

Annual Review of Environment and Resources
**Island Biodiversity in the
Anthropocene**

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Abstract

Biodiversity on marine islands is characterized by unique biogeographic, phylogenetic and functional characteristics. Islands hold a disproportionate amount of the world's biodiversity, and they have also experienced a disproportionate loss of it. Following human contact, island biodiversity has sustained negative human impacts increasing in rate and magnitude as islands transitioned from primary through secondary to tertiary economies. On islands, habitat transformation and invasive non-native species have historically been the major threats to biodiversity, and although these threats will continue in new forms, new impacts such as human-induced climate change and sea-level rise are emerging. Island biodiversity is changing with some species going extinct, others changing in abundance, non-native species becoming a part of many ecosystems, and humans shaping many ecological processes. Islands thus are microcosms for the emerging biodiversity and socioecological landscapes of the Anthropocene. Islands will require new strategies for the protection and restoration of their biodiversity, including maintaining biological and cultural heritage through regenerative practices, mainstreaming biodiversity in cultural and production landscapes, and engaging with the reality of novel ecosystems.

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Contents

INTRODUCTION	32
The Anthropocene	32
Islands	33
FORMATION	34
Species Diversity	34
Functional Diversity	36
Habitat Diversity	37
HUMANS	38
First Contact	38
Modern History	39
Contemporary Era	39
DRIVERS	40
Current Threats	40
Emerging Patterns	43
ADAPTATION	45
Protection and Restoration	45
Cultural Landscapes	47
Novel Ecosystems	50
CONCLUSIONS	51

INTRODUCTION

Biodiversity is considered important, for both its own sake and the values and services it provides to humans (1). However, it is widely recognized that biodiversity is declining rapidly, conferring risk of extinction to unique species and interactions, as well as to the important ecosystem services provided to human society. This has been exemplified on islands, where biodiversity has declined at some of the fastest rates (2). In this article, we review island biodiversity as we enter the Anthropocene. In the first part, we consider the concept of the Anthropocene and define the scope of islands treated in this review. In the second part, we review the ecological and evolutionary formation of island biodiversity prior to human contact. In the third part, we review how humans have affected and altered the current status and future fate of island biodiversity. In the fourth part, we describe emerging patterns of island biodiversity in heavily disturbed anthropogenic landscapes, and we review emerging adaptation strategies for the island landscapes of the Anthropocene.

The Anthropocene

Since the emergence of *Homo sapiens*, the scale of the influence of our species on the ecology of ecosystems has continuously increased. The extent of ecosystems within which humans have become a dominant ecological force, often by purposely changing them, has expanded, and especially since the mid twentieth century. Depending on definition, up to 78% of the planet's surface is today considered anthropogenic biomes (anthromes) (3). However, the effects of humans on the ecology of the planet reaches far beyond the boundaries of anthromes, through unbounded processes such as human-induced climate change, biological invasions, and pollution. Nowadays, humans are a global force in the sense that they change the functioning of the whole planetary ecosystem (4).

Biodiversity: the variety of life found in a location, comprising genetic, species, phylogenetic, functional, and habitat diversity

Anthropocene: the period in the Earth's history during which human activity has been a dominant influence on the ecology of the planet

Anthrome: a biome with globally significant ecological patterns created by sustained interactions between humans and ecosystems

This planetary scale of the effects of humans on physical, chemical, and biological processes led scientists to introduce the concept of the Anthropocene. Depending on different disciplinary perspectives and criteria, the start date of this new era differs, but there is little doubt that we have entered a time of massive human impact at a planetary scale (5; though see 6). In this review, we use the term Anthropocene to make explicit that anthromes cover today a very considerable part of the planet and human actions substantially change ecological processes and patterns beyond anthromes at local to global scales. Human impacts on the environment in the Anthropocene threaten biodiversity and ecosystem services. Up to 58% of vertebrate species might go extinct in the twenty-first century (7); relatively undisturbed natural areas across the world's biomes have been diminished to a fraction of prehuman extents (8); and ecosystem services such as pollination, water supply and purification, or soil regeneration have been severely reduced (9). In the Anthropocene, these human effects will remain and likely grow. As a society we have to better learn to minimize negative impacts and maximize positive effects of human land use, first and foremost on islands where these effects are strongest (10, 11).

Adaptive radiation:

a process in which organisms diversify rapidly from an ancestral species into new forms with different ecological adaptations

Islands

Although only making up a few percent of the planet's land area, islands are critical systems for considering the fate of biodiversity in the Anthropocene. Islands are home to a significant part of global biodiversity due to a very high level of species endemism, unique functional traits, and spectacular evolutionary patterns, such as adaptive radiations or examples of replicated convergent evolution (12, 13). Island livelihoods are made from tightly formed cultural bonds with local biodiversity, leading to unique socioecological systems (14). In total, one-quarter of the world's countries are islands or archipelagos, and more than two-thirds include islands (15). However, beyond being hotspots of biodiversity, islands are also hotspots of past, present, and predicted future biodiversity loss and habitat transformation (16). Due to the small size of islands, human environmental impacts were often very rapid and substantial, and they tended to occur earlier across whole landscapes, including remote areas, as compared to adjacent continents. Islands are in this sense early warning systems where the wholesale ecological transformation of landscapes can first be observed (17), but also where comprehensive solutions to environmental problems can be first tested (18, 19). Many islands experienced sequences of different phases of human exploitation with first traditional land use by indigenous people, followed by rapid extractive exploitation upon arrival of colonial settlers, and thereafter attempts at nature conservation and ecological regeneration. Islands are in ecology, evolution, and environmental sciences (as well as many other fields) considered real-world model systems due to their small size, complex interactions of multiple factors (including broad abiotic gradients within islands), and manifold replication across all world regions and climate zones (20). Such independent replications allow for multisite comparative studies.

There are different types of islands, including mountaintops, lakes, and habitat fragments. In this review, we focus on islands surrounded by water and more specifically those in oceans and seas, and we term them in a broad sense as marine islands, thereby excluding islands in freshwater bodies; however, some of the ideas also apply to them. Islands in the ocean include volcanoes, atolls, islands on a continental shelf, and continental fragments (i.e., islands that originated from a continental plate but are now isolated in the ocean). Biogeographers use the term oceanic island strictly for volcanic islands that formed through the accumulation of submarine magma and were never connected to continents. Land bridge islands and other islands on a continental shelf, as well as continental fragments or microcontinents (e.g., Madagascar, New Zealand), are built on a continental crust and consequently are characterized by a different geology (e.g., granites rather

Alpha diversity:

the average species diversity found in a particular locality, such as an island

Beta diversity: the ratio between regional and local species diversity, such as between an archipelago and an island

Gamma diversity: the total species diversity within a region, such as an archipelago or the planet

Phylogeny:

the relatedness of the evolutionary history of species determined based upon similarities and differences in their physical or genetic characteristics

than basalts in oceanic crust). Although volcanic islands reach a maximum age of approximately tens of millions of years, the presence of islands in an archipelago lasts beyond this, and continental islands can be much older. This review focuses on terrestrial biodiversity, and therefore seamounts that rise from the seabed but do not reach the ocean's surface are not considered. The Global Island Database identifies 175,000 marine islands larger than 0.1 km², and the 17,883 of the world's marine islands larger than 1 km² make up 5.3% of the planet's land area (http://www.globalislands.net/about/gid_functions.php).

The marine islands of the world are diverse in their abiotic characteristics and occur in all regions and at all latitudes. Depending on definition, the smallest islands have a size of only a few square meters (i.e., a single rock), whereas the largest landmasses typically considered islands have areas of more than hundreds of thousands of square kilometers, respectively. Equally diverse is the topography of islands (21). Low-lying islands such as atolls reach only a few meters above sea level (MASL), while the tallest ones are major mountains that can be higher than 4,000 MASL. Due to the buffering effect of the oceans, islands tend to have higher precipitation and lower temperature than continents. However, low-lying islands and islands at high and low latitudes tend to have dry climates with little precipitation, and high-rising islands in the subtropics are characterized by a strong contrast between a very wet windward and a very dry leeward side of mountain chains. Islands are thus a nonrandom subset of environments found on the planet. These abiotic traits of island environments accordingly shape the biotic components found in them.

FORMATION

Biodiversity can be defined and measured in different ways (**Figure 1**). Often, the total number of species is used as a measure of biodiversity and can be further decomposed to alpha diversity, beta diversity, and gamma diversity (22). However, biodiversity is not just the number of species, it is also their relative and total abundances, their relative and total uniqueness (phylogeny) and the variation within species (i.e., genetic diversity). Biodiversity is also more than just species, comprising the functional diversity of species and the interactions among them and with their habitat (23). As a broader concept (24), defining and measuring biodiversity can be as much a philosophical endeavor (25) as it is one of enumeration (26). Only by operationalizing the different components of biodiversity definitively can we understand how it is changing in the Anthropocene.

