

OPINION ARTICLE

The Use of Extant Non-Indigenous Tortoises as a Restoration Tool to Replace Extinct Ecosystem Engineers

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Abstract

We argue that the introduction of non-native extant tortoises as ecological replacements for extinct giant tortoises is a realistic restoration management scheme, which is easy to implement. We discuss how the recent extinctions of endemic giant *Cylindraspis* tortoises on the Mascarene Islands have left a legacy of ecosystem dysfunction threatening the remnants of native biota, focusing on the island of Mauritius because this is where most has been inferred about plant–tortoise interactions. There is a pressing need to restore and preserve several Mauritian habitats and plant communities that suffer from ecosystem dysfunction. We discuss ongoing restoration efforts on the Mauritian offshore Round Island, which provide a case study highlighting how tortoise substitutes are being used in an experimental and hypothesis-driven conservation and restoration project. The immediate conservation concern was to

prevent the extinction and further degradation of Round Island's threatened flora and fauna. In the long term, the introduction of tortoises to Round Island will lead to valuable management and restoration insights for subsequent larger-scale mainland restoration projects. This case study further highlights the feasibility, versatility and low-risk nature of using tortoises in restoration programs, with particular reference to their introduction to island ecosystems. Overall, the use of extant tortoises as replacements for extinct ones is a good example of how conservation and restoration biology concepts applied at a smaller scale can be microcosms for more grandiose schemes and addresses more immediate conservation priorities than large-scale ecosystem rewilding projects.

Key words: ecological analogs, islands, proxy species, restoration, tortoise, translocations.

Introduction

Islands harbor a plethora of unique flora and fauna, but many continue to suffer disproportionately high levels of extinction. The Mascarene Islands, for instance, have lost the majority of their endemic large-bodied vertebrates (Cheke & Hume 2008). There is increasing evidence that this has led to the disruption of important interactions and ecosystem processes, such as herbivory and seed dispersal (Maunder et al. 2002; Cheke & Hume 2008; Hansen et al. 2008). Due to their isolation

and relatively simple ecosystems, the Mascarenes are an ideal system in which to study both the effects of extinction and disruption, and also to explore how lost interactions and habitat dynamics can at least partly be resurrected.

The abundant populations of giant *Cylindraspis* tortoises that once roamed the Mascarene Islands became extinct by the early nineteenth century (Stoddart et al. 1979). *Cylindraspis* tortoises were the predominant large endemic herbivores of the Mascarenes. Given their long evolutionary association with the Mascarenes (N. Arnold 2007, Natural History Museum, London, personal communication) and large populations (Barnwell 1948), these tortoises probably exerted strong selective pressures on the native plant communities (Cheke & Hume 2008). Early references to their feeding ecology (Leguat 1707 cited in Cheke & Hume 2008; Tafforet 1726 cited in Cheke & Hume 2008) suggest that *Cylindraspis*, like extant giant tortoises elsewhere (Grubb 1971; Merton et al. 1976; Cayot 1987), were important grazers, browsers, and seed dispersers. Today, *Geochelone nigra* in Galapagos and *Aldabrachelys gigantea* in Aldabra are the only surviving giant tortoises.

Our specific aim is threefold: first, we briefly describe the ecology of the extinct Mascarene giant tortoises and discuss

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the evidence that their extinction has left a legacy of ecosystem dysfunction threatening the remnants of native biota. Second, we argue that extant tortoises can be used as ecological proxies for the extinct species to recreate some of the lost dynamics. Finally, we highlight how tortoise substitutes are being used to aid the restoration of Round Island, a small Mauritian island.

Tortoises as Grazers, Browsers, and Seed Dispersers

The Mascarene Islands were home to five endemic species of giant tortoises, *Cylindraspis triserrata* and *C. inepta* on Mauritius, *C. vosmaeri* and *C. peltastes* on Rodrigues, and *C. indica* on Réunion. The occurrence of two distinct shell morphologies suggests differential niche exploitation (Arnold 1979). The saddlebacked shells of *C. triserrata*, *C. vosmaeri*, and some individuals of *C. indica* are purportedly adaptations to dry habitats with sparse vegetation, whereby the raised front permits the upward extension of their long necks to exploit taller plants by browsing. In contrast, the domed shells of *C. inepta*, *C. peltastes*, and some individuals of *C. indica* suggest that they were predominantly grazers. This shell type may also have enabled easy passage through dense forests (Arnold 1979). Fossil evidence (Bour 1981; Austin & Arnold 2001; Florens 2002), historical records (Barnwell 1948), and the behavior of extant giant tortoises on some Galapagos islands (Cayot 1987) suggest that the extinct Mascarene giant tortoises utilized both lowland and upland habitats, ranging from open, palm-dominated forest to dense rainforest (Vaughan & Wiehe 1937; Cheke & Hume 2008). However, the greatest tortoise densities are thought to have been in the lowland palm-dominated open forest which was likely to have been maintained (i.e., engineered) by grazing giant tortoises of both shell morphologies (Cheke & Hume 2008).

