Islands and Evolution (2010). Pérez-Mellado, V. and Ramon, C. (eds.) Institut Menorquí d'Estudis. Recerca, 19: 111-146

ON THE USE OF TAXON SUBSTITUTES IN REWILDING PROJECTS ON ISLANDS

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Abstract. Recent proposals to rewild continental ecosystems with taxon substitutes –replacing extinct species with extant analogues– have met with controversy, chiefly because the involved species are extinct Pleistocene megafauna and their still-extant counterparts, and because of the massive areas required. In contrast, I argue that island rewilding offers ideal and much less controversial scenarios to rapidly advance our empirical understanding of taxon substitutions. The main reasons are twofold: firstly, anthropogenic extinctions happened very recently on islands, often within the last few centuries; secondly, island species are much smaller and require less space to implement rewilding projects. Island rewilding offers hope for restoring even highly degraded island ecosystems where many species have been lost, and allows radically different restoration trajectories to be pursued than those available with the surviving native species pools. I here present an overview of currently ongoing, planned, and proposed taxon substitution projects on islands, discuss several salient points, and highlight promising avenues for future research and restoration management.

Key words: naturalness, extinction, restoration, ecological analogues, plant-animal interactions, ecosystem functioning, assisted migration.

Resumen. Las recientes propuestas para repoblar ecosistemas continentales con taxones sustitutivos (reemplazando las especies extinguidas con otras vivientes análogas) han sido objeto de controversia, especialmente porque las especies involucradas formaban parte de la megafauna extinguida del Pleistoceno, al igual que sus todavía vivientes contrapartes y también porque se precisan áreas de una gran extensión. Por el contrario, propongo que la repoblación de las islas ofrece escenarios ideales y mucho menos controvertidos, para avanzar rápidamente en nuestra comprensión empírica de la sustitución de taxones. Las razones principales son dobles: en primer lugar, las extinciones antropogénicas han sucedido en las islas muy recientemente, frecuentemente en los últimos siglos; en segundo lugar,

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las especies insulares son mucho más pequeñas y requieren menos espacio para implementar los proyectos de repoblación. La repoblación insular ofrece una esperanza para restaurar incluso ecosistemas insulares intensamente degradados, donde muchas especies se han perdido y permite seguir trayectorias de restauración radicalmente diferentes de aquéllas disponibles con el conjunto de especies nativas supervivientes. Presento aquí el panorama de los proyectos de sustitución en islas que se hallan en curso de realización, en planificación o propuestos, discuto numerosos puntos a resaltar y señalo las prometedoras líneas de futura investigación y de manejo de la restauración.

Palabras clave. Naturalidad, extinción, restauración, análogos ecológicos, interacciones planta-animal, funcionamiento de los ecosistemas, migración asistida.

Resum. Les recents propostes per repoblar ecosistemes continentals amb taxons substitutius (reemplaçant les espècies extingides amb altres vivents anàlogues) han estat objecte de controvèrsia, especialment perquè les espècies involucrades formaven part de la megafauna extingida del Plistocè, igual que els seus encara vivents contrapartes i també perquè es precisen àrees d'una gran extensió. Per contra, proposo que la repoblació de les illes ofereix escenaris ideals i molt menys controvertits, per avançar ràpidament en la nostra comprensió empírica de la substitució de taxons. Les raons principals són dobles: en primer lloc, les extincions antropogèniques han succeït a les illes molt recentment, freqüentment als últims segles; en segon lloc, les espècies insulars són molt més petites i requereixen menys espai per implementar els projectes de repoblació. La repoblació insular ofereix una esperança per restaurar fins i tot ecosistemes insulars intensament degradats, on moltes espècies s'han perdut i permet seguir trajectòries de restauració radicalment diferents d'aquelles disponibles amb el conjunt d'espècies natives supervivents. Presento aquí el panorama dels projectes de substitució en illes que es troben en curs de realització, en planificació o proposats, discuteixo nombrosos punts a ressaltar i assenyalo les prometedores línies de futura investigació i de maneig de la restauració.

Paraules clau. Naturalitat, extinció, restauració, anàlegs ecològics, interaccions planta-animal, funcionament dels ecosistemes, migració assistida.

INTRODUCTION

> *"...stars, comets and extinct species share another convenient property that appeals to people. Not only are they very interesting, but there is nothing we can actually do about them either. By this I mean that we are powerless to intervene to change what happens to them or what they do (or did). So discovering more about them carries no responsibility; they are the ultimate, free, intellectual curiosity trip, devoid of any need to 'do' anything when we discover more about them"*
>
> *Lawton, 1995*

> *"The ecology of the afterlife is alive and well"*
>
> *Lawton, 1995*

Many studies have documented how the majority of island ecosystems are badly damaged after catastrophic anthropogenic impacts that mainly occurred within the last two millennia, depending on the date of human colonisation. However, adding to the already overwhelming litany of ecosystem destruction on islands is not the topic of the present contribution. As Donlan et al. (2005) succinctly put it, more than enough has sadly been written about the "doom and gloom" facing Earth's biodiversity.

Between the two opening quotes by John Lawton, one could say, lies the emerging field of rewilding with taxon substitutes, resurrecting the lost ecosystem functions of recently extinct species by substituting them with extant species (unless stated otherwise, 'rewilding' hereafter refers to restoration practices involving taxon substitutes). Even though extinctions on islands happened so recently, and are being increasingly well documented through the discovery of subfossil material, there is still a widespread disregard of the ecological and evolutionary roles played by many of these 'ghost species'–yet there is no doubt that on many islands they fulfilled important functional roles until very recently, for example as herbivores, frugivores and pollinators (e.g. Cox and Elmqvist, 2000; McConkey and Drake, 2002; Godfrey et al., 2008; Hansen and Galetti, 2009). As essential as modern-day conservation of endangered species and habitats is in halting the sixth mass extinction, some ecologists and practitioners have come to realise that we ignore the ecological and evolutionary consequences of these functional gaps at our own peril.

For continental ecosystems, these views have resulted in several recent suggestions to rewild large tracts of continental ecosystems, in North America, South America and Eurasia (Galetti, 2004; Donlan et al., 2005; Zimov, 2005; Donlan et al., 2006), all of which aim to replace extinct Pleistocene megafauna and restore lost ecosystem dynamics. The notion that it may be possible to get one up on that most ultimate of anthropogenic disturbance regimes, extinction, may seem heretic to some, and certainly has sparked controversy (Rubenstein et al., 2006; Caro, 2007; Caro and Sherman, 2009; Donlan and Greene, 2010).

In contrast to this, I believe islands offer some of the best suited scenarios to rapidly advance our empirical understanding of rewilding and exploring the use of taxon substitutions in conservation and restoration (see also Griffiths and Harris, 2010; Griffiths et al., 2010; Hansen et al., 2010; Kaiser-Bunbury et al., 2010). This is chiefly because the relevant temporal and spatial scales are much smaller on islands. Temporally, the majority of island species went extinct very recently, often within the last five centuries. This contrasts greatly with the peak of continental megafauna extinctions thousands of years ago, in the Pleistocene, and puts most island ghosts squarely in the youngest category of Lawton's (1995) poetically termed 'noveau-dead'. Spatially, the involved species are physically smaller than continental megafauna, making it more feasible to manage them in restoration projects. As a consequence, the size of the areas required to establish ecologically meaningful rewilding projects is also much smaller on islands, compared to the grand vistas required for continental rewilding.

