Conservation Palaeoecology

The application of palaeoecological research in the conservation and restoration of oceanic islands

"Earth is now nowhere pristine. Human economics, politics, demographics and chemicals pervade every ecosystem."
- Sandom et al., 2013

"Human arrogance toward nature ... has carved deep gashes in the landscape and defined our modern environmental history."
- Minteer & Collins, 2010

"Everything that should not be done to an island has been done to Mauritius. Except, perhaps, nuclear testing."
- Adams & Cawardine, 1990

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1 Introduction

1.1 *The importance of protecting and restoring island ecosystems*

Global climate is changing at the hands of many human-mediated processes, such as the release of greenhouse gasses into the Earth's atmosphere (IPCC, 2013). These processes may affect local, or global, ecosystems directly (e.g. the collapse of fish populations due to overfishing; Rose, 2004; Jackson *et al*., 2001) or indirectly (e.g. climatic change leading to increased extinction risk; Thomas *et al*., 2004). The indirect influence of anthropogenic activity on continental flora and fauna may be partially mitigated by migration into newly suitable habitats (Walther *et al*., 2002), yet this is entirely dependent on the migratory capacity of individual species – meaning that some species may be 'too slow' to survive (Pearson, 2006). The ability of undergoing appropriate range shifts with regard to changes in global climate may be affected by several factors, such as the natural rate of migration, environmental tolerance, or even anthropogenic barriers causing landscape fragmentation (Honnay *et al*., 2002). However, range shifts will be a problem in island ecosystems which often do not allow for migration over long distances.

Global climatic change is not the only problem faced by island ecosystems. The flora and fauna present on islands are more than often directly endangered as a result of human activities (Burney *et al*., 2004; Burney & Flannery, 2005), including overexploitation (e.g. by hunting), habitat modification (e.g. agriculture; Gillespie *et al*., 2008), and invasive species (Traveset & Richardson, 2006; Kaiser-Bunbury *et al*., 2010). This has led to native island species overrepresented on the IUCN Red List of threatened taxa. The protection of flora and fauna is not only important for the sake of maintaining biodiversity, as these systems also offer ecosystem services (Sandom *et al*., 2013) and act as natural laboratories for studying ecological and evolutionary processes due to their small size and relatively simple ecosystems (Gillespie *et al*., 2008). There are several oceanic islands with particularly high rates of endemism (Kier *et al*., 2009; figure 1) where many of these unique species are being lost due to the presence of human influences (Florens, 2014). The incredible scope of potential losses of biodiversity becomes evident when considering that islands cover only five percent of the Earth's land surface, yet hold a quarter of the planet's endemic vascular plants (Kreft *et al*., 2008) which means they contain the highest number of endemics per unit area (Caujapé-Castells *et al*., 2010), or that 20 out of 34 biodiversity hotspots are islands (Myers *et al*., 2000). Many species are threatened, but others have unfortunately already gone extinct, and out of some 80 documented extinctions in the past 400 years, about 50 occurred on islands (Sax & Gaines, 2008). The global loss of biodiversity is a problem on both islands and continents, but island ecosystems should be a priority as they are more threatened than continents (Kier *et al*., 2009).

One example of how global climate change is a threat to island ecosystems, is that of rising sea-levels. The size of islands is a major factor in their resilience against global climate change (Caujapé-Castells *et al*., 2010), with habitat loss acting as one of the primary threats to island resilience and biodiversity (Brooks *et al*., 2002). This habitat loss may occur directly or indirectly. Direct loss of habitat may occur due to human intervention of the ecosystem, but could also occur due to the predicted increases in sea levels (Wetzel *et al*., 2012). Increasing sea levels could also indirectly affect habitat loss, as human refugees (as a result of increased sea levels) may have to create new habitat for themselves where there formerly was none. This is but one of many dangers potentially affecting island ecosystems.

Among these severely endangered islands, or archipelagos, are the Canary Islands, the Hawaiian Islands, the Galápagos Islands, Madagascar, Mauritius, and New

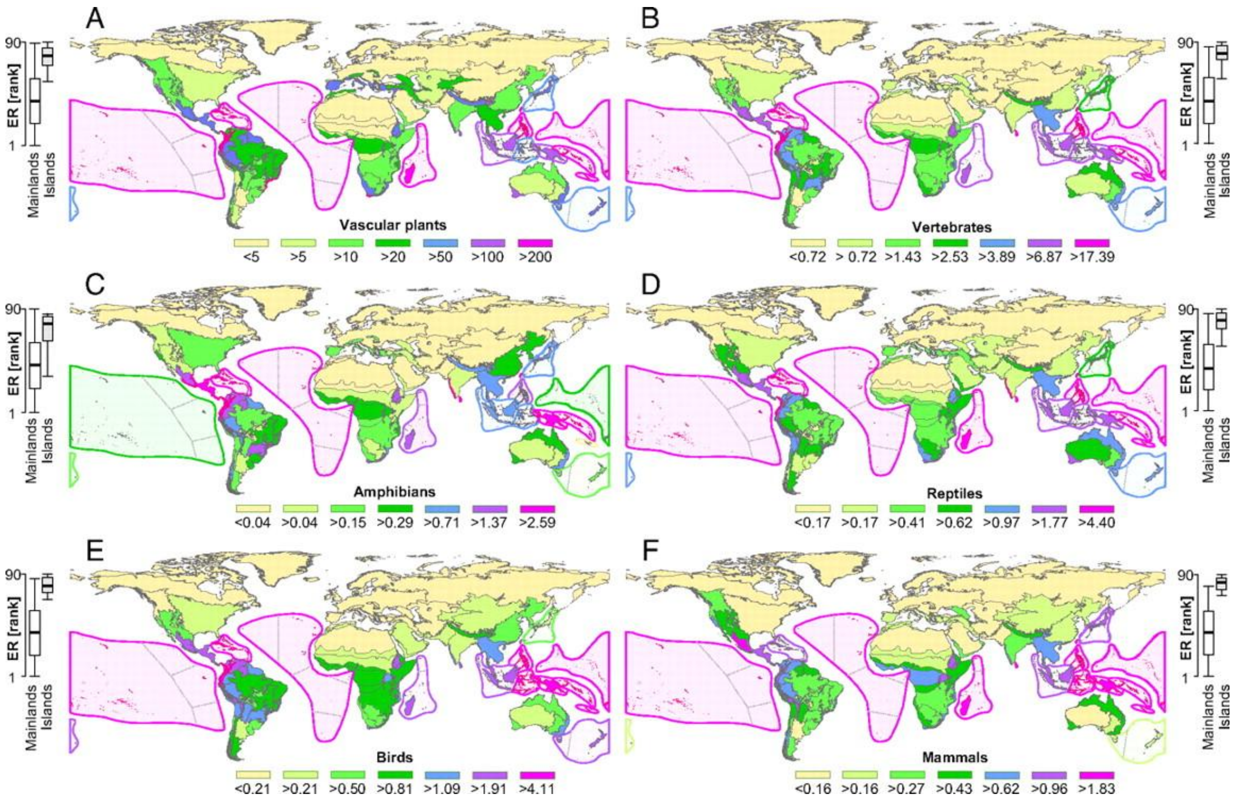

Figure 1. Geographic distribution of endemism richness for (**A**) vascular plants, (**B**) terrestrial vertebrates, (**C**) amphibians, (**D**) reptiles, (**E**) birds and (**F**) mammals across the world. A similar number of regions is contained within each colour class. Rank-based differences in endemic species richness are displayed by the box-and-whisker-plots for the mainland (white) and island regions (gray). Figure adapted from Kier *et al*. (2009).

Zealand (table 1). This thesis addresses several key questions concerning the conservation and restoration of oceanic island ecosystems. Its aim is to assess the potential of incorporating new fields of research, primarily palaeoecology, into nature conservation and promote the use of these novel applications to improve upon current conservation and restoration efforts.

This thesis will start off with an analysis of the current state of island ecosystems, followed by a description of how palaeoecology may be integrated into existing conservation networks, examples of current issues in conservation biology, how both recent and future palaeoecological studies will and might contribute to the conservation and restoration of island ecosystems, and will finally conclude with a summary and call-to-arms.

1.2 *The current state of island ecosystems*

1.2.1 *The Canary Islands*

The native flora of the Canary islands, just off the northwest coast of continental Africa, contains over 680 endemic taxa, comprising over half of the total native flora (Reyes-Betancort *et al*., 2008). Despite current efforts of protecting the remaining natural vegetation in the Natura 2000 network and national reserves, some of the vegetation has already declined to a point where only little possibility of recovery remains (Aguilar *et al*., 2010). Several taxa of the endangered endemic flora are increasingly being threatened by goats (*Capra hircus*), muflon (*Ovis aries musimon*), rabbits (*Oryctolagus cuniculus*) and ground squirrels (*Atlantoxerus getulus*) introduced to the islands. The impact of these introduced