Species Diversity

Islands are tumultuous places; raised from the oceans or divided from continents, they undergo change at a pace faster than most other biomes (27). The species that colonize and persist upon islands react and adapt to this constant change, making islands engines of evolution and laboratories of ecology (28–30), and biodiversity hotspots across the planet (31). MacArthur & Wilson's equilibrium theory of island biogeography (ETIB; 32, 33) focused on the paramount role of island size and isolation in regulating species richness on islands, through extinction and immigration rates. The ETIB heralded a shift from pattern- to process-based investigation of island biodiversity (13, 28, 30). Studies of island biodiversity blossomed, including classic texts by Carlquist (34), Williamson (35), and Whittaker (36), and the biodiversity of islands has since come to be understood in light of the interaction among ecology, evolution, and biogeography. MacArthur & Wilson's ETIB was ecological in scope, and it did not incorporate the geological processes of island creation and disappearance in regulating island biodiversity. Expanding the scope of the ETIB required incorporating island ontogeny (37, 38) and the effects of Pleistocene glaciations on shaping the islands and their biota (24). Volcanic oceanic archipelagos in particular have

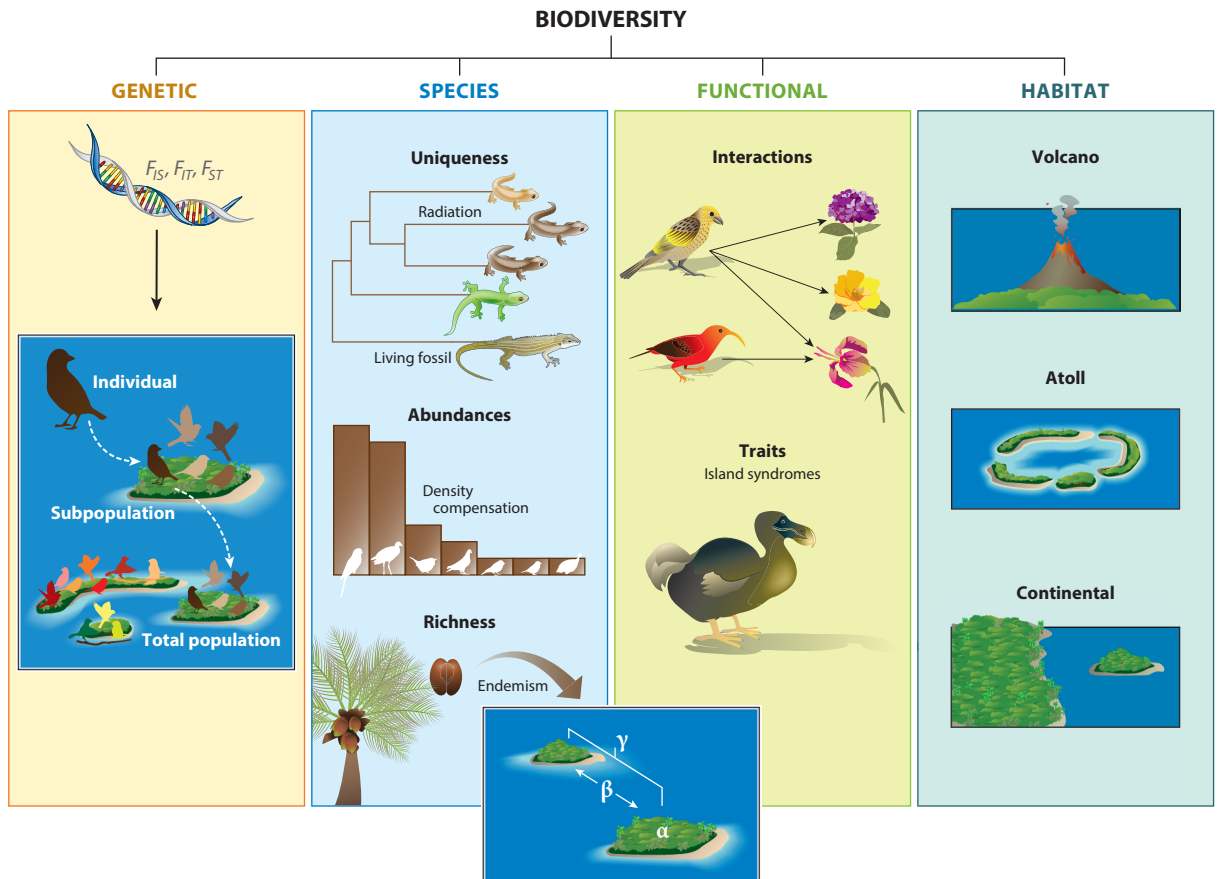


Figure 1

Decomposition of biodiversity to genetic (individual, subpopulation, and total population), species (uniqueness, abundances, and richness), functional (interactions and traits), and habitat diversity (island types and abiotic heterogeneity within them). The inset box decomposes species richness to alpha (within islands), beta (between islands), and gamma (across islands). On islands, the distinct characteristics of species diversity include the presence of unique adaptive radiations and living fossils in terms of phylogeny, the presence of density compensation in abundances, and high levels of endemism in species richness.

facilitated a refined understanding of community assembly and speciation across multiple islands that were present at different times in an archipelago (39).

Species diversity on islands is the result of a number of filters and selective processes acting upon individuals and populations (**Figure 2**). The ecological communities on islands are often young, with species having formed from few founding individuals that had successfully dispersed and established on islands. The sorting filters of dispersal act on individuals (40), affecting species establishment (41), ultimately creating impoverishment and disharmony in island biotas (42). Island assemblies are also subjected to historical contingency bringing an element of chance to island biotas. Changes in species composition on islands occur naturally over time through processes such as the taxon cycle and following assembly rules. Especially on larger and older islands, an important proportion of species diversity has been formed through in situ speciation, including adaptive radiations, derived from few founder species (cladogenesis). Alternatively, species adapt and evolve on islands without separation into multiple species (anagenesis). Islands

Disharmony: the biased representation of higher taxa (e.g., genera, families) on islands compared to nearby continents

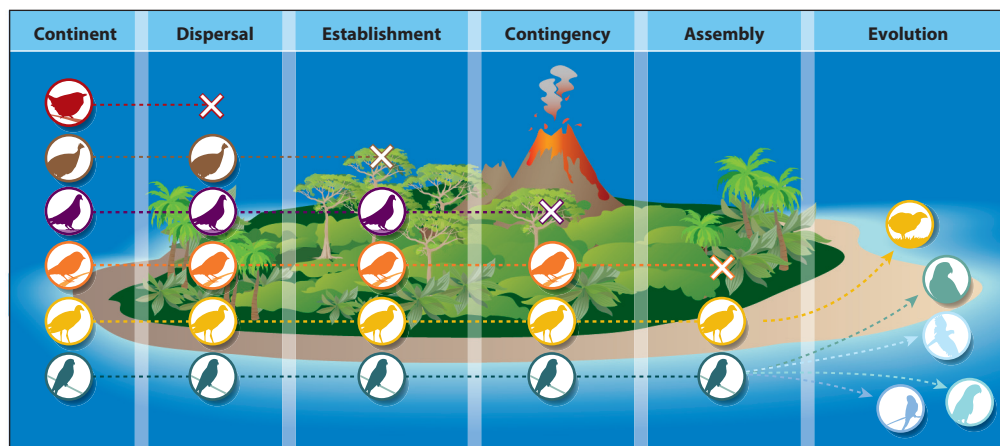


Figure 2

An illustration using birds of the major filters and processes in the assembly of species diversity on oceanic islands. Species are filtered on their ability to disperse to islands and successfully establish. Although not necessarily occurring consecutively in this order, historical contingency creates unique circumstances for which species persist, while community assembly occurs through taxon cycles and assembly rules, and eventually evolution through anagenesis and cladogenesis (e.g., adaptive radiations) occurs [Losos & Ricklefs (28), Losos et al. (190), Gillespie (191)].

Historical contingency:

unique past events in archipelagos which affect the trajectory of biodiversity patterns (e.g., which species persist and which perish)

Taxon cycle:

sequential phases of expansion and contraction of the ranges of species thereby undergoing evolutionary change and associated niche shifts

Assembly rules: rules which govern species co-occurrence patterns in developing and established biological communities

are also important refugia for ancient species and lineages that have since gone extinct on continents, therefore representing unique phylogenetic lineages (43). Alpha and beta species diversity per unit area is often low on islands because some species population densities tend to be overabundant, through a pattern termed density compensation, and ecological generalists dominate across different habitats. However, because of high endemism from radiations or relict species, islands contribute disproportionately to global species diversity.

The proliferation of island biodiversity data has enabled macroecological studies (e.g., 44, 45) that have revisited the role of founder effects and dominance (incumbent advantage or priority effect) in shaping island populations and species (46, 47), as well as the relative importance of colonization versus in situ speciation for the formation of island biodiversity (48). There has also recently been a return to pattern-based investigation comparing islands to continents, and native to non-native species, across multiple taxa (e.g., 49–51), revealing in particular how the human introduction of species has replaced biogeographic filters to island colonization with social ones (52, 53). The application of molecular biology tools has also widened our understanding of the role of genetic diversity and phylogenetics on islands (54). Genetic diversity can be measured in many ways with many different markers, but F-statistics provide a measure analogous to species diversity measures that partition variation among population levels (55). Genetic diversity of island species is generally expected to be lower than continental counterparts, given population bottlenecks following founder events and persistent small population sizes relative to continents (56). However, this need not always be the case (57), and prolonged small population sizes on islands may have also purged deleterious genes, making species more resilient to genetic fitness effects such as inbreeding depression (58).