My point of view is rooted in the long-standing tradition of evolutionary biologists and ecologists to regard islands as natural laboratories: due to their relative simple ecosystems, islands offer ideal setups to answer complex questions that are difficult to address in more complex mainland settings. However, taking this metaphor at face value, Holocene extinction events on islands worldwide have left the laboratories more than half empty and sorely in need of equipment—from a plethora of pipet-tips and test tubes to lumbering gas-chromatographs. Properly applied, rewilding is an explicit, hypothesis-driven and adaptive management option that adds a promising tool to the growing arsenal available to island restoration projects—re-stocking the laboratories, so to speak.

Island rewilding is inherently part of a whole-ecosystem view of restoration (Steadman and Martin, 2003; Lazell, 2005; Hutton et al., 2007; Jones, 2008), and is closely allied to the concept of 'inter-situ' conservation championed by Burney and Burney (2007), which they define as: "The establishment of species by reintroduction to locations outside the current range but within the recent past range of the species. In some cases, closest living relatives or ecological surrogates may be substituted for globally extinct species that are regarded as essential to maintain a process believed critical to the function of the target ecosystem. Inter-situ conservation, in effect, bridges the gaps between in-situ and ex-situ conservation.". In both rewilding and inter-situ conservation, the emphasis is on maintaining or restoring ecosystem functioning rather than on species conservation, even though the two are often intimately linked. In essence, for highly degraded island ecosystems where many species have been lost, rewilding allows radically different restoration trajectories to be pursued than those available with the surviving native species pools. Depending on how degraded the targeted ecosystem is, island rewilding spans the scale between 'ecological restoration' and 'ecological engineering' on the management continuum visualised by Atkinson (2001), and should be considered as conservation translocations (*sensu* Seddon et al., 2007; Seddon et al., in press) within an expanded definition of the IUCN reintroduction guidelines (Hansen et al., 2010).

In this contribution, I aim to firstly present an overview of selected ongoing, planned and suggested rewilding projects on islands around the world; secondly, to discuss how we can derive the information needed to assess the appropriateness of a taxon substitute candidate for a rewilding project; and thirdly to argue some salient points that arise about how island rewilding can offer fruitful research and management avenues.

Island rewilding: current state and future options

> *"Reintroduction of the 'missing' forest fauna [of Hong Kong] would bring ecological, conservation and educational benefits, but depending, as at present, on accidental escapes and kind-hearted Buddhists to do this is a recipe for disaster"*
>
> *Corlett, 2002*

Opponents of rewilding with taxon substitutions claim that these schemes are doomed to create more problems than they can solve. It is true that islands have suffered more havoc at the hands of introduced species than most ecosystems, and the utmost caution should be taken in any rewilding project. Examples of necessary cautionary measures are covered elsewhere (Donlan et al., 2006; Caro, 2007; Griffiths et al., 2010; Hansen et al., in 2010), and I will not be elaborating on this point in great detail here. Instead, I hope the examples below, as well as the case studies covered in greater detail in Boxes 1–3, will illustrate the potential for taxon substitution to rapidly move beyond the status of gimmick and become an integral part of restoration schemes for some of the most degraded habitats on our planet. Encouragingly, a vital first step in island rewilding—to address and manage or remove the known or suspected causal agents that led to extinctions in the first place—is increasingly being achieved on islands around the world, e.g. eradications of invasive mammals (Veitch and Clout, 2002; Nogales et al., 2004), setting the stage for the potential use of taxon substitutions in many dysfunctional island ecosystems around the world.

Animal rewilding

Probably reflecting the traditional high visibility of research on island avifauna, birds have until now been the focus of the majority of island rewilding projects (see also Box 1). Lately, tortoises have joined the fray (Griffiths et al., 2010; Hansen, et al., 2010), and other 'typical' island taxa like fruitbats and lizards offer similarly well-suited scenarios. Conservation and restoration of invertebrates on islands is sadly lagging far behind that of vertebrates (New, 2008) and the following overview is restricted to examples of vertebrate rewilding.

Box 1: New Zealand—taking the lead in avian rewilding?

In New Zealand, island restoration plans are strongly influenced by progress in the scientific understanding of pre-anthropogenic ecosystems. Most recently, a special issue of the New Zealand Journal of Ecology, "Feathers to Fur" (Sullivan et al., 2010), has brilliantly highlighted how the dramatic shift from avian- to mammal-dominated ecological guilds has had large impacts on ecosystem dynamics, often to the detriment of native species (e.g. Forsyth et al., 2010; Lee et al., 2010; see also Greenwood and Atkinson, 1977; Caughley, 1989; Atkinson and Cameron, 1993; Cooper et al., 1993; Bond et al., 2004; Wood et al., 2008).

In response, following the inspiring address by Atkinson (1988), a flurry of New Zealand island restoration plans have advocated translocations of extant species within the New Zealand archipelago to replace extinct species or subspecies, focusing on birds. In relation to taxon substitutions New Zealand is therefore—as is the case with many aspects of island conservation and restoration—ahead of much of the rest of the world. Most of these restoration plans stress the ecosystem approach behind the proposed taxon substitutions, aiming to restore lost trophic interactions as well as mutualistic interactions like pollination and seed dispersal.

An early example, perhaps far-flung to some, Meurk (1990, cited in Norton et al., 2005) suggested using extant ratites from outside New Zealand to replace extinct moas on Quail Island. More realistically, Miskelly (1999) proposed to use the extant Chatham Island snipe *Coenocorypha pusilla* as a substitute for the extinct North Island snipe *C. barrierensis*. However, this could be complicated by politics if the Chatham Island community is resistant to endemic taxa being moved elsewhere. In this case, their approval could perhaps be secured after 'preciprocal' translocations from elsewhere in New Zealand to replace extinct Chatham Island taxa (C. Miskelly, pers. comm.). For example, the Snares Island fernbird *Bowdleria punctata caudata*, could be introduced to replace the extinct Chatham Island fernbird *B. rufescens* (Miskelly, 1999). A few years later, in 2001, the management plan for threatened birds on Chatham Islands included a list with nine extinct birds that could be replaced by extant species and subspecies (Table 3 in Aikman et al., 2001), which was expanded to 11 species by Atkinson (Table 3 in Atkinson, 2001). Roberts and Miskelly (2003) developed further restoration and rewilding plans for snipe. Together with recent advances in New Zealand snipe taxonomy (Miskelly and Baker, 2009; Baker et al.,(2010), all these restoration plans provide an ideal template for scientifically rigorous implementation of snipe rewilding projects in New Zealand.

In 2005, the first thoroughly planned taxon substitution in New Zealand took place when 30 Snares Island snipe *C. huegeli* were translocated to Putauhinu Island to replace the extinct Stewart Island snipe *C. iredalei* (Charteris and Miskelly, 2005). The second New Zealand taxon substitution project, translocating North Island kokako *Callaeas wilsoni* to Secretary Island as a substitute for the extinct South Island kokako *C. cinerea*, took place in 2008 and 2009, where a total of 17 birds were translocated. This substitution is part of a well-laid restoration plan for Secretary Island, aiming to restore lost herbivory, pollination and seed dispersal interactions (Seddon et al., in press). Lastly, earlier translocations of South island takahe *Porphyrio mantelli* to sites on North Island and some of its islets, which used to be home to the extinct takahe *P. hochstetteri* (Lee and Jamieson, 2001), were in fact taxon substitutions even though they weren't embedded in a rewilding framework but rather part of the species' recovery programme.

