Isolated and vulnerable: the history and future of Pacific Island terrestrial biodiversity

GUNNAR KEPPEL[1], CLARE MORRISON[2], JEAN-YVES MEYER[3] and HANS JUERGEN BOEHMER[4]

Islands in the tropical Pacific have a rich and unique biota produced by island biogeographic processes and modified by recent anthropogenic influences. This biota has been shaped by four overlapping phases: natural colonization and dynamics (phase 1), impacts of indigenous (phase 2) and non-indigenous (phase 3) settlers, and increasing environmental awareness (phase 4). Island ecosystems are resilient to natural disturbance regimes but highly vulnerable to invasive species and other human-related influences, due to comparatively low alpha diversity, isolated evolution and the absence of certain functional groups. Habitat loss, overexploitation, invasive alien species and pollution continue to threaten terrestrial biodiversity, compounded by limited environmental awareness, minimal conservation funding, project mismanagement, limited local capacity and inadequate and/or unsuitable conservation policies. To achieve effective conservation of terrestrial biodiversity in the region, biophysical threats need to be mitigated with improved scientific, institutional and management capacity.

Key words: anthropogenic impacts, conservation, disturbance, environmental awareness, extinction, habitat degradation, invasive species, local capacity, multiple threats

INTRODUCTION

THE insular tropical Pacific includes independent nations and dependent territories between New Guinea in the west and the Galápagos Islands in the east (see Fig. 1.1 in Mueller-Dombois and Fosberg 1989). It has exceptional terrestrial biodiversity (Keast and Miller 1996, Table 1), recognized by the identification of four biodiversity hotspots: Polynesia and Micronesia, East Melanesian Islands, Melanesia, New Caledonia, and Galápagos, as part of Tumbes-Chocó-Magdalena (Mittermeier *et al.* 2004). Furthermore, New Guinea is widely recognized as a centre of high biodiversity (Legra *et al.* 2008).

Isolation through separation by inhospitable oceans that limit dispersal has produced high terrestrial species turnover among islands and considerable localized endemism (Keppel *et al.* 2009, Kier *et al.* 2009). This results in low alpha and high gamma diversity, compared to similar ecosystems on continents. Furthermore, island floras often lack important biotic elements of the mainland (Thorne 1963, Keppel *et al.* 2009).

Insular ecosystems in the Pacific are highly susceptible to anthropogenic disturbance (Kier *et al.* 2009), demonstrated by the extinction of large proportions of the Pacific bird fauna (Steadman 2006). High vulnerability to anthropogenic influences may be related to low alpha diversity, the absence of certain functional groups, small population sizes and limited genetic diversity (Frankham 1998, Mueller-Dombois 2008). Currently, habitat destruction and degradation, and invasive species threaten numerous species and ecosystems in the tropical Pacific (Kingsford *et al.* 2009, Woinarski 2010).

We review the history, current threats and predicted future of terrestrial ecosystems on oceanic islands of the tropical Pacific. These islands lack continental connections but share histories of colonization, disharmonic biotas and biological invasions. We highlight ecological and socio-economic challenges to conservation in Pacific Island countries and suggest ways these could be overcome.

HISTORY

Pacific Island ecosystems are the result of four key historical phases: natural colonization and dynamics; impacts of indigenous settlers; impacts of non-indigenous settlers; and environmental awareness (Fig. 1). The first phase covers the geological appearance, and subsequent colonization by species, of an island before human arrival. The second and third phases include the impacts of humans on the environment. The final phase is the current one, with increasing concerns about environmental degradation and biodiversity loss. While there is considerable overlap between different phases, they illustrate the major changes in Pacific Island socio-ecological environments.

Natural colonization and dynamics

Volcanic, limestone or atoll islands in the tropical Pacific are geologically relatively young, not exceeding 40 million years (Mueller-

[1]School of Natural and Built Environments and Barbara Hardy Institute, University of South Australia, Mawson Lakes Campus, GPO Box 2471, Adelaide, SA 5001, Australia. E-mail: Gunnar.Keppel@gmail.com.
[2]School of Environment, Griffith University Gold Coast, QLD 4222, Australia.
[3]Délégation à la Recherche, Government of French Polynesia, B.P. 20981, Papeete, Tahiti.
[4]Department of Ecology and Ecosystem Management, Chair for Strategic Landscape Planning and Management, Technical University of Munich, Emil-Ramann-Strasse 6, 85350 Freising-Weihenstephan, Germany.

PACIFIC CONSERVATION BIOLOGY Vol. **20(2):** ??–??. Surrey Beatty & Sons, Sydney. 2014.

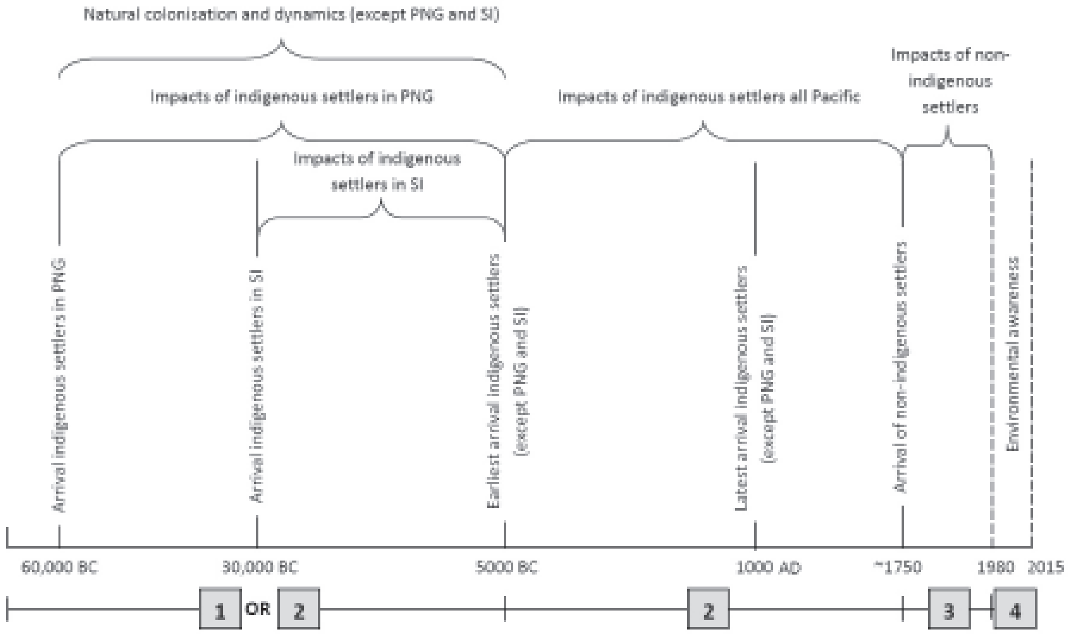

Fig. 1. Schematic timeline of the four historical phases of Pacific ecosystems (not to scale). 1 = natural colonization, 2 = impacts of indigenous settlers, 3 = impacts of non-indigenous settlers, 4 = environmental awareness. PNG = Papua New Guinea, SI = Solomon Islands.

