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

Katia Sanchez-Ortiz[1, 2 *], Kara J. M. Taylor[3], Adriana De Palma[1], Christian König[4, 5], Petr Pyšek[6, 7], Patrick Weigelt[4], Franz Essl[8], Andy Purvis[1, 2]

1 Department of Life Sciences, Natural History Museum, London, United Kingdom
2 Department of Life Sciences, Imperial College London, London, United Kingdom
3 Food Animal Health Research Program, Ohio Agricultural Research and Development Center, The Ohio State University, Wooster, Ohio, United States of America
4 Biodiversity, Macroecology & Biogeography, University of Goettingen, Göttingen, Germany
5 Department of Geography, Humboldt-Universität zu Berlin, Berlin, Germany
6 Department of Invasion Ecology, Institute of Botany, The Czech Academy of Sciences, Průhonice, Czech Republic
7 Department of Ecology, Faculty of Science, Charles University, Prague, Czech Republic
8 Department of Botany and Biodiversity Research, University Vienna, Vienna, Austria

* Corresponding author
E-mail: k.sanchez-ortiz@nhm.ac.uk

Abstract

Island species and habitats are particularly vulnerable to human disturbances, and anthropogenic changes are increasingly overwriting natural island biogeographic patterns. However, quantitative comparisons of how native and alien assemblages respond to human disturbances are scarce. Using data from 6,252 species (vertebrates, invertebrates and plants), 7,731 sites and 80 islands, we model how land-use change, human population density and distance to the nearest road affect local assemblages of alien and native species on islands. We found that these pressures reduce both richness and abundance of natives, whereas the number and abundance of alien species are high in plantation forests and agricultural or urban sites. In contrast to the long-established pattern for native species, more isolated islands have a higher number of alien species across most land uses than do less isolated islands. Finally, our models of compositional similarity comparing sites in minimally-disturbed primary vegetation with other land uses, and sites within the same land use show that alien species play a major role in the turnover and homogenization of island assemblages. The declines of native species on islands in the face of human pressures, and the proneness to invasions of even the more remote islands, highlight the need to reduce the intensity of human pressures on islands and so far as possible to prevent the establishment of alien species.

Introduction

Land use and related pressures strongly modify the diversity within local ecological assemblages [1–3] and turnover between them [4], in ways that can differ significantly between ecological systems or geographic regions [1,5,6]. This study focuses on islands – landmasses completely surrounded by ocean – worldwide, and models statistically how land use and related pressures affect two disjunct subsets of their local ecological assemblages: natives and aliens. Studying alien and native responses to human pressures on islands is important for two main reasons. First, islands have been highlighted as hotspots of alien species [7–10] and as systems at higher risk of invasions [11–14]. Second, many species native to islands have characteristics – e.g., narrow-range endemism, small population size – that make them both irreplaceable and particularly vulnerable to human disturbances [15–17].

Natural and anthropogenic factors combine to make islands, and their site-level communities, prone to invasion. Islands – especially remote islands – may have a relatively small source pool of native species [18] from which their communities are assembled. The resulting low species richness for their area [19] is in turn hypothesised to result in more available resources [12], low pressures from predators or pathogens, and disharmonic communities [13,20]. Additionally, many native species have low competitive ability [13] and have evolved reduced dispersal abilities [20] and reproductive output [21–23]. These natural factors combine to facilitate establishment by alien colonists, especially in disturbed sites [24–26]. Land-use change involves site-level disturbance, favouring the establishment of alien species (often good dispersers that reproduce rapidly and tolerate a broad range of conditions [27–29]). Additionally, humans have directly introduced many alien species to islands, with propagule pressure (i.e., number of released individuals [30]) and the presence of other groups of introduced species [31] both influencing the probability of establishment.

Anthropogenic disturbances may favour alien species, but disturbed habitats can represent novel environments for some native species, to which they are not adapted [12]. Natives with traits related to a high extinction risk – such as large size [32,33], low fecundity, limited dispersal abilities, stenotopy [34] and small range-size [33,35] – are particularly unlikely to tolerate human impacts, whereas those with the opposite traits are likely to be more resilient. Both the addition of aliens and the accelerated turnover of natives can drive changes in among-site species turnover, including biotic homogenization [36]: their relative importance remains an open question.

If alien species follow natural island biogeographic patterns, large islands and islands close to continents or other islands would have more alien species than small and isolated islands [37].

However, anthropogenic processes have particularly changed the species–isolation relationship [9,38–40]. Currently, anthropogenic factors such as colonisation pressure (i.e., number of species introduced to a defined location [8,41]) or economic isolation of islands [39] may be more important than geographic isolation. Measures of economic activity are related to propagule pressure (e.g., trade volumes), ecological disturbances [42] and infrastructure development [43] (e.g., roads), all of which ease the arrival and establishment of alien species [42,43]. Here, as a simple proxy for islands' economic connectance, we use per-capita GDP, which has previously been shown to correlate across countries globally with the numbers of alien introductions [8] and, among countries within regions, with numbers of established alien amphibian and reptile species [7].

In this paper, we use data from 6,252 species (vertebrates, invertebrates and plants), 7,731 sites and 80 islands in the PREDICTS database [44] whose native/alien status could be determined, to model how land-use change and related pressures affect local native and alien assemblages on 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 site-level total abundance and species richness, we show that three human pressures (land use, human population density and distance to the nearest road) affect alien assemblages differently from native assemblages. Additionally, we test whether richness and abundance of alien species is predicted by measures of island size, geographic isolation and economic connectance. To evaluate the turnover of native and alien assemblages caused by land-use change on islands, we estimate how species composition of alien and native communities in minimally-disturbed sites is affected by land-use change. Finally, for native and alien assemblages separately, we estimate the homogeneity of assemblages among sites within the same land use.