A fitting first stop on our round the (rewilded) world tour is the tiny island of Guana in the British Virgin Islands. In the eminent edited volume on the natural history of Guana, Lazell (2005) highlights how conservation translocations are a powerful tool in the restoration of islands. The island has been the focus of several reintroductions of locally extinct species, and Lazell (2005) argues that the logical next step is to use analogous species from elsewhere to replace globally extinct taxa. The list includes Hawaiian monk seal *Monachus schauinslandi*, Guam rail *Rallus owstoni*, and Puerto Rican iguaca *Amazonia vittata vittata* as stand-ins for the extinct Caribbean monk seal *M. tropicalis*, DeBooy's rail *Nesotrochis debooyi*, and Virgin Islands parrot *Amazonia vittata* ssp. indet., respectively. Another groundbreaking example comes from Nonsuch Island near Bermuda, where rewilding spans from the introduction of a scale-insect resistant genotype of the endemic Bermuda cedar *Juniperus bermudiana* to the replacement of the extinct night heron *Nyctanassa carcinocatactes* with the widespread *N. violacea* (Wingate, 2001; Olson and Wingate, 2006).

On to the often heavily populated archipelagos of the Indomalayan region, where, even on urban metropole islands like Hong Kong, rewilding offers a way to drive restoration forward. As succinctly summarised in the opening quote of this section, Corlett (2002) highlights how a scientifically rigorous rewilding approach, rather than relying on present-day haphazard non-conservation introductions, is likely to result in significant conservation benefits.

The islands in the Indian Ocean offer yet another eminently suited laboratory for rewilding experiments. Recently, Cheke (2008) gave an inspiring overview of the vast potential for avifaunal reintroductions and taxon substitutions on the oceanic islands of the Western Indian Ocean (see also Box 2). On the largest island in the Western Indian Ocean, Madagascar, rewilding may be the only way to resurrect some of the lost interactions of the extinct elephant birds, giant lemurs, and giant tortoises (Burney, 2003; Hansen et al., 2010).

Box 2: The Mascarene Islands: a taxon substitution laboratory in the making

> *"Indeed the Mascarene Islands, in a nutshell, encapsulate both the fascination and frustration of working on the ecology of the afterlife; ghosts are not easy to pin down."*
>
> *Lawton, 1995*

The Mascarene Islands—Mauritius, Rodrigues and Réunion, located between 600–1100 km east of Madagascar—perfectly illustrate how, from an ecosystem function point-of-view, taxon substitutions can bring about a more holistic ecosystem restoration practice than conservation of extant native species and control of alien invasive species on their own. There have been several proposals for the use of carefully selected taxon substitutes in the Mascarene Islands (Jones, 1993; Jones, 1996; Jones, 2002; Cheke and Hume, 2008; Hansen et al., 2008; Jones, 2008 and refs therein). Potential rewilding options have recently been discussed in greater detail for two taxon groups: tortoises (Griffiths et al., 2010; Hansen et al., 2010) and birds (Cheke, 2008). Instead of repeating all of the proposed taxa, I here want to give a sense of the kind of Mascarene restoration schemes, where taxon substitutes would likely be most useful.

Mauritius

On Mauritius, walking through the last remnants of native forests, one is surrounded by ghosts. Since human colonisation in the 17th century, Mauritius has suffered the extinction of most large-bodied native vertebrates. The litany includes the famous flightless Dodo, but also giant tortoises, parrots, pigeons, fruitbats and giant lizards (Cheke and Hume, 2008). Many of the extinct vertebrates were generalist herbivores and frugivores. The loss has consequently led native Mauritian habitats and species to suffer from disrupted herbivory and seed dispersal interactions that once were pivotal for creating and maintaining ecosystem heterogeneity and dynamics on the island (Baider and Florens, 2006; Hansen et al., 2008; Virah-Sawmy et al., 2009; Griffiths et al., 2010). The real ghosts in the Mauritian forests are therefore not as much the extinct animals themselves, but more importantly the more or less extinct networks of interactions.

What about the few remaining extant endemic vertebrate species? Intense conservation efforts since the early 1980s have pulled back several endemic species from the literal brink of extinction. The 'Big Three' in this regard are the Mauritius kestrel, *Falco punctatus*, the pink pigeon, *Nesoenas mayeri*, and the echo parakeet, *Psittacula echo*; all three were down to or rapidly approaching single-digit numbers of surviving individuals. The rescue projects of these three species are-rightly so!-widely hailed as success stories that should inspire us to realise that until the last breeding pair dies, there is hope to save a species from extinction.

However, a key question in the restoration of Mauritian habitats is whether the regeneration dynamics of native plant species in Mauritian forests —themselves struggling under massive incursions by invasive alien plants and animals— are being restored as well? An example of a controversial but relevant question could be whether the Mauritian forests are 'better or worse off' with the successful species conservation projects bringing, for example, the pigeons and parakeets back up in numbers? From the point of view of at least one critical functional component, seed dispersal, the answer may, perhaps surprisingly, be 'worse'. Both pink pigeons and echo parakeets feed on a variety of plant material, including substantial amounts of fruits and seeds. However, both birds are chiefly seed predators, rather than seed dispersers; the powerful gizzard of the pink pigeon crushes all but the hardest of seeds, while the echo parakeet mostly feeds destructively on fruits and seeds before they ripen. Another example is the need to reinstate a suitable Mauritian herbivory regime that can promote habitat heterogeneity and native biodiversity. Currently, the lack of appropriate large herbivores in areas under restoration necessitates continuous weeding of invasive plants by humans; this state of affairs is certainly not restoring for the future, but rather only gardening for the present.

Therefore, in parallel to the conservation projects focusing on endangered species, the use of suitable taxon substitutes to specifically resurrect efficient seed dispersal and herbivory interactions should be an equally important focus. This would likely not only directly benefit Mauritian plant species, but also indirectly benefit long-term conservation of e.g. pink pigeons and echo parakeets by ensuring the regeneration of biodiverse and productive native habitats.

Consequently, the situation in Mauritius is (over-)ripe for the use of taxon substitutes, but, as Lawton rightly pointed out, 'ghosts are not easy to pin down', much less to resurrect! With so many ghosts to choose between, where do you start? Substitution of which species and resurrection of which functions should be attempted first? (Figure 1). The iconic dodo *Raphus cucullatus* would of course be an eye-catching start, but the world's islands are sadly short on giant, flightless pigeons. Also, despite early claims that dodos might be essential for forest regeneration (Temple, 1977), their role was likely more that of a seed predator than a seed disperser (Witmer and Cheke, 1991; Hansen et al., 2008). Instead, the choice fell on the extinct *Cylindraspis* tortoises. Studies of extant species have painted an increasingly clear picture of tortoises as keystone ecosystem components, in particular with respect to herbivory and seed dispersal. Accordingly, Mauritius is emerging as a leader in rewilding of island megafauna, with successful tortoise taxon substitution projects already implemented on two offshore islands, Round Island and Ile aux Aigrettes (Jones, 2002; Jones, 2008; Griffiths et al., 2010), and more are likely to follow.