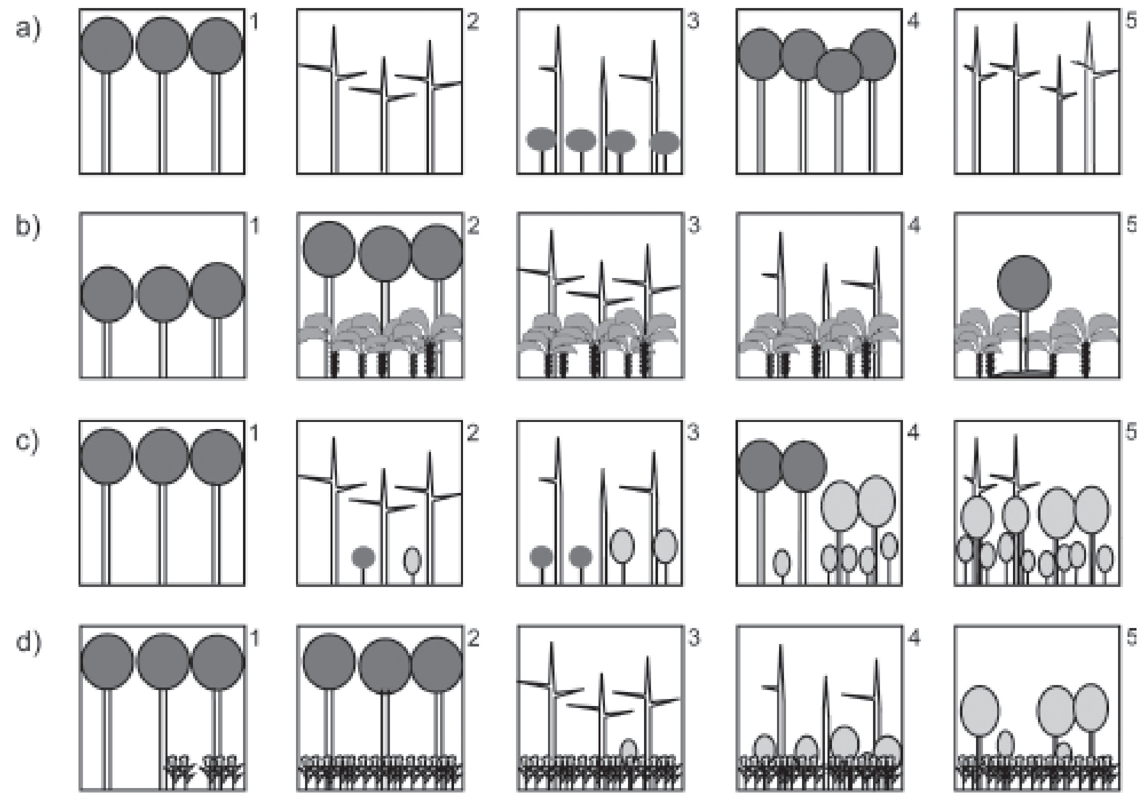

Fig. 2. Long-term dynamics of Hawai'i´s montane ohia rainforest under natural conditions (a and b) and with potential long-term effects of alien plant species (c and d), after Boehmer and Niemand (2009). a) Replacement dieback: regular cohort dynamics of native ohia (*Metrosideros polymorpha*) with subsequent replacement of the dead canopy cohort after dieback. b) Displacement dieback: displacement of ohia by native hapu´u tree ferns *Cibotium* sp. after dieback; dense treefern canopy inhibits ohia regeneration on nutrient rich ash soils. c) New displacement dieback, Type 1: displacement of ohia by cohorts of non-native strawberry guava *Psidium cattleianum*, producing guava-dominated forest. d) New displacement dieback, Type 2: invasion of non-native kahili ginger *Hedychium gardnerianum* and subsequent dominance in the understory, inhibiting ohia regeneration after dieback and facilitating displacement by *Psidium cattleianum*, producing a *Psidium*-forest with *Hedychium*-dominated understory.

Dombois and Fosberg 1998), and harbour more than 12 000 plant and 500 bird species (Mittermeier *et al*. 2004). For islands in the tropical Pacific, these biota originated recently from continents, particularly Australia, Southeast Asia and the Americas. Colonization was probably continuous, with various lineages arriving at different times, within the last 10 million years (Keppel *et al*. 2009).

The diversity and endemism of Pacific Islands' biota reflects the age, area and isolation of islands, decreasing eastwards from the large and less isolated islands in the western Pacific (e.g. Diamond and Mayr 1976, Keppel *et al*. 2010). Speciation within and among islands has also contributed to diversity (e.g. Cronk *et al.* 2005, Percy *et al.* 2008). Intra-island speciation was likely facilitated by the presence of diverse ecosystems (Mueller-Dombois and Fosberg 1998), the natural fragmentation of some ecosystems (e.g. tropical montane cloud forest) into isolated communities (Merlin and Juvik 1993), and microhabitat specialization (Webb 1999, Keppel *et al.* 2011).

Low alpha diversity in Pacific Island ecosystems has simplified some ecological processes, compared to continental environments. For example, secondary succession, through auto-succession, involves the same species in some ecosystems of Hawai'i (e.g. Mueller-Dombois and Boehmer 2013) and Galápagos (Itow and Mueller-Dombois 1988). Despite such simplicity, ecosystems on tropical Pacific Islands display considerable resilience. For example, Western Polynesian and Eastern Melanesian rainforests are adapted to frequent cyclones, surviving or recovering quickly, even after severe damage (e.g. Burslem *et al.* 2000, Webb *et al.* 2011). However, repeated intense disturbances can alter successional pathways, producing alternate communities (Elmqvist *et al.* 1994, Franklin 2007).