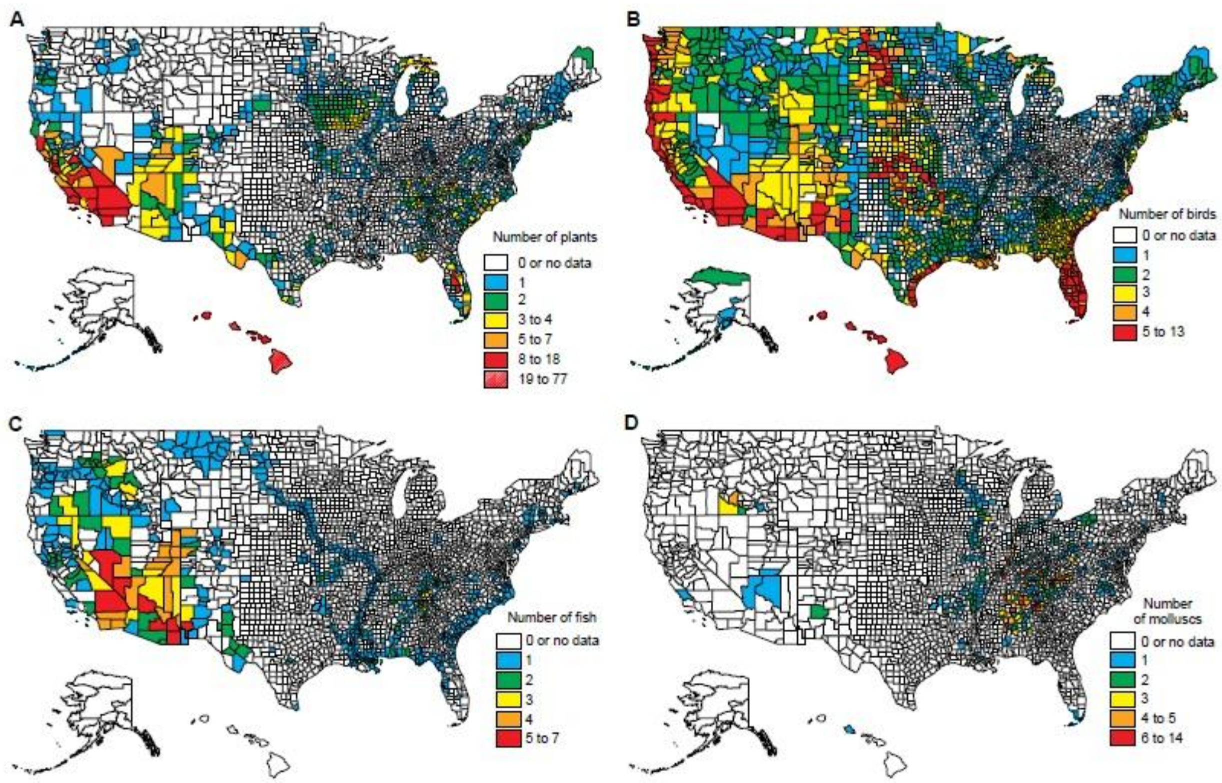

Figure 2. The geographic distribution of endangered species across the United States: (**A**) Plants, (**B**) birds, (**C**) fish, and (**D**) mollusks. The bottom left-hand corner shows Alaska and Hawaii. Adapted from Dobson *et al.* (1997).

animals may seem negative, but their carcasses help maintain three endangered bird subspecies endemic to the Canary Islands (Gangoso *et al*., 2006). These birds likely relied on carcasses of species which have now gone extinct, possibly due to human influences. Removing these harmful species from the ecosystem is still recommended, as long as they are replaced by extant taxa which may fulfill a similar function without endangering the ecosystem. This particular situation describes a conflict of interest between agricultural and conservation viewpoints, as the number of goats keeps increasing via funding by the European Common Agricultural Policy, yet European LIFE projects provide funding for the conservation of endemics – a conflict that has yet to be resolved (Gangoso *et al*., 2006). On a more positive note, the Natura 2000 network and the local natural reserves cover almost half of the islands' surface, causing several of the more prominent vegetation types to recover slowly (Aguilar *et al*., 2010).

Finally, one example of the endangered fauna on the islands is that of the Egyptian vulture (*Neophron percnopterus*). This bird of prey now relies on high preadult survival for maintaining a viable population, as many adults are killed by power lines, lead accumulation (lead shot during hunting season), and poisoning as an indirect effect of human persecution of possible livestock predators (Donázar *et al*., 2002). The locals would have to reconsider certain power lines and adjust their hunting habits to lower adult mortality, and maintain a considerable distance to the breeding grounds to allow for preadult survival.

The flora and fauna of the Canary Islands are precious and require protection, and despite current efforts to protect the native taxa, a more active approach may be necessary in the restoration of this archipelago.

1.2.2 *The Hawaiian Islands*

In the Pacific Ocean halfway between Japan and the United States, the Hawaiian Islands comprise an archipelago far less fortunate in terms of conservation (figure 2). These islands are a hotspot for bird and plant taxa, many of which are endemic to this island chain, and they are also home of the greatest number of endangered species in the United States (Dobson *et al.,* 1997). The exact number of endangered species, and the pressure they are under, differs between the islands (e.g. smaller islands contain a higher proportion of endemic taxa at risk). Many of the islands experience anthropogenic influences, ranging from the introduction of alien species to the loss of crucial habitat (Sakai *et al*., 2002). While predation and landscape change by humans have most certainly taken a toll on the islands, it is the indirect influence of mankind which has harmed the archipelago's native biodiversity most (Burney & Burney, 2007).

Similar to the Canary Islands, introduced species on the Hawaiian Islands seemingly threaten many of the native flora and fauna. While plants are mostly at risk from goats and pigs (*Sus scrofa*), the animals of the archipelago are hunted by pigs, rodents, feral dogs (*Canis familiaris*) and cats (*Felis domesticus*), and the mongoose (*Herpestes auropunctatus*; Loope *et al*., 1988). All of this pressure on the ecosystem has led to the extinction of nine percent of the 1159 native plant taxa, and 52.5% of those that still remain are now at risk (Sakai *et al*., 2002). To prevent invasive plants from getting the upper hand in this struggle for survival, several plans have been made with the government and locals to manage the spread of invasive species and protect the native populations. These plans include assessments of introduced species, biological control of the invasive species, actively working to chemically and mechanically protect local populations of native plants, and the education at a high-school level to promote the understanding of island ecosystems and stimulating actively taking part in the preservation of native flora (Loope *et al*., 2004).

The conservation of the Hawaiian native populations of both plants and animals (birds in particular) is seemingly underway, yet it is likely not without its problems. Current efforts seem to focus on maintaining current populations and managing the abundance of introduced species, and therefore the next step should be to restore some of the lost taxa and ecological interactions. However, determining how to efficiently restore an ecosystem might require the application of novel methods and fields of research.

1.2.3 *The Galápagos Islands*

The Galápagos Islands form an archipelago roughly 925 kilometres to the west of continental Ecuador and are well known for the scientific expeditions of Charles Darwin. Before the island was permanently colonized, it had been a transient home to Incas, pirates, and whalers. The Galápagos archipelago was first colonized in the early 19th century, which by human standards may be considered relatively late. The islands have not experienced the brunt of the destructive capabilities of mankind, though our influence is definitely affecting the Galápagos. While it is currently not as threatened as some of the world's other island systems yet, it seems to be well underway (Snell *et al*., 2002). The hunt for several of the native animals has had a definite negative impact on the fauna of the Galápagos since before the islands were colonized, as nearby whaling ships would take from the islands whatever they deemed necessary. Despite much of the surface of the Galápagos Islands being protected, illegal hunting persists to this day. For example, the mortality of giant tortoises by poaching exceeds natural mortality, which is a large threat to these long-lived and slow-reproducing animals (Márquez *et al*., 2007). Furthermore, shark populations in the

Galápagos Marine Reserve are at risk due to illegal fishing activities (Carr *et al*., 2013).

Yet not all threats are caused by illegal activities, as several additions to the island fauna by humans are a cause for concern (Loope *et al*., 1988). These include goats which threaten much of the native plant life, and the introduced pigs damage both plant life and eat the eggs of tortoises (*Geochelone elephantopus*), Pacific green turtles (*Chelonia mydas agassizii*), and marine and land iguanas (*Amblyrhynchus cristatus* and *Conolophus* spp.). The introduction of black rats (*Rattus rattus*) has had a negative impact on dark-rumped petrels (*Pterodroma phaeopygia*), rice rats (*Oryzomis* spp.), and tortoises by killing their young. Before their population control started, feral dogs were considered serious predators on the Galápagos Islands, where they fed on marine and land iguanas, fur seals (*Arctocephalus australis*), blue-footed boobies (*Sula nebouxi*), and penguins (*Spheniscus mendiculus*). The giant tortoises of the Galápagos are arguably the most endangered of all the fauna on this islands, which has had its impact on the habitat types found on the islands due to their function as the only large native herbivore (Froyd *et al*., 2014).

Considering all of these direct and indirect paths by which humans have affected organisms native to the Galápagos, it becomes apparent that there is a definite need for the protection and restoration of some of the flora and fauna. Poaching will likely have to be resolved by increasing numbers of security guards on the islands. Additionally, it has been difficult to establish a baseline for the Galápagos Islands, as historical records do not go back very far. Conservationists will have to take new methods into consideration to learn more about the past ecosystems of the Galápagos.

1.2.4 *Madagascar*

Slightly east of Mozambique, across the Mozambique Channel, lies the island nation of Madagascar. It is the fourth-largest island in the world and is considered one of the 'hottest' biodiversity hotspots (Myers *et al*., 2000). Roughly 90% of (vascular) plants and vertebrates found on the island are endemic and are hence found nowhere else in the world (Goodman & Benstead, 2005). The pressure exerted by centuries of human predation and habitat modification on large, endemic animals is high, and several periods of human activity (i.e. first arrival, establishment of settlements, European arrival) coeval with large declines in the native fauna (Crowley, 2010). These anthropogenic factors, along with competition for resources with the introduced cattle, have heavily impacted the megafauna of Madagascar.

The effects of the human presence may have been amplified by several droughts occurring in the late Holocene (2,500 years BP – present), which illustrate the increasingly arid conditions on the island (Virah-Sawmy *et al*., 2010). It is unfortunate that the anthropogenic forces which once likely led to the demise of several now-extinct taxa persist to this very day. Among these forces is a mining operation for ilmenite in southeastern Madagascar, which destroys much of the native forest. This has been allowed to continue due to the assumption that the patchy, heterogeneous nature of the forest has been achieved through human impacts, yet a recent study shows that the local ecosystem is dynamic and has maintained this heterogeneous landscape for millennia (Virah-Sawmy *et al*., 2009a). The continued degradation of this area would therefore serve only to destroy a native littoral forest with high concentrations of precious endemic plant life.

