CONSERVATION BIOLOGY

Globally threatened vertebrates on islands with invasive species

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Global biodiversity loss is disproportionately rapid on islands, where invasive species are a major driver of extinctions. To inform conservation planning aimed at preventing extinctions, we identify the distribution and biogeographic patterns of highly threatened terrestrial vertebrates (classified by the International Union for Conservation of Nature) and invasive vertebrates on ~465,000 islands worldwide by conducting a comprehensive literature review and interviews with more than 500 experts. We found that 1189 highly threatened vertebrate species (319 amphibians, 282 reptiles, 296 birds, and 292 mammals) breed on 1288 islands. These taxa represent only 5% of Earth's terrestrial vertebrates and 41% of all highly threatened terrestrial vertebrates, which occur in <1% of islands worldwide. Information about invasive vertebrates was available for 1030 islands (80% of islands with highly threatened vertebrates). Invasive vertebrates were absent from 24% of these islands, where biosecurity to prevent invasions is a critical management tool. On the 76% of islands where invasive vertebrates were present, management could benefit 39% of Earth's highly threatened vertebrates. Invasive mammals occurred in 97% of these islands, with *Rattus sp.* as the most common invasive vertebrate (78%; 609 islands). Our results provide an important baseline for identifying islands for invasive species eradication and other island conservation actions that reduce biodiversity loss.

INTRODUCTION

The loss of biodiversity is one of the most acute global issues linked with severe negative impacts on people and the environment (*1*–*3*). Consequently, urgent action is required to reduce biodiversity loss (*4*, *5*). The decline of populations and disappearance of species from islands and freshwater systems are disproportionately more rapid than anywhere else worldwide (*6*, *7*). Islands, in particular, comprise only 5.3% of global land area (*8*) yet are hotspots of biodiversity (*7*, *9*, *10*). Islands are also epicenters of biodiversity loss. They host 61% of known extinctions and 37% of critically endangered species (*7*).

Here, we examine the distribution of highly threatened vertebrates [using the classification by the International Union for Conservation of Nature (IUCN) Red List (*11*)] on the world's ~465,000 islands (*8*) as well as the co-occurrence of invasive species, the primary driver of their extinction (*12*–*14*) on these islands. Islands are isolated land masses that often maintain simplified ecological systems containing highly adapted and unique species with typically small population sizes, low reproductive rates, and a lack of predator defenses compared with continental counterparts (*9*, *15*, *16*). These traits make island species more prone to human-related impacts. There are many examples of human-mediated extinctions of island vertebrates, such as the Dodo (*Raphus cucullatus*) and the Navassa Rhinoceros Iguana (*Cyclura onchiopsis*), which were extirpated by human exploitation and introduced predators (*11*, *17*).

Invasive species are the primary driver of island extinctions (*12*, *17*, *18*). They are implicated in 86% of extinctions of island species since 1500 A.D. (*18*) and currently endanger 596 species of birds, mammals, and reptiles listed as threatened on the IUCN Red List (*17*). The ecological consequences of population decline and extinction are widespread (*19*). For example, the loss of island-breeding seabirds by introduced predators can alter soil fertility and ultimately transform plant and below-ground ecological communities (*20*, *21*). Extinctions also result in lost mutualistic interactions. The extinction of large frugivores (for example, *R. cucullatus* and *Cylindraspis triserrata*) from Mauritius left endemic plants, which are dependent on germination via digestion by these frugivores, without the ability to reproduce (*22*, *23*). The extinction of honeycreepers from Hawaii disrupted pollination of native lobelioids, which are now critically endangered (*11*, *24*).

Fortunately, island restoration activities can stop and even reverse some of these trends (*25*). Many vertebrates are highly threatened, but also often socially valued, and well studied (*26*, *27*), making them important targets for conservation that can also benefit whole-island ecosystems and lesser known taxa (*28*–*30*). For example, invasive mammal eradications have provided beneficial outcomes for many threatened island endemics (*31*, *32*), including 62 species classified as threatened on the IUCN Red List (*33*). Prevention, control, and eradication of invasive species is identified as one of the 20 Aichi Biodiversity Targets for global biodiversity conservation (*34*). However, few studies have elucidated the specific island locations of island breeding species and where they overlap with potentially damaging invasive species (*35*). Defining this overlap is necessary to pinpoint where conservation actions can prevent extinctions (*35*, *36*). To address this gap, we created a unique data set [the Threatened Island Biodiversity Database (*37*); fig. S1 and table S1]. The database documents which of the world's islands support breeding populations of terrestrial vertebrates (amphibians, reptiles, birds, and mammals) classified as critically endangered or endangered by the IUCN [hereafter, "highly threatened"; (*11*)]. In addition, we examine which islands with highly threatened vertebrates are colonized by invasive vertebrates (fig. S2 and table S2).

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Here, we address the following questions: (i) How many highly threatened island vertebrate species and populations occur on islands? (ii) What are the biogeographic and socioeconomic patterns in the distribution of these highly threatened vertebrates? (iii) Where do invasive vertebrates co-occur with highly threatened vertebrates on islands? (iv) Which vertebrate groups co-occur most frequently with invasive vertebrates? This is a novel comprehensive global synthesis of the biogeography of highly threatened island vertebrates and invasive species on islands. It underpins ongoing work to identify the most important islands for invasive vertebrate eradications and can be used in systematic planning to conserve island biota and as a baseline to document future changes in the status of highly threatened insular vertebrate taxa.

RESULTS

Highly threatened vertebrates on islands

We identified 1189 highly threatened vertebrate species that breed on islands, including 319 amphibians, 282 reptiles, 296 birds, and 292 mammals (Fig. 1 and Table 1). Ninety-two percent (1094) of these vertebrates breed exclusively on islands, and the remaining 8% (95) breed on both islands and continents (data file S1). These taxa represent only 5% of all IUCN-assessed extant terrestrial vertebrates but a disproportionately higher percentage (41%) of all highly threatened terrestrial vertebrates when compared with species on continental land masses (*11*).

The 1189 highly threatened vertebrate species breed on 1288 islands. These islands represented only 0.3% of the ~465,000 islands worldwide (*8*) but comprise 61% of global island area. Highly threatened vertebrates occur on some of the largest islands in the world (mean ± SD = 3684.8 ± 37,871.8 km^2; median, 3.58 km^2), although the island size was variable (range, 5.5×10^{-04} to 773,848.3 km^2), compared with islands without highly threatened vertebrates (all other islands worldwide; Fig. 2A). Similarly, 63% of these islands are in the tropics (versus 19% of other islands; Fig. 2B), most often in the central Indo-Pacific biogeographic region (32%; Fig. 3A), particularly in Oceania (21%; Fig. 3B), and are likely to support tropical and subtropical moist broadleaf forest habitat (42%; Fig. 3C and data file S2). Islands with highly threatened vertebrates occur in 102 countries or territories, of which 51% are considered high income [median gross domestic product (GDP) per capita = $32,696], yet this was lower than expected when compared with other islands (85% high income; median GDP per capita = $42,337; Fig. 2C and data file S2). These islands were broadly distributed across countries yet were most often found in Micronesia, New Zealand, and Indonesia (each with 7% of their islands supporting breeding populations of highly threatened vertebrates), compared with islands without threatened vertebrates, which were most often found in Canada.

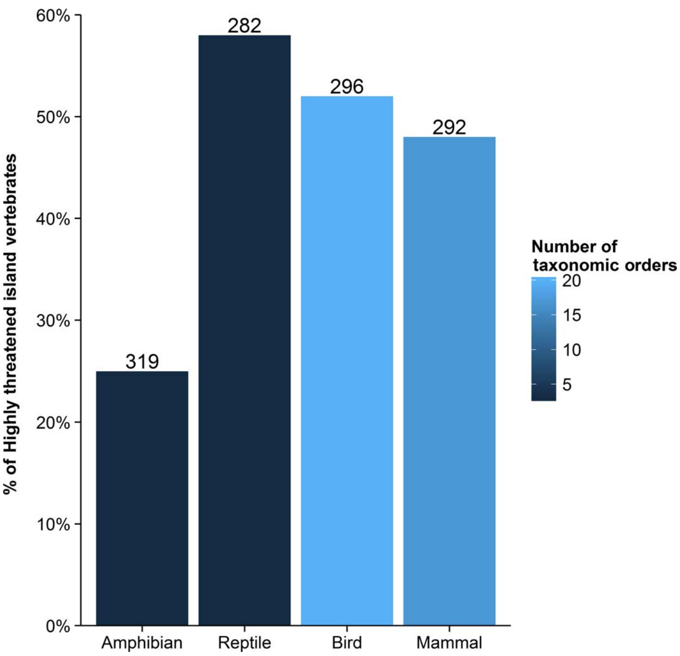

Fig. 1. Percentage of highly threatened vertebrates breeding on islands by vertebrate class. Numbers above the bar give the total number of highly threatened species that breed on islands. Color shading indicates the number of taxonomic orders within each island vertebrate class.

Breeding populations

Of the 1189 highly threatened terrestrial vertebrate species, there were 2890 populations breeding on 1288 islands (a population represents one species breeding on one island; Fig. 4). The number of highly threatened species on an island increased nonlinearly with island size ($R^2 = 0.38$, $F = 823.4$, $df = 1$, $P < 0.01$). Islands with the most highly threatened vertebrate populations included Madagascar (156 species), Sri Lanka (76 species), Hispaniola (68 species), and Cuba (60 species). Cumulatively, these four islands were home to 30% (360) of highly threatened vertebrates, including 56% of amphibian, 33% of reptile, 9% of bird, and 21% of mammal species.