Natural disturbance regimes drive vegetation dynamics (Boehmer and Richter 1997). In many archipelagos of the tropical Pacific these include extreme climatic events, such as cyclones (Keppel *et al*. 2010), and extreme geologic events, such as volcanic eruptions. In Hawai'i, *Metrosideros polymorpha* trees establish after eruption, producing an even-aged cohort with an estimated life span of 400–600 years (Kitayama *et al.* 1995). Such cohorts may be maintained for thousands of years, sometimes affected by landscape-level canopy dieback triggered by extreme climatic events (Boehmer *et al.* 2013, Fig. 2). *M. polymorpha* displays enormous resilience, persisting over millions of years as the keystone species in rainforests through severe climatic changes (Hotchkiss *et al.* 2000, Mueller-Dombois and Boehmer 2013). Similarly, the regeneration dynamics of Araucariaceae in New Caledonia and New Guinea, and *Scalesia* species in Galápagos, depend on large-scale disturbances and cyclic regeneration of successive cohorts (Itow and Mueller-Dombois 1998, Enright *et al.* 1999).

Impacts of indigenous settlers

Humans arrived on oceanic Pacific Islands 5 000–700 years ago (Anderson 2009, Wilmhurst *et al.* 2011), with severe environmental consequences. For example, giant, now-extinct megapodes, pigeons, frogs, tortoises and iguanas (Pregill and Worthy 2003) lived in Fiji before humans arrived. On other Pacific Islands, large-bodied animals were also rapidly driven to extinction by early human colonizers (e.g. Steadman 2006).

The first colonizers also introduced numerous plant and animal species, with rats and pigs particularly impacting ecosystems (Anderson 2009). After initial rapid impacts, the synergistic effects of habitat conversion, species extinctions, species introductions, and novel pathogens continued to change ecosystems, driving more species to extinction (Burney *et al.* 2001). The extinction of large-bodied animals may continue to affect the present dispersal ability of large-seeded tree species (McConkey and Drake 2002).

Large-scale changes in vegetation also occurred. Vegetation was cleared for agriculture, introduced animals preyed on seeds (McConkey *et al.* 2003, Meyer and Butaud 2009), and the frequency of fire increased (Hope *et al.* 2009). As a result, prevalent species and vegetation types disappeared, sometimes within decades of human arrival (e.g. Flenley and King 1984, Prebble and Dowe 2008). In dry regions (e.g. western Viti Levu, Fiji), forests were replaced by herbaceous landscapes (Rolett and Diamond 2004, Hope *et al*. 2009).

Impacts of non-indigenous settlers

European settlers further exacerbated environmental impacts by increasing habitat destruction and/or conversion, hunting and harvesting native species, and introducing additional non-native plants, animals and pathogenic diseases (Cuddihy and Stone 1990). As a result, little primary forest remains and there are now more than 1500 terrestrial species listed on the IUCN Red List of threatened species for the Pacific region (Morrison 2012, Table 1). The Pacific region also has the highest proportion of threatened birds in the world and more than 90% (201 species) of all Pacific terrestrial gastropods are listed as threatened. Terrestrial species are most impacted by habitat loss (55%; includes modification, degradation, fragmentation), followed by overexploitation (32%; hunting and gathering, logging), invasive alien species (22%; flora, fauna, pathogens) and pollution (14%; airborne, water, terrestrial), with many species affected by more than one threatening process (Morrison 2012). These impacts stem from local threats (e.g. land clearing for plantations, construction of tourist resorts), to landscape level factors (e.g. downstream pollution from urban areas or industry, overharvesting of local flora/fauna populations), to ecosystem scale events such as widespread logging, large-scale commercial agriculture, urban spread and mining (Kingsford *et al*. 2009, Woinarski 2010).

Logging and intensive agriculture are two of the bigger threats that have destroyed large areas of native ecosystems (Kingsford *et al*. 2009, Wardell-Johnson *et al*. 2011). Logging continues at high rates in the Solomon Islands and New Guinea, with considerable social and environmental consequences (Kabutaulaka 2000, Shearman *et al.* 2009). Commercial plantations of non-native trees, including mahogany, Caribbean pine and oil palms are replacing native forests (Varmola 2002, Nelson *et al.* 2014). In addition, agriculture extent and intensity increases with growing human populations and a demand-driven market, exemplified by kava cultivation on Pohnpei Island (Merlin and Raynor 2005). Furthermore, extensive mining has considerably damaged ecosystems on islands such as Nauru and Grande Terre, New Caledonia (e.g. Manner *et al*. 1984)

Few habitats are currently free from non-native plant and animal species and, although the impacts of invasive species are variable and complex (Fischer *et al.* 2009, Minden *et al.* 2010, Fig. 2), they often have devastating effects, with many current island habitats becoming "novel" or "hybrid" ecosystems, with abundant invasive alien species (Pouteau *et al.* 2013). Ungulates (goats, sheep, horses, cattle), introduced in the 18th century, dramatically affected the vegetation of the Hawai`ian and Marquesas Islands (Merlin and Juvik 1992). The accidental introduction of the black rat *Rattus rattus* from European ships caused numerous extinctions of endemic land birds on several Polynesian archipelagos (Thibault *et al.* 2002). Other faunal introductions with catastrophic impacts on the native fauna of Pacific Islands include the small Indian mongoose *Herpetes javanicus* in Fiji and Hawai`i (Morley and Winder 2013), the carnivorous rosy-wolf snail *Euglandina rosea* in Hawai`i, Samoa and French Polynesia (Cowie 2001), the little fire ant *Wasmannia auropunctata* in New Caledonia (Le Brenton *et al.* 2003), and the brown tree snake *Boiga irregularis* on Guam (Wiles *et al.* 2003). Alien birds, such as the common mynah *Acridotheres tristis* or bulbuls *Pycnonotus* spp. compete with native birds for food and nesting sites and disperse invasive plants, changing the seed dispersal networks in forest ecosystems (Spotswood *et al.* 2012).

Continuously increasing numbers of invasive alien plants are also changing the structure and processes of Pacific Island ecosystems. Several introduced plant species are now dominant in native forests (see Meyer 2004, 2014, Fig. 2), including strawberry guava *Psidium cattleianum*, rose-apple *Syzygium jambos*, *Miconia calvescens* and *Clidemia hirta* in rain- and cloud forest. Invasive, flammable grasses have invaded many dry habitats, establishing new fire regimes, community dynamics and nutrient cycling (D'Antonio and Vitousek 1992). Other potential threats to native forests include the African tulip tree *Spathodea campanulata* and octopus tree *Schefflera actinophylla*, now widely naturalized in Fiji, Hawai'i and Tahiti (e.g. Meyer 2000). Furthermore, invasive plants may possess traits previously absent in native ecosystems that change ecosystem processes. For example, the non-native tree *Morella faya* has quadrupled the amount of nitrogen entering soils in Hawai'i (Vitousek *et al.* 1987).

