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Reconciling conflicting perspectives for biodiversity conservation in the Anthropocene

Christoph Kueffer^{1*} and Christopher N Kaiser-Bunbury²

We introduce here a framework – based on experiences from oceanic islands – for conserving biodiversity in the Anthropocene. In an increasingly human-dominated world, the context for conservation-oriented action is extremely variable, attributable to three largely independent factors: the degree of anthropogenic change, the importance of deliberate versus inadvertent human influence on ecosystems, and land-use priorities. Given this variability, we discuss the need to integrate four strategies, often considered incompatible, for safeguarding biodiversity: maintaining relicts of historical biodiversity through intensive and continuous management, creating artificial in situ, inter situ, and ex situ conservation settings that are resilient to anthropogenic change, co-opting novel ecosystems and associated "opportunistic biodiversity" as the wild-lands of the future, and promoting biodiversity in cultural landscapes by adapting economic activities.

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Human-mediated environmental impacts are now so extensive and pervasive that many consider that the planet has entered a new geological epoch – the Anthropocene. Increasingly, efforts to conserve biodiversity are confronted with new challenges resulting from profound changes to many biotic and abiotic processes (Steffen *et al.* 2004; MA 2005), which require reassessing current management strategies (Rosenzweig 2003; Koh and Gardner 2010; Kareiva *et al.* 2011; Rudd 2011). Driven by the need to find solutions to these emerging challenges, biodiversity conservation is entering a phase of prolific innovation. Here, we focus on the biological challenges and examine some of the novel approaches under consideration – such as implementing inter situ conservation (Burney and Burney 2007), rewilding (Hansen *et al.* 2010), reassessing the negative image of

In a nutshell:

- In human-dominated landscapes, conservation depends on reconciling conflicting concepts; preserving the qualities of historical (or pristine) nature will rely on human design, and novel ecosystems will dominate wildlands
- Much biodiversity will survive only in "artificial" conservation habitat created through ex situ, inter situ, or in situ management
- Rapid up-scaling of management efforts (including restoration) and rigorous prevention of threats are urgently needed to conserve relicts of historical biodiversity
- Ultimately, maintenance of rare species, ecological interactions, and ecosystem services requires large-scale planning of mosaics of strictly protected areas, "artificial" biodiversity habitats, novel ecosystems, and biodiverse cultural landscapes

¹Institute of Integrative Biology, Swiss Federal Institute of Technology (ETH), Zurich, Switzerland ^{*}(kueffer@env.ethz.ch); ²Department of Bioscience, Aarhus University, Aarhus, Denmark

alien species (Ewel and Putz 2004), and promoting biodiversity in novel ecosystems (Hobbs *et al.* 2013) and cultural landscapes (Daily *et al.* 2001; Rosenzweig 2003; Koh and Gardner 2010). With this upheaval of new ideas, ranging from vague proposals to fully fledged pilot projects, there is a genuine risk of the conservation community fragmenting into different schools of thought (for controversial debates, see Caro *et al.* 2012; Vitule *et al.* 2012; Hobbs *et al.* 2013). In an attempt to minimize that risk, we introduce a conceptual framework that moves beyond established dichotomies and offers ways to reconcile conflicting perspectives.

We focus on oceanic islands, which possess several characteristics that make them a good model system for conservation in the Anthropocene. First, many islands have a high human population density, a heavily altered and fragmented environment, and small remnant populations of native species. These same attributes will increasingly be relevant across continental land masses as wildlands shrink and human land use expands (Rosenzweig 2003; MA 2005; Koh and Gardner 2010). Second, species that are highly sensitive to anthropogenic influences and species with the ability to adapt to such influences are both represented in island biotas; conservation should embrace species that depend on undisturbed habitat (Gibson et al. 2011) as well as those that tolerate anthropogenic conditions or even benefit from humans (Rosenzweig 2003; Kareiva et al. 2011). Finally, islands are an ideal testing ground for new conservation approaches for several practical reasons. Low species richness, small spatial extent of associated ecosystems, and the presence of thousands of islands with similar ecologies and conservation challenges facilitate replicated comparative studies of integrative strategies (Kueffer 2012). Islands have long supported pioneering development in biodiversity conservation (Whittaker and Fernández-