Highly threatened vertebrates bred on an average of 2.5 islands (median, 1; range, 1 to 77; Fig. 2), and 70% (829) of species were restricted to breeding on a single island, including 87% of amphibian, 67% of reptile, 51% of bird, and 65% of mammal species. Biogeographic patterns in threatened birds and reptiles tended to be different from amphibians and mammals (Table 2). Threatened birds and reptiles occurred on more islands (mean ± SD islands = 3 ± 6 and 3 ± 7 and maximum islands of 40 and 77, respectively) that were smaller (median, 23.5 and 19.8 km^2, respectively) and in higher income countries (55 and 46%, respectively) than other highly threatened vertebrates. Although threatened birds and reptiles overlapped in similar realms across the tropics, threatened reptiles were concentrated on tropical islands (734 populations; 84%), particularly in Oceania (209 populations) and the Neotropics (206 populations). Meanwhile, threatened bird populations were distributed across both tropical (499 populations; 49%) and temperate (465 populations; 46%) climates, primarily driven by the distribution of threatened seabirds.

Population extinctions

Of the 1189 highly threatened vertebrates, 8% (99 species) experienced population extinctions (that is, an extirpation, the total loss of a species from an island, but not globally; table S1). The 99 species lost an average of three populations (mean ± SD = 2.7 ± 3.6; median, 2; range, 1 to 28), which predictably scaled nonlinearly with the number of islands from which a species was originally breeding ($R^2 = 0.3$, $F = 2.1$, $P < 0.01$). In total, 273 population extinctions occurred in recent centuries from 202 islands. The largest numbers of population extinctions occurred in French Polynesia (Tuamotus, Marquesas) and the United States (Northern Marianas, Hawaii; data file S2). Guam experienced the largest number of population extinctions from a single island (8 species, including 2 reptiles, 5 birds, and 1 mammal population). Forty highly threatened vertebrates have become extinct from ≥50% of their islands (table S3), and birds have lost more populations than other highly threatened vertebrate: 19% (56) of highly threatened birds have experienced ≥1 population extinction (islands lost: mean ± SD = 3 ± 4.5; median, 1; maximum, 28).

People and invasive vertebrates on islands

Nearly half of the 1288 islands (597; 47%) were uninhabited (data file S2), whereas 130 (10%) were minimally inhabited (1 to 100 people), and 220 (27%) had greater than 10,000 people. The number of human

Table 1. Taxonomic comparisons of the 2919 highly threatened terrestrial vertebrates and the 1189 highly threatened terrestrial vertebrates on islands. CR, critically endangered; EN, endangered.

Taxonomic class	All terrestrial vertebrates (*11*)				All terrestrial vertebrates from islands		
	Total taxa (% of described taxa)	# of CR and EN (% of total)	Red List category (% of total)		Total CR and EN (% of total CR and EN)	Red List category (% of total CR and EN)	
			CR	EN		CR	EN
Amphibia	6106 (24%)	1255 (21%)	498 (8%)	757 (12%)	319 (25%)	109 (34%)	210 (34%)
Reptilia	4160 (17%)	486 (12%)	162 (4%)	324 (8%)	282 (58%)	105 (58%)	177 (37%)
Aves	9538 (38%)	566 (6%)	187 (2%)	379 (4%)	296 (52%)	119 (52%)	177 (40%)
Mammalia	5337 (21%)	612 (11%)	187 (4%)	425 (8%)	292 (48%)	96 (48%)	196 (33%)
Total	25,141	2919 (12%)	1034 (4%)	1885 (7%)	1189 (41%)	429 (36%)	760 (64%)

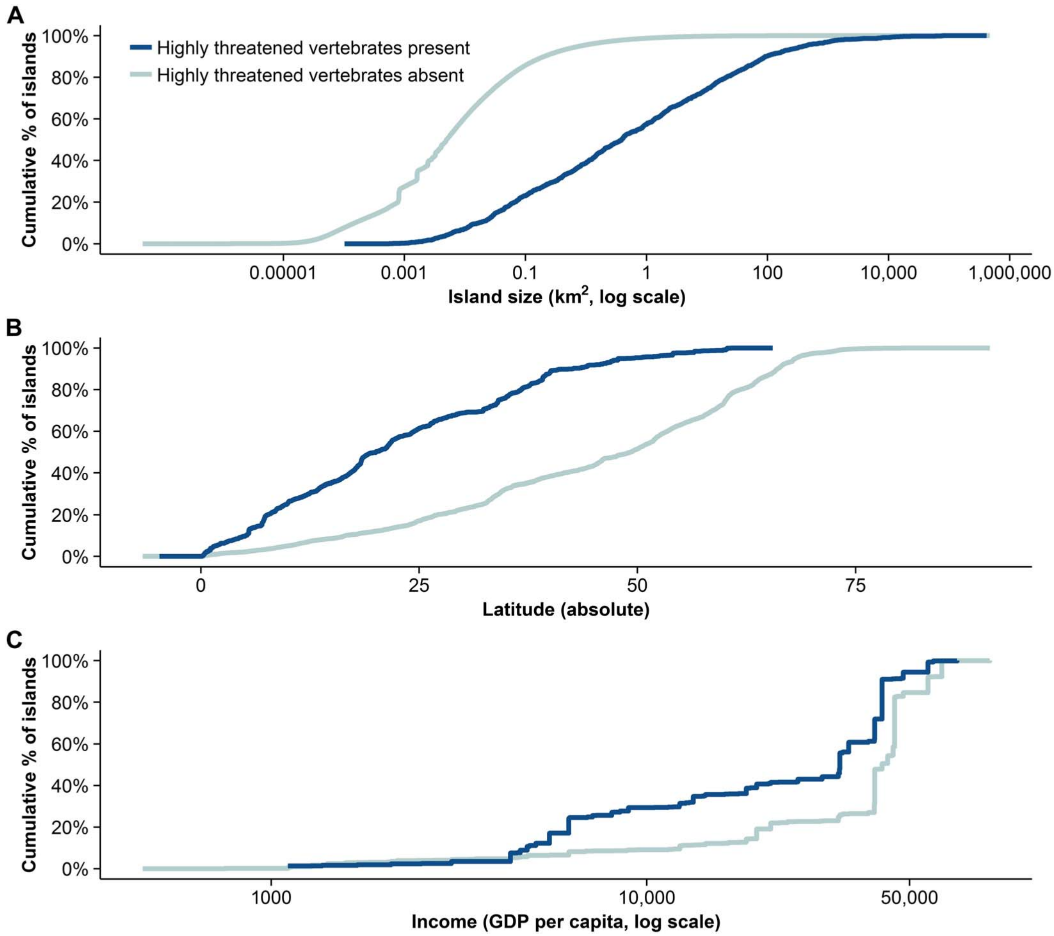

Fig. 2. Attributes of islands globally with and without highly threatened vertebrates. Comparisons of (**A**) island size (km^2), (**B**) absolute latitude, and (**C**) GDP between islands with and without highly threatened terrestrial vertebrate species. Islands with highly threatened vertebrates were larger, more equatorial, and in countries with lower GDP per capita.

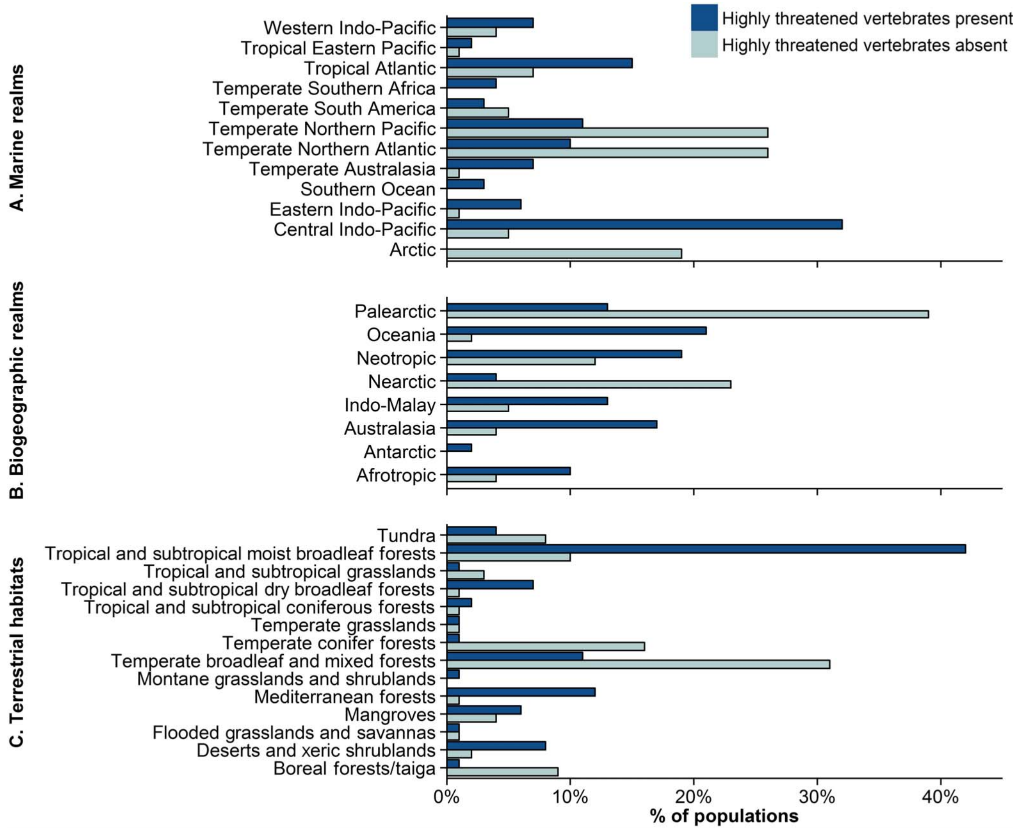

Fig. 3. The ecoregions of islands globally with and without highly threatened vertebrates. Comparisons across (**A**) marine realms, (**B**) biogeographic realms, and (**C**) terrestrial habitats for islands with and without highly threatened terrestrial vertebrate species present. Islands with highly threatened vertebrates were located primarily in the central Indo-Pacific, Oceania, and the Neotropics and supported primarily tropical and subtropical moist broadleaf forest habitats.

inhabitants on islands increased nonlinearly with island size (R^2 = 0.39, F = 163.58, P < 0.01).