Environmental Awareness

Over the last few decades, there has been increasing awareness about the environmental consequences of human activities and the need to protect native biodiversity on tropical Pacific Islands. This is manifested through international and regional agreements designed to protect the environment. For example, most Pacific Island countries have committed to monitoring biodiversity as part of the United Nation's Millennium Goals and the Convention on Biological Diversity's 2011–2020 Strategic Plan for Biodiversity (CBD 2010) and through the Convention for the protection of Natural Resources and Environment of the South Pacific Region (Osmundsen 1992). Furthermore, most nations have some protected areas (Table 1) and legislation protecting flora and fauna. There are also a growing number of international and local non-government environmental organizations (NGOs) working in the region (Lees and Siwatibau 2009).

Increasing environmental awareness has led to the emergence of some successful conservation initiatives at various levels. Several, mostly community-managed, protected areas have been in existence for decades, sometimes providing important local revenue (Keppel *et al*. 2012a). Furthermore, some NGO- and government-driven projects have successfully eradicated invasive species on mostly uninhabited Pacific Islands (e.g. Veitch *et al*. 2011). On the national level, Fiji has established a multi-institutional

Table 1. Estimates of the extent (land area) and relative amount (%) of terrestrial habitats (forest remaining, primary forest, protected forest), biodiversity (plant, vertebrate), and threat indicators (threatened species, invasive species) for countries and territories in the tropical Pacific. Note that information was obtained from global databases for consistency and that better estimates are available for some aspects from different sources.

Country	Land Area (x1000 ha)[a]	Land area forested (%)[a,f]	Land area classified as primary forest (%)[a]	Land area protected (%)[b]	Number of plant species[c]	Number of terrestrial vertebrate species[c]	Number of IUCN red-listed species[d]	Number of invasive species[e]
American Samoa	20	90.0	unavailable	0	269	77	33	79
Cook Islands	24	66.7	0.0	7	667	76	43	100
Fiji	1827	55.5	24.6	2.2	2660	172	213	147
French Polynesia	352	42.3	10.9	1.1	1611	130	233	192
Galápagos	801	unavailable	unavailable	unavailable	unavailable	unavailable	132	70
Guam	55	47.3	unavailable	20.9	361	158	39	129
Hawai'i	1656	unavailable	unavailable	unavailable	unavailable	unavailable	308	310
Kiribati	81	14.8	0.0	13	163	69	26	66
Marshall Islands	18	72.2	44.4	2	371	105	19	75
Micronesia (Federated States of)	70	91.4	68.6	8	755	175	50	98
Nauru	2	0.0	0.0	0	35	50	13	42
New Caledonia	1857	45.9	23.6	7.4	6451	294	420	196
Niue	26	73.1	23.1	unavailable	148	53	21	65
Northern Mariana Islands	46	65.2	17.4	4.4	100	161	39	99
Palau	46	87.0	unavailable	1.3	328	178	68	93
Papua New Guinea	45286	63.4	57.9	9.7	18894	1483	363	100
Rapa Nui (Easter Island)	17	0	unavailable	unavailable	unavailable	unavailable	1	1
Samoa	283	60.4	unavailable	3.6	1005	96	33	82
Solomon Islands	2799	79.1	39.5	0.8	2597	426	121	86
Tokelau	1	0.0	0.0	unavailable	56	22	15	16
Tonga	72	12.5	5.6	25.5	581	84	36	85
Tuvalu	3	33.3	unavailable	0	121	46	19	23
Vanuatu	1220	36.1	unavailable	4.5	1994	156	55	66
Wallis and Futuna	14	42.9	unavailable	0	351	57	22	52

[a]Food and Agricultural Organization (FAO; http://www.fao.org)
[b]World Bank (http://www.worldbank.org)
[c]Morrison (2012)
[d]International Union for Conservation of Nature (http://www.iucnredlist.org)
[e]Global Invasive Species Database (http://www.issg.org/database)
[f]includes any forest cover (primary, secondary, exotic).

protected area committee, making considerable progress towards protecting 20% of remaining forests (Keppel 2014).

IMPLEMENTING CONSERVATION

Despite increased environmental awareness and funding and some conservation successes, few new terrestrial protected areas have been established over the last two decades to halt habitat conversion and degradation, and the number of species listed on the IUCN Red List is growing (Keppel *et al.* 2012b, Morrison 2012, Table 1). Rapidly growing and more mobile human populations, related pressures from natural resource extraction and species introductions, and the imminent impacts of climate change, are intensifying threats for the unique terrestrial biodiversity of Pacific islands (Wardell-Johnson *et al*. 2011, Woinarski 2010). This is compounded by the limited amount and quality of conservation data available, poor collaboration among stakeholders, limited and mismanaged funding, and limited political and public awareness of conservation principles.

Ecological challenges

Controlling invasive species is difficult, especially when a species is widespread. Most successful eradications have been achieved on localized scales (e.g. Veitch *et al*. 2011). Biological control is an efficient tool, but can negatively impact on native biodiversity where host-specificity of the agent was not adequately ascertained (Kuris 2003). Similarly, restoring degraded landscapes with depleted soils, non-native seed banks and altered ecosystem dynamics is challenging (Gardener *et al*. 2013).

Anthropogenic climate change directly impacts on the biodiversity of the region as well as indirectly through other environmental threats, intensifying current pressures (Wardell-Johnson *et al.* 2011). Sea level rise, changes to rainfall patterns and hydrological regimes, more extreme weather events, and increased temperatures will impact on terrestrial biodiversity (Leslie *et al.* 2007, IPCC 2013), increasingly threatening many species and their ecosystems. For example, tropical montane cloud forests are experiencing altered precipitation, humidity, temperature, and storm frequency and duration (Foster 2001), with these impacts probably exacerbated by complex synergetic effects (Boehmer 2011).