Functional Diversity

Existing on an island shapes the biology of organisms, from the traits of species to the interactions among them, and this functional diversity is as important as species diversity (59). Functional traits

more common in island species include gigantism and dwarfism, reduced dispersal ability, longer life spans, reduced reproductive output, loss of defenses, flightlessness in birds and insects, and woodiness in herbaceous plants. Such functional traits recurrently emerged in atypical taxa, creating a suite of traits that can be considered adaptations to island life. Classic studies of how island traits are formed focused on the island rule—whereby the size of an organism on isolated islands changes predictably in comparison to continental counterparts (60), the evolution of flightlessness (61), and the evolution of woodiness (62). In some cases, this occurred as species established on islands expanded their trait space to that vacated by functional groups characteristically absent from islands [e.g., the Komodo dragon (*Varanus komodoensis*) replacing mammalian predators, giant tortoises replacing large mammalian herbivores, lizards replacing insects as pollinators]. This has led some to argue that vacant niches are more prevalent on islands (63).

In addition to traits, the island syndrome sees systematic differences in demography, reproduction, behavior, and morphology on islands (64), given the modulating biogeographic effects of island size and isolation. Life on small and isolated landmasses reduces the benefits of dispersal and the co-occurrence of predators and competitors. This affects population density, which has cascading short-term effects on reproduction, body size, and behavior, and long-term effects on reproductive output and body size. The principles of the island syndrome have been derived from studies on island populations of rodents (65) and reptiles (66), although the framework likely has validity in application to birds (e.g., 67) and plants (e.g., 64), among other taxa, and their interactions (68). The island syndrome paradigm provides a guiding framework for understanding what shapes the biology of organisms on islands. However, the forces that structure the biology of organisms on islands are scale dependent on the ecology of the organisms. When the island is relatively large compared to the ecology of the organism, the organism will become less distinguishable from continental counterparts.

Species interactions are also a critical component of functional biodiversity, maintaining ecosystem processes in ecological networks (23). Islands tend to be dominated by highly generalized species and interactions (69), but with low redundancy due to limited species diversity (70). As for species diversity, these interactions tend to be dominated by high degrees of uniqueness and endemism. The functional role of species in island networks is also relevant, particularly the strength of their interactions (69). Loss of key functional groups, such as seed dispersers, has cascading consequences throughout the ecosystem (71). The outcomes of species interactions on islands are also heavily dependent on the mode of trophic regulation, which on islands is bottom-up controlled in the absence of apex species found on continents such as large mammalian predators and herbivores (72).

Habitat Diversity

Habitat diversity within islands, correlated with island area, also shapes species diversity (73), and hence contributes to biodiversity (74). Habitat diversity is limited on islands at high and low latitudes, and also on low-lying islands, but is greater on topographically diverse islands due to broad climatic gradients (e.g., elevational gradients, as well as the contrast between windward and leeward sides of mountain chains). Habitat diversity fosters meta-communities that exchange species, interactions, and energy flow across boundaries and gradients (75). Within archipelagos, geophysical and associated habitat diversity is often high especially when they include volcanic islands of different ages (76). In the first phase of their ontogeny, characterized by volcanic activity, volcanic islands grow to tall mountains that, at their climax, typically reach more than 4,000 m above sea level and up to 10,000 m from the ocean floor (e.g., Mauna Kea in the Hawaiian archipelago). Once volcanic activity stops, the work of erosion becomes increasingly visible and shapes island

Density

compensation:

elevated population densities of particular species on islands caused by reduced species richness

Island syndrome:

a suite of behaviors, traits, and population dynamics found in species on islands

landforms. Old volcanic islands are characterized by deep valleys, rugged topography and steep slopes carved by erosion, before submerging and becoming coral atolls or sea mounts. Whereas soils on young islands are nitrogen-limited, those on old islands become phosphorus-limited (77). On some islands, unique geological formations have facilitated the evolution of a unique flora (78). Such abiotic variation among and within islands drives species variation on islands, leading to the establishment and evolution of different species (79).

HUMANS

Humans have arisen as a driving force shaping biodiversity. Human impacts on island biodiversity, from first contact through colonial times, bear both similarities, but also contrasts, to impacts on continental biodiversity. On islands, impacts have often been more rapid and affected more land surface area. Although many islands were among the last places on the planet to be colonized by humans, impacts have been particularly severe thereafter (80). Indeed, most known extinctions have happened on islands throughout all phases of human settlement history (16, 81). Deconstructing the types of impacts humans have had on island biodiversity allows us to understand the current state of island biodiversity.

First Contact

Knowing the date of first human contact on an island is critical for interpreting human impacts, most clearly species extinctions, and distinguishing them from climatic events (16, 82). New discoveries and recent advances in paleoecology have refined some of the dates of first contact by humans, but it often remains controversial when first contact occurred [e.g., recent estimates for Madagascar range from 3,000 to 10,000 years BP (83, 84)]. Nonetheless, typically when humans arrived vulnerable species were rapidly exploited to extinction (81, 85). However, this might not have always been the case, particularly for very early cultures with limited technology (86), and impacts can vary greatly based on circumstances such as area, isolation, geology, or climate (87, 88).

Humans on islands typically ate their way down trophic levels (89). Insular species were more vulnerable than continental ones both because of their island syndromes and the lack of refugia on small islands (90). Megafauna were the first extinctions, typically endemic mammals (91) and birds (92). Estimates from the Pacific are that 20% of the avifauna, at least 1,000 species, went extinct following first contact (85, 93). Following the extinctions of megafauna, the diet of indigenous people shifted rapidly to less rewarding but also less easily exhausted marine resources such as fish and shellfish (94). This often drove a shift from nomadic hunting to settled agrarian societies (95). Human consumption was not the only driver of negative impacts on island populations; predation by non-native species (e.g., mammals) was substantial, and some species were also harvested to extinction for ornamental purposes (e.g., birds for feathers). The deliberate or accidental introduction of non-native species also caused habitat transformation, which indirectly further exacerbated extinctions (96).

The measure of impact of humans on island biodiversity should not just be numbers of species extinctions. In the pursuit of a primary economy based around raw materials, humans also whole-scale transformed landscapes, including extensive deforestation (88), especially of coastal and low-land habitats (94), and degradation of soils (97). Non-native species introductions (98) led to concomitant reductions in the abundances and distributions of native species (16, 87), and loss of interactions (99, 100). Often, these factors acted in synergy (16). How human societies culturally responded to their negative impacts on island biodiversity, particularly the extinctions, is considered today in light of the ongoing social injustices following European colonization and loss of

sovereignty (101). Indigenous people were certainly aware of, and lamented, extinctions (102), and adopted new cultural practices in response (87). Over time biological diversity and cultural diversity on islands became intrinsically linked (103) as early signs of the Anthropocene emerged (80).

Modern History

The modern era is generally considered to have commenced around 1500 AD with the Age of Discovery, but its timing on islands typically coincided with colonization originating from Europe or European descendants. European culture came to dominate much of the world due to extensive overseas exploration, and (re)discovery of remote islands. Many of these islands were claimed and colonized regardless of the presence of indigenous people upon them. Economies continued to exploit natural resources but shifted toward a secondary economy exporting manufactured goods to continental homelands. This was typically done with no regard to sustainability, and following extensive land-use change led to degraded land or monocultures. Habitat transformation was extensive, with typically at least two-thirds of original habitat lost in its entirety, and the remaining one-third substantially altered (104). These colonizations exacerbated the decline of native biodiversity on islands (16). Ninety percent of bird extinctions during this period have been on islands (105). Intrinsically linked to biodiversity, the population size and cultural diversity of indigenous people on islands also often declined dramatically (14).

Colonization also caused elevated rates of species introductions from continents. Many species introductions to islands were intentional and involved acclimatization (53, 106). The establishment of regular shipping lines enabled the repeated introduction of individuals, ultimately facilitating establishment (107). Unintentional introductions of animals and plants also occurred. Invasive non-native rodents from Europe were accidentally introduced to more than 80% of the world's island groups (108), and following them intentional introductions of companion animals such as cats and dogs. These mammalian predators are most responsible for vertebrate extinctions during this period (109).

European culture also brought Judeo-Christian anthropocentric worldviews about how humans and nature relate (110). This anthropocentric sense that humans were separate from nature and had dominion over it, coupled with the technological innovations of the Industrial Revolution, enabled the continued transformation of biodiversity on islands (111). In the Western world the co-occurrence of imperialism, industrialism, and rationalism gave birth to modern ecology and environmental ethics at the start of the twentieth century (112), and then the field of conservation biology by the middle of the twentieth century (113). This was followed by a renaissance of indigenous culture and local biocultural knowledge and heritage on islands (20) that sets the scene for island conservation in modern times.