Methods

Data assemblage

All data on species abundance and occurrence at sites on islands (including Australia) were extracted from the PREDICTS database [44] in October 2016. The database collates data from published research that compared local biodiversity across sites in different land uses, and is structured hierarchically into Data Sources (publications), Studies (different sampling methods within a source), Blocks (spatial blocks, if present in the study) and Sites [45]. Australia was treated as an island because of its island-like characteristics– e.g., long isolation history (complete isolation from other continents ~ 33 Mya [46]) and relatively small size. 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 [47]. All data processing and statistical analyses were performed using R Version 3.3.3 [48].

The island data from PREDICTS included 17,776 species and 1,339,339 biodiversity records (each one being a single diversity record of a species at a site within a study). Only 42 of the168 data sources had already classified the sampled species as aliens or natives at the sites sampled. To classify as many remaining species as possible, we matched PREDICTS records with 27 external sources of information on native and alien ranges (Table 1 in S1 File). Three global databases provide island-specific (rather than country-level) species classifications: the Global Naturalized Alien Flora database (GloNAF; [49,50]), the Global Inventory of Floras and Traits (GIFT; [51]) and the Threatened Island Biodiversity database (TIB; [52]). We identified all matching species-island combinations between these three databases and PREDICTS island data. For remaining taxa, we queried additional databases for species status at a country level, via either downloadable datasets or an application programming interface (API). We also used data from GloNAF to determine the status of plant species at a country 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, we first extracted the status for the matching species-country combinations, but also classified species according to the geographic ranges provided by these sources: i.e., species whose sampling location in our dataset was not included in their native range were classified as alien. In a final step, we searched for data sources that could help classifying species with many records in our data set that 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.

Statistical modelling

Models of total abundance and species richness

For each site, we split the PREDICTS data into native species and alien species, discarding data that could not be classified. For aliens and natives separately, we calculated each site's total abundance (sum of abundances of all present taxa) and species richness (number of unique present taxa). 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.

The studies in the PREDICTS database differ greatly in their sampling methods, taxonomic focus and locations; and some studies have spatial blocks or split-plot designs. To accommodate the resulting heterogeneity and non-independence, we fitted mixed-effect models ('*lme4'* package ver. 1.1-15 – [53]) to model the responses of alien and native species richness and total abundance to human pressures.

As fixed-effects, the full 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. Because not all abundance data were counts of individuals, Poisson or quasipoisson models could not be used: instead, sites' total abundance was rescaled to a zero-to-one scale within each study to reduce the variance among studies, square-root transformed (which gave a better residual distribution than log transformation), and modelled using a Gaussian error structure. Species richness (always a count) was modelled using a Poisson error structure and log link.

Site-level data for human population density (for the year 2000) and distance to the nearest road were obtained from the Global Rural-Urban Mapping Project, ver. 1 (GRUMPv1) [54] and the Global Roads Open Access Data Set, ver. 1 [55], respectively. HPD and DistRd were log transformed (to reduce skew) and rescaled to a zero-to-one scale (to reduce collinearity) prior to modelling, and fitted as quadratic orthogonal polynomials. Sites in the PREDICTS database had previously been classified into 10 land-use categories and three land-use intensities within each land use [45]. For our models, these categories were collapsed into seven final land use/use intensity classes: 1) Primary vegetation with minimal use (henceforth PriMin; used as a baseline representing minimally disturbed sites), 2) Primary vegetation (other than minimal use), 3) Secondary vegetation, 4) Plantation forest, 5) Cropland, 6) Pasture and 7) Urban. These collapsed classes gave reasonable sample sizes (at least 100 sites) within each land-use class for both alien and native data (Table 5 in S1 File). Sites missing data for any of the human pressures were excluded from these models.

To identify the best random-effects structure, we compared two possibilities following the procedure in [56]: (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 [57]. Finally, the fixed-effects structure of the final models was determined using backwards stepwise model simplification and likelihood ratio tests with models fitted using Maximum Likelihood [56]. Generalized Variance Inflation Factors (GVIFs) [56] did not indicate strong collinearity among

the explanatory variables and model diagnostics showed that the final abundance and richness models fulfilled homogeneity and normality assumptions (Fig 1 in S1 File).

Models including island traits as predictors

We tested whether any of three island characteristics – area, isolation and GDP per capita – predicted total abundance or richness of aliens. Island area (in km^2) was calculated using a global layer of land polygons taken from OpenStreetMap [58] in cylindrical equal area projection. As a proxy for island isolation, we used Weigelt et al.'s [59] 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), which has been shown to predict diversity of plants on islands at a global scale [60]. Data for three Japanese islands and Australia (Table 9 in S1 File) were missing from Weigelt et al. [59], so these four islands were not included in the surrounding landmass models. GDP per capita (in current US dollars for the year 2005) for each site's country came from World Bank Open Data.

Using only the alien data, we fitted six mixed-effects models – testing each of the three island characteristics in turn as predictors of richness and abundance – with the same modelling approach as used above except as follows. As fixed effects, each initial model included one two-way interaction between land use and the island trait. To reduce skew and improve the distribution of residuals [61], island area was square-root transformed and GDP per capita log-transformed. Surrounding landmass did not require transformation. We considered two possible random-effects structures for the models: (i) random intercepts of study (ii) random intercepts of study and island. We performed post hoc analysis (package '*phia*' ver. 0.2-1 – [62]) to test whether the coefficients of the interaction between the land uses and the island trait were significantly non-zero.

Models of compositional similarity

To model how land-use change affects the turnover of native and alien assemblages on islands, we model pairwise differences in assemblage composition among sites using a modified matrix regression – explained in more detail below. Under this approach, the non-independence among the pairwise comparisons necessitates the use of permutation tests to assess statistical significance [63].

