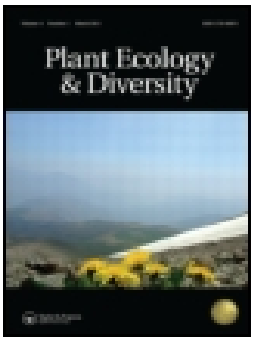

Plant Ecology & Diversity

ISSN: 1755-0874 (Print) 1755-1668 (Online) Journal homepage: https://www.tandfonline.com/loi/tped20

Short-term recovery of native vegetation and threatened species after restoration of a remnant forest in a small oceanic island of the South Pacific

Jean-Yves Meyer, Tiffany Laitame & Jean-Claude Gaertner

PLANT ECOLOGY & DIVERSITY
https://doi.org/10.1080/17550874.2019.1584651

ARTICLE

Short-term recovery of native vegetation and threatened species after restoration of a remnant forest in a small oceanic island of the South Pacific

Jean-Yves Meyer[a], Tiffany Laitame[b] and Jean-Claude Gaertner[c]

[a]Délégation à la Recherche, Gouvernement de la Polynésie française, Tahiti, French Polynesia; [b]UMR-241 EIO, Université de la Polynésie française, Tahiti, French Polynesia; [c]UMR-241 EIO, Institut de Recherche pour le Développement, Tahiti, French Polynesia

ABSTRACT

Background: Invasive alien species have transformed many natural ecosystems, especially on islands where endemic species are critically endangered, and where habitat restoration is a challenge.

Aims: We set up an experimental protocol to aid the restoration of a native remnant forest by excluding feral ungulates and suppressing an invasive tree.

Methods: Sixteen plots of 144 m^2 were delimited in a dry-mesic forest located on the small oceanic island of Rapa Iti (South Pacific) and half of them were fenced. The invasive tree *Psidium cattleianum* was manually cut in four fenced and four unfenced plots. We monitored understorey species diversity and abundance every 6 months for a period of 30 months in twenty-four 4-m^2 quadrats randomly selected in each plot.

Results: A significant increase of native species richness occurred in the fenced plots where the invasive tree was suppressed, and a decrease of alien species diversity in the fenced plots. The abundance of native and alien species was significantly reduced in the fenced plots, where recruitment of endemic threatened species was observed.

Conclusion: Rapid vegetation change occurred in 30 months. The understorey plant community response to ungulate exclusion and invasive tree removal strongly differed between native and alien species, with the recovery of native vegetation.

ARTICLE HISTORY
Received 17 July 2018
Accepted 6 February 2019

KEYWORDS
Exclosure; feral ungulates; invasive alien species; plant succession; restoration; threatened plants

Introduction

The globalisation of Earth's biota by introduced exotic species has been transforming local and regional floras and faunas (Wilson 1992; Davis 2003). One of its most striking consequences has been the increase of invasive alien plant and animal species (Soulé 1990; Perrings et al. 2005; Meyerson and Mooney 2007) which are recognised as a primary cause of the decline of native and endemic species, and sometimes their complete extinction (Mack et al. 2000; Vilà et al. 2011; Pyšek et al. 2012), especially in the more vulnerable island ecosystems (Paulay 1994; Cowie 2001; Steadman 2006; Castro and Jaksic 2008; Sax and Gaines 2008; Caujapé-Castells et al. 2010; Kraus and Duffy 2010; Kueffer et al. 2010). Restoration of island ecosystems by controlling invasive species or excluding them can significantly contribute to *in situ* conservation and recovery of rare endemic plants (Towns and Ballantine 1993; Loope and Medeiros 1994; Medeiros et al. 2014).