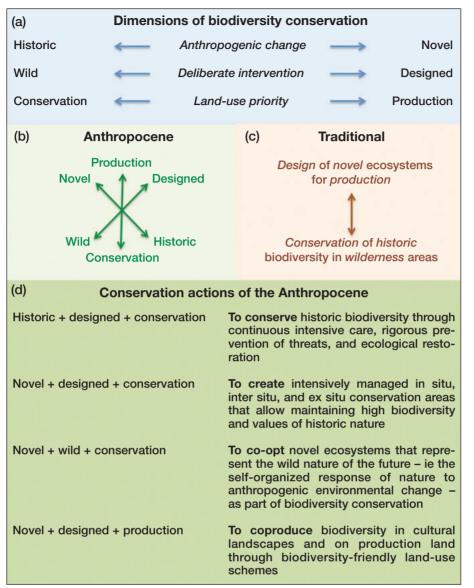


Figure 1. The role of human action in biodiversity conservation in the Anthropocene is defined by three dimensions (a): (1) the degree of anthropogenic change from pre-human historical (or pristine) nature to anthropogenic novel nature; (2) deliberate (eg land use) versus inadvertent (eg climate change) human influence on an ecosystem, resulting in wild or designed nature; and (3) land-use priority that can be determined as biodiversity maintenance or generation of products and ecosystem services. Traditionally, these dimensions were assumed to be aligned; that is, the parameters on the left and right side of the axes were associated with biodiversity conservation and with man-made environments, respectively (c). In the Anthropocene, however, the dimensions are largely independent (b), allowing for the definition of multiple combinations along the three axes. We highlight four combinations (d), which might, when synergistically applied, maximize the potential of biodiversity conservation. Other combinations are also worthwhile, such as "novel + wild + production", which represents the use of ecosystem services produced through novel ecosystems.

Palacios 2007), and many emerging concepts were first applied and fine-tuned on islands (Burney and Burney 2007; Hansen *et al.* 2010; Kaiser-Bunbury *et al.* 2010). In this article, we argue that islands are also well suited to testing how multiple strategies can be integrated and implemented to address the conservation challenges of the Anthropocene.

C Kueffer and CN Kaiser-Bunbury

A biodiversity conservation framework for an anthropogenic world

It was traditionally accepted that biodiversity is conserved most effectively by protecting nature from human influence (cf Rosenzweig 2003; Kareiva *et al.* 2011). Because humans and their impacts are omnipresent, however, this view is becoming increasingly untenable. We believe that a new paradigm, based on three sets of considerations (Figure 1a), is required for guiding conservation efforts.

First, the *historical* abiotic and biotic conditions of habitats prior to major disturbances are an important reference for understanding and valuing the *novel* conditions that occur in human-influenced systems (Hobbs *et al.* 2013). Anthropogenic impacts on ecosystems have often resulted in biodiversity loss and homogenization. Understanding and quantifying these changes remains essential for determining and conserving the value of historical ecosystem characteristics under novel conditions.

Second, humans affect ecosystems either deliberately (eg land use) or inadvertently (eg climate change, invasive species, pollution). Deliberate actions can be altered and directed toward augmenting biodiversity conservation. Nature that is deliberately shaped by humans may be termed designed in contrast to wild (Higgs 2003; Kueffer and Daehler 2009). There thus exists a spectrum - from wildlands, which are scarcely affected by humans' deliberate actions, to designed nature, which is deliberately influenced and created by humans. The negative effects of inadvertent actions on biodiversity appear to be increasing in most biomes of the world (MA 2005). This implies that, even in wild nature,

historical habitat conditions are increasingly being lost as a result of past disturbances (eg fragmentation, small populations, loss of mutualisms, changed abiotic conditions) or unbounded anthropogenic effects. Consequently, historical habitat conditions can be conserved only through continuous major human intervention.

Third, in areas affected by deliberate human action,

conservation must take account of the prevailing types and spatial patterns of land use. This can result in another spectrum – from *biodiversity areas*, which are reserved exclusively for biodiversity conservation, to *production land*, where biodiversity is at best a byproduct of other land-use types.

Thus, conservation actions in a human-dominated landscape can be defined by three largely independent dimensions (Figure 1b): (1) historical to novel habitat conditions (abiotic and biotic), (2) wild to designed nature, and (3) biodiversity areas to production land. A framework that distinguishes these dimensions contrasts with traditional conservation thinking, which assumes that they are congruent: historical nature is to be found in wildlands that should be protected for the sole purpose of biodiversity conservation (Figure 1c). This changing perspective leads to at least four scenarios that are often considered conflicting (Figure 1d):

- Ways must be found to actively *conserve* remnants and values of historical nature that would cease to exist without direct human assistance. Depending on the intensity of interventions, the resulting state can be considered wild or designed.
- In a human-dominated world, biodiversity will depend on humans' ability to *create* habitats through ex situ, inter situ, or in situ conservation that can withstand anthropogenic impacts and better ensure its persistence.
- Novel ecosystems are emerging that represent the wildlands of the future (ie the self-organized response of nature to anthropogenic impacts). Such ecosystems should be *co-opted* as part of biodiversity conservation.
- Cultural landscapes provide the opportunity to *coproduce* biodiversity through biodiversity-friendly and sustainable land-use schemes. This action falls within the remit of "reconciliation ecology" (Rosenzweig 2003) and "countryside biogeography" (Daily *et al.* 2001).