We first calculated compositional similarity (for aliens and natives separately) for all possible pairwise comparisons between sites (including both forward and reverse comparisons) within each study using the abundance-based (J_A) and richness-based (J_R) asymmetric Jaccard

Index, calculated as: $J_R = S_{ij} / S_j$, where S_{ij} is the number of species common to both sites and S_j is the number of species in site *j*; $J_A = A_{ij} / A_j$, 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* [64]. These asymmetric measures reflect the possibility of one site's assemblage being largely nested within another [65]. Both measures are one if all taxa at site *j* are also present at site *i*, zero if the two sites share no taxa in common, and undefined (and dropped from analyses) if neither site had any organisms sampled. Low J_A and J_R values mainly result from a high number or high abundance of novel or unique species in site *j* (i.e., species recorded at site *j* but missing in site *i*).

We fitted mixed-effect models to model both J_A and J_R as a function of the sites' land uses (henceforth land-use contrast; e.g, PriMin-Pasture), the geographic and environmental distance between the sites (to account for similarity decay with geographic [66] and environmental distance) and the assemblage status (native or alien). Land-use contrast was a 49-level factor (i.e., all possible combinations for the seven land-use categories); however, we only focus on results for 13 land-use contrasts (Table 14 in S1 File): – 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 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, the land-use contrasts of interest had sample sizes >1900 and included data from five or more studies (Table 14 in S1 File); the only exception was PriMin-Urban, for which data only came from one study for aliens and two studies for natives. Because estimates based on so few studies are unreliable [67], we do not report the results for this contrast (model coefficients for all land-use contrasts are presented in Table 16 in S1 File). Geographic distance between sites was calculated from the sites' coordinates using the *distHaversine*' function in the '*geosphere*' package ver. 1.5-7 [68], while environmental distance was estimated as the 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 [69] and using the '*gower_dist*' function in the '*gower*' package ver. 0.1.2 [70]. We excluded pairwise comparisons for which environmental distance could not be calculated due to missing data or where geographic distance was zero as a result of coordinate imprecision. We also excluded studies sampling a single species or where sampling effort varied among sites.

As fixed effects, the models included two-way interactions between assemblage status (alien/native) and each of geographic distance, environmental distance and land-use contrast. Study identity was included as a random intercept. We used the PriMin-PriMin contrast as the intercept level in the models and a baseline against which to compare the other land-use

contrasts, since it represents the natural spatial turnover of species. Prior to modelling, compositional similarity was logit-transformed (using an adjustment of 0.01 to deal with 0 and 1 values [71]). To deal with extreme values [61] and normalise the data distribution, environmental distance was transformed using cube root, and geographic distance was first divided by the median maximum linear extent of the sites in the dataset (which reflects site size [72]) and then log-transformed; as a result, a transformed geographic distance of zero corresponds to adjacent sites. The final models for J_A and J_R fulfilled homogeneity and normality assumptions (Fig 11 in S1 File).

Because these models use all pairwise comparisons, they have extensive pseudo-replication, precluding the use of standard statistical approaches to simplify the fixed effects of the models. We therefore used permutation tests [63] to assess significance of terms during backwards stepwise model simplification based on likelihood ratios. The model dataset was permuted 199 times by randomly shuffling the response variable data within studies while holding data for all explanatory variables constant. The likelihood ratio between models at successive stages of model simplification (i.e., between a more complex and a less complex model) was compared against a null distribution of ratios of initial and reduced models fitted with the 199 permuted datasets (function '*as.randtest*' in the the '*ade4*' package ver. 1.7-10 – [73]). The statistical significance of the model coefficients for interactions between alien/native status and the other explanatory variables was tested in the same way, except that the comparisons between the model coefficients and the coefficients obtained from the permutation trials were two-tailed.

Results

3,059 species recorded from 2,840 island sites in the PREDICTS database were already classified as native or aliens by 42 data sources. There were 13,060 unique combinations of island and species with a Latin binomial, of which 1,109 (for 1,039 species) could be classified using the island-specific databases, 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.

The resulting data (available at https://doi.org/10.5519/0047472) included 799 alien species (Table 2 in S1 File) from 4,799 sites in 99 studies, 38 islands and 21 countries as well as 5,522 native species (Table 2 in S1 File) from 7,354 sites, in 157 studies, 79 islands and 29 countries. In total, we were able to classify ~52% of the island biodiversity records in the PREDICTS database as native or alien (Table 3 in S1 File), and retained ~70% of the island studies and ~75% of island sites in the PREDICTS database.

Effects of human pressures on native and alien species

The best random-effects structure for the abundance and richness models included random slopes for land uses within study and random intercepts of study and block within study (Table 6 in S1 File); however, failure of richness models with random slopes to converge caused us to model richness without random slopes. Aliens and natives responded very differently to human pressures, in terms of both overall abundance (Table 7 in S1 File) and species richness (Table 8 in S1 File).

On average, ~17% of the species and total abundance in sites in minimally-disturbed primary vegetation (PriMin) corresponded to alien species (and ~83% to native species) (Figs 5 and 6 in S1 File). Compared with PriMin, three land uses had significantly lower overall abundance of natives: pastures (-33%), plantation forests (-24%) and secondary vegetation (-13%) (Fig 1). By contrast, aliens were very much more abundant in all land uses – especially the human-dominated land uses – than in PriMin (Fig 1). Though the effects of DistRd on abundance were weaker and less clear (Table 7 in S1 File), native abundance increased with DistRd (Fig 2 in S1 File). Native abundance in urban, pasture and cropland sites also tended to be lower with higher HPD (Fig 2), while alien abundance in pastures increases with HPD (Fig 3 in S1 File).