Social and economic challenges

There is limited reliable quantitative data on species diversity and distributions, the quality and availability of habitats, or conservation threats (e.g. Solomon Islands and Vanuatu lack published floras). There are publicly available estimates (cf. Table 1), but with severe inaccuracies. For example, the Cook Islands have primary forest remaining (Keppel *et al*. 2012a) and only 890 of the 1611 vascular plant species reported for French Polynesia are native, while the terrestrial protected area coverage in French Polynesia is almost twice the extent reported (Meyer and Salvat 2009). Many other environmental indicators, such as the species listed in the IUCN Red List (Morrison 2012), are based on data with major knowledge gaps for certain taxonomic groups and geographic areas.

Numerous stakeholders, including government departments, United Nations agencies, regional intergovernmental agencies, local and international NGOs, community-based groups, academic institutions and landowners, are involved in conservation of Pacific Island ecosystems (Lees and Siwatibau 2009). Despite this large number, or because of it, there is often little consultation or collaboration, duplicated conservation effort and wasted resources. Conflict and competition may also exist among the different groups that pursue their own goals and responsibilities to donor agencies, which are frequently unrelated to national and local conservation priorities (Hunnam 2002, Keppel *et al*. 2012b, Lees and Siwatibau 2009).

Active participation of landowners in the conservation and management of biodiversity is critical because most land (>80%) in Pacific Island nations is under customary (or traditional) ownership and managed by customary groups and processes, often linked to social and spiritual/religious beliefs (Ward 2000, Keppel *et al*. 2012b). Land is highly valued, providing almost all subsistence requirements, status, psychological security and identity or a place to belong (Kamikamica 1987). The complex land tenure systems and relatively limited government authority, compared to countries with central governance of the land, makes creating and maintaining protected areas more complicated (Keppel *et al*. 2012b).

Management of conservation resources is often inefficient. Most resources are with international NGOs, often with excessive administration costs, repetitive or redundant processes, and poor prioritization of conservation targets (Bottrill *et al*. 2011, Keppel *et al*. 2012b). Most Pacific Island countries are developing nations and environmental sectors of governments are generally poorly underfunded and considered low priority as governments and landowners often rely heavily on natural resource extraction for income (Morrison 2012). Further, international donor-assisted programmes usually have short-funding cycles of 3–5 years, insufficient for successful implementation of conservation programmes that meet the needs of local landowning communities (Hunnam 2002, Sayer and Campbell 2004).

Increasing environmental and conservation knowledge and awareness at all levels is essential for effective management of Pacific Island ecosystems and biodiversity. This includes increasing regional awareness about the importance of ecosystem management (e.g. large-scale and long-term ecosystem impacts of kava cultivation triggered establishment of the Pohnpei Watershed Forest Reserve), invasive species prevention (e.g. ongoing community workshops are slowing the spread of green iguanas, *Iguana iguana*, in Fiji), and sustainable harvesting of biodiversity (e.g. ongoing government workshops about the impacts of large-scale logging and palm oil plantations in the Solomon Islands). Such information is critical for local government and community support for conservation programmes, as well as improving the ability of politicians, government employees and local communities to make informed decisions about their natural resources.

FUTURE DIRECTIONS

Effective policies that protect Pacific Island biodiversity, addressing current and emerging ecological, political and social challenges are required. Such policies have been proposed but their implementation needs to build local capacity at all levels (Kingsford *et al*. 2009). They need to be linked to clear, specific, national targets with quantifiable outcomes (e.g. reducing the number of plants listed as threatened on the IUCN Red List by a certain percentage by 2030). Such targets should be identified and strategically prioritized, based on national importance, producing concerted and concentrated conservation actions. To evaluate effectiveness, regular state of the environment quantitative reporting is essential. This involves national monitoring the extent of and threats to ecosystems, including the distribution and abundance of species.

Functional ecosystems are especially important for developing island nations, with large rural populations, dependent on natural resources. The importance of these ecosystems and their species is not always recognized (Scanlon *et al*. 2014), highlighting the need for increased environmental awareness. A greater understanding of the central role of ecosystems and biodiversity to the well-being of Pacific Island societies should increase willingness and responsibility for environmental protection, potentially reducing current inefficiencies affecting conservation.

The effects of multiple threats are more difficult to predict, constituting one of the major dangers posed by anthropogenic climate change in Oceania (Wardell-Johnson *et al*. 2011). For example, Hawai'ian montane forests are fundamentally threatened by alien invasive species, exacerbated by projected increased frequency of climatic anomalies, due to climate change (Loope and Giambelluca 1998). The latter will increase the vulnerability of the indigenous key tree species, making forests more susceptible to biological invasions. If invading alien species colonize before indigenous species establish, the composition and structure of the native ecosystem will change (Minden *et al.* 2010, Fig. 2). This may produce completely new ecosystems with few native plant species, as on some islands of French Polynesia (Pouteau *et al.* 2013).

Pacific Island ecosystems have displayed great resilience to natural disturbances and climatic changes over thousands of years, which should be utilized in restoration and conservation efforts. More recently, many ecosystems are becoming increasingly vulnerable to anthropogenic effects, making them among the most threatened on our planet (Gillespie *et al*. 2012). Only a concerted effort, focussed on alleviating and mitigating key threats through effective policies and the collaboration of key stakeholders, will halt or minimize the continuing loss of biodiversity. Such an effort would need to be based on increased local capacity and environmental awareness.

ACKNOWLEDGEMENTS

The authors are members of the Pacific-Asia Biodiversity Transect (PABITRA) network and the concept of four phases of island development were inspired by a presentation on 'Biodiversity, ecosystem services, and resilient societies' (9 July 2013, 12th Pacific Science Inter-Congress, Suva, Fiji by Prof. Dieter Mueller-Dombois, the founder of PABITRA.

REFERENCES

Anderson, A., 2009. The rat and the octopus: initial human colonization and the prehistoric introduction of domestic animals to Remote Oceania. *Biolog. Invasions* **11:** 1503–1519.

Boehmer, H. J., 2011. Vulnerability of tropical montane rain forest ecosystems due to climate change. Pp. 789–802 *in* Coping with Global Environmental Change, Disasters and Security — Threats, Challenges, Vulnerabilities and Risks ed by H. G. Brauch, Ú. Oswald Spring, C. Mesjasz, J. Grin, P. Kameri-Mbote, B. Chourou, P. Dunay and J. Birkmann. Springer-Verlag, Berlin, Germany.

Boehmer, H. J. and Niemand, C., 2009. Die neue Vegetationsdynamik pazifischer Wälder. Wie Klimaextreme und biologische Invasionen Inselökosysteme verändern. *Geographische Rundschau* **61:** 32–37.