Conserving relicts of historical biodiversity requires rapid up-scaling of conservation efforts

A large proportion of island species persist today as isolated individuals or small populations in small habitat fragments (WebTable 1). Although these remnants may still harbor high levels of biodiversity (WebTable 1), much of it is likely to represent an extinction debt (Triantis *et al.* 2010). On many islands, major habitat damage has occurred only during the past 50 to 200 years, and the consequences of recent sharp declines in recruitment, especially for long-lived species, have not yet been fully realized. For example, regeneration of the palm *Lodoicea maldivica* has declined markedly in recent years but will be reflected in a declining adult population only after 200 to 300 years (Rist *et al.* 2010). Species that are restricted to one or a few small areas are also susceptible to stochastic events (Caujapé-Castells *et al.* 2010). Thus, outbreaks of pests and diseases may decimate populations of (even common) native species within a few years (Caujapé-Castells *et al.* 2010).

In the past, to conserve biodiversity meant primarily to restrict human interference in natural areas (cf Rosenzweig 2003; Kareiva *et al.* 2011). Now, as multiple threats affect historical biodiversity even in protected areas (Figure 2), active interventions must be undertaken speedily, at an adequate scale, and must be maintained indefinitely. Such intervention requires: (1) removing existing threats; (2) preventing further impacts; (3) reinforcing remnant populations, which are often too small to be viable; and (4) restoring vital ecological interactions and processes.

Recent advances in invasive species control and eradication on islands demonstrate that such rigorous actions can be effective (Veitch *et al.* 2011; Database of Island Invasive Species Eradications [http://eradicationsdb.fos. auckland.ac.nz/]). Eradication of invasive species from small- to medium-sized and sparsely populated islands has become a key element for the survival of critically endangered endemics (WebTable 2; Anderson *et al.* 2011). On large islands, a combination of containment, local eradication, and exclusion can have a dramatic positive effect on native biodiversity. For example, only 10 years after measures were introduced to control *Psidium cattleianum* in Conservation Management Areas on Mauritius, populations of many native plants and animals (some previously considered extinct) had re-emerged or increased



Figure 2. In human-dominated landscapes, threat factors to biodiversity are strongly interconnected. Among the most severe threats to species, habitats, and ecosystem functions are climate change and pollution; habitat fragmentation and alterations (such as fires); natural and disturbance-caused rarity of biodiversity; alien animals, plants, and pathogens; and the loss of biotic interactions, such as pollination and seed dispersal. Photo credits: (a) J Olesen, (b) D Hansen, (c, d) PCA.

(Florens and Baider 2013). Up-scaling control to large areas has been increasingly successful, even on populated islands (Oppel et al. 2011; Burns et al. 2012). Prevention should address even minor disturbances, such as those due to ecotourism, and should include establishing buffer zones and developing contingency plans for threats like fire or biological invasions. Reinforcing small populations should build on a combination of in situ management, ex situ or inter situ propagation for restocking, and the creation of ecological corridors or the active translocation between isolated populations to maintain genetic diversity (Caujapé-Castells et al. 2010; Baret et al. 2012). Finally, because of past or current disturbances and edge effects, it may be necessary to restore some ecosystem functions and ecological interactions even in relatively undisturbed habitats. These measures need to be applied rapidly and at an appropriate scale, but few island-based human communities have the experience, financial resources, and personnel to undertake such work.

Creating resilient habitat for conservation-reliant biodiversity

Despite efforts to conserve the least-disturbed habitat fragments, biodiversity on many islands will continue to decrease. To mitigate biodiversity losses, we recommend that natural areas be transformed to improve resilience or that novel habitats be created. Biodiversity that cannot be conserved in situ should be managed through an inter situ approach that conserves biodiversity in locations outside their past distribution but with the aim of maintaining essential ecological interactions (eg pollination, seed dispersal, trophic interactions; WebTable 2). More imminently, however, many species can be conserved only through ex situ management in botanical gardens and zoos (WebTable 2).

