green spaces.

APPENDIX B

Supplement for Chapter 2

Table B.1. Final dataset for compositional similarity models including all taxa. The table shows the number of pairs of sites per each land-use contrast generated from pairwise comparisons within studies in the PREDICTS database. Numbers in brackets show the number of studies from which data came from. Only land-use contrasts of interest are shown.

Land-use contrast	Islands	Mainlands
PriMin- PriMin	19950 (45)	391994 (118)
PriMin- Primary	6147 (16)	15047 (53)
PriMin- Secondary	13757 (38)	16563 (80)
PriMin- Cropland	4338 (14)	7375 (23)
PriMin- Pasture	9094 (13)	19317 (42)
PriMin- Plantation	14494 (27)	3755 (42)
PriMin- Urban	59 (2)	8636 (12)
Primary-Primary	67331 (31)	30315 (72)
Secondary- Secondary	285330 (82)	120720 (164)
Cropland - Cropland	8899 (14)	201053 (86)
Pasture - Pasture	444906 (39)	629932 (91)
Plantation - Plantation	62113 (34)	70060 (68)
Urban - Urban	38530 (17)	15317 (30)

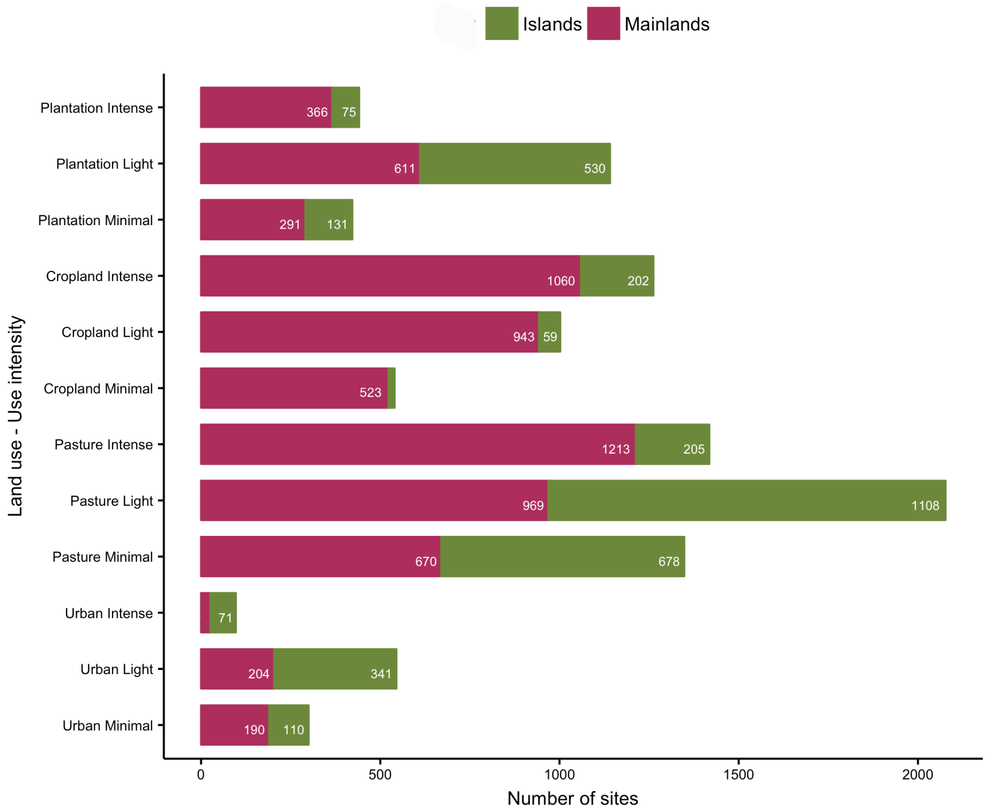


Figure B.1. Number of sites (on islands and mainlands) per land use/use intensity combination in the dataset used for the all-taxa compositional similarity models. The figure only shows human-dominated land uses, which are the ones that are addressed in the discussion. The number of sites in Urban Intense on mainlands is 26 and number of sites in Cropland Minimal on islands is 17.

Table B.2. Numbers of species (by major taxonomic group) included in the island and mainland data used for the all-taxa compositional similarity models.

Taxon	Islands	Mainlands
Vertebrates	1135	3239
Amphibia	33	289
Aves	857	2398
Mammalia	96	319
Reptilia	149	233
Invertebrates	6266	13952
Annelida	54	136
Arachnida	632	2320
Archaeognatha	9	4
Blattodea	37	19
Chilopoda	48	46
Coleoptera	1713	3196
Collembola	50	130
Dermaptera	9	10
Diplopoda	80	72
Diplura	2	1
Diptera	397	1027
Embioptera	2	2
Ephemeroptera	2	2
Hemiptera	837	713
Hymenoptera	1379	3294
Isoptera	17	90
Lepidoptera	602	2203
Malacostraca	51	45
Mantodea	5	25
Maxillopoda	1	0
Mecoptera	1	2
Megaloptera	0	1
Mollusca	195	79
Nematoda	1	308
Neuroptera	14	34
Odonata	2	4

Onychophora	3	0
Orthoptera	37	152
Pauropoda	2	2
Phasmida	1	1
Phthiraptera	1	1
Platyhelminthes	4	1
Plecoptera	6	0
Protura	1	1
Psocodea	33	3
Raphidioptera	0	1
Siphonaptera	1	1
Symphyla	5	1
Thysanoptera	25	18
Trichoptera	5	6
Zoraptera	1	0
Zygentoma	1	1
Plants	3863	7945
Bryophyta	15	495
Cycadopsida	0	2
Equisetopsida	3	1
Gnetopsida	13	6
Liliopsida	781	1303
Lycopodiopsida	16	9
Magnoliopsida	2807	5986
Marattiopsida	1	1
Pinopsida	12	30
Polypodiopsida	207	111
Psilotopsida	8	1
Fungi	474	2
Ascomycota	41	2
Basidiomycota	413	0
Glomeromycota	20	0
Protozoans	2	0
Mycetozoa	2	0
Not specified	53	174

Table B.3. Number of island and mainland studies (per biome) which were included in the dataset used for the all-taxa compositional similarity models.

Biome	Islands	Mainlands
Tundra	0	1
Boreal Forests/Taiga	0	18
Temperate Conifer Forests	7	11
Temperate Broadleaf & Mixed Forests	72	103
Montane Grasslands & Shrublands	5	11
Temperate Grasslands, Savannas & Shrublands	11	16
Mediterranean Forests, Woodlands & Scrub	7	29
Deserts & Xeric Shrublands	5	13
Tropical & Subtropical Grasslands, Savannas & Shrublands	10	23
Tropical & Subtropical Coniferous Forests	0	6
Flooded Grasslands & Savannas	0	1
Tropical & Subtropical Dry Broadleaf Forests	3	17
Tropical & Subtropical Moist Broadleaf Forests	42	120
Mangroves	1	6

Table B.4. Akaike's information criterion (AIC) values for all-taxa compositional similarity models using transformed and untransformed explanatory variables. ∆AIC values are shown relative to the best model.

	Richness-based			Abundance-based		
	d.f.	AIC	∆AIC	d.f.	AIC	∆AIC
Transformed variables	104	16897868	--	104	17575011	--
Untransformed variables	104	16899902	2034	104	17577713	2702

Table B.5. Coefficients from the all-taxa compositional similarity models (abundance-based and richness-based). Mainland coefficients (i.e., interaction coefficients) are expressed as the difference from the island coefficients. Significance (indicated by stars) is shown for the land-use contrasts of interest (first section of the table), for which "two-tailed" tests were performed to compare the observed values against null distributions. Although I only reported significance for the interaction coefficients, I also tested for significance of island coefficients (baseline in model). The two coefficients for PriMin-Urb of islands correspond to the original coefficients from the models and coefficients that were calculated indirectly (inside brackets). The coefficients in brackets for PriMin-Urb of mainlands correspond to the difference from the island coefficients that were calculated indirectly. Significance for PriMin-Urban is not shown since it could not be estimated using island coefficients that were caculated indirectly. Significance codes: >0.05^{--},<0.05**, and 0.005***

	Richness-based model		Abundance-based model	
	Islands	Mainlands	Islands	Mainlands
PriMin- PriMin	0.603 ***	0.403 ***	1.439 ***	0.501 ***
Geographic distance	-0.050 ***	-0.029 ***	-0.055 ***	-0.037 ***
Environmental distance	-1.204 ***	0.289 ***	-1.511 ***	0.534 ***
PriMin-Primary	-0.357 ***	-0.077 **	-0.460 ***	-0.079 **
PriMin-Secondary	-0.100 ***	-0.140 ***	-0.287 ***	0.060 $^{--}$
PriMin-Plantation	-0.576 ***	-0.687 ***	-0.745 ***	-0.740 ***
PriMin-Cropland	-0.920 ***	-0.142 ***	-1.231 ***	-0.114 **
PriMin-Pasture	-0.889 ***	-0.645 ***	-1.330 ***	-0.539 ***
PriMin-Urban	-0.370 (-1.360)	-0.934 (0.055)	-0.312 (-1.333)	-1.392 (-0.372)

Primary-Primary	0.843 ***	-1.084 ***	0.931 ***	-1.301 ***
Secondary-Secondary	0.622 ***	-1.056 ***	0.656 ***	-1.274 ***
Plantation-Plantation	0.767 ***	-1.225 ***	0.832 ***	-1.505 ***
Cropland-Cropland	-0.619 ***	0.506 ***	-0.776 ***	0.581 ***
Pasture-Pasture	-0.223 ***	0.072 ***	-0.191 ***	-0.009 --
Urban-Urban	-0.246 ***	0.680 ***	-0.315 ***	0.732 ***
Cropland-Pasture	-0.528	-0.004	-0.592	-0.015
Cropland-Plantation	-0.964	-0.286	-1.142	-0.748
Cropland-PriMin	-1.289	0.197	-1.463	0.188
Cropland-Primary	-0.366	-0.915	-0.440	-1.053
Cropland-Secondary	-1.062	0.356	-1.230	0.225
Cropland-Urban	-1.085	0.110	-1.163	-0.136
Pasture-Cropland	0.078	-0.181	-0.053	-0.170
Pasture-Plantation	-1.633	0.502	-1.730	-0.263
Pasture-PriMin	-0.609	-0.898	-0.864	-0.996
Pasture-Primary	-1.210	0.031	-1.322	-0.183
Pasture-Secondary	-1.595	0.815	-1.751	0.609
Pasture-Urban	0.243	-0.304	0.182	-0.386
Plantation-Cropland	-0.289	-1.350	-0.561	-1.622
Plantation-Pasture	-1.702	-0.352	-1.810	-0.849
Plantation-PriMin	-0.532	-0.218	-0.669	-0.372
Plantation-Primary	-0.743	0.102	-0.732	-0.075
Plantation-Secondary	-0.008	-0.858	-0.111	-1.068
Plantation-Urban	-0.729	-0.146	-0.811	-0.506
Primary-Cropland	-0.060	-0.861	-0.028	-1.119
Primary-Pasture	-0.265	-0.844	-0.360	-1.069
Primary-Plantation	0.663	-1.392	0.061	-1.003
Primary-PriMin	-0.294	-0.291	-0.459	-0.302
Primary-Secondary	0.192	-0.820	0.007	-0.862
Primary-Urban	-1.246	0.677	-1.440	0.538
Secondary-Cropland	-0.361	-0.308	-0.679	-0.295
Secondary-Pasture	-0.548	-0.385	-0.695	-0.610
Secondary-Plantation	0.030	-0.769	-0.149	-0.862
Secondary-PriMin	-0.142	0.106	-0.258	0.256
Secondary-Primary	0.534	-1.293	0.535	-1.514
Secondary-Urban	-0.585	-0.526	-0.660	-0.706
Urban-Cropland	-0.152	-0.702	-0.330	-0.686
Urban-Pasture	-0.001	-0.468	-0.069	-0.518
Urban-Plantation	-0.501	-0.279	-0.567	-0.351
Urban-PriMin	-0.315	-0.999	-0.350	-1.188
Urban-Primary	-0.880	0.276	-1.363	0.590
Urban-Secondary	-0.573	-0.169	-0.649	-0.336

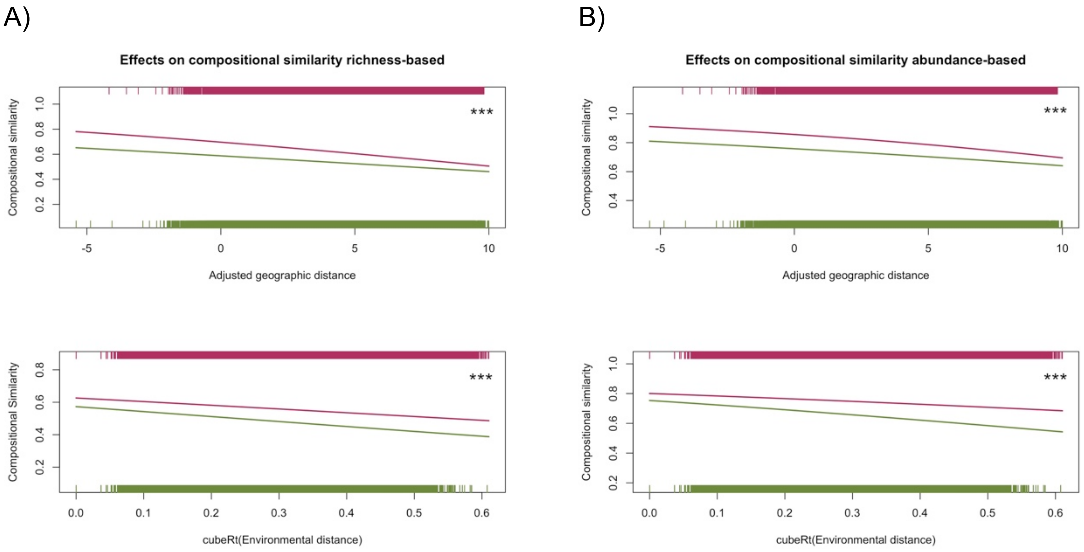


Figure B.2. Effects of geographic and environmental distance between sites on compositional similarity of island (green) and mainland (purple) assemblages. The two figures in panel A show the results for the richness-based model and the figures in panel B results for abundance-based model. The rugs in the figures show the distribution of data for islands and mainlands. Significance (indicated by stars) corresponds to p-values calculated from “two-tailed” tests using the interaction coefficients (to compare the observed values against null distributions) to test for significant differences between responses of islands and mainlands. Significance code: 0.005***

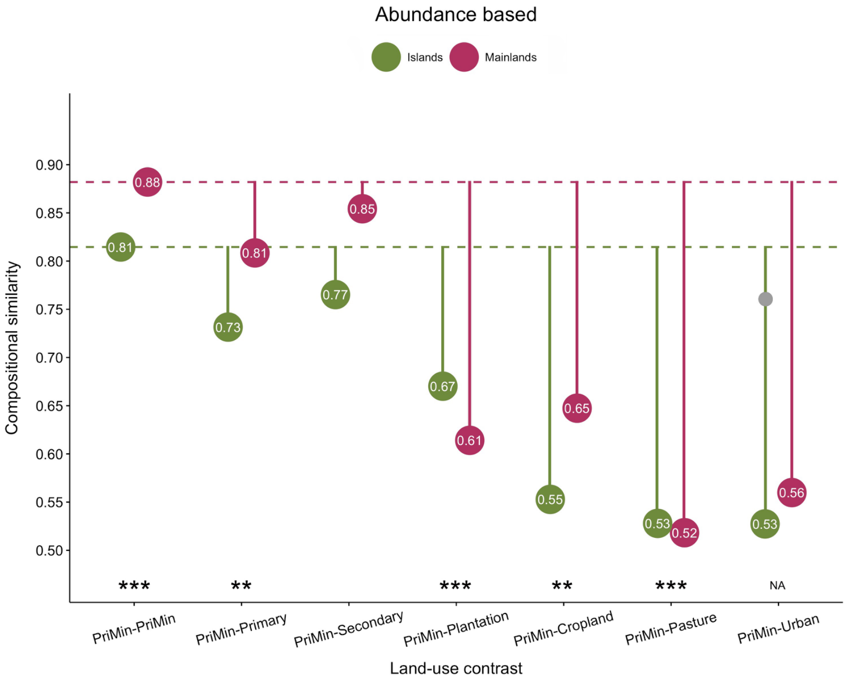


Figure B.3. J_A estimates for land-use contrasts where site *i* is in PriMin. Solid lines show the magnitude of change in J_A driven by change to different land uses, the baseline is compositional similarity between PriMin sites on islands and mainlands respectively (dashed lines). The grey circle in the PriMin-Urban contrast for islands shows the original estimate from the model, while the displayed value corresponds to the estimate that was calculated indirectly. Significance (indicated by stars) is shown for island/mainland differences for J_A changes from PriMin-PriMin on a logit scale. Significance for PriMin-Urban is not shown since it could not be estimated using island coefficients that were caculated indirectly. When using the original coefficients islands and mainlands showed significant differences for PriMin-Urban. Significance codes: <0.05**, and 0.005***

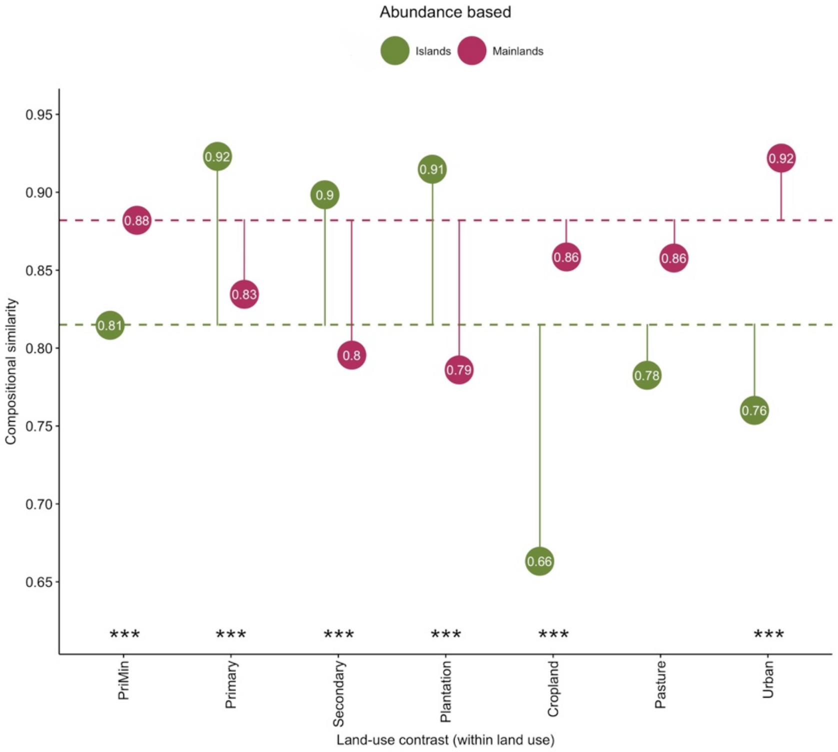


Figure B.4. J_A estimates for sites within the same land use on islands and mainlands. Each category corresponds to a land-use contrast (i.e., Cropland= Cropland-Cropland). Solid lines show the magnitude of change in J_A for islands and mainlands, using compositional similarity between PriMin sites as baseline (dashed lines). Significance connotation and codes as in Figure B.3.

Table B.6. Coefficients from the all-taxa compositional similarity models where Australia was classified as mainland. The table only shows land-use contrasts of interest and significance (indicated by stars) for the interaction coefficients (i.e, mainland coefficients). The two coefficients for PriMin-Urb on islands correspond to the original coefficients from the models and coefficients that were calculated indirectly (inside brackets). The coefficients in brackets for PriMin-Urb of mainlands correspond to the difference from the island coefficients that were calculated indirectly. Significance codes: >0.05--,<0.05**, and 0.005***

	Richness-based model		Abundance-based model	
	Islands	Mainlands	Islands	Mainlands
PriMin- PriMin	0.584	0.430 ***	1.439	0.499 ***
Geographic distance	-0.050	-0.030 ***	-0.055	-0.039 ***
Environmental distance	-1.067	0.069 --	-1.354	0.274 ***
PriMin- Primary	-0.414	-0.009 --	-0.535	0.011 --
PriMin- Secondary	-0.087	-0.147 ***	-0.285	0.063 --
PriMin- Plantation	-0.571	-0.521 ***	-0.746	-0.568 ***
PriMin- Cropland	-0.866	-0.178 **	-1.181	-0.137 ***
PriMin- Pasture	-0.897	-0.629 ***	-1.352	-0.494 ***
PriMin- Urban	-0.354 (-1.369)	-0.921 (0.094)	-0.302 (-1.354)	-1.361 (-0.309)
Primary- Primary	1.101	-1.360 ***	1.231	-1.627 ***
Secondary- Secondary	0.662	-1.070 ***	0.682	-1.256 ***
Plantation- Plantation	0.893	-1.329 ***	0.970	-1.606 ***
Cropland-Cropland	-0.597	0.481 ***	-0.758	0.572 ***
Pasture- Pasture	-0.218	0.064 **	-0.193	0.002 --
Urban- Urban	-0.269	0.714 ***	-0.358	0.800 ***

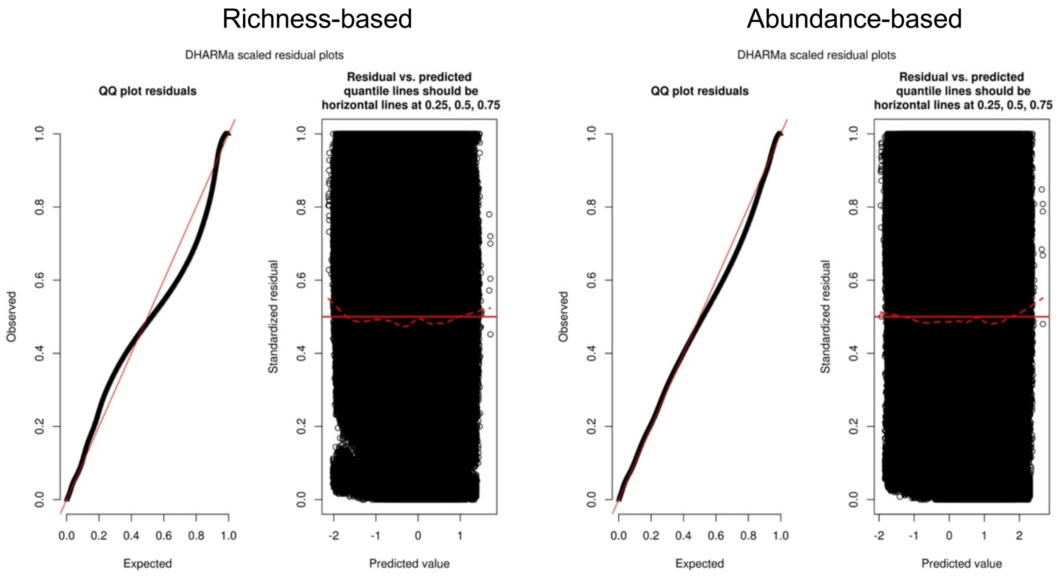


Figure B.5 . Diagnostic plots for the final compositional similarity models including all taxa.