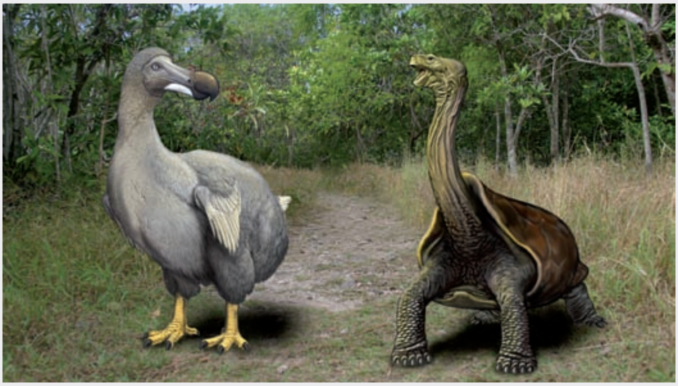

Figure 1. How to select which functional island ghosts to resurrect? On Mauritius the dodo *Raphus cucullatus* (left) may be the most famous ghost, but empirical evidence strongly suggests that substituting the extinct *Cylindraspis* tortoises (right) with extant counterparts will bring more benefits to habitat restoration (animal illustrations by Carl Buell; *Cylindraspis* drawing modified from Hansen and Galetti 2009)

Rodrigues

Rodrigues has been hit harder than most islands; the island today is largely covered with grassland and a few stands of exotic trees (Gade, 1985; Cheke and Hume, 2008). However, this also means that there is great scope for intelligently tinkering together novel ecosystems that can provide much-needed habitat for the remaining native Rodrigues biota. In fact, survival and recent population growth of all three surviving endemic vertebrates, a fruitbat and two passerines, has been largely attributed to the existence of (non-conservation) plantings of exotic trees in the 1970s (Impey et al., 2002; Showler et al., 2002; Fox, 2003). Restoration projects involving replanting forests with native species are on their way on Grande Montagne and in the Francois Leguat Giant Tortoise Reserve, as well as on some smaller islets (Jones, 2008; Weaver and Griffiths, 2008). These will soon provide further habitat for the remaining native species, as well as an ideal scenario for the introduction of taxon substitutes to re-start essential ecosystem functions like herbivory, pollination, and seed dispersal (Hansen et al., 2010; Kaiser-Bunbury et al., 2010).

Réunion

On Réunion, the largest and youngest of the three Mascarene Islands, there are still fairly large tracts of native forests left in the mountainous interior of the island (Strasberg et al., 2005). Much of this region was included in a national park created in 2007. However, like Mauritius and Rodrigues, Réunion has lost the majority of its vertebrates (Cheke and Hume, 2008). Also here there is evidence that plant species with fleshy fruits may be suffering from seed dispersal limitation (Strasberg, 1996), especially on newly formed lava flows from the still-active volcano, Piton de la Fournaise (Thebaud and Strasberg, 1997).

Temple (1981) suggested that the large native forests on Réunion may be good sites to introduce analogues from the neighbouring islands, particularly the Mauritian pink pigeon *Nesoenas mayeri* and the echo parakeet *P. echo* because of empty 'frugivorous pigeon' and 'frugivorous parrot' niches. There are ongoing discussions and nascent plans to replace the extinct Réunion parakeets, *Psittacula eques* and *P. bensoni*, with *P. echo* from Mauritius (A. Reuleaux, pers. comm). While these schemes make perfect sense from a species conservation point of view—literally putting valuable eggs in more than one basket—the case may not be as clear from the point of view of ecosystem function. The same argumentation as for Mauritius, above, applies to the situation in Réunion. To facilitate forest regeneration—and for this active, volcanic island in particular also to enable native plants to colonise recent lava flows—it would make more sense to introduce generalist, efficient seed dispersers. Among prime candidates could be blue pigeons (genus *Alectroenas*) from other islands in the Western Indian Ocean, where species of this genus are still extant (Comoros, Madagascar, or the Seychelles). Tortoises are another excellent candidate group for taxon substitutions in Réunion. Radiated tortoises *Astrochelys radiata* from Madagascar have been introduced to Réunion as pets many years ago and are widely bred in captivity; as many as 40,000 *A. radiata* are estimated to be kept on the island (Boullay, 1995). While the species isn't naturalised on the island, animals could easily be sourced from the captive population and used as substitutes for the extinct endemic species, *Cylindraspis indica*.

Another candidate taxon would be *Pteropus* fruitbats. Réunion once harboured two species, *P. niger* and *P. subniger*; while the former is still extant and common on Mauritius, the latter is extinct. Interestingly, Réunion is currently the scene of a natural re-colonisation event: a few individuals of *P. niger*, have recently found their way to Réunion from Mauritius (Mauritian Wildlife Foundation, 2009). Should they fail to establish here, conservationists have a very strong case to translocate *P. niger*, or potentially use *P. rodricensis* from Rodrigues as a taxon substitute for *P. subniger*. Inter-island movements of fruit bats have been observed in several archipelagos (Wiles and Glass, 1990; McConkey and Drake, 2007), and within-archipelago taxon substitution with fruitbats would thus closely mimic natural colonisation events.

The countless islands of the Pacific Ocean are also ideally suited candidate ecosystems for rewilding. For the Galapagos Islands, we have recently discussed options for tortoises elsewhere (Hansen et al., 2010). More outlandish Pacific rewilding proposals that involve tortoises include some of the recently extinct meiolaniid tortoises in the Austral-Pacific region and the giant flightless anatids of Hawaii (Box 3). For the Australian Lord Howe Island, Hutton et al. (2007) provide a candidate list with eight extinct animals and their potential substitutes in their Table 2. As a good example of socio-cultural barriers to rewilding, they caution that one driver of extinction of the parakeet *Cyanoramphus novaezelandiae subflavescens* was people killing the parakeet to protect their fruit crop—underscoring the need for acceptance by locals in cases where they may otherwise cause a newly rewilded species to go extinct.

In their evocatively titled paper about paleoecology and "the future resurrection of birds on Pacific islands", Steadman and Martin (2003) advocated the use of *Didunculus strigirostris* as replacement for an extinct *Didunculus* on the island of Tofua, Tonga, and the Guam rail *Gallirallus* owstoni as replacement for an extinct undescribed *Gallirallus* on Aguiguan. These two examples were not suggested with a specific emphasis on ecosystem dynamics, but rather on conservation of the extant species. However, in the third example, replacing the extinct *Ducula aurorae* of Mangaia, Cook Islands, they referred to the candidate D. pacifica as an "ecological analog" for the extinct species, hinting at the possible resurrection of lost interactions here, too–a point elaborated on later by Steadman (2006).

Hawaii is another potential Pacific rewilding laboratory. Being another of the world's island extinction hotspots, there are sadly also more than enough candidate ghosts that could be resurrected here. Progress is being made on the island of Kaua`i, which is home to one of the most promising habitat recreation projects anywhere (Burney and Burney, 2007) that could benefit greatly from using taxon substitutes (see Box 3). Some of the small, northwestern islands in the archipelago also represent good scenarios for rewilding projects that could be rapidly implemented. For example, on the once-barren but recuperating Laysan Island, Sincock and

Kridler (1977 cited in Morin and Conant, 1998) suggested introducing Nihoa Millerbirds *Acrocephalus familiaris kingi* to replace an extinct subspecies of *A. familiaris*. Indeed, the first translocation is scheduled to go ahead in 2011 (H. Freifeld and S. Plentovich, pers. comm.). Additionally, Morin and Conant (1998) proposed translocating the main island honeycreeper *Himatione sanguinea* as a substitute for the extinct subspecies *H. s. freethii*, and replacing the extinct flightless Laysan Island rail *Porzana palmeri* with the widely distributed, flighted and closely related rail *Porzana pusilla*. The difference in flight capabilities of the taxa in the final example hints at a promising avenue of research: can rewilding projects "re-start" evolutionary trajectories or states that were occupied by extinct species? (see below).

Box 3. Outlandish tortoise taxon substitutions?

In two recent papers, we have highlighted how replacing recently extinct large and giant tortoises with extant tortoises represent a low-risk, high-impact restoration scenario for many ecosystems where tortoises once occurred, especially on islands (Griffiths et al., 2010; Hansen et al., 2010). In the following two case studies, I illustrate how the use of extant tortoises as taxon substitutes could also be extended beyond the taxonomic realm of the true land tortoises, Testudinidae.

