

Island biodiversity conservation needs palaeoecology

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The discovery and colonization of islands by humans has invariably resulted in their widespread ecological transformation. The small and isolated populations of many island taxa, and their evolution in the absence of humans and their introduced taxa, mean that they are particularly vulnerable to human activities. Consequently, even the most degraded islands are a focus for restoration, eradication, and monitoring programmes to protect the remaining endemic and/or relict populations. Here, we build a framework that incorporates an assessment of the degree of change from multiple baseline reference periods using long-term ecological data. The use of multiple reference points may provide information on both the variability of natural systems and responses to successive waves of cultural transformation of island ecosystems, involving, for example, the alteration of fire and grazing regimes and the introduction of non-native species. We provide exemplification of how such approaches can provide valuable information for biodiversity conservation managers of island ecosystems.

Island ecosystems have always played a leading role in conservation biology. They are often described as natural laboratories, providing model systems for the testing of evolutionary, ecological and biogeographic theories^{1,2}. Remote island ecosystems are hotspots of biodiversity, with legacies of relatively recent human impact and native species' extinctions, and therefore provide significant challenges when considering how to conserve biodiversity. They also offer some of the best-suited scenarios for rapidly advancing our understanding of fundamental aspects of human relationships with nature, and of conservation strategies, including restoration and eradication programmes³⁻⁷. Examples of programmes specifically tailored to islands include the Global Island Partnership, the International Union for Conservation of Nature (IUCN) Island Initiative Program, and the Small Island Developing States Network.

The isolated nature of remote islands is both part of the problem, creating 'naive' native ecosystems, especially vulnerable to non-native invasions; and a positive, in that the natural barriers to colonization can, for example, enable successful programmes eradicating non-native vertebrates⁵ and/or translocating endangered species. However, success in managing island ecosystems and conserving biodiversity, as well as invasive species eradication, may be contingent upon a sound understanding of an island's specific ecological history. Recent work within restoration ecology has highlighted that ecological history is important, not only to determine the degree of change that has occurred from baselines or reference conditions, but also the level of intervention required to restore an ecosystem towards particular desired states⁸⁻¹⁰. Establishing points in time (and accompanying baseline states) of first human impact can therefore be important for decision-making and provide

guidance on what to restore and where, when managing both native and novel ecosystems¹¹⁻¹³.

Baselines are frequently derived from historical literature or from palaeoecological studies based on biological proxy, fossil or sub-fossil evidence, especially pollen, spores, plant macrofossils and charcoal records^{14,15}. Indeed, numerous decadal-to-millennial scale time-series have been generated from islands (Fig. 1). Collectively, these records provide a rich picture of past environmental change and the ecological impacts of initial and subsequent human settlement of island ecosystems globally (Fig. 2)¹⁶⁻¹⁸. Such studies can also provide information on the native/non-native status of particular species, pre-human ecological conditions and how achievable restoration targets may be^{8,11}. As most oceanic islands are relatively recently settled (many <10,000 years) compared with continental regions, pre-human baselines can often be more clearly distinguished and dated and such data can be of direct relevance to conservation decisions. A good example is provided by the Hawaiian island of Kaua'i, where fossil pollen data recovered from ancient caves and marshes revealed the character and scale of human-induced ecological transformation and was used in refining a list of appropriate native plants for forest restoration initiatives¹⁹.

Whereas ecological baselines can be conceived of as a referring to a single state, derived from a particular point in time (for example, a pre-human baseline), herein we discuss the potential value of using palaeoecological techniques to determine multiple past baselines. For instance, in addition to the consideration of pre-human states reflecting natural variability and responses to environmental stressors (for example, natural disturbances), we may also identify key points in time where human cultures exerted different types of

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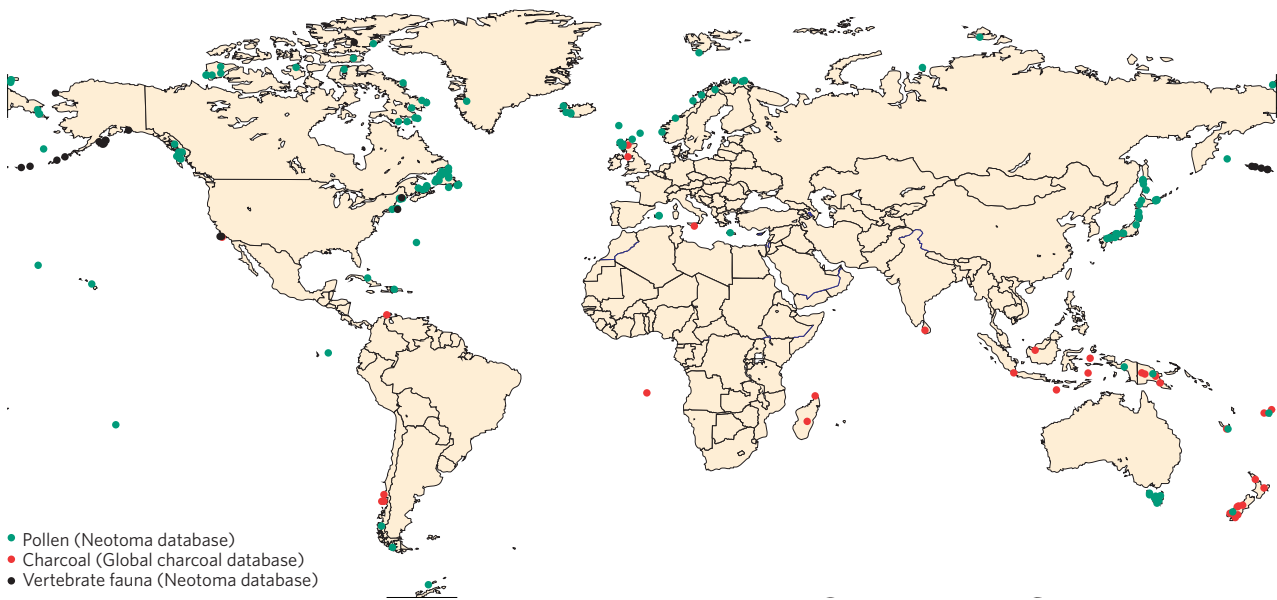


Figure 1 | To encourage the use of palaeoecological datasets in conservation we ideally need freely available online datasets. This figure shows some geolocations for fossil pollen (indicators of past vegetation change), bone assemblage (presence of vertebrates), and fossil charcoal (indicators of past fires) datasets currently available from islands around the world in the Neotoma database and the Global Charcoal Database (last accessed January 2017).