The presence or absence of non-native terrestrial invasive vertebrate species (amphibians, reptiles, birds, and mammals; hereafter, "invasive vertebrates") was confirmed on 1030 islands with highly threatened vertebrates, of which 779 (76%) had at least one invasive vertebrate present (Fig. 5). We identified 37 islands with invasive vertebrates that are subject to ongoing eradication efforts where at least one invasive vertebrate species is undergoing removal. Invasive vertebrates were absent from 251 islands (24%). We were unable to determine the status of invasive vertebrates on 258 islands.

We identified 4178 populations of 320 species of invasive vertebrates (table S4). Invasive mammals were found on 753 islands (97% of islands with an invasive vertebrate) and were the most common invasive class (3361 populations of 175 species). Invasive rats (*Rattus sp.*) occurred on 609 islands (47% of all islands and 78% of islands with invasive vertebrates; table S5). Other common invasive vertebrates included ungulates (on 446 islands), such as pigs (*Suidae*), cows (*Bovidae*), and goats (*Cervidae*); carnivores, such as cats (*Felidae*; on 419 islands) and dogs (*Canidae*; on 350 islands); and rodents, such as mice (*Mus sp.*; on 352 islands).

In total, 2217 highly threatened vertebrate populations (77%) co-occurred with an invasive vertebrate, representing at least one population of 1145 species (96%) and 39% of all highly threatened terrestrial vertebrates on the IUCN Red List. Invasive vertebrates occurred on all of the breeding islands for 87% of highly threatened vertebrates (all islands of 97% of amphibian, 83% of reptile, 80% of bird, and 89% of mammal species contained an invasive vertebrate). Human habitation was a strong predictor of the presence of invasives: 546 of 685 islands with people (80%) supported invasive vertebrates (χ^2 = 279, df = 1, P < 0.0001). Invasive vertebrates were on 230 uninhabited islands (30%), and an additional 90 islands (12%) were minimally inhabited (<100 inhabitants). Invasive vertebrate management on these islands could potentially benefit up to 226 populations of 162 threatened vertebrate species. Highly threatened birds (Procellariformes, 20 species; Passeriformes, 19 species) and reptiles (Squamata, 49 species) most frequently occurred on these islands, yet the list represents 3% of amphibian, 18% of reptile, 26% of bird, and 9% of mammal species, including 27 single-island endemics (table S6) and 5.5% of all highly threatened terrestrial vertebrates on the IUCN Red List (table S6).

DISCUSSION

Biogeographic patterns in highly threatened vertebrate species

Highly threatened vertebrates were found on islands across all oceans and habitats and within 102 countries or territories. Larger islands tended to have more species as well as more people and invasive vertebrates, which was expected on the basis of island biogeography theory (*38*) and recent studies showing area as a predictor of the number of native species, humans, and invasive species present (*39*). Although most highly threatened vertebrates were highly endemic (most were restricted to a single island), there were differences in biogeographic patterns among

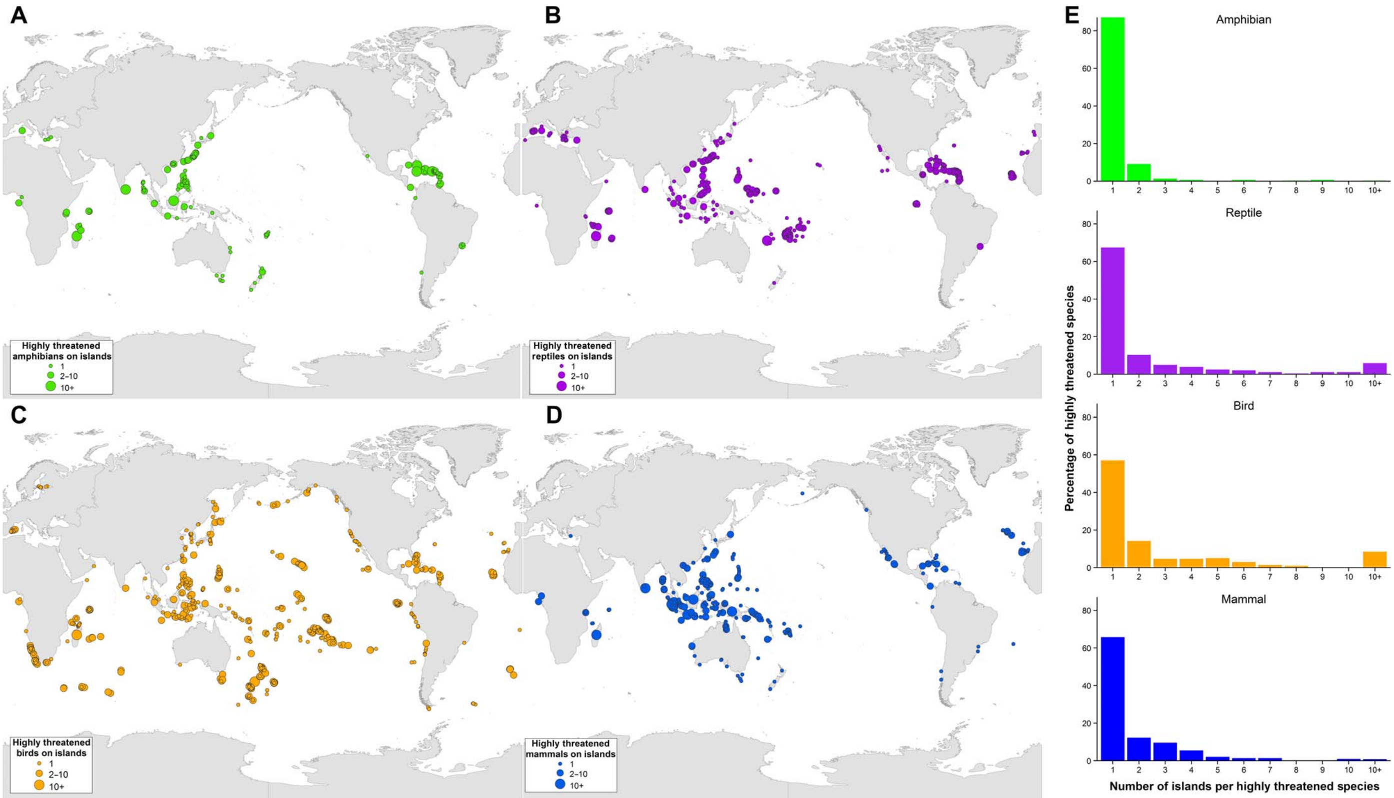

Fig. 4. The global distribution of highly threatened vertebrates. Location of islands supporting populations of highly threatened (**A**) amphibians, (**B**) reptiles, (**C**) birds, (**D**) mammals, and the number of islands with breeding populations per highly threatened species (**E**).

amphibians, reptiles, birds, and mammals, which are consistent with their different life histories (Table 2). For example, amphibians require access to freshwater and do not easily disperse across saltwater (*40*, *41*). Unsurprisingly, this group was found to be highly endemic and most often found on large continental islands, such as Hispaniola and Sri Lanka. These islands are inhabited by people, with a relatively low per capita income, and nearly all supported invasive vertebrates. Although these biogeographic patterns were similar for highly threatened mammals, particularly nonvolant mammals, mammalian distributions were different from amphibians: Large numbers occurred on Madagascar (36 species; 12% of all threatened island mammals), and 53% of all populations were in the central Indo-Pacific region. Amphibian and mammalian conservation efforts in these regions are often complex and underfunded (*42*), suggesting that a diversity of conservation approaches and funding strategies (for example, national, international, and private) will be necessary to effectively conserve these species.

Highly threatened birds and reptiles tended to have similar biogeographic patterns, occurring on islands that were more often small and uninhabited or minimally inhabited, compared to amphibians or mammals. Birds and reptiles also have higher numbers of population extinctions. Birds were lost from a greater percentage of islands (table S3) than any other taxa, with most population extinctions in French Polynesia (for example, Polynesian ground dove, *Gallicolumba erythroptera*; 80% of islands lost), a known extinction hotspot (*43*, *44*). Although extinctions are linked to susceptibility and timing of threats (*12*, *44*), birds and reptiles that bred on many islands were more likely to have lost populations than those that bred on fewer islands.

Although overarching biogeographic patterns were similar between birds and reptiles, there were some differences. Birds disperse more easily and are a highly diverse class with many different life history strategies (*45*). These factors likely contributed to the broad variability in island characteristics and endemicity patterns observed in highly threatened birds. There was less variation in patterns for reptilian geography, which tended to be confined to specific regions: 25% of all highly threatened island reptiles were in Madagascar, and almost all other reptile populations (48%) occurred in the Neotropics and Oceania (for example, Fiji and Micronesia).