The strange case of the meiolaniids

Meiolaniid tortoises—an ancient reptilian lineage that went extinct within the last few thousand years—were bizarre–looking creatures with horned heads and spiked, club–like tails. Some species grew to gigantic proportions with likely total lengths of more than three meters. Their diet was probably that of a highly generalised herbivore. While not closely related to testudinid tortoises, meiolaniids were also Eucryptodires (Gaffney, 1996). They most recently inhabited continental and insular regions in the Australian-Pacific region (Gaffney, 1996; Worthy et al., 1999; White et al, 2010). In New Caledonia there is evidence that humans co-occurred with meiloaniids, and may have caused their demise (Gaffney, 1984). In Vanuatu, a recently discovered early Lapita settler site dating to between 3000–2800 BP (Bedford et al., 2006) includes extensive midden deposits containing many subfossil remains of a meiolaniid tortoise; remains that have not been found at any later sites throughout the archipelago to date, suggesting a rapid anthropogenic 'blitzkrieg' extinction of this species (White et al. 2010; S. Bedford, pers. comm.), as so often documented for birds on isolated islands (Steadman, 2006). However, in at least one case, Lord Howe Island, *M. platyceps* apparently went extinct before human arrival for unknown reasons (Gaffney, 1996).

Because virtually nothing is known about the biology of the meiolaniids, suggestions to replace them with extant taxa could be deemed highly speculative with no practical application. For islands where meiolaniids went extinct very recently, the case may be different. Here, giant extant testudinid tortoises may well be able to act as ecological replacements for extinct meiolaniids, restoring recently lost megafaunal plant-animal interactions. Intriguingly, in his description of the extinct giant flightless pigeon of Fiji, Worthy (2001) mentions that, “Fiji has an abundance of trees with large fruits, whose dropped fruit probably composed the bulk of the diet [of the giant pigeon]”. It is not inconceivable that the extinct Fijian meiolaniid tortoises once had a sizeable share of this bounty, too—and that extant testudinid tortoises therefore would be excellent substitute frugivores.

Taxon	Distribution	Last record
Meiolania platyceps	Lord Howe Island, Australia	Late Pleistocene
Meiolania mackayi	Walpole Island, New Caledonia	Late Pleistocene
Meiolania sp. "Wyandotte"	Queensland, Australia	Late Pleistocene
Ninjemys oweni	Queensland, Australia	Late Pleistocene
Meiolania? sp.	Viti Levu, Fiji	Late Pleistocene-Recent
Meiolania? *damelipi*	Efate, Vanuatu	Recent

Table 1. Recently extinct meioloaniid tortoises

Hawaii: from tortoise-beaked giant ducks to tortoises?

In Hawaii, restoration ecologists have suggested to examine the use of giant tortoises as restoration tools under controlled circumstances in enclosures (D.A. Burney, pers. comm.), even though tortoises never ocurred on Hawaiian islands. What may initially sound like an eccentric proposal has in fact got solid arguments behind it. Giant tortoises are likely to be closely aligned with the type of pre-human grazer/browser regime once present on Hawaii. This was dominated by now-extinct large flightless anatids, often referred to as moa-nalo, many of which had beaks with tortoise-like features–so much so that one of the moa-nalo genera was named *Chelychelynechen* or ‘tortoise-jawed goose’ (Olson and James, 1991). Furthermore, some endemic Hawaiian plant lineages have traits such as spines and heterophyllly, which have been suggested to have evolved as anti-browser adaptations against moa-nalos (Givnish et al., 1984); similar traits have been associated with anti-browsing adaptations against giant tortoises in the Mascarene Islands (Eskildsen et al., 2004). A study of coprolites from the moa-nalo *Thambetochen chauliodous* showed that it was a browser, feeding on coarse material (James and Burney, 1997). It is thus not inconceivable that large or giant tortoises could play key roles in Hawaiian restoration projects, e.g. the Makauwahi Cave project on Kaua`i, that aims to reconstruct a native ecosystem more or less from scratch in former agricultural lands (Burney and Burney, 2007). Moreover, using giant tortoises rather than large extant exotic geese in restoration projects in Hawaii has the important added advantage of completely removing any risk of avifaunal disease transfer to endangered endemic birds, such as the ne-ne goose (D.A. Burney, pers. comm).

In summary, because of their great versatility and ease of management, I envisage that large and giant tortoises could be used as substitutes for extinct non-chelonians. In fact, tortoises could be used as a generalised restoration tool in many island habitats, where other non-native browsers or grazers, such as cattle, sheep or goats, would be too disruptive or too difficult to manage. Rewilding with large and giant tortoises thus has the potential to be a multifunctional 'Swiss army knife' of ecosystem restoration in numerous degraded insular (and continental) ecosystems, where generalist herbivores and frugivores are deemed necessary to achieve specific, desired restoration trajectories.

Figure 2. Outlandish tortoise taxon substitutions. Even across high-order taxonomical borders, ecologically sound arguments can be made for the use of taxon substitutes. Two examples would be substituting the extinct Hawaiian flightless anatid moa-nalo *Chelychelynechen quassus* or meiloaniid tortoises *Meioloania spp*. from islands in the Austral-Pacific region (right) with extant giant tortoises, e.g. *Aldabrachelys gigantea* (left) (illustrations of extinct animals by Carl Buell)

Plant rewilding

Native island plants are beset by habitat loss, invasive plants, introduced seed- and seedling predators, and introduced herbivores (Strahm, 1994; Maunder et al., 1998; Sakai et al., 2002; Meyer and Butaud, 2009). Even though there have been comparatively few documented extinctions of plants on islands (Sax and Gaines, 2008), there is no doubt that many native island floras today are composed of the living dead (*sensu* Janzen, 1986)—species, which are reduced to such pitiful numbers that natural regeneration is impossible, and extinction without active intervention is extremely likely. While species conservation and habitat restoration clearly has the most important role to play in conserving island plants, the role of plant rewilding should not be underestimated, particularly when recreating native ecosystems more or less from scratch in severely degraded islands (Burney and Burney, 2007).

Like in animals, it is perhaps easier for large plants to get the attention of researchers and practitioners. A good example is the extinct giant palm

Paschalococos disperta (Arecaceae) from the now largely denuded Easter Island (Dransfield et al., 1984), where theories have abounded on its distribution, usage by humans, and why it went extinct (Hunt, 2007; Hunt and Lipo, 2009 and references therein). Even if recent studies have questioned to what extent Easter Island was forested before human arrival (Rull et al., 2010), there can be no doubt that this huge, endemic palm was a keystone component of the ecosystem, and thus a prime candidate for rewilding. A good substitute could be the equally giant and likely closely related Chilean palm *Jubaea chilensis*. Some people believe that the Easter Island palm is indeed identical with *J. chilensis* (even though no clear supporting evidence exists), and have planted several small populations of *J. chilensis* on Easter Island already (Moreno and Fernández, 2004). Such replanting could easily be expanded within a proper rewilding framework.

Another example comes from the northwesternmost Hawaiian Islands, where the restoration plan for Laysan Island (Morin and Conant, 1998) proposes that several extinct species or subspecies from this island could be replaced with extant taxa from nearby islands—in concert with the suggestions to rewild the Laysan avifauna (see above). The restoration plan stresses the need for careful studies to determine the suitability of the substitutions, and includes detailed information on steps that should be taken to assess if and how the extinct *Achyranthes atollensis* (Amaranthaceae) could be replaced by *A. splendens* var. *rotundata*, and *Cenchrus agrimonioides* var. *laysanensis* (Poaceae) by *C. agrimonioides* var. *agrimonioides*, respectively. It also mentions the possibility to replace an extinct *Pritchardia* palm, once an important component of the Laysan ecosystem (Athens et al., 2007), with an extant *Pritchardia* species, potentially *P. remota* from Nihoa (Rauzon, 2001). A final example comes from Lord Howe Island, where Hutton et al. (2007) speculated that the extinct *Solanum bauerianum* (Solanaceae) could be replaced with *S. viride*.