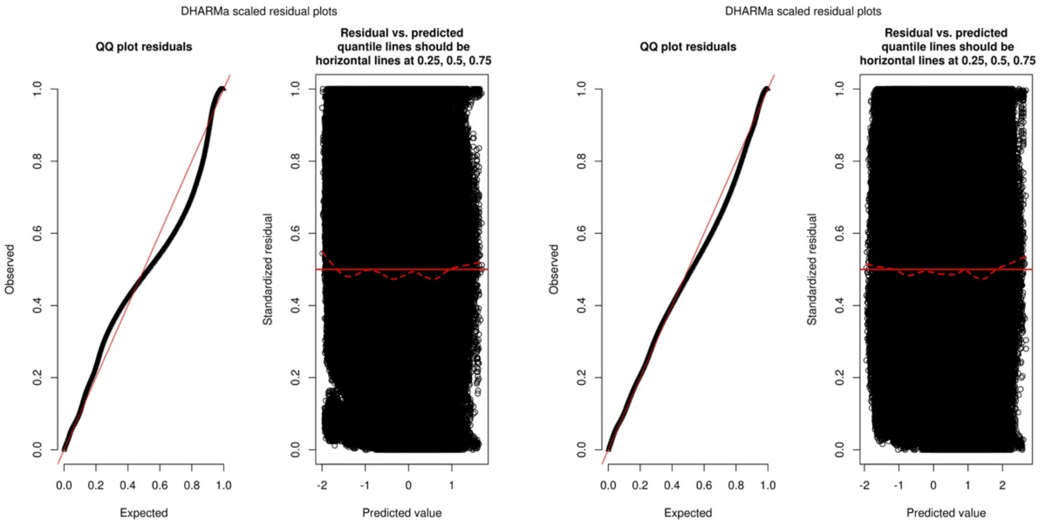
Table B.7. Final datasets for the animal and plant/fungal compositional similarity models. The table shows the number of pairs of sites per each land-use contrast generated from pairwise comparisons within studies in the PREDICTS database. Numbers in brackets show the number of studies from which data came from. Only land-use contrasts of interest are shown.

	Animal data		Plant/fungal data	
Land-use contrast	Islands	Mainlands	Islands	Mainlands
PriMin- PriMin	10900 (35)	63078 (94)	9050 (10)	326660 (23)
PriMin- Primary	398 (13)	13969 (47)	5749 (3)	1078 (6)
PriMin- Secondary	8587 (28)	14968 (68)	5170 (10)	1595 (12)
PriMin- Cropland	2415 (8)	6982 (21)	1923 (6)	393 (2)
PriMin- Pasture	3997 (10)	9740 (35)	5097 (3)	745 (6)
PriMin- Plantation	8143 (20)	3393 (38)	6351 (7)	362 (4)
PriMin- Urban	59 (2)	8198 (10)	0	438 (2)
Primary-Primary	62229 (26)	26445 (63)	5102 (5)	3870 (9)
Secondary- Secondary	277105 (70)	94171 (138)	8225 (12)	26477 (25)
Cropland - Cropland	6377 (9)	200535 (81)	2522 (5)	518 (5)
Pasture - Pasture	424876 (32)	585927 (75)	20030 (7)	10333 (15)
Plantation - Plantation	42253 (27)	66307 (55)	19860 (7)	3753 (13)
Urban - Urban	38530 (17)	11599 (26)	0	3712 (3)

Table B.8. Significance of the interaction terms in the compositional similarity models for plant/fungal assemblages. Significance of environmental distance as main effect was also tested since this variable did not interact significantly with the Island/Mainland term. Values correspond to p-values calculated by performing a “greater” hypothesis test, where I compared the likelihood ratio for my observed models (maximum model and model excluding each interaction) against a distribution of null likelihood ratios generated from comparisons of models using permuted datasets.

Interaction term	Richness-based model	Abundance-based model
Geographic distance × Island/Mainland	0.005	0.005
Environmental distance × Island/Mainland	0.115	0.5
Land-use contrast × Island/Mainland	0.005	0.005
Environmental distance	0.005	0.005

Richness-based (animals) Abundance-based (animals)



Richness-based (plants/fungi) Abundance-based (plants/fungi)

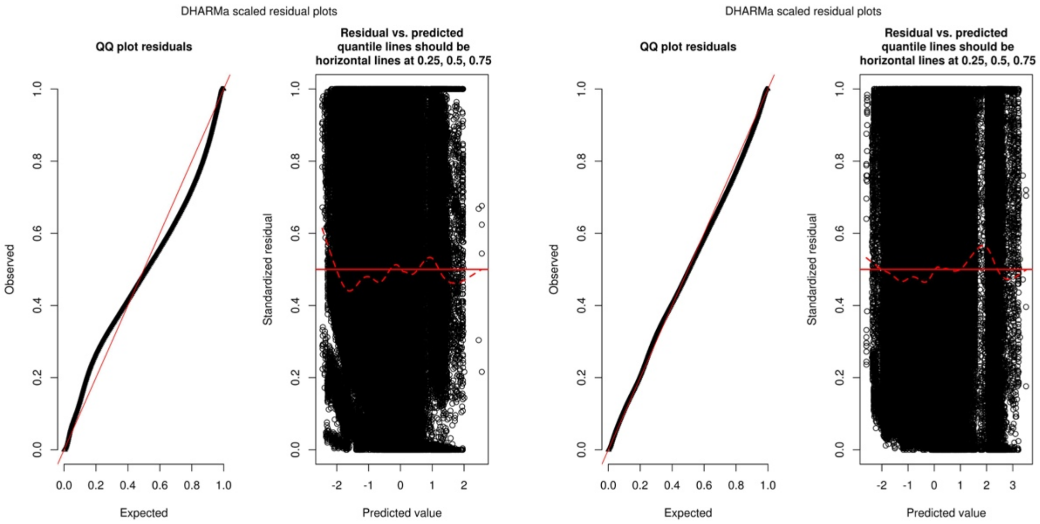


Figure B.6 . Diagnostic plots for the final compositional similarity models for animals and plants/fungi.

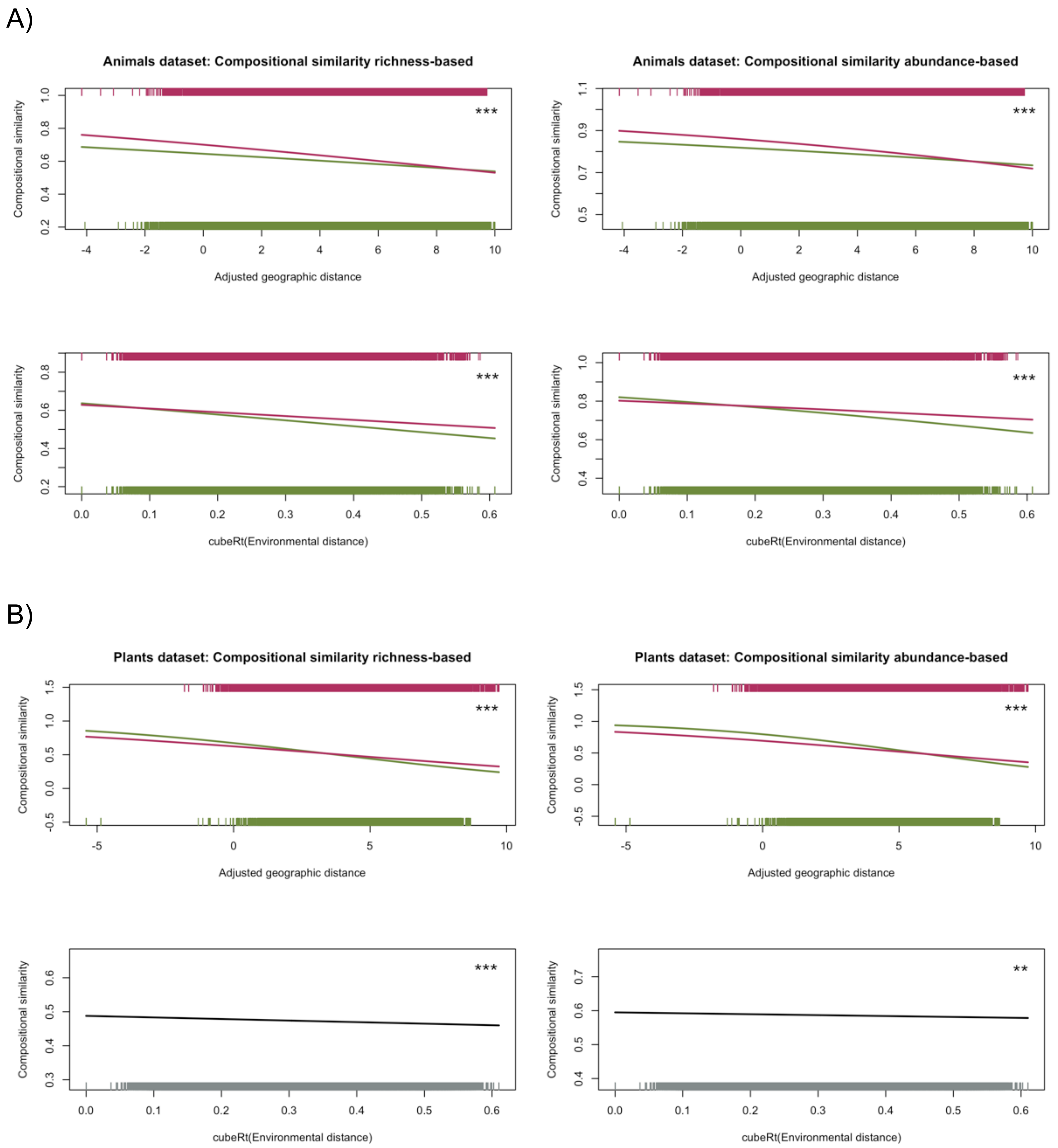


Figure B.7. Effects of geographic and environmental distance between sites on compositional similarity of animal and plant/fungal assemblages. Islands results are shown in green and mainlands in purple. The four figures in panel A show the results for the richness-based and abundance-based models for animals and the four figures in panel B show results for richness-based and abundance-based models for plants/fungi. The rugs in the figures show the distribution of data for islands, mainlands or all data (grey). Significance (indicated by stars) corresponds to p-values calculated from “two-tailed” tests using the interaction coefficients (to compare the observed values against null distributions) to test for significant differences between responses of islands and mainlands. In the case of plant/fungal models, p-values for environmental distance were calculated for the single term since this variable did not interact significantly with the Island/Mainland term. Significance codes: <0.05**, 0.005***

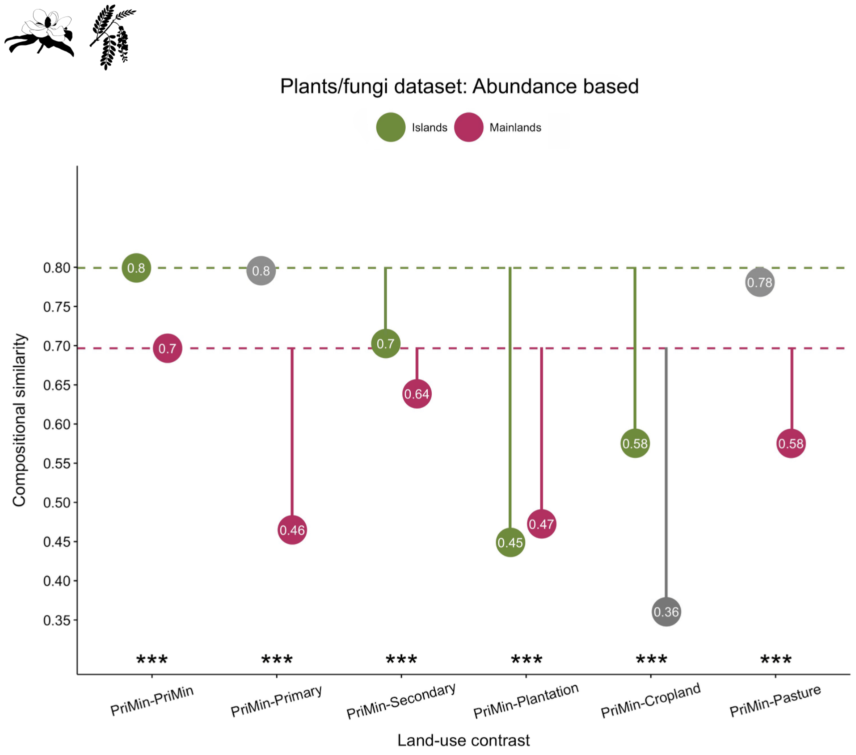


Figure B.8. J_A estimates for plant/fungal assemblages in land-use contrasts where site *i* is in PriMin. Solid lines show the magnitude of change in J_A on islands and mainlands driven by change to different land uses. Circles in grey indicate contrasts with limited data (i.e., data from three or less studies). PriMin-Urban results are not shown since no plant/fungal data was available for this contrast for islands. Significance connotation and codes as in Figure B.3.

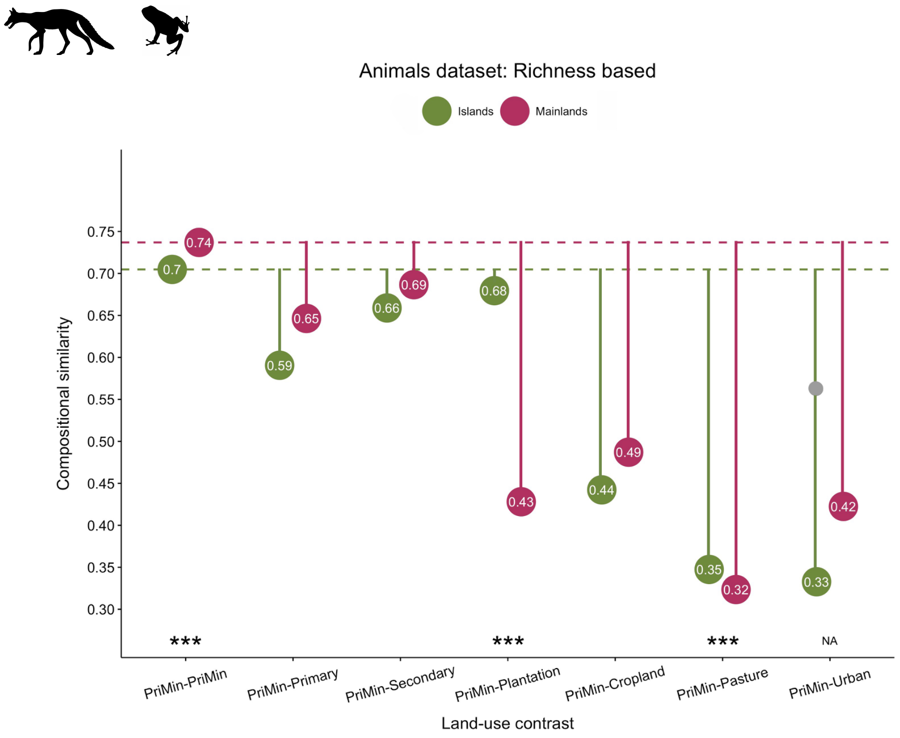


Figure B.9. J_R estimates for animal assemblages in land-use contrasts where site *i* is in PriMin. Solid lines show the magnitude of change in J_R on islands and mainlands driven by change to different land uses. The grey circle in the PriMin-Urban island contrast shows the original estimate from the model, while the displayed value corresponds to the estimate that was calculated indirectly. When using the original coefficients, islands and mainlands showed significant differences for PriMin-Urban. Significance connotation and codes as in Figure B.3.

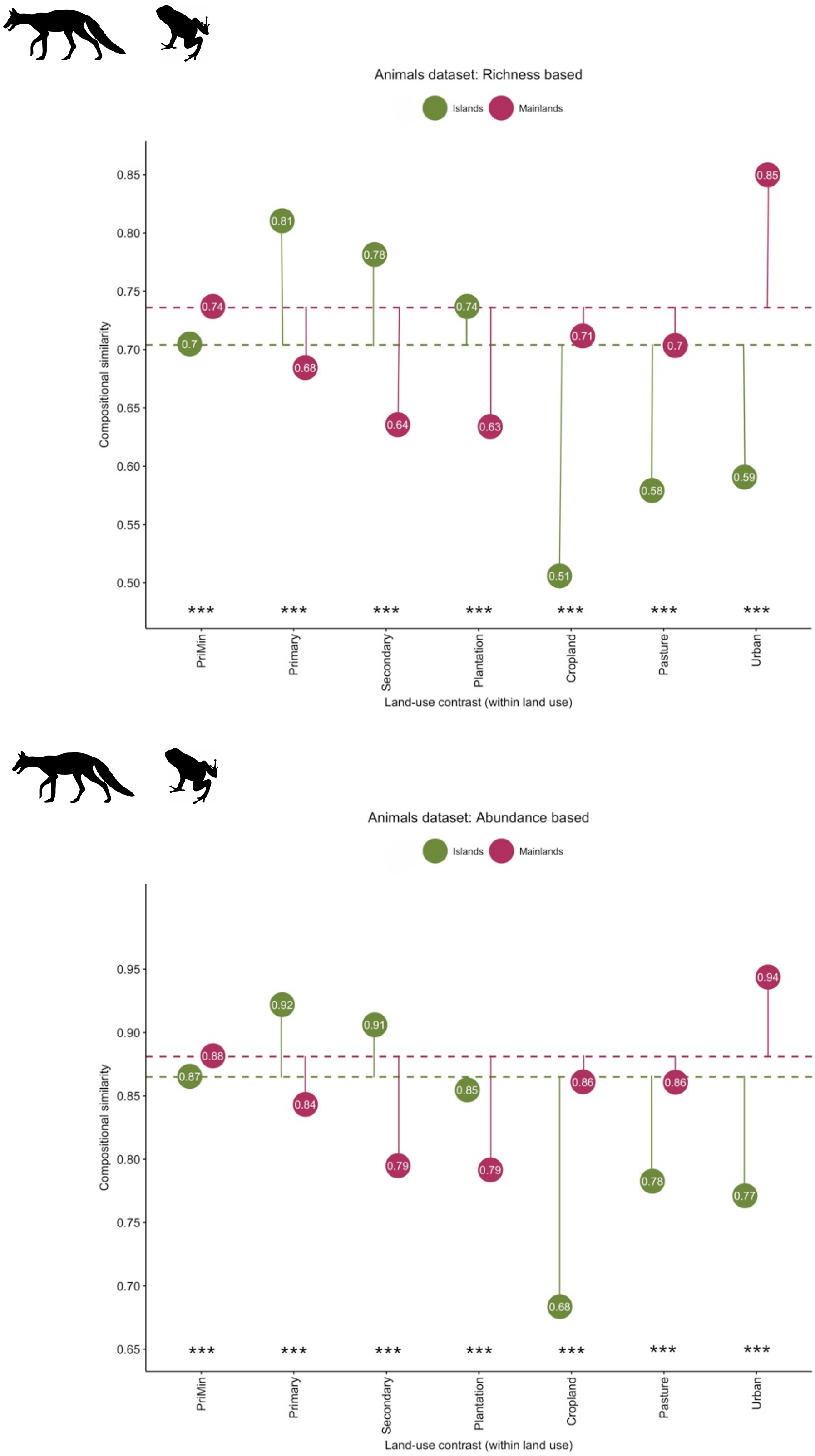


Figure B.10. J_R and J_A estimates for animal assemblages of sites within the same land use on islands and mainlands. Each category corresponds to a land-use contrast (i.e., Primary= Primary-Primary). Solid lines show the magnitude of change in J_R and J_A for islands and mainlands using compositional similarity between PriMin sites as baseline (dashed lines). Significance connotation and codes as in Figure B.3.

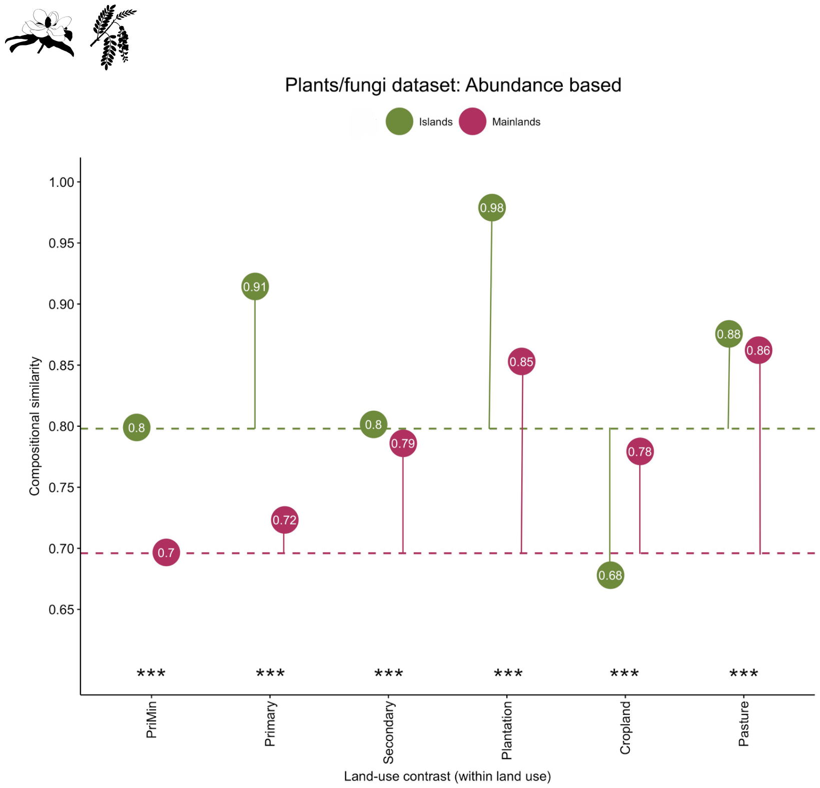


Figure B.11. J_A estimates for plant/fungal assemblages of sites within the same land use on islands and mainlands. Solid lines show the magnitude of change in J_A for islands and mainlands using compositional similarity between PriMin sites as baseline (dashed lines). Urban-Urban results are not shown since no plant/fungal data was available for this contrast for islands. Significance connotation and codes as in Figure B.3.

Table B.9. Islands included in the all-taxa compositional similarity models. The islands marked with NAs are those that were excluded from the models evaluating the effects of island area and isolation on compositional similarity. The country or countries listed for each island correspond to where sites in the PREDICTS database are located.