Boehmer, H. J. and Richter, M., 1997. Regeneration of plant communities — an attempt to establish a typology and zonal system. *Plant Res. & Devel.* **45:** 74–88.

Boehmer, H. J., Wagner, H. H., Jacobi, J. D., Gerrish, G. C. and Mueller-Dombois, D., 2013. Rebuilding after collapse: evidence for long-term cohort dynamics in the native Hawaiian rain forest. *J. Vegetation Sci.* **24:** 639–650.

Bottrill, M. C., Hockings, M. and Possingham, H. P., 2011. In pursuit of knowledge: addressing barriers to effective conservation evaluation. *Ecol. & Soc.* **16:** 14.

Burney, D. A., James, H. F., Burney, L. P., Olson, S. L., Kikuchi, W., Wagner, W. L., Burney, M., McCloskey, D., Kikuchi, D., Grady, F. V., Gage II, R. and Nishek, R., 2001. Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. *Ecolog. Monogr.* **71:** 615–641.

Burslem, D. F. R. P., Whitmore, T. C. and Brown, G. C., 2000. Short-term effects of cyclone impact and long-term recovery of tropical rain forest on Kolombangara, Solomon Islands. *J. Ecol.* **88:** 1063–1087.

CBD, 2010. COP 10 Decision X/2 — Strategic plan for biodiversity 2011–2020, available at: http://www.cbd.int/sp.

Cowie, R. H., 2001. Invertebrate invasions on Pacific Islands and the replacement of unique native faunas: a synthesis of the land and freshwater snails. *Biolog. Invasions* **3:** 119–136.

Cronk, Q. C. B., Kiehn, M., Wagner, W. L. and Smith, J. F., 2005. Evolution of *Cyrtandra* (Gesneriaceae) in the Pacific Ocean: the origin of a supertramp clade. *Amer. J. Botany* **92:** 1017–1024.

Cuddihy, J. W. and Stone, C. P., 1990. Alteration of native Hawaiian vegetation: effects of humans, their activities and introductions. University of Hawai'i Press, Honolulu, Hawai'i, USA.

D'Antonio, C. M. and Vitousek, P. M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Ann. Rev. Ecol. & Syst.* **23:** 63–87.

Diamond, J. M. and Mayr, E., 1976. Species-area relation for birds of the Solomon Archipelago. *Proc. Nat. Acad. Sci., USA* **73:** 262–266.

Elmqvist, T., Rainey, W. E., Pierson, E. D. and Cox, P. A., 1994. Effects of tropical cyclones Ofa and Val on the structure of a Samoan lowland rain forest. *Biotropica* **26:** 384–391.

Enright, N. J., Ogden, J. and Rigg, L. S., 1999. Dynamics of forests with Araucariaceae in the western Pacific. *J. Vegetation Sci.* **10:** 793–804.

Fischer, L. K., von der Lippe, M. and Kowarik, I., 2009. Tree invasion in managed tropical forest facilitates endemic species. *J. Biogeog.* **36:** 2251–2263.

Flenley, J. R. and King, S. M., 1984. Late Quaternary pollen records from Easter Island. *Nat.* **307:** 47–50.

Foster, P., 2001. The potential negative impacts of global climate change on tropical montane cloud forests. *Earth-Sci. Rev.* **55:** 73–106.

Frankham, R., 1998. Inbreeding and extiction: island populations. *Cons. Biol.* **12:** 665–675.

Franklin, J., 2007. Recovery from clearing, cyclone and fire in rain forests of Tonga, South Pacific: vegetation dynamics 1995–2005. *Austral Ecol.* **32:** 789–797.

Gardener, M. R., Trueman, M., Buddenhagen, C., Heleno, R., Jaeger, H., Atkinson, R. and Tye, A., 2013. A pragmatic approach to the management of plant invasions in Galapagos. Pp. 349–374 *in* Plant Invasions in Protected Areas: Patterns, Problems and Challenges ed by L. C. Foxcroft, P. Pyšek, D. M. Richardson and P. Genovesi. Springer-Verlag, Dordrecht, Netherlands.

Gillespie, T. W., Lipkin, B., Sullivan, L., Benowits, D. R., Pau, S. and Keppel, G., 2012. The rarest and least protected forests in biodiversity hotspots. *Biodiv. & Cons.* **21:** 3597–3611.

Hope, G., Stevenson, J. and Southern, W., 2009. Vegetation histories from the Fijian Islands: Alternative records of human impact. Pp. 63–86 *in* The Early Prehistory of Fiji (Terra Australis 31) ed by G. Clark and A. Anderson. ANU ePress, Canberra, Australia.

Hotchkiss, S., Vitousek, P. M., Chadwick, O. A. and Price, J. P., 2000. Climate cycles, geomorphological change, and the interpretation of soil and ecosystem development. *Ecosyst.* **3:** 522–533.

Hunnam, P., 2002. Lessons in Conservation for People and Projects in the Pacific Islands Region. United Nations Development Programme, New York, USA.

IPCC, 2013. Climate Change 2013: the Physical Science Basis. Summary for Policy Makers. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

Itow, S. and Mueller-Dombois, D., 1988. Population structure, stand-level dieback and recovery of *Scalesia pedunculata* forest in the Galápagos Islands. *Ecolog. Res.* **3:** 333–339.

Kabutaulaka, T. T., 2000. Rumble in the jungle: land, culture and (un)sustainable logging in Solomon Islands. Pp. 88–97 *in* Culture and Sustainable Development in the Pacific ed by A. Hooper. Asia Pacific Press, Canberra, Australia.

Kamikamica, J. N., 1987. Fiji. Making native land productive. Pp. 226–239 *in* Land Tenure in the Pacific ed by R. Crocombe. University of the South Pacific, Suva, Fiji.

Keast, A. and Miller, S. E., 1996. The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes. SPB Academic Publishing, Amsterdam, Netherlands.

Keppel, G., 2014. The importance of expert knowledge in conservation planning — Comment to an article by C.J. Klein *et al*. *Marine Policy*: early view.

Keppel, G., Lowe, A. J. and Possingham, H. P., 2009. Changing perspectives on the biogeography of the tropical South Pacific: influences of dispersal, vicariance and extinction. *J. Biogeog.* **36:** 1035–1054.

Keppel, G., Buckley, Y. M. and Possingham, H. P., 2010. Drivers of lowland rain forest community assembly, species diversity and forest structure on islands in the tropical South Pacific. *J. Ecol.* **98:** 87–95.