However, apart from obvious cases like the *Pritchardia* palm on Laysan, or the giant wine palm on Easter Island—i.e. large plants in an otherwise denuded landscape—it is very difficult to confirm when/if a plant has gone extinct (Maunder, 1992), and thus could become a 'candidate ghost' to be rewilded. Indeed, some island plants that were thought to be extinct have been rediscovered (Strahm, 1983; IUCN, 2001; Simbaña and Tye, 2009), underscoring the need for extreme caution when determining the appropriateness of plant rewilding projects. However, once a project is deemed to be desirable, its implementation can benefit a lot from the lessons learnt in plant reintroduction and translocation projects (Maunder, 1992; Allen, 1994). On the plus side of things, rewilded plant individuals or populations are obviously easier to monitor than rewilded animals (Maunder, 1992).

How to select taxon substitutes: help from beyond the grave

> *"Most of the research about species extinction has been conducted on islands because islands are controlled environments and scientists can get drinks with little umbrellas in them there"*
>
> *O'Rourke, 1994*

In general, for rewilding projects on islands it is possible to suggest at least two prioritised lists for selecting extant proxy taxa. First, in relation to source areas a reasonable initial list of options, in order of most preferred to least preferred, could be: 1) translocation within an island (including smaller surrounding islets), 2) translocation between islands within an archipelago, 3) translocations between archipelagos within a region, and 4) translocations from islands in other regions or from continental regions. Second, in relation to the relevance of genetic relatedness when selecting analogue species, Hutton et al. (2007) argue that a similar approach should be taken. That is, preferably 1) reintroducing the same species, before 2) substituting with a different subspecies, or 3) a congeneric. In their opinion, substitutions that involve taxa above subspecies level or that are based on ecological function should be avoided. However, both lists may be too restrictive and indeed fundamentally flawed when considering islands, which are home to many of the world's most spectacular examples of adaptive radiation—speciation events, where close relatives on neighbouring islands are often the ones most morphologically, and thus also potentially ecologically, dissimilar. Classical examples of this include Galapagos finches and Hawaiian honeycreepers. On the other hand, there are also several groups of closely related animals within and between archipelagos that seemingly fulfill the same function, for example congeneric species of frugivorous pigeons and fruitbats acting as seed dispersers. Moreover, it is conceivable that extinct taxa could be replaced with functionally similar extant taxa even across genera or higher-order taxonomical borders (see Box 3). What is clear is that the more we know about the extinct species, and the pre-anthropogenic islands they inhabited, the better we will be able to judge the relative merits of specific taxon substitute candidates.

Learning about the ghosts

Lawton (1995) said that endeavours to learn about ghosts were interesting, but ultimately of little practical use. However, both paleoecologists and conservation biologists now realise that conservation and restoration projects stand to gain tremendously from precise and detailed information about extinct species and their pre-anthropogenic ecosystems (e.g. Lyman, 2006; Froyd and Willis, 2008; Frazier, 2010; Hadley and Barnosky, 2009; Stewart, 2009)—and it is clear that rewilding projects would, too.

An obvious first step is to discover and identify as many of the recently extinct species on an island as possible. While there are historical records or even scientific studies available for some of the most recent island ghosts, most oftenly paleobiologists have to dig a bit deeper. Tremendous progress in this field has been made on many islands around the world in recent decades. The pioneering work of island paleoecologists working in Hawaii and other Pacific islands, the Mascarenes, New Zealand, Madagascar, and islands in the Caribbean, have unearthed invaluable subfossil material and increased the known tally of recently extinct species manifold (e.g. Olson and James, 1991; Burney, 1997; Worthy et al., 1999; Burney et al., 2001; Worthy and Holdaway, 2002; Burney et al., 2004; Stead-man, 2006; Steadman et al., 2007; Cheke and Hume, 2008).

After building a reasonably complete understanding of an island's pre-anthropogenic species communities comes the need to reconstruct the evolution and ecology of the species. In many cases, DNA can be extracted from museum specimens or subfossil remains, and used for molecular phylogenetic analyses to shed light on e.g. relationships, origins, and rates of speciation (e.g. Cooper et al., 1996; Sorenson et al., 1999; Austin and Arnold, 2001; Shapiro et al., 2002; James, 2004; Karanth et al., 2005; Austin and Arnold, 2006). Again, while such studies often provide important information for conservation of still-extant species (Leonard, 2008), it is clear that they offer similarly central insights for identifying suited taxon substitute candidates.

Subfossil remains can also yield treasure troves of data on a central question in re-assembling a partially lost island ecosystem: what was the diet of the extinct species? Such insights can be gained from studying dentition and patterns of dental wear (Godfrey et al., 2004), stable isotopes (Burleigh and Arnold, 1986; Koch et al., 2009; Crowley et al., 2010), and coprolite content (James and Burney, 1997; Wood et al., 2008). For community-level information, Burney et al. (2003) used an innovative approach to establish body mass indices of extinct herbivores in Madagascar by analysing abundances of fungal spores associated with dung from large herbivores. Pre-anthropogenic plant communities can also be studied via analyses of seeds and pollen in sediments from e.g. wetlands and lakes (Colinvaux and Schofield, 1976; Burney et al., 2004; Athens et al., 2007; Rijsdijk et al., 2009).

A final, more indirect line of inquiry is examining putative links between traits in extant island species and the causal evolutionary pressures once exerted by extinct island species; for example, how herbivores may have shaped the plant communities (Greenwood and Atkinson, 1977; Caughley, 1989; Givnish et al., 1994; Bond et al., 2004; Eskildsen et al., 2004; Hansen et al., 2004; Burns and Dawson, 2006; Bond and Silander, 2007; Godfrey et al., 2008; Fadzly et al., 2009; Griffiths et al., 2010), how frugivores may have interacted with fruit-bearing plants (Lord et al., 2002; McConkey and Drake, 2002; Godfrey et al., 2008), or assessing which flowers and pollinators may once have interacted (Lammers and Freeman, 1986; Cox and Elmqvist, 2000).

Equipped with all of these detailed tools, paleoecologists can envision entire prehistoric island ecosystems with a great deal of detail (Burney, 2003; Cheke and Hume, 2008; Godfrey et al., 2008), and rewilding practitioners are armed with a solid scientific basis on which to progress when selecting specific taxon substitute candidates.

Future research and management directions

> *"The pragmatic reality is probably that restoration is more about creating a new future than recreating the past"*
>
> *Macdonald, 2009*

> *"I have found a strong inverse correlation between peoples'ecological purity and the spatial extent of restoration they have personally achieved"*
>
> *Cabin, 2007*

In this section I will highlight some questions raised, and opportunities offered, by island rewilding. Some have direct bearing on larger-scale continental rewilding, while others are relevant only for islands.

Alien exotic or *de facto* substitute?

While negative impacts of introduced species are often readily apparent, it can be more complex to disentangle their overall function, including potential positive roles they may play in their new home. It is thus not always a clear-cut case that eradication or control is the cure-all for introduced species, and effects of removal may be difficult to predict (Zavaleta et al., 2001). This becomes especially important to understand in cases where native species may have come to rely on the introduced species for survival or reproduction (Westman, 1990; Ewel and Putz, 2004). Warren (2007) therefore suggests to rather focus on problematic versus non-problematic species. Such deliberations raise an important point in relation to rewilding: in ecosystems where introduced species have far more positive than negative effects and where they fulfill roles of extinct species, should they be tolerated and indeed be considered *de facto* taxon substitutes?