Invasive vertebrates on islands

For the islands with highly threatened vertebrates that were free of invasive vertebrates, biosecurity will be an important strategy for preventing invasives from becoming established (*46*). This is the most cost-effective long-term strategy for managing invasive species on islands (*46*, *47*). However, the majority of islands with highly threatened vertebrates also had invasive vertebrates, most commonly invasive mammals. Rats (*Rattus sp.*) occurred on 78% of these islands, close to the estimated proportion of island regions worldwide with invasive rodents (*48*, *49*). Although not every threatened vertebrate will be affected by an invasive species, invasive mammals such as rats, ungulates, and cats, the three most common invasive vertebrates on islands, are a major driver in vertebrate extinction and endangerment on islands (*17*, *18*). The control or eradication of invasive mammals is a widely applied tool that has likely benefitted more than 200 vertebrate species worldwide (*33*). However, only 11% of previous invasive species eradications from

Table 2. Biogeographic island patterns (total and % of total) for the 2890 breeding populations of highly threatened amphibians, reptiles, birds, and mammal species.

Island characteristic	Amphibian	Reptile	Bird	Mammal
Latitude				
Polar	0 (0%)	0 (0%)	58 (5.68%)	1 (0.17%)
Temperate	56 (13.8%)	137 (15.7%)	465 (45.5%)	97 (16.4%)
Tropical	351 (86.2%)	734 (84.3%)	499 (48.8%)	492 (83.4%)
Biome*				
Boreal forests/taiga	0 (0%)	0 (0%)	14 (1.4%)	0 (0%)
Deserts and xeric shrublands	10 (2.5%)	62 (7.1%)	93 (9.1%)	14 (2.4%)
Flooded grasslands and savannas	2 (0.5%)	7 (0.8%)	2 (0.2%)	4 (0.7%)
Mangroves	48 (11.8%)	61 (7%)	24 (2.3%)	26 (4.4%)
Mediterranean forests, woodlands, and scrub	7 (1.7%)	84 (9.6%)	97 (9.5%)	18 (3.1%)
Montane Grasslands and Shrublands	38 (9.3%)	72 (8.3%)	38 (3.7%)	36 (6.1%)
Temperate broadleaf and mixed forests	14 (3.4%)	11 (1.3%)	188 (18.4%)	22 (3.7%)
Temperate conifer forests	3 (0.7%)	2 (0.2%)	12 (1.2%)	5 (0.8%)
Temperate grasslands, savannas, and shrublands	0 (0%)	0 (0%)	30 (2.9%)	0 (0%)
Tropical and subtropical coniferous forests	0 (0%)	24 (2.8%)	12 (1.2%)	3 (0.5%)
Tropical and subtropical dry broadleaf forests	74 (18.2%)	92 (10.6%)	113 (11.1%)	67 (11.4%)
Tropical and subtropical grasslands, savannas and shrublands	0 (0%)	0 (0%)	7 (0.7%)	15 (2.5%)
Tropical and subtropical moist broadleaf forests	211 (51.8%)	443 (50.9%)	297 (29.1%)	379 (64.2%)
Tundra	0 (0%)	0 (0%)	68 (6.7%)	1 (0.2%)
Biogeographical realm*				
Afrotropic	61 (15%)	125 (14.4%)	209 (20.5%)	55 (9.3%)
Antarctic	0 (0%)	0 (0%)	33 (3.2%)	0 (0%)
Australasia	17 (4.2%)	54 (6.2%)	263 (25.7%)	150 (25.4%)
Indo-Malay	157 (38.6%)	153 (17.6%)	97 (9.5%)	232 (39.3%)
Nearctic	1 (0.2%)	14 (1.6%)	37 (3.6%)	7 (1.2%)
Neotropic	150 (36.9%)	206 (23.7%)	109 (10.7%)	54 (9.2%)
None	0 (0%)	13 (1.5%)	27 (2.6%)	0 (0%)
Oceania	9 (2.2%)	209 (22.3%)	160 (15.7%)	61 (10%)
Palearctic	12 (2.9%)	97 (11.1%)	87 (8.5%)	31 (5.3%)
Marine realm†				
Arctic	0 (0%)	0 (0%)	0 (0%)	1 (0.2%)
Central Indo-Pacific	81 (19.9%)	362 (41.6%)	223 (21.8%)	317 (53.7%)
Eastern Indo-Pacific	0 (0%)	25 (2.9%)	106 (10.4%)	2 (0.3%)
Southern Ocean	0 (0%)	0 (0%)	58 (5.7%)	0 (0%)
Temperate Australasia	12 (2.9%)	1 (0.1%)	160 (15.7%)	16 (2.7%)
Temperate Northern Atlantic	6 (1.5%)	84 (9.6%)	39 (3.8%)	25 (4.2%)
Temperate Northern Pacific	33 (8.1%)	50 (5.7%)	106 (10.4%)	51 (8.6%)

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Island characteristic	Amphibian	Reptile	Bird	Mammal
Temperate South America	5 (1.2%)	2 (0.2%)	51 (5%)	5 (0.8%)
Temperate Southern Africa	0 (0%)	0 (0%)	109 (10.7%)	0 (0%)
Tropical Atlantic	145 (35.6%)	225 (25.8%)	69 (6.8%)	34 (5.8%)
Tropical Eastern Pacific	3 (0.7%)	3 (0.3%)	35 (3.4%)	3 (0.5%)
Western Indo-Pacific	122 (30%)	119 (13.7%)	66 (6.5%)	136 (23.1%)
Island area (km^2)				
Mean (SD)	115,509.54 (199,904.4)	66,076.1 (179,042.9)	21,439.87 (88,367.3)	112,081.68 (233,663.7)
Median	65,721.01	19.82	23.475567	852.55
Income (GDP)‡				
High income	111 (28.2%)	396 (46.2%)	558 (55.6%)	129 (23.5%)
Upper middle income	135 (34.3%)	166 (19.3%)	224 (22.3%)	81 (14.8%)
Lower middle income	100 (25.4%)	214 (24.9%)	184 (18.3%)	294 (53.6%)
Low income	48 (12.2%)	82 (9.6%)	37 (3.7%)	44 (8%)
Human inhabitants				
Absent	9 (2.2%)	260 (30.2%)	428 (41.9%)	87 (14.7%)
Present	398 (97.8%)	606 (69.6%)	594 (58.1%)	502 (85.1%)
Unknown	0 (0%)	2 (0.2%)	0 (0%)	1 (0.2%)
Invasive vertebrates				
Present	387 (95.1%)	640 (73.5%)	666 (65.2%)	524 (88.8%)
Absent	5 (1.2%)	65 (7.5%)	279 (27.3%)	23 (3.9%)
Unknown	15 (3.7%)	166 (19.1%)	77 (7.5%)	43 (7.3%)
Endemism (# of breeding islands)				
Mean (SD)	1.3 (1.1)	3.1 (6.6)	3.5 (5.6)	1.9 (2.4)
Minimum	1	1	1	1
25%	1	1	1	1
50%	1	1	1	1
75%	1	2	3	2
Maximum	13	77	40	26

*Data from Spatz *et al.* (*77*). †Data from Spalding *et al.* (*70*). ‡Data from the International Monetary and World Bank Open Data (*72*, *73*).

islands worldwide have taken place on islands with highly threatened species (*50*). This likely reflects a focus on national or local conservation priorities and, until recently, a lack of consolidated data on the global distribution of threatened species and invasive species that is needed to guide eradiation planning at this scale. Thus, there is considerable scope to effectively expand island eradication efforts to benefit globally threatened species. Models based on our database suggest that controlling or eradicating rats and other damaging invasive mammals could prevent 41 to 75% of predicted island vertebrate population extinctions (*51*). Furthermore, investigating the feasibility of eradications on the most promising of the 1288 islands with highly threatened island vertebrates can help meet many global biodiversity targets (*52*).

Ninety-five percent of the human inhabited islands in our data set also contained invasive vertebrates. The presence of invasive species is often associated with the presence of people (*12*, *53*). However, of the 779 islands with invasive vertebrates, 42% were uninhabited or minimally inhabited. Of all highly threatened vertebrates, birds and reptiles most frequently occurred on these islands, particularly seabirds, passerines, lizards, and snakes. These islands may offer the most unique invasive vertebrate management opportunities because invasive vertebrate management is often easier to implement in locations with no or small human populations (*54*). From this list of islands, it is informative to consider which islands may emerge as particularly important for management that would deliver major impacts for the conservation of island species. Six islands (Table 3) can be highlighted because they support at least two highly threatened vertebrates, including species found nowhere else in the world (that is, single-island endemics or species that have lost populations and occur on only one island), and at least one of the most damaging invasive vertebrates [rodents, cats, dogs, stoats, mongoose, and pigs (*17*)]. Cumulatively, these islands support 22 populations of 18 highly threatened vertebrates. A thorough assessment of sociopolitical and operational feasibility, as well as a more detailed evaluation of the threat that invasives pose to these threatened species, is now needed.