Keppel, G., Tuiwawa, M. V., Naikatini, A. and Rounds, I. A., 2011. Microhabitat specialization of tropical rain forest canopy trees in the Sovi Basin, Viti Levu, Fiji Islands. *J. Tropical Ecol.* **27:** 491–501.

Keppel, G., Morrison, C., Hardcastle, J., Rounds, I. A., Wilmott, I. K., Hurahura, F. and Patterson, K. S., 2012a. Conservation in tropical Pacific Island countries: case studies of successful programmes. *PARKS* **18:** 111–123.

Keppel, G., Morrison, C., Watling, D., Tuiwawa, M. and Rounds, I. A., 2012b. Conservation in tropical Pacific Island countries: why most current approaches are failing. *Cons. Letters* **5:** 256–265.

Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P. L., Nowicki, C., Mutke, J. and Barthlott, W., 2009. A global assessment of endemism and species richness across island and mainland regions. *Proc. Nat. Acad. Nat. Sci., USA* **106:** 9322–9327.

Kingsford, R. T., Watson, J. E. M., Lundquist, C. J., Venter, O., Hughes, L., Johnston, E. L., Atherton, J., Gawel, M., Keith, D. A., Mackey, B. G., Morley, C., Possingham, H. P., Raynor, B., Recher, H. F. and Wilson, K. A., 2009. Major conservation policy issues for biodiversity in Oceania. *Cons. Biol.* **23:** 834–840.

Kitayama, K., Mueller-Dombois, D. and Vitousek, P. M., 1995. Primary succession of Hawaiian montane forest on a chronosequence of eight lava flows. *J. Vegetation Sci.* **6:** 211–222.

Kuris, A. M., 2003. Did biological control cause extinction of the coconut moth, *Levuana iridescens*, in Fiji? *Biolog. Invasions* **5:** 133–141.

Le Brenton, J., Chazeau, J. and Jourdan, H., 2003. Immediate impacts of invasion by *Wasmannia auropunctata* (Hymenoptera: Formicidae) on native litter ant fauna in a New Caledonian rainforest. *Austral Ecol.* **28:** 204–209.

Lees, A. and Siwatibau, S., 2009. Strategies for effective and just conservation: the Austral Foundation's review of conservation in Fiji. *Curr. Cons.* **4:** 21–23.

Legra, L., Li, X. and Peterson, A. T., 2008. Biodiversity consequences of sea level rise in New Guinea. *Pac. Cons. Biol.* **14:** 191–199.

Leslie, L. M., Karoly, D. J., Leplastrier, M. and Buckley, B. W., 2007. Variability of tropical cyclones over the southwest Pacific Ocean. *Meteorol. & Atmospheric Physics* **97:** 171–180.

Loope, L. L. and Giambelluca, T., 1998. Vulnerability of island tropical montane cloud forests to climate change, with special reference to East Maui, Hawai'i. *Climatic Change* **39:** 503–517.

Manner, H. I., Thaman, R. R. and Hassal, D. C., 1984. Phosphate mining induced vegetation changes on Nauru Island. *Ecol.* **65:** 1454–1465.

McConkey, K. R. and Drake, D. R., 2002. Extinct pigeons and declining bat populations: are large seeds still being dispersed in the Tropical Pacific? Pp. 381–395 *in* Seed Dispersal and Frugivory: Ecology, Evolution and Conservation ed by D. J. Levey, W. R. Silva and M. Galetti. CAB Publishing, Wallingford, UK.

McConkey, K. R., Drake, D. R., Meehan, H. J. and Parsons, N., 2003. Husking stations provide evidence of seed predation by introduced rodents in Tongan rainforest. *Biolog. Cons.* **109:** 221–225.

Merlin, M. D. and Juvik, J. O., 1992. Relationships among native and alien plants on Pacific Islands with and without significant human disturbance and feral ungulates. Pp. 597–624 *in* Alien Plant Invasions in Native Ecosystems of Hawai'i: Management and Research ed by C. P. Stone, C. W. Smith and J. T. Tunison. University of Hawaii Cooperative National Park Resources Studies Unit, Honolulu, Hawai'i, USA.

Merlin, M. D. and Juvik, J. O., 1993. Montane cloud forests in the tropical Pacific: some aspects of their floristics, biogeography, ecology and conservation. Pp. 234–253 *in* Tropical Montane Cloud Forests. Proceedings of an International Symposium ed by L. S. Hamilton, J. O. Juvik and F. N. Scatena. East-West Center, Honolulu, Hawai'i, USA.

Merlin, M. D. and Raynor, W., 2005. Kava cultivation, native species conservation and integrated watershed resource management on Pohnpei Island. *Pac. Sci.* **59:** 241–260.

Meyer, J.-Y., 2000. Preliminary review of the invasive plants in the Pacific islands (SPREP Member Countries). Pp. 85–114 *in* Invasive Species in the Pacific: a Technical Review and Draft Regional Strategy ed by G. Sherley. South Pacific Regional Environment Programme (SPREP), Apia, Samoa.

Meyer, J.-Y., 2004. Threat of invasive alien plants to native flora and forest vegetation of Eastern Polynesia. *Pac. Sci.* **58:** 357–375.

Meyer, J.-Y., 2014. Critical issues and new challenges for the research and management of invasive plants in the Pacific Islands. *Pac. Cons. Biol.* in press.

Meyer, J.-Y. and Butaud, J. F., 2009. The impacts of rats on the endangered native flora of French Polynesia (Pacific Islands): drivers of plant extinction or coup de grâce species? *Biolog. Invasions* **11:** 1569–1585.

Meyer, J.-Y. and Salvat, B., 2009. French Polynesia: biology. Pp. 332–338 *in* Encyclopedia of Islands ed by R. Gillespie and D. Clague. University of California Press, Berkeley, California, USA.

Minden, V., Jacobi, J. D., Porembski, S. and Boehmer, H. J., 2010. Effects of invasive alien kahili ginger (*Hedychium gardnerianum*) on native plant species regeneration in a Hawaiian rainforest. *App. Vegetation Sci.* **13:** 5–14.

Mittermeier, R. A., Gil, P. R., Hoffman, M., Pilgrim, J., Brooks, T., Mittermeier, C. G., Lamoreux, J. and da Fonseca, G. A. B., 2004. Hotspots revisited: Earth's Biologically Richest and Most Threatened Terrestrial Ecoregions. Agrupación Sierra Madre, Mexico City, Mexico.