Continental restoration projects and nature reserve managers have long made use of livestock to provide controllable, desired levels of herbivory (Posada et al., 2000; Papanastasis, 2009). Even if not employed within an explicit rewilding framework, such large mammals are, in fact, often *de facto* taxon substitutes, replacing recently extinct, local mammalian herbivore megafauna. While it may be difficult to assess if, and to what extent, e.g. an introduced herbivore benefits the functioning of an island ecosystem (Lee et al., 2010), it is easier to understand the advantage of an introduced species resurrecting extinct mutualistic interactions, such as pollination and seed dispersal.

In relation to seed dispersal, some studies have illustrated how introduced birds can efficiently disperse native seeds on islands (Cole et al., 1995; Ferguson and Drake, 1999; Foster and Robinson, 2007; Kawakami et al., 2009), while other studies found the opposite pattern, with introduced birds largely dispersing seeds of introduced and invasive plants (Lewin and Lewin, 1984; Linnebjerg et al., 2010; Chimera and Drake, 2010; Staddon et al., 2010). In the Balearic Islands, Riera et al. (2002) highlighted how introduced mammals did consume native fruits, but that they were not providing as good a seed dispersal service to the endangered *Cneorum tricoccon* (Cneoraceae) as the endemic *Podarcis* lizards. In New Zealand, introduced rodents and possums may feed on fruits and seeds of some native plant species, but destroy the majority of seeds and should thus be considered inefficient substitutes (Williams et al., 2000; Kelly et al., 2006). Likewise for pollination interactions, where introduced species can be functional substitutes for extinct pollinators (Cox, 1983; Lord, 1991), but where they more oftenly disrupt native interactions, to the detriment of native plants and/or animal mutualists (Traveset and Richardson, 2006).

These examples stress how the roles of introduced species in native island ecosystems are idiosyncratic, and how detailed case-by-case studies are required to determine whether already-present exotic species should be regarded as unwanted pests, or, in specific cases, as welcome additions to degraded habitats (Rodriguez, 2006).

Conservation politics, human culture, and taxon substitutions on islands

Many islands form, or are part of, small independent states, especially in the Caribbean and in the Pacific Ocean. Tourism often forms a major part of the economy of these states, and pictures of the ‘unspoiled paradise island’ are among the most frequently used advertisement gimmicks. With an increasing emphasis on the environment, it is in the interest of such islands to maintain or enhance their ‘green’ eco-tourism image, and restoration of native habitats is a good way to achieve this. Therefore, parallel to the ecological and evolutionary arguments about islands being relatively simple ecosystems, stakeholders in such island states, including parliamentary politicians, may be more likely to support ecosystem rewilding with taxon substitutes than politicians from more economically complex continental countries. The republic of Mauritius in the Mascarene Islands offers a good example of this (Box 2). In general, conservation management on islands is often very hands-on, and adaptive management is frequently used. Both governmental and non-governmental conservation agencies are thus well-poised to capitalise on the development of rewilding with taxon substitutes, and indeed to contribute significantly to the maturation of rewilding as a management option and to its mainstream acceptance elsewhere.

Within a small island nation there is a great need to ensure local support for taxon substitution projects. This could be achieved via economical or cultural pathways. While economical benefits are easy to envision, cultural ones may be more difficult to imagine. A good example of the latter comes from Mangaia, Cook Islands, where people expressed their "desire to establish and protect populations of pigeons and doves, thereby restoring some of the auditory and visual enchantment that these forests once offered" (Steadman and Martin, 2003). An even more charismatic example is linked to a snipe taxon substitution project in New Zealand (see Box 1). After an investigation worthy of Agatha Christie, Miskelly (1987) identified the call of a legendary nocturnal bird, the hakawai, as the sounds created by the night-time aerial displays of endemic snipe (Miskelly, 1987). Two of the male Snares Island snipe *Coenocorypha huegeli* introduced to Putauhinu Island in 2005 as substitutes for the extinct *C. iredalei* had a pattern of tail feather wear suggestive of hakawai displays, causing elation among the people involved that they had resurrected not only a real but also a legendary bird! (Charteris and Miskelly, 2005). To hear the hakawai was earlier considered a bad omen (Miskelly, 1987), but in an interesting twist to the story, local muttonbirders enthusiastic about the snipe's return may now consider hearing the hakawai a boon—demonstrating another way in which rewilding can garner local support.

Of course, many island species went extinct very soon after human colonisation; these taxa do not often persist in the memory of local folklore. For such species, though, a creative use of nomenclature by the scientists that discover the remnants may have an important role to play in paving the way for cultural acceptance of taxon substitutes to replace them. A good example of this is could be the evocative name coined by Olson and James (1991) for the extinct giant, flightless anatids of Hawaii, the moa-nalo, "from Hawaiian moa, fowl, and nalo, meaning lost, vanished, forgotten"—after all, who wouldn't want to be the one to find long-lost fowls? (see Box 3).

Managing ecosystems for the future

Despite early calls for an integration of ecosystem dynamics in the then-emerging field of restoration ecology (Pickett and Parker, 1994), the goal of many restoration projects is still to achieve a 'natural' state where the restored ecosystem is as close as possible to the way it was before anthropogenic impacts (Hilderbrand et al., 2005). There has been a long discussion of what is natural, and several schemes and metrics have been proposed on how to classify and quantify ‘naturalness’ e.g. (Anderson, 1991; Machado, 2004). It should by now be clear, though, that there is not a single non-anthropogenic ecosystem left anywhere on this planet. Moreover, our knowledge of ecosystems have progressed to an understanding that ecosystems are not static, but rather are fluid and dynamic (Wu and Loucks, 1995; Bengtsson et al., 2003; Manning et al., 2009), an especially important point in relation to conservation and restoration (Gillson and Willis, 2004; Manning et al., 2009; Bellingham et al., 2010; Hall, 2010). In face of an uncertain future, a strong case can therefore be made for also restoring towards future resilience rather than only according to past history (Swetnam et al., 1999; Choi, 2007; Hayward, 2009; Jackson and Hobbs, 2009). Ideally, rewilding combines key aspects of both these approaches by aiming to restore lost ecosystem functions *and* dynamics, based on recent ecological history, rather than aiming to achieve or maintain a specific ecosystem state or species roster. Rewilders and restoration ecologists should work together as mediators and creators of desired ecosystem trajectories and optimal landscape fluidity (*sensu* Manning et al., 2009).

An interesting parallel has recently been drawn between how we view human health and ecosystem health, and specifically how approaches to ecosystem restoration ideally could mirror human medicine in how to diagnose ‘unhealthy’ ecosystems, and how to ‘heal’ them (Temperton, 2007; Keulartz, 2010; Lowenthal, 2010). Just like human health is easier to maintain via prevention than to restore via cure, rewilding with taxon substitutes therefore has potential as a ‘future’ management option in another sense. Cole et al. (2008) argued that, “Although controversial, [practitioners could] consider functional substitutes for species that cannot survive under current conditions”. This could become important for many oceanic island ecosystems, where even the most focused conservation efforts may not be enough to save a species, or where climate change will transform a restricted habitat type in a way that renders survival impossible (Harris et al. 2006; see also Box 4). In such cases, investigating the possible use of taxon substitutions ‘ahead of time’ would mean that if a species goes extinct, taxon substitution as a restoration measure could be undertaken fast enough to prevent undesirable trajectories of ecosystem dynamics.