Much of contemporary Madagascar has been heavily impacted by humans and its future as a biodiversity hotspot relies on halting of hunting and illegal trafficking, and the fragmentation and loss of forest cover (Dewar & Richard, 2012). Determining what the 'natural' state of Madagascar is in its current predicament is difficult, and will therefore require the integration of methods

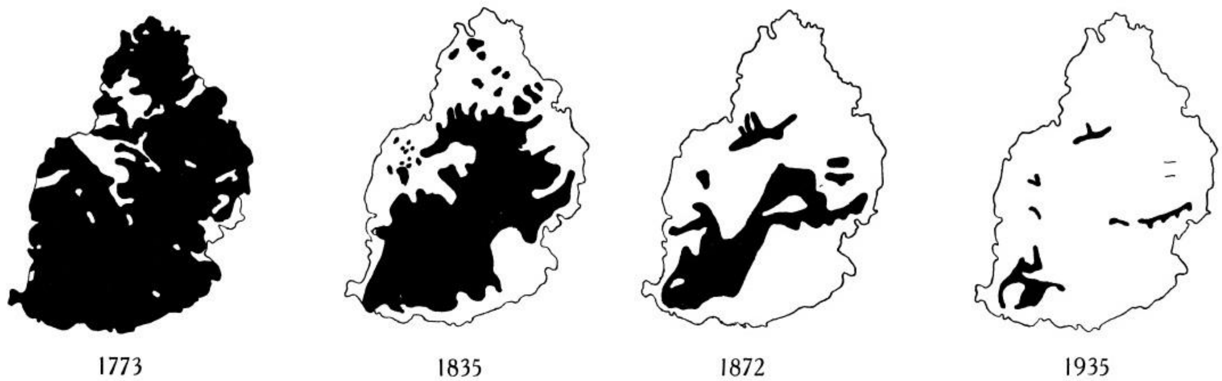

Figure 3. A map showing the distribution of indigenous forests (black) across Mauritius over time. Adapted from Vaughan & Wiehe (1937).

which look back before the arrival of humans on its shores.

1.2.5 *Mauritius*

Roughly 2,000 kilometres off the southeast coast of the African continent, just east of Madagascar, lies a small island nation by the name of Mauritius, former home of the extinct Dodo (*Raphus cucullatus*). The island remained uninhabited until the arrival of the Dutch Republic in 1638 CE, by whom the first colony was established and the island was given its current name. Not much is known about the natural vegetation on the island as it took the inhabitants of Mauritius (i.e. the Dutch, French and British) less than four centuries to almost completely deforest the island (figure 3; De Boer, 2014a). The remaining knowledge about the Mauritian flora came mostly from old ship logs and what little pristine vegetation remained until recent reconstructions of past vegetation and climate were carried out (De Boer, 2014, PhD thesis).

Characteristic of human arrival on islands is the introduction of several invasive species, often along with other anthropogenic influences such as landscape modification. The arrival of the Dutch did indeed coincide with the appearance of several exotic plant taxa, such as pine (*Pinus* spp.), tea (*Camellia sinensis*) and sugar cane (*Saccharum officinarum*; De Boer *et al*., 2013a). However, the Mauritian flora was not the only group affected by the human presence. The fauna of Mauritius suffered at the hands of humans as well, be it via habitat loss or through hunting. Two of the most famous examples are those of the Dodo and the giant *Cylindraspis* tortoises, both of which are now extinct. It is likely that the Dodo was unable to cope with the overharvesting by the colonists and the introduction of rats and pigs which ate its eggs, thereby leading to the downfall of the Dodo (De Boer *et al*., in press). Not much is known about the Dodo's ecology and feeding habits, therefore the effects of the Dodo extinction on the Mauritian ecosystem remain a mystery. Large herbivores are known to play an important role in ecosystems in their interactions with plants, including pollination, maintaining certain ecotopes via population control, and seed dispersal (Kaiser-Bunbury *et al*., 2010). The loss of giant tortoises and Dodos as the primary large herbivores is therefore likely to have led to further extinctions of several plant and animal taxa, whose absence has left a functional gap ever since their extinction.

Most of Mauritius' natural vegetation has already been lost to time at the hands of the human colonists and the invasive organisms they brought with them, and restoring the ecosystem to its original state will prove nearly impossible. The restoration of the ecosystem to a functioning state similar to the original will be a difficult, but possible, alternative. Combining information regarding past conditions with current conservation strategies may prove necessary for the effective restoration of Mauritius, where reestablishing ecological interactions may take priority over reconstructing the exact species composition.

1.2.6 *New Zealand*

Another biodiversity hotspot can be found 1,500 kilometres east of Australia, the island nation of New Zealand. It was colonized by humans relatively late and its native flora and fauna therefore had enough time to develop. Yet, as is the case with many other islands, the plant life has been deteriorating ever since the exposure to humans. Several taxa have already gone extinct (6 taxa) and an increasing number of plants is classified as 'threatened' (180 taxa) or 'at risk' (651 taxa; De Lange *et al*., 2008). The indigenous birds of New Zealand are not faring much better (Miskelly *et al*., 2008) with 20 extinct, 77 threatened, 93 at risk, and only 36 not threatened taxa. The reasons for such biodiversity loss vary across taxa, but habitat loss or fragmentation and other human impact factors are likely to be the main culprits. Introduced species are among the main threats to native taxa, be it bird or plant. In the case of the kaka *Nestor meridionalis*, an endemic forest parrot, both introduced wasps and mammals which pose a threat (Beggs & Wilson, 1991). The kaka feeds mostly on honeydew excreted by the scale insect *Ultracoelostoma assimile*. The introduced wasps also consume the honeydew and in autumn their numbers are so great that no honeydew remains for the kaka. The lack of energy that results from this lowers their reproductive rate and the chicks of those that do reproduce are at risk of being predated by (introduced) stoats (*Mustela erminea*). This is but one of many example of how invasive species are threatening indigenous animals, and will eventually drive them to extinction if we do not intervene.

The over-exploitation of terrestrial communities, overharvesting of marine ecosystems, introduction of exotic organisms, and habitat destruction have ravaged much of the New Zealand ecosystem (Towns & Ballantine, 1993). Conservation efforts now focus on protecting species and habitats, and attempts to eradicate pests from the islands to allow recovery of native flora and fauna.

Table 1. Details of each island (group), including the approximate time of colonization by the indigenous people, the Europeans, and current major threats to biodiversity.

	Colonization by natives	*European colonization*	*Major threats*
Canary Islands	1000 BCE	15th century* *no exact date known	Introduced flora & fauna Agriculture Human habitation and infrastructure
Hawaiian Islands	300 CE	1778 CE	Introduced flora & fauna Human habitation and infrastructure
Galápagos Islands	N/A	1832 CE	Introduced flora & fauna (Illegal) hunting
Madagascar	490 CE	1894 CE	Introduced fauna (Illegal) hunting Mining operations
Mauritius	N/A	1638 CE	Introduced flora & fauna Agriculture Human habitation & infrastructure (Illegal) hunting
New Zealand	1280 CE	1822 CE	Introduced flora & fauna Human habitation & infrastructure (Illegal) hunting

Unfortunately, these efforts come too late for some species, and their loss may have disrupted certain ecological interactions.

Establishing a baseline of which taxa occurred in the past, along with the ecological interactions they are likely to have supported, will be necessary to formulate new and appropriate plans for the restoration of New Zealand.

1.3 *The integration of palaeoecology in the conservation and restoration of islands*

Palaeoecology is the study of fossils and subfossils for the purpose of reconstructing the ecosystems of the past. These (sub)fossils are often acquired from sediment cores recovered from lakes, wetlands or bogs, where sedimentary layers have been deposited over the course of centuries, millennia or even longer. Many different types of (sub)fossils, or proxies, can be found within these sediments, and each one has its own uses. For example, subfossil pollen may be used to infer regional climate by reconstructing past vegetation (Van Geel *et al*., 2010), whereas the subfossil head capsules of larval Chironomidae (non-biting midges) are used to accurately estimate past temperatures (Heiri *et al*., 2007) or lake depth (Engels *et al*., 2012). It is even possible to utilize biomarkers in determining local conditions (Van Bentum *et al*., 2009) or identifying the presence of certain animal groups (Van den Bos *et al*., 2014). These proxies allow palaeoecologists to provide a reliable, long-term record of past ecosystem dynamics and climate change (Willis *et al*., 2007), especially in high-resolution multi-proxy studies. The use of these long-term records therefore provide conservationists with an extension of historical accounts, as they are based on empirical evidence and therefore far more reliable.

The conservation and restoration of ecosystems to their former states relies on several key factors which should be taken into consideration: what is 'natural' (Willis & Birks, 2006), what is an ecosystem's baseline (e.g. Nascimento *et al*., 2009), how dynamic is that baseline (e.g. Willis *et al*., 2010; Seddon *et al*., 2011), and what were the most important

Box 1 Terminology

Natural (state)	The state wherein an ecosystem is able to sustain itself without human intervention and approximates pre-human conditions, including ecological interactions and containing most remaining native taxa.
(Re)introduction	The addition of formerly native or non-native plants and animals to an ecosystem.
Native, indigenous	The current or past plant and animal inhabitants of an island, whose range is not limited to the island.
Endemic	The current or past plant and animal inhabitants of an island, which are unique to that island.
Non-native, exotic	The taxa introduced directly or indirectly by human exposure, the ranges of which did not originally include the island.
Invasive	Introduced plant or animal taxa which proliferate rapidly within the new environment and are able to outcompete and endanger the native flora and/or fauna.
Ecological or plant-animal interactions	Interactions between plants, animals, or plants and animals which are crucial to maintaining the natural state of an ecosystem. These include seed dispersal, pollination, grazing, and more.
(Dynamic) baseline	An ecosystem's composition of plant and animal life in the absence of human impact, also referred to as pre-human conditions. These may be dynamic as ecosystems respond to changing conditions, such as global climate change, local hydrological shifts, etc.
Keystone species	A species that has a far greater effect on its environment relative to other species. Such species may play a critical role in maintaining an ecosystem as they affect many other organisms.

ecosystem processes at that time (e.g. Wood *et al.*, 2013)? Palaeoecological records spanning several millennia are capable of answering most of these questions by providing a valuable glimpse into the past, when humans had yet to colonize many oceanic islands. Researchers can use these records to determine the pre-human state of the ecosystem (Wilmshurst *et al.*, 2013), the human impact on ecosystems (Leeuwen *et al.*, 2008; Nascimento *et al.*, 2009; Connor *et al.*, 2012; Van Der Knaap *et al.*, 2012; Nogué *et al.*, 2013), the loss of certain ecological interactions (Crowley *et al.*, 2011; Wood *et al.*, 2012), as well as providing valuable knowledge on how to restore and manage ecosystems (Burney & Burney, 2007; Gilson & Duffin, 2007). The aforementioned subjects all refer to the restoration of ecosystems affected by anthropogenic forces, yet it is worth mentioning the predictive power of palaeoecological studies and the new perspectives that they offers (Vegas-Vilarrúbia *et al.*, 2011). The assessment of possible future scenarios using records of the past is necessary in the continued conservation of protected and restored ecosystems. While it is true that the forces responsible for past climatic changes were dramatically different (i.e. natural rather than anthropogenic), the rate and magnitude of these changes is often not much different than the predictions for the coming century (Willis & MacDonald, 2011). Combining these predictions with palaeoecological and contemporary data on species and ecosystems will provide conservationists with a strong and reliable method of minimizing the risk of extinction for many species and ecosystems in the face of climate change (Dawson *et al.*, 2011).