There is ample evidence that intensive grazing and browsing in Mascarene ecosystems has exerted strong selective pressures on the flora. For example, prostrate growth, small leaves, and coarse tough foliage, common characteristics in the native and endemic Mauritian grassland community, are functional traits of grazed communities (Huntly 1991). We believe that tortoises, the predominant endemic herbivores, were the most likely selective agents.

Another line of evidence for the significance of giant tortoises in shaping the Mascarene flora is the prevalence of heterophylly, a widespread leaf dimorphism trait reported in 28 families of endemic woody Mascarene plants (Friedmann & Cadet 1976; Hansen et al. 2003; Eskildsen et al. 2004). It is likely that heterophylly at least partly evolved in response to browsing pressures from giant tortoises. Indirect evidence comes from feeding experiments with *Aldabrachelys gigantea*, which avoid the low-growing “juvenile” leaves, often characterized by red coloration and different shape and size foliage, in preference for the higher-growing mature leaves (Eskildsen et al. 2004). In many heterophyllous species the transition in leaf form occurs between 0.6 and 1.7 m (C.J.G., unpublished data). A reconstruction of *C. vosmaeri* (the large Rodriguan

species) suggests that saddlebacked animals could browse up to 1.2 m (Jones 2002), showing that most of the palatable adult leaves were beyond the reach of even saddlebacked tortoises.

Plant species with fleshy fruits are abundant in most tropical forests (Howe & Smallwood 1982), and forests once covered at least 85% of Mauritius (Vaughan & Wiehe 1937), with possibly the same cover on Réunion and Rodrigues (Cheke & Hume 2008). The main fruiting season of palm and hardwood species on the Mascarenes coincides with the late dry season when grasses, a major constituent of giant tortoise diet (Gibson & Hamilton 1983; Cayot 1987), are dry or absent. So it is highly probable that tortoises fed on fruits during this period. Several early explorers refer to tortoises eating fruits (Leguat 1707 cited in Cheke & Hume 2008; Tafforet 1726 cited in Cheke & Hume 2008), which are an important part of tortoise diet elsewhere (Grubb 1971; Hnatiuk 1978; Leuteritz 2003). We envisage that the domed-shell tortoises, which were more manoeuvrable through dense forest, would have moved inland to wetter areas to exploit hardwood fruits, while their saddlebacked counterparts utilized the more open coastal palm forest.

Extinctions and the Loss of Ecological Connectivity

The eradication of introduced mammalian herbivores in the 1970s and 1980s from Round Island, which had become a palm savannah habitat (Bullock et al. 2002), has given some comparative insights into the trophic cascades which may have followed the extinction of the tortoise populations. The once common Round Island tussock-forming grass, *Vetiveria arguta*, rapidly declined in abundance and distribution following the eradication of introduced goats (*Capra hircus*) and rabbits (*Oryctolagus cuniculus*) (North et al. 1994). Its decline was concomitant with an increase of grazing-intolerant invasive grasses, e.g., *Cenchrus echinatus* and *Chloris barbata* (Bullock et al. 2002), which have encroached on the shorter-stature and slow-growing native grassland community, a complex of grasses, sedges, and herbs. This replacement process has previously been documented on Gunner’s Quoin, another Mauritian island (North & Bullock 1986). We believe, therefore, that the loss of tortoises would have initiated this degeneration of the native grassland community, to the extent that modern botanists did not include it in their classification of Mascarene habitats (Vaughan & Wiehe 1937). Today, remnant patches of Mauritius’ native grassland community are restricted to Round Island and, to a lesser extent, Gunner’s Quoin.