Island	Country	Distance to mainland (km)	Area (km^2)	Surrounding landmass (summed proportions)
Anijima	Japan	NA	NA	NA
Australia	Australia	NA	NA	NA
Bioko	Equatorial Guinea	73.03	1950.46	1.148
Borneo	Indonesia/Malaysia	1104.78	725098.05	0.501
Chichijima	Japan	NA	NA	NA
Cuba	Cuba	422.54	106901.26	0.423
Cyprus	Cyprus	113.75	9267.65	1.097
Faial	Portugal	NA	NA	NA
Flores	Portugal	NA	NA	NA
Grande Comoro	Comoros	307.45	1021.61	0.736
Great Britain	United Kingdom	441.35	219236.05	0.858
Hainan	China	115.16	34042.9	0.946
Hawai'i	United States	3727.76	10457.22	0.245
Honshu	Japan	756.22	227522.73	0.573
Ireland	Ireland	582.2	84037.84	0.692
Kolombangara	Solomon Islands	1492.05	693.85	0.384
Luzon	Philippines	930.47	104973.97	0.478
Madagascar	Madagascar	780.51	590547.38	0.46
Negros	Philippines	1506.29	12796.25	0.648
New Guinea	Papua New Guinea	616.21	773633.97	0.38
North Island	New Zealand	2201.51	114253.63	0.171
North Uist	United Kingdom	756.37	330.66	0.776
Palawan	Philippines	1041.98	11456.92	0.494
Puerto Rico	Puerto Rico	765.49	8728.54	0.381
Santa Catharina	Brazil	8.09	424.89	1.203
Santa Maria	Portugal	NA	NA	NA
Sao Tome	Sao Tome and Principe	283.63	854.8	0.753
Shikoku	Japan	420.87	18313.93	0.832
Shimono-shima	Japan	357.35	1.53	1.231
Sjaelland	Denmark	62.53	7080.12	1.526
South Island	New Zealand	1868.86	150576.24	0.163
Sulawesi	Indonesia	1423.52	169020.98	0.51
Sumatra	Indonesia	287.22	429003.21	0.557
Tasmania	Australia	320.86	64363.4	0.346
Terceira	Portugal	1537.24	400.56	0.46
Tierra del Fuego	Argentina	153.75	47732.31	0.59
Wight	United Kingdom	107.93	387.76	1.394

Table B.10. ANOVA table for richness-based compositional similarity models including island area or island isolation metrics as explanatory variables. The table shows results for the full models since none of the isolation metrics or area were significant as main effect when the models were simplified. LUc= Land-use contrast, Dist= Distance to the nearest mainland, Land= Surrounding landmass. Stars indicate the level of significance (Sig): <0.05*, <0.01** and <0.001***

Term	χ^2	d.f.	Sig
Model including distance to the nearest mainland			
LUc	156.8931	48	***
Dist	1.1041	1	
LUc * Dist	34.6093	48	
Model including surrounding landmass			
LUc	162.2306	48	***
Land	0.6024	1	
LUc * Land	56.3036	48	
Model including area			
LUc	165.8644	48	***
Area	0.1377	1	
LUc * Area	66.7575	48	*

Table B.11. ANOVA table for abundance-based compositional similarity models including island area or island isolation metrics as explanatory variables. Acronyms and significance codes as in Table B.10.

Term	χ^2	d.f.	Sig
Model including distance to the nearest mainland			
LUc	189.6315	48	***
Dist	1.5048	1	
LUc * Dist	37.0433	48	
Model including surrounding landmass			
LUc	199.222	48	***
Land	0.793	1	
LUc * Land	69.708	48	*
Model including area			
LUc	198.273	48	***
Area	0.173	1	
LUc * Area	61.577	48	

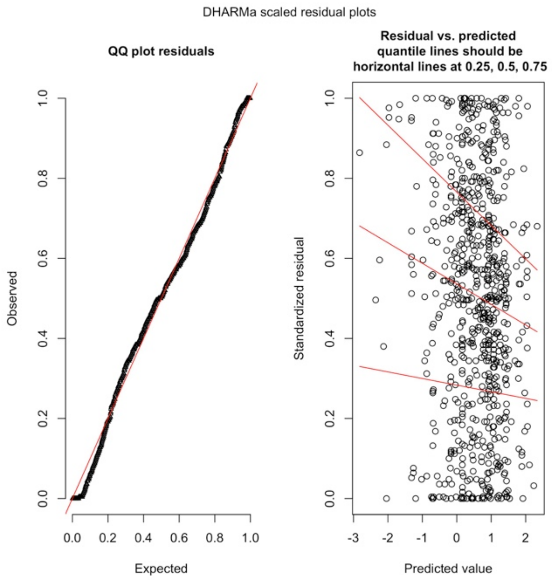


Figure B.12 . Diagnostic plot for the model where average J_A of each land-use contrast within each study was modelled as a function of land-use contrast and landmass surrounding the island.

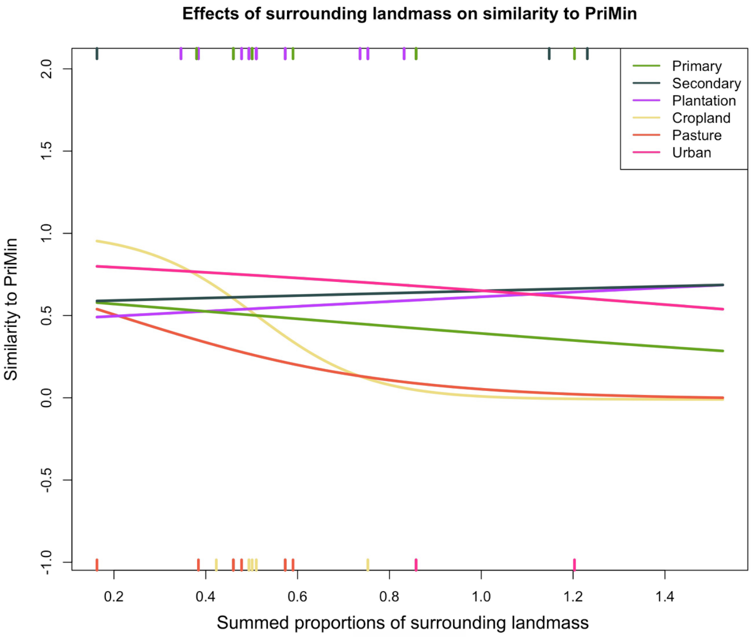


Figure B.13. Effects of surrounding landmass on compositional similarity to PriMin (abundance-based). Only one slope is significantly different from zero: PriMin-Cropland (-8.12, P=0.006). The rugs in the figure show the landmass values represented in the model dataset (exclusively for land-use contrasts where site *i* is in PriMin).

APPENDIX C

Supplement for Chapter 3

Table C.1. Final datasets for the abundance and richness models that were used to estimate BII. The table shows the number of sites on islands and mainlands across land use/use intensity categories (LUI) and the total number of island and mainland sites in the datasets (bottom row). Numbers in brackets show the number of studies from which data came from. The abundance dataset included island data from 63 different islands, while the richness dataset included data from 74 different islands.

LUI	Abundance dataset		Richness dataset	
	Islands	Mainlands	Islands	Mainlands
Primary Vegetation Minimal use	1012 (85)	3299 (212)	1370 (100)	3778 (245)
Primary Vegetation Light use	467 (38)	1486 (108)	520 (43)	2026 (130)
Primary Vegetation Intense use	252 (9)	295 (35)	266 (12)	351 (41)
Secondary Vegetation Minimal use	801 (82)	1792 (166)	944 (90)	2200 (185)
Secondary Vegetation Light use	633 (47)	772 (90)	715 (54)	985 (97)
Secondary Vegetation Intense use	393 (23)	285 (41)	414 (28)	314 (44)
Pasture Minimal use	911 (24)	666 (53)	911 (24)	673 (57)
Pasture Light use	1165 (38)	1074 (66)	1173 (40)	1104 (72)
Pasture Intense use	228 (22)	1226 (22)	241 (24)	1232 (23)
Plantation forest Minimal use	133 (20)	354 (52)	198 (24)	507 (61)
Plantation forest Light use	664 (30)	686 (51)	714 (36)	722 (55)
Plantation forest Intense use	76 (10)	377 (28)	90 (12)	389 (31)
Cropland Minimal use	49 (18)	622 (50)	51 (20)	659 (54)
Cropland Light use	78 (11)	1111 (65)	78 (11)	1291 (69)
Cropland Intense use	291 (17)	1077 (45)	292 (18)	1176 (48)
Urban Minimal use	147 (18)	218 (20)	149 (19)	251 (27)
Urban Light use	412 (21)	221 (26)	428 (22)	273 (33)
Urban Intense use	74 (8)	38 (13)	74 (8)	196 (20)
Total sites and studies	7786 (202)	15599 (432)	8628 (225)	18127 (490)

Table C.2. Number of island and mainland sites per biome in the final datasets for the abundance and richness models that were used to estimate BII.

Biome	Abundance dataset		Richness dataset	
	Islands	Mainlands	Islands	Mainlands
Boreal Forests/Taiga	0	1049	0	1075
Deserts & Xeric Shrublands	55	210	55	218
Flooded Grasslands & Savannas	0	39	0	51
Mangroves	6	24	6	24
Mediterranean Forests, Woodlands & Scrub	303	1422	304	1614
Montane Grasslands & Shrublands	485	277	485	488
Temperate Broadleaf & Mixed Forests	3764	6790	4051	7607
Temperate Conifer Forests	98	422	98	512
Temperate Grasslands, Savannas & Shrublands	280	271	456	704
Tropical & Subtropical Coniferous Forests	0	277	0	367
Tropical & Subtropical Dry Broadleaf Forests	82	400	82	430
Tropical & Subtropical Grasslands, Savannas & Shrublands	545	1386	571	1721
Tropical & Subtropical Moist Broadleaf Forests	2168	3011	2520	3266
Tundra	0	21	0	50

Table C.3. Numbers of species (by major taxonomic group) included in the island and mainland data for the abundance and richness models that were used to estimate BII.

Taxon	Abundance dataset		Richness dataset	
	Islands	Mainlands	Islands	Mainlands
Vertebrates	1547	4340	1635	4815
Amphibia	136	291	136	317
Aves	1012	3383	1077	3792
Mammalia	216	427	225	463
Reptilia	183	239	197	243
Invertebrates	8552	16430	9289	17017
Annelida	160	136	160	136
Arachnida	973	2554	974	2555
Archaeognatha	9	4	9	4
Blattodea	37	19	40	19

Chilopoda	56	46	56	46
Coleoptera	2689	4092	2784	4094
Collembola	113	130	113	193
Dermaptera	9	10	9	10
Diplopoda	87	72	87	72
Diplura	2	1	2	1
Diptera	410	1128	521	1129
Embioptera	2	2	2	2
Ephemeroptera	2	2	2	2
Hemiptera	837	713	878	713
Hymenoptera	1349	3715	1654	3809
Isoptera	17	124	17	124
Lepidoptera	932	2881	1045	3197
Malacostraca	54	47	54	47
Mantodea	5	25	5	25
Maxillopoda	1	0	1	0
Mecoptera	1	2	1	2
Megaloptera	1	0	0	1
Mollusca	195	114	196	205
Nematoda	380	386	380	386
Neuroptera	14	34	17	34
Odonata	91	4	92	4
Onychophora	3	0	3	0
Orthoptera	37	152	99	170
Pauropoda	2	2	2	2
Phasmida	1	1	1	1
Phthiraptera	1	1	1	1
Platyhelminthes	4	1	5	1
Plecoptera	6	0	6	0
Protura	1	1	1	1
Psocodea	33	3	33	3
Raphidioptera	0	1	0	1

Siphonaptera	1	1	1	1
Symphyla	5	1	5	1
Thysanoptera	25	18	25	18
Trichoptera	5	6	5	6
Zoraptera	1	0	1	0
Zygentoma	1	1	2	1
Plants	4170	8268	5651	10482
Bryophyta	271	918	302	1139
Cycadopsida	0	2	0	2
Equisetopsida	3	1	4	6
Gnetopsida	13	5	13	5
Liliopsida	785	1348	993	1623
Lycopodiopsida	16	9	18	11
Magnoliopsida	2853	5825	4053	7479
Marattiopsida	1	1	1	1
Pinopsida	12	33	23	45
Polypodiopsida	208	125	234	170
Psilotopsida	8	1	10	1
Fungi	902	720	903	930
Ascomycota	469	340	470	400
Basidiomycota	413	369	413	519
Glomeromycota	20	11	20	11
Protozoans	2	1	2	1
Mycetozoa	2	1	2	1

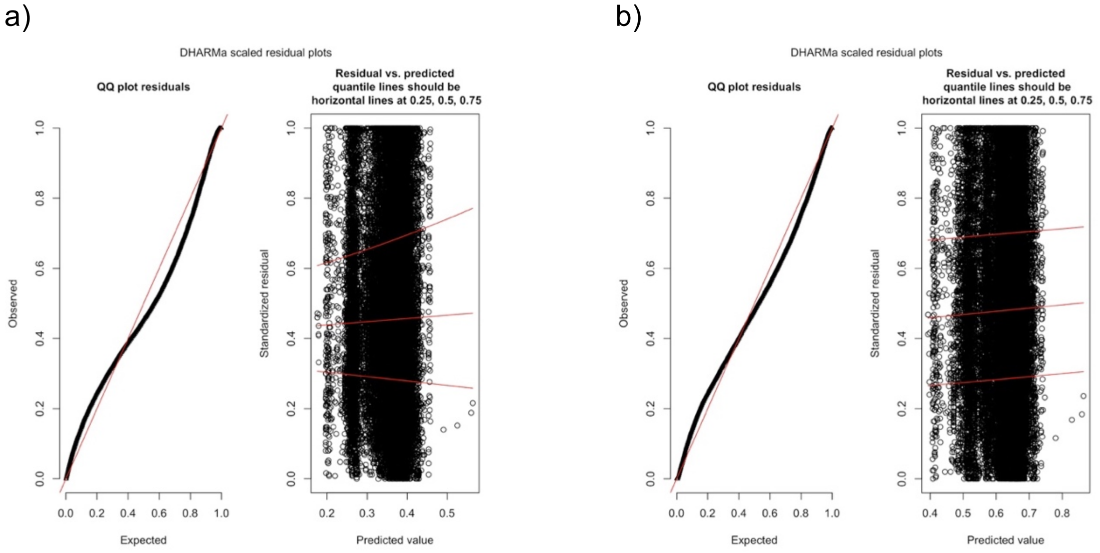


Figure C.1. Diagnostic plots for the abundance model that was used to estimate BII. a) Minimum adequate model (MAM) using log transformation for rescaled total abundance. b) MAM using square root transformation for rescaled total abundance (final model).

Table C.4. Akaike's information criterion (AIC) values for models of total abundance (for BII estimation) using the three random-effects structures that were tested. ∆AIC values are shown relative to the best model. SS= study, SSB= block within study.

Random-effects structure	d.f.	AIC	∆AIC
(1+LandUse+UseIntensity|SS)+(1|SSB)	122	-13073.31	--
(1+LandUse|SS)+(1|SSB)	107	-12738.73	334.58
(1|SS)+(1|SSB)	87	-10771.61	2301.7

Table C.5. ANOVA table for the minimum adequate model of total abundance that was used to estimate BII. LUI= land use/use intensity, HPD= human population density, DistRd= distance to the nearest road. Stars indicate the level of significance (Sig): <0.05*, <0.01** and <0.001***

Term	χ^2	d.f.	Sig
LUI	96.23	17	***
Island/Mainland	0.11	1	
HPD	25.71	2	***
DistRd	15.67	2	***
LUI × Island/Mainland	29.28	17	*
HPD × Island/Mainland	1.69	2	
LandUse × HPD	47.38	10	***
LandUse × HPD × Island/Mainland	48.82	10	***

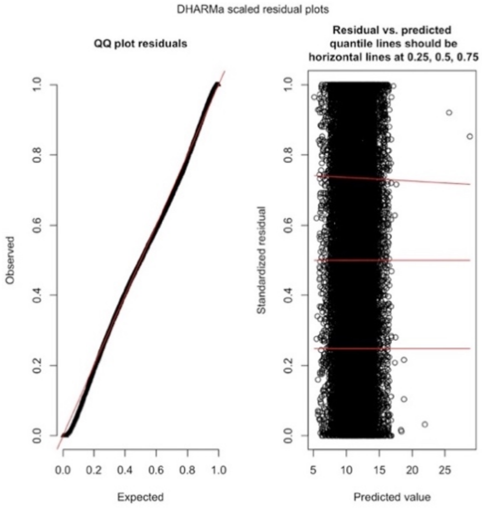


Figure C.2. Diagnostic plot for the minimum adequate model of species richness that was used to estimate BII.

Table C.6. AIC values for models of species richness (for BII estimation) using the three random-effects structures that were tested. ∆AIC values are shown relative to the best model. SS= study, SSB= block within study.

Random-effects structure	d.f.	AIC	∆AIC
(1+LandUse+UseIntensity|SS)+(1|SSB)	121	156923.5	--
(1+LandUse|SS)+(1|SSB)	106	157851.2	927.7
(1|SS)+(1|SSB)	86	163368.6	6445.1

Table C.7. ANOVA table for the minimum adequate model of species richness that was used to estimate BII. LUI= land use/use intensity, HPD= human population density, DistRd= distance to the nearest road. Stars indicate the level of significance (Sig): <0.05*, <0.01** and <0.001***

Term	χ^2	d.f.	p-value
LUI	404.30	17	***
Island/Mainland	2.92	1	
HPD	0.08	2	
DistRd	15.42	2	***
LUI × Island/Mainland	70.29	17	***
HPD × Island/Mainland	28.02	2	***
LandUse × HPD	147.39	10	***
DistRd × Island/Mainland	4.31	2	
LandUse × DistRd	80.11	10	***
LandUse × HPD × Island/Mainland	64.25	10	***
LandUse × DistRd × Island/Mainland	55.18	10	***

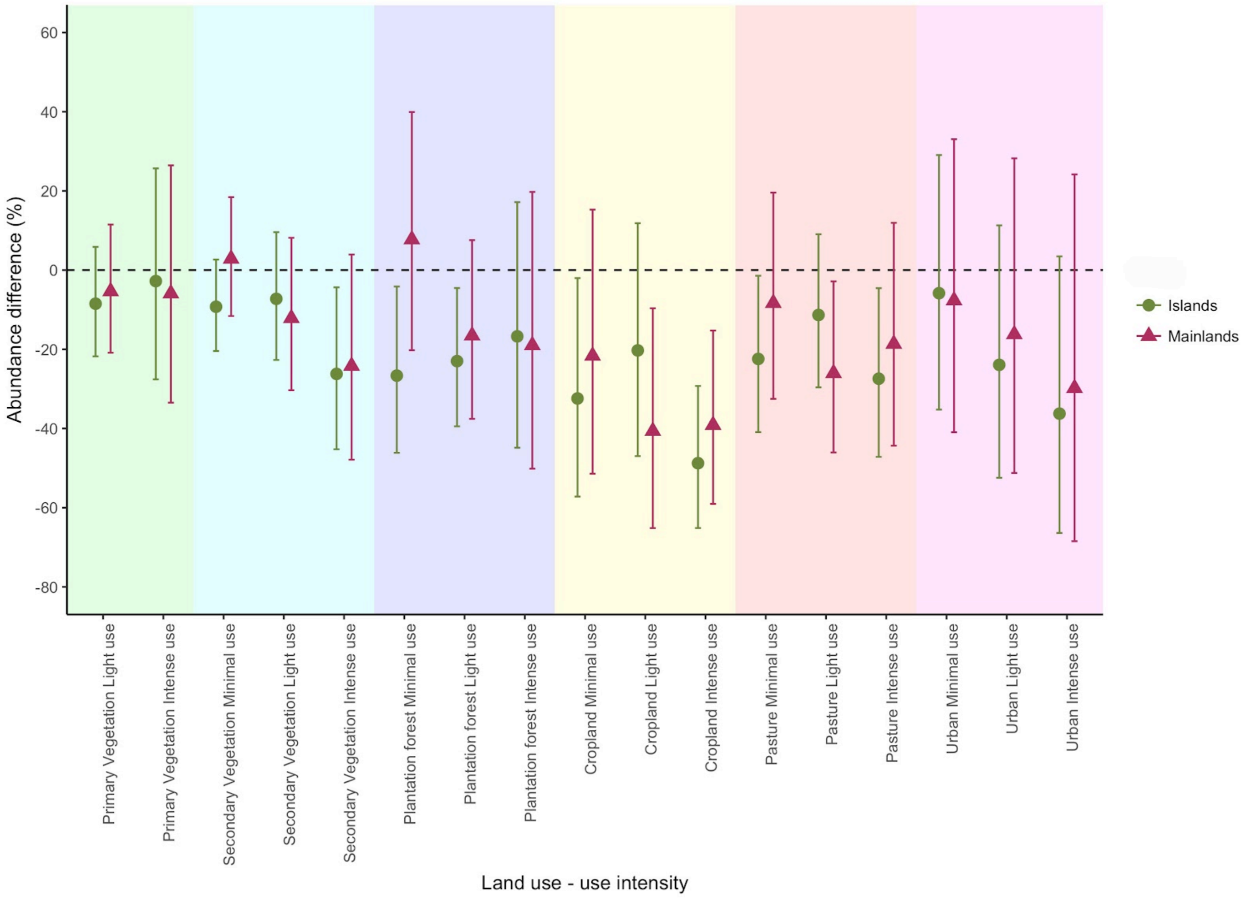


Figure C.3. Response of total abundance to land use/use intensity on islands and mainlands. Values indicate decrease or increase in percentage of total abundance using minimally-used primary vegetation as baseline (dashed line). Bars indicate 95% confidence intervals.