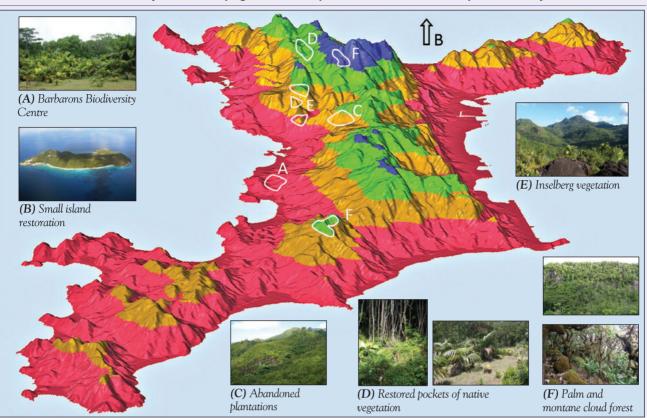
On most islands, biodiverse areas will be destroyed or degraded unless in situ management enhances the resilience of conservation-reliant biodiversity to anthropogenic change, which will require ecological design of biotic and abiotic conditions. Biological manipulation may involve the introduction and augmentation of "analog" species closely related to extinct native species to restore ecological interactions (Hansen et al. 2010; Kaiser-Bunbury et al. 2010). For instance, Aldabra giant tortoises (Aldabrachelys gigantea) act as seed dispersers of the endemic ebony (Diospyros tessellaria) on Ile aux Aigrettes in Mauritius (Kaiser-Bunbury et al. 2010). Establishing a new balance in disturbed food webs may require introduction of alien species (eg biological control), or control or removal of specific native species (Sahasrabudhe and Motter 2011). Many of these tasks will necessitate continuous management efforts.

Inter situ conservation creates new spaces for imperiled species and biotic interactions associated with these species outside their original habitat (Burney and Burney 2007). These habitats and communities differ in the degree

to which they resemble natural systems. The principal goal is to design ecosystems that are resilient to anthropogenic change and allow cost-effective conservation of multiple species. Examples include the Makauwahi Cave restoration project in the Hawaiian Archipelago, in which native species are reintroduced to their former range (Burney and Burney 2007), and offshore islets in the Seychelles Archipelago (Panel 1), where inter situ communities consist of designed assemblages of threatened species (Kueffer et al. 2013). Although many conservationists still aim to ensure that reconstructed and original species assemblies are taxonomically and functionally similar, inter situ conservation areas on islands may increasingly be considered as refugia where biodiversity is preserved irrespective of historical communities (eg Towns et al. 1990). One example is the conservation of rocky inselberg (steep-sided monolithic outcrops) habitat in the Seychelles. Many tree species formerly present in lowland forest still survive as dwarf individuals in this ecologically marginal habitat (Kueffer et al. 2013). Conserving or actively introducing such moist forest trees to dry inselbergs, where some survive only as "bonsai" ecotypes of rocky habitats, could be considered a combination of in situ and inter situ conservation (Panel 1). Similarly, in situ and ex situ strategies merge when rare native species are planted in a park setting close to natural areas, which ensures maintenance of ecological interactions; for instance, after placement within a botanical garden, the rare endemic tree Colea sechellarum is pollinated by the endemic Seychelles sunbird Cinnyris dussumieri visiting from nearby forests (Panel 1).

Novel ecosystems – a chance for wild nature and a need for containment

An increasing proportion of the world's natural areas contain wild but disturbed habitat, especially on islands (WebTable 3). Such ecosystems have been termed "novel ecosystems" (Hobbs et al. 2013) and contain many alien or native species that thrive on anthropogenic disturbances (ie opportunistic biodiversity). Novel ecosystems and their opportunistic biodiversity deliver important ecosystem services, entail qualities of wildness, and ensure unrestricted evolution (WebTable 3; Kueffer and Daehler 2009; Carroll 2011; Hobbs et al. 2013). For example, forests in the Seychelles dominated by alien cinnamon (Cinnamomum verum) effectively prevent more problematic alien plant species from spreading, while allowing endemic plants to reproduce (Kueffer et al. 2010). In Hawaii, novel lowland forest maintains or increases ecosystem services such as productivity, nutrient turnover, or belowground carbon storage as compared with native stands (Mascaro et al. 2012). Further, novel ecosystems provide suitable habitat and functionally analogous ecological interactions, which allow some native species to persist despite detrimental change (Kueffer and Daehler 2009; Carroll 2011; Lugo et al. 2012). The introduced honey bee Apis mellifera, although often considered a competitor of endemic pollinators, is one of



Panel 1. Toward biodiversity-rich anthropogenic landscapes on islands - the example of the Seychelles

Figure 3. Mahé Island (Republic of Seychelles) is an illustrative example of the importance of landscape-scale conservation approaches in the Anthropocene.