Knowledge gaps and moving forward

Despite being identified as vital locations for biodiversity, islands are often underrepresented in important analyses of opportunities for biodiversity conservation [for example, the studies of Myers *et al.* (*55*), Geldmann *et al.* (*56*), and Pimm *et al.* (*57*)]. Islands make up a minimal amount of global land area, are often remote, and are less easily accessible (*58*), contributing to an overall lack of information about islands in general compared to continental areas. Consequently, the attributes used in our analysis were coarse (for example, documenting the presence and absence of highly threatened vertebrates rather than their population sizes or specific colony locations) and directed at a subset of vertebrates to conserve (for example, those that are highly threatened instead of all vertebrates), and the breeding status for some highly threatened vertebrates is still unconfirmed, including 45 species that could possibly be extinct (see the Supplementary Materials). Similarly,

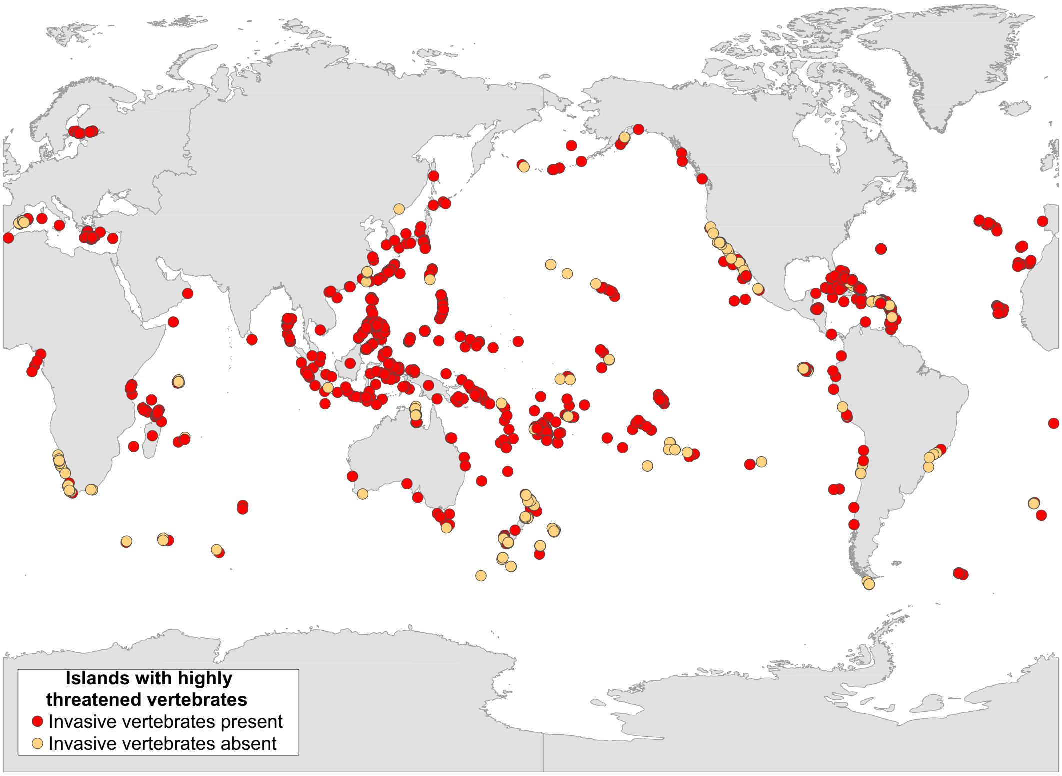

Fig. 5. The 1030 islands with highly threatened native vertebrates and information on the presence or absence of invasive vertebrates. Of these, 779 (76%) had at least one invasive vertebrate species present. Mammals were the most common invader on these islands (753 islands; 97% of islands with highly threatened vertebrates).

Table 3. Highlighted islands from the threatened island biodiversity database that support highly threatened vertebrate species, including those which are found nowhere else in the world. These islands are uninhabited or minimally inhabited and contain at least one of the most damaging invasive species known (*17*). Consideration of these islands for invasive species management would deliver major impacts for the conservation of island species.

Island	Country/territory	Number of highly threatened vertebrates present	Damaging invasives present
Gough	Saint Helena, Ascension and Tristan da Cunha	6	*Mus musculus*
Mona	Puerto Rico	5	*Felis catus*, *M. musculus*, *Rattus rattus*, and *Sus scrofa*
Amsterdam	French southern territories	4	*F. catus*, *M. musculus*, and *Rattus norvegicus*
Socorro	Mexico	3	*F. catus* and *M. musculus*
San Jose	Mexico	2	*Canis familiaris* and *F. catus*
Moho Tani	French Polynesia	2	*F. catus* and *Rattus exulans*

20% of islands analyzed lacked any information about invasive vertebrates; thus, general knowledge on the presence or absence of invasives is not complete at the global scale. Finally, although 58% of highly threatened reptiles are from islands, making them the most threatened island vertebrate class, less than 50% of known reptiles have been assessed on the IUCN Red List. Hence, our estimates of island biodiversity, threat, and co-occurrence of invasive vertebrates on these islands are likely underestimates. The enhancement of monitoring methods and genetic tools to find cryptic island species will no doubt fill these knowledge gaps over time.

CONCLUSIONS

To inform assessments of limited conservation resources and guide national and international initiatives to protect threatened biodiversity (*5*, *59*), we created the Threatened Island Biodiversity Database (*37*), which assembles, for the first time, distribution information on all critically endangered and endangered island breeding vertebrates. The data set itself is a dynamic product, reflecting the nature of biodiversity data and management needs, and is informed by the best information available globally at the time of collection. It includes information on which islands threatened species currently and historically bred on and the physical characteristics and socioeconomic attributes of each island. In addition, it includes the distribution of threats from the primary driver of island vertebrate extinction and endangerment, invasive vertebrates. This database provides the ability to identify and prioritize conservation actions, such as prevention, control, and eradication of invasive vertebrates, which could benefit the 41% of the world's highly threatened terrestrial vertebrates largely confined to islands.

Given current technical constraints on successful eradications, eradication of invasives may not be a feasible intervention for some highly threatened vertebrates, particularly amphibians and mammals, because they mostly occur on large and inhabited islands where whole-island interventions are less tractable (*54*, *60*) than on smaller or uninhabited islands. For these and other threatened taxa on such islands, localized approaches, such as local control and fencing out invasive species, translocating threatened species to safe habitats, implementing education programs, and enhancing policy for addressing invasions are critical (*45*, *61*). These alternative actions may be sufficient to tackle the threat of invasive species and facilitate partial or full long-term species recovery or may be important short- to medium-term measures that can maintain highly threatened species until improvements in eradication techniques make these more complex eradications possible (*62*–*64*).

The Aichi Biodiversity Targets 9 and 12 of the UN Strategic Plan for Biodiversity 2020 and the UN Sustainable Development Goals 15.5 and 15.8 call to reduce the rate of extinction, particularly by reducing the impact of invasive species (*4*, *65*). However, a recent review of the progress toward international targets to prevent extinctions highlights the limited progress that governments and international bodies have made toward eliminating threats from invasive species (*66*, *67*). The Threatened Island Biodiversity Database is an important conservation tool for addressing this gap. To date, the database (which is publicly available at tib.islandconservation.org) has been provided to dozens of researchers and conservationists and cited in 10 peer-reviewed articles. The data are being used in global island conservation assessments, evaluations of the impact of invasives on native species and human health, and measures of conservation successes [for example, the studies of Dawson *et al.* (*68*), McCreless *et al.* (*51*), de Wit *et al.* (*69*), and Jones *et al.* (*33*)], underpinning ongoing efforts to identify the most important islands globally and regionally for eradicating invasive species to benefit threatened biodiversity. These interventions will likely also benefit less well-studied taxa, such as plants and terrestrial invertebrates, many of which are concentrated on the same islands as highly threatened vertebrates and are susceptible to invasive species (*9*, *28*).

MATERIALS AND METHODS

Threatened vertebrates on islands

We created the Threatened Island Biodiversity Database (*37*), which contains data on the island distribution of highly threatened terrestrial species of amphibians, reptiles, birds, and mammals recognized by the IUCN Red List of Threatened Species (version 2013). Seabirds breeding on islands were included, but marine mammals and sea turtles were excluded because of the broad global distribution of many of these species' breeding sites. We downloaded all vertebrate taxa assessed as critically endangered or endangered, then identified those that breed on islands or on both islands and continents. With this list, we followed a systematic review to identify each island with a breeding population of a highly threatened vertebrate species (a species breeding on an island was considered a single population), documenting the present (1990 to 2015, when the data collection process was concluded) and historic (<1990 to 1500 A.D.) breeding status for each population on each island, followed by a review of the data by more than 500 experts (fig. S1 and table S1).

Island biogeography

We linked each island with an extant breeding population of a threatened vertebrate to the global island database (*8*) via a unique identification number and spatial reference for each island. This data set provided coordinates, island size (km^2), and ISO (International Organization for Standardization) alpha-2 codes for each island, country, or territory. Islands ranged in size from 0.00001 km^2 (offshore rocks) to 773,848 km^2 (New Guinea). To place these islands into a biogeographic context that can be applied to strategizing conservation of threatened island species, we supplemented the data set with the following metrics downloaded from global online databases: marine ecoregions (*70*), terrestrial biomes and realms (*71*), and GDP per capita (*72*) and as income groups (*73*). We subsequently compared the distributions of island attributes between the islands with and without highly threatened vertebrates using Kolmogorov-Smirnov tests for continuous variables (for example, island size) and Pearson χ^2 tests for ordinal data (for example, ecoregion).