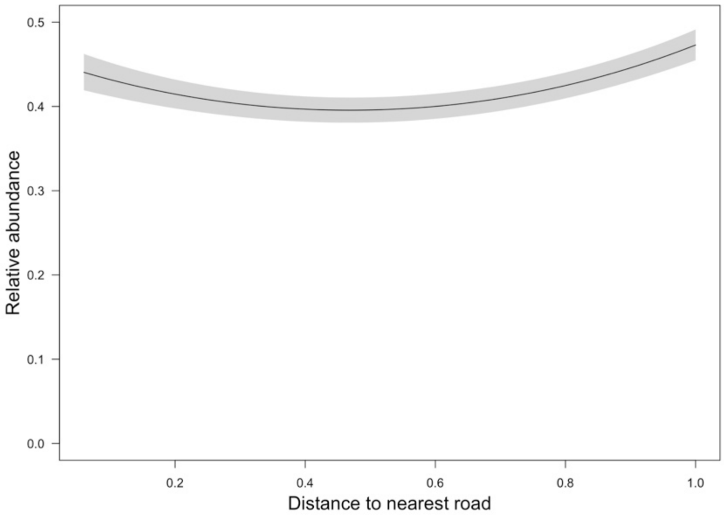
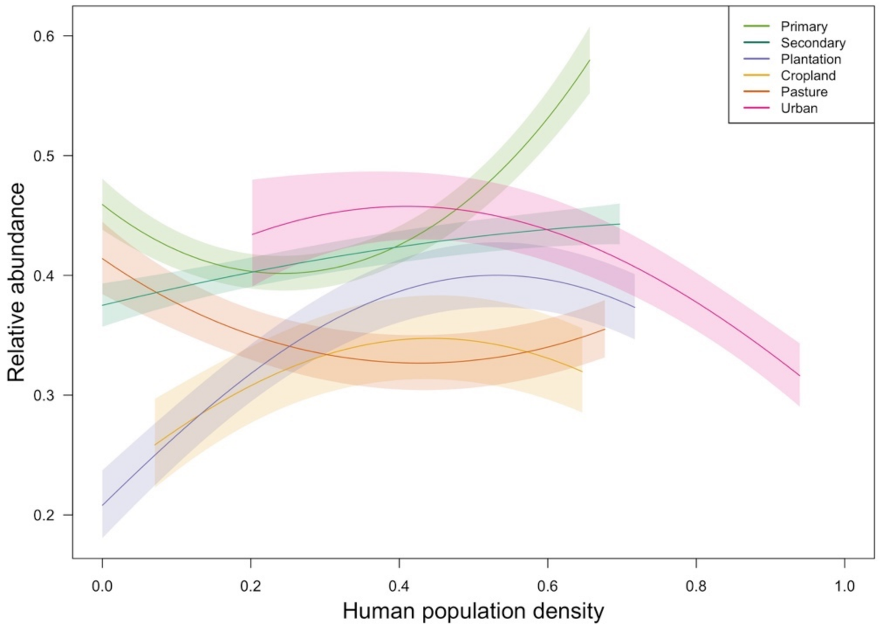


Figure C.4. Response of total abundance to distance to the nearest road (DistRd). The error bar shows half the standard error. In the abundance model that was used for BII estimation, DistRd was significant as a main effect but did not interact significantly with any other variable. DistRd values are shown on a rescaled axis (as fitted in the models). Abundance is shown on a zero-to-one scale (as fitted in the models; i.e., abundance rescaled within studies).

a)



b)

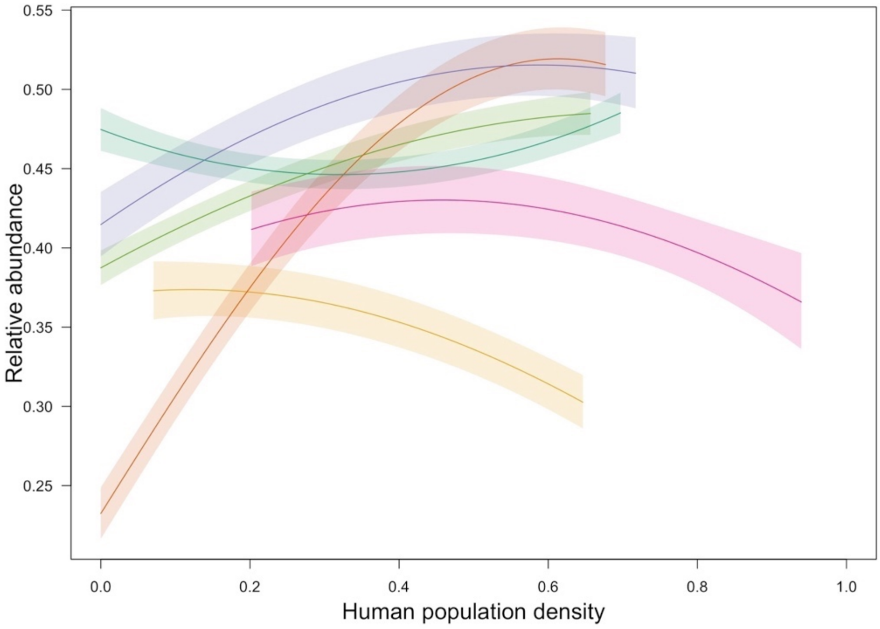


Figure C.5. Response of total abundance to human population density (HPD) across land uses on a) islands and b) mainlands. The x limits of each coloured line indicate the 2.5th and 97.5th percentiles for the values of HPD represented in each land use in the model dataset. For clarity, the error bars show half the standard error. HPD values are shown on a rescaled axis (as fitted in the models). Abundance is shown on a zero-to-one scale (as fitted in the models; i.e., abundance rescaled within studies).

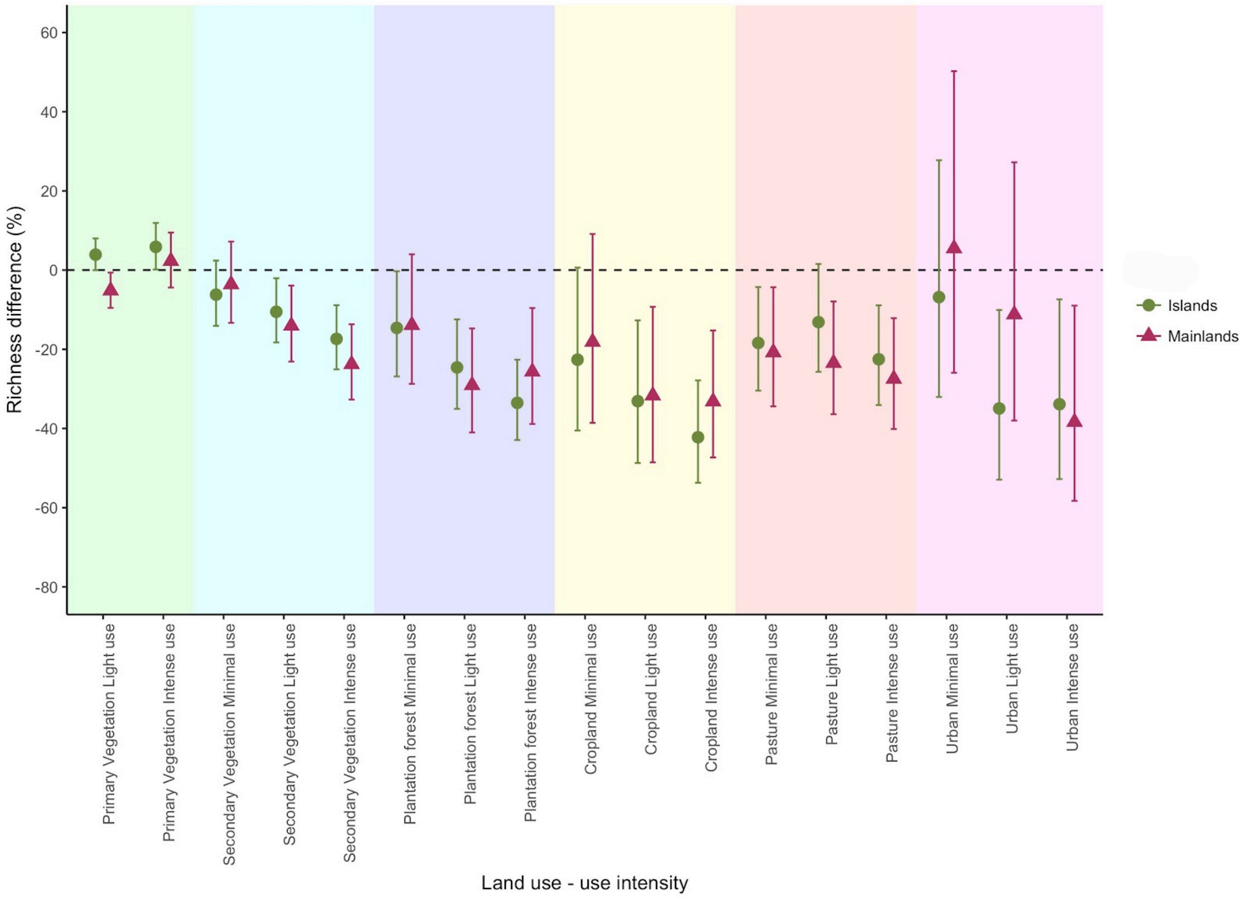


Figure C.6. Response of species richness to land use/use intensity on islands and mainlands. Values indicate decrease or increase in percentage of species richness using minimally-used primary vegetation as baseline (dashed line). Bars indicate 95% confidence intervals.

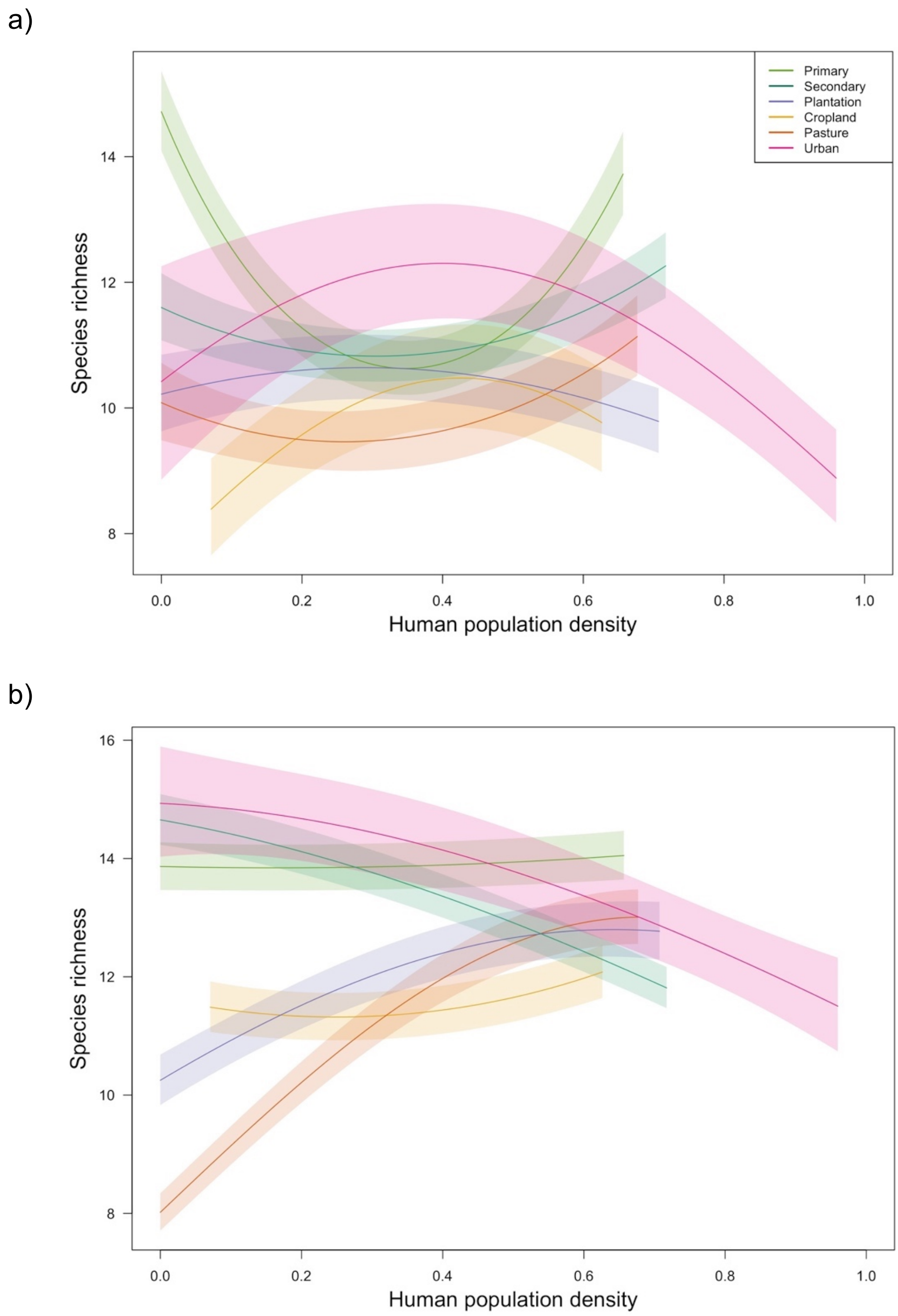


Figure C.7. Response of species richness to human population density across land uses on a) islands and b) mainlands. Values of human population density are shown on a rescaled axis (as fitted in the models).

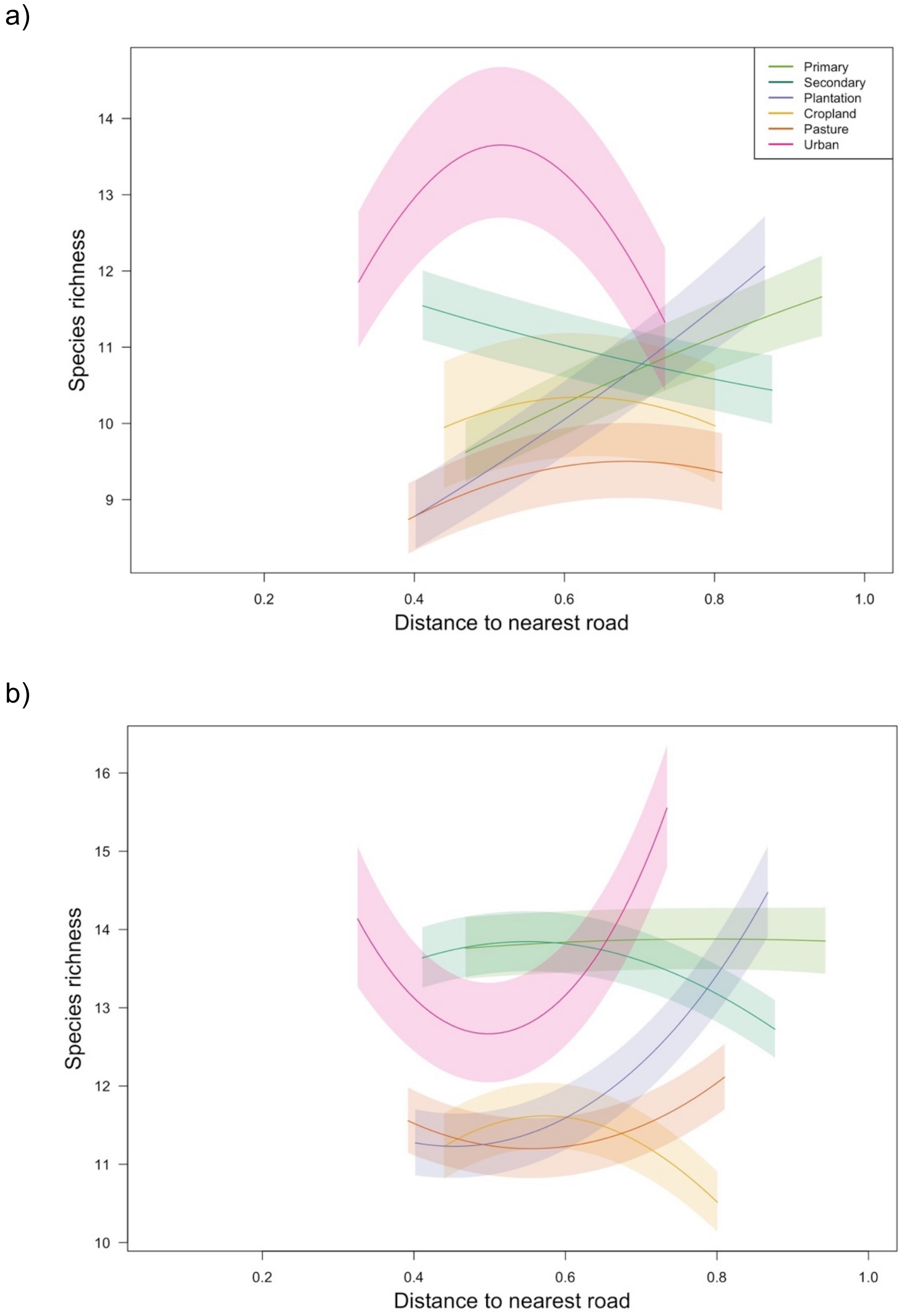


Figure C.8. Response of species richness to distance to the nearest road across land uses on a) islands and b) mainlands. Values of distance to the nearest road are shown on a rescaled axis (as fitted in the models).

Table C.8. Compositional similarity between minimally-disturbed primary vegetation (PriMin) and other land uses on islands and mainlands. The estimates (from abundance- and richness-based models in Chapter 2) are expressed relative to compositional similarity between adjacent sites in PriMin with identical environments. For islands, PriMin-Urban compositional similarity inside brackets corresponds to the estimates that were calculated indirectly (product of estimated PriMin-Secondary and Secondary-Urban compositional similarities – see Chapter 2– that in this case is expressed relative to PriMin-PriMin).

	Abundance-based model		Richness-based model	
	Islands	Mainlands	Islands	Mainlands
PriMin- PriMin	1	1	1	1
PriMin- Primary	0.898	0.917	0.866	0.871
PriMin- Secondary	0.939	0.969	0.963	0.931
PriMin- Plantation	0.823	0.696	0.780	0.590
PriMin- Cropland	0.679	0.734	0.647	0.659
PriMin- Pasture	0.648	0.587	0.658	0.500
PriMin- Urban	0.93 (0.647)	0.635	0.86 (0.486)	0.576

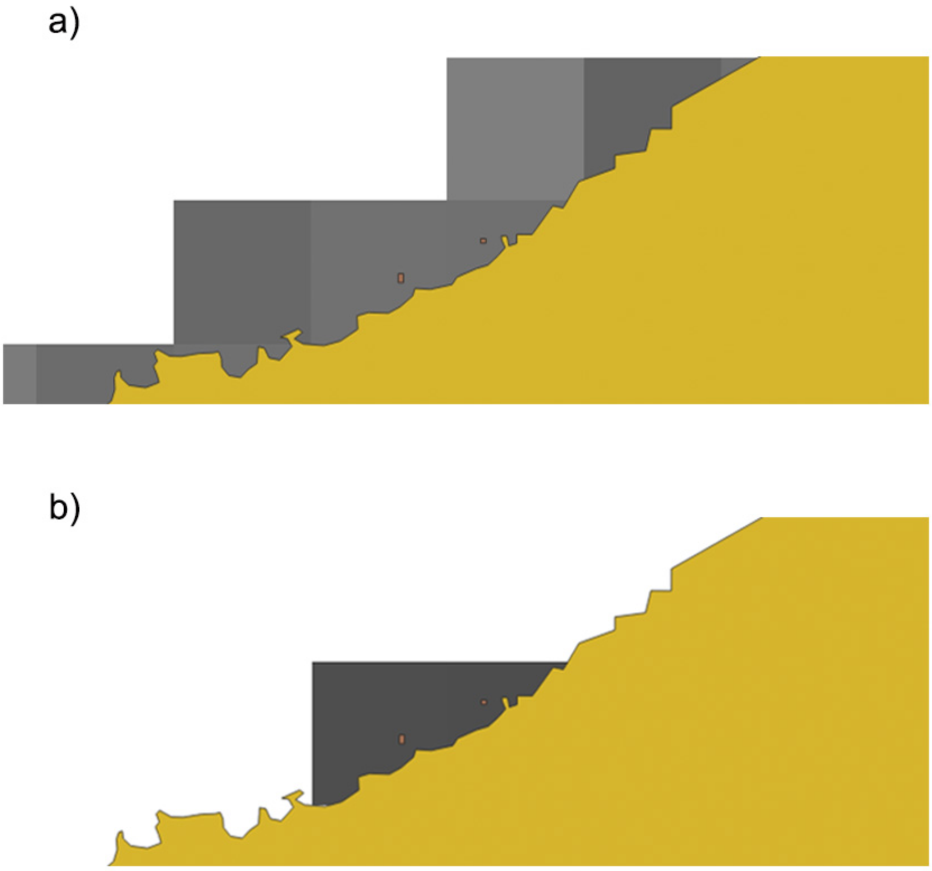


Figure C.9. Example of shared cells between islands and mainlands in the final BII maps. Two small islands (<1km^2) are located close to the mainland coast. The yellow polygons correspond to the mainland shapefile and the small islands are shown in orange. Grey cells show the final BII maps for a) mainlands and b) islands; in this case, two cells of the BII maps are shared between islands and mainlands, since they intersect with both island and mainland shapefiles.

Table C.9. Average BII (abundance-based and richness-based) for terrestrial biomes of islands and mainlands. s.d. are shown within parenthesis. BII values are shown in a 0 to 1 scale (1= 100% intactness).

Biome	Abundance-based BII		Richness-based BII	
	Islands	Mainlands	Islands	Mainlands
Temperate Grasslands, Savannas and Shrublands	0.62 (0.12)	0.49 (0.13)	0.52 (0.10)	0.48 (0.12)
Mediterranean Forests, Woodlands and Scrub	0.59 (0.11)	0.61 (0.12)	0.51 (0.09)	0.57 (0.12)
Montane Grasslands and Shrublands	0.65 (0.08)	0.60 (0.16)	0.55 (0.10)	0.58 (0.15)
Tropical and Subtropical Grasslands, Savannas and Shrublands	0.70 (0.05)	0.67 (0.13)	0.59 (0.05)	0.62 (0.12)
Flooded Grasslands and Savannas	0.63 (0.08)	0.65 (0.16)	0.55 (0.10)	0.61 (0.15)
Temperate Broadleaf and Mixed Forests	0.59 (0.13)	0.69 (0.13)	0.52 (0.12)	0.66 (0.13)
Tropical and Subtropical Dry Broadleaf Forests	0.59 (0.07)	0.69 (0.11)	0.49 (0.07)	0.67 (0.10)
Deserts and Xeric Shrublands	0.70 (0.05)	0.73 (0.21)	0.56 (0.04)	0.71 (0.18)
Tropical and Subtropical Coniferous Forests	0.62 (0.07)	0.71 (0.12)	0.52 (0.07)	0.68 (0.13)
Mangroves	0.71 (0.09)	0.74 (0.13)	0.62 (0.11)	0.70 (0.11)
Temperate Conifer Forests	0.71 (0.11)	0.76 (0.14)	0.67 (0.14)	0.75 (0.15)
Tropical and Subtropical Moist Broadleaf Forests	0.69 (0.09)	0.83 (0.15)	0.60 (0.11)	0.79 (0.15)
Boreal Forests/Taiga	0.77 (0.09)	0.90 (0.06)	0.75 (0.11)	0.92 (0.07)
Tundra	0.96 (0.03)	0.92 (0.05)	0.97 (0.04)	0.97 (0.03)

Table C.10. Average BII (abundance-based and richness-based) for biodiversity hotspots of islands and mainlands. s.d. are shown within parenthesis. BII values are shown in a 0 to 1 scale (1= 100% intactness).