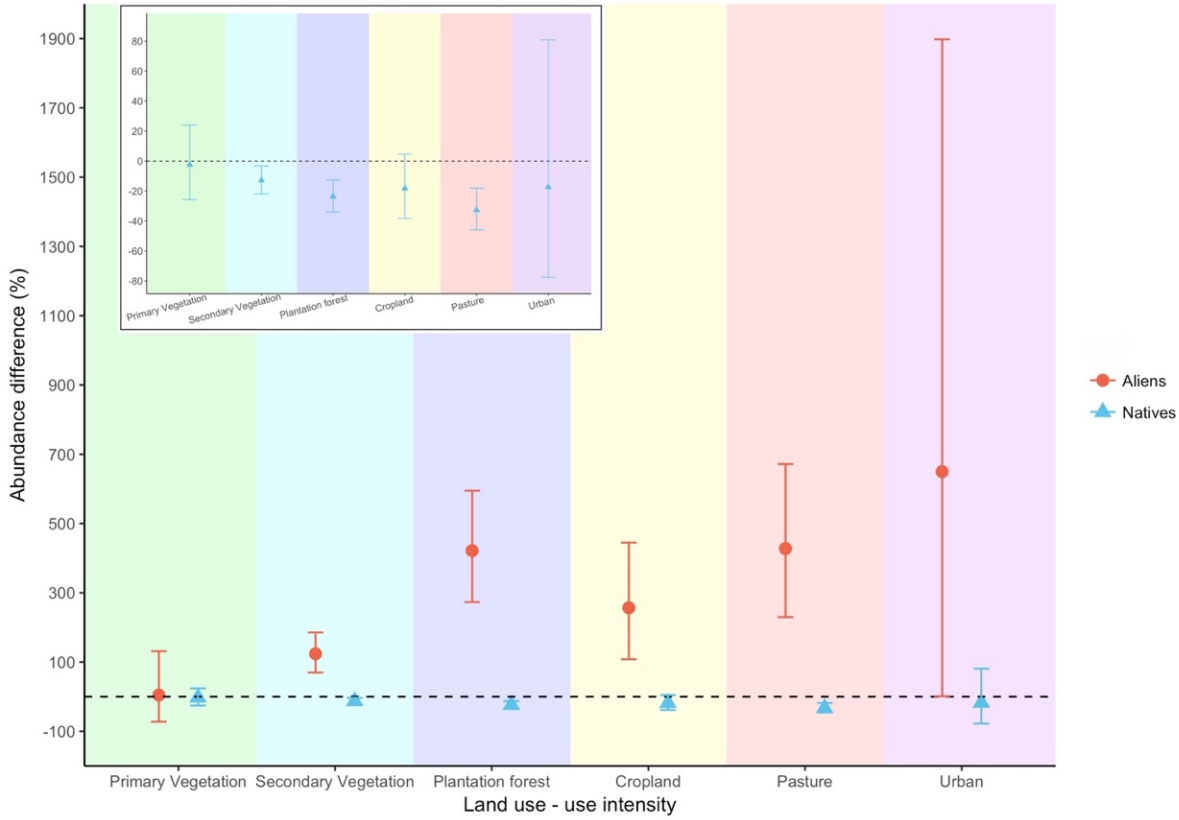

Fig 1. Response of total abundance of aliens and natives to land use. Values indicate decrease or increase in percentage of total abundance using minimally-used primary vegetation as baseline (dashed line). Bars indicate 95% confidence intervals, which are asymmetric because of back-transformation from the square-root scale. The inset expands the y-axis for natives, which are not clearly visible in the main plot.

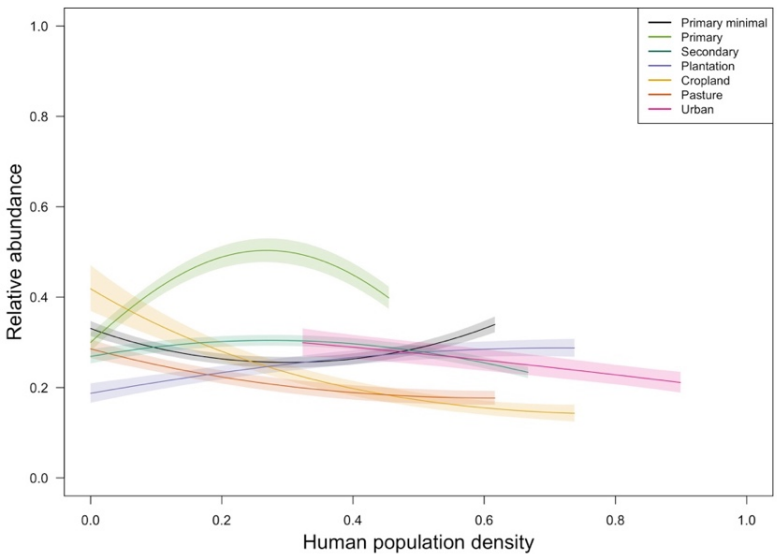

Fig 2. Response of total abundance of natives to human population density (HPD) across land uses. The x limits of each coloured line indicate the 2.5th and 97.5th percentiles for the values of HPD represented in each land use in the model dataset. For clarity, the error bars show half the standard error. HPD values are shown on a rescaled axis (as fitted in the models). Abundance is shown on a zero-to-one scale (i.e., abundance rescaled within studies but back-transformed from the square-root scale).

Agricultural land uses had markedly lower native species-richness, but very much higher alien species-richness, than seen in PriMin sites (Fig 3). HPD had only weak effects on numbers of native (Fig 4) and alien (Fig 4 in S1 File) species within most land uses, but the number of native species in some land uses tended to decline as HPD increases (Fig 4). Native species-richness tended to be lower nearer to roads in human-dominated land uses, whereas (except in urban sites) alien species-richness tended to be higher nearer to roads (Fig 5).