A major challenge of conservation in the Anthropocene is to integrate threatened biodiversity into a heterogeneous mosaic of habitats characterized by strongly contrasting anthropogenic, biotic, and environmental conditions (Koh and Gardner 2010). On islands, for instance, anthropogenic and environmental gradients are often steep, habitat fragments are small, and the distances between fragments are short. An illustrative example is Mahé, the 154-km² main inhabited island of the inner group of granitic islands of the Republic of Seychelles (western Indian Ocean; Kueffer et al. 2013). The island is divided into four broad habitat zones (Figure 3). Lowland regions from the coast to approximately 200 m above sea level (asl) are highly managed urban and agricultural areas characterized by tourism infrastructure along the coasts, urban development in the lowlands to approximately 100 m asl, and residential areas intermixed with abandoned secondary vegetation and private gardens to approximately 200 m asl (indicated in red in Figure 3). Biodiversity-poor, abandoned timber and cinnamon (Cinnamomum verum) plantations dominate an altitudinal belt between 200 m and 400 m asl (yellow in Figure 3). Between 400 m and 600 m asl, the island is covered almost entirely by abandoned cinnamon plantations (green in Figure 3). In contrast to lower elevations, these "novel" forests are still rich in native biodiversity, albeit scattered, and are mostly included within protected areas. Above approximately 600 m asl, 3 km² of montane cloud forest persists that is still composed of mostly native vegetation, although alien trees such as cinnamon are common (blue in Figure 3). Inselberg ("glacis") are steep-sided monolithic rock outcrops that occur throughout the elevation gradient but primarily from 250 m to 650 m. Inselberg vegetation harbors some of the last remaining endemic plant communities in the Seychelles and consists of shrubs, small trees, palms, and screw palms (Pandanus sp). Each of these habitat zones provides particular opportunities for biodiversity conservation. In the populated lowland zone, ex situ propagation, inter situ conservation, agroforestry, and ecotourism are important elements of conservation strategies. For instance, at the Barbarons Biodiversity Center, part of the Seychelles Botanical Gardens (Figure 3, polygon A), rare species are propagated and planted in a park-like setting bordering wildlands, which ensures that basic ecological interactions are maintained. North Island, a 210-ha island, is one example of the role of ecotourism in inter situ biodiversity conservation. The island is managed by a luxury hotel that is in the process of eradicating invasive species, restoring native vegetation, and (re-)introducing rare plant and animal species (Figure 3, arrow B). Abandoned plantation and cinnamon forest is currently underutilized and mostly unmanaged (Figure 3, polygon C). It holds promise for sustainable timber production and the harvesting of non-timber forest products, and as a managed forest it can serve as a buffer zone for high biodiversity areas. To manage the cinnamon-dominated novel forests at mid-elevations as a mixed native-alien forest, it has been proposed that small patches of native vegetation interspersed in the cinnamon forest should be restored (Figure 3, polygon D). Such patches would serve as native fruit sources for the surrounding forest while the alien matrix maintains important ecological functions for the forest (eg erosion control, food source for native fauna, barrier against other plant invasions; Kueffer et al. 2013). Inselberg vegetation is also a seed source of native species in the alien-dominated landscape. Managing and conserving rare plants on inselbergs, including some for which this habitat is only marginally suitable, may be considered a combination of in situ and inter situ conservation (Figure 3, polygon E). Only small pockets of montane cloud forest and mid-elevation native palm forest survive across the island (Figure 3, polygon F). These forests are imperiled by invasive plants and animals, climate change, and other human disturbances, and only continuous and intensive in situ management will be able to preserve these sensitive habitats.

the most abundant pollinators of many native island plants (Kaiser-Bunbury *et al.* 2010). Because some of these native plants have lost their endemic mutualisms, introduced honey bees now provide vital pollinator services. Similarly, alien birds and mammals often act as "substitute" seed dispersers for native plants (eg Riera *et al.* 2002).

Novel ecosystems and their opportunistic biodiversity are no panacea for biodiversity conservation, partly because many native species will not persist in novel habitats and opportunistic biodiversity may threaten to invade refugia of vulnerable native species. Despite its benefits to mid-elevation novel forests in the Seychelles, cinnamon threatens nearby montane cloud forests and must be prevented from spreading therein (Kueffer et al. 2013). Opportunistic biodiversity can also introduce problematic features to landscapes, such as increased fire risk. Because it is often unfeasible or undesirable to replace novel with native habitats (eg Kueffer *et al.* 2010; Carroll 2011; Hobbs et al. 2013), studying novel ecosystem functioning is essential to identify positive features that can be used in sustainable biodiversity management. Such management could, for instance, involve the largescale replacement of problematic alien species, which invade nearby natural areas or increase fire risk, with easy to propagate native or less problematic alien species. If well managed, novel ecosystems may harbor valuable opportunistic native and alien biodiversity, facilitate evolution of new biodiversity, increase resilience to climate change, establish ecological connectivity, or act as buffer zones for high biodiversity areas, all of which can aid conservation.