Hotspot	Abundance-based BII		Richness-based BII	
	Islands	Mainlands	Islands	Mainlands
Atlantic Forest	0.68 (0.06)	0.67 (0.11)	0.57 (0.06)	0.61 (0.11)
California Floristic Province	0.75 (0.1)	0.69 (0.17)	0.65 (0.12)	0.68 (0.18)
Cape Floristic Region	--	0.45 (0.12)	--	0.44 (0.1)
Caribbean Islands	0.58 (0.06)	--	0.49 (0.07)	--
Caucasus	0.69 (0.06)	0.64 (0.12)	0.57 (0.04)	0.6 (0.11)
Cerrado	--	0.62 (0.12)	--	0.59 (0.11)
Chilean Winter Rainfall and Valdivian Forests	0.77 (0.05)	0.78 (0.12)	0.65 (0.05)	0.76 (0.12)
Coastal Forests of Eastern Africa	0.56 (0.08)	0.72 (0.09)	0.49 (0.05)	0.65 (0.08)
East Melanesian Islands	0.74 (0.04)	--	0.66 (0.3)	--
Eastern Afromontane	--	0.75 (0.1)	--	0.68 (0.1)
Guinean Forests of West Africa	0.66 (0.04)	0.74 (0.1)	0.57 (0.03)	0.68 (0.1)
Himalaya	--	0.68 (0.16)	--	0.65 (0.14)
Horn of Africa	0.6 (0.07)	0.66 (0.1)	0.49 (0.06)	0.61 (0.1)
Indo-Burma	0.64 (0.09)	0.79 (0.13)	0.52 (0.08)	0.77 (0.12)
Irano-Anatolian	--	0.66 (0.09)	--	0.6 (0.09)
Japan	0.64 (0.09)	--	0.55 (0.08)	--
Madagascar and the Indian Ocean Islands	0.58 (0.06)	--	0.49 (0.05)	--
Madrean Pine-Oak Woodlands	--	0.7 (0.13)	--	0.67 (0.14)
Maputaland-Pondoland-Albany	0.63 (0.06)	0.59 (0.15)	0.5 (0.06)	0.56 (0.12)
Mediterranean Basin	0.55 (0.08)	0.61 (0.11)	0.47 (0.07)	0.57 (0.11)
Mesoamerica	0.68 (0.06)	0.75 (0.1)	0.57 (0.06)	0.7 (0.12)
Mountains of Central Asia	--	0.61 (0.12)	--	0.56 (0.12)
Mountains of Southwest China	--	0.66 (0.13)	--	0.61 (0.13)
New Caledonia	0.7 (0.04)	--	0.68 (0.07)	--
New Zealand	0.58 (0.1)	--	0.5 (0.1)	--
Philippines	0.62 (0.07)	--	0.5 (0.06)	--
Polynesia-Micronesia	0.64 (0.09)	--	0.54 (0.1)	--

Southwest Australia	0.6 (0.1)	--	0.52 (0.07)	--
Succulent Karoo	0.67 (0.03)	0.4 (0.14)	0.57 (0.05)	0.43 (0.13)
Sundaland	0.68 (0.09)	0.8 (0.11)	0.59 (0.11)	0.78 (0.1)
Tropical Andes	0.72 (0.01)	0.77 (0.1)	0.58 (0.01)	0.74 (0.12)
Tumbes-Choco-Magdalena	0.8 (0.09)	0.76 (0.1)	0.75 (0.12)	0.71 (0.1)
Wallacea	0.69 (0.06)	--	0.59 (0.08)	--
Western Ghats and Sri Lanka	0.66 (0.07)	0.75 (0.13)	0.54 (0.06)	0.72 (0.09)

Table C.11. Percentage of land surface under each land use /use intensity category (LUI) in the island (including and excluding Australia) and mainland BII maps.

LUI	Percentage on islands	Percentage on mainlands	Percentage on islands excluding Australia
Primary Vegetation Minimal use	38.45	28.48	45.21
Primary Vegetation Light use	8.35	8.79	14.40
Primary Vegetation Intense use	1.03	0.94	2.07
Secondary Vegetation Minimal use	7.40	16.75	8.21
Secondary Vegetation Light use	2.29	6.15	3.84
Secondary Vegetation Intense use	0.61	1.52	1.22
Cropland Minimal use	1.14	2.65	1.91
Cropland Light use	2.99	4.24	4.19
Cropland Intense use	4.85	5.40	5.67
Pasture Minimal use	0.29	0.11	0.25
Pasture Light use	29.74	21.61	9.62
Pasture Intense use	2.35	2.96	2.59
Urban Minimal use	0.32	0.23	0.54
Urban Light use	0.01	0.0007	0.01
Urban Intense use	0.16	0.16	0.29

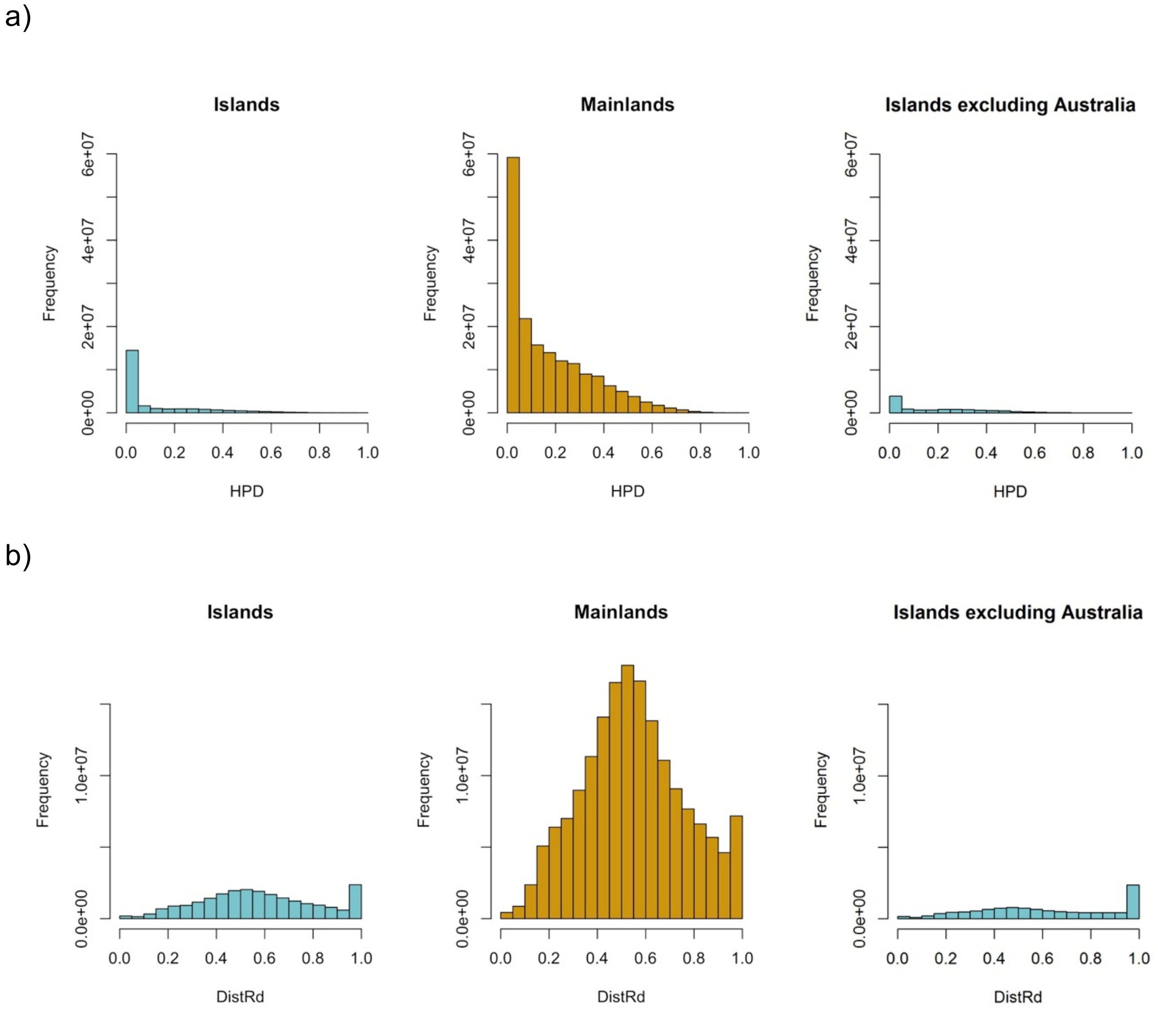


Figure C.10. Data distribution for a) human population density (HPD) and b) distance to the nearest road (DistRd) in island (including and excluding Australia) and mainland BII maps. Frequency indicates number of cells in the maps. HPD and DistRd are shown on rescaled axes (as fitted in the models); the 0 to 1 scales are the same for island and mainland datasets. The high frequency of cells with a high value for distance to road might evidence the lack of data in gROADSv1 maps for some regions, especially for islands.

Table C.12. Percentage of land surface with different values of human population density (HPD) and distance to the nearest road (DistRd) in the island (including and excluding Australia) and mainland BII maps. Three classes with different range of values were established for HPD and DistRd: Low (0 - 0.3), Medium (0.3 - 0.6) and High (0.6 - 1). Note that the ‘High’ category means a higher pressure intensity for HPD but a lower pressure for DistRd.

Human population density			
	Percentage on islands	Percentage on mainlands	Percentage on islands excluding Australia
Low	84.30	77.48	69.10
Medium	13.47	20.19	26.51
High	2.24	2.33	4.39
Distance to the nearest road			
Low	13.42	12.80	15.41
Medium	43.49	49.23	35.81
High	43.09	37.98	48.78

APPENDIX D

Supplement for Chapter 4

Table D.1. External sources that were used to determine the status of species in the PREDICTS database at either island or country level.

Source acronym	Citation/Description	Access to data	Species status in
AGDAWR	Australian Government Department of Agriculture and Water Resources.	Search for specific species at: http://www.agriculture.gov.au/ [Accessed March 2017]	Country
ALA	Atlas of Living Australia.	Search for specific species at: https://www.ala.org.au/ [Accessed March 2017]	Country
AntMaps	Janicki, J., Narula, N., Ziegler, M., Guénard, B. Economo, E.P. (2016). Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: The design andimplementation of antmaps.org. Ecological Informatics 32: 185-193.	Search for specific species at: http://antmaps.org/ [Accessed March 2017]	Country
AntWeb	AntWeb v8.0.5.	Search for specific species at: https://www.antweb.org [Accessed May 2017]	Country
BirdLife	BirdLife Australia.	Downloaded from: http://birdlife.org.au/conservation/science/taxonomy [Accessed April 2015]	Country
	BirdLife International.	Downloaded from: http://datazone.birdlife.org/species/search [Accessed March 2017] (Search for endemic species in countries included in PREDICTS database)	Country
C.Vink, Canterbury Museum, NZ	Taxonomic expert at Canterbury Museum, New Zealand	Direct contact with taxonomic expert to classify species from the order Araneae in New Zealand	Country
CITES	UNEP (2017). The Species + Website. Nairobi, Kenya. Compiled by UNEP-WCMC, Cambridge, UK.	Downloaded from: https://www.speciesplus.net/species [Accessed March 2017]	Country
CMS	UNEP (2017). The Species + Website. Nairobi, Kenya. Compiled by UNEP-WCMC, Cambridge, UK.	Downloaded from: https://www.speciesplus.net/species [Accessed March 2017]	Country
DLO	Discover Life.	Search for specific species at: http://discoverlife.org [Accessed March 2017]	Country
FEO	Flora Europaea. Euro+Med (2006). Euro+Med PlantBase - the information resource for Euro-Mediterranean plant diversity. Published on the Internet.	Data accessed through R package 'originr' function 'is_native') [Accessed March 2019]	Country
GAVIA	Dyer, E. E., Redding, D. W., & Blackburn, T. M. (2017). The global avian invasions atlas, a database of alien bird distributions worldwide. *Scientific data*, *4*, 170041.	Downloaded from: https://figshare.com/articles/Data_from_The_Global_Avian_Invasions_Atlas_-_A_database_of_alien_bird_distributions_worldwide/4234850 [Accessed May 2017]	Country

GIFT	Weigelt, P., König, C. & Kreft, H. (2017) The Global Inventory of Floras and Traits (GIFT) database. Available at: http://gift.uni-goettingen.de	Data provided by the GIFT team (July, 2017)	Island
GISD	IUCN Invasive Species Specialist Group (ISSG) (2015). The Global Invasive Species Database. Version 2015.1. (http://www.iucngisd.org/gisd)	Data accessed through R package 'originr' function 'gisd') [Accessed March 2019]	Country
GloNAF	van Kleunen, M., Pyšek, P., Dawson, W., Essl, F., Kreft, H., Pergl, J., ... & Lenzner, B. (2019). The Global Naturalized Alien Flora (GloNAF) database. *Ecology*, *100*(1), e02542.	Data provided by the GloNAF team (July 2017)	Island
GloNAF-country	van Kleunen, M., Pyšek, P., Dawson, W., Essl, F., Kreft, H., Pergl, J., ... & Lenzner, B. (2019). The Global Naturalized Alien Flora (GloNAF) database. *Ecology*, *100*(1), e02542.	Data provided by the GloNAF team (September 2015)	Country
GRIIS	Pagad, S., Genovesi, P., Carnevali, L., Schigel, D., & McGeoch, M. A. (2018). Introducing the global register of introduced and invasive species. Scientific data, 5, 170202.	Downloaded from: http://www.griis.org/ [Accessed May 2017] (Selected terms: "terrestrial", "freshwater", "verified record")	Country
IUCN	The IUCN Red List of Threatened Species. Version 2017-1.	Data accessed through R package 'rredlist' function 'rl_occ_country' [Accessed March 2019]	Country
Knight (1974)	Knight, W. J. (1974). Leaf hoppers of New Zealand: Subfamilies Aphrodinae, Jassinae, Xestocephalinae, Idiocerinae, and Macropsinae (Homoptera: Cicadellidae). *New Zealand journal of zoology*, *1*(4), 475-493.	Data taken from publication	Country
LCR-NZ	Landcare Research New Zealand.	Search for specific species at: https://www.landcareresearch.co.nz/science/plants-animals-fungi [Accessed May 2017]	Country
N.Wyatt, NHM, UK	Taxonomic expert at the Natural History Museum, United Kingdom.	Direct contact with taxonomic expert to classify species from the order Diptera in different countries	Country
NZTCS	New Zealand Threat Classification System.	Search for specific species at: https://nztcs.org.nz/ [Accessed March 2017]	Country
OSF	Orthoptera Species File.	Search for specific species at: http://orthoptera.speciesfile.org/HomePage/Orthoptera/HomePage.aspx [Accessed May 2017]	Country
TEARA	Te Ara: The encyclopedia of New Zealand.	Search for specific species at: https://teara.govt.nz/en [Accessed March 2017]	Country
TIBD-IAS	Threatened Island Biodiversity Database Partners. (2017). The Threatened Island Biodiversity Database: developed by Island Conservation, University of California Santa Cruz Coastal Conservation Action Lab, BirdLife International and IUCN Invasive Species Specialist Group. Version 2017.	Data provided by the TIB team (May 2017) (Invasive species on islands)	Island

TIBD-TSpI	Threatened Island Biodiversity Database Partners. (2017). The Threatened Island Biodiversity Database: developed by Island Conservation, University of California Santa Cruz Coastal Conservation Action Lab, BirdLife International and IUCN Invasive Species Specialist Group. Version 2017.	Data provided by the TIB team (May 2017) (Threatened species on islands)	Island
WCSP	World Checklist of Selected Plant Families.	Search for specific species at: http://wcsp.science.kew.org [Accessed March 2017]	Country
WPB	Checklist of the Western Palaearctic Bees (Hymenoptera: Apoidea: Anthophila).	Search for specific species at: http://westpalbees.myspecies.info. [Accessed March 2017]	Country

Table D.2. Number of alien and native species (by major taxonomic group) included in the island data in the PREDICTS database.

Taxon	Native species	Alien species
Vertebrates	1248	112
Amphibia	107	2
Aves	794	84
Mammalia	183	22
Reptilia	164	4
Invertebrates	2125	384
Annelida	13	1
Arachnida	63	51
Archaeognatha	3	0
Blattodea	2	0
Chilopoda	12	2
Coleoptera	1315	185
Collembola	1	0
Dermaptera	1	2
Diplopoda	5	13
Diptera	190	26
Hemiptera	54	23
Hymenoptera	232	26
Lepidoptera	73	33
Malacostraca	5	0
Mollusca	45	9
Neuroptera	3	0
Odonata	61	0
Onychophora	2	0
Orthoptera	30	5
Pauropoda	1	0
Psocodea	8	5
Thysanoptera	4	3
Trichoptera	2	0
Plants	2149	303
Bryophyta	5	0
Equisetopsida	4	0

Gnetopsida	11	0
Liliopsida	551	86
Lycopodiopsida	5	0
Magnoliopsida	1450	210
Pinopsida	18	5
Polypodiopsida	99	1
Psilotopsida	6	1

Table D.3. Number of biodiversity records per species status for island data in the PREDICTS database.

Status	Number of records
Alien	89472
Native	607586
Not classified	642281

Table D.4. Number of biodiversity records that were classified by external sources or data sources in the PREDICTS database. The table shows the number of records classified by each external source (first row shows the total records classified by all external sources), but only the total records classified by all PREDICTS data sources (bottom row). Full names of the external sources are provided in Table D.1. If a source in Table D.1 is not listed, there were no matches for the species-country combinations in that data source or matching combinations were classified first by other sources.

Source	Records
All external sources	281981
AGDAWR	52
ALA	20
AntMaps	281
AntWeb	1934
BirdLife	33704
C.Vink, Canterbury Museum, NZ	1830
CITES	10399
CMS	735
DLO/NZH	86
GAVIA	3833
GIFT	122833
GISD	13612
GloNAF	11508
GloNAF-Nature	1165
GRIIS	16497
IUCN	58467
Knight (1974)	20
LCR-NZ	360
N.Wyatt, NHM, UK	2326
NZTCS	236
OSF	754
TEARA	360

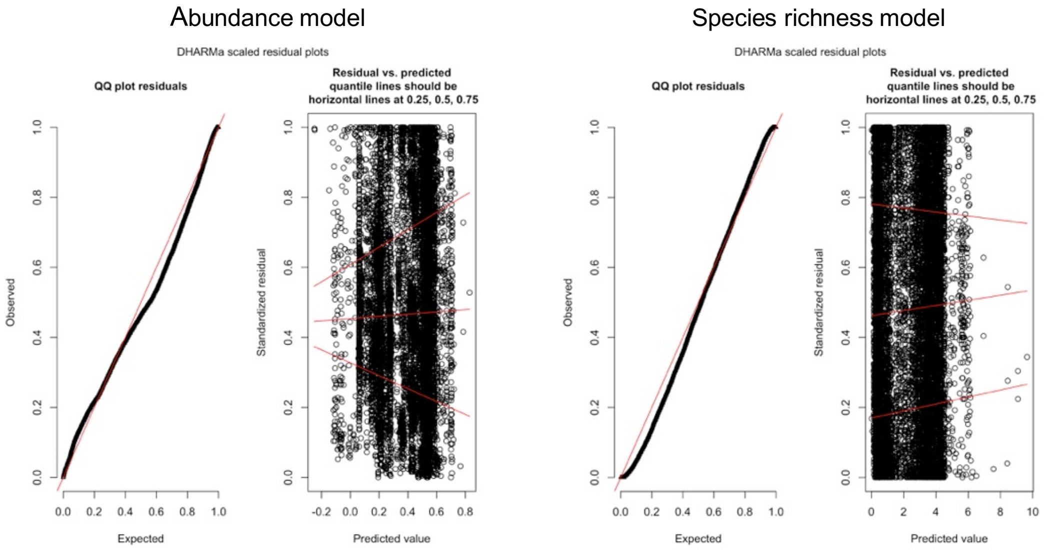
TIBD-IAS	440
TIBD-TSpl	379
WCSP	10
WPB	140
PREDICTS data sources	415077

Table D.5. Final datasets for the abundance and richness models for alien and native species. The table shows the number of sites and (in parentheses) studies including alien and native data across land use/use intensity categories (LUI).

LUI	Abundance dataset		Richness dataset	
	Alien	Native	Alien	Native
Primary Vegetation Minimal use	772 (43)	833 (64)	1077 (52)	1171 (75)
Primary Vegetation	398 (18)	486 (32)	464 (22)	553 (37)
Secondary Vegetation	1065 (51)	1564 (91)	1239 (58)	1797 (102)
Plantation forest	596 (22)	669 (39)	719 (30)	792 (47)
Cropland	188 (14)	328 (30)	197 (16)	338 (33)
Pasture	724 (26)	1893 (44)	912 (28)	2090 (47)
Urban	137 (8)	473 (13)	155 (9)	491 (14)

Table D.6. Akaike's information criterion (AIC) values for the initial models of total abundance and richness of aliens and natives using the two different random-effects structures that were tested. ΔAIC values are shown relative to the best model. SS= study, SSB= block within study.

Random-effects structure	d.f.	AIC	ΔAIC
Abundance model			
(1+LandUse|SS)+(1|SSB)	100	-3193.219	--
(1|SS)+(1|SSB)	73	-3025.870	167.349
Richness model			
(1+LandUse|SS)+(1|SSB)	99	47739.72	--
(1|SS)+(1|SSB)	72	48949.59	1209.87



Abundance model

Species richness model

Figure D.1. Diagnostic plots for the minimum adequate models of total abundance and species richness of alien and native species.