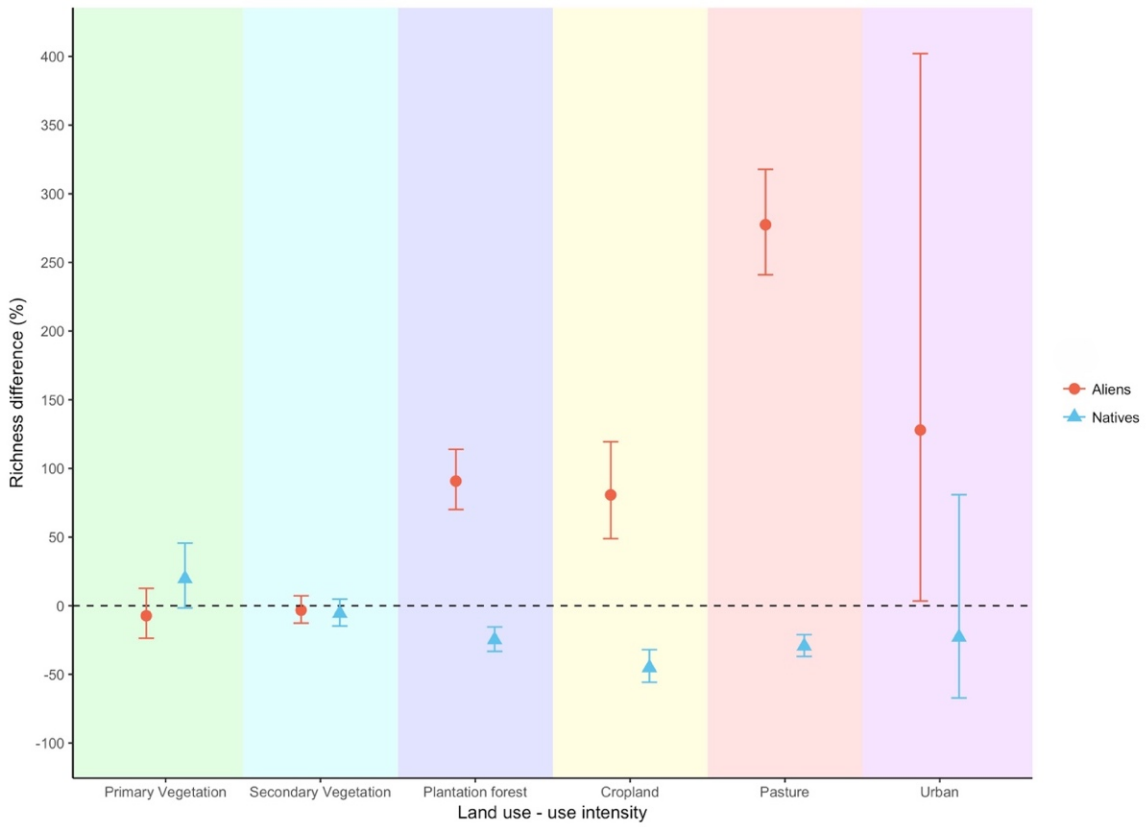

Fig 3. Response of richness of aliens and natives to land use. Values indicate decrease or increase in percentage of species richness using minimally-used primary vegetation as baseline (dashed line). Bars indicate 95% confidence intervals and are asymmetric because of back-transformation from the logarithmic scale of the models.

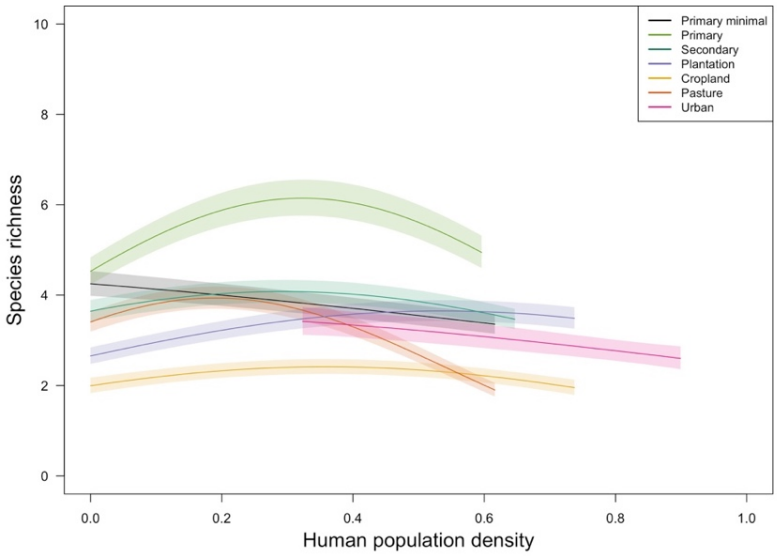

Fig 4. Response of richness of natives to human population density across land uses. Values of human population density are shown on a rescaled axis (as fitted in the models).

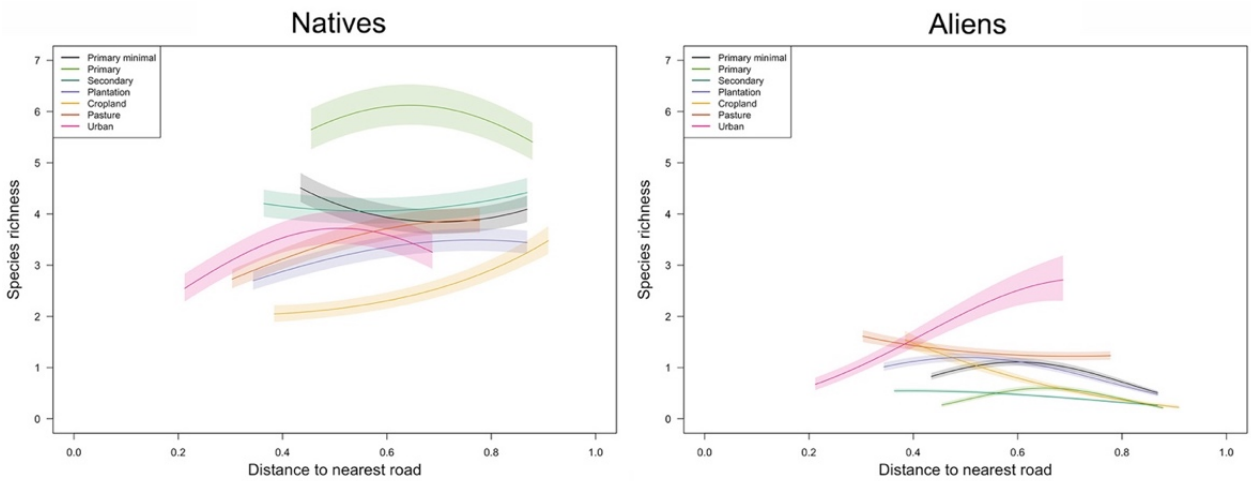

Fig 5. Response of richness of aliens and natives to distance to the nearest road. Distance to road values are shown on a rescaled axis (as fitted in the models).