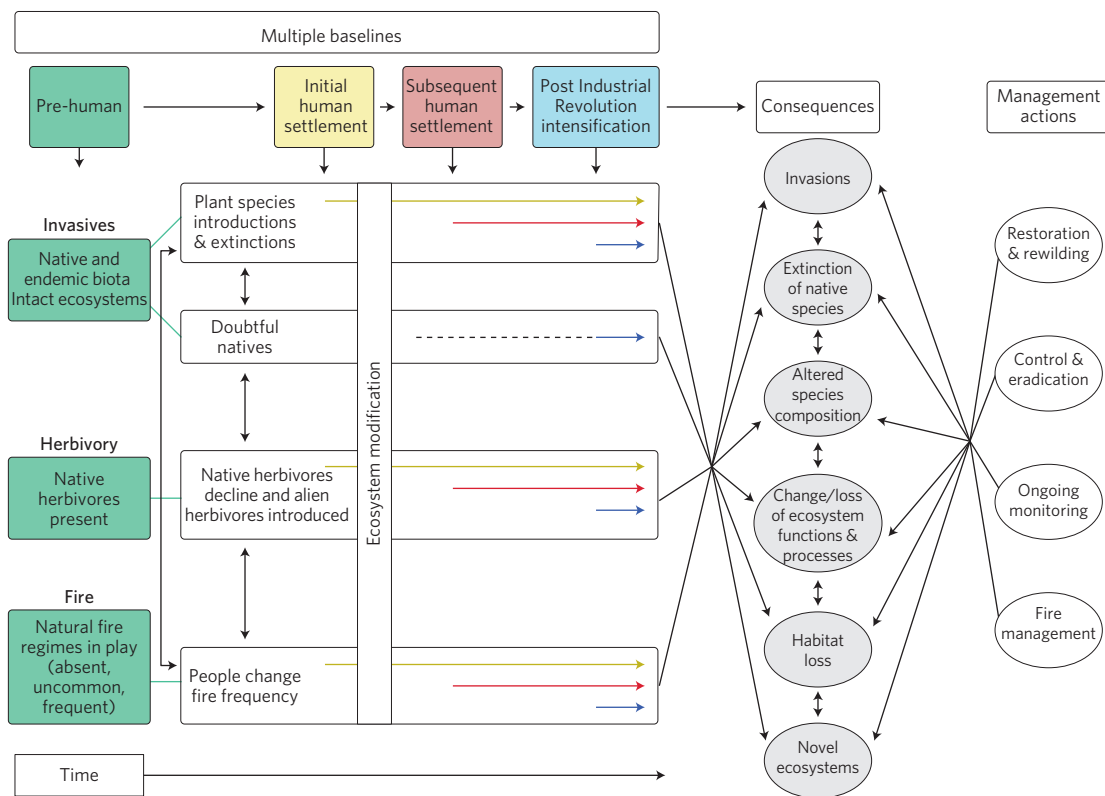


Figure 2 | Conceptual diagram summarizing the main concepts discussed within the text and the suggested management actions. The diagram focuses on the degree of change and main human impacts on island ecosystems over time, taking into consideration multiple baselines (indicated by yellow, red and blue arrows). We show how the introduction of invasive species, herbivores, and human-induced changes of the fire frequency may impact the native and endemic island biota and lead to varied management actions. Colour of the arrows is related to the relevant baseline above.

influences on islands over time, and transformed ecosystems in distinct ways. Such multiple baselines provide invaluable insights and opportunities for conservation practitioners and policymakers and may also be particularly informative for restoration programmes that take both an ecological and cultural perspective^{8,10,16}. The use

of fossil pollen data alongside other historical and pre-historical archives on Kaua'i again provides illustration, as efforts have been made to develop management and interpretive programmes for centuries-old working cultural landscapes owned by the National Tropical Botanical Garden and on other privately owned sites¹⁹.

Table 1 | The set of biological proxies, management questions and informed conservation actions used within the text to track back human impacts on island ecosystems.

Impact	Biological proxy	Management questions	Informed conservation action
Invasive and non-native species	Plant microfossils, plant macrofossils, ancient DNA	(1) Timing of species introduction (2) Resolving the species provenance (3) Rate and pattern of spread (4) Assessment of the impact on native ecosystems	Eradication, restoration, monitoring
Fire	Plant microfossils, charcoal (macro- and micro), tree ring fire-scars*, charred plant macrofossils*	(5) Determine natural versus human-induced fire regimes (6) Determine ecosystem thresholds in response to fire (7) Assessing the interaction with other anthropogenic disturbances	Fire suppression, fire prevention, restoration
Herbivory	Fungal spores (for example, <i>Sporormiella</i>), plant microfossils, ancient DNA, faunal remains (for example, bones)	(8) Determine the origin and presence of herbivores (9) Analyse the rate and pattern of the introduction (10) Assessment of the impact on native ecosystems	Eradication, restoration, monitoring

Note that some biological proxies can be used to characterize different impacts. *Not discussed in the text.

In this Perspective, we select three relevant topics that are closely related to human colonization and subsequent activities and each of which have been shown to have profound impacts on island ecosystems (Table 1)^{1–7,19}: (1) invasive and non-native species, (2) altered fire regimes, and (3) altered grazing regimes. Using case studies from islands that draw particularly upon plant microfossils and charcoal records, we describe how palaeoecological data and the reconstruction of past baselines can be applied to inform and improve management plans for island ecosystems.

Invasive and non-native species

The distinction between ‘native’ and ‘(alien) non-native’ species and determination of the ‘natural range’ of a species when considering longer timescales can become the subject of much philosophical debate. Pragmatically, however, two approaches dominate in the restoration ecology literature: (1) humans as the agency for introduction and (2) the historic Holocene species’ range²⁰. These distinctions can often be much more clearly drawn on islands in contrast with continental ecosystems, as human arrival times are generally both more recent and more precisely known. In the absence of definitive data, the status determination of non-native plant species on islands is often based on conjecture, derived from a combination of factors including: date and site of first recorded presence (particularly post-European settlement); non-native status designations in neighbouring regions; active change in current species distributions; ability to transform habitats; individual species’ characteristics, including association with humans and history as a non-native^{21,22}.

Key questions in any ecological restoration programme are which species should be conserved, which are priorities for eradication, and which should be closely monitored for potential deleterious ecological future impacts⁵. Palaeoecological methodologies such as the analysis of plant macro- and microfossils (such as pollen and phytoliths), and preserved DNA can be powerful tools, particularly when used in conjunction with historical evidence, to determine the provenance of plant species on islands, for example, to determine whether they are native, historical or more recent introductions and to provide insight to address conservation management questions^{20,23,24} through:

- Analysis of native species’ ranges and historical distributions²⁵.
- Developing clear criteria for designation of non-native species status²⁶.
- Resolving the origin of ‘cryptogenic species’ (species that cannot be reliably classed as either native or non-native)²⁷.
- Analysing the origin, dispersal, and rate of spread of invasive species over time^{24,28}.
- Assessing the long-term impact of (invasive) non-native species on native species.

- Predicting future outcomes of invasions and responses to environmental change^{24,29}.

For example, combined palaeoecological analyses and historical records confirmed the non-native status of the daisy tree (*Olearia lyallii*) in the sub-Antarctic Auckland Islands²⁸. Their results indicate that although endemic to the New Zealand region, *O. lyallii* became established in these remote islands approx. 1807–1810, probably facilitated by localized habitat disturbances associated with European sealers (Fig. 3). Similarly, in an example from the Galápagos Islands, palaeoecological analyses revealed that nine plant species presumed to be either introduced after European discovery of the islands in 1597 or of doubtful native status were, in fact, native to the archipelago^{21,30}. One of these species, *Hibiscus diversifolius*, an identified ‘habitat transformer’ appearing to be expanding its distributional range, had previously been considered for potential control or eradication. In addition, palaeoecological analyses in Mauritius also recorded over a dozen plant species that are currently not considered native to this Indian Ocean island³¹. Most of these taxa, including several palm tree species, had been extirpated from the island prior to the first reliable vegetation surveys, less than two centuries following first human colonization. These species were abundant in pre-human ecosystems and illustrate a considerable proportion of ‘unknown lost’ biodiversity^{31,32}.