Morley, C. G. and Winder, L., 2013. The effect of the small Indian mongoose (*Urva auropunctatus*), island quality and habitat on the distribution of native and endemic birds on small islands within Fiji. *PLoS One* **8:** e53842.

Morrison, C., 2012. Impacts of tourism on threatened species in the Pacific region: a review. *Pac. Cons. Biol.* **18:** 227–239.

Mueller-Dombois, D. and Fosberg, F. R., 1998. Vegetation of the Tropical Pacific Islands. Springer-Verlag, New York, USA.

Mueller-Dombois, D., 2008. Pacific island forest: successionally impoverished and now threatened to be overgrown by aliens? *Pac. Sci.* **62:** 303–308.

Mueller-Dombois, D. and Boehmer, H. J., 2013. Origin of the Hawaiian rainforest and its transition states in long-term primary succession. *Biogeosci.* **10:** 5171–5182.

Nelson, P. N., Gabriel, J., Filer, C., Banabas, M., Sayer, J. A., Curry, G. N., Koczberski, G. and Venter, O., 2014. Oil palm and deforestation in Papua New Guinea. *Cons. Letters* **7:** early view.

Osmundsen, L., 1992. Paradise preserved? The contribution of the SPREP convention to the environmental welfare of the South Pacific. *Ecol. Law Quart.* **19:** 727–793.

Percy, D. M., Garver, A. M., Wagner, W. L., James, H. F., Cunningham, C. W., Miller, S. E. and Fleischer, R. C., 2008. Progressive island colonization and ancient origin of Hawaiian *Metrosideros* (Myrtaceae). *Proc. Roy. Soc. Lond., Series B (Biolog. Sci.)* **275:** 1479–1490.

Pouteau, R., Meyer, J.-Y., Fourdrigniez, M. and Taputuarai, R., 2013. Novel ecosystems in the Pacific Islands: assessing loss, fragmentation and alteration of native forests by invasive alien plants on the island of Moorea (French Polynesia). Pp. 19–33 *in* Biodiversity and Societies in the Pacific Islands ed by S. Larrue. Presses Universitaires de Provence & The Australian National University e-Press, Aix-en-Provence, France & Canberra, Australia.

Prebble, M. and Dowe, J. L., 2008. The late Quaternary decline and extinction of palms on oceanic Pacific Islands. *Quaternary Sci. Rev.* **27:** 2546–2567.

Pregill, G. K. and Worthy, T. H., 2003. A new iguanid lizard (*Squamata, Iguanidae*) from the late Quaternary of Fiji, Southwest Pacific. *Herpetologica* **59:** 57–67.

Rolett, B. and Diamond, J., 2004. Environmental predictors of pre-European deforestation on Pacific Islands. *Nat.* **431:** 443–446.

Sayer, J. A. and Campbell, B. M., 2004. The science of sustainable development: local livelihoods and the global environment. Cambridge University Press, Cambridge, UK.

Scanlon, A. T., Petit, S., Tuiwawa, M., and Naikatini, A., 2014. High similarity between a bat-services plant assemblage and that used by humans. *Biolog. Cons.* **174:** 111–119.

Shearman, P. L., Ash, J., Mackey, B., Bryan, J. E. and Lokes, B., 2009. Forest conversion and degradation in Papua New Guinea 1972–2002. *Biotropica* **41:** 379–390.

Spotswood, E. N., Meyer, J.-Y. and Bartolome, J. W., 2012. An invasive tree alters the structure of seed dispersal networks between birds and plants in French Polynesia. *J. Biogeog.* **39:** 2007–2020.

Steadman, D. W., 2006. Extinction and Biogeography of Tropical Pacific Birds. The University of Chicago Press, Chicago, USA.

Thibault, J.-C., Martin, J.-L., Penloup, A. and Meyer, J.-Y., 2002. Understanding the decline and extinction of Monarchs (Aves) in Polynesian islands. *Biolog. Cons.* **108:** 161–174.

Thorne, F., 1963. Biotic distribution patterns in the Pacific. Pp. 311–354 *in* Pacific Basin Biogeography: A Symposium ed by J. L. Gressit. Bishop Museum Press, Honolulu, Hawai'i, USA.

Varmola, M. (ed), 2002. Hardwood programmes in Fiji, Solomon Islands and Papua New Guinea. Forestry Department, Food and Agriculture Organization of the United Nations, Rome, Italy.

Veitch, C. R., Clout, M. N. and Towns, D. R. (eds), 2011. Island Invasives: Eradiaction and Management. Proceedings of the International Conference on Island Invasives. IUCN, Gland, Switzerland and Auckland, New Zealand.

Vitousek, P. M., Walker, L. R., Whiteaker, L. D., Mueller-Dombois, D. and Matson, P. A., 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Sci.* **238:** 802–804.

Ward, R. G., 2000. Land tenure in Pacific Islands: changing patterns and implications for land acquisition. Pp. 75–87 *in* Resettlement Policy and Practice in South East Asia and the Pacific ed by Asia Development Bank, Sydney, Australia.

Wardell-Johnson, G. W., Keppel, G. and Sander, J., 2011. Climate change impacts on the terrestrial biodiversity and carbon stocks of Oceania. *Pac. Cons. Biol.* **17:** 220–240.

Webb, E. L., 1999. Effects of topography on rainforest tree community structure and diversity in American Samoa and implications for frugivore and nectarivore populations. *J. Biogeog.* **26:** 887–897.

Webb, E. L., Seamon, J. O. and Fa'aumu, S., 2011. Frequent, low-amplitude disturbances drive high tree turnover rates on a remote, cyclone-prone Polynesian island. *J. Biogeog.* **38:** 1240–1252.

Wiles, G. J., Bart, J., Beck Jr., R. E. and Aguon, C. F., 2003. Impacts of the brown tree snake: patterns of decline and species persistence in Guam's avifauna. *Cons. Biol.* **17:** 1350–1360.

Wilmhurst, J. M., Hunt, T. L., Lipo, C. P. and Anderson, A. J., 2011. High-precision radiocarbon dating shows recent and rapid initial human colonization of East Polynesia. *Proc. Nat. Acad. Nat. Sci., USA* **108:** 1815–1820.

Woinarski, J. C. Z., 2010. Biodiversity conservation in tropical forest landscapes of Oceania. *Biolog. Cons.* **143:** 2385–2394.