Promoting biodiversity in cultural landscapes toward long-term coexistence

Another promising avenue for conservation is the promotion of native biodiversity in a cultural landscape and on production land (Daily et al. 2001; Rosenzweig 2003; Koh and Gardner 2010). Some island animals are ecologically plastic and can adapt to, or benefit from, man-made environments and new food sources (Kaiser-Bunbury et al. 2010; Lugo et al. 2012). For example, endemic geckos use coconut trees and domestic houses for shelter, and frugivorous endemic birds and fruit bats have expanded their diets to include alien fruits grown in gardens and plantations (eg Luskin 2010). To coproduce biodiversity, human activities such as landscaping, sustainable forest production, agroforestry, low-intensity agriculture, and home gardening have to be tailored to the needs of native species (eg Thaman 2002; Atkinson et al. 2010). One advantage of coproduced biodiversity is the provision of additional land for biodiversity conservation and its economically sustainable management (Rosenzweig 2003). For instance, invasive species control (eg of rats and weeds) on production land may benefit some conservation-reliant biodiversity that cannot be conserved on wildlands.

On islands, coproducing biodiversity in cultural land-

scapes is important for several reasons. First, distances between urban areas, agricultural land, and (semi-)natural areas are often very short (Panel 1), allowing native fauna to move between anthropogenic and natural areas for different activities (eg foraging and roosting; Luskin 2010). Second, maintenance of agriculture and (agro)forestry is essential for economic and ecological sustainability, subsistence, and food security of island communities. Consequently, biodiversity-friendly land use such as indigenous land-use systems, agroforestry, or domestic gardens have a long tradition on islands (Esquivell and Hammer 1992; Clarke and Thaman 1993; Thaman 2002), and sustainable forestry with native tree species is increasingly being implemented (eg Baret et al. 2012). Third, ecotourism provides opportunities for landscaping with native biodiversity and cofinancing of conservation actions (Panel 1; eg Baret et al. 2012; Kueffer et al. 2013). In return, biodiversity-rich cultural landscapes can help to increase awareness of biodiversity among tourists and local citizens. Guiding and promoting the coexistence of production and biodiversity is thus integral to biodiversity conservation and sustainable development on islands.

Conclusions

More than 80% of conservation scientists agree that current conservation goals and standards of success should be reassessed (Rudd 2011). We have reviewed some of the new approaches that integrate traditional and novel perspectives. Most of these require a landscape-scale approach, with different types of management adapted to specific habitats (Panel 1), and a move beyond simplistic dichotomies such as wildlands versus man-made ecosystems. In essence, biodiversity conservation can be improved by embracing a multipronged approach, including: *conserving* relicts of historical biodiversity, *creating* artificial biodiversity conservation areas, *co-opting* novel ecosystems and their opportunistic biodiversity as a fundamental part of biodiversity conservation, and *coproducing* biodiversity in cultural landscapes.

The views proposed here should not distract attention from the immediate need to protect and restore remaining large tracts of relatively undisturbed wildlands on continents (Caro et al. 2012). Instead, lessons learned from island settings can equip managers with a broader set of skills and approaches to address emerging conservation challenges on continents. At a global scale, wildland extent is rapidly shrinking (Steffen et al. 2004; MA 2005; Koh and Gardner 2010; Hobbs et al. 2013) and vulnerable biodiversity is dependent on ever smaller fragments of natural areas (Gibson *et al.* 2011) while novel ecosystems are expanding (Hobbs et al. 2013); consequently, designing landscapescale mosaics of wild and anthropogenic nature is an emerging global conservation priority (Koh and Gardner 2010). In this sense, conservation on islands provides a preview of what conservation on continents may be like in the future.