Island traits as predictors of alien abundance and richness

The models relating alien abundance to island area or GDP per capita used data from 85 studies in 30 islands, whereas the corresponding species-richness models used data from 99 studies and 39 islands. Because some islands lacked data for surrounding landmass, the model relating this factor to alien abundance used data from 65 studies from 26 islands, whereas the alien richness model used 76 studies from 35 islands (Table 9 in S1 File).

For all six models, the best random-effects structure included random intercepts of study and island. None of the models could be simplified – land use interacted significantly with each island characteristic (Tables 11 and 13 in S1 File). However, only a few land uses had significant interaction coefficients (Figs 8 and 10 in S1 File), 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 (Fig 6): sites within most land uses (but not pastures or plantation forests) have most alien species on those islands with least surrounding landmass. This trend was particularly strong in PriMin and urban sites.

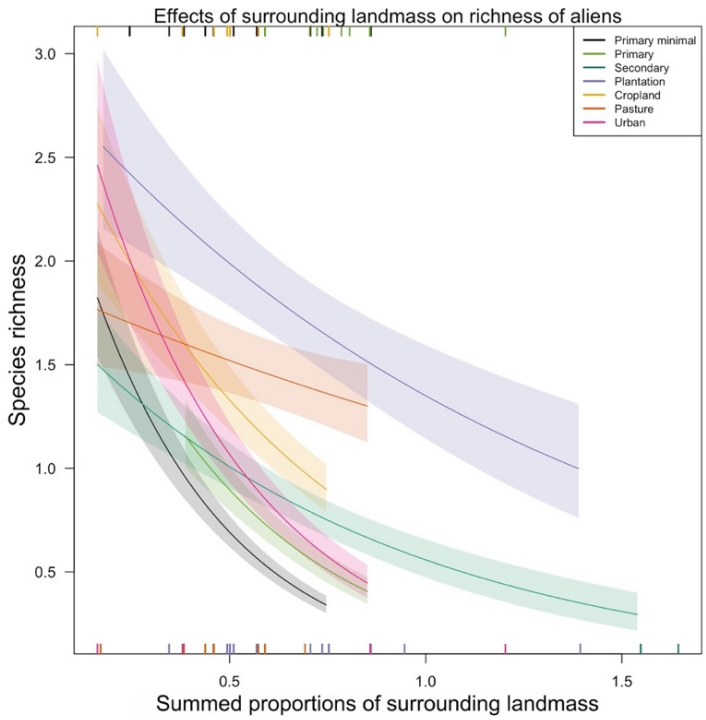

Fig 6. Effects of surrounding landmass on richness of alien species across land uses. For clarity, the error bars show half the standard error. The lines are curved because the response variable has been back-transformed from the logarithmic scale of the model. Slopes that are significantly different from zero: Primary minimal (-2.9, P= <0.001), Primary vegetation (-2.3, P= <0.01), Secondary vegetation (-1.2, P=0.05), Cropland (-1.6, P= <0.05) and Urban (-2.5, 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 overlap, so some data is not visible.

Land use and compositional similarity of native vs alien assemblages

The models of compositional similarity included 91 studies, 60 having data for alien assemblages (2,780 sites; 25 islands; 597 species) and 90 having data for natives (4,293 sites; 32 islands; 3,199 species). All interactions were significant in both models (Table 15 in S1 File). For both J_A and J_R, the decline in similarity with geographic distance is significantly

steeper for alien assemblages than for native, whereas the reverse is true for the decline with environmental distance (Table 16 and Fig 12 in S1 File).

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 than native assemblages, for both J_A and J_R (Fig 7; Fig 13 in S1 File). Alien assemblages of PriMin sites were more compositionally similar to each other than to those in other land uses, especially agriculture. In contrast, native assemblages of PriMin sites were slightly less similar to each other than to assemblages of sites in most other land uses.