Monitoring plant succession, defined as the change in species composition and abundance over time (Walker et al. 2007), is crucial to assess the success of forest restoration programmes (Aronson and Van Andel 2006; Suding 2011). However, controlling invasive alien plants can be a long-term and difficult process, especially when they are widespread and dominant (Florens and Baider 2013). Excluding feral ungulates through fencing may facilitate the regeneration of native plant species (Cabin et al. 2000; Cole et al. 2012). However, the increase of both alien species diversity and cover after excluding ungulates and/or controlling invasive plants has also been noticed (Cabin et al. 2000; Cabin et al. 2002; Cuevas and Quesne 2006; Shimizu 2006; Jäger and Kowarik 2010; Weller et al. 2011; Cole and Litton 2014). Multiple studies have shown that once established, alien herbaceous weeds and woody species can increase in cover following the removal of feral ungulates (Eckhardt 1972; Scowcroft and Hobdy 1987; Aplet et al. 1991; Scowcroft and Conrad 1992; Tunison et al. 1994; Zavaleta et al. 2001; Kessler 2002). Moreover, even when alien grasses are removed and native seed sources are present, natural or passive regeneration (i.e. seedling recruitment) may be rare (Loope and Medeiros 1994; Cabin et al. 2002). Nevertheless, when

CONTACT Jean-Yves Meyer jean-yves.meyer@recherche.gov.pf
The supplemental material for this article can be accessed here.

restoration efforts have been maintained for several years, recruitment of native species is stimulated (Thaxton et al. 2010).

In this study, we conducted a relatively short-term (2.5 years) plant recovery experiment using two restoration treatments (fencing to exclude feral ungulates and removing an invasive tree species by cutting its trunks and stems) with a relatively high frequency of surveys (every 6 months) to investigate the following questions:

- What are the effects of ungulate exclusion and/or invasive plant removal on both native and alien plant communities?
- What are the short-term changes in species diversity, composition, abundance and species turnover following these restoration treatments?

Materials and methods

Study site

Rapa Iti (27°37′S; 144°20′W) is a small (40 km^2) and remote oceanic island (4.1–4.8 Myr old) in the South Pacific located at ca. 1200 km south-east of Tahiti, French Polynesia (Meyer and Claridge 2014). The climate is subtropical with a mean annual rainfall of 2560 mm and temperature of 20.6°C (with a recorded absolute minimum of 8.5°C), and without a pronounced dry or wet season (>150 mm monthly rainfall) (Laurent et al. 2004). The island comprises 507 inhabitants (2017 census) living in two villages (Area and Haurei), and is only accessible by a cargo boat (a 36-h trip, once every 2 months) from the neighbouring island of Raivavae located 550 km north-west.

The native vascular flora of Rapa Iti is unique in the South Pacific with ca. 60 local endemic species (31% of endemism), three monotypic genera (*Apostates* and *Pacifigeron*, Asteraceae; *Metatrophis*, Urticaceae), and several other endemic species belonging to four other south-eastern Polynesian endemic genera (*Fitchia* and *Oparanthus*, Asteraceae; *Apetahia*, Campanulaceae; *Haroldiella*, Urticaceae) (Meyer 2011; Meyer et al. 2014; Motley et al. 2014). The native forests of Rapa Iti have been severely degraded by past and current anthropogenic activities such as logging, fires, feral ungulates (goats, pigs and cattle) and invasive alien plants (Meyer et al. 2014). Dry-mesic forests are among the most threatened native habitats, and currently represent only 1% of the island surface, i.e. less than 40 ha (Motley et al. 2014) (Figure 1). These remnant forests host several critically endangered taxa (considered CR using IUCN Red List criteria) such as the island endemic sandalwood *Santalum insulare* var. *margaretae* (Santalaceae) with fewer than 10 plants known in the wild, and thus are of crucial conservation