In addition to recognition of ‘lost species’ through plant microfossil identification, syntheses of palaeobotanical, historical, ecological and molecular evidence have also been increasingly used to resolve the conservation status of species with cryptic origins^{6,33–35} for example Krauss’ clubmoss (*Selaginella kraussiana*) in the Azores³³ and eastern bluebirds (*Sialia sialis bermudensis*) on Bermuda⁶. However, many oceanic islands now have high numbers and proportions of species that are considered to be non-natives, in many cases outnumbering native species. Few would argue that all such species should be targeted for control or eradication: many are valued by human societies as food plants, for aesthetic reasons, or for their ecological functions, in some cases replacing or supplementing extinct (or extirpated) native species¹⁶.

From a biodiversity perspective, we may also use palaeo-data to address how human colonization and subsequent cultural phases, such as the introduction of livestock, crops and new land-use techniques have influenced the abundance of particular island species over time, recognizing that there may be winners as well as losers. Unique island species and subspecies may even have developed as a result of the genetic divergence of an anthropogenically introduced or facilitated founder species. An example of this is the Canarian Egyptian vulture, a genetically distinct, insular population of the Endangered (IUCN) Egyptian vulture (*Neophron percnopterus*). Genetic analyses indicate that vultures first colonized the Canary

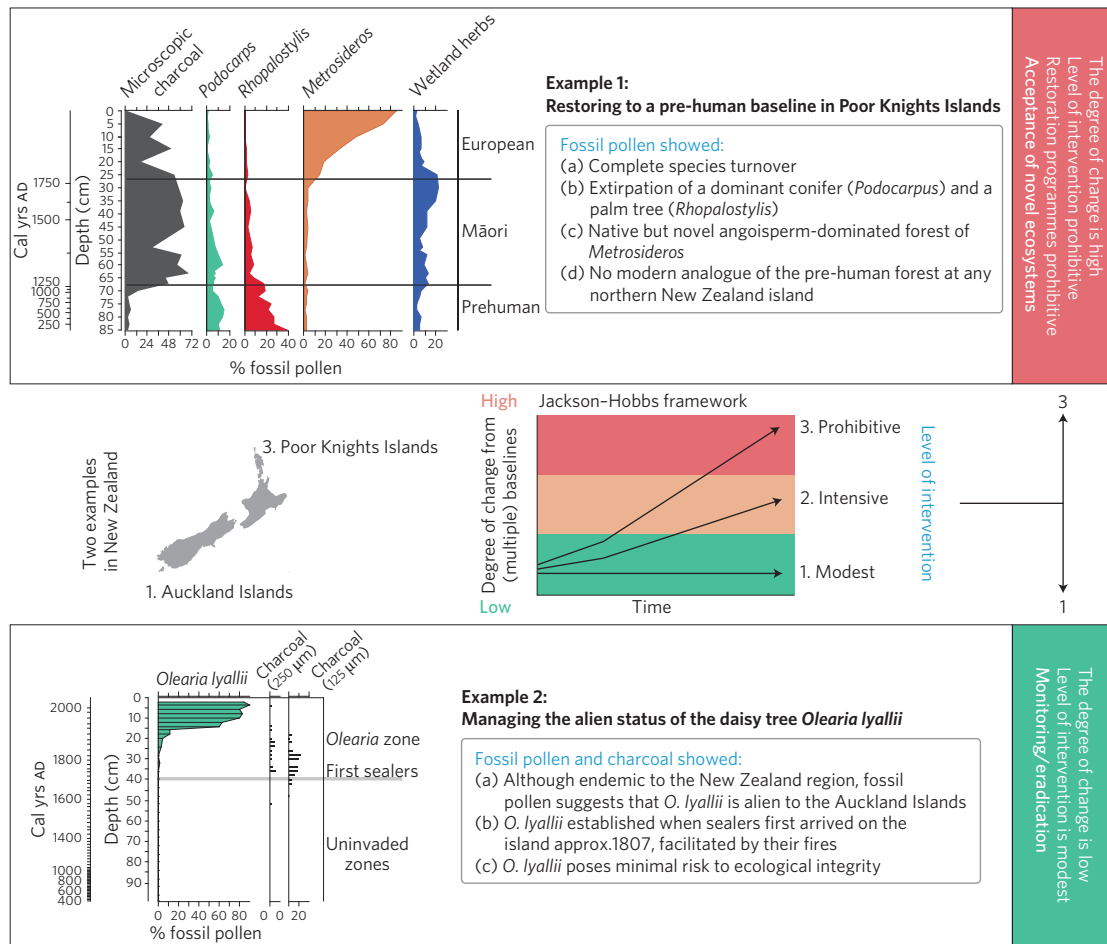


Figure 3 | Two palaeoecological examples from New Zealand showing different potential conservation practices. This figure assumes a context where the most desired state is the least altered by humans, although we recognize that this may not always be the key goal of conservation managers in practice. We are showing a modified Jackson-Hobbs framework⁸ applied to two palaeoecological examples in New Zealand, Tawhiti Rahi Island of the Poor Knights Islands¹⁶ and the Auckland Islands²⁸. In the first example, the pollen shows that the current vegetation composition on the Poor Knights is completely different to the pre-human state, and the level of intervention required to return it to its undisturbed state would be prohibitive. Furthermore, palaeoecological insights from the Poor Knights have revealed that the native *Metrosideros* forest is not a good analogue for a pre-human restoration endpoint on other more degraded islands in northern New Zealand. In the second example, pollen and charcoal analyses were able to resolve the non-native status of a tree daisy on sub-Antarctic Auckland Islands, and show that although its establishment was facilitated by anthropogenic disturbance, the tree has been slow to spread. Pollen and charcoal records suggest this non-native tree poses a low risk to the Auckland Islands’ ecological integrity, and the level of intervention required to return the invaded sites to a pre-invaded state would be relatively modest. However, current management practices of ongoing monitoring and no intervention are also appropriate. Figure adapted with permission from ref. ¹⁶, Wiley-Blackwell (top); ref. ⁸, AAAS (middle); and ref. ²⁸, Oxford Univ. Press (bottom).

Islands 2,500 years ago³⁶, a date coincident with the timing of human colonization of the archipelago determined from archaeological remains. The vultures are believed to have colonized the islands naturally, but the colonization was likely facilitated by the introduction of domesticated livestock, as suitable food sources were previously lacking³⁶.

The role of long-term ecological data (spanning palaeoecological and long-term population monitoring studies) can thus be much more than simply determining whether colonization was anthropogenically assisted, but also to provide quantitative information on changing abundances, distribution and responses to environmental change within the island system, and the processes explaining present-day island biodiversity.