In conclusion, the palaeoecological field of research has high potential to improve current nature conservation efforts by offering unique insights into the Earth's past. This enables researchers and conservationists to more effectively restore island ecosystems to their former glory and to reduce the risks associated with predicted future climate change.

2 Key issues in the conservation and restoration of ecosystems

2.1 *What is natural?*

"You are stationed on a tropical island, the flora and fauna of which have rapidly deteriorated ever since human colonization, and you are tasked with restoring the island's ecosystem to its natural state. What would you do?"

When confronted with this question and asked to define a 'natural' state, it quickly becomes clear how different people's opinions on this subject are. Nonetheless, there are several common views on what the natural state of an ecosystem entails, what follows are but three of many opinions. First and foremost, there is the opinion that the state the ecosystem was in before the arrival of humans should be considered the original, and therefore natural, state of the island. Some would therefore argue that it is the responsibility of humans to eliminate the invasive, non-native species and nurture the native flora and fauna back to their original state. The second popular view on the question posed would mean that whatever plants and animals would inhabit the island in its current state with minimal human interference is considered the natural state. This argument focuses mostly on excluding the human factor from the island, and allowing nature (species and processes) to regain control of the ecosystem. This opinion seems similar to what is happening in the Dutch Oostvaardersplassen (Staatsbosbeheer, 2013; figure 4). Finally, a considerable minority of people considers humans and their influence on their surroundings natural, which is an interesting and appropriate philosophical issue, yet seems rather out-of-place and inappropriate as a conservation and restoration goal. Within this view, one may differentiate between the aboriginal inhabitants and European colonists, arguing that the native lifestyle was less taxing on the ecosystem. Palaeoecological studies on the Canary Islands have shown that some areas experienced minimal deterioration in spite of the aboriginal human population (Nogúe *et al*., 2013), while the effect of the natives on other islands may have been underestimated (Nascimento *et al*., 2009). Considering this significant difference in human impact among different islands within the same archipelago, it would be safer to assume that current human populations, native or otherwise, would have a negative impact on the ecosystem.

Unfortunately, there does not seem to be one definitive answer to the question of what 'natural' is. The pre-human conditions of an ecosystem would provide an appropriate answer, as human impact has been the main threat to many of the ecosystems. However, it is unlikely that this is a feasible goal for conservation efforts due to continued human activities. Feasibility is not the sole issue at hand, as problems also arise with a number of other factors, including the status of introduced species (Willis & Birks, 2006). If a particular plant species was introduced to an island hundreds of years ago and has been part of the ecosystem since, do we still consider it non-native? Where do we draw the line between native and exotic? Fortunately, palaeoecological studies are able to shed a new light on the species composition before and after exposure to human impact. The colonization, continued inhabitation, and landscape modification of islands have changed the conditions prevalent in these ecosystems. It is therefore likely that many of the species, native and introduced, will have to be reevaluated in regards to the current circumstances.

This individual approach should not be limited to the classification of species alone, but should be expanded to include entire habitats and ecosystems. After all, an ecosystem as a whole may react differently to similar factors depending on its location and species composition. Past forests underwent complete overhauls in response to changing climate (Jeffers *et al*., 2011), while others may have reacted mostly to changes in local conditions (Virah-Sawmy *et al*., 2009a). This same argument can be made for the spatial distribution of species in certain habitats, some originally composed of closed canopy forest and others containing a natural heterogeneous landscape (Virah-Sawmy *et al*., 2009a). It is important to consider it a general rule that each ecosystem responds differently to local, regional, and global changes. As climatic variables on different scales change, it will depend on the ecosystem's resilience whether a threshold is crossed, which may lead to complete turnovers in species composition and dominance (Dearing, 2008; Andersen *et al*., 2009; Virah-Sawmy *et al*., 2009b; Seddon *et al*., 2011). As such, the restoration to a more natural, pre-human state will require island and site-specific analyses to be performed.

'Doom-and-gloom' scenarios in which a threshold is crossed leading to the degradation or demise of an entire ecosystem are common, this makes it important to increase the understanding that nature will likely persevere, but not necessarily in the way we humans prefer. The crossing of such a threshold may simply lead to an alternate steady state of a different composition (Willis *et al*., 2010; Wilmshurst *et al*., 2013). This offers an entire array of new problems, most importantly the disruption of previous plant-animal interactions. As such interactions are an integral part of sustaining current and past vegetation, these should be preserved to the best of our abilities. In this thesis, the natural state of an ecosystem that must be protected, preserved and restored will therefore be defined as follows:

"The state wherein an ecosystem is able to sustain itself without human intervention and approximates pre-human conditions, including ecological interactions and containing most remaining native taxa."

Figure 4. Current and potential rewilding efforts: (**A**) The Oostvaardersplassen in the Netherlands is a successful initiative in which a large area has been allowed to flourish with minimal human intervention, whereas the possible (re)introduction of (**B**) lions (*Panthera leo*) to North-America could help manage populations of grazing (**C**) mustang horses (*Equus caballus*). Images property of Bart Jekel (**A**), Joachim S. Müller (**B**), and John Harwood (**C**). Used under Creative Commons license.

2.2 *Is it still possible to restore ecosystems to their natural state?*

The conservation and restoration of island ecosystems will require a great number of changes to be made to local and global policies, as well as needing extensive research on the islands of interest. It is therefore necessary to be aware of some important questions, such as how to deal with the human presence, identify and restore lost ecological processes and interactions, and handle introduced taxa.

Removing the human population from an island would solve part of the problems encountered in conserving ecosystems, yet this goal is unrealistic. Humans have conquered and claimed much of the Earth's territories and with over seven billion individuals, it is necessary to involve the population in conserving and restoring nature (Dewar & Richard, 2012), rather than excluding them. There are several ways to get local inhabitants interested besides depending on their good nature, one of which is financial compensation (Zabel & Roe, 2009). This tactic may have some short-term usefulness with current landowners, as these will likely appreciate the payment for extra efforts on their part. This approach does require constant monitoring of participants to prevent cheaters entering this system, much like the evolution of cooperation with punisher-roles assigned to a select few.

A long-term solution could be to invest more in certain education plans to make children aware of both the integral value of a fully-functioning ecosystem, as well as what it offers them (Loope *et al*., 2004). Many of the plans to promote active participation in ecosystem conservation and restoration require compensation of some sort and unfortunately these resources are often limited. While the application of multiple plans is recommended to get as many people involved as possible, the improved education of children (and possibly adults) seems the most promising option due to the long-term plans involved with protecting the ecosystem. After all, it is they who will one day inherit the Earth.

Many types of ecological interactions, including plant-animal interactions, have been endangered and lost directly or indirectly by anthropogenic forces (Wood *et al*., 2012). These interactions are often crucial for the survival of the species involved, as is the case with pollination and seed dispersal. These processes are necessary for an ecosystem to function properly and their restoration should therefore take priority (Thorpe & Stanley, 2011). The disruption of reproductive interactions poses a serious problem, and the restoration of one partner or component does not necessarily create favourable conditions for the other. On islands, pollination is often invertebrate-mediated and seed dispersal is carried out mostly by vertebrates, and as such it may be easier to restore pollination than seed dispersal depending on the size of the island (Kaiser-Bunbury *et al*., 2010). Seed dispersal may have to take place over fairly large distances (with regard to minimum pollination distances), as Janzen-Connell patterns act strongly on arboreal vegetation on present-day islands (Hansen *et al*., 2008). Contrary to seed dispersal, island size is less of an issue for pollinator taxa whose minimal space requirements are far less than those of seed dispersers. The restoration of pollination interactions may therefore take priority over seed dispersal interactions on some islands, especially small islands. Many of the pollinators and particularly seed dispersers on islands are threatened, or may be extinct already (Virah-Sawmy *et al*., 2010).

The taxa responsible for these ecological interactions, and many others, may be unable to meet all the demands in order to restore many of these mutualisms. Therefore, alternative possibilities will have to be explored. One of these is the possibility of replacing extinct taxa with either related or unrelated non-native taxa able to fill the ecological gap left by their predecessors (Atkinson, 1988). The introduction of new taxa to islands will require an appropriate amount of research to be performed beforehand, as introducing the wrong taxon to this environment may have catastrophic consequences. It will be necessary to first identify the missing interaction, then find a species capable of fulfilling this role, and subsequently determining whether that species will not destabilize other valuable interactions (Sandom *et al*., 2013). Only after a taxon meets the entirety of the criteria, will it be allowed to introduce it into the ecosystem where it will hopefully restore part of its function.

An (hypothetical) example provided by Sandom *et al*. (2013) is that reintroducing lions (*Panthera leo*; figure 4) to North America would restore apex predator presence in order to compensate for overgrazing by mustang horses (*Equus caballus*; figure 4), which would in turn diminish the need for continued anthropogenic intervention, effectively creating a naturally self-regulating system. Such an approach is not without its dangers, as stated by Rubenstein *et al*. (2006), as introduced species may jeopardize the status of some indigenous species and ecosystems. They argue that resources should be spent preserving currently threatened organisms, as well as reintroducing these native species into their historical ranges.

The reintroduction of herbivores may have to be supplemented with the introduction of predators if the ecosystem is to regulate itself to complement other regulating processes such as food availability. Unfortunately, the average citizen is unlikely to become excited at the idea of large predatory animals roaming the island freely. Public opinion would have to be changed in favour of the reintroduction of predators, and doing so would require the cooperation of biologists, conservationists and public figures. In today's society, the education of the masses via internet, social media, television programmes, books, public events and other outreach efforts is feasible, given that the arguments provided in favour of such (re)introductions are well-supported by scientific evidence.

This should stimulate researchers to join the scientific discussion on the introduction of extant related or unrelated organisms, and to consider both the benefits and disadvantages. There is still much we do not know about the effects of these introductions and such uncertainties should be met by performing more research. More than anything, this provides new ideas and possibilities of proactively restoring habitats rather than observing populations decline, species go extinct and habitat being destroyed (Caro, 2007). This alone could make it worth the effort despite some of the risks involved, as it may not only restore damaged ecosystems, but also reinvigorate many of the weary conservation biologists out there.