People and invasive vertebrates on islands

The presence of human populations on islands plays a significant role in extinction risk for native species (*51*). Human settlements are associated with major drivers of extinctions and endangerment, including the transport and maintenance of invasive species on islands (*43*). The presence and relative density of people on islands and the types of invasive species present are important determinants of the strategies available for managing invasive species (*46*, *54*). We conducted a systematic review of the literature and online databases to document the distribution and number of invasive vertebrate species and human inhabitants on islands. With this information, we examined how many islands with invasive vertebrates were either uninhabited or minimally inhabited by people to understand the potential scope of conservation opportunities on islands that would be the most simple to achieve.

To identify the presence or absence of people on islands, we referred to human censuses data (through 2014) in government reports, literature, and websites (for example, Wikipedia, tourism websites, and travel blogs). When this was not available, we contacted local experts. Because not all islands had detailed data on the number of human inhabitants, we pooled human population sizes into ordinal categories of 0, 1 to 100, 101 to 1000, 1001 to 10,000, >10,000, or not found.

To identify the presence or absence of terrestrial non-native alien vertebrates (hereafter, invasive vertebrates) on islands, we conducted a systematic review of the literature, websites, databases [for example, the Global Invasive Species Database (*74*)], and expert advice (fig. S2). We focused on non-native terrestrial vertebrates, defined as some of the most damaging terrestrial invaders (*75*), whose introduction spreads outside their natural range, and which are documented as negatively affecting native terrestrial vertebrates on islands (*33*, *76*). We identified each invasive to the species level when possible or to the most specific taxonomic group possible, then grouped them as: amphibian, reptile (subgroup: snake, turtle, large reptile, and small reptile), mammal [subgroup: cat, dog, rat (*Rattus*), mouse (*Mus*), rabbit/hare, mongoose/weasel, primate, raccoon, ungulate, and other], and bird (subgroup: raptor and nonraptor; tables S3 and S4). For each island, invasive vertebrate presence was defined as present, absent, or unknown. Islands were considered to have invasive vertebrates if they were confirmed or suspected to be present or if there was an ongoing eradication (table S2). We did not investigate the impacts of these invasive groups, but we described their co-occurrence on islands with highly threatened vertebrates.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at http://advances.sciencemag.org/cgi/content/full/3/10/e1603080/DC1

Supplementary Materials and Methods

fig. S1. Systematic review process flowchart for identifying islands with breeding populations of highly threatened terrestrial vertebrate species.

fig. S2. Systematic review process flowchart for identifying islands with non-native terrestrial invasive vertebrate species (invasive vertebrates) on islands with highly threatened vertebrate species.

table S1. Current and historic breeding status assigned to each highly threatened terrestrial vertebrate species on an island.

table S2. Island status category definitions describing the presence or absence of invasive non-native vertebrates on each island and the status applied to each invasive vertebrate on each island.

table S3. The 40 highly threatened vertebrate species that experienced population extinctions (extirpations) across ≥50% of their islands.

table S4. The 320 species of invasive vertebrates found on islands with highly threatened vertebrates.

table S5. The number and percentage of each invasive vertebrate group on islands with highly threatened vertebrate species.

table S6. The highly threatened vertebrate species on islands with invasive vertebrates and minimal human populations (<100 people).

data file S1. The 1189 highly threatened vertebrate taxa from the IUCN Red List (version 2013.2).

data file S2. The 1288 islands with highly threatened terrestrial vertebrates.

References (*78*–*86*)

REFERENCES AND NOTES

1. G. M. Mace, K. Norris, A. H. Fitter, Biodiversity and ecosystem services: A multilayered relationship. *Trends Ecol. Evol.* **27**, 19–26 (2012).
2. G. Ceballos, P. R. Ehrlich, A. D. Barnosky, A. García, R. M. Pringle, T. M. Palmer, Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Sci. Adv.* **1**, e1400253 (2015).
3. J. Rockström, W. Steffen, K. Noone, Å. Persson, F. S. Chapin III, E. Lambin, T. Lenton, M. Scheffer, C. Folke, H. J. Schellnhuber, B. Nykvist, C. A. de Wit, T. Hughes, S. van der Leeuw, H. Rodhe, S. Sörlin, P. K. Snyder, R. Costanza, U. Svedin, M. Falkenmark, L. Karlberg, R. W. Corell, V. J. Fabry, J. Hansen, B. Walker, D. Liverman, K. Richardson, P. Crutzen, J. A. Foley, Planetary boundaries: Exploring the safe operating space for humanity. *Nature* **461**, 472–475 (2009).
4. United Nations, "Sustainable Development Goals" (2015); www.un.org/sustainabledevelopment/sustainable-development-goals/.
5. Secretariat of the Convention on Biological Diversity, "Strategic Plan for Biodiversity 2011-2020. COP 10 Outcomes" (Nagoya, Japan, 2010); www.cbd.int/cop10/doc/default.shtml.
6. D. Dudgeon, A. H. Arthington, M. O. Gessner, Z.-I. Kawabata, D. J. Knowler, C. Lévêque, R. J. Naiman, A.-H. Prieur-Richard, D. Soto, M. L. J. Stiassny, C. A. Sullivan, Freshwater biodiversity: Importance, threats, status and conservation challenges. *Biol. Rev. Camb. Philos. Soc.* **81**, 163–182 (2006).
7. B. R. Tershy, K.-W. Shen, K. M. Newton, N. D. Holmes, D. A. Croll, The importance of islands for the protection of biological and linguistic diversity. *Bioscience* **65**, 592–597 (2015).
8. UNEP-WCMC, "Global distribution of islands. Global Island Database (version 2.1, November 2015). Based on Open Street Map data (© OpenStreetMap contributors)" (Cambridge, UK, 2015); www.unep-wcmc.org.
9. G. Kier H. Kreft, T. M. Lee, W. Jetz, P. L. Ibisch, C. Nowicki, J. Mutke, W. Barthlott, A global assessment of endemism and species richness across island and mainland regions. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 9322–9327 (2009).
10. H. Kreft, W. Jetz, J. Mutke, G. Kier, W. Barthlott, Global diversity of island floras from a macroecological perspective. *Ecol. Lett.* **11**, 116–127 (2008).
11. International Union for Conservation Nature, "The IUCN Red List of Threatened Species" (2013); www.iucnredlist.org/.
12. T. M. Blackburn, P. Cassey, R. P. Duncan, K. L. Evans, K. J. Gaston, Avian extinction and mammalian introductions on oceanic islands. *Science* **305**, 1955–1958 (2004).
13. F. M. Medina, E. Bonnaud, E. Vidal, B. R. Tershy, E. S. Zavaleta, C. J. Donlan, B. S. Keitt, M. Le Corre, S. V. Horwath, M. Nogales, A global review of the impacts of invasive cats on island endangered vertebrates. *Glob. Chang. Biol.* **17**, 3503–3510 (2011).
14. D. Simberloff, Invasive Species, in *Conservation Biology for All*, N. S. Sodhi, P. R. Ehrlich, Eds. (Oxford Univ. Press Inc., 2010), pp. 131–152.
15. D. T. Blumstein, J. C. Daniel, The loss of anti-predator behaviour following isolation on islands. *Proc. Biol. Sci.* **272**, 1663–1668 (2005).
16. E. O. Wilson, R. H. MacArthur, *Theory of Island Biogeography* (Princeton Univ. Press, 1967).
17. T. S. Doherty, A. S. Glen, D. G. Nimmo, E. G. Ritchie, C. R. Dickman, Invasive predators and global biodiversity loss. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 11261–11265 (2016).
18. C. Bellard, P. Cassey, T. M. Blackburn, Alien species as a driver of recent extinctions. *Biol. Lett.* **12**, 20150623 (2016).
19. R. Dirzo, H. S. Young, M. Galletti, G. Ceballos, N. J. B. Isaac, B. Collen, Defaunation in the Anthropocene. *Science* **345**, 401–406 (2014).
20. D. A. Croll, J. L. Maron, J. A. Estes, E. M. Danner, G. V. Byrd, Introduced predators transform subarctic islands from grassland to tundra. *Science* **307**, 1959–1961 (2005).
21. T. Fukami, D. A. Wardle, P. J. Bellingham, C. P. H. Mulder, D. R. Towns, G. W. Yeates, K. I. Bonner, M. S. Durrett, M. N. Grant-Hoffman, W. M. Williamson, Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecol. Lett.* **9**, 1299–1307 (2006).
22. S. A. Temple, Plant-animal mutualism: Coevolution with dodo leads to near extinction of plant. *Science* **197**, 885–886 (1977).
23. D. M. Hansen, M. Galetti, The forgotten megafauna. *Science* **324**, 42–43 (2009).
24. C. E. Aslan, E. S. Zavaleta, B. Tershy, D. Croll, Mutualism disruption threatens global plant biodiversity: A systematic review. *PLOS ONE* **8**, e66993 (2013).
25. M. Hoffmann, C. Hilton-Taylor, A. Angulo, M. Böhm, T. M. Brooks, S. H. M. Butchart, K. E. Carpenter, J. Chanson, B. Collen, N. A. Cox, W. R. T. Darwall, N. K. Dulvy, L. R. Harrison, V. Katariya, C. M. Pollock, S. Quader, N. I. Richman, A. S. L. Rodrigues, M. F. Tognelli, J.-C. Vié, J. M. Aguiar, D. J. Allen, G. R. Allen, G. Amori, N. B. Ananjeva, F. Andreone, P. Andrew, A. L. Aquino Ortiz, J. E. M. Baillie, R. Baldi, B. D. Bell, S. D. Biju, J. P. Bird, P. Black-Decima, J. J. Blanc, F. Bolaños, W. Bolivar-G., I. J. Burfield, J. A. Burton, D. R. Capper, F. Castro, G. Catullo, R. D. Cavanagh, A. Channing, N. L. Chao, A. M. Chenery, F. Chiozza, V. Clausnitzer, N. J. Collar, L. C. Collett, B. B. Collette, C. F. Cortez Fernandez, M. T. Craig, M. J. Crosby, N. Cumberlidge, A. Cuttelod, A. E. Derocher, A. C. Diesmos, J. S. Donaldson, J. W. Duckworth, G. Dutson, S. K. Dutta, R. H. Emslie, A. Farjon, S. Fowler, J. Freyhof, D. L. Garshelis, J. Gerlach, D. J. Gower, T. D. Grant, G. A. Hammerson, R. B. Harris, L. R. Heaney, S. B. Hedges, J.-M. Hero, B. Hughes, S. A. Hussain, J. Icochea M., R. F. Inger, N. Ishii, D. T. Iskandar, R. K. B. Jenkins, Y. Kaneko, M. Kottelat, K. M. Kovacs, S. L. Kuzmin, E. La Marca, J. F. Lamoreux, M. W. N. Lau, E. O. Lavilla, K. Leus, R. L. Lewison, G. Lichtenstein, S. R. Livingstone, V. Lukoschek, D. P. Mallon, P. J. K. McGowan, A. McIvor, P. D. Moehlman, S. Molur, A. Muñoz Alonso, J. A. Musick, K. Nowell, R. A. Nussbaum, W. Olech, N. L. Orlov, T. J. Papenfuss, G. Parra-Olea, W. F. Perrin, B. A. Polidoro, M. Pourkazemi, P. A. Racey, J. S. Ragle, M. Ram, G. Rathbun, R. P. Reynolds, A. G. J. Rhodin, S. J. Richards, L. O. Rodríguez, S. R. Ron, C. Rondinini, A. B. Rylands, Y. Sadovy de Mitcheson, J. C. Sanciangco, K. L. Sanders, G. Santos-Barrera, J. Schipper, C. Self-Sullivan, Y. Shi, A. Shoemaker, F. T. Short, C. Sillero-Zubiri, D. L. Silvano, K. G. Smith, A. T. Smith, J. Snoeks, A. J. Stattersfield, A. J. Symes, A. B. Taber, B. K. Talukdar, H. J. Temple, R. Timmins,