Changes in fire regime

Humans have modified fire regimes in most ecosystem types around the world, as they have colonized and increased in abundance over time³⁷. On islands, human modifications of the fire

regime typically occurred much later than in continental regions, especially on islands where human presence is more recent (for example, in the past 500–5,000 years) and where natural ignitions were rare³⁸. Knowledge of long-term fire ecology is fundamental to understanding the natural variability of fire regimes (fire history) and the responses and resilience of ecosystems to fire (both natural and human ignited). On islands where fire was a naturally occurring disturbance before human arrival, resource managers face a complicated scenario. They must consider whether fires should be suppressed or prescribed in particular ecosystems, what the long-term ecosystem responses to a particular fire regime will be, and whether post-fire restoration is necessary. Consequently, there is an increasing awareness among scientists and managers that long-term research, including various forms of palaeoecological data, holds significance for contemporary fire management policy³⁹.

Current management of forest fires consists mainly of prevention (management of fuel), control (fire suppression), and recovery (ecosystem restoration). Palaeoecological proxies such as charcoal,

pollen and fungal spores found in sediments, and tree rings with fire scars, among other indicators, provide information on different spatial-temporal resolutions of fire occurrence and fire regime characteristics³⁹. In addition, these datasets allow reconstructions of both fire regimes and vegetation dynamics, and can be used to address key issues related to fire–ecosystem interactions such as:

- Determining natural fire regimes on islands (that is, caused by volcanism or lightning strikes), providing a reference for resilience to fire on islands where fire was uncommon or rare before human arrival, or to emulate fire suppression and prescribed burning on islands where fire was an important and naturally common form of disturbance before human arrival⁴⁰.
- Differentiating between natural and cultural fire regimes⁴¹, that is, how have fire regimes changed over time following human arrival?
- Determining ecosystem thresholds in response to fire (that is, how or if species recover after repeated fire) and the necessity to intervene through restoration^{42,43}.
- Assessing the role of other anthropic disturbances on fire behaviour such as invasive species, climate change, forest logging, landscape fragmentation, and the combined effects on ecosystems^{43,44}.

Several palaeoecological studies have shown the applicability of long-term reconstructions in fire ecology and management on islands. For example, in New Zealand, fossil charcoal records from lakes in the South Island indicate that severe fires occurred soon after initial settlement by the indigenous Māori, resulting in significant reduction of the native forest and subsequent soil erosion⁴⁵. Charcoal analysis of high temporal resolution, from multiple sites, allowed the establishment of a robust fire chronology before and after Māori arrival (in the thirteenth century). The reconstructions showed that fire was rare and infrequent before human arrival, and rapidly increased in frequency and extent following initial human arrival, with the development of a novel anthropogenic fire regime, with fires every 50–100 years, a pattern sustained until European contact, when fire frequency increased again⁴⁶. Some understanding of spatial variation was also achieved, with key predictors of forest loss during the initial burning period in New Zealand relating to gradients in moisture and topography rather than human behaviour; the mere introduction of a novel anthropogenic ignition source made deforestation of New Zealand and most of other Pacific islands inevitable⁴⁷. The virtual absence of fires in the immediate period prior to human arrival (pre-Māori) and the rapid replacement of trees by ferns, shrubs and grasses after the initial burning period, indicate that although native forests were paradoxically highly flammable, they are not adapted or resilient to frequent and repeated anthropogenic fires. There are other cases where the charcoal record clearly shows different fire regimes associated with specific periods of human occupation. For instance, in Hispaniola, the second largest island in the Caribbean, there is evidence that natural fires occurred within dry forests, where several tree species (for example, *Pinus occidentalis*) are fire-adapted⁴⁸. This natural fire regime was significantly modified from approx. 5,400 cal. years BP, coinciding with the occurrence of early settlers in the island. Following European settlement, fires became generally less frequent than during the pre-Columbian phase. Another key example is provided by pollen and charcoal data from Tenerife in the Canary Islands (Fig. 4), where two burning baselines can be linked with human arrivals: (1) the first colonists from North Africa and (2) Europeans. Before human arrival the concentration of charcoal was relatively low in Tenerife. After initial settlement fires increased in frequency, with an associated decline and later extinction of some tree species (for example, *Quercus* and *Carpinus*)³².

Finally, there are island ecosystems that are known to be dependent on fire. Black pine woodlands in Corsica are a key example of such a fire-dependent system: a high-resolution charcoal record, together with plant macrofossils, has revealed that this fire-prone

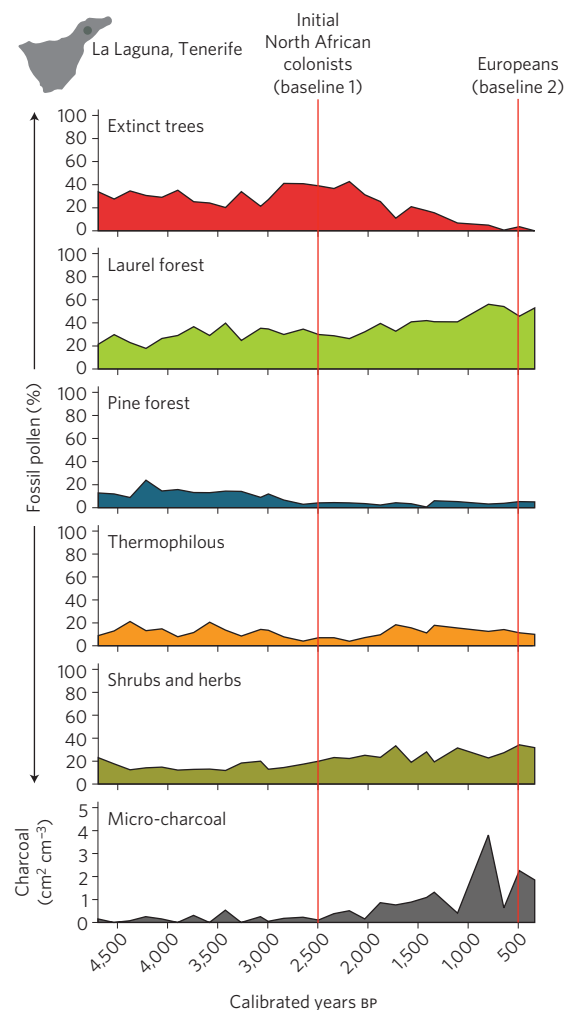


Figure 4 | Summary time-series from a sedimentary sequence from Tenerife (Canary Islands). We show the long-term dynamics of main Canarian vegetation types: extinct trees (for example, *Quercus* and *Carpinus*), laurel forest (for example, *Morella* and *Erica*), pine forest (for example, *Pinus canariensis*), thermophilous woodland (for example, *Juniperus* and *Phoenix*), and shrubs and herbs (for example, *Poaceae*). In addition, we show micro-charcoal counts to depict fire regimes. We have highlighted in red two obvious points for calculation of alternative baselines for La Laguna, Tenerife. Figure adapted with permission from ref. ³², Wiley-Blackwell (see original for full details).

ecosystem has persisted and very likely been favoured by frequent fires occurring on the island during the last 13,200 years, both under naturally ignited and human-induced fire regimes⁴⁹.