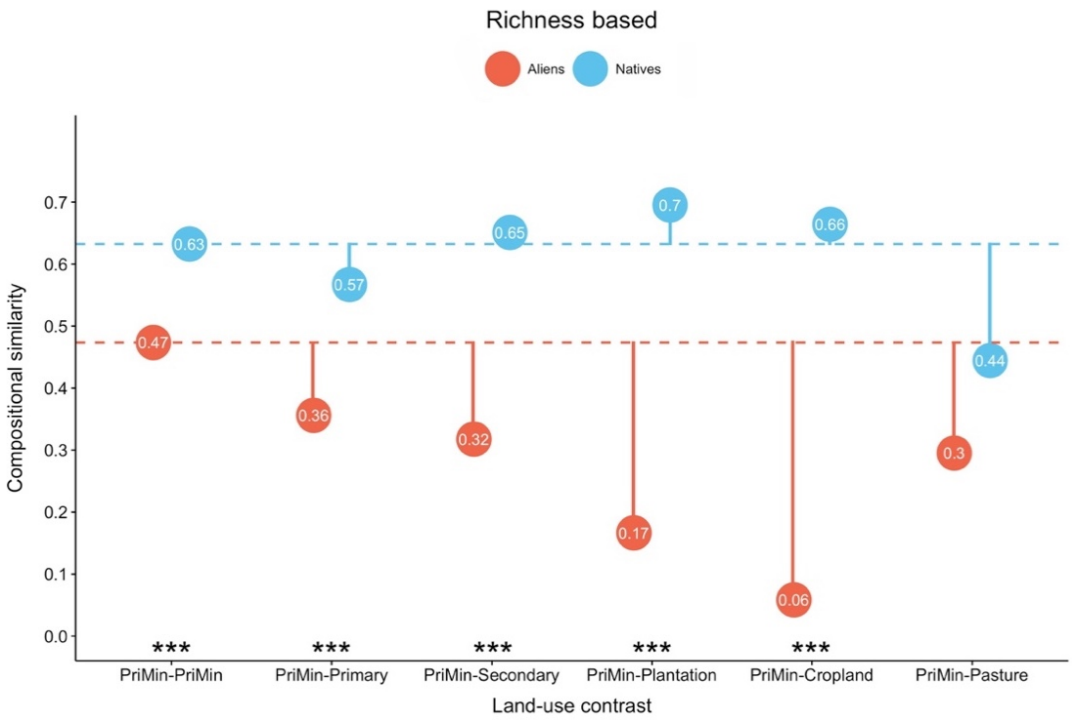

Fig 7. J_R estimates for land-use contrasts where site *i* is in PriMin. Solid lines show the magnitude of change in J_R driven by change to different land uses; the baseline is compositional similarity between PriMin sites for alien and native assemblages respectively (dashed lines). Significance (indicated 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 (for these coefficients, see Table 16 in S1 File) Significance code: 0.005***

Moving to compositional similarity within a land use, pairs of sites within most land uses tend to have more similar assemblages than do pairs of PriMin sites, for both alien and native assemblages and for both J_A and J_R (Fig 8; Fig 14 in S1 File). 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. Reduction of spatial beta diversity was stronger in native than alien assemblages only in models for J_A in secondary vegetation and pastures – and then only slightly so (Fig 14 in S1 File).

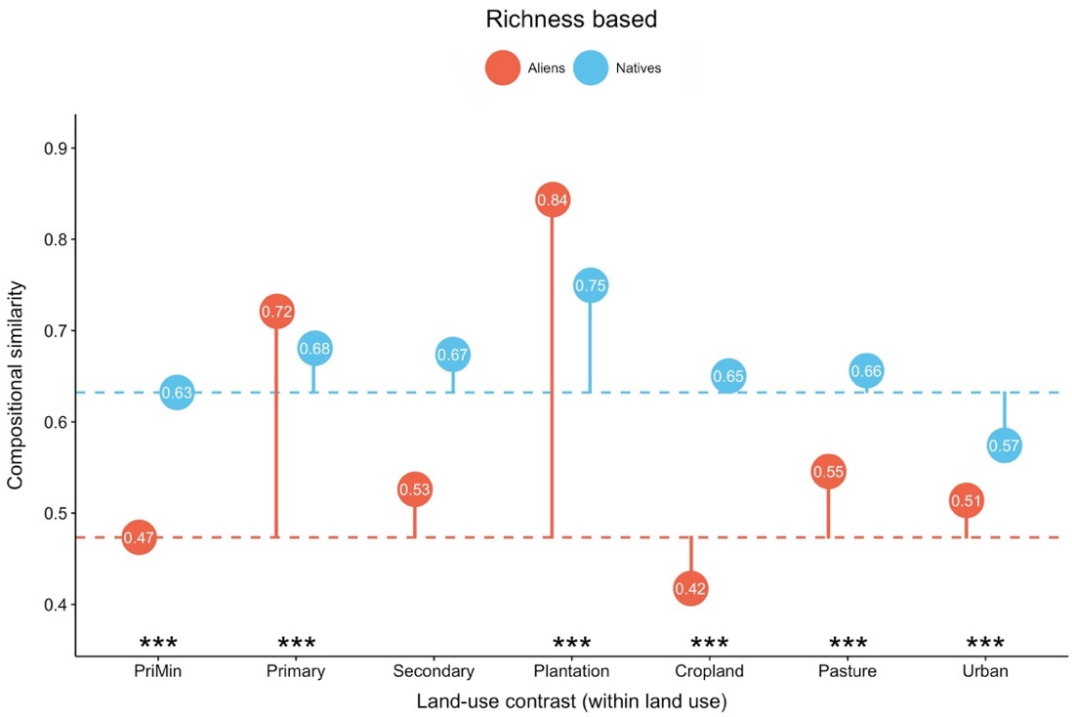

Fig 8. J_R estimates for alien and native assemblages in sites within the same land use. Each category corresponds to a land-use contrast (i.e., Cropland= Cropland-Cropland). Solid lines show the magnitude of change in J_R using PriMin-PriMin compositional similarity as baseline (dashed lines). Significance connotation and codes as in Fig 7.

Discussion

Human-dominated land uses markedly decrease the abundance and richness of native species in island sites 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 native [34,74] and narrow-range species [75], and with the hypothesis that alien species can be very successful in disturbed habitats [12,76–78]. Our results also agree with syntheses that have highlighted agriculture as a main cause of biodiversity loss [79,80]: croplands and pastures showed the largest reductions in native species-richness and, in pastures, abundance.

Most sites in minimally-disturbed primary vegetation have very few alien species with a low total abundance (although there are exceptions – Figs 5 and 6 in S1 File), contributing to the

extreme percentage increases seen in human-dominated land uses. In our final dataset, on average, ~17% of the species and total abundance in minimally-disturbed sites corresponded to alien species. Although this proportion is small, the presence of alien species even among the sites with least human impact violates the assumption of space-for-time substitution and means that statistical models are likely to underestimate the net effects of land-use change on local assemblages [81]. Our data do not permit estimation of the proportion of aliens in minimally-impacted mainland sites: it might be either higher (because of greater connectivity) or lower (because mainland assemblages are less likely be undersaturated).