J. A. Tobias, K. Tsytsulina, D. Tweddle, C. Ubeda, S. V. Valenti, P. P. van Dijk, L. M. Veiga, A. Veloso, D. C. Wege, M. Wilkinson, E. A. Williamson, F. Xie, B. E. Young, H. R. Akçakaya, L. Bennun, T. M. Blackburn, L. Boitani, H. T. Dublin, G. A. B. da Fonseca, C. Gascon, T. E. Lacher Jr., G. M. Mace, S. A. Mainka, J. A. McNeely, R. A. Mittermeier, G. M. Reid, J. P. Rodriguez, A. A. Rosenberg, M. J. Samways, J. Smart, B. A. Stein, S. N. Stuart, The impact of conservation on the status of the world's vertebrates. *Science* **330**, 1503–1509 (2010).
26. R. Grenyer, C. D. L. Orme, S. F. Jackson, G. H. Thomas, R. G. Davies, T. J. Davies, K. E. Jones, V. A. Olson, R. S. Ridgely, P. C. Rasmussen, T.-S. Ding, P. M. Bennett, T. M. Blackburn, K. J. Gaston, J. L. Gittleman, I. P. F. Owens, Global distribution and conservation of rare and threatened vertebrates. *Nature* **444**, 93–96 (2006).
27. C. N. Jenkins, S. L. Pimm, L. N. Joppa, Global patterns of terrestrial vertebrate diversity and conservation. *Proc. Natl. Acad. Sci. U.S.A.* **110**, E2602–E2610 (2013).
28. C. Aslan, N. Holmes, B. Tershy, D. Spatz, D. A. Croll, Benefits to poorly studied taxa of conservation of bird and mammal diversity on islands. *Conserv. Biol.* **29**, 133–142 (2015).
29. Ç. H. Şekercioğlu, G. C. Daily, P. R. Ehrlich, Ecosystem consequences of bird declines. *Proc. Natl. Acad. Sci. U.S.A.* **101**, 18042–18047 (2004).
30. J. L. Smith, C. P. H. Mulder, J. C. Ellis, Seabirds as ecosystem engineers: Nutrient inputs and physical disturbance, in *Seabird Islands: Ecology, Invasion, and Restoration*, C. P. H. Mulder, W. B. Anderson, D. R. Towns, P. J. Bellingham, Eds. (Oxford Univ. Press Inc., 2011), pp. 27–55.
31. C. J. Donlan, K. Campbell, W. Cabrera, C. Lavoie, V. Carrion, F. Cruz, Recovery of the Galápagos rail (*Laterallus spilonotus*) following the removal of invasive mammals. *Biol. Conserv.* **138**, 520–524 (2007).
32. D. L. Whitworth, H. R. Carter, F. Gress, Recovery of a threatened seabird after eradication of an introduced predator: Eight years of progress for Scripps's murrelet at Anacapa Island, California. *Biol. Conserv.* **162**, 52–59 (2013).
33. H. P. Jones, N. D. Holmes, S. H. M. Butchart, B. R. Tershy, P. J. Kappes, I. Corkery, A. Aguirre-Muñoz, D. P. Armstrong, E. Bonnaud, A. A. Burbidge, K. Campbell, F. Courchamp, P. E. Cowan, R. J. Cuthbert, S. Ebbert, P. Genovesi, G. R. Howald, B. S. Keitt, S. W. Kress, C. M. Miskelly, S. Oppel, S. Poncet, M. J. Rauzon, G. Rocamora, J. C. Russell, A. Samaniego-Herrera, P. J. Seddon, D. R. Spatz, D. R. Towns, D. A. Croll, Invasive mammal eradication on islands results in substantial conservation gains. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 4033–4038 (2016).
34. Convention on Biological Diversity, "X/2.Strategic Plan for Biodiversity 2011-2020" (Conference of the Parties to the Convention on Biological Diversity, 2010), pp. 1–13; www.cbd.int/decision/cop/?id=12268.
35. L. N. Joppa, B. O'Connor, P. Visconti, C. Smith, J. Geldmann, M. Hoffmann, J. E. M. Watson, S. H. M. Butchart, M. Virah-Sawmy, B. S. Halpern, S. E. Ahmed, A. Balmford, W. J. Sutherland, M. Harfoot, C. Hilton-Taylor, W. Foden, E. Di Minin, S. Pagad, P. Genovesi, J. Hutton, N. D. Burgess, Filling in biodiversity threat gaps. *Science* **352**, 416–418 (2016).
36. T. H. Ricketts, E. Dinerstein, T. Boucher, T. M. Brooks, S. H. M. Butchart, M. Hoffmann, J. F. Lamoreux, J. Morrison, M. Parr, J. D. Pilgrim, A. S. L. Rodrigues, W. Sechrest, G. E. Wallace, K. Berlin, J. Bielby, N. D. Burgess, D. R. Church, N. Cox, D. Knox, C. Loucks, G. W. Luck, L. L. Master, R. Moore, R. Naidoo, R. Ridgely, G. E. Schatz, G. Shire, H. Strand, W. Wettengel, E. Wikramanayake, Pinpointing and preventing imminent extinctions. *Proc. Natl. Acad. Sci. U.S.A.* **102**, 18497–18501 (2005).
37. Threatened Island Biodiversity Database Partners, 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 2016.1 (2016); http://tib.islandconservation.org.
38. R. H. MacArthur, E. O. Wilson, *The Theory of Island Biogeography* (Princeton Univ. Press, 1967).
39. J. M. Jeschke, P. Genovesi, Do biodiversity and human impact influence the introduction or establishment of alien mammals? *Oikos* **120**, 57–64 (2011).
40. W. E. Duellman, L. Trueb, *Biology of Amphibians* (John Hopkins Univ. Press, 1994).
41. R. F. Inger, H. K. Voris, The biogeographical relations of the frogs and snakes of Sundaland. *J. Biogeogr.* **28**, 863–891 (2016).
42. A. Waldron, A. O. Mooers, D. C. Miller, N. Nibbelink, D. Redding, T. S. Kuhn, J. T. Roberts, J. L. Gittleman, Targeting global conservation funding to limit immediate biodiversity declines. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 12144–12148 (2013).
43. D. W. Steadman, *Extinction and Biogeography of Tropical Pacific Birds* (Chicago Univ. Press, 2006).
44. J. K. Szabo, N. Khwaja, S. T. Garnett, S. H. M. Butchart, Global patterns and drivers of avian extinctions at the species and subspecies level. *PLOS ONE* **7**, 1–9 (2012).
45. BirdLife International, Data Zone (2013); available at www.birdlife.org/datazone.
46. J. Parkes, E. Murphy, Management of introduced mammals in New Zealand. *New Zeal. J. Zool.* **30**, 335–359 (2003).
47. J. L. Moore, T. M. Rout, C. E. Hauser, D. Moro, M. Jones, C. Wilcox, H. P. Possingham, Protecting islands from pest invasion: Optimal allocation of biosecurity resources between quarantine and surveillance. *Biol. Conserv.* **143**, 1068–1078 (2010).
48. J. C. Russell, D. R. Towns, M. N. Clout, *Review of Rat Invasion Biology: Implications for Island Biosecurity* (Department of Conservation, Wellington, New Zealand, 2008).
49. I. A. E. Atkinson, The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas, in *Conservation of Island Birds: Case Studies for the Management of Threatened Island Species*, P. J. Moors, Ed. (International Council for Bird Preservation, 1985), pp. 35–81.
50. Database of Island Invasive Species Eradications (DIISE), developed by Island Conservation, Coastal Conservation Action Laboratory UCSC, IUCN SSC Invasive Species Specialist Group, University of Auckland and Landcare Research New Zealand (2015); http://diise.islandconservation.org/).
51. E. E. McCreless, D. D. Huff, D. A. Croll, B. R. Tershy, D. R. Spatz, N. D. Holmes, S. H. M. Butchart, C. Wilcox, Past and estimated future impact of invasive alien mammals on insular threatened vertebrate populations. *Nat. Commun.* **7**, 12488 (2016).
52. S. H. M. Butchart, A. J. Stattersfield, N. J. Collar, How many bird extinctions have we prevented? *Oryx* **40**, 266–278 (2006).
53. D. W. Steadman, Prehistoric extinctions of Pacific island birds: Biodiversity meets zooarchaeology. *Science* **267**, 1123–1131 (1995).
54. S. Oppel, B. M. Beaven, M. Bolton, J. Vickery, T. W. Bodey, Eradication of invasive mammals on islands inhabited by humans and domestic animals. *Conserv. Biol.* **25**, 232–240 (2011).
55. N. Myers, R. A. Mittermeier, C. G. Mittermeier, G. A. B. da Fonseca, J. Kent, Biodiversity hotspots for conservation priorities. *Nature* **403**, 853–858 (2000).
56. J. Geldmann, L. N. Joppa, N. D. Burgess, Mapping change in human pressure globally on land and within protected areas. *Conserv. Biol.* **28**, 1604–1616 (2014).
57. S. L. Pimm, C. N. Jenkins, R. Abell, T. M. Brooks, J. L. Gittleman, L. N. Joppa, P. H. Raven, C. M. Roberts, J. O. Sexton, The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**, 1246752 (2014).
58. R. J. Whittaker, J. M. Fernández-Palacios, *Island Biogeography: Ecology, Evolution, and Conservation* (Oxford Univ. Press, 2007).
59. P. Genovesi, C. Carboneras, M. Vilà, P. Walton, EU adopts innovative legislation on invasive species: A step towards a global response to biological invasions? *Biol. Invasions* **17**, 1307–1311 (2015).
60. G. Howald, C. J. Donlan, J. P. Galván, J. C. Russell, J. Parkes, A. Samaniego, Y. Wang, D. Veitch, P. Genovesi, M. Pascal, A. Saunders, B. Tershy, Invasive rodent eradication on islands. *Conserv. Biol.* **21**, 1258–1268 (2007).
61. F. Courchamp, J.-L. Chapuis, M. Pascal, Mammal invaders on islands: Impact, control and control impact. *Biol. Rev. Camb. Philos. Soc.* **78**, 347–383 (2003).
62. K. Campbell, C. J. Donlan, Feral goat eradications on islands. *Conserv. Biol.* **19**, 1362–1374 (2005).
63. E. T. Game, G. Lipsett-Moore, R. Hamilton, N. Peterson, J. Kereseka, W. Atu, M. Watts, H. Possingham, Informed opportunism for conservation planning in the Solomon Islands. *Conserv. Lett.* **4**, 38–46 (2011).
64. M. Bode, C. M. Baker, M. Plein, Eradicating down the food chain: Optimal multispecies eradication schedules for a commonly encountered invaded island ecosystem. *J. Appl. Ecol.* **52**, 571–579 (2015).
65. UNEP CBD, Conference of the Parties to the Convention on Biological Diversity, COP 10 (2010), p. 13; www.cbd.int/decision/cop/?id=12268).
66. Secretariat of the Convention on Biological Diversity, in *Global Biodiversity Outlook 4* (Montréal, 2014), p. 155.
67. D. P. Tittensor, M. Walpole, S. L. L. Hill, D. G. Boyce, G. L. Britten, N. D. Burgess, S. H. M. Butchart, P. W. Leadley, E. C. Regan, R. Alkemade, R. Baumung, C. Bellard, L. Bouwman, N. J. Bowles-Newark, A. M. Chenery, W. W. L. Cheung, V. Christensen, H. D. Cooper, A. R. Crowther, M. J. R. Dixon, A. Galli, V. Gaveau, R. D. Gregory, N. L. Gutierrez, T. L. Hirsch, R. Höft, S. R. Januchowski-Hartley, M. Karmann, C. B. Krug, F. J. Leverington, J. Loh, R. K. Lojenga, K. Malsch, A. Marques, D. H. W. Morgan, P. J. Mumby, T. Newbold, K. Noonan-Mooney, S. N. Pagad, B. C. Parks, H. M. Pereira, T. Robertson, C. Rondinini, L. Santini, J. P. W. Scharlemann, S. Schindler, U. R. Sumaila, L. S. L. Teh, J. van Kolck, P. Visconti, Y. Ye, A mid-term analysis of progress toward international biodiversity targets. *Science* **346**, 241–244 (2014).
68. J. Dawson, S. Oppel, R. J. Cuthbert, N. Holmes, J. P. Bird, S. H. M. Butchart, D. R. Spatz, B. Tershy, Prioritizing islands for the eradication of invasive vertebrates in the United Kingdom overseas territories. *Conserv. Biol.* **29**, 143–153 (2015).
69. L. A. de Wit, D. A. Croll, B. Tershy, K. M. Newton, D. R. Spatz, N. D. Holmes, A. M. Kilpatric, Estimating burdens of neglected tropical zoonotic diseases on islands with introduced mammals. *Am. J. Trop. Med. Hyg.* **96**, 749–757 (2017).
70. M. D. Spalding, H. E. Fox, G. R. Allen, N. C. Davidson, Z. A. Ferdaña, M. Finlayson, B. S. Halpern, M. A. Jorge, A. Lombana, S. A. Lourie, K. D. Martin, E. McManus, J. Molnar, C. A. Recchia, J. Robertson, Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *Bioscience* **57**, 573–583 (2007).
71. D. M. Olson, E. Dinersteing, The Global 200: Priority ecoregions for global conservation. *Ann. Missouri Bot. Gard.* **89**, 199–224 (2002).
72. International Monetary Foundation, World Economic Outlook Database (2015); www.imf.org/external/pubs/ft/weo/2015/01/weodata/index.aspx.