Contemporary Era

The greatest change to impact island biodiversity in the twentieth century was the advent of globalization. With rapid international transit, the diversity of vectors and pathways for introducing new species and diseases increased substantially (114), and with it the number of species introductions (51). The more remote an island, the more likely it appears to have non-native species established on it (50), possibly reflecting elevated introduction efforts (aka propagule pressure) to such sites (106). The types of species being introduced also changed (115, 116), with shorter travel times increasing survival in transit, and hence the establishment rate, of unintentional introductions.

Ultimately, the historical biogeographic barriers that delineated the world, and particularly islands from continents, were broken down (52). The factors that control species richness on islands

in the Anthropocene are now social rather than natural (117). The full extent of this is only now being revealed through macroecological studies of global datasets, which reveal no decrease in the accumulation of non-native species worldwide (118) due to new source species pools of species being accessed (119). Ironically, the newly found accessibility of islands also drove a diversification to tertiary economies that was focused on tourism and founded on the remoteness of islands and their natural landscapes and unique biodiversity (120, 121). At the same time, exposure to a volatile global economy forces island economies to periodically opportunistically readjust their primary and secondary economies, leading to ever-changing exploitative land use.

The twentieth century also saw geopolitical upheaval, particularly following the World Wars given the diminishment of the colonial Western European powers, prompting a return to independence for many islands (122); however, dependences remain high (20) and sovereignty is still contested for others that remain subnations of continental powers (101). This shift in power dynamics created a new geopolitical class of islands—small island developing states (SIDS). Thirty-three entirely insular SIDS are now recognized globally, and these are not randomly distributed across the planet. They tend to be tropical, with high biodiversity, but relatively low financial capital (123).

DRIVERS

The smaller size of islands compared to continents renders them more vulnerable to novel disturbances (90), making them epicenters of defaunation in the Anthropocene (124, 125). The status of island biodiversity today is a result of the historical, although novel at the time they first occurred, impacts on islands generated by humans. Today, approximately half of island species that have been assessed for threat status are at some risk of extinction (126). As well as the direct losses associated with species extinctions, disappearance of species can negatively affect their mutualists, leading to extinction cascades and changes of ecosystem functioning (72). The loss of large vertebrate seed dispersers, in particular, has been demonstrated to affect many island plants (71, 127).

Current Threats

The availability of comprehensive global datasets such as the IUCN Red List of Threatened Species, Global Islands Database, and Global Invasive Species Database has facilitated analyses of contrasting factors historically affecting island biodiversity, particularly extinctions (**Table 1**). For both plants and animals, islands have higher densities of extinct and critically endangered species, and also human languages, compared to continents, and invasive non-native species and habitat loss were the largest threats to island biodiversity (14). Just under half of all species at risk of extinction are found on islands. For threatened species found on islands, almost all are found exclusively on islands, and mostly restricted to one island, whereas invasive mammals are only absent from one-quarter of the islands (128).

The current status of threats to island biodiversity today can be assessed relative to continents. The IUCN Red List considers 12 categories of threat to species, although the two categories “geological events” and “other options” are typically excluded when considering anthropogenic impacts only. Maxwell et al. (129) compared these threats for all near threatened, vulnerable, endangered, and critically endangered species ($n = 8,688$ where threat data were available). Leclerc et al. (126) compare these same threats to all vulnerable, endangered, and critically endangered species ($n = 4,127$ where threat data were available, but excluding near threatened taxa) and extinct or extinct in the wild species ($n = 249$ where threat data were available) on islands, but only on a subset of well-documented geographic subregions (15 insular regions with > 50 species assessed). The tabulated results of Leclerc et al. and Maxwell et al. reveal the relative importance of the 10

Table 1 Summary of studies using the IUCN Red List to investigate threats to biodiversity on islands

Study	IUCN Red List	Threat status	Taxa	Location	Summary
Tershy et al. (14)	2010.1	CR and EX	Animals and plants	Species exclusively on islands	Compared number of species of plants and animals between islands and continents, and a subset of threat categories
Spatz et al. (128)	2013.2	EN and CR	Birds, mammals, reptiles, and amphibians	Species totally or partly on islands	Compared distribution of native species to distribution of invasive vertebrate species
Doherty et al. (109)	2014.3	VU, EN, CR, EW, and EX	Birds, mammals, and reptiles	All species	Determined impact of introduced mammalian predators
Bellard et al. (133)	2015.4	LC, NT, VU, EN, and CR	Birds, mammals, reptiles, and amphibians	All species	Determined impact of invasive species

Abbreviations: CR, critically endangered; EN, endangered; EW, extinct in the wild; EX, extinct; IUCN, International Union for Conservation of Nature; LC, least concern; NT, near threatened; VU, vulnerable.

different threat categories for insular species listed in the IUCN Red List where threat data were available (**Table 2, Figure 3**). However, other indirect threats to island biodiversity also exist, such as the consequences of habitat transformation on habitat diversity, the loss of traditional knowledge, and the impacts of free trade and globalization on island biocultural diversity (130). Similar to threatened continental species, the most prevalent threats to island species are overexploitation and agricultural activity. However, species on islands are much more likely to be threatened by invasive species and disease; indeed, almost three-quarters of threatened species impacted by invasive species and disease are found on islands. In contrast, threats such as transport, pollution, human disturbance, and urban development have so far been much less likely to impact island species. However, these studies are not exactly comparable as the IUCN Red List dataset versions used—and filters applied—differ slightly, and in any case the IUCN Red List is itself also a biased subset of biodiversity (131).

Analyses of historical and current threats to island species consistently show that invasive species (see the sidebar titled Defining an Invasive Non-Native Species) and diseases have been

Table 2 Number of International Union for Conservation of Nature (IUCN) Red List species impacted by a threat category

	Overexploitation	Agricultural activity	Urban development	Invasion and disease	Pollution	System modification	Climate change	Human disturbance	Transport	Energy production
All species ^a	6,241	5,407	3,014	2,298	1,901	1,865	1,688	1,223	1,219	913
Insular species ^b	2,356	2,345	986	1,684	372	923	702	359	217	428
Percentage insular species ^c	38%	43%	33%	73%	20%	49%	42%	29%	18%	47%

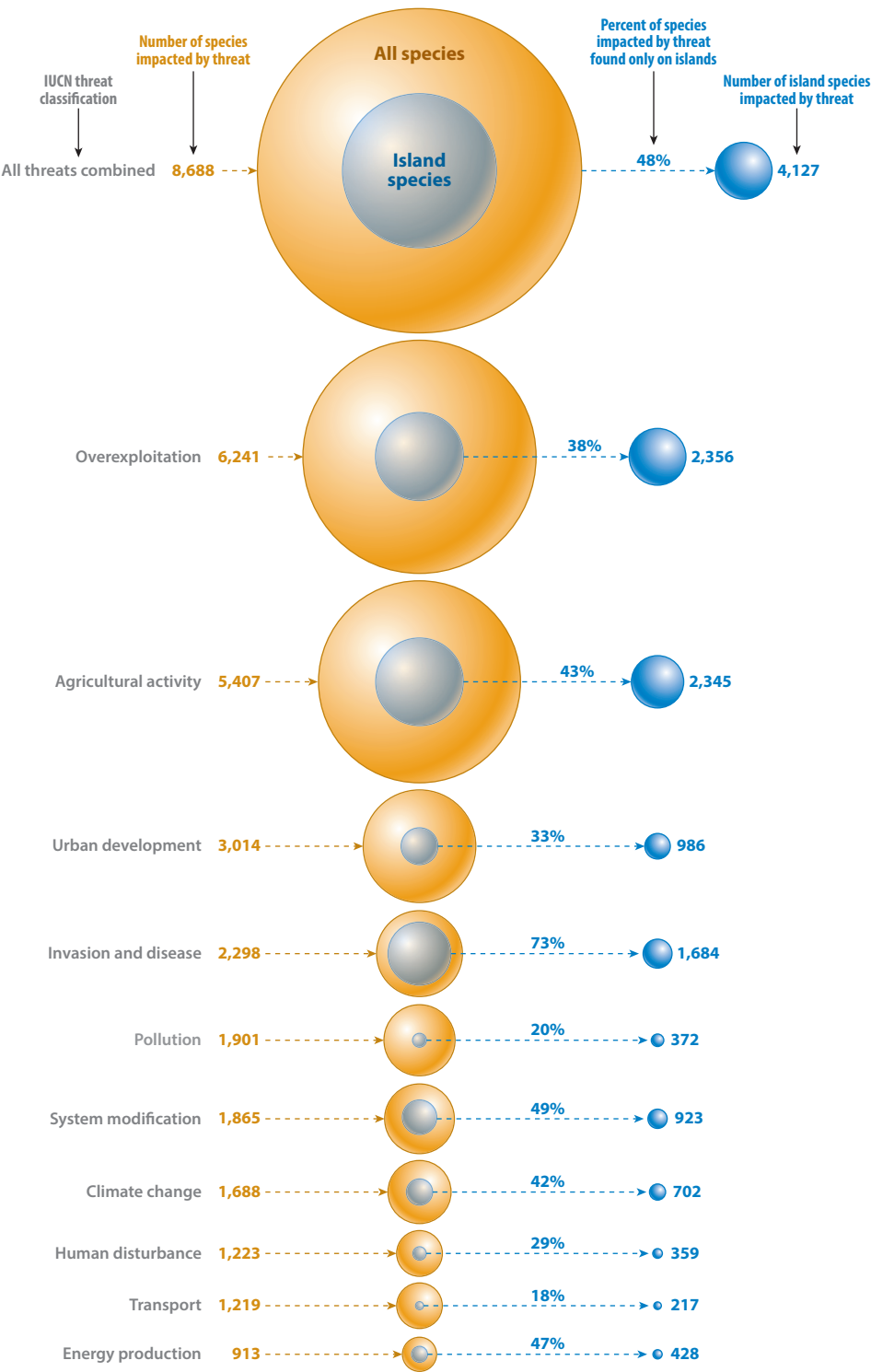
^aData are from Maxwell et al. (129) for IUCN Red List 2016.1.