Box 4. Kindred spirits: rewilding and assisted migration

Models and projections increasingly demonstrate how the distributions of many species will have to change to respond to climate change. However, some species or groups of species will likely not be able to respond and migrate fast enough, or even to disperse across anthropogenically altered and disconnected landscapes to new, suitable habitats (Walther et al., 2002; Colwell et al., 2008; Devictor et al., 2008).

In response, some scientists and practitioners have proposed to proactively translocate populations of plants and animals—confusingly using four different names for the same process: assisted migration (Keel, 2007; McLachlan et al., 2007), assisted colonisation (Hunter, 2007; Hoegh-Guldberg et al., 2008), facilitated range shift (Manning et al., 2009), or managed relocation (Schwartz et al., 2009). All these terms describe an approach aiming at identifying species that are particularly at risk due to climate change and moving them to other, more suited, parts of the 'same broad biogeographic region' (Hoegh-Guldberg et al., 2008). The concerns raised against this practise largely mirror the ones against taxon substitutions, mainly the inherent risk of creating new invasive species or pests (Ricciardi and Simberloff, 2009). However, this risk is very likely small. Mueller and Hellmann (2008) found that introduced species that had been moved within a continent were unlikely to become invasive, compared to species that had been moved to another continent. Moving species within one island, or between islands in an archipelago, would in all likelihood be even less risky, given the much smaller geographical ranges involved.

In parallel to the arguments in favour of rewilding islands with taxon substitutes, islands thus also appear eminently suitable as both donors and recipients of species targeted for assisted migration. Within their relatively small areas, many islands harbour very different climatic regimes. Even within a dramatic future scenario for climate change, it is thus conceivable that slowly migrating native species, e.g. plants and invertebrates, can be translocated within an island. Moreover, within or between archipelagos, or even between regions, there may be opportunities to combine taxon substitutions and assisted migration, by using 'climatic refugees' (Hunter, 2007) from one island as substitutes for extinct, similar species on another. Carter et al. (2001) take a conservative view and argue that adaptation options are limited to broadscale measures such as slowing invasion rates, optimising conservation policies, and increasing public awareness. For species at risk of extinction, such measures will appear more than a little 'fluffy', with little, if any, practical actions before it's too late.

A metapopulation approach to island rewilding

Even more so than in many continental ecosystems, current conservation or restoration areas on islands are often very small and disjunct. The use of the same taxon substitute species in a network of small intra- or inter-island conservation management areas (CMAs) could take place within a 'managed metapopulation' strategy (Davies-Mostert et al., 2009), which would have important implications for long-term management. For example, human-mediated dispersal of individuals between CMAs could be employed to mimic natural levels of gene flow or simply to maintain genetic diversity, or to prevent populations from fluctuating towards zero. The metapopulation management approach may be more prudent on small oceanic islands than on larger continental islands, where larger areas can be rewilded and ideally harbour long-term self-sustaining populations of the substitute species. Obviously, though, the metapopulation metaphor should not be taken too far; for example, it would be undesirable to let populations in one CMA go extinct before supplementing them with individuals from another.

Island rewilding as (re-)evolutionary experiments

With proper planning and monitoring, introducing taxon substitutes onto one or several islands may function as long term, replicable evolutionary 're–speciation' or 're–evolution' experiments—as Atkinson (1988) asked: "Can carefully planned species translocations reinstate the evolutionary processes formerly acting on related but extinct species?". Extant and extinct island rails (Rallidae), most but not all of whom are/were flightless, and their islands offer an ideal candidate setup. Until recently these birds were widespread, especially in the Pacific region (Steadman, 2006), and Steadman and Martin (2003) envisioned the need for an "innovative, proactive conservation strategy... to restart evolution of some of the lineages that have suffered the most loss, such as flightless rails" (see also Lazell, 2005). We know that traits of island species can respond evolutionarily to changes in their environment within a very short time (Grant, 1998). Initial stages of 're-evolution' of flightlessness in flighted substitutes of island birds, such as behavioural modifications and extended ground feeding, could perhaps be detected within relatively few generations.

Concluding remarks

> *"those who repair the earth should ultimately marvel at nature's ways even more than lament nature's losses"*
>
> *Hall, 2010*

> *"Restoration is fencing, planting, fertilizing, tilling, and weeding the wildland garden: succession, bioremediation, reforestation, aforestation, fire control, proscribed burning, crowd control, biological control, reintroduction, mitigation, and much more"*
>
> *Janzen, 1998*

Public perception and understanding of concepts in ecology and conservation is usually lagging behind scientific research (Ladle and Gillson, 2009). Rewilding with taxon substitutions represents a case where public and political perception—and hence prioritisation and funding—could well be ahead of ecologists in the decades ahead. Even among scientists, the fascination with the 'ecology of the afterlife', and debating the relative merits of tinkering with species and ecosystems for restoration purposes, causes creative coining of terms like 'resurrection ecology' (Pyle, 2000), or 'recombinant ecology' (Soulé, 1990).

Interestingly, many of the positive responses to the suggestions to rewild North America with substitute megafauna have come from a perhaps unexpected side: landowners and ranchers, who are willing to put their lands at the disposal of rewilders (Donlan and Greene, 2010). Thus, advances in applied rewilding may also be driven by private conservation entrepreneurs, one example of which is the recent rewilding of the Bolson tortoise in New Mexico on lands owned by the Turner Endangered Species Fund (Truett and Phillips, 2009). Similarly, many small islands or parts of larger islands are privately owned, and in cases where the owners are sympathetic to the rewilding concept these could be used for taxon substitutions.

Opponents against taxon substitutions most frequently invoke the fear of creating new invasive species problems, often proceeding to listing the many well-known examples from introduced biocontrol agents gone out of control. While this concern is valid and important, in some cases it makes little sense, especially in relation to rewilding on islands. For example, Ricciardi and Simberloff (2009) recount how "human-assisted introductions of predators have…caused species loss in insular habitats worldwide"—but noone in their right mind would advocate replacing an extinct island species with a mainland predator! More drastically, in a recent comment, Caro and Sherman (2009) go as far as to say there should be "an international moratorium" on the use of non-native megafauna in rewilding projects. Quite apart from lacking suggestions as to how such a moratorium could be achieved, the question remains who should enforce it? An underlying thread in the argumentation of rewilding opponents is to say that "we shouldn't allow any rewilding projects because there is too little empirical evidence from rewilding projects". However, as rightly pointed out by Griffiths and Harris (2010), this is quite an unconstructive catch-22.

Instead of blanket condemnation of taxon substitution as a restoration tool on islands, we need case-by-case judgments based on the particular natural, economical, political, and cultural idiosyncrasies of each case. Moreover, to avoid creating eco-tourist gimmicks only, rewilding projects should comprise explicit and quantifiable short- and long-term objectives. Properly applied, rewilding with taxon substitutes represents a very clear case of evidence-based conservation (*sensu* Sutherland et al., 2004).

I conclude this contribution with a call to nations and organisations that are custodians of appropriate species or populations to consider sharing this essentially global natural heritage with nations or organisations that are planning restoration projects, where the best available evidence demonstrates how these species could be successfully used as taxon substitutes.

ACKNOWLEDGEMENTS

My greatest gratitude goes to Valentín Pérez-Mellado, M.M. Ramon, and the organising committee of the Island Evolution Symposium in Menorca for the opportunity to join the Symposium and to present my thoughts and views here. I am also grateful to David Burney, Trevor Worthy, Stuart Bedford, Colin Miskelly, and Anthony Cheke for sharing information and unpublished data, to Christine Griffiths, Josh Donlan, Karl Campbell, Rachel Atkinson, and Christopher Kaiser-Bunbury for many inspiring discussions, and to the many other colleagues and friends in the Mascarene Islands and elsewhere, with whom I have discussed island rewilding during the last few years.

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