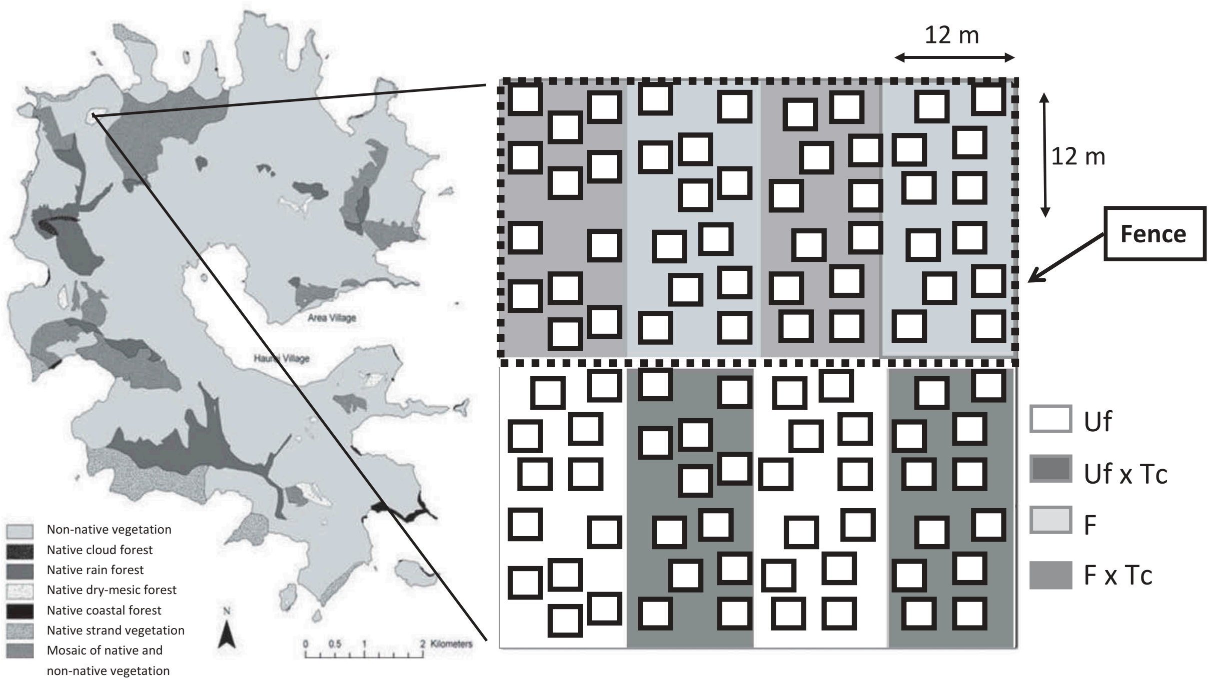

Figure 1. Vegetation map of Rapa Iti, French Polynesia (after Motley et al. 2014) and the sampling design of the restoration experiment.

The experimental treatments included: unfenced control (Uf), unfenced with removal of *Psidium cattleianum* (Uf × Tc), fenced (f), and fenced with removal of *Psidium cattleianum* (F × Tc).

importance (UICN France, MNHN, & DIREN Polynésie française 2015).

The study site is a ca. 1-ha patch of dry-mesic forest located on the north side of the island (27°34.922′S; 144°22.071′W; Figure 1), between 150 and 250 m elevation, and on a relatively steep slope (ca. 45° or 100%) (Figure 2). It is only accessible by small motor boats from the two villages (about 1 h) or by foot (several hours hike) as there is no road or track crossing the island. The forest is characterised by a semi-open canopy, reaching 6–8 m in height (Motley et al. 2014, and J.-Y.M., pers. obs.) with the presence of threatened endemic trees such as *Ixora stokesii* (Rubiaceae, endangered or EN according to IUCN), *Nesoluma* (syn. *Sideroxylon*) *polynesicum* (Sapotaceae, VU), *Sophora rapaensis* (Fabaceae, EN) and *Zanthoxylum* sp. (Rutaceae, EN) and other native species which are locally rare such as *Metrosideros collina* (Myrtaceae) (Table 1). The overstorey vegetation is dominated by strawberry guava *Psidium cattleianum* (Myrtaceae), a small tree native to Brazil, probably introduced in Rapa Iti in the 1930s (first collected by botanist Harold St-John in 1934) for its edible fleshy fruits. This shade-tolerant species with an abundant fruit production (Wessels et al. 2007; Uowolo and Denslow 2008) is particularly invasive in tropical and subtropical rainforests of the Pacific islands, including the Bonin Islands (Shimizu 2006), the Hawaiian Islands (Huenneke and Vitousek 1990; Cole et al. 2012), Lord Howe (Auld and Hutton 2004) and the Society Islands, French Polynesia (Meyer 2004), as well as in the Indian Ocean islands including Mauritius (Lorence and Sussman 1986; Florens et al. 2010, 2016), La Réunion (McDonald et al. 1991; Baret et al. 2006) and the Seychelles (Gerlach 2004; Rocamora and Henriette 2015) where it forms dense thickets excluding native and endemic plant species.