^bData are from Leclerc et al. (126) for IUCN Red List 2015.4.

^cHere Leclerc et al. exclude 1% of insular species, and near threatened species, so island percentages are an underestimate. Data here exclude extinct and extinct in wild species.

Figure 3

The major threats to all IUCN Red Listed threatened species (numbers of species and circles in *gold*) and those found only on islands (percentages, numbers of species and circles in *blue*). Figure adapted from Maxwell et al. (129) using Leclerc et al. (126).



DEFINING AN INVASIVE NON-NATIVE SPECIES

Non-native (introduced or alien) species have been transported to new locations outside their prehuman distribution range by human agency. To become invasive, they must pass successfully through the stages of transport, introduction, establishment, and spread (186), and be considered to have some form of negative impact (187). Negative impacts arise from invasive species exceeding a damage threshold on some ecological, social, or economic value (188). Non-native invasive species are distinguished from native invasive species (189).

the major drivers of extinction on islands in modern history (i.e., in anthropogenic landscapes characterized by fragmented natural areas), particularly for native vertebrate species (132). Introduced mammalian predators were implicated in just over half of vertebrate extinctions on islands (109), and the only other invasive species of comparable magnitude of global impact is the chytrid fungus affecting amphibians (133). Whereas all threats interacted to cause widespread declines in native species abundances on islands, so far only invasive species, especially introduced predators and diseases, appear to have had the efficiency to completely extinguish species. This is possibly because invasive species impacts are spatially unbounded.

In the contemporary era, invasive species are not the most common threat in the current declines of island species, but remain an ongoing important threat, especially relative to their lesser role in the decline of continental species. The ecological and socioeconomic impacts of invasive species in island ecosystems occur at all levels of ecological organization (134). However, it is not necessarily that islands are more invadable per se, as once believed, but that they are places where, relative to the native biota, more species introductions have taken place or more extensive habitat transformation has happened (53, 135), and the endemic species are in relatively smaller numbers and occupy smaller areas, making them more vulnerable to the impacts of invasive species and subsequent extinction (16, 72).

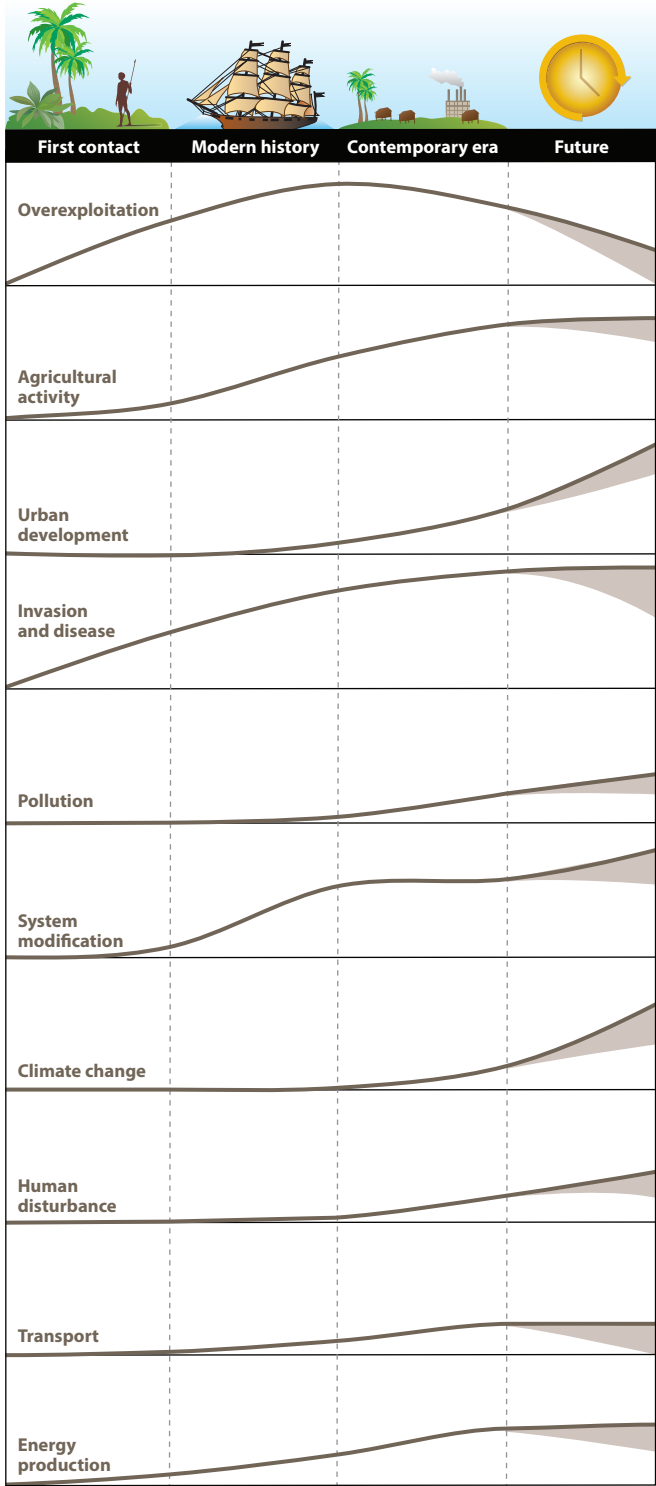
Emerging Patterns

The current threat status of island biodiversity is largely a result of past impacts, and some effects of the past will still only become visible in the future. Some native species extinctions are yet to be realized, as populations exist in a transient state between the initialization of an impact and its end point. Sometimes, this transient state can occur over centuries, creating an extinction debt from the legacy of past impacts such as habitat transformation (136, 137). Even where species have not gone extinct, substantial reductions in range and abundance erode genetic diversity and population resilience, and reduce species participation in ecological networks. Nonetheless, what is clear is that the biodiversity of islands has in most cases already been irrevocably transformed at all levels, and the future threats to island biodiversity will be different in type and magnitude (**Figure 4**). The accumulation rate of non-native species on islands is not slowing down (118), and the invasive species and diseases of the future will differ in type from those historically. Already emerging invasive species groups on islands include reptiles from the pet trade, microorganisms, and diseases, all of which can readily occupy vacant trait space on islands. These novel invasive species will create further novel assemblages and interactions on islands, with far-reaching ecological consequences (72).

Some non-native species will remain an important threat to island biodiversity (i.e., those considered invasive), whereas others might have to be evaluated and understood differently. Introductions of non-native species to islands have increased local species richness far beyond historical levels, leading to novel biogeographic patterns determined by anthropogenic factors (53, 138–140).

Figure 4

Threat intensity over time on islands through first contact, modern history, the contemporary era, and projected into the future. Whereas some threats will continue to expand (e.g., invasion and disease) and new threats will emerge (e.g., climate change), other threats will remain low (e.g., human disturbance) or will diminish (e.g., overexploitation). Shading indicates potential alternative future trajectories if threats are appropriately managed.



These empirical patterns have led some to argue that the extinction of native species is offset by the introduction of new species (141). However, this increase in species richness is scale and taxon dependent (142, 143). Regionally (e.g., at the scale of archipelagos), often the same pool of species are being introduced, but different species (sometimes of different ecological function) are going extinct; thus, evaluating different dimensions of biodiversity is critical when assessing changing species richness (**Figure 5**). Furthermore, counts of summed native and non-native species richness on islands or archipelagos do not reflect underlying biological processes at the scale of habitats. Within islands, many threatened endemic species are found only in small fragments of relatively undisturbed and uninvaded natural habitat and do not interact with non-native species that dominate the surrounding disturbed landscape. The increase of total species richness in the short term and at an island level (141) therefore cannot be interpreted as evidence of long-term coexistence of the two groups of species. When considering the impacts of species introductions on island biodiversity, one must distinguish alpha diversity, beta diversity, and gamma diversity (144), native from non-native biodiversity (145), and be clear if specifically considering species richness (146), or biodiversity more broadly than species numbers alone.