Alien species are much more common on human-dominated sites than on more natural sites (especially minimally-used primary vegetation), as expected from their tolerance to disturbed conditions, their colonisation ability and the incumbency advantage of native species in undisturbed sites [12]. The high abundance of aliens in pastures and cities (Figure 1) has been highlighted previously [25,82–85], and often follows from intentional introduction (e.g., for livestock forage [86]; or, in cities, for trade [87]). Overall, land-use change boosted alien abundance more than alien richness, suggesting that aliens able to tolerate the extreme conditions of these drastically altered habitats can become very successful [88,89], perhaps partly because island natives are poor competitors in human-dominated land uses [12].

Many island natives seem to need 'people-free land' [90–92]: higher human population density reduces native abundance and richness not only in most human-dominated land uses but also in minimally-used primary vegetation. Even without their influences on habitat modification or invasive species, human populations in natural ecosystems may represent a threat to native species, e.g., through hunter-gathering [79,90].

Sites closer to roads have more alien species but – in human-dominated land uses – fewer natives. These effects, though not particularly strong, were as expected: the development of roads or other infrastructure involves a direct traffic of vehicles and goods and severe modification of natural habitats [43,93,94], all of which can promote the arrival and establishment of alien species [42,43,94,95]. Additionally, road development can worsen the conditions of sites that have seen land conversion, causes habitat fragmentation [96] and leads to collisions with vehicles, all of which increase mortality [93,94] potentially leading to the loss of vulnerable native species.

Sites on more isolated islands have higher absolute numbers of alien species across most land uses and higher alien abundance in primary vegetation (Fig 8 in S1 File). These results support a recent suggestion that island remoteness promotes invasions by alien species worldwide [40], and provide further evidence that island biogeography of exotic species is not defined by the natural species–isolation relationship [38,39]. Redding et al. [31] recently found

that the presence of other groups of introduced species at the introduction location is one of the main determinants of successful establishment, suggesting an important role for location-specific factors. The reduced diversity of remote islands [37] can make them more invasible [39,97] (but see [98]) because of their high resource availability, missing functional groups and/or low pressures from competitors, pathogens or predators [13,99]. Isolated islands are expected to have particularly small species pools because of restricted immigration [37], leading to lower species richness per unit area and smaller samples from the set of potential species that can survive in different conditions [18]. 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. We found that alien richness and abundance in minimally-disturbed primary vegetation decreases rapidly as surrounding landmass (and hence the source pool of natural colonists) increases, suggesting that saturated native assemblages are able to stem the influx of aliens [100].

Factors related to the arrival or introduction of alien species are also likely to partly drive the high alien richness in human-dominated sites on isolated islands. In particular, propagule and/or colonisation pressure – positively related to the establishment of aliens [8,31] – might be higher in remote islands [38]: because such islands often have few native species that can be used for farming, hunting, as sources of fuel or for other economic purposes [13,38], there may be more intentional releases of alien species and high levels of imports [14].

Conversion of minimally-used primary vegetation to other land uses affects composition of alien assemblages more dramatically than native assemblages: the low number and abundance of alien species in natural habitats (Figs 5 and 6 in S1 File) means that other land uses are less likely to have alien species in common with minimally-disturbed sites. The native assemblages at disturbed sites on islands are likely to be nested subsets of undisturbed communities, given the small source pool of potential native colonists, their lack of adaptation to disturbed sites, and their poor competitiveness [13,18,101]. Pastures seem to be an important exception, including some native novel species. The pasture sites that are compared with minimally-used primary vegetation are mostly (133 out of 141 sites) not used intensively, and they are largely from South Island (New Zealand), Australia, Madagascar and Tierra del Fuego, where rangeland (i.e., ecosystems where the native vegetation has the potential to be grazed [102]) is common [103]. Resilient species among the natives may be able to establish in such rangelands and other low-intensity grazed sites.

Most land uses have lower spatial beta diversity than minimally-disturbed sites, for both alien and native assemblages. This biotic homogenization is stronger for alien assemblages, in line with previous studies of particular human-dominated land uses [104], suggesting that the gain

of alien species in disturbed sites might be the main cause of assemblage homogenization on islands [104,105]. Addition of alien species drives homogenization if the same species become widespread across disturbed sites [36]. Our results suggest that such homogenization may be occurring in forested land uses (i.e., particularly in plantations and primary vegetation with light or intense use): these are likely to harbour few alien species (since competition is higher than in significantly disturbed habitats) that are common across these sites. In contrast, alien assemblages in croplands are more heterogeneous than assemblages within minimally-disturbed sites, suggesting that the new alien species in this land use are not ubiquitous across sites [36,106], perhaps due to different aliens establishing with different crops. 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 [36] and the persistence of common species.

Because we were not able to classify all species as alien or natives, our dataset includes a restricted number of islands. Expanding the dataset to more islands with more different characteristics would increase the power to detect effects of island characteristics. 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 site-level richness and abundance of alien species might simply be outweighed by anthropogenic factors such as colonisation pressure. High economic activity is expected to ease the arrival and establishment of alien species [7,8,107], which we did not find; but the country-level values of per-capita GDP may not be a good reflection of the economic activity of the islands.

Our models suggest that natives can be replaced by alien or invasive species in degraded habitats [77,108] and that, on islands, species turnover caused by land-use change might be driven mainly by novel alien species rather than novel native species. In contrast, it is likely that mainland settings, having larger species pools than islands, could provide a larger number resilient natives able to establish and compete in disturbed sites [18]. Hence, effects of land-use change on mainland assemblage composition may be driven by both alien and native synanthropic species missing from natural habitats but assembling into novel human-dominated ecosystems.

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 [109]. We did not account for the effects of alien richness or abundance on native communities, but previous studies have highlighted habitat modification as the main driver of biodiversity decline, outcompeting other drivers such as invasive species or climate change [79,110]. However, on islands, alien species are important drivers of native extinctions [92,111]; therefore, more comprehensive

analyses evaluating interactions between different human pressures are needed to disentangle the importance of different threats in driving losses of island biodiversity.

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Supporting information

S1 File. Supporting figures and tables.