Having discussed the possible advantages of introducing alien organisms into other ecosystems, it would be foolish to not consider the risks involved. Introduced plants have the potential of invading ecosystems, possibly outcompeting the native plant life (Morales & Aizen, 2006; Lopezaraiza-Mikel *et al*., 2007). Despite interfering with one or several other native plants, non-native plants may actually have an overall positive effect on the ecosystem (Kaiser-Bunbury *et al*., 2010), due to increases in connectivity or by engaging in certain mutualistic interactions with native taxa. The same could be true for introduced fauna, for example the introduction of honey bees on Mauritius has led to competition with local pollinators as well as potentially aiding native plants in pollination (Kaiser, 2006).

For those invasive organisms that do seem to do more harm than good, there are multiple approaches available. These include active extermination by humans (Loope *et al*., 2004), biological control via another introduced species (Loope *et al*., 2004), and simulating natural disturbances which have minimal impacts on the native species (Thorpe & Stanley, 2011). These disturbances could, for example, include reintroducing a fire regime in certain ecosystems (see 2.3). The line separating one group of introduced organisms from the other is blurry at best. On Tawhiti Rahi, one of the New Zealand islands, a fifth of the flora consists of alien plant species (De Lange & Cameron, 1999) and 5 of 13 terrestrial bird species are not native to the area (McCallum, 1981). As these introductions are not recent, these organisms have led to entirely new interactions both positive and negative between the native and non-native populations, which means that one cannot simply remove the invasive organisms from their habitat there. Additional research, both site- and species-specific, is required here as well, to determine the type of impact these introduced taxa have on native species and the ecosystem as a whole. Therefore, it seems that it is not safe to either introduce or remove non-native taxa from an ecosystem without first researching their interactions with others, lest our attempts at restoration accidentally further the deterioration of the islands.

It is not only the limitations of nature which may affect the success of restoring a natural state. The dedication of the local government and the available funds to restoring their ecosystem are equally important. Island nations may not have the financial resources to fund conservation efforts, especially those in the Third World. In these cases, it may be important to stress the potential profit of a functional ecosystem via, for example, (eco)tourism. Especially the islands with attractive flora or fauna with a high 'cuteness factor' could profit from this. Some nations may be reluctant to spend a substantial part of their income to invest in "potential profit." Financial assistance from First World countries or organizations could potentially solve part of these problems by either funding the conservation effort directly or by rewarding the local government for achieving certain stretch goals.

The overpopulation of many islands poses yet another problem for conservation. As the removal of humans from the ecosystem itself is unlikely, involving them in the conservation plans seems to be the next best solution. Rather than considering the local communities as a hindrance to restoring ecosystems, they could be employed as tools to achieve conservation goals (Agrawal & Gibson, 1999; Cooper *et al*., 2007). Involving the local populace, along with improved education, could help mediate the negative effects of overpopulation and turn some of the overpopulation to good use in the restoration of the local ecosystem.

After having discussed several (of many) key issues in the conservation and restoration of ecosystems to their natural state, it is safe to say that there is no single answer on how to act in the face of habitat destruction, invasive species, and climate change. The possibilities we are presented with will require immense dedication, high investments, and – most of all – far more research until we can be certain about the choices made for the benefit of the islands. Though difficult, the restoration of ecosystems to their natural state may still be possible, and any progress made in the successful conservation of island ecosystems may significantly impact the way we look at nature conservation on the continents.

2.3 *Which important processes within ecosystems ought to be restored?*

The restoration of an ecosystem should include the ability to sustain and maintain itself. To do so, several important processes will need to be restored. Three of these processes (Landscape management, plant-animal interactions, and fire regimes) will be highlighted along with the associated risks and benefits. In addition, I will discuss how palaeoecological research may benefit restoration.

2.3.1 *Megafaunal landscape management and plant-animal interactions*

The megafauna of an island ecosystem (figure 5) affects many aspects of the landscape, including seed dispersal, plant properties, and plant spatial distribution (Griffiths *et al*., 2010). The loss of large herbivores could reduce the distance over which seeds are dispersed, hamper the pollination of some plants or allow formerly grazed plant species to outcompete other native species. When this occurs, rewilding (i.e. limiting the human impact and reintroducing species) could benefit the ecosystem by restoring these important interactions, thereby restoring the lost balance. One example is that of the abundance of C3 or C4 plants in some areas of Madagascar. These were affected by some of the now-extinct lemur species, which dispersed the seeds of C3 and/or C4 plants (Crowley *et al*., 2011). The introduction of similar species could therefore have a significant impact on the landscape, such as the distribution and abundance of certain plants. Such (re)introductions may serve to reestablish many of these lost interactions and to reshape current ecosystems back to their former states. It is unfortunate that (re)introductions of species are rarely simple because ecosystem conditions have changed in their absence. Giant tortoises may have functioned as ecological engineers as their consumption and trampling of plants may have created or maintained open habitats, which in their absence were eventually replaced by bogs (Froyd *et al*., 2014). Such dramatic landscape-scale changes caused by the extinction of a keystone species was quite likely accompanied by a decline or even extinction of certain plant taxa, and might have partially disturbed the ecohydrology of the island. Possibly even worse is that the loss of an open landscape reduces the spatial heterogeneity of an area, which could then reduce the resilience to (future) climate change due to less variety in plants and animals able to cope with such changes (Virah-Sawmy *et* al., 2009a). Each individual habitat should therefore be evaluated to determine whether a return to the previous conditions is still possible, or whether a threshold has been crossed by which some processes gained the upper hand and forced the ecosystem into an alternative steady state (Scheffer *et al*., 2001). In such cases, a decision would have to be made whether to restore the ecosystem to its previous state, with all risks involved, or to preserve the current state where possible. Ecosystems that are on the verge of shifting to an alternative state should be preserved by maintaining or improving the resilience of the habitat to external influences (Seddon *et al*., 2011). The ability of reintroduced taxa to reshape the habitat and to sustain a viable population under new ecological circumstances are most relevant when reintroducing extant species which have may only experienced a range shift, for example. A return to their former habitat could therefore be problematic. The introduction of related extant taxa, or unrelated taxa with similar functions, once again puts the emphasis on issues relating to invasiveness and the consequences of new interactions.

The risks associated with introducing a foreign species into an ecosystem in order to restore lost functionality of an extinct species are high. The results could be catastrophic if the introduced taxon endangers the native flora and fauna by predation, competition, or some other way (Rubenstein *et al*., 2006; Caro, 2007). This problem may be resolved by introducing and monitoring a small population of the foreign species in a somewhat controlled environment. This would allow researchers to determine the risk this species poses to the island, and whether releasing them into the wild uncontrolled would be advisable (Griffiths *et al*., 2011). In a cruel twist of fate, reintroduced native species may have to be monitored and managed rather than the established invasive species (Garrett *et al*., 2007). A gap of knowledge about extinct, native species may yield yet another problem as their former role in the ecosystem may not be known, making the identification of replacement taxa difficult to impossible. The use of palaeoecological research in identifying the niches occupied by the extinct species in question may provide unique insights into their functions (Wood *et al*., 2012). The identification of a niche may lead to the choice of an appropriate replacement species, or the unfortunate conclusion that the extinction of a species resulted in an irreplaceable loss of function.

The restoration of plant-animal interactions is difficult, especially when not concerned with merely megafaunal reintroductions (Traveset & Richardson, 2006). Human colonization and landscape modification is often the reason for the endangerment and extirpation of many plant species, which in turn may affect many other organisms, such as pollinators. The reintroduction of such plants, or the introduction of alien plants, may have a wide variety of effects. The foreign plants may invade the ecosystem and disrupt existing plant-pollinator mutualisms, for example, by offering more resources than the native plants (Traveset & Richardson, 2006). As was discussed earlier (see 2.2), the overall effect of the introduced taxa could potentially also be positive. While some of the interactions between plants and animals may be disrupted by the invasive taxa, they could facilitate a multitude of processes which benefit other taxa and the ecosystem as a whole (Lopezaraiza-Mikel *et al*., 2007; Kaiser-Bunbury *et al*., 2010), especially for those taxa that do not overlap in blooming (Morales & Aizen, 2006). On-site or greenhouse-situated comparative studies between the native flora and the taxa to be introduced seem a reasonable solution to prevent the ecosystem-wide disruption of plant-animal interactions. However, despite our best efforts, it is unlikely that it is possible to eliminate all the risks of introducing foreign taxa into a new

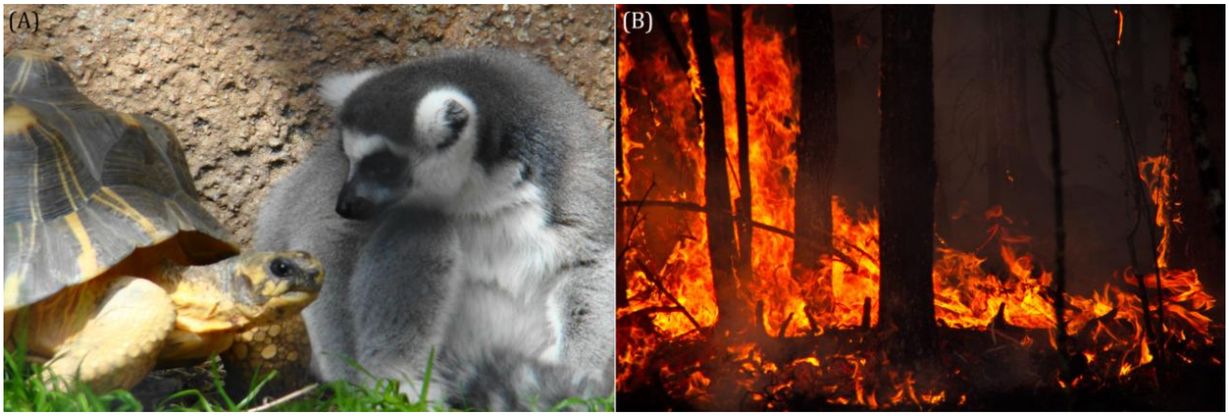

Figure 5. The ecological functions of megafauna can be diverse, but among their 'roles' are those of seed dispersers and fire preventers. The Madagascan radiated tortoise (*Astrochelys radiata*) and ring-tailed lemur (*Lemur catta*) are important players in these processes on Madagascar (**A**). However, it is important to realize that in some ecosystem fires are a natural occurrence and shape the landscape, rather than acting as solely a destructive force, as in the Yugansky nature reserve in Russia (**B**). Images property of Mario Pineda (**A**) and Tatiana Bulyonkova (**B**), and used under Creative Commons license.

environment. Despite the risks involved, it is likely well worth the trouble of studying both past and present ecological circumstances and combining the resulting data so that ecosystems may return to a state in which they may sustain themselves with minimal anthropogenic interference.