The strongest emerging threat is likely to be human-induced climate change, which will increasingly affect terrestrial biodiversity on islands (147). This will occur through multiple mechanisms, including more extreme climates and climatic events, as well as coastal inundation and sea-level rise (148). Island biodiversity will be particularly vulnerable due to small population sizes and limited extents of particular habitats (often already fragmented through habitat transformation), as well as limited opportunities for dispersal to favored climates (149). These vulnerabilities will be exacerbated through the interaction of other increasing threat factors, especially habitat transformation and fragmentation and emerging invasive species. Chytrid fungus and avian malaria will invade new habitat due to climate change, thereby threatening endemic island birds and amphibians previously surviving in climate refugia (e.g., 150). Secondary consequences will follow from human adaptation, as development into natural areas might take place due to displacement from coastal areas as a result of sea-level rise (151).

ADAPTATION

Clearly, challenges for biodiversity conservation on islands are enormous, and no single strategy will suffice (152). Although protection of island biodiversity is considered a global conservation priority, analyses of global spending show that island conservation efforts are underfunded relative to continents (153). A multipronged conservation strategy has emerged that integrates traditional conservation strategies such as protection and restoration with ideas including mainstreaming biodiversity in different land-use systems and incorporating the realities of emerging novel ecosystems (19). At the same time, there has also been a resurgence acknowledging the crucial role of islanders in the renewal of human-nature relationships (20). Although some efforts build on the opportunities provided by the isolation of islands that can be managed and often restored in their entirety (e.g., small offshore islands), much island biodiversity will have to be saved amid human land-use and in heavily used and disturbed cultural landscapes. This will require multiscale strategies that combine targeted local interventions for protection and restoration at local scales, with the mainstreaming of biodiversity across mosaic cultural and novel landscapes (16).

Protection and Restoration

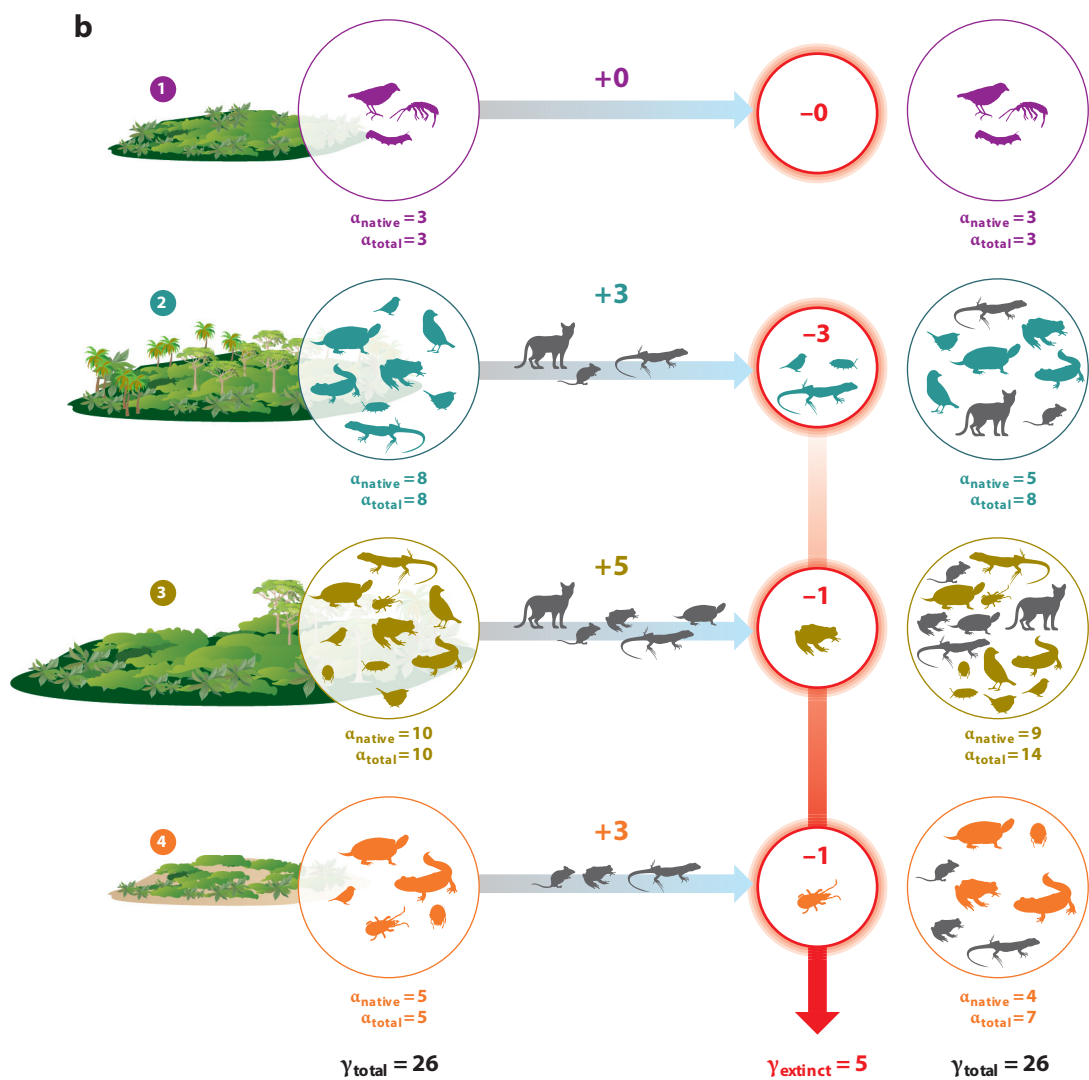
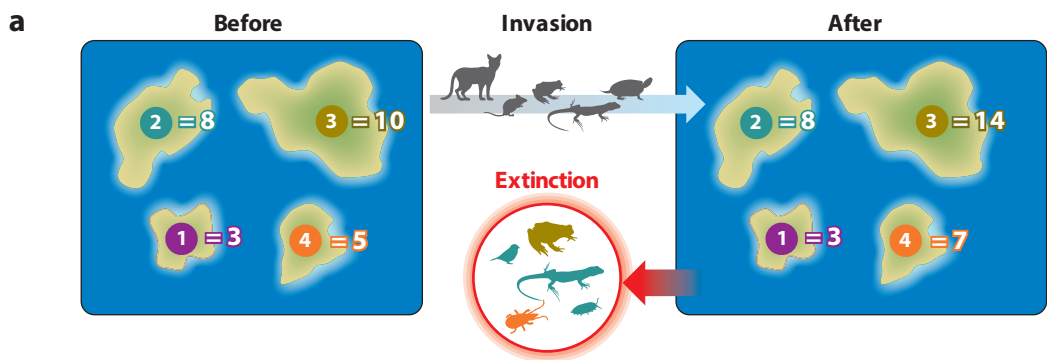
Protected areas are established on most islands (**Figure 6**), but relatively undisturbed natural habitat remains only in small pockets on most inhabited islands, often in inaccessible places such as steep slopes, ridges, and deep valleys or at high elevation (19). The only extensive natural areas left

Novel ecosystem:

a self-sustaining ecosystem of human agency with a significantly altered species composition compared to a prehuman state and in which ecological thresholds have been crossed

Cultural landscape:

a landscape with cultural properties representing the combined works of nature and humans



(Caption appears on following page)

Figure 5 (Figure appears on preceding page)

A hypothetical example illustrating the role of scale in assessing species richness changes following invasion in a simple four island archipelago. (a) Before invasion, the archipelago contains a total of 26 unique species, all of which are native and endemic to single islands (*Before* column). Following the establishment of five identical introduced species in different numbers across islands of the archipelago (*Invasion* column), five of the native island endemic species are driven extinct (*After* column). (b) Although island species richness (α) has remained the same (islands ❶ and ❷) or increased (islands ❸ and ❹), and archipelago species richness (γ) has remained the same at 26 unique species, native species richness has declined with five extinctions, affecting global species richness given these are endemics. Distinguishing native from non-native species richness is critical. Island ❶ might be a candidate for species conservation and biosecurity, island ❷ might be a diverse novel ecosystem composed of different assemblies of native and non-native species, island ❸ might be where native and introduced species co-exist in different habitats, and island ❹ might be where native species are protected through intensive ex situ, inter situ, and in situ conservation.

are at high elevations in subalpine and alpine habitat, on remote islands at high and low latitudes, and on low-lying atolls. Although these habitats do harbor unique biodiversity, species numbers are low. Much island biodiversity is therefore left in small and highly fragmented protected areas scattered across anthropogenic landscapes. Protection of this native biodiversity depends increasingly on continuous maintenance work such as invasive species management and species recovery programs (e.g., 154). Indeed, there are many examples of successful species recovery programs for species that were close to extinction (155).

Restoration efforts have been particularly successful on small uninhabited offshore islands where invasive species can be eradicated, native vegetation replanted, and native animals reintroduced or translocated, for instance islands in New Zealand (156) or the Western Indian Ocean (155). Eradication efforts are increasingly focusing on larger islands (157), and deliver a substantial return on investment for conservation funding (158), as well as being a necessary precursor to island restoration. Restoration of small areas on inhabited islands has also been possible through intensive management (159). Suppression of invasive species below damage thresholds can lead to the rapid recovery of native plants and animals (160) and can restore species interactions (161). However, where multiple threats interact and threat levels are maintained by strong stakeholder interests, protection and restoration are difficult, as exemplified by the continuing decline of native biodiversity on many inhabited islands (e.g., 162, 163).