Table D.7. ANOVA table for the minimum adequate model of total abundance of alien and native species. LUI= land use/use intensity, HPD= human population density, DistRd= distance to the nearest road. Stars indicate the level of significance (Sig): <0.05*, <0.01** and <0.001***

Term	χ^2	d.f.	Sig
LUI	13.868	6	*
Alien/Native	4914.875	1	***
HPD	4.222	2	
DistRd	0.250	2	
LUI × Alien/Native	355.756	6	***
HPD × Alien/Native	28.354	2	***
LUI × HPD	24.401	12	*
DistRd × Alien/Native	42.792	2	***
LUI × DistRd	31.945	12	**
LUI × HPD × Alien/Native	306.764	12	***

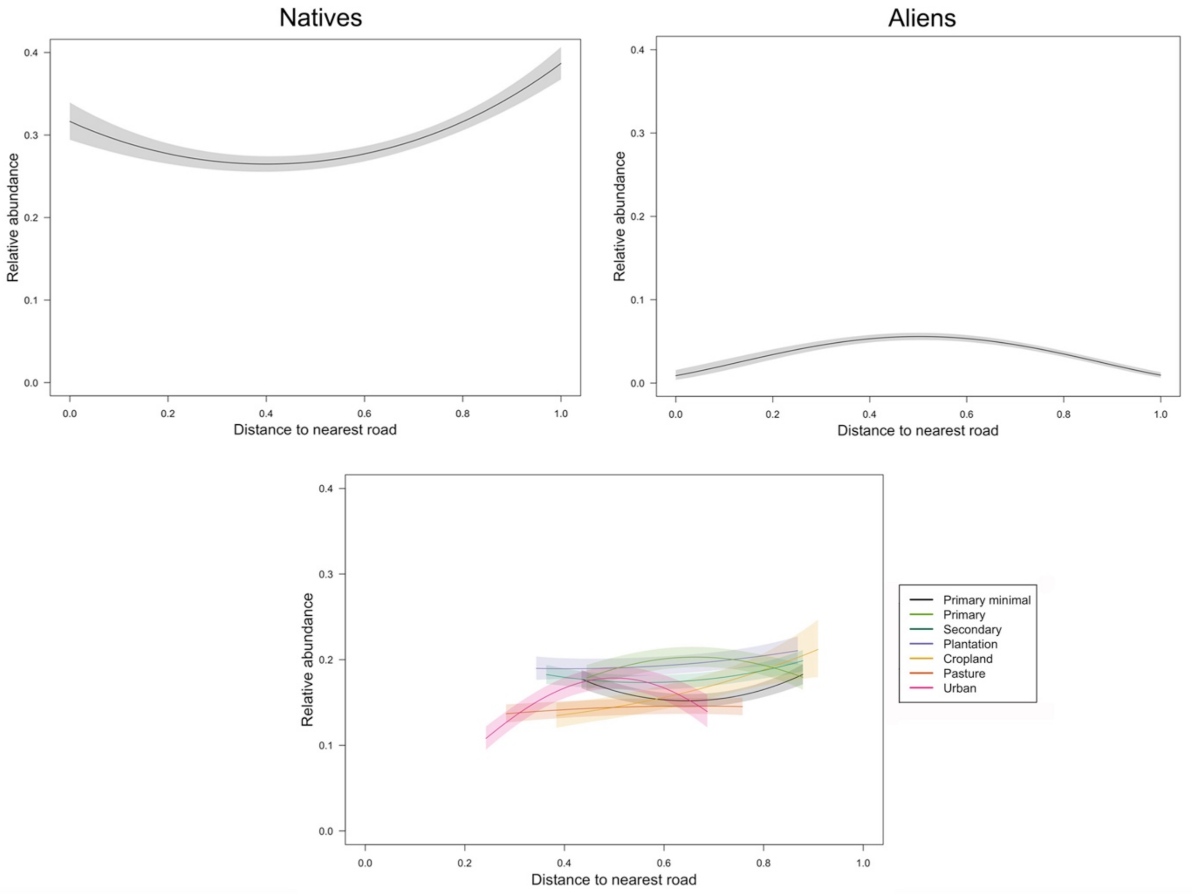


Figure D.2. Response of total abundance of aliens and natives to distance to the nearest road. The figure at the bottom shows the overall effect of distance to road on total abundance across land uses (the effects of this interaction did not differ for alien and native species –i.e., three-way interaction was dropped from the model (Table D.7)). For clarity, the error bars show half the standard error. The values of distance to road are shown on a rescaled axis (as fitted in the models). Abundance is shown on a zero-to-one scale (as fitted in the models; i.e., abundance rescaled within studies).

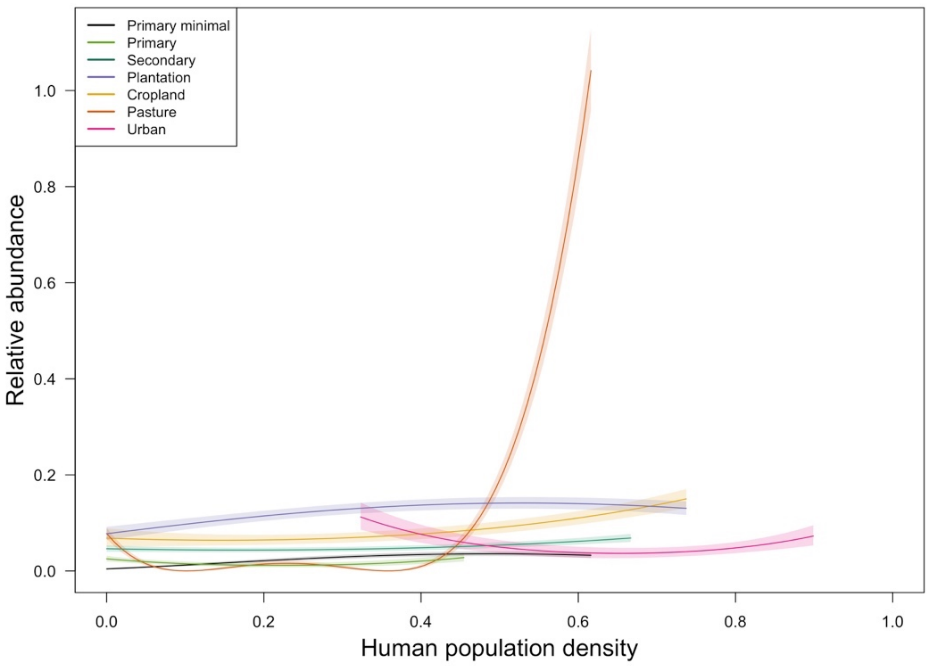


Figure D.3. Response of total abundance of aliens to human population density (HPD). The x limits of each coloured line indicate the 2.5th and 97.5th percentiles for the values of HPD represented in each land use in the model dataset. For clarity, the error bars show half the standard error. HPD values are shown on a rescaled axis (as fitted in the models). Abundance is shown on a zero-to-one scale (as fitted in the models; i.e., abundance rescaled within studies).

Table D.8. ANOVA table for the minimum adequate model of richness of alien and native species. LUI= land use/use intensity, HPD= human population density, DistRd= distance to the nearest road. Stars indicate the level of significance (Sig): <0.05*, <0.01** and <0.001***

Term	χ^2	d.f.	Sig
LUI	230.962	6	***
Alien/Native	17615.899	1	***
HPD	29.366	2	***
DistRd	1.260	2	
LUI × Alien/Native	1117.428	6	***
HPD × Alien/Native	1249.040	2	***
LUI × HPD	146.637	12	***
DistRd × Alien/Native	213.849	2	***
LUI × DistRd	106.856	12	***
LUI × HPD × Alien/Native	868.620	12	***
LUI × DistRd × Alien/Native	176.951	12	***

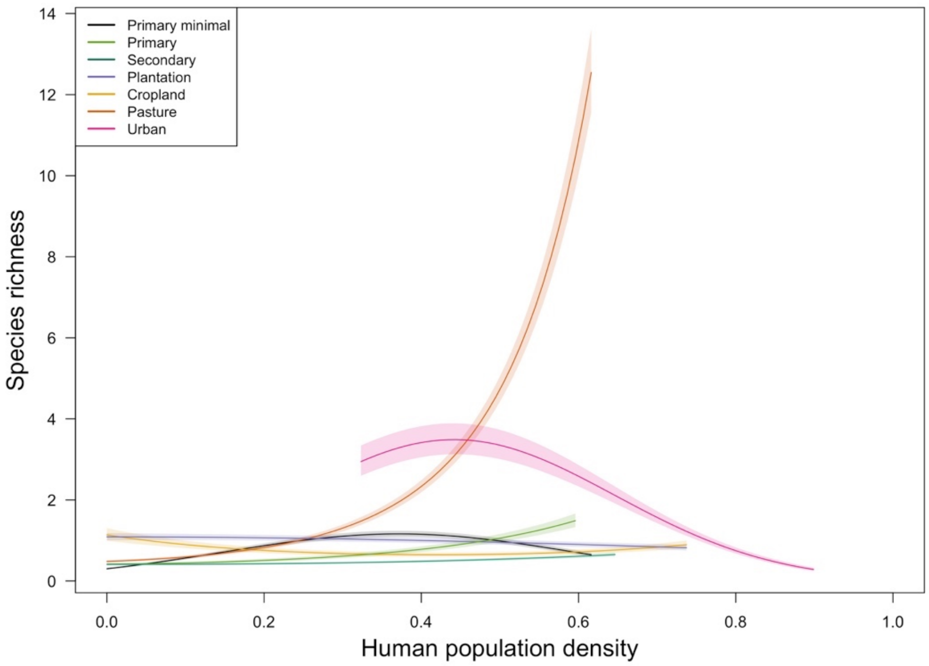


Figure D.4. Response of species richness of aliens to human population density. Values of human population density are shown on a rescaled axis (as fitted in the models).

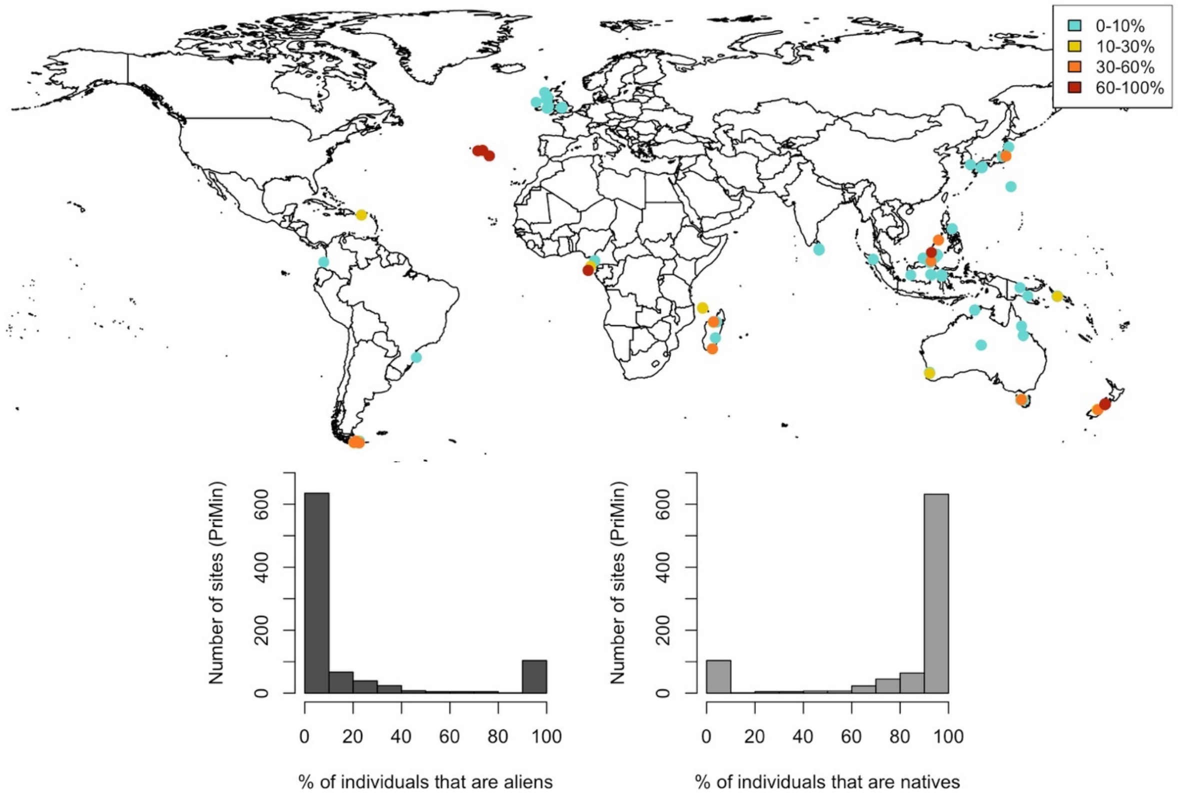


Figure D.5. Percentage of individuals that are aliens in sites in minimally-disturbed primary vegetation. Percentages were calculated using exclusively data for alien and native species; species that could not be classified were excluded from these calculations. Only sites that were included in the abundance model are shown. Sites with higher percentages were the last to be plotted, so that they would be highlighted. Histograms show the percentage of individuals that are aliens and natives across sites in minimally-disturbed primary vegetation.

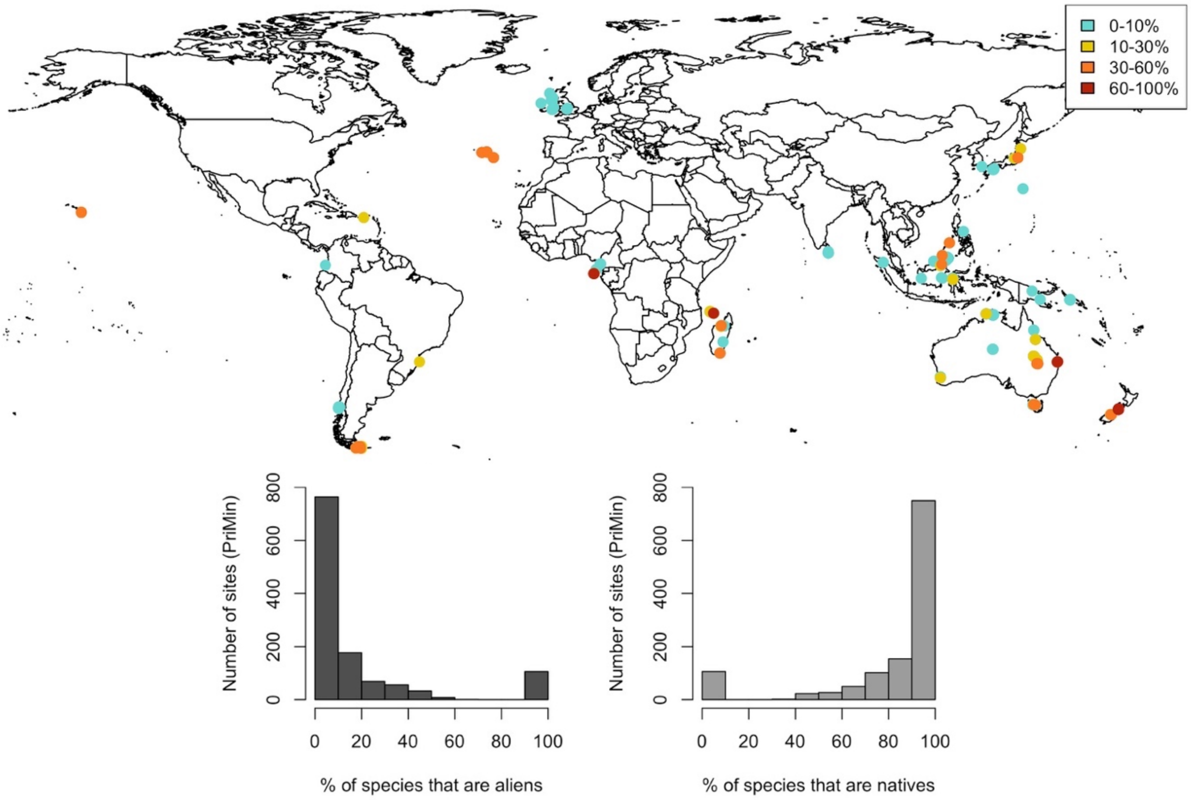


Figure D.6. Percentage of species that are aliens in sites in minimally-disturbed primary vegetation. Percentages were calculated using exclusively data for alien and native species; species that could not be classified were excluded from these calculations. Only sites that were included in the richness model are shown. Histograms show the percentage of species that are aliens and natives across sites in minimally-disturbed primary vegetation.

Table D.9. Islands included in the models for abundance and richness of aliens using island traits as explanatory variables. Islands marked with a star were included in the abundance and richness models, the rest were only included in richness models. The four islands with missing data for surrounding landmass (i.e., no data in Weigelt et al., 2013) were not included in the models including this variable. The country listed for each island corresponds to where sites (with data for aliens) in the PREDICTS database are located; i.e., only sites in Borneo were located in two different countries.

Island	Country	Island area (km^2)	Surrounding landmass (summed proportions)	Country per capita GDP (current US dollars – year 2005)	Calculated island GDP per capita
Anijima *	Japan	7.879	NA	37217.649	0.805
Anjouan	Comoros	426.580	0.706	1068.600	244.945
Australia *	Australia	7588924.738	NA	33961.682	33961.682
Balambangan	Malaysia	103.175	0.704	5593.823	1.757
Banggi	Malaysia	431.372	0.723	5593.823	7.344
Bintan	Indonesia	1169.873	0.806	1260.929	0.814
Borneo *	Malaysia	732289.104	0.501	5593.823	509.704
Borneo *	Indonesia	732289.104	0.501	1260.929	509.704
Chichijima *	Japan	23.757	NA	37217.649	2.426
Faial *	Portugal	172.857	0.46	18784.949	35.499
Flores *	Portugal	140.943	0.438	18784.949	28.945
Grande Comoro *	Comoros	1015.564	0.736	1068.600	583.145
Great Britain *	United Kingdom	218670.015	0.858	41732.641	37720.320
Hainan *	China	34023.685	0.946	1753.418	6.355
Hawai'i	United States	10431.594	0.245	44307.921	50.448
Honshu *	Japan	227947.264	0.573	37217.649	23274.791
Ilha das Rosas *	Brazil	3.066	1.644	4770.184	0.002
Ireland *	Ireland	83531.769	0.692	50878.640	61692.303
Kolombangara *	Solomon Islands	693.585	0.384	880.875	21.828
Madagascar *	Madagascar	587926.700	0.46	274.820	274.820
Mallawalli	Malaysia	38.321	0.785	5593.823	0.652
New Guinea *	Papua New Guinea	777319.960	0.38	770.565	1322.650
Nishi-jima *	Japan	0.484	NA	37217.649	0.049
North Island *	New Zealand	113707.769	0.171	27750.725	11983.871
Osel	Estonia	2891.685	1.548	10338.313	705.241
Palawan *	Philippines	11448.371	0.494	1194.697	45.871
Principe *	Sao Tome and Principe	138.754	0.86	804.128	116.225
Puerto Rico *	Puerto Rico	8703.443	0.381	21959.323	21959.323
Pulau Mangalum	Malaysia	5.165	0.739	5593.823	0.088
Pulau Mantanai Besar	Malaysia	2.118	0.857	5593.823	0.036
Santa Catharina *	Brazil	422.290	1.203	4770.184	0.241
Santa Maria *	Portugal	96.926	0.459	18784.949	19.905
Sao Tome *	Sao Tome and Principe	849.266	0.753	804.128	711.374

South Island *	New Zealand	150437.674	0.163	27750.725	15854.903
Sri Lanka *	Sri Lanka	65724.996	0.569	1250.005	1250.005
Sulawesi*	Indonesia	168821.235	0.51	1260.929	117.507
Tasmania *	Australia	63584.062	0.346	33961.682	281.091
Terceira *	Portugal	400.714	0.46	18784.949	82.294
Tierra del Fuego *	Argentina	47419.119	0.59	5076.884	485.670
Wight *	United Kingdom	381.948	1.394	41732.641	65.886

Table D.10. AIC values for models of total abundance of aliens (including island traits) using the two different random-effects structures that were tested. ∆AIC values are shown relative to the best model. SS= study.

Random-effects structure	d.f.	AIC	∆AIC
Model including area			
(1|SS) + (1|Island)	17	-81.232	--
(1|SS)	16	-76.872	4.360
Model including surrounding landmass			
(1|SS) + (1|Island)	17	-341.808	--
(1|SS)	16	-341.005	0.8029
Model including country GDP per capita			
(1|SS) + (1|Island)	17	-177.543	--
(1|SS)	16	-174.4930	3.050
Model including island GDP per capita			
(1|SS) + (1|Island)	17	-183.346	--
(1|SS)	16	-181.993	1.353

Table D.11. ANOVA tables for models of total abundance of aliens including island traits as explanatory variables. LUI= land use/use intensity. Stars indicate the level of significance (Sig): <0.05*, <0.01** and <0.001***

Term	χ^2	d.f.	Sig
Model including area			
LUI	126.799	6	***
Area	0.004	1	
LUI × Area	56.117	6	***
Model including surrounding landmass			
LUI	138.127	6	***
Landmass	0.005	1	
LUI × Landmass	73.056	6	***
Model including country GDP per capita			
LUI	126.937	6	***
Country GDP	0.013	1	
LUI × Country GDP	65.277	6	***
Model including island GDP per capita			
LUI	127.386	6	***
Island GDP	0.277	1	
LUI × Island GDP	79.678	6	***

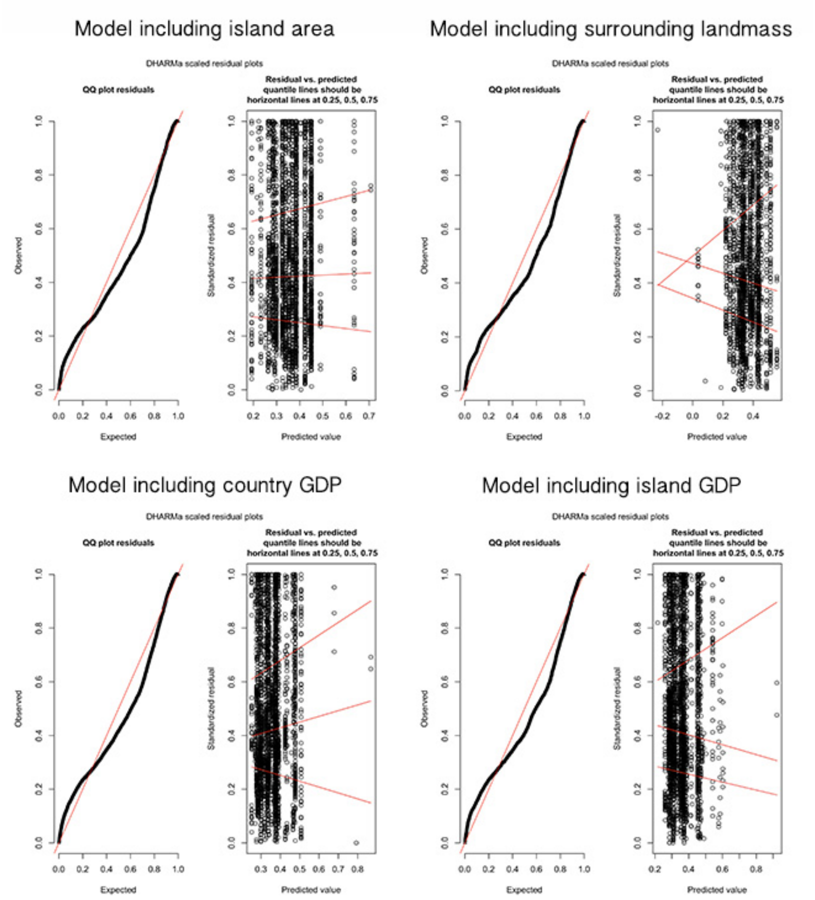


Figure D.7. Diagnostic plots for the four models of total abundance of aliens including the different island traits as explanatory variables.