The second main threat to this remnant dry-mesic forest is grazing by feral ungulates which

Figure 2. A view of the study site, Rapa Iti, French Polynesia in 2011 with the dry-mesic forest remnant on the right side (photographic credit: T. Laitame).

Table 1. List of woody species recorded in the study and in surrounding areas, Rapa Iti, French Polynesia.

Species	Family	Chorology	Conservation status	Habit (life form)	Elevation range (habitat type)	Frequency/abundance on island
Allophylus rhomboidalis	Sapindaceae	IND	LR	Tree	Mid elev. (slope)	Rare
Alyxia stellata	Apocynaceae	IND		Shrub	Mid elev. (slope)	Common
Celtis pacifica[a]	Ulmaceae	IND		Tree	Mid elev. (slope)	Rare
Cordyline fruticosa[a]	Liliaceae	POL		Herb	Mid elev. (cliff)	Common
Fagraea berteroana	Loganiaceae	IND		Tree	Low elev. (valley)	Common
Ficus tinctoria	Moraceae	POL		Tree	Low elev. (valley)	Common
Freycinetia impavida[a]	Pandanaceae	IND		Liana	Mid elev. (slope)	Abundant
Glochidion longfieldiae	Phyllantaceae	END Rapa	VU	Tree	Mid elev. (slope)	Common
Heliotropium foertherianum	Boraginaceae	IND		Shrub	Low elev.(littoral)	Common
Ixora stokesii[a]	Rubiaceae	END Rapa	VU	Tree	Mid elev. (slope)	Rare
Macropiper puberulum[a]	Piperaceae	IND		Shrub	Mid elev. (slope)	Common
Meryta cf. *choristantha*	Araliaceae	END Rapa	EN	Tree	Mid elev. (slope)	Rare
Metrosideros collina[a]	Myrtaceae	IND		Tree	Mid elev. (cliff)	Common
Myoporum rapense[a]	Myoporaceae	END Rapa	VU	Shrub	Low (littoral) and mid elev. (slope)	Rare
Nesoluma polynesicum[a]	Sapotaceae	IND	EN	Tree	Mid elev. (slope)	Very rare
Pandanus tectorius	Pandanaceae	IND		Tree	Low elev. (littoral)	Common
Psidium cattleianum[a]	Myrtaceae	EUR		Tree	Low and mid elev.	Abundant
Psydrax odorata	Rubiaceae	IND		Tree	Mid elev. (cliff)	Common
Sophora rapaensis[a]	Fabaceae	END Rapa	EN	Tree	Mid elev. (slope)	Rare
Weinmannia rapensis	Cunoniaceae	END Rapa	VU	Tree	Mid elev. (slope)	Common
Zanthoxylum sp.[a]	Rutaceae	END Rapa?	NE	Tree	Mid elev. (slope)	Very rare

For each species their chorology, conservation status, habit and habitat type (low elevation = 0–100 m; mid elevation >100–300 m) and frequency/abundance (assessed at an island-scale and based on the authors' personal observations). Chorology follows the 'Inventaire national du Patrimoine Naturel', https://inpn.mnhn.fr/): EUR = European introduction; POL = Polynesian introduction; IND = Indigenous/Native; END Aust = Endemic to the Australs; END Rapa = Endemic to the island of Rapa Iti. Conservation status is given for the endemic taxa only (according to the 'Red Lists of Threatened Species in France', UICN France, MNHN, & DIREN Polynésie française 2015): CR = Critically endangered; EN = Endangered; VU = Vulnerable; NT = Near threatened; LR = Low risk; NE = Not evaluated; DD = Data deficient.