Restoration must be based around clear social and ecological goals (164) and can draw on the analyses of current ecosystem states (165) as well as paleoecological studies of prehuman island biodiversity (166). In some cases, dramatic and rapid returns of many characteristics of historical natural ecosystem states have been possible, particularly where they focus on restoring keystone species and processes (167). The use of ecological design efforts is becoming more common. One strategy, sometimes called inter situ conservation as it moves between ex and in situ conservation practices (168), is to create new communities or ecosystems that are partly managed and partly wild. Inter situ conservation has been particularly successful when threatened species have had to be removed from their extant range due to threats, and conserved in a new site where threats could be effectively mitigated or were not present, e.g., on small offshore islands. This has often been the case for species at risk from invasive mammals (169), but may become increasingly common to conserve species at risk from climate change (170). Restoration projects on islands also benefit from the support and involvement of people, as restoration is essentially a human endeavor, which also brings wider benefits to people's health and wellbeing (171).

Cultural Landscapes

Although protection and restoration of natural areas on islands will remain important in conservation agendas, biodiversity conservation in the Anthropocene requires moving beyond the mind set of protectionism and protected areas (172). Cultural landscapes express the long-standing

Countries 46–90 next panel

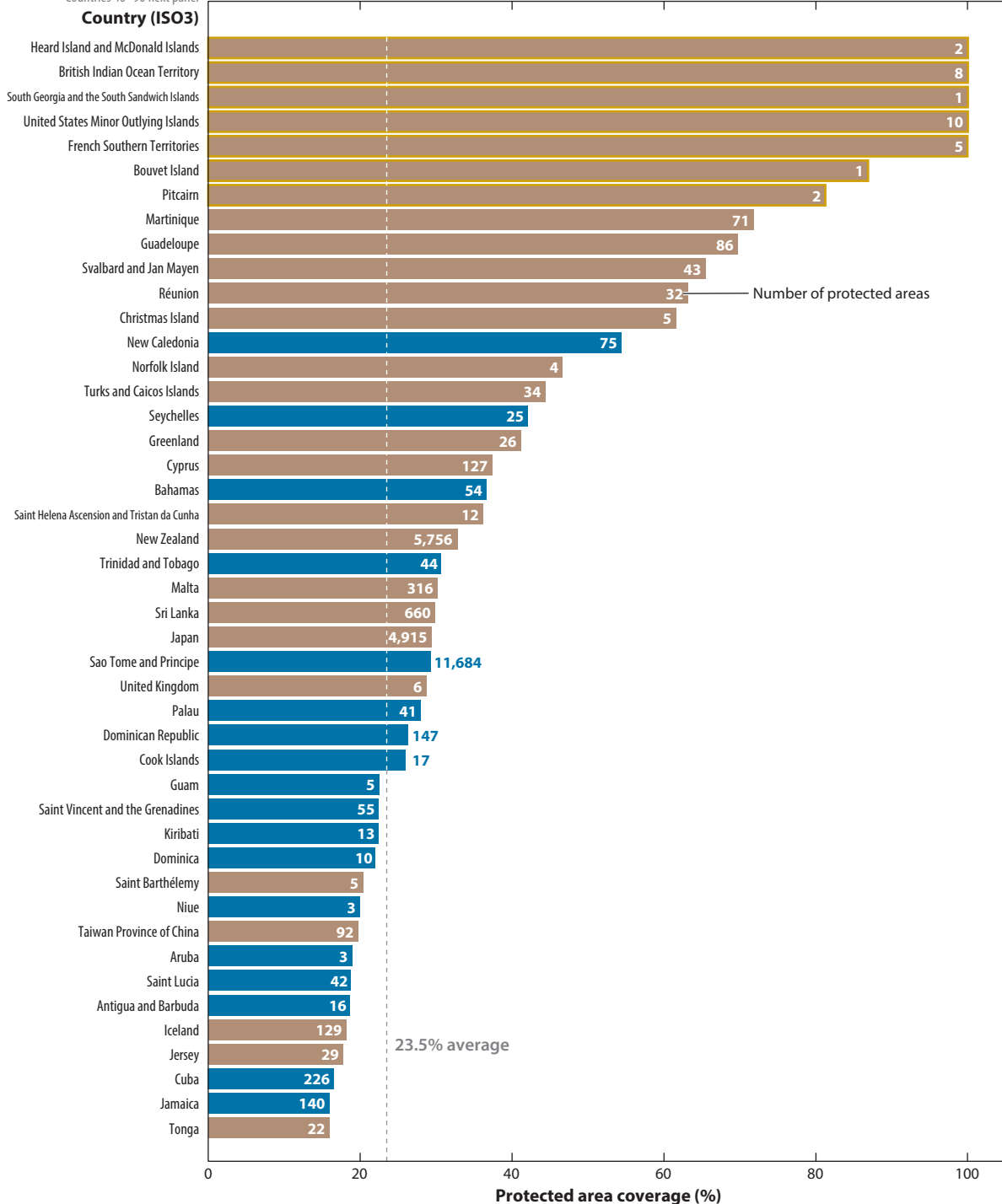
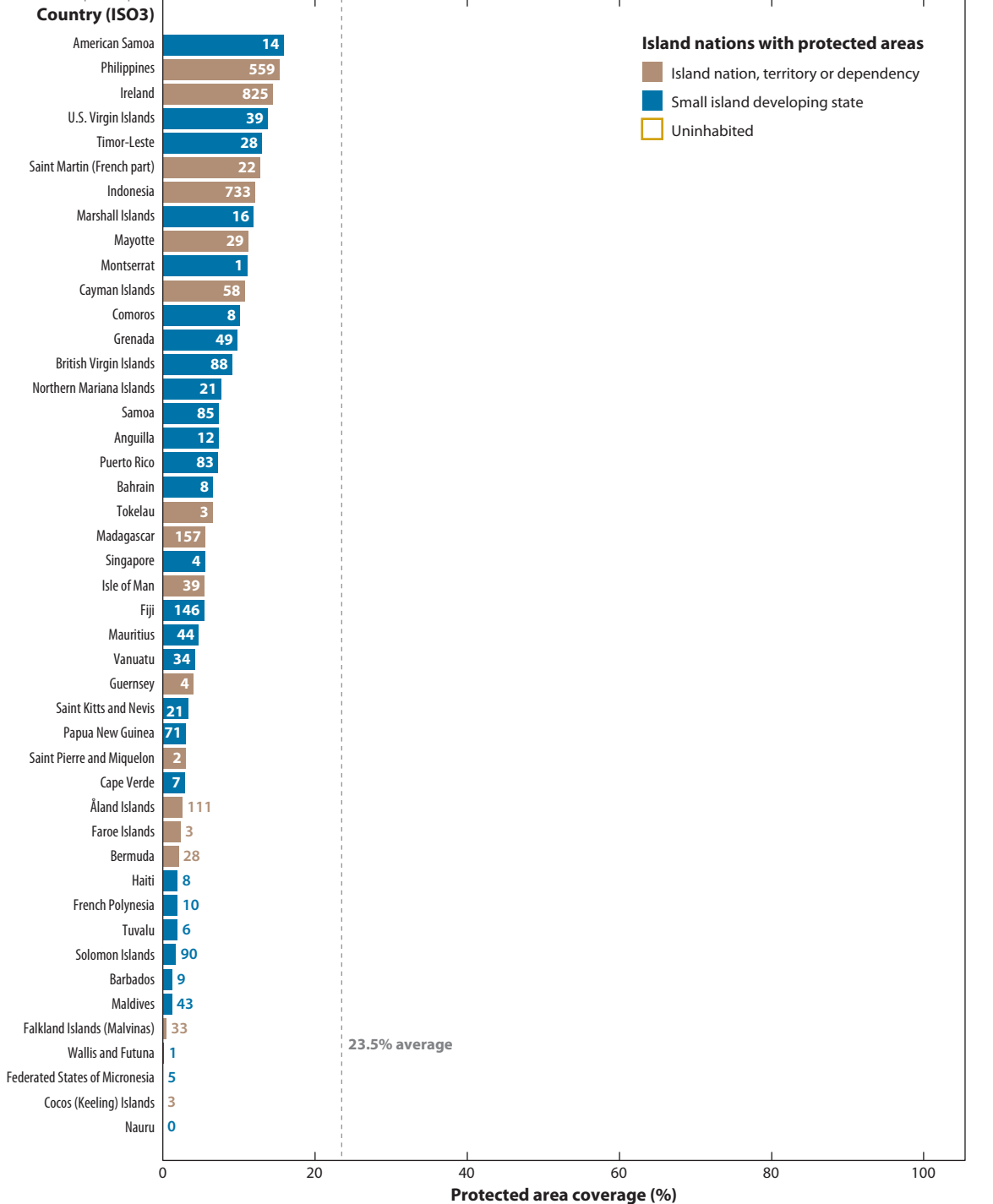


Figure 6

(Continued)

Countries 1–45 previous panel



(Caption appears on following page)

Figure 6 (*Figure appears on preceding page*)

There are a total of 28,559 protected areas on 90 wholly island nations, territories, or dependencies (number of protected areas per island nation listed inside bars; *right margin*). Protected area coverage on islands ranges from 0 to 100%, and across all islands a total of 23.5% of terrestrial land area is in protected areas. Only one-third of islands ($n = 30$) exceed the global average, and the six most protected islands with more than 85% coverage are all uninhabited (outlined in *yellow*). Just over half of these islands ($n = 49$) are Small Island Developing States (*blue bars*) that are overly represented in below average protected area coverage. Designation of a protected area does not necessarily ensure management effectiveness. Data are from <http://www.protectedplanet.net>.

relationship between peoples and their natural environment. Some native biodiversity persists across cultural landscapes, and subtle changes in land management practices and human behaviors can promote it (19). Many island species are adaptable and given appropriate land-use practices persist in anthropogenic environments and benefit from novel resources (69, 173). Non-native species can sometimes have beneficial functions in cultural landscapes (174), alongside any negative impacts (145).