A final issue is which species to reintroduce, as the financial capabilities of the island nations involved are often limited. Decisions will have to be made as to the restoration of which species is more important. The identification of so-called 'keystone species' (Mills *et al*., 1993; Paine, 1995) could help to smoothen this process. Keystone species are taxa which have a disproportionally large effect on their environment relative to their abundance, meaning they are involved in many more different interactions than other organisms in the ecosystem. (Re)introducing these species first could help to rebalance the ecosystem before introducing species whose impact on the ecosystem is smaller. After all, the first goal of restoration should be to restore the ecosystem to a functioning state.

2.3.2 *The fires and flames*

Fire is often considered a purely destructive force by humans and it is therefore often attempted to minimize the impact of wildfires. However, while the effects of fire are detrimental to some species (Burney & Burney, 2007), they are beneficial to those adapted to regular fire events (Cowling & Lamont, 1987). Natural fires have always occurred in some parts of the world (figure 5), but have become either less or more frequent due to contemporary climate change and other human-mediated processes (Vegas-Vilarrúbia *et al*., 2011). The extinctions of the giant tortoises of Madagascar and the Moa of New Zealand have likely led to changes in fire regimes in their habitats (Pedrono *et al*., 2013; Wood *et al*., 2013). It is likely that their consumption of the vegetation minimized the above ground biomass, which is potential fuel load. Fires have occurred naturally on Madagascar before humans set foot on the island, but it is the dramatic increase in burning associated with human settlement which now threatens parts of the island (Burney *et al*., 2004). This example serves to show that fire is not a bad thing in of itself, but it is rather the human-mediated overexposure to it which is dangerous. Natural fires are not limited to arid regions (Lynch *et al*., 2004), and may even possess an important role in the conservation of some species. For example, several beetles from forests in southeast

Sweden likely require forest fires or the resulting structural changes to survive (Lindbladh *et al*., 2003). Bond & Keeley (2005) have stated that fire is not unlike a herbivore, as it plays an important role in determining plant distribution and abundance, community composition, and the structural composition of a habitat. Furthermore, as fire consumes material, it converts complex organic molecules into organic and mineral products. This process will in turn enrich the soils of the area, allowing successful establishment of new life.

It would be unwise, of course, to allow every natural fire to take its course. There are often human settlements nearby which require protection from the flames, or current climate change may have led to increased fire frequencies which are unsustainable for the ecosystem itself. Once more, additional research is required to make an appropriate decision concerning the management of wildfires. Palaeoecological research has its own role to play in this by providing data on past fire regimes via, for example, the study of charcoal particles found within sediment cores. Learning more about past fire regimes could inform us about what fire intensities and frequencies are sustainable and would allow the natural vegetation (type) to prosper. It is time to reconsider the role of fire in the conservation and even restoration of ecosystems as it brings more than just destruction, it creates opportunities for new life to flourish.

The conservation and restoration of ecosystems using (re)introductions of (non)native taxa and fire regimes seems possible, but will likely be difficult. Novel methods are required to assess how to best achieve our goals, and palaeoecology will likely be of great assistance due to the unique perspective it offers. The identification of lost ecological interactions and the frequency and intensity of burning are but two of many applications of palaeoecological research, but serve to show the immense potential of this field of research.

3 Present and future palaeoecology

3.1 *Palaeoecology in conservation*

The applications of palaeoecological research discussed so far have mostly been hypothetical, based on a variety of proxies and their functions. The field of restoration palaeoecology is relatively young and it is for this reason that most available studies were performed in the past decade, particularly the previous five years. Several of these studies are already being applied to conservation and restorations policies on a number of islands. As stated before, island systems are relatively and are consequently used as natural laboratories (Gillespie *et al*., 2008). The section below will highlight several of the studies which have successfully applied palaeoecological data to the conservation and restoration of island ecosystems.

3.1.1 *The Canary Islands*

In 2009, Nascimento *et al*. published a study in which they described the long-term ecology of Tenerife in order to establish a pre-human baseline and determine the effects of human activity and climatic variation on the island's vegetation. They did so by studying the fossil pollen and charcoal remains found within a sediment core recovered from a former lake bed. Between 4,700 and 2,000 cal. yr BP, the forests surrounding the lake were dominated by oak (*Quercus*) and hornbeam (*Carpinus*), with pine (*Pinus canariensis*) forests present in the region as well. It was after the arrival of humans roughly 2,500 years ago (Rando *et al*., 1999) that the abundance of oak and hornbeam declined, leading to the establishment of present-day laurel forest and a more open vegetation type. This study by Nascimento *et al*. (2009) has shown that the human impact on the vegetation of Tenerife was stronger than hitherto realized. More importantly, this study showed that both the oak and hornbeam – once considered non-native – formed a significant part of the natural vegetation. This could be crucial information for restoring the ecosystem as both genera are currently extinct on the island.

Further evidence for the requirement of site-specific studies is provided by Nogué *et al*. (2013) in their study of the forests of La Gomera. Using the same proxies as Nascimento *et al*. (2009), fossil pollen and charcoal, they set out to reconstruct the long-term dynamics of a forest located near the summit of Garajonay National Park. Their record covered the last 9,600 cal. years and showed signs of both climatic changes and burning. A rapid change in climate seems to have induced a sudden shift in forest taxa roughly 5,500 years ago, predating the arrival of humans on the island by some ~3,000 years. Furthermore, the frequency of fires over the last 800 years was by far the lowest of the entire 9,600 year sequence, further proof of low human impact on the island. This study by Nogué *et al*. (2013) therefore suggests that the current vegetation in Garajonay National Park is an ancient, mostly natural relict of pre-human times. This shows the necessity of site-specific analyses, and also that largely natural ecosystems still exist.

These two studies highlight the effectiveness of the methods applied here. The study of fossil pollen to reconstruct past vegetation on these islands proved to be useful in estimating the human impact on the ecosystem, and hence assessing the naturalness of the vegetation. Furthermore, the charcoal remains show two sides of the same coin. Human-induced burning on Tenerife likely destroyed much of the vegetation, while natural fires were far more common on La Gomera and may have played an important role in maintaining landscape diversity. In both cases, the value of palaeoecological research to ecosystem conservation is apparent and will hopefully lead to increased cooperation between palaeoecologists and conservationists.

3.1.2 *The Hawaiian Islands*

Burney & Burney (2007) have shown how restoration based on palaeoecological data may be put into practice successfully on Kaua`i, Hawaii. According to these authors, both in-situ (i.e. conservation of species in its current habitat) and ex-situ (i.e. conservation of species in human-controlled environments such as botanical gardens) conservation of plants was ineffective in preserving many of the threatened plant taxa. The use of palaeoecological methods (e.g. pollen analysis) here not only showed the extent of human impact on the island, but also showed the past ranges of certain plants. This led to a policy of so-called inter-situ conservation based on palaeoecological data, in which species are reintroduced outside of their current range into regions in which they lived in the recent past. One success story is that of Makauwahi Cave (figure 6), where much of these original vegetation has been restored, albeit under continued intensive supervision of two palaeoecologists. With continued research and cooperation, this will lead to many successful restorations of natural vegetation.

3.1.3 *The Galápagos Islands*

The introduction of non-native plants by the Europeans to the Galápagos has been detrimental to the local plant life. It is for this reason that the removal of these invasive species has become a priority in the conservation and restoration policy of these islands (Kaiser, 2001). One role of conservation palaeoecology is to differentiate natives from non-natives, as Van Leeuwen *et al*. (2008) did by analyzing four sediment sequences from different sites. Using analysis of fossil pollen, they were able to show that at least six of the taxa currently presumed to be non-native or doubtfully native actually predated first human contact in 1535 (Suggs, 1967). This highlights how a knowledge gap may lead to the inappropriate control of what are in fact native species, and how data on

Figure 6. Several photos of the Makauwahi Cave on the Hawaiian archipelago. Two palaeoecologists, David A. Burney and Lida Pigott Burney, are responsible for the successful restoration of much of the original vegetation of this site. All images above are property of Wolfram Burner and used under Creative Commons license.

past vegetation may improve current management strategies.

Palaeoecological proxies come in all shapes and sizes, and may be used in a variety of ways. Seddon *et al*. (2011) used a variety of methods to study the processes operating in the coastal zone, whether there was a threshold response, and how information about an ecosystem's past serves to inform us about the current resilience of the system. They used AMS radiocarbon dating along with stable carbon isotopes ($\delta^{13}C$) to reconstruct sedimentation rates and ecological change, bulk geochemical analysis to determine local changes in the environment, and the analysis of diatom remains to reconstruct the salinity of the Diablas lagoon on Isabela, Galápagos. Using this combination of methods, they were able to determine that a combination of climatic changes and disturbances over time were able to trigger a threshold response which caused the local mangrove community to shift towards a microbial mat. This remarkable shift into an alternate steady state describes non-linear behaviour of an ecosystem. Palaeoecology can therefore provide important information concerning baselines, thresholds and the ecological responses to environmental change.

Another study on the Galápagos Islands has shown how microfossils may be utilized in order to reconstruct the possible effects of megafaunal loss on an island ecosystem (Froyd *et al*., 2014). Here, a reconstruction of past vegetation using fossil pollen was made and subsequently combined with the past abundances of giant tortoises, as inferred from the analysis of coprophilous fungal spores. This combination of data shows that giant tortoise populations declined some 500-700 years ago as a result of either human impact or climate change. While it is unfortunate that the exact reason for the decline of tortoise populations is uncertain, what came next may be considered far more interesting. The loss of tortoise presence on

Santa Cruz Island caused a shift from freshwater wetland habitats to *Sphagnum* bogs, which in turn very likely led to the decline or extinction of several plant species. As such, this study has supports the importance of large herbivores in maintaining a healthy, natural ecosystem. They achieve this by grazing, trampling and wallowing, all of which structure the plant community and thereby indirectly also sustain many plant taxa specific to the habitat in question.