[a]Species present in the study area (150–250 m a.s.l.)

were introduced in the nineteenth century (Meyer 2011). About 50 heads of cattle, a dozen of horses and 30 goats were free-roaming in the study site and surrounding areas of the ca. 110 ha valley during our study period (information supplied by local hunters, T.L. pers. obs.). Feral ungulates also facilitate the spread of strawberry guava by eating the fruits and disturbing the soil, providing suitable micro-habitats for establishment (Meyer 2004).

Restoration treatments and plant succession study

A total of sixteen 12 m × 12 m (144 m^2) plots were established in the study site (representing a total area of ca. 0.2 ha), eight were surrounded by a fence and eight left unfenced. The fenced and unfenced areas were adjacent because of the small size of the selected dry-mesic forest remnant and to avoid heterogeneity in plant species composition due to topography (Figures 1 and 2). The fence was made of stainless steel with a 30 mm × 30 mm wire mesh, and 1.5 m tall iron fence posts were installed every 2 m. In addition, strawberry guava was manually cut in four fenced and four unfenced plots (Figure 1).Their trunks and stems were cut with a machete as low as possible to avoid resprouts. Herbicide was not applied to avoid potential detrimental effects on native and endemic plants found in the understorey.

In each plot, the density (number of stems m^{-2}) of each woody species (with a dbh ≥1.5 cm) and their basal area (cm^2 ha^{-1}) were calculated before treatments. To study plant succession in the understorey, we followed each individual (<1 m in height) in six 2 m × 2 m (4 m^2) quadrats randomly chosen within each plot, representing a total of 24 quadrats for each of the four treatments: fencing (F), unfenced (Uf), fencing with tree cutting (F × Tc) and unfenced with tree cutting (Uf × Tc). Plant diversity or richness (i.e. the number of species) was recorded and cover (i.e. the percentage of area covered by all individuals of each species) was estimated by eye in each quadrat. Plants were identified at the species level or genus if they were too small to identify to species. They were classified as native, endemic or alien species, and by tolerance to shade (light demanding, intermediate or shade-tolerant species) based on relevant literature. Plots were monitored before and after fencing and tree removal (weeding), for a total of four to five surveys (after 6, 12, 18, 24 and 30 months for the F and F × Tc treatments) during the study period.

Data analysis

Because the initial surveys conducted in December 2011 (T0) in the fenced plots (F and F × Tc) were made 6 months before the unfenced plots (Uf and Uf × Tc) conducted in July 2012 (T1 = T0 + 6) due to strong logistical constraints (restricted time spent on Rapa Iti during each field-trip, and a small field crew of local volunteers), understorey species number and cover were only compared in the F-F × Tc and Uf-Uf × Tc pair treatments.

We used a non-parametric Wilcoxon-test to verify that species richness and plant cover for all native and alien plants (total richness or cover), for native species only (native richness or cover) and for alien species only (alien richness or cover) were not significantly different during the initial surveys (T0 and T1) in order to be able to compare them during the following surveys. As total cover, native richness and alien cover were not significantly different ($P > 0.05$), suggesting limited differences between T0 and T1, they were compared over time in all treatments.

In order to assess the effects of treatments and/or time on the understorey vegetation (for natives, aliens and total species), we used permutational multivariate analysis of variance (PERMANOVA) carried out with the 'Adonis' function of the R-vegan package which avoids normality assumption by doing permutations among our observations. A fourth-root transformation was applied on our data which were permuted 999 times to calculate P values for a pseudo F statistic (Anderson 2001). When PERMANOVA was significant, pair-wise tests were computed using Wilcoxon-test to identify significant differences between treatments or survey times. All statistical analyses were conducted in R v3.0.2.