Island cultures around the world hold a unique biocultural heritage including traditional knowledge of ecosystem management (175). Promotion of biodiversity in cultural landscapes must build on this local knowledge and culture, and their sense of guardianship over the land (20). However, that is not to say that such island cultures are static; they too have continued to evolve and adapt as new cultures have been, and will continue to be, integrated into them (176). Such recognition of the uniqueness and value of biocultural heritage on islands has been growing in recent decades both locally and internationally, and it is enshrined in international conservation and sustainability targets (177). Working with local people and incorporating their local knowledge and practices is today considered a crucial component of any effective ecosystem management program on an island (175), but still faces challenges overcoming past legacies of colonialism and ongoing disputes over sovereignty and embedded social injustice (101).

Modern production within cultural landscapes also provides opportunities for biodiversity conservation, particularly through synergies that arise from land-use practices such as pest control and promotion of ecosystem processes (such as pollination), both of which can enhance native biodiversity. This ultimately brings shared benefits of biodiversity improvement to both the biodiversity itself and human livelihoods, and encourages cofinancing of conservation actions (165). Such whole-landscape management of biodiversity across contrasting landscape elements is especially critical on islands, where smaller land areas and higher degrees of fragmentation mean biodiversity, both native and non-native, is more often moving between landscapes and dependent on different landscape contexts. Cultural landscapes with high native biodiversity can then maintain exposure to biodiversity among increasingly urbanized island inhabitants (178), and deliver the uniqueness that makes islands attractive as ecotourism destinations (179).

Novel Ecosystems

Increasingly more land on islands, and often as part of protected areas, can be classified as novel ecosystems. With the transition away from primary economies, cultural landscapes have been abandoned on many islands. As a result of former land use and its legacies, contingent novel ecosystems develop that are characterized by mixed species compositions of native species from different habitats as well as non-native species and cultivated species (19, 180). Although not a replacement for native habitats, these new biotic communities can provide habitat for threatened native species (173, 181), provide ecosystem services (174), and include non-native species of conservation value in their native range (182) or of cultural value, for instance, among species introduced by indigenous people (98).

Studies on emerging novel species communities composed of native and non-native species on islands are only beginning (180). Some native species can survive in habitats dominated by non-native species, providing threats to their population are mitigated (173, 181). Non-native species in novel ecosystems are as much interacting with one another as they are with native species (72), and non-native species on islands appear to evolve in the same direction as native species (183), potentially enabling coevolution between newly assembled species. Species identity and origin in novel ecosystems is typically considered less important than functional role. In an effort to restore ecological function, the introduction of non-native species as functional analogues of extinct native species might also be undertaken, if it is not already taking place by extant non-native species, with the aim to restore ecological functions in the ecosystem (184).

Decisions around management of novel ecosystems include a large values component and, more so than in natural areas, competing views often exist on what the target ecosystem state should be (185). This includes considering the relative abundances of native versus non-native species, and the purpose of the ecosystem, such as protection of intrinsic biodiversity values versus provision of ecosystem services. However, management of biodiversity on islands should not simplistically contrast different conservation strategies such as working with the realities of novel ecosystems versus conserving remaining native-dominated habitat (19). Rather, biodiversity conservation on islands should consider where sites fall along important gradients such as the degree of anthropogenic change (historical to novel), the level of deliberate intervention (wild to designed), and land-use priorities (conservation to production).

CONCLUSIONS

Across the entire planet, humans have transformed biomes to anthromes, heralding the epoch of the Anthropocene. Concomitant with this has been widespread defaunation and degeneration of ecosystems and their processes. Islands have been at the epicenter of these impacts, their small size and unique biodiversity that evolved in isolation rendering them acutely vulnerable. Islands can serve as model systems for biodiversity conservation in the Anthropocene. In particular, they teach us the importance of holistic approaches.

Biodiversity takes many forms, and it is far more than species richness alone. Species diversity describes not only the total number of species, but also their population abundances and genetic diversity, and phylogenetic uniqueness. Functional diversity describes the variation in traits and interactions among species, and their effects on ecosystem processes. Only by taking into account the totality of biodiversity is it possible to understand how it has changed on islands with human contact over time. Different phases of human colonization and land use had different effects on biodiversity. Extinctions of large and vulnerable fauna happened rapidly after first contact, but following a period of Western colonialism that commenced around 1500 AD, there was a step change in the levels of habitat transformation and species introductions to islands. Today, the biogeographic boundaries of islands have been removed by globalization, but there has been a resurgence of indigeneity and return to independence, especially for SIDS. Accordingly, depending on future population size and land-use scenarios, the fate of island biodiversity will likely be very different. Conservation strategies in the Anthropocene must take into account multiple threats and their simultaneous interactions. Although the impacts of biological invasions have consistently been pronounced on island ecological communities, emerging threats such as human-induced climate change will become more pronounced. This will require a multipronged conservation approach that integrates different strategies. Protection and restoration of ever-diminishing natural areas will remain critical, but biodiversity can also be enhanced in cultural landscapes that combine natural and human values and activities. On many islands, novel ecosystems of mixed native

and non-native species will need to be accepted and managed in perpetuity, presenting new challenges and opportunities for island conservation. The future of island biodiversity will depend on envisioning new human-nature relationships on islands that build on the biocultural knowledge of indigenous and local people, are in line with local and global pathways of long-term sustainability, and integrate island biodiversity into culture practices ranging from stewardship (protection and restoration of qualities of prehuman biodiversity) to biodiversity-friendly land-use practice and the regeneration of the cultural and ecological potentials of island life.

SUMMARY POINTS

1. Islands and their unique biodiversity are at the epicenter of the defaunation and ecosystem degradation crisis of the Anthropocene.
2. Biodiversity is complex and entails many interacting components, including species, functional, habitat, and genetic diversity, that all are unique on islands.
3. Island biodiversity differs markedly from continents due to the filters and processes in the assembly and evolution of biodiversity on marine islands.
4. Human impacts on island biodiversity have grown over time as islands underwent multiple waves of human colonizations and socioeconomic transformations.
5. Overexploitation and agricultural activity are the major threats to island species, but relative to continents biological invasions are proportionally a more important threat.
6. Emerging threats to island biodiversity include human-induced climate change and new invasive species and diseases.
7. Protection and restoration of functioning communities of native biodiversity is critical but resource-demanding and therefore only possible in contexts where threats can be efficiently managed.
8. Promotion of biodiversity in cultural landscapes and novel ecosystems is crucial for maintaining biodiversity across island landscapes and as an integral part of island livelihoods.

FUTURE ISSUES

1. Are there biodiversity patterns other than species distributions (e.g., genetic, phylogenetic, functional) specific to islands and consistent across them?
2. What is the contribution of understudied taxa (e.g., soil biota, invertebrates, nonvascular plants) to island biodiversity?
3. How do community assembly (including coevolution) and ecosystem processes differ between island and continental ecosystems?
4. Can human histories and their interactions with specific island environments in different time periods explain differences in current threat levels of island taxonomic groups?
5. What can we learn from indigenous and historic human-nature relationships on islands for biodiversity conservation and sustainable land use in the Anthropocene?

6. How do contemporary threats to island biodiversity differ from past ones and how can future ones be anticipated and prevented (e.g., extinction debts, human-induced climate change, emerging novel invasive species and diseases)?
7. Which aspects of island biodiversity (e.g., genetic, phylogenetic, functional) will experience disproportionately more threats at present or in the near future?
8. What are the ecological and social values of emerging novel ecosystems on islands and what are effective management strategies for them?
9. How can invasive species eradications be scaled up to larger islands and multiple species for taxonomic groups other than mammals?
10. How can biocultural knowledge best be harnessed, and empowerment of local livelihoods and indigenous people be ensured, for the stewardship of island biodiversity?
11. What are ecologically, socially, and economically sustainable development paths and limits for island societies in the Anthropocene?
12. How can more attention and resources be devoted to island biodiversity research and management on islands and particularly in small island developing states?

DISCLOSURE STATEMENT

J.C.R. discloses that he is a member of the IUCN Invasive Species Specialist Group and a science advisor to Zero Invasive Predators. The authors are not aware of any other affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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