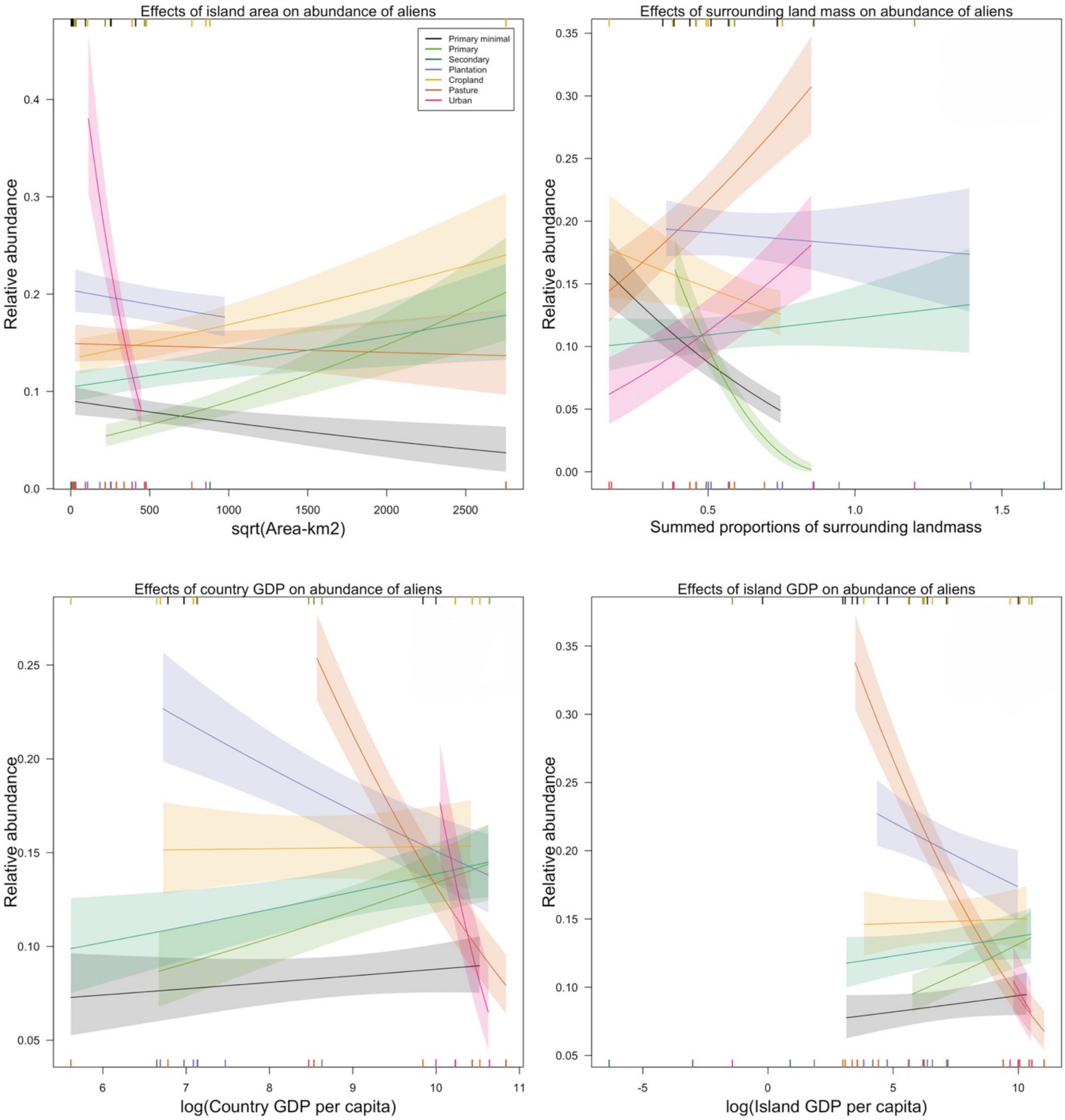


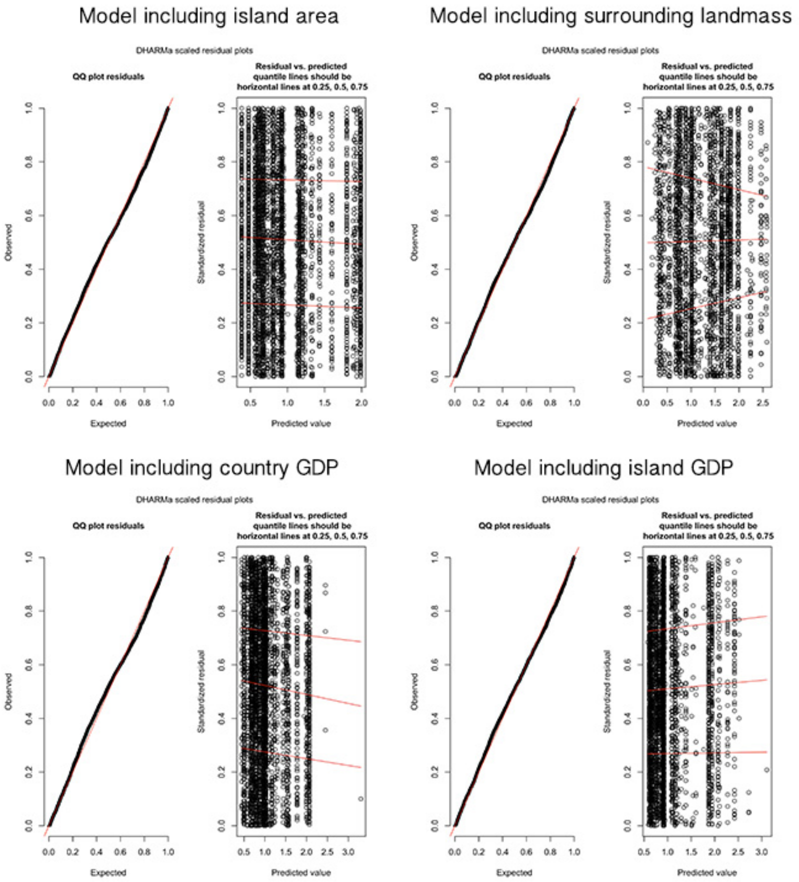
Figure D.8. Effects of island area, surrounding landmass, country-level and island-level GDP per capita on total abundance of aliens. For clarity, the error bars show half the standard error. Rugs along the horizontal margins show values of the explanatory variables represented (across land uses) in the model data set (rugs for minimally-used primary vegetation, primary vegetation and croplands along the top margin and rugs for the rest of the land uses along the bottom margin). Rugs for land uses can overlap, therefore some data is not visible. The slopes that are significantly different from zero in each model are: Urban (-9.935 e-4, P= <0.05) in model including island area; Primary minimal (-0.302, P=<0.05) and Primary Vegetation (-0.776, P= <0.001) in model including surrounding landmass; Pasture (-0.098, P= <0.001) and Urban (-0.284, P= <0.01) in model including country GDP; Pasture (-0.042, P= <0.001) and Urban (-0.053, P= <0.01) in model including island GDP.

Table D.12. AIC values for models of alien species richness (including island traits) using the two different random-effects structures that were tested. ∆AIC values are shown relative to the best model.

Random-effects structure	d.f.	AIC	∆AIC
Model including area			
(1|SS) + (1|Island)	16	11734.18	--
(1|SS)	15	11816.31	82.13
Model including surrounding landmass			
(1|SS) + (1|Island)	16	8721.123	--
(1|SS)	15	8798.617	77.494
Model including country GDP per capita			
(1|SS) + (1|Island)	16	11726.16	--
(1|SS)	15	11818.45	92.96
Model including island GDP per capita			
(1|SS) + (1|Island)	16	11703.97	--
(1|SS)	15	11754.98	51.01

Table D.13. ANOVA tables for models of alien species richness including island traits as explanatory variables. LUI= land use/use intensity. Stars indicate the level of significance (Sig): <0.05*, <0.01** and <0.001***

Term	χ^2	d.f.	Sig
Model including area			
LUI	501.121	6	***
Area	0.385	1	
LUI × Area	64.541	6	***
Model including surrounding landmass			
LUI	496.870	6	***
Landmass	5.207	1	*
LUI × Landmass	67.668	6	***
Model including country GDP per capita			
LUI	484.492	6	***
Country GDP	0.058	1	
LUI × Country GDP	74.280	6	***
Model including island GDP per capita			
LUI	498.715	6	***
Island GDP	0.102	1	
LUI × Island GDP	95.903	6	***


Model including island area

Model including surrounding landmass

Model including country GDP

Model including island GDP

Figure D.9. Diagnostic plots for the four models of alien species richness including the different island traits as explanatory variables.

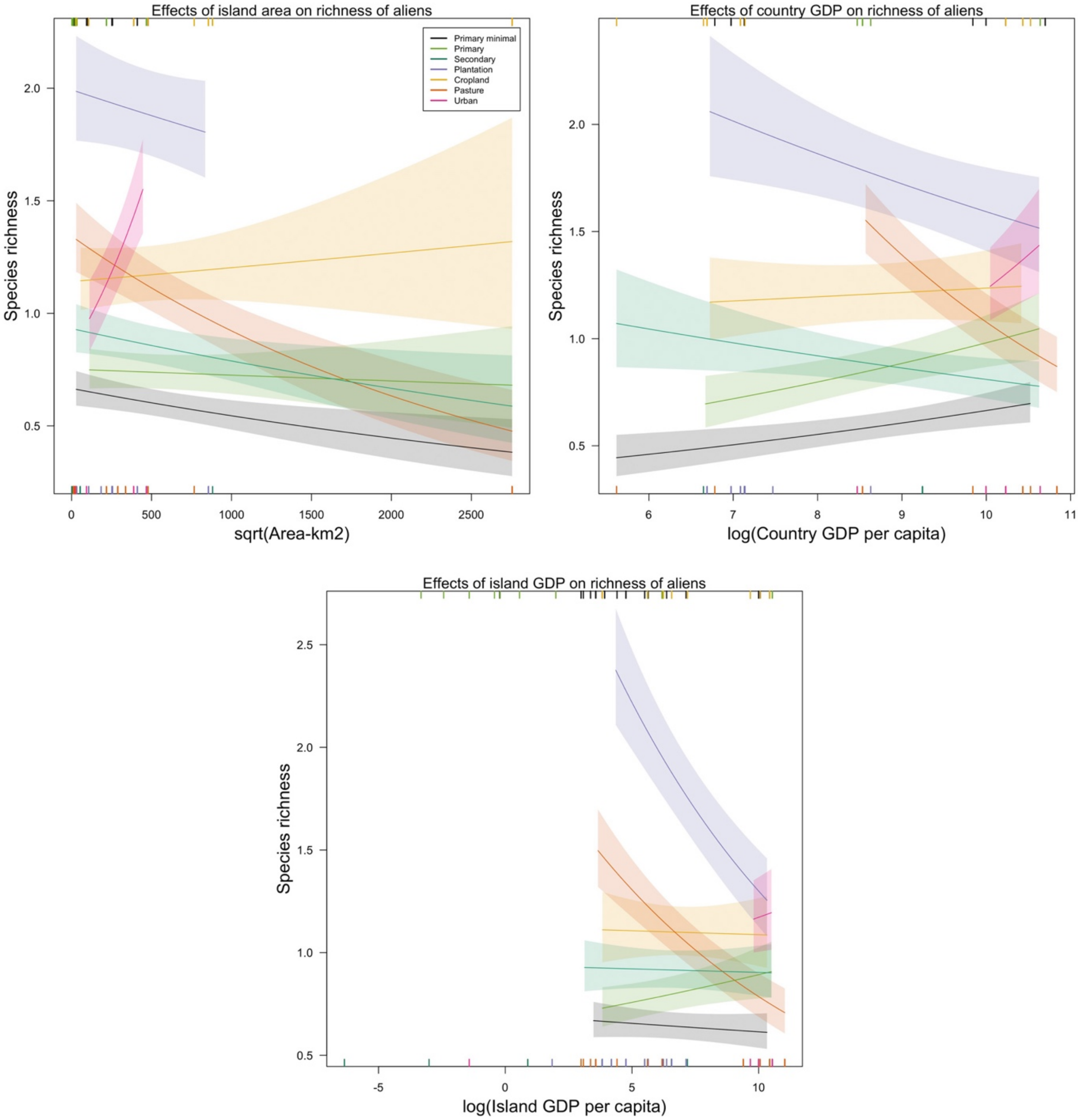
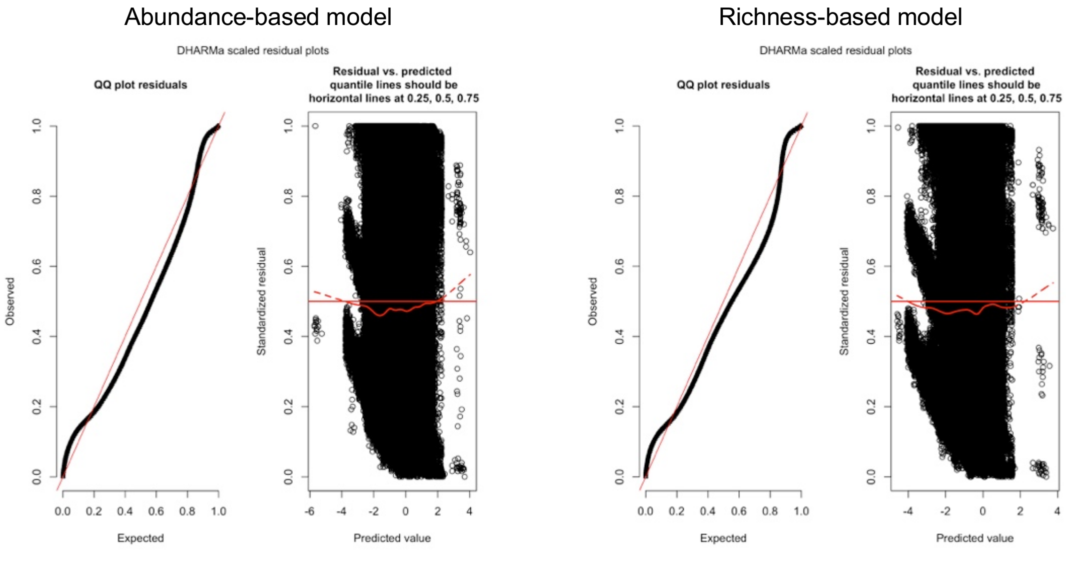


Figure D.10. Effects of island area, country-level and island-level GDP per capita on species richness of aliens. Rugs along the horizontal margins show values of the explanatory variables represented (across land uses) in the model data set (rugs for minimally-used primary vegetation, primary vegetation and croplands along the top margin and rugs for the rest of the land uses along the bottom margin). Rugs for land uses can overlap, therefore some data is not visible. No slopes were significantly different from zero in the models including island area or island GDP. In the model including country GDP only Pasture (-0.255, P= <0.05) had a slope significantly different from zero.

Table D.14. Final dataset for the compositional similarity models for alien and native assemblages. The table shows the number of pair of sites per each land-use contrast generated from pairwise comparisons within studies in the PREDICTS database. Numbers inside brackets show the number of studies from which data came from. Only land-use contrasts of interest are shown.

Land-use contrast	Aliens	Natives
PriMin- PriMin	11038 (21)	19053 (35)
PriMin- Primary	4139 (8)	5627 (12)
PriMin- Secondary	6405 (19)	12847 (32)
PriMin- Cropland	2712 (7)	3477 (9)
PriMin- Pasture	8390 (6)	9066 (10)
PriMin- Plantation	8994 (11)	10718 (17)
PriMin- Urban	2 (1)	50 (2)
Primary-Primary	13046 (7)	22714 (18)
Secondary- Secondary	11736 (29)	31379 (53)
Cropland - Cropland	3720 (5)	4975 (6)
Pasture - Pasture	19108 (15)	117488 (25)
Plantation - Plantation	28163 (15)	33374 (22)
Urban - Urban	1901 (6)	14906 (10)


Abundance-based model

Richness-based model

Figure D.11. Diagnostic plots for the minimum adequate models of abundance-based and richness-based compositional similarity for alien and native assemblages.

Table D.15. Significance of the interaction terms in the compositional similarity models (abundance-based and richness-based) for native and alien assemblages. p-values were calculated by performing a "greater" hypothesis test, where I compared the likelihood ratio for my observed models (maximum model and model excluding each interaction) against a distribution of null likelihood ratios generated from comparisons of models using permuted datasets (model comparisons with the same difference in degrees of freedom as my observed models, but representing no real loss of explanatory power). LUc= Land-use contrast, EnvDist= Environmental distance, GeogDist= Geographic distance.

Interaction term	Abundance-based model	Richness-based model
LUc × Alien/Native	0.005	0.005
EnvDist × Alien/Native	0.005	0.01
GeogDist × Alien/Native	0.005	0.005

Table D.16. Coefficients from the final compositional similarity models (abundance-based and richness-based) for native and alien assemblages. Coefficients for native species (i.e., interaction coefficients) are expressed as the difference from the alien coefficients. Significance (indicated by stars) is shown for the coefficients of interest (first section of the table), for which "two-tailed" tests were performed to compare the observed values against null distributions. Although I only reported significance for the interaction coefficients, I also tested for significance of alien coefficients (baseline in model). Significance codes: >0.05 --,<0.05**, and 0.005***

	Abundance-based model		Richness-based model	
	Aliens	Natives	Aliens	Natives
PriMin-PriMin	0.422 ***	0.658 ***	-0.104 ***	0.635 ***
Geographic distance	-0.125 ***	0.064 ***	-0.1 ***	0.042 ***
Environmental distance	-0.987 ***	-0.925 ***	-1.212 ***	-0.205 **
PriMin-Primary	-0.655 ***	0.237 ***	-0.476 ***	0.21 ***
PriMin-Secondary	-0.976 ***	1.071 ***	-0.644 ***	0.724 ***
PriMin-Plantation	-1.729 ***	2.074 ***	-1.46 ***	1.736 ***
PriMin-Cropland	-2.761 ***	2.876 ***	-2.526 ***	2.663 ***
PriMin-Pasture	-1.361 ***	0.285 ***	-0.747 ***	-0.003 --
PriMin-Urban	0.191 --	-1.26 --	-0.271 --	-0.839 --
Primary-Primary	0.814 ***	-0.726 ***	1.032 ***	-0.822 ***
Secondary-Secondary	-0.02 --	0.155 ***	0.206 ***	-0.027 --
Plantation-Plantation	1.916 ***	-1.339 ***	1.737 ***	-1.198 ***
Cropland-Cropland	-0.326 ***	0.323 ***	-0.222 ***	0.299 ***
Pasture-Pasture	0.153 ***	0.131 ***	0.284 ***	-0.182 ***
Urban-Urban	-0.455 ***	0.132 --	0.159 --	-0.396 ***
Cropland-Pasture	1.783	-3.52	2.159	-3.792
Cropland-Plantation	-0.751	0.408	-0.506	0.17
Cropland-PriMin	-1.224	0.134	-0.971	-0.101
Cropland-Primary	3.89	-4.285	4.08	-4.426
Cropland-Secondary	-0.839	0.05	-0.607	-0.15
Cropland-Urban	-0.016	-1.571	0.397	-1.967
Pasture-Cropland	0.577	-1.446	0.94	-1.789
Pasture-Plantation	-0.271	-1.504	0.002	-1.701
Pasture-PriMin	-0.376	-0.728	-0.07	-0.729
Pasture-Primary	-0.097	-0.69	0.096	-0.633
Pasture-Secondary	-0.553	-0.801	0.045	-1.191

Pasture-Urban	0.409	-1.077	0.956	-1.547
Plantation-Cropland	-1.288	1.815	-1.144	1.711
Plantation-Pasture	-0.122	-0.46	0.558	-1.08
Plantation-PriMin	-0.591	0.175	-0.28	-0.166
Plantation-Primary	-1.922	1.491	-1.371	1.075
Plantation-Secondary	0.506	-0.444	0.729	-0.66
Plantation-Urban	0.311	0.516	1.112	-0.327
Primary-Cropland	0.076	-0.426	0.272	-0.677
Primary-Pasture	-0.076	-0.497	0.166	-0.542
Primary-Plantation	-1.95	1.944	-1.685	1.751
Primary-PriMin	-0.493	0.078	-0.338	0.149
Primary-Secondary	0.686	-0.717	0.92	-0.814
Primary-Urban	0.302	-1.969	2.582	-4.019
Secondary-Cropland	-2.221	2.833	-2.022	2.686
Secondary-Pasture	-0.981	0.015	-0.23	-0.352
Secondary-Plantation	-0.913	1.485	-0.604	1.126
Secondary-PriMin	-0.006	-0.196	0.165	-0.405
Secondary-Primary	-0.045	-0.151	0.2	-0.247
Secondary-Urban	-3.182	3.192	-2.065	2.15
Urban-Cropland	1.121	-1.288	1.82	-1.89
Urban-Pasture	0.781	-1.077	1.833	-2.046
Urban-Plantation	0.889	-1.02	1.088	-1.166
Urban-PriMin	0.656	-1.253	2.975	-3.494
Urban-Primary	0.297	-2.574	0.194	-2.049
Urban-Secondary	-5.428	4.899	-3.843	3.409

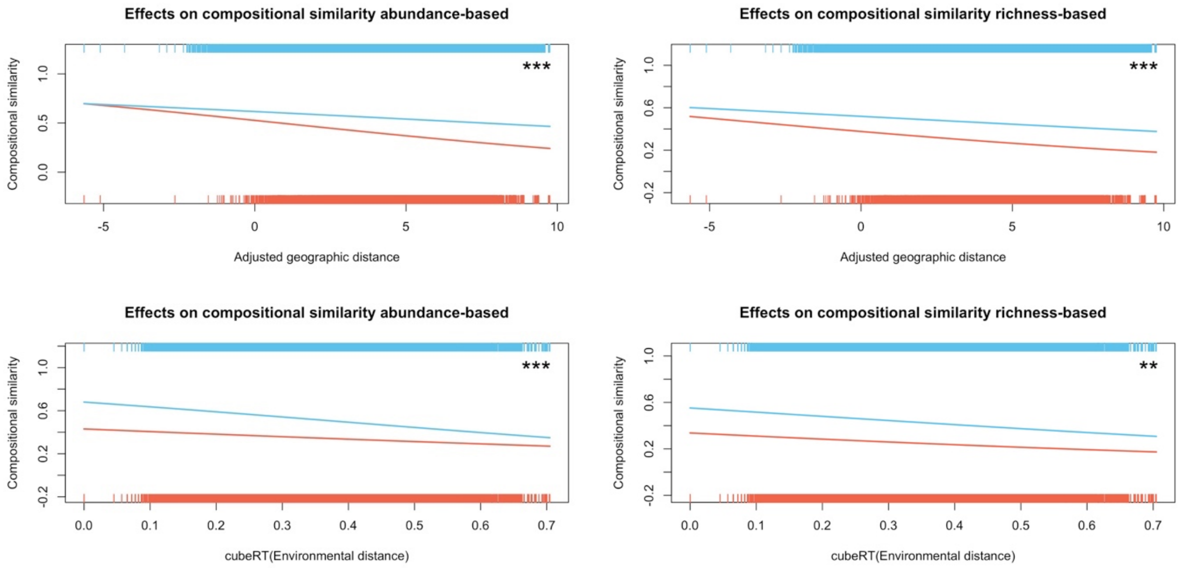


Figure D.12. Effects of geographic and environmental distance between sites on compositional similarity (J_A and J_R) of alien (orange) and native (blue) assemblages. The rugs in the figures show the distribution of data for aliens and natives. Significance (indicated by stars) corresponds to p-values calculated from “two-tailed” tests using the interaction coefficients (to compare the observed values against null distributions) to test for significant differences between responses of aliens and natives. Significance code: <0.05**, 0.005***