Large, fleshy-pulped, and highly aromatic fruits are considered adaptations to entice vertebrate consumers (van der Pijl 1969). Such fruits are produced by many Mauritian trees, which are at greater risk of extinction than trees which produce smaller fruits (Maunder et al. 2002; von Bethlenfalvy 2006). Today, the only extant native vertebrate capable of dispersing at least some large fruits is the bat *Pteropus niger* (Nyhagen et al. 2005). However, by virtue of their sheer abundance, association with the island’s forests and more catholic diet, tortoises were probably key seed dispersers of the fruits they consumed. Many of the introduced vertebrates are seed predators (Cheke & Hume 2008) and so fail to compensate for

the loss of native dispersers. Limited seed-dispersal and poor seedling recruitment is widespread in Mauritian habitats and hampers natural regeneration (Hansen et al. 2008).

Ecological Proxy Candidates

The lack of selective grazing and seed dispersal functions has important implications for the conservation and restoration of native biota in Mauritius. One solution is to use ecological substitutes to restore lost ecosystem functions (Donlan et al. 2006; Hutton et al. 2007; Hansen et al. 2008). *Aldabrachelys gigantea* and *Astrochelys radiata* (Madagascan radiated tortoise), which belong to the same family (Testudinidae) as the extinct species, were considered suitable proxies (Jones 2002; Donlan et al. 2006). Both species are selective grazers and capable of consuming and dispersing large-seeded fruits (Grubb 1971; Gibson & Hamilton 1983; Leuteritz 2003).

Aldabran giant tortoises have previously been used as surrogates for extinct species on other Indian Ocean islands, e.g. Ile aux Aigrettes (Jones 2002), Rodrigues (Weaver & Griffiths 2008), Curieuse, Cousin, and Frégate Islands (Stoddart et al. 1982). There is no evidence that tortoises have a negative impact on the native vegetation on any of these islands (Hamblen 1994; B. Sachse 2005, personal communication; C.J.G., unpublished data).

Tortoises and Round Island – A Case Study

Historical records document that giant tortoises were once present on Round Island (Lloyd 1846). To determine whether some lost ecosystem functions can be recreated using surrogate species, the Government of Mauritius and a local nongovernmental organization, the Mauritian Wildlife Foundation, introduced small populations of unknown sex subadult Aldabran giant and adult male Madagascan radiated tortoises to Round Island in June 2007. Round Island's native plant communities are relatively intact and harbor the best remnants of palm-rich forest, where tortoises would once have created and maintained open grassy areas. Invasive weeds are the greatest prevailing threat. Tortoises, like other herbivores, influence plant communities by altering the competitive balance between plant species, providing a competitive advantage to those species least sensitive to grazing damage (Grubb 1971; Cayot 1987). Theoretically, the introduced tortoises should graze the faster-growing, more abundant fleshier exotic grasses in preference to the less prevalent native species, which often possess anti-herbivorous traits specific against tortoise grazing. This should benefit the less competitive shade-intolerant natives (Moretto & Distel 1997). Whilst small areas are weeded manually and native grasses planted in an attempt to control the exotics and encourage natives, weeding is restricted to 2% of Round Island's 215 ha and is an enormous drain on financial and human resources. Planting natives is a short-term solution and fails to address the primary cause of decline, which is vital for the restoration of ecosystem function (Hobbs & Norton 1996).

Sustained grazing is predicted to reduce seed production of the palatable nonindigenous species, thereby reducing tortoise-mediated exotic seed dispersal potential and the size of their seed bank (O'Connor & Pickett 1992). We believe that their dispersal will be negligible comparable to present conditions, in which weeds seed unhindered and the exotic grasses are already ubiquitous. Furthermore, the initial rapid regeneration of the palm forest following the eradication of alien mammals has declined, as non-native plants swamp the young seedlings, which are further limited by a lack of suitable seed beds (Bullock et al. 2002). However, more important is the lack of dispersal of palm seeds into new, suitable sites; few fruits are dispersed beyond the shadow of maternal trees. The consumption and dispersal of large fruits would create a more dynamic forest.

Tortoises were initially kept in enclosures and their impact on the plant community studied. Preliminary observations suggested that, as predicted, they preferentially grazed the exotic vegetation, avoiding native plants, which were regenerating in areas previously dominated by exotic plants. Following their release from the enclosures in May to July 2008, tortoises were seen consuming and dispersing the large seeds of the endemic palm, *Latania loddigesii*, which is believed to be dispersal limited. Further investigation is necessary to ensure that the tortoises do not have any negative indirect effects on the native biota. Long-term monitoring is planned as it is likely that there will be a time lag before all costs and benefits are apparent.