73. The World Bank, World Bank Open Data (2015); http://data.worldbank.org/.
74. Invasive Species Specialist Group, Global Invasive Species Database (2013); www.issg.org/database).
75. S. Lowe, M. Browne, S. Boudjelas, M. De Poorter, *100 of the World's Worst Invasive Alien Species: A selection from the Global Invasive Species Database* (IUCN Invasive Species Specialist Group, 2000).
76. IUCN SSC Invasive Species Specialist Group, "About Invasive Species" (2011); www.issg.org/about_is.htm.
77. D. R. Spatz, K. M. Newton, R. Heinz, B. Tershy, N. D. Holmes, S. H. M. Butchart, D. A. Croll, The biogeography of globally threatened seabirds and island conservation opportunities. *Conserv. Biol.* **28**, 1282–1290 (2014).
78. M. P. Marchetti, T. Engstrom, The conservation paradox of endangered and invasive species. *Conserv. Biol.* **30**, 434–437 (2016).
79. F. Yildirim, A. Kaya, Selecting map projections in minimizing area distortions in GIS applications. *Sensors* **8**, 7809–7817 (2008).
80. A. S. L. Rodrigues, J. D. Pilgrim, J. F. Lamoreux, M. Hoffmann, T. M. Brooks, The value of the IUCN Red List for conservation. *Trends Ecol. Evol.* **21**, 71–76 (2006).
81. G. M. Mace, N. J. Collar, K. J. Gaston, C. Hilton-Taylor, H. R. Akçakaya, N. Leader-Williams, E. J. Milner-Gulland, S. N. Stuart, Quantification of extinction risk: IUCN's system for classifying threatened species. *Conserv. Biol.* **22**, 1424–1442 (2008).
82. S. H. M. Butchart, A. J. Stattersfield, L. A. Bennun, S. M. Shutes, H. R. Akçakaya, J. E. M. Baillie, S. N. Stuart, C. Hilton-Taylor, G. M. Mace, Measuring global trends in the status of biodiversity: Red list indices for birds. *PLOS Biol.* **2**, e383 (2004).
83. A. Farina, N. Pieretti, The soundscape ecology: A new frontier of landscape research and its application to islands and coastal systems. *J. Mar. Isl. Cult.* **1**, 21–26 (2012).
84. A. L. Borker, M. W. McKown, J. T. Ackerman, C. A. Eagles-Smith, B. R. Tershy, D. A. Croll, Vocal activity as a low cost and scalable index of seabird colony size. *Conserv. Biol.* **28**, 1100–1108 (2014).
85. W. Turner, Sensing biodiversity. *Science* **346**, 301–302 (2014).
86. D. Simberloff, J.-L. Martin, P. Genovesi, V. Maris, D. A. Wardle, J. Aronson, F. Courchamp, B. Gali, E. García-Berthou, M. Pascal, P. Pyšek, R. Sousa, E. Tabacchi, M. Vilà, Impacts of biological invasions: What's what and the way forward. *Trends Ecol. Evol.* **28**, 58–66 (2013).

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