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Location	Specifications	References
Hawaiian flora	512 taxa (44.2% of flora) are restricted to 20 or fewer populations in the wild. >100 species are known from 20 or fewer remaining individuals.	Sakai et <i>al.</i> (2002); Oldfield (2011)
Forest cover (Haiti)	In Haiti (27750 km ²), less than 4% of the land area is covered with forest and no primary forest remains. The flora of Haiti is composed of more than 5000 vascular plants with an endemism of about one-third, and more than 2000 animal species. Globally, many of the rarest forest ecoregions occur on islands, with often only a few square kilometers remaining and typically only few percentages of cover included in protected areas.	Sergile and Woods (2001); FAO (2010); Diamond and Robinson (2011); Gillespie <i>et al.</i> (2012)
High-altitude habitat (New Caledonia)	182 endemic vascular plants are found in 1 km ² of high-altitude maquis vegetation.	Jaffre et al. (1998)
Montane cloud forest (French Polynesia)	60–70% of the endemic flora of French Polynesia is found in montane cloud forest, and 25–50% is restricted to this habitat. Predicted climate change may reduce the area of this habitat to 1500 ha (90% reduction) by 2100. Already today, the extent of the habitat is only on three islands >200 ha.	Meyer (2010); Pouteau <i>et al.</i> (2010)
Wet forest (Mauritius)	56% of all woody native species of this habitat (108 species) were recorded in 0.75 ha of the best preserved habitat patches.	Florens et al. (2012)
Juniper woodlands (Tenerife, Canary Islands)	47% of all endemic perennial plants of Tenerife (189 species) were recorded in 34 ha of juniper woodlands.	Otto et al. (2012)
Lowland dry forest (New Caledonia, La Réunion, and Hawaii)	In New Caledonia, less than 2% of lowland dry vegetation remains intact, mostly as patches of less than 5 ha, the largest one being 200 ha. 223 endemic plant species are found in this habitat, 59 of which are restricted to it. I 18 native woody plant species were recorded in 7 sites of 0.1 ha. Virtually no intact lowland dry vegetation remains on many other islands, including La Réunion and Hawaii.	Bouchet <i>et al.</i> (1995); Juvik and Juvik (1998); Strasberg <i>et al.</i> (2005); Gillespie <i>et al.</i> (2011)
Small islands	There are >500 named islands of <100 km ² in the world; 24 islands of less than 100 km ² in the Atlantic and Pacific oceans (total area of 913 km ²) together host 585 endemic plant species. For example, in the Bonin Islands (Japan), 140 endemic species are found on 20 (highly disturbed) islands of a total area of 80 km ² (the largest being 24 km ²).	Ono (1998);Trusty et al (2011)
Rodrigues (western Indian Ocean)	Rodrigues (109 km ²) has approximately 130 native flowering plants (about 50% are island or archipelago endemics), all of which are threatened. Relict native-species-dominated vegetation consists of around 40 ha of restored habitat.	Kueffer and Mauremootoo (2004); Cheke and Hume (2008

WebTable 1. Examples of relict historical plant diversity on oceanic islands

Notes: The table lists typical examples of relict island plant diversity that illustrate the great importance of extinction debts for island biotas. Examples include small population sizes of species and small remnant areas of habitats that are the result of natural processes, past and current anthropogenic impacts, expected future impacts (eg climate change), or a combination of these factors. One highlighted feature is that, at present, very small patches of little-disturbed island vegetation still harbor high diversity.

Ex situ conservation	Botanical gardens on many oceanic islands have living ex situ collections in park-like settings and are close to natural areas. Species from the same habitat are planted in groups, or ex situ sites are placed within the respective habitat zone (eg El Portillo Visitor Center has a living collection of rare plants inside subalpine vegetation of Teide National Park on Tenerife, Canary Islands). Native animals use these areas as habitat. Close proximity between ex situ collections and adjacent natural areas facilitates ecological interactions within and between ex situ areas and surrounding habitat.
Restoration and inter situ conservation on small islands	It has been recognized for at least 30 years that small islands can act as refuges for highly threatened island plants and animals due to effective invasive species control and habitat restoration, for example, in New Zealand, Australia, Mascarenes, Seychelles, Hawaii, and the Californian Channel Islands (Towns et al. 1990; Safford and Jones 1998; Roemer et al. 2002; Komdeur and Pels 2005; Hutton et al. 2007; Samways et al. 2010; Anderson et al. 2011; Towns et al. 2012; Kueffer et al. 2013). Island conservationists increasingly consider these islands as inter situ conservation areas for biota that was historically absent on the island.
Restoration and inter situ conservation on large islands	Restoration or complete re-creation of native-species-dominated habitat is also possible on large and highly populated islands, but this often requires initial major investments for removal of invasive plants, replanting of native vegetation, and fencing to exclude invasive animals. Continuous management includes fence maintenance and regular weeding due to high propagule pressure from the surrounding alien vegetation. These restored habitats of 10–100 ha are vital to the persistance of rare plants and animals and can be used for the reintroduction of rare species to the wild. Examples include Hakalau Forest National Wildlife Refuge on the Big Island (www.fws.gov/hakalauforest/) and Makauwahi Cave on Kauai (both in the Hawaiian Archipelago, Pacific Ocean; Burney and Burney 2007, 2009), Conservation Management Areas (CMA) in Mauritius and Rodrigues (Mascarenes, Indian Ocean; Impey <i>et al.</i> 2002; Mauremootoo and Payendee 2002; Kueffer and Mauremootoo 2004; Cheke and Hume 2008; Kaiser <i>et al.</i> 2008; Kaiser-Bunbury <i>et al.</i> 2009; Florens <i>et al.</i> 2010; Baider and Florens 2011; Hugel 2012), or a pilot project in the Azores (Heleno <i>et al.</i> 2010).
Rewilding on islands	Hansen (2010) recently reviewed planned and implemented introductions of alien "analog" plant and animal species of extinct native species to island ecosystems ("rewilding"). Many of these approaches are first tested on small islands, where it is possible to monitor and if necessary revert experiments.