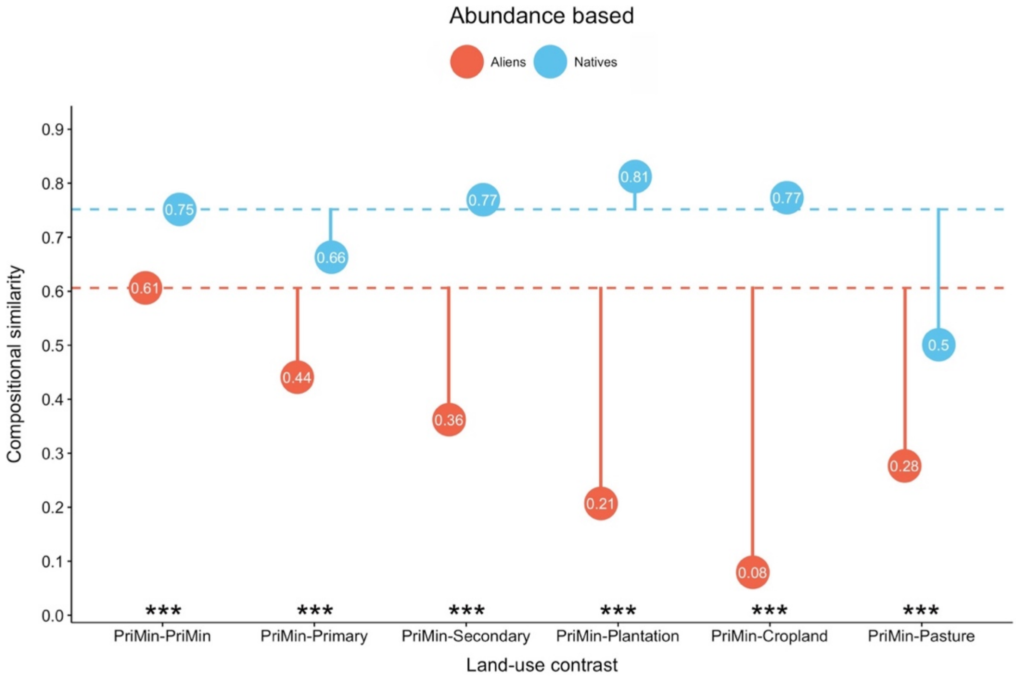


Figure D.13. J_A estimates for alien and native assemblages for land-use contrasts where site *i* is in PriMin. Solid lines show the magnitude of change in J_A driven by change to different land uses; the baseline is compositional similarity between PriMin sites for alien and native assemblages respectively (dashed lines). Significance (indicated by stars) is shown for alien/native differences for J_A changes from PriMin-PriMin on a logit scale (results from "two-tailed" tests comparing the coefficients for interaction between alien/native and land-use contrast to null distributions). Results for the PriMin-Urban contrast are not shown because sample sizes for this contrast were very small (but see the coefficients in Table D.16) Significance code: 0.005***

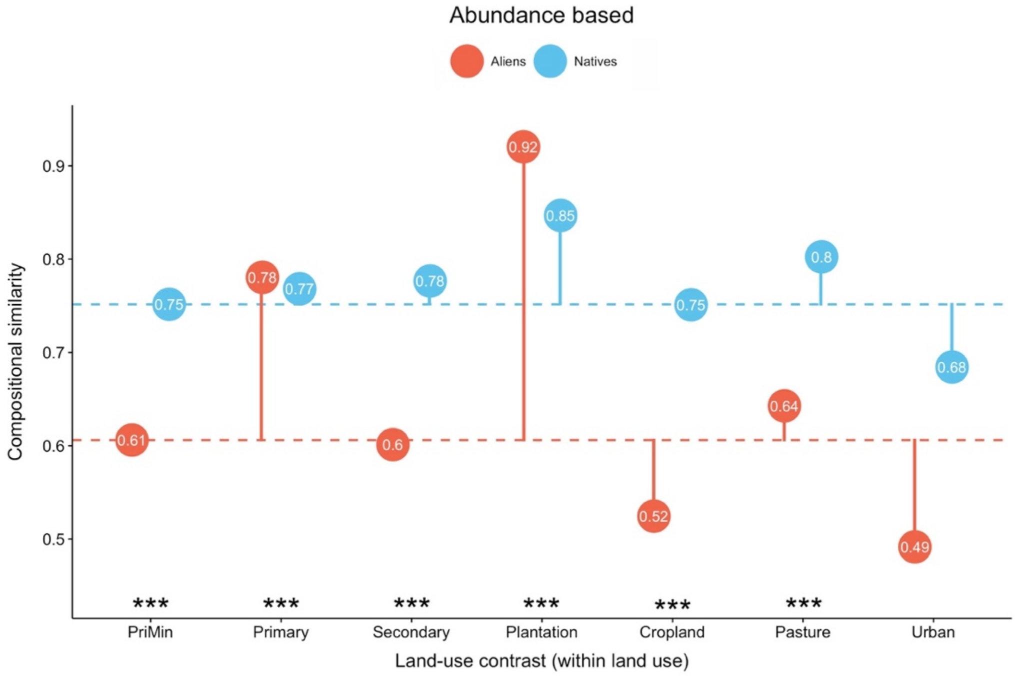


Figure D.14. J_A estimates for alien and native assemblages in sites within the same land use. Each category corresponds to a land-use contrast (i.e., Cropland= Cropland-Cropland). Solid lines show the magnitude of change in J_A using PriMin-PriMin compositional similarity as baseline (dashed lines). Significance connotation and codes as in Figure D.13.

APPENDIX E

Supplement for Chapter 5

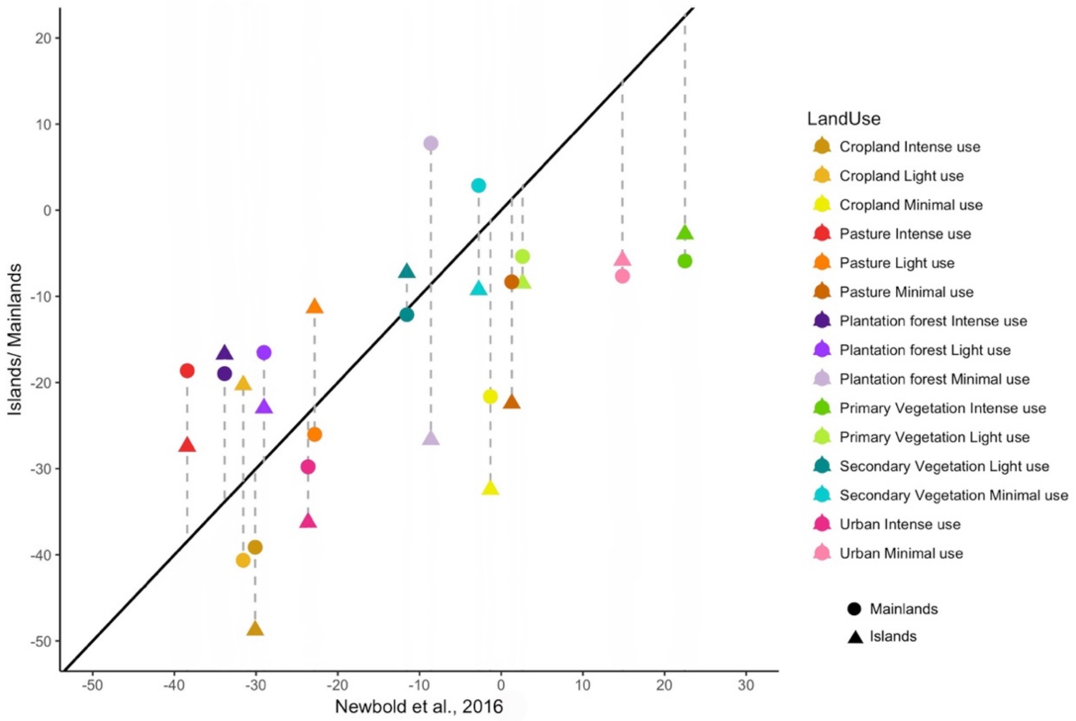


Figure E.1. Response of total abundance to land use/use intensity: Island and mainland estimates are compared against global estimates from Newbold et al. (2016a). Values indicate decrease or increase in percentage of total abundance using minimally-used primary vegetation as baseline. Secondary vegetation with intense use and Urban with light use are not included in the comparisons since in Newbold et al. (2016a) these land-use classes were collapsed with Secondary vegetation with light use and Urban with minimal use, respectively.

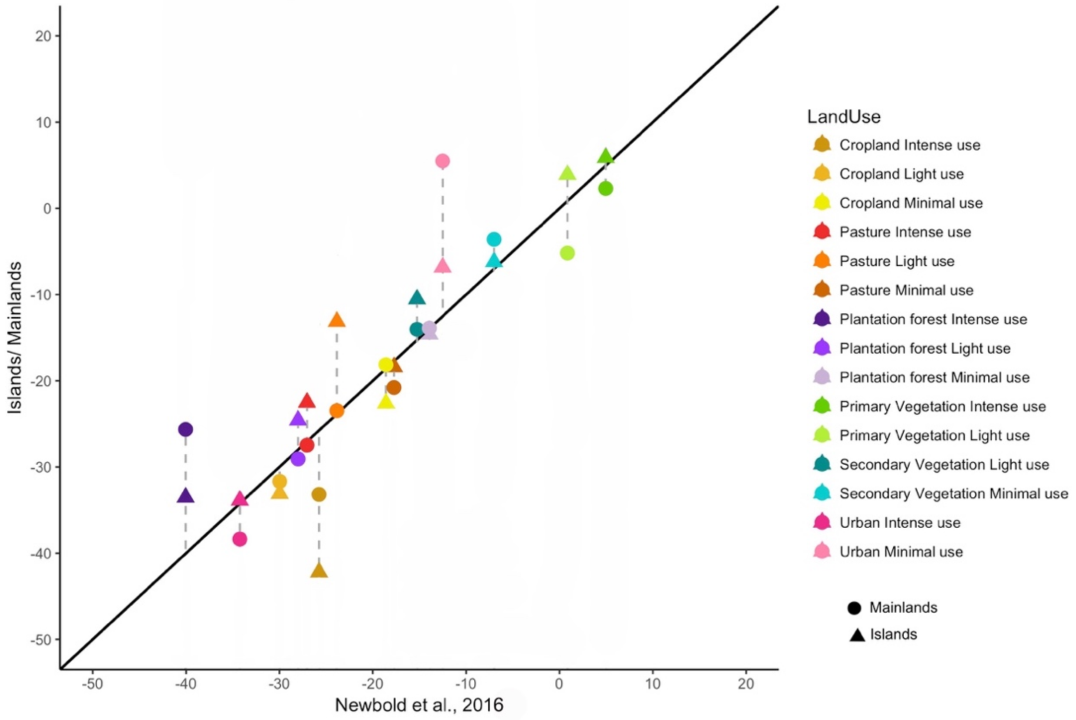


Figure E.2. Response of species richness to land use/use intensity: Island and mainland estimates are compared against global estimates from Newbold et al. (2016a). Values indicate decrease or increase in percentage of species richness using minimally-used primary vegetation as baseline.

Table E.1. Results from the compositional similarity model (abundance-based) using log transformation for all variables but keeping PriMin as baseline in the land-use contrasts. The table shows backtransformed values (0 to 1 scale) for compositional similarity and rescaled values (so that the contrast of PriMin against itself had a value of 1). Only results for mainlands and land use contrasts of interest are shown.

	Log transformation	
	Compositional similarity	Rescaled compositional similarity
PriMin-PriMin	0.832	1
PriMin-Primary	0.720	0.865
PriMin-Secondary	0.791	0.952
PriMin-Plantation	0.591	0.710
PriMin-Cropland	0.594	0.714
PriMin-Pasture	0.539	0.648
PriMin-Urban	0.524	0.630

Table E.2. Results from compositional similarity models (abundance-based) using collapsed primary vegetation as baseline in the land-use contrasts. The table shows the results of two models: a model using log transformation for all variables (as in Newbold et al. (2016a)) and a model using data transformations from Chapter 2 (referred as Logit transformation). The table shows backtransformed (0 to 1 scale) compositional similarity values and rescaled values (so that the contrast of Primary against itself had a value of 1). Only results for mainlands and land use contrasts of interest are shown.

	Logit transformation		Log transformation	
	Compositional similarity	Rescaled compositional similarity	Compositional similarity	Rescaled compositional similarity
Primary-Primary	0.842	1	0.785	1
Primary-Secondary	0.806	0.957	0.742	0.945
Primary-Plantation	0.715	0.849	0.665	0.847
Primary-Cropland	0.642	0.762	0.595	0.758
Primary-Pasture	0.531	0.630	0.551	0.702
Primary-Urban	0.635	0.754	0.598	0.762

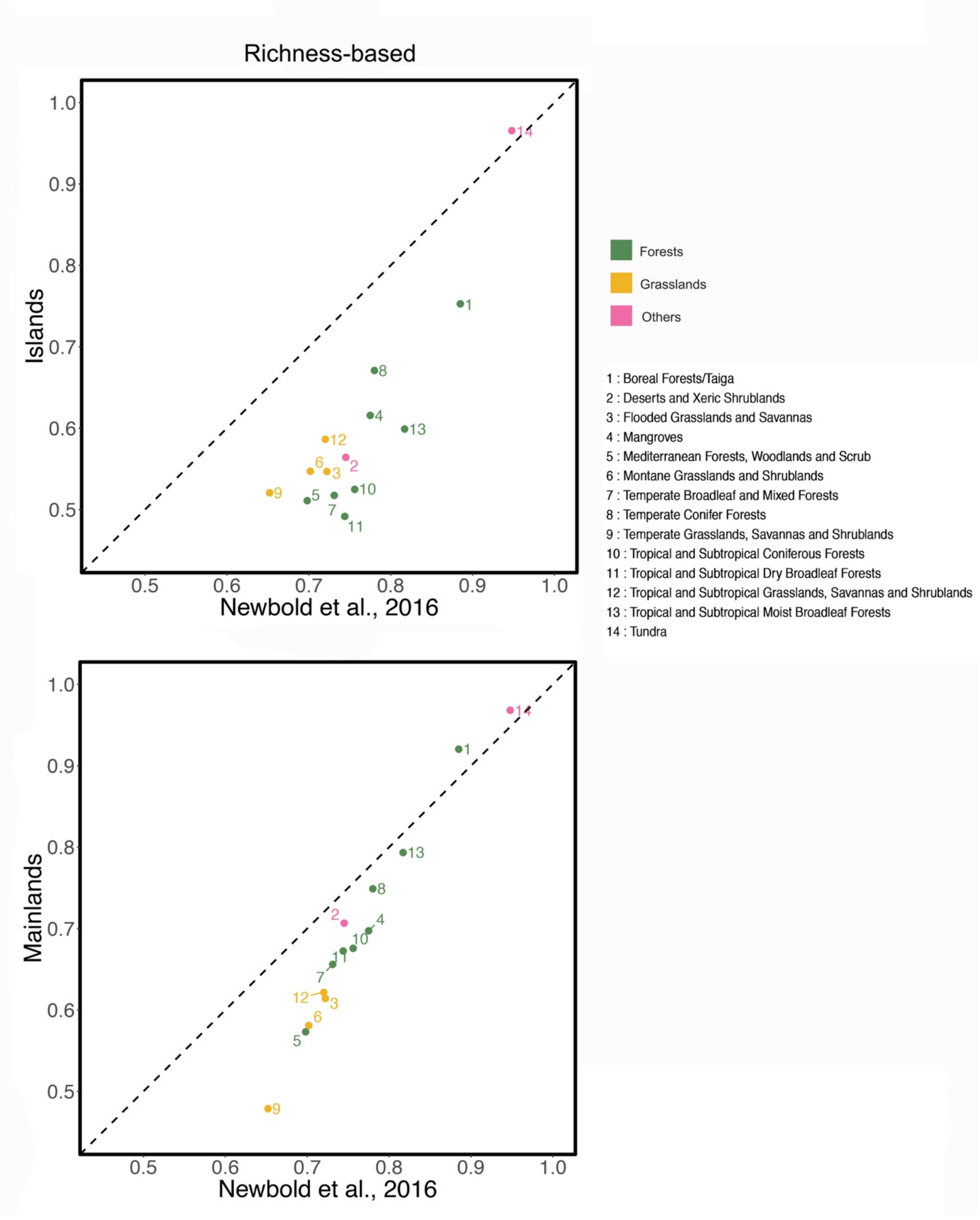


Figure E.3. BII estimates (richness-based) for biomes on islands and mainlands compared with global estimates from Newbold et al. (2016a). Colours indicate major biome type. Values from 0 to 1 correspond to BII (1= 100% intactness).

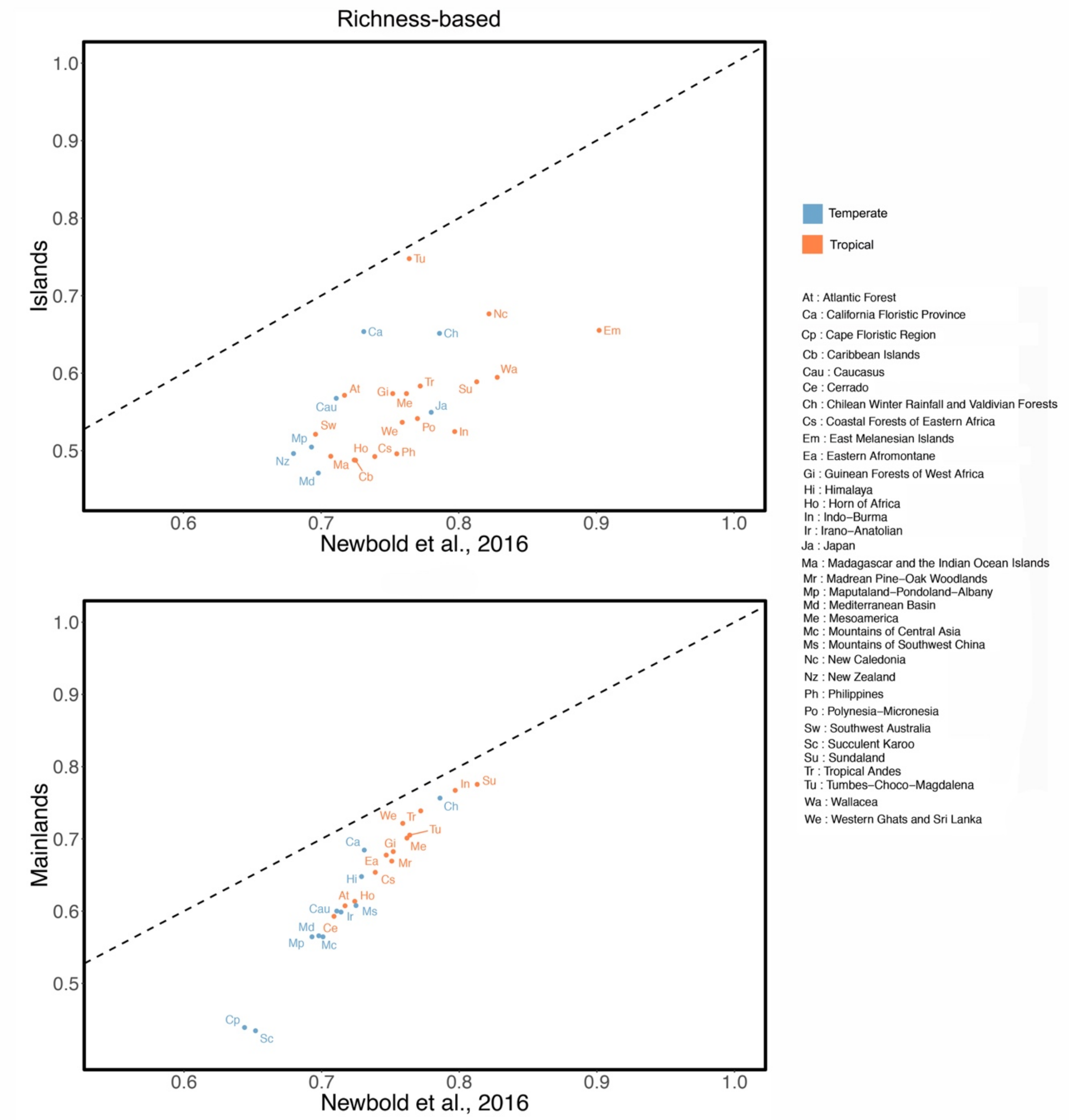


Figure E.4. BII estimates (richness-based) for biodiversity hotspots on islands and mainlands compared with global estimates from Newbold et al. (2016a). Some hotspots are exclusively located on islands or mainlands. Colours indicate whether hotspots are in the tropical or temperate realms. Values from 0 to 1 correspond to BII (1= 100% intactness).

Table E.3. Number of island sites per biome in the final datasets for the abundance and richness models fitted for BII calculation (Chapter 3) and for estimation of alien/native responses (Chapter 4). For the latter model only data for native species is shown. For a few biomes, there were more sites in the dataset for island natives than in the island dataset used for models fitted for BII calculation. This is the result of the exclusion of sites without a defined use intensity in the BII models; use intensity was not included in models for responses of island natives.

Biome	Abundance models		Richness models	
	Island data in BII model	Island natives data in alien/native model	Island data in BII model	Island natives data in alien/native model
Boreal Forests/Taiga	0	0	0	0
Deserts & Xeric Shrublands	55	64	55	64
Flooded Grasslands & Savannas	0	0	0	0
Mangroves	6	3	6	3
Mediterranean Forests, Woodlands & Scrub	303	82	304	83
Montane Grasslands & Shrublands	485	260	485	260
Temperate Broadleaf & Mixed Forests	3764	3059	4051	3346
Temperate Conifer Forests	98	86	98	86
Temperate Grasslands, Savannas & Shrublands	280	190	456	542
Tropical & Subtropical Coniferous Forests	0	0	0	0
Tropical & Subtropical Dry Broadleaf Forests	82	82	82	82
Tropical & Subtropical Grasslands, Savannas & Shrublands	545	537	571	563
Tropical & Subtropical Moist Broadleaf Forests	2168	1883	2520	2203
Tundra	0	0	0	0

Table E.4. Numbers of species by Phylum represented in the final datasets for the abundance and richness models fitted for BII calculation (Chapter 3) and for estimation of alien/native responses (Chapter 4). For the latter model only data for native species is shown.

Taxon	Abundance models		Richness models	
	Island data in BII model	Island natives data in alien/native model	Island data in BII model	Island natives data in alien/native model
Annelida	160	13	160	13
Arthropoda	7819	1974	8556	2057
Ascomycota	469	0	470	0
Basidiomycota	413	0	413	0
Bryophyta	271	0	302	5
Chordata	1547	1185	1635	1248
Glomeromycota	20	0	20	0
Mollusca	195	45	196	45
Mycetozoa	2	0	2	0
Nematoda	380	0	380	0
Onychophora	3	2	3	2
Platyhelminthes	4	0	5	0
Tracheophyta	3914	1419	5371	2144