Herbivore density over time

The impacts of long-term herbivory by introduced taxa on island ecosystems remain the subject of debate^{50,51}. Several authors have argued for the eradication of non-native herbivores (for example, feral goats and rabbits) to promote the conservation of native vegetation^{52–54}. Others have argued that herbivory provides the only means to preserve certain cultural ecosystems, such as agroforestry systems that depart from the pre-human baseline but nonetheless are valued for biodiversity and/or cultural values⁵⁵. Herbivores can also be important ecosystem engineers on islands, altering fire and disturbance regimes through changes in availability of biomass^{17,56,57}, or helping to control plant invasions^{58,59}. It has been shown that eradication of introduced herbivores can be successful in many islands⁵³ with significant conservation benefits^{5,60}. However, in certain

contexts, the eradication or exclusion of non-native herbivores may entail some negative consequences, for example, through perverse outcomes such as the increase in rat populations and their associated impacts upon for example, nesting birds, seeds, and invertebrates⁶¹, or unexpected cascading effects facilitating the increase of invasive plant species⁵⁹. Therefore, techniques such as trapping, hunting, biocontrol, or any combination of them to remove herbivores from a particular site may be unsuccessful if not carefully coordinated and implemented^{62,63}. Finally, native herbivores also occur on many islands worldwide and their decline or extinction after human arrival has had consequences on ecosystem dynamics⁶⁴. Palaeoecological proxies (fossil pollen, fungal spores, faunal assemblages, aDNA (ancient DNA) in sediments, and coprolites) can provide information to help understand and manage both native and non-native herbivores in island ecosystems by:

- Determining whether large native herbivores (for example, tortoises, rodents and birds) have been extirpated in the past from some islands but introduced to others, and whether population fluxes and extinctions have been anthropogenic and/or natural in origin.
- Allowing the rate and pattern of herbivore introduction over time to be assessed²⁵.
- Demonstrating the long-term impact of changes in herbivore population on native ecosystems (for example, ref. ⁶⁵).

Determining when herbivores were introduced to an island is also relevant to understand the role of herbivory and its impact upon vegetation⁵⁶. In this context, the coprophilous genus of fungi *Sporormiella* provides a powerful tool to trace changing herbivory regimes and when coupled with fossil pollen records, the resulting impact on plant diversity^{18,65,66}. Spores of these dung-affiliated taxa are considered to be one of the most broadly applicable palaeoecological proxies for quantifying herbivore densities because of their low dispersal capacity^{66–68}. *Sporormiella* and other coprophilous fungi are useful for tracing mammalian herbivores on islands (for example, refs ^{65,69}), as well as native avian and reptile herbivores on islands that were almost free of terrestrial mammals before human arrival (for example all the Polynesian islands, Mauritius and Galápagos). *Sporormiella* has been successfully used to identify both native avian herbivores, and introduced herbivore presence in New Zealand peat records¹⁸, and it has been used in studies of the decline of giant tortoise populations in the Galápagos Islands, revealing the previously unappreciated impact of this decline on wetland habitats¹⁷. *Sphagnum* bogs currently found in the Galápagos uplands were revealed to have developed only over the past 500 years, replacing former open-water wetland habitats. *Sporormiella* data indicate that giant tortoises were formerly present at these sites. The authors postulate that wallowing tortoises helped maintain open water conditions; but as tortoise populations declined throughout the historic period, this led to a series of cascading ecological impacts with the conversion of wetlands to *Sphagnum* bogs and resultant deleterious impact on wetland-dependent species.

In many islands, early (pre-historic) human colonists introduced commensal mammals such as pigs (*Sus domesticus*), goats (*Capra hircus*), sheep (*Ovis aries*), rats (*Rattus* spp.), and rabbits (*Oryctolagus cuniculus*). These introductions typically had significant negative impacts on the vegetation^{32,70}, promoting increased erosion, and sometimes being implicated in the extinction of native fauna as, for example, species of avifauna in Macaronesia (for example, ref. ⁷¹), and of many small birds on Pacific islands^{72,73}. Native island herbivores usually fulfil an important role in their ecosystems, mostly by control of biomass, influencing landscape heterogeneity, seed-dispersal and nutrient cycling³. Whereas remote oceanic islands mostly lacked terrestrial mammals prior to human colonization, many less remote or past land-bridge islands did possess their own indigenous assemblages of terrestrial mammals (see ref. ⁷⁴). Many of these island herbivores experienced reduction of their population

size, population collapse, and extinction following human colonization. On theoretical and empirical grounds, we know that the removal (or addition) of a major trophic level or function has wide-ranging impacts on ecosystem process and form, often out of proportion to the number of extinctions initially involved. For example, palaeoecological studies from Mauritius show that the now extinct dodo and two species of giant tortoise lived in dense populations in the coastal lowlands⁷⁵. These populations experienced regular environmental hazards from tropical storms and seasonal droughts⁷⁶. A prolonged drought 4,200 years ago caused a mass death in the Mare aux Songes⁷⁶. This wetland was the primary source of drinking water in the southwest of the island, as open freshwater is scarce in the Mauritian lowlands due to its recent basaltic nature. In excess of 100,000 giant tortoise and dodos died within 100 years when decreased precipitation caused salinization and algal blooming. In another example from an Alaskan island, it has been shown that the extinction of the mammoth population on Saint Paul also related to diminished freshwater availability combined synergistically with shrinking island area and regional climate change, in this case entirely independently of and before human colonization⁷⁷. These examples show how larger vertebrate species, especially those of former land-bridge islands, have been subject to fluctuations in resources (especially related to water and island size), of large ecological impact, independent of human action. This also serves to highlight the importance of developing longer-term chronologies of changing island environments and carrying capacities in order to develop understanding of the resilience of insular fauna and systems to environmental change.

The future for integrating palaeoecology and conservation

It is apparent from the examples we have provided that the choice of baseline or reference condition could have significance for conservation targets and strategy, and that identification of multiple baselines and assessment of natural variability in response to past change should be important goals of conservation palaeoecologists^{8,19}. The complexity of managing island ecosystems varies depending on what baseline(s) is (are) used, and what goals are prioritized, for example: (1) a functioning and biodiverse ecosystem, (2) a particular cultural landscape, or (3) restoration of a pre-human ecosystem. This complexity opens an important knowledge gap, as many island ecosystem management decisions usually occur without knowledge of their pre-human vegetation and faunal baselines, and without a direct measure of ecosystem change through time¹⁴. In this context, the potential level of intervention and the associated implementation costs are unknown. For example, in Fig. 3 we illustrate the case of Poor Knights Islands in New Zealand where a complete compositional turnover from the pre-human baseline was reported, including the extirpation of a dominant conifer from the Podocarpaceae family (*Dacrydium cupressinum*) and a palm tree (*Rhopalostylis*). On this island, a novel (but native) and successional angiosperm-dominated forest (*Metrosideros*) is currently dominant and there is no modern equivalent of the pre-human conifer- and palm-dominated forests on any other northern offshore New Zealand island¹⁶. Although fossil pollen and aDNA data show that the current ecosystem is significantly altered from the pre-human baseline, in this case the analyses can be used to suggest that accepting the novel successional ecosystem with no further intervention may be more beneficial and cost-effective than trying to restore the vegetation to its pre-human baseline.

In addition, the notion that multiple baselines may each be valued and part of the cultural and biological heritage of an island and its peoples, and thus worthy of consideration by managers in a conservation and landscape management (and tourist and recreation) context is one that arguably deserves wider attention. Recently, an example was presented¹⁰ where palaeoecological data about past ecological states were integrated with traditional knowledge to help

island managers inform their restoration goals. This is relevant if we aim to recognize the long-term role of humans in re-shaping island ecosystems and that managing to conserve particular cultural landscapes may have a place within an overarching conservation strategy. Multiple baselines can guide managers interested in restoring some parts of their islands to pre-human vegetation baselines in order to enhance native biodiversity, while also allowing other areas to be developed for cultural purposes such as harvesting or traditional activities, which can also often be compatible with healthy populations of native species.

Palaeoecological records and the multiple baseline framework also help to inform the likely trajectories of future natural successions and to evaluate pre-human responses of the vegetation to natural disturbances⁷⁸. For example, detailed Holocene plant microfossils and sediment records can document the response of vegetation to a range of natural disturbances over time and allow these to be compared with the more recent impacts of human arrival on an island. As such records can reveal the time taken for successions to take place and for ecosystems to recover to their pre-disturbed state after a natural disturbance (for example, fire, storms, volcanism, etc.), they can provide important information about ecosystem resilience, especially when they have occurred under similar climatic conditions to the present⁷⁹. This is illustrated in the Poor Knights Island records, where the pre-human vegetation had a high β -diversity and the forest composition remained tightly homogeneous despite disturbance from volcanism¹⁶. In contrast, following human arrival, β -diversity declined and the vegetation composition not only diverged completely away from its pre-human baseline, but became highly variable, suggesting decreasing resilience to disturbance.

On Alexander Selkirk Island (Juan Fernández Islands, Chile), the palaeo-pollen records show that although the vegetation communities (for example, subalpine heath-shrubland) were highly dynamic over millennial-to-decadal timescales, all taxa persisted through periods of rapid and significant climate change, including the lowering of sea level by approx. 135 m at the Last Glacial Maximum. However, following European arrival in the sixteenth century, the next four centuries saw drastic reductions in native species abundance and diversity as a result of a novel fire regime and the introduction of goats, and of invasive plant species (for example, *Rumex acetosella*)⁸⁰. In a final example, palaeoecological records identified a clear link⁶⁵ between introduced mammalian herbivores and vegetation change in the dune system on the uninhabited sub-Antarctic Enderby Island, in the Auckland Islands archipelago⁶⁵. Here, in the nineteenth century, after humans introduced rabbits, pigs, goats, cattle and sheep, intense grazing pressure caused a rapid decline of palatable native tussock grasses (*Poa litorosa*) and megaherbs, which were replaced with an exotic sward community. As the dates of introduced animal eradications from the islands are known, and could be pinpointed in the age–depth profiles of the pollen and dung fungal spore records, cattle and rabbits could be identified as the key drivers of vegetation change. The records also showed that the native palatable species re-established within years of their removal from the island. These examples and many others appear to suggest a consistent impact on vegetation variability when humans settle islands. However, outcomes are varied and thus further research is needed to understand the links between vegetation change and specific drivers of change (for example, fires, invasive plant species and herbivory or a combination) of all three.

We have reviewed examples where palaeoecological records can, and should, be used to complement conservation strategies and management frameworks. Good sources of palaeoecological information are online databases such as Neotoma (<http://www.neotomadb.org>) and the European Pollen Database (<http://www.europeanpollendatabase.net/index.php>). These are continually growing as new data are organized and made available. Although the

availability of palaeoecological records for smaller and more remote endemic-rich islands is limited, the information can provide a solid first step to determine, for example, pre-human floral and faunal states, the category of invasive and native species, fire regimes, and the impacts of non-native herbivores. By our estimation, at least 155 fossil pollen datasets are currently publicly available from island ecosystems and there are many more faunal reconstructions from sediment and cave deposits. In addition, there is also a Global Charcoal Database (<https://www.paleofire.org/>), which includes 35 ‘palaeofire datasets’ from islands (Fig. 1).

To maximize the value of palaeoecological data in island conservation we need to incorporate the following considerations: (1) how to more effectively disseminate knowledge about the legacy of a landscape in a manner that will influence the design of planning frameworks for biodiversity conservation; and (2) the limitations of each palaeoecological proxy, such as low taxonomic and temporal resolution, and potential bias towards islands with suitable conditions for fossil preservation. Finally, we advocate establishing routine palaeoecological investigations involving fossil proxies and other biomarkers, as a key step in developing science-based evidence for biodiversity conservation plans for island ecosystems, whether focused on restoration, eradication or the acceptance of novel ecosystems^{81–83}. Such data can lead to a more flexible view on the management of future ecosystems that now include humans and their introduced taxa, and to better-informed debate on the type of nature to be conserved or restored.

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References

1. Caujapé-Castells, J. *et al.* Conservation of oceanic island floras: Present and future global challenges. *Persp. Plant Ecol. Evol. System.* **12**, 107–129 (2010).
2. Vitousek, P. M. Oceanic islands as model systems for ecological studies. *J. Biogeogr.* **29**, 573–582 (2002).
3. Kaiser-Bunbury, C. N., Traveset, A. & Hansen, D. M. Conservation and restoration of plant–animal mutualisms on oceanic islands. *Persp. Plant Ecol. Evol. System.* **12**, 131–143 (2010).
4. Kueffer, C. *et al.* A global comparison of plant invasions on oceanic islands. *Persp. Plant Ecol. Evol. System.* **12**, 145–161 (2010).
5. Jones, H. P. *et al.* Invasive mammal eradication on islands results in substantial conservation gains. *Proc. Natl Acad. Sci. USA* **113**, 4033–4038 (2016).
6. Avery, J. D., Fonseca, D. M., Campagne, P. & Lockwood, J. L. Cryptic introductions and the interpretation of island biodiversity. *Mol. Ecol.* **22**, 2313–2324 (2013).
7. Whittaker R. J. & Fernández-Palacios J. M. *Island Biogeography: Ecology, Evolution, and Conservation*. (Oxford Univ. Press, 2007).
8. Jackson, S. T. & Hobbs, R. J. Ecological restoration in the light of ecological history. *Science* **325**, 567–569 (2009).
9. Bellingham, B. J. *et al.* New Zealand island restoration: seabirds, predators, and the importance of history. *New Zeal. J. Ecol.* **34**, 115–136 (2010).
10. Lyver, P. O. B. *et al.* Looking back for the future: local knowledge and palaeoecology inform biocultural restoration of coastal ecosystems in New Zealand. *Hum. Ecol.* **43**, 681–695 (2015).
11. Burney, D. A. Tropical islands as paleoecological laboratories: gauging the consequences of human arrival. *Hum. Ecol.* **25**, 437–457 (1997).
12. Hobbs, R. J., Higgs, E. & Harris, J. A. Novel ecosystems: implications for conservation and restoration. *Trends Ecol. Evol.* **24**, 599–605 (2009).
13. Dietl, G. P. *et al.* Conservation paleobiology: leveraging knowledge of the past to inform conservation and restoration. *Annu. Rev. Earth Planet. Sci.* **43**, 79 (2015).
14. Gillson, L., Ladle, R. J. & Araújo, M. B. in *Conservation Biogeography* 31–44 (John Wiley & Sons, 2011).
15. Willis, K. J., Bailey, R. M., Bhagwat, S. A. & Birks, H. J. B. Biodiversity baselines, thresholds and resilience: testing predictions and assumptions using palaeoecological data. *Trends Ecol. Evol.* **25**, 583–591 (2010).
16. Wilmshurst, J. M. *et al.* Use of pollen and ancient DNA as conservation baselines for offshore islands in New Zealand. *Conserv. Biol.* **28**, 202–212 (2014).
17. Froyd, C. A. *et al.* The ecological consequences of megafaunal loss: giant tortoises and wetland biodiversity. *Ecol. Lett.* **17**, 144–154 (2014).
18. Wood, J. R., Wilmshurst, J. M., Worthy, T. H. & Cooper, A. *Sporormiella* as a proxy for non-mammalian herbivores in island ecosystems. *Quat. Sci. Rev.* **30**, 915–920 (2011).

19. Burney, D. A. & Burney, L. P. Paleoecology and “inter-situ” restoration on Kaua’i, Hawai’i. *Front. Ecol. Environ.* **5**, 483–490 (2007).
20. Callicott, J. B. The pragmatic power and promise of theoretical environmental ethics: forging a new discourse. *Environ. Values* **11**, 3–25 (2002).
21. van Leeuwen, J. F. N. *et al.* Fossil pollen as a guide to conservation in the Galápagos. *Science* **322**, 1206–1206 (2008).
22. Delisle, F., Lavoie, C., Jean, M. & Lachance, D. Reconstructing the spread of invasive plants: taking into account biases associated with herbarium specimens. *J. Biogeogr.* **30**, 1033–1042 (2003).
23. Cañellas-Boltà, N., Rull, V., Sáez, A., Prebble, M. & Margalef, O. First records and potential palaeoecological significance of *Dianella* (Xanthorrhoeaceae), an extinct representative of the native flora of Rapa Nui (Easter Island). *Veg. Hist. Archaeobot.* **23**, 331–338 (2014).
24. Froyd, C. A. & Willis, K. J. Emerging issues in biodiversity & conservation management: the need for a palaeoecological perspective. *Quat. Sci. Rev.* **27**, 1723–1732 (2008).
25. Willis, K. J. *et al.* How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. *Philos. Trans. R. Soc. Lon. B* **362**, 175–187 (2007).
26. Bean, A. R. A new system for determining which plant species are indigenous in Australia. *Aust. Syst. Bot.* **20**, 1–43 (2007).
27. Carlton, J. T. Biological invasions and cryptogenic species. *Ecology* **77**, 1653–1655 (1996).
28. Wilmshurst, J. M., McGlone, M. S. & Turney, C. S. M. Long-term ecology resolves the timing, region of origin and process of establishment for a disputed alien tree. *AoB Plants* **7**, plv104 (2015).
29. Benning, T. L., LaPointe, D., Atkinson, C. T. & Vitousek, P. M. Interactions of climate change with biological invasions and land use in the Hawaiian Islands: modeling the fate of endemic birds using a geographic information system. *Proc. Natl Acad. Sci. USA* **99**, 14246–14249 (2002).
30. Coffey, E. E. D., Froyd, C. A. & Willis, K. J. When is an invasive not an invasive? Macrofossil evidence of doubtful native plant species in the Galápagos Islands. *Ecology* **92**, 805–812 (2011).
31. de Boer, E. J. *et al.* Multi-proxy reconstruction of environmental dynamics and colonization impacts in the Mauritian uplands. *Palaeogeogr. Palaeoclim. Palaeoecol.* **383–384**, 42–51 (2013).
32. de Nascimento, L., Willis, K. J., Fernández-Palacios, J. M., Criado, C. & Whittaker, R. J. The long-term ecology of the lost forests of La Laguna, Tenerife (Canary Islands). *J. Biogeogr.* **36**, 499–514 (2009).
33. van Leeuwen, J. F. *et al.* Native or introduced? Fossil pollen and spores may say. An example from the Azores Islands. *Neobiota* **6**, 27–34 (2005).
34. Evans, J. *Pistia stratiotes* L. in the Florida Peninsula: biogeographic evidence and conservation implications of native tenure for an ‘invasive’ aquatic plant. *Conserv. Soc.* **11**, 233–246 (2013).
35. Rosati, L., Masi, A., Giardini, M. & Marignani, M. Under the shadow of a big plane tree: Why *Platanus orientalis* should be considered an archaeophyte in Italy. *Plant Biosyst.* **149**, 185–194 (2015).
36. Agudo, R., Rico, C., Vilà, C., Hiraldo, F. & Donazar, J. A. The role of humans in the diversification of a threatened island raptor. *BMC Evol. Biol.* **10**, 384 (2010).
37. Roebroeks, W. & Villa, P. On the earliest evidence for habitual use of fire in Europe. *Proc. Natl Acad. Sci. USA* **108**, 5209–5214 (2011).
38. Rolett, B. & Diamond, J. Environmental predictors of pre-European deforestation on Pacific islands. *Nature* **431**, 443–446 (2004).
39. Conedera, M. *et al.* Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. *Quat. Sci. Rev.* **28**, 555–576 (2009).
40. Scott, A. C., Hardiman, M., Pinter, N. & Anderson, R. S. Evidence of fire regimes in the Pleistocene of the California Islands. *SAGVNTVM Extra* **11**, 59–60 (2011).
41. Iglesias, V., Yospin, G. I. & Whitlock, C. Reconstruction of fire regimes through integrated paleoecological proxy data and ecological modeling. *Front. Plant Sci.* **5**, 785 (2015).
42. Gil-Romera, G. *et al.* Biomass-modulated fire dynamics during the Last Glacial–Interglacial Transition at the Central Pyrenees (Spain). *Palaeogeogr. Palaeoclim. Palaeoecol.* **402**, 113–124 (2014).
43. Perry, G. L. W., Wilmshurst, J. M., Ogden, J. & Enright, N. J. Exotic mammals and invasive plants alter fire-related thresholds in southern temperate forested landscapes. *Ecosystems* **18**, 1290–1305 (2015).
44. Brooks, M. L. *et al.* Effects of invasive alien plants on fire regimes. *BioScience* **54**, 677–688 (2004).
45. McWethy, D. B. *et al.* Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. *Proc. Natl Acad. Sci. USA* **107**, 21343–21348 (2010).
46. McWethy, D. B., Wilmshurst, J. M., Whitlock, C., Wood, J. R. & McGlone, M. S. A high-resolution chronology of rapid forest transitions following Polynesian arrival in New Zealand. *PLoS ONE* **9**, e111328 (2014).
47. Perry, G. L. W., Wilmshurst, J. M., McGlone, M. S. & Napier, A. Reconstructing spatial vulnerability to forest loss by fire in pre-historic New Zealand. *Glob. Ecol. Biogeogr.* **21**, 1029–1041 (2012).
48. Higuera-Gundy, A. *et al.* A 10,300 ¹⁴C yr record of climate and vegetation change from Haiti. *Quat. Res.* **52**, 159–170 (1999).
49. Leys, B., Finsinger, W. & Carcaillet, C. Historical range of fire frequency is not the Achilles’ heel of the Corsican black pine ecosystem. *J. Ecol.* **102**, 381–395 (2014).
50. Garzón-Machado, V., del-Arco-Aguilar, M. J. & Pérez-de-Paz, P. L. Threat or threatened species? A paradox in conservation biology. *J. Nat. Conserv.* **20**, 228–230 (2012).
51. Bowen, L. & Vuren, D. V. Insular endemic plants lack defenses against herbivores. *Conserv. Biol.* **11**, 1249–1254 (1997).
52. Fraser, I. & Chisholm, T. Conservation or cultural heritage? Cattle grazing in the Victoria Alpine National Park. *Ecol. Econ.* **33**, 63–75 (2000).
53. Campbell, K. & Donlan, C. J. Feral goat eradication on Islands. *Conserv. Biol.* **19**, 1362–1374 (2005).
54. Garzón-Machado, V. *et al.* Strong negative effect of alien herbivores on endemic legumes of the Canary pine forest. *Biol. Conserv.* **143**, 2685–2694 (2010).
55. Peco, B., Sánchez, A. M. & Azcárate, F. M. Abandonment in grazing systems: consequences for vegetation and soil. *Agr. Ecosyst. Environ.* **113**, 284–294 (2006).
56. Burney, D. A., Robinson, G. S. & Burney, L. P. *Sporormiella* and the late Holocene extinctions in Madagascar. *Proc. Natl Acad. Sci. USA* **100**, 10800–10805 (2003).
57. Gill, J. L., Williams, J. W., Jackson, S. T., Lininger, K. B. & Robinson, G. S. Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America. *Science* **326**, 1100–1103 (2009).
58. Hansen, D. M. Non-native megaherbivores: the case for novel function to manage plant invasions on islands. *AoB Plants* **7**, plv085 (2015).
59. Chapuis, J. L. *et al.* Eradication of invasive herbivores: usefulness and limits for biological conservation in a changing world. *Anim. Conserv.* **14**, 471–473 (2011).
60. Schweizer, D., Jones, H. P. & Holmes, N. D. Literature review and meta-analysis of vegetation responses to goat and European rabbit eradications on islands. *Pacific Sci.* **70**, 55–71 (2015).
61. Innes, J. *et al.* Effect of grazing on ship rat density in forest fragments of lowland Waikato, New Zealand. *New Zeal. J. Ecol.* **34**, 227–232 (2010).
62. Veitch, C.R. & Clout, M. N. (eds) *Turning the Tide: The Eradication of Invasive Species* (IUCN, 2002).
63. Bergstrom, D. M. *et al.* Indirect effects of invasive species removal devastate World Heritage Island. *J. Appl. Ecol.* **46**, 73–81 (2009).
64. Hansen, D. M., Donlan, C. J., Griffiths, C. J. & Campbell, K. J. Ecological history and latent conservation potential: large and giant tortoises as a model for taxon substitutions. *Ecography* **33**, 272–284 (2010).
65. Wood, J. R., Wilmshurst, J. M., Turney, C. S. M. & Fogwill, C. J. Palaeoecological signatures of vegetation change induced by herbivory regime shifts on subantarctic Enderby Island. *Quat. Sci. Rev.* **134**, 51–58 (2016).
66. Baker, A. G., Bhagwat, S. A. & Willis, K. J. Do dung fungal spores make a good proxy for past distribution of large herbivores? *Quat. Sci. Rev.* **62**, 21–31 (2013).
67. Davis, O. K. Spores of the dung fungus *Sporormiella*: increased abundance in historic sediments and before Pleistocene megafaunal extinction. *Quat. Res.* **28**, 290–294 (1987).
68. Gill, J. L. *et al.* Linking abundances of the dung fungus *Sporormiella* to the density of bison: implications for assessing grazing by megaherbivores in palaeorecords. *J. Ecol.* **101**, 1125–1136 (2013).
69. Raczka, M. F., Bush, M. B., Folcik, A. M. & McMichael, C. H. *Sporormiella* as a tool for detecting the presence of large herbivores in the Neotropics. *Biota Neotropica* **16**, e20150090 (2016).
70. Athens, J. S. *Rattus exulans* and the catastrophic disappearance of Hawai’i’s native lowland forest. *Biol. Invasions* **11**, 1489 (2008).
71. Illera, J. C., Rando, J. C., Richardson, D. S. & Emerson, B. C. Age, origins and extinctions of the avifauna of Macaronesia: a synthesis of phylogenetic and fossil information. *Quat. Sci. Rev.* **50**, 14–22 (2012).
72. Steadman, D. W. *Extinction and Biogeography of Tropical Pacific Birds* (Univ. Chicago Press, 2006).
73. Taylor, R. H. How the Macquaire island parakeet became extinct. *New Zeal. J. Ecol.* **2**, 42–45 (1979).
74. Lomolino, M. V. *et al.* Of mice and mammoths: generality and antiquity of the island rule. *J. Biogeography* **40**, 1427–1439 (2013).
75. Rijdsdijk, K. F. *et al.* A review of the dodo and its ecosystem: insights from a vertebrate concentration Lagerstätte in Mauritius. *J. Vert. Paleontol.* **35**, 3–20 (2015).
76. de Boer, E. J. *et al.* A deadly cocktail: how a drought around 4200 cal. yr BP caused mass mortality events at the infamous ‘dodo swamp’ in Mauritius. *Holocene* **25**, 758–771 (2015).

77. Graham, R. W. *et al.* Timing and causes of mid-Holocene mammoth extinction on St. Paul Island, Alaska. *Proc. Natl Acad. Sci. USA* **113**, 9310–9314 (2016).
78. Wilmshurst, J. M., McGlone, M. S. & Partridge, T. R. A late Holocene history of natural disturbance in lowland podocarp/hardwood forest, Hawke's Bay, New Zealand. *New Zeal. J. Bot.* **35**, 79–96 (1997).
79. Wilmshurst, J. M., McGlone, M. S., Leathwick, J. R. & Newnham, R. M. A pre-deforestation pollen-climate calibration model for New Zealand and quantitative temperature reconstructions for the past 18 000 years BP. *J. Quat. Sci.* **22**, 535–547 (2007).
80. Haberle, S. G. Late Quaternary vegetation dynamics and human impact on Alexander Selkirk Island, Chile. *J. Biogeogr.* **30**, 239–255 (2003).
81. Gillson, L. & Marchant, R. From myopia to clarity: sharpening the focus of ecosystem management through the lens of palaeoecology. *Trends Ecol. Evol.* **29**, 317–325 (2014).
82. McCarroll, J., Chambers, F. M., Webb, J. C. & Thom, T. Using palaeoecology to advise peatland conservation: An example from West Arkengarthdale, Yorkshire, UK. *J. Nat. Conserv.* **30**, 90–102 (2016).
83. Barnosky, A. D. *et al.* Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. *Science* <http://doi.org/10.1126/science.aah4787> (2017).

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Author contributions

S.N. lead the Perspective and wrote the paper together with all authors: L.d.N., C.F., J.M.W., E.J.d.B., E.E.D.C., R.J.W., J.M.F.P. and K.J.W. All authors contributed in the discussion.

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Competing interests

The authors declare no competing financial interests.