Palaeoecological research on the Galápagos Islands has shown how it may be applied to establishing whether taxa are native or non-native, determining the resilience of an ecosystem to climatic change, as well as the importance of herbivores on islands. These three highlighted studies all have practical applications in the management of islands which aim to conserve and restore their natural ecosystems, some of which is already being applied (see 3.1.4 and 3.1.5).

3.1.4 *Madagascar*

The island of Madagascar is a valuable biodiversity hotspot threatened by human impacts and climate change. Burney *et al.* (2004) have showed the destructive impact of the human presence on the island. Having assembled a database of 278 age determinations of sediments, plant macrofossils, bones, teeth, eggshells, speleothems and pottery, they were able to construct a timeline of sorts. The dates of the many megafauna remains strongly suggest that most of the now-extinct taxa were still alive when humans arrived on the island. A drastic decrease in coprophilous fungal spores after human arrival infers the beginning of the end for many of the indigenous wildlife, and is followed by strong increases in charcoal particles in sediment cores. These are signs of a catastrophic cascade of events kickstarted by the human presence on the island. It is likely that the megafauna was concentrated in the presently rare wooded savannas of Madagascar, where they were soon hunted down by the human settlers. Following this megafaunal collapse, a buildup of above-ground biomass resulting from the absence of grazers and browsers probably changed the fire regime on the island, hence the increased presence of charcoal particles. This in turn could have been the cause for some of the greatest landscape transformations observed on Madagascar, which could confound current restoration efforts. This study shows how human presence may have affected an entire ecosystem solely by removing the megafauna, but may fortunately also provide us with invaluable information which may assist us in restoring much of the ecosystem.

Spatial heterogeneity is often attributed to human-mediated landscape fragmentation, yet some ecosystems are naturally heterogeneous, as shown by Virah-Sawmy *et al.* (2009a). Before the arrival of humans, local variation in groundwater, nutrients and fires maintained a highly heterogeneous landscape. The effects of future climate change on a threatened and already fragmented landscape could be disastrous if anthropogenic forces remain as they are. A second study by Virah-Sawmy *et al.* (2009b) focuses on the resilience and threshold response of Madagascar's coastal habitats, similar to the study later performed by Seddon *et al.* (2011) on the Galápagos. Both studies by Virah-Sawmy *et al.* made extensive use of the pollen records of the area, but their study on ecosystem resilience added diatom, charcoal and geochemical records. These proxies combined showed that a synergistic effect of sea-level rise and rainfall deficits triggered a threshold response which led to the transformation of two types of littoral forest to a heath-grassland. The identification of a threshold response and the naturally heterogeneous landscape have led them (i.e. Virah-Sawmy *et al.*, 2009ab) to argue a different approach to conservation, one which takes into consideration the resilience and threshold of an ecosystem. Current conservation efforts focus mostly on species distribution and dispersal, and ecosystem resilience would make for an appropriate addition as it decreases the probability of biodiversity loss due to external forcings. Nonetheless, habitats may differ in their sensitivity to certain factors, and as such it seems important to once again stress the use of site-specific analyses.

The importance of large herbivores did not go unnoticed by Pedrono *et al*. as they present a plan for the reintroduction of giant tortoises to Madagascar in their 2013 paper. The giant tortoises of Madagascar have been extinct for some time, but there is evidence that the extant Aldabra giant tortoise (*Aldabrachelys gigantean*) is closely related to the extinct *Aldabrachelys abrupta*. The ecological functions of several extinct megafauna could potentially be fulfilled by the Aldabra giant tortoises, at least partially. Once introduced, the introduced tortoises would likely aid in the recovery of island ecosystems by, for example, reducing flammable plant material and thereby decreasing the frequency of burning. Additionally, the potential and unique tourist experience this offers could help finance some of the ongoing restoration projects on Madagascar. As Pedrono *et al*. (2013) so adequately described it, "…this proposed giant tortoise translocation could represent a welcome break-through in the struggle to retain and restore the unique biological riches of Madagascar."

The ongoing conservation and restoration efforts on Madagascar at times seem to be fighting a losing battle, yet the new insights into the past offered by palaeoecological studies as the ones described above offer new chances to learn and adapt current policies. Information concerning lost megafauna may help restore these (i.e. species and/or ecological functions) in the future, the discovery of a natural heterogeneity in the landscape requires us to reevaluate the conservation efforts along the coasts of Madagascar, and the possible reintroduction of giant tortoises offers a glimmer hope in the face of insurmountable odds.

3.1.5 *Mauritius*

A common trait of many tropical islands is the presence of giant tortoises as megafauna. Unfortunately, it is also common for these herbivores to be either threatened or extinct, and Mauritius is no different. Griffiths *et al*. (2010, 2011) argue in favour of reintroducing the giant tortoise to Mauritius as part of the conservation and restoration strategies. The endemic giant tortoises have gone extinct shortly after human colonization, but they may be replaced by the same Aldabran tortoises which are to be introduced in Madagascar (see 3.1.4). Fortunately, Griffiths *et al*. are able to support their claims with two important examples, as the extant giant tortoises have been introduced to nearby Round Island and Ile aux Aigrettes. On Round Island, subadult Aldabran giant and adult male Madagascan radiated tortoises have been introduced and are being monitored to determine their impact on the island. As most oceanic islands, Round Island is plagued by invasive plant species, but the reintroduction of tortoises may provide a solution. The tortoises do not only restore ecological interactions, but they also devour many invasive plants. This is partially due to the faster-growing, more abundant, and fleshier nature of the non-native plant life, and partially due to the anti-herbivorous traits of the native species – traits which offer specific protection against tortoise grazing (Griffiths *et al*., 2010). The situation on Ile aux Aigrettes is similar to that of Round Island, and here tortoises have proved their worth by minimizing damage to native species and even being advantageous for the restoration of plant taxa reliant on animal-mediated seed dispersal. Furthermore, tortoises are relatively easy to keep and will probably not become invasive as they are easy to monitor and unlikely to run away. Additionally, their influence on the local ecosystem may be tracked via, for example, the study of dung samples for plant material. These examples show how the replacement of extinct taxa by extant, related taxa may work and benefit the ecosystem as a whole, whilst also reducing the costs of human intervention (e.g. removal of exotics).

More recently, studies by De Boer *et al*. (2013ab, 2014; De Boer, 2014) have provided a detailed reconstruction of the past vegetation and climate of Mauritius, which may serve any conservation or restoration efforts well. Much of the original vegetation has been lost (figure 3) to human activities and has been replaced by predominantly sugar cane plantations. As so little of the original flora and fauna remains, it will be very difficult to properly restore the Mauritian ecosystem. Its potential for conservation and restoration is high however, as almost any addition to the island is sure to be an improvement over its current state.

At present, conservation palaeoecology offers the best future prospects for restoring parts of Mauritius to a more natural state, as very little natural vegetation remains.

3.1.6 *New Zealand*

The final island to be discussed is New Zealand, another victim of the activities of mankind. Often, little is known about the plant-animal interactions in pre-human times, as was the case with the kakapo, a rare and threatened nocturnal, flightless parrot. It is fortunate that the discovery of a rare, but possible valuable, proxy was able to shed light on lost interactions with the kakapo in a study performed by Wood *et al*. (2012). Using coprolites, or fossil feces, they were able to infer a former direct feeding interaction between the kakapo and a root-parasite (*Dactylanthus taylorii*). The analysis of ancient DNA (aDNA) obtained from the coprolite was used to determine that it was in fact a kakapo which deposited the feces in the first place, while the analysis of pollen and spores from the coprolite showed a high abundance of *D. taylorii* pollen. The current distributions of these species no longer overlap, and it seems likely that this means that *D. taylorii* has lost at least one of its pollinators. The application of inter-situ conservation methods could potentially restore this interaction if the New Zealand conservationists deem this necessary.

Wood *et al*. (2013) do seem to have an affection for fossil feces, as a second study uses coprolites once more. This time, however, they set out to increase the understanding of the lost herbivore community structure of the extinct moa of New Zealand. Using aDNA, four sympatric moa species were identified, while the analysis of pollen, plant macrofossils and plant aDNA offer unique insights into the diet of these avian herbivores, 400 years before their extinction (~1450 CE). Sadly, the authors had to conclude that there are no extant ecological replacements for the moa, which means their extinction is an incredible loss to New Zealand's ecosystems. In this case, a species and its ecological function has truly been lost to time, unlike the case of the kakapo. However, Wood *et al*. (2013) mention that there is not one organism capable of replacing the entire range of moa interactions. Given enough detailed information on the possible replacements is available, the functions of the moa could be fulfilled by multiple introductions of non-native species. However, there is likely a shortage of information concerning the moa's interactions and such replacements are therefore likely to be too dangerous at this time.

Finally, a study by Wilmshurst *et al*. (2013) utilized fossil pollen and aDNA to study changes in vegetation composition over the last 2,000 years. Several changes in the species composition of Tawhiti Rahi, one of the offshore islands of New Zealand, occurred before human arrival. The human arrival affected species composition far more than the natural change preceding it, however, as the dominant species of pre-human vegetation no longer occur on the island itself nor on any of the other islands in the region. A complete turnover has occurred now that forest has been allowed to redevelop in the past 180 years, before which it was gardened land. The only extant forests of similar composition now occur in northern North Island of New Zealand, which could be the last hope for the restoration of the offshore islands of New Zealand. Managers of these islands could manipulate the existing successional pathways or actively replant the absent taxa to start the restoration of the islands, but changes which have occurred since human colonization may make these plans difficult to execute. The introduction of non-native taxa, the novel interactions, and the difficulty of reproducing natural disturbances are but three of many issues facing conservationists on New Zealand. However, palaeoecological records such as the one provided by Wilmshurst *et al*. (2013) may provide valuable goals for conservation and restoration, and could allow managers to make more informed decisions.

The three studies discussed above emphasize the versatility of conservation palaeoecology, which allows for the use of completely different proxies to reconstruct lost interactions, the niches of extinct taxa, and past environments. This may allow the conservationists of New Zealand to restore what was lost by (re)introducing organisms to past or new habitat.