Past restoration techniques on Round Island have failed to address the cause of decline of the grassland community and were limited in scale. A landscape-based restoration program appears necessary to preserve and restore Round Island's biota. The use of tortoises as ecological proxies is essentially synonymous to adopting biological control agents, and thus requires careful consideration of the risks involved (Simberloff & Stiling 1996). We believe that introducing tortoises to Round Island was a low-risk, high reward strategy (Table 1), based on the biological characteristics of these tortoises and the attributes of Round Island.

According to fossil evidence, the low lying Aldabra atoll, home to *A. gigantea*, was colonized at least three times by these giant tortoises, following periods when it was submerged (Braithwaite et al. 1973). Colonists most likely originated from Madagascar, which had two species of giant tortoise (Arnold 1979). Today, their ancestors are extinct and future natural colonization is impossible. Assisting colonization to other Indian Ocean islands could prevent their potential extinction as a result of contemporary climate change. Using tortoises to restore habitat would simultaneously secure their future survival.

We argue that blanket condemnation of using exotic species in restoration and conservation contexts to either restore ecological interactions or prevent the extinction of a species, respectively (Rubenstein et al. 2006; Ricciardi & Simberloff 2009), is counterproductive. Each introduction proposal should be rigorously examined on a case-by-case and locality-by-locality basis as proposed by Donlan et al. (2006). For

Table 1. Summary risk assessment of introducing tortoises to Round Island based on parameters considered important for biological control agents (Howarth 1991 and references therein).

<i>Risk Assessment Parameters</i>	<i>Risk Assessment for Tortoises</i>
Potential to predict response outcomes accurately	<p>Low Risk:</p> <p>Ability to predict plant responses to grazing from:</p> <ul style="list-style-type: none"> • simple plant traits (Vesk & Westoby 2001; Eskildsen et al. 2004); • similar feeding observations of different tortoise species and plant responses to tortoise grazing (Grubb 1971; Cayot 1987; Hambler 1994; Leuteritz 2003); • the response of the Round Island flora to the eradication of mammalian herbivores (North et al. 1994; Bullock et al. 2002); • Ile aux Aigrettes plant–tortoise study (C.J.G., unpublished data).
Potential to disperse from intended target environment	<p>No/Low Risk:</p> <p>Tortoises were initially restricted to enclosures and subsequent radio-tracked. Dispersal to neighboring islands is highly unlikely.</p>
Potential to self-perpetuate	<p>No Risk:</p> <p>Initial introduction of 12 subadult (i.e. nonreproducing) Aldabran giant tortoises, and 12 male adult radiated tortoises.</p>
Potential to monitor impacts on native biota	<p>Low Risk:</p> <p>Enclosures facilitate close monitoring of interactions with biota. Tortoises are large, noncryptic, sluggish, aboveground animals. When released from enclosures, animals were fitted with radio transmitters. Long-term monitoring (>30 yr) of biota provides valuable baseline data to identify any detrimental impacts. Permanent occupation of the island by wardens facilitates long-term monitoring.</p>
Potential nontarget effects and irreversible consequences	<p>No/Low Risk:</p> <p>See above.</p> <p>Ability to remove all individuals from island easily and rapidly. Disease screening and the general species-specificity of reptile diseases (Cooper & Jackson 1981) minimize the risk to the endemic reptile populations. Quarantining animals and strict control of their diet prior to translocation prevented the introduction of non-indigenous plant material.</p>
Potential economic cost-benefit analysis	<p>Low maintenance, long-term weed control solution.</p> <p>Opportunity to direct funding and human resources to alternative restoration activities.</p>

example, there are major differences between suitable candidate species and sites we suggest and those of Donlan and colleagues (2006; Table 2). Ricciardi and Simberloff's (2009) generalist conclusions are based on species that are difficult to control, whose impacts were not assessed prior to mass translocation, and whose translocations are irrevocable. As highlighted in the risk assessment (Table 1), tortoises can be removed relatively easily from islands allowing temporal and spatial changes in their impact to be appraised and addressed.