Results

In the initial survey (i.e. before treatments), the abundance of alien woody species (only represented by *Psidium cattleianum* with mean density of 0.29 stem m^{-2} per plot for plants with a dbh ≥1.5 cm), was significantly higher than the native and endemic woody species in our study site. The average basal area of *P. cattleianum* (1.45 m^2/ha) appeared to be lower than native species, but the difference was not significant (Figure 3).

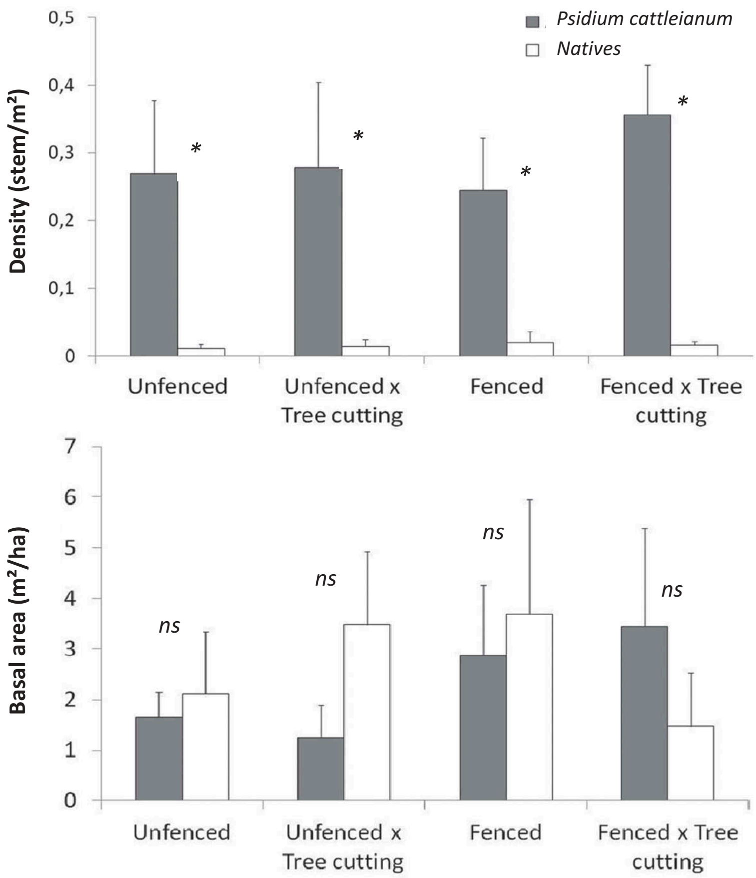

Figure 3. Density (a) and basal area (b) (mean ± SE, $N = 4$ plots) of *Psidium cattleianum* and those of native species (dbh > 1.5 cm) in the initial survey before applying the treatments, Rapa Iti, French Polynesia, 2012.
Significant differences (T, $P < 0.05$) between natives and aliens are indicated by asterisks (n.s. for non-significant).

Species composition and diversity after fencing and weeding

A total of 56 vascular plant species was found in the plots during the 30-month period, including 21 native herbs and ferns, 5 native woody species (of which three island endemics), 3 naturalised woody alien species and 32 weedy alien herbs (Table S1).

By using PERMANOVA, the total, alien and native plant species richness and cover showed a strong time and treatment effects, as well as a strong interaction between time and treatment (Table 2). The total species richness did not differ in the F × Tc treatment with time but showed a significant decrease in the F treatment after 18–30 months, the Uf × Tc treatment after 12–18 months and in the Uf treatment after 18 months only (Figure 4). Alien species richness remained higher than that by native species in all treatments over time. Native species richness showed a significant increase in F × Tc after 18–24 and 30 months (T, $P < 0.05$). In contrast, alien species richness decreased after 24 months for Uf (T, $P < 0.01$), and after 12–18 months for Uf × Tc (T, $P < 0.05$) while this statistical difference disappeared after 24 months. In the F × Tc treatment, alien species richness was

Table 2. Effects of time and treatments on plant cover and species richness of understorey plants (PERMANOVA, $N = 24$ quadrats).