Biodiversity in novel ecosystems	Novel ecosystems on islands provide important habitat for common and rare native species (eg Safford and Jones 1998; Kueffer and Daehler 2009; Pawson et al. 2009; Kueffer et al. 2010; Lugo et al. 2012; Meyer 2012; Ewel et al. 2013), and it can be more cost-effective to conserve certain species in novel ecosystems than restoring natural areas (Safford and Jones 1998). Some native species benefit from novel conditions: for example, open canopy (Lugo et al. 2012) or novel trophic interactions such as alien top predators (eg cats) that support native animals by controlling alien mesopredators (eg rats; Kueffer 2012; Lugo et al. 2012). Maintaining common native species in high abundance in novel ecosystems allows conservation efforts to be focused on rare species in relicts of historical biodiversity or inter situ habitat. Biodiversity in novel habitat can have cultural value; for example, traditional gathering of native wild plants (Ticktin et al. 2006), and alien species threatened in their native range are worth conserving in novel ecosystems within the alien range (Lugo et al. 2012).
Ecosystem services in novel ecosystems	Novel ecosystems produce important ecosystem services (Daily <i>et al.</i> 2009; Kueffer and Daehler 2009; Mascaro <i>et al.</i> 2012; Ewel <i>et al.</i> 2013). Maintaining and enhancing ecosystem services cost-effectively in such areas while minimizing impact on nearby biodiversity-rich habitat is an important management challenge.
Ecotourism	On many islands, ecotourism has become a major economic component, which can help cofinancing landscaping programs with native species or biodiversity management on privately owned land (eg Baret <i>et al.</i> 2012; Kueffer <i>et al.</i> 2013).
Forestry	Forestry contributes substantially to the national economy of many island states (Wilkie <i>et al.</i> 2002). Forestry with native species has been trialed on different islands (eg Baret <i>et al.</i> 2012), and such native tree plantations can be relatively rich in native biodiversity (Goldman <i>et al.</i> 2008).
Agroforestry	Agroforestry can support endangered island biodiversity (eg Clarke and Thaman 1993, 1997; Thaman 2002). On islands, agroforestry plantations may have been important refuge areas for native fauna during periods of deforestation (eg in Puerto Rico; Lugo <i>et al.</i> 2012).
Home gardens	Home gardens, which have a long tradition in island societies (Esquivell and Hammer 1992; Ceccolini 2002), can be used to propagate rare plants (Atkinson <i>et al.</i> 2010; Baret <i>et al.</i> 2012) or to substitute wild collection of valuable species (eg roof thatching, medicinal plants; eg Beaver and Kueffer 2005).
Ecological interactions between novel habitat/production land and conservation areas	Novel ecosystems and production land can serve functional roles for native island species that complement those of conservation areas. For instance, in Mauritius some endangered forest birds breed in alien <i>Cryptomeria</i> forest where they are less prone to rat predation, but forage in nearby natural areas (Safford and Jones 1998). Some frugivores have been documented to forage in gardens or plantations and roost in natural areas (Luskin 2010). More generally, native frugivores on islands have been reported to forage on alien fruits (eg Nelson <i>et al.</i> 2000; Kueffer <i>et al.</i> 2009), and native plants are dispersed or pollinated by alien animals (eg Cox and Elmqvist 2000; Riera <i>et al.</i> 2002; Kelly <i>et al.</i> 2006; Foster and Robinson 2007). Understanding such interactions is critical for landscape-scale management of biodiversity that depends on novel ecosystems/production land and protected areas.

Notes: The list of examples is not exhaustive but is representative of the diversity of conservation actions on islands.

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