Conclusions

The extinction of the endemic giant tortoises in Mauritius has left dysfunctional ecosystems. Fortunately, their partial rehabilitation is feasible because tortoise extinctions were relatively recent. Offshore islands such as Round Island offer the best opportunities and most pressing concerns for restoration. Current management of Round Island's biota is failing to compensate for the loss of tortoises, which were an important component of the open palm-rich forest. Evidence

suggests that long-term restoration can only be achieved by reinstating the functional processes performed by the extinct tortoises. We introduced non-indigenous tortoises as suitable substitute species and justify why they will alter resource levels and disturbance regimes to favour native species, most of which are threatened. Tortoises are ideal surrogates, as they present no apparent risks. The use of substitutes as a restoration technique is likely to be directly applicable to many other island ecosystems that suffer from similar ecosystem dysfunctionality, especially those which were home to species of giant tortoises that have become extinct relatively recently (Auffenberg 1974). Additionally, we believe that more degraded mainland Mauritian habitats that lack grazing pressures and seed dispersal by large animals could also benefit from the introduction of tortoise proxies. Successful exclusion of exotic mammalian herbivores from mainland forests within the Black River National Park has enabled regeneration of native species (Cheke & Hume 2008), but many endemic and native species within these small protected areas suffer from seed-dispersal limitation (Hansen et al. 2008). Control of

Table 2. Main contrasts between the American Pleistocene rewilding proposal (Donlan et al. 2006) and the use of tortoises as analogs on Round Island.

	<i>Pleistocene Rewilding</i>	<i>Tortoise Analogs</i>
Rationale	Reconstruct ecosystems.	Recreate lost ecosystem functions.
Extinction history	~13,000 yr ago.	~200 yr ago.
Ecological consequences of historical losses	Largely unknown and difficult to infer as high species loss from complex continental communities.	Detailed knowledge of fossil record and recent extinctions provides valuable insight into the species that were present and the concomitant impact of their loss.
Habitat condition	Hard to predict due to long timescale since extinctions. Flora and habitat have been severely modified.	Detailed historical records due to recent human colonization. Islands harbor remnants of semipristine habitat and many associated species still present.
Scale	Large: continental context. Candidate species globally sourced.	Small islands. Candidate species sourced from captivity.
Species	Multiple species from a wide variety of taxa. Span several trophic levels and include predators, some of which are considered dangerous. Little to no assessment of candidate species in a comparable system to the intended release site.	Tortoise taxa. Herbivores; both tortoise species are regarded as natives by locals due to the large captive populations within Mauritius. Preliminary trials conducted on a small island (Ile aux Aigrettes).
Project acceptance	Potential conflicts and less readily accepted by public. High cost as a need for secure fencing and expensive translocation costs to source animals. Animals would have to come from a wide variety of sources. Captive bred predators will be less adapted to new habitat than herbivores.	No direct human conflict on uninhabited islands. Main costs needed for translocation; islands act as a natural barrier. Healthy animals are widely available in captivity. Generalistic nature of tortoises enables them to adapt readily to new habitats.
Prevention of disease transmission	Hard as in some cases proposed species have related taxa within the suggested area.	No other conspecific tortoises occur in the habitat. Risk of interspecies disease transmission is low.
Predicting food web and habitat response	Hard to predict indirect effects when introducing animals at a multitude of trophic levels.	More accurate predictions possible as introducing only herbivores into simple ecosystems.
Monitoring potential	Difficult to measure the impact of each species on the other biota in large areas.	Opportunity to pen animals and make prior assessments. Limited vagility eases monitoring.
Dispersal potential	High, fast moving, continents lack boundaries.	Limited, slow moving, restricted to islands.

invasive weeds is still paramount. Only 57.6 ha of Mauritius' upland forest (Cheke & Hume 2008) is regularly weeded manually, less than 0.04% of the island's forest cover in 1753 (Vaughan & Wiehe 1937). Introducing grazing and browsing tortoises could be a relatively easy, simple and cost-effective way to restore some of these lost dynamics and allow invasive weeds to be managed in far larger areas of native forest.

While large-scale restoration projects with taxon substitutes, like the one suggested by Donlan et al. (2006), are difficult to implement, we believe that much can be learnt about using species substitutes from smaller-scale projects, in particular when implemented on islands, which are "microcosms" of continents. Their recent human colonization, high intrinsic

conservation value, and relative biological simplicity make islands ideal "model systems" for restoration (Wardle 2002). Furthermore, the isolation and lack of human habitation on many islands will result in fewer objections to restoration plans here than to more ambitious projects in more densely populated continental areas.

Implications for Practice

- Restoration will only be fully achieved by incorporating ecosystem processes which originally shaped communities, such as herbivory and seed dispersal.

- These ecosystem processes can be restored by carefully selecting proxy species, thereby reducing human interference.
- Translocation of large, slow reproducing species with relatively small ranges as replacements for extinct natives should be considered, as such biocontrol agents will be easy to monitor and manipulate.
- Experimental studies on offshore islands or similar contained areas should be undertaken prior to large-scale releases in mainland habitats.

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