3.2 *The limitations of palaeoecology*

The application of palaeoecological research methods has a lot of potential, but it is not without its limitations in location, time, and proxies. Despite the necessity for site-specific studies, local palaeoecological studies are not always possible. The cores used in research have to be recovered from sites where sediment has been or is being deposited, and such sites (e.g. lakes, bogs) are not always available. As such, some study sites may have to settle for a regional study of past climate and vegetation, rather than a site-specific one.

The study location is not the only limiting factor, however. Any study targeting a specific time period should keep in mind the time encompassed within and resolution of a recovered sediment core. Depending on the geological origins of a lake, the sediments contained within may span a varying amount of time. This could significantly hamper a study's progress in the absence of appropriate pilot studies. Furthermore, if past sediment deposition was particularly slow, the study material may contain the time period of interest but have a lower resolution (i.e. 'years per centimeter'). Any data acquired from such a sediment core could provide information on a timescale too large for the application in conservation biology (e.g. in establishing baseline dynamics). Taking this into account in designing a study and performing pilot studies could minimize this risk.

The proxies themselves often have limitations. Proxies are used to reconstruct a vast number of variables, yet for some it remains difficult to distinguish which external factors are forcing changes. In the study of subfossil pollen, determining whether it is local conditions (e.g. nutrient availability) or climatic conditions that primarily affect changes in vegetation composition can be difficult. Another example is that of subfossil chironomids, the distribution of which may be affected by water temperature, water depth, lake nutrient status, and more. Fortunately, there are often ways of resolving such issues. In the case of coprophilous fungal spores it may be hard to determine what species deposited the dung in the first place. Froyd *et al*. (2014) studied the effects of the loss of giant tortoises on the Galápagos Islands. The fungal spores found are not characteristic for the feces of giant tortoises, but Froyd *et al*. were able to determine the depositor via the process of elimination. There are only two other animal (groups) possibly capable of depositing sufficiently abundant quantities of dung, the now-extinct giant rice rat (*Megaoryzomys* sp.) and birds. It is unclear whether the giant rice rat would have used the upland wetland habitats to such an extent and the Galápagos do not support any avian taxa which favour these habitats, in contrast to the giant tortoises for which this is consistent with known preferences.

Therefore, despite the limitations of the proxy, the available information on other local species were able to resolve this mystery.

It is crucial to acknowledge the inherent imperfection of palaeoecological methods, but also to develop ways to work around them. Further development of proxies could lead to a better understanding of these, and thereby improve our interpretations of them. However, in recent years the number of multi-proxy studies has increased dramatically, and this seems the preferred research method as it not only provides a wealth of information, it also assists in eliminating some of the uncertainties of the other proxies used. As stated above, the conclusions drawn from palaeoecological studies are interpretations of data, and as such do not provide definitive evidence of past conditions. The interpretations of these data are often the most logical options based on knowledge of contemporary ecosystems and species, yet different researchers may interpret the same dataset differently. Below, two example studies will be given a second glance to show the duality of palaeoecological research.

3.2.1 *The kakapo*

The study performed by Wood *et al*. (2012) described the ecological role of the threatened kakapo in New Zealand. The authors suggest that the presence of pollen and spores in kakapo coprolites are related to its function as a pollinator. Their paper focuses mostly on the newly discovered interactions between the kakapo and parasitic plant *Dactylanthus*, including the potential pollination by the kakapo. However, many parrot species are known for their destructive feeding habits, something which may have been detrimental to *Dactylanthus* rather than advantageous. The authors acknowledge this possibility and provide several arguments to support their claim.

Firstly, if destructive feeding occurs, pollen may still adhere to the feathers surround the kakapo's face and subsequently be transferred to female inflorescences. Kakapos feed selectively on a variety of plant species, but it is not known whether they feed on *Dactylanthus* indiscriminately. If they discriminate between *Dactylanthus* and other plant species, this could possibly offset the potential benefits of pollination. The authors cite several studies showing successful pollination in *Dactylanthus* via ship rats, despite destructive feeding on the male inflorescence (Wood *et al*., 2012 and references therein). In their 2012 paper, the authors also mention several parrot species which do engage in nectar feeding and pollination, and as such it is not unthinkable that the kakapo could do the same.

Wood *et al*. (2012) provide good arguments to support their claim of the kakapo as a potential pollinator of *Dactylanthus*. Despite these arguments, the interpretations of their data are not concrete evidence of the kakapo's function and other researchers could potentially dispute these claims. The authors themselves call for new studies investigating the feeding habits of the remaining kakapo. This case study illustrates the advantages and disadvantages of palaeoecological research, in this case it led to new insights but is unable to provide all the answers by itself. Palaeoecology is an important tool to be utilized alongside a broad spectrum of methods, as it is not a solution in and of itself.

3.2.2 *The "Van Geel versus Vera" discussion*

The appearance of primeval forests in northwest Europe has been a subject of discussion for the past several decades (Birks, 2005). In the Netherlands, this discussion is spearheaded by two outspoken biologists: Bas van Geel, palaeoecologist at the University of Amsterdam, and Frans W. M. Vera, ecologist and conservationist for the Foundation Natural Processes. Based on personal experience and past palaeoecological studies (e.g. Iversen, 1973), Van Geel has argued that the primeval landscape of northwestern Europe consisted of closed-canopy forests and associated underbrush. Vera, however, claims that a more open vegetation type dominated the landscape (Vera, 2000). Vera's open landscape was a mosaic of open grassland and regenerating shrubs and forests created and maintained by large herbivores. Despite the strong contrast between their respective views, both parties have sometimes made use of the same data. Their interpretations of such data differ, and both Van Geel and Vera have continued gathering evidence for their claims as this discussion went on.

Modern analogues of primeval forests are lacking in northwestern and central Europe. Therefore, unlike the ecological role of the kakapo (see 3.2.1), it is impossible test either hypothesis directly. Any experiments involving the 'natural development' of an ecosystem have to therefore involve rewilding projects such as the Oostvaardersplassen in the Netherlands. Considering the human influence in creating many of these areas and differences with past climate, however, they are unlikely to reflect natural conditions as they were thousands of years ago.

This conflict of opinions originated from the Achilles' heel of palaeoecology: the indirect evidence provided by proxies is open to interpretation. Compensating for this inherent weakness is difficult, but the utilization of multiple proxies as well as including other fields of research may mitigate its effects.

3.3 *The future of conservation palaeoecology*

Distinguishing between native and non-native organisms, assessing ecosystem resilience, reconstructing past ecological interactions, determining natural baseline dynamics, identifying threshold responses. All of this and more is made possible by researching past environments and climate. The above examples (3.1.1-3.1.6) serve to illustrate how far palaeoecology has come in the conservation and restoration of island ecosystems in less than a decade. Many of the current predictions regarding the loss of biodiversity in the face of climate change still rely on old, or relatively short-term, data. By including the unique insights offered by palaeoecological research with our current knowledge, the new generation of predictions will assuredly become far more accurate and reliable.

Realizing the value of palaeoecological research is but the first step in a long process. The results from such studies have yet to reach a wider audience, including conservationists. Palaeoecologists will have to approach new groups and journals themselves in order to introduce their field of research and to convince scientists and journals alike of their value to conservation efforts. Efforts by palaeoecologists will increase understanding among conservation scientists, which could in turn lead more collaborative studies. Spreading the word among policy makers may prove to be more difficult, but the writing of reports on palaeoecological research in a more accessible (e.g. less jargon) way could help.

Palaeoecological studies are time-demanding and most certainly have their limitations. Despite this, they offer us glimpses of the past which are invaluable to further the understanding of our world (Jackson & Hobbs, 2009). The integration of this field of research into the existing network of conservation sciences will open new windows of opportunity for research, as well as improve the quality of conservation and restoration decisions. Performing site-specific analyses will allow a network of many small-scale projects across the world to improve the overall condition of the earth. Such projects would likely have a higher probability of success as they are adapted to the environment to which they are applied, rather than making uninformed decisions based on a rudimentary understanding of the world as a whole. It is often better to handle smaller parts of the problem individually than to face the entire problem head-on. As such, I believe that any decision made concerning the conservation or restoration of any area should be supported by knowledge on both past and present. After all, is the past not the key to the future?

4 Conclusion

This thesis has sought to highlight the role palaeoecology can fulfill in conservation and restoration. It has described the current predicament of six islands in the Pacific, Atlantic, and Indian Ocean. I subsequently addressed several of many issues facing conservation and restoration efforts, especially those where palaeoecology offered new insights and solutions. Finally, by highlighting important studies which seek to restore the aforementioned islands I have hopefully shown how useful the application of conservation palaeoecology is, and how it has the potential to change and improve current conservation efforts.

The introduction of palaeoecology may provide invaluable assistance in the restoration of the Canary Islands, the Hawaiian Islands, the Galápagos Islands, Madagascar, Mauritius, New Zealand, and other islands. Conservation methods successfully developed and tested on these islands may someday lead to new ideas for the restoration of continental ecosystems, although the latter are likely far more complex than the isolated island communities.

There are no perfect fields of research, however, and palaeoecology is no different. Over the course of time, it has become far more accurate and reliable with an increase in the number of proxies available, the possibility of high-resolution studies, and better understanding of the resulting data. Despite this, researchers ought to take into account that palaeoecological data mostly yield indirect evidence and that their interpretation depends on our understanding of current interactions between biota and climate. Those studying subfossil chironomids, for example, are well-aware that the distribution of chironomids is not only related to temperature, but may be affected by other factors as well, such as water depth or nutrient availability. It is only by carefully studying the evidence presented by multiple proxies that we are able to determine which variable is affecting the proxy of interest. Such practices have fortunately become more commonplace in modern palaeoecology, which has dramatically increased the reliability of interpretations. The highlighted studies above (see 3.1) have shown the potential value of palaeoecological research and demonstrated how their results are already changing conservation and restoration strategies.

The future outlook of many threatened ecosystems seems to be a little brighter with the introduction of palaeoecology, as it offers us chances to better understand the past. The necessity of site-specific analyses and the sheer amount of factors to be investigated will make restoration a difficult and time-consuming process, however. Consider this thesis a call-to-arms for palaeoecologists to invest in the practical applications of their research, as well as for conservationists, for whom it is time to start taking palaeoecology seriously and to realize the potential it holds. Be it via discussions or joint projects, working together is the only way forward. It is time for mankind to take responsibility for its transgressions against nature and to restore what has been lost, and I believe that the utilization of conservation palaeoecology is crucial in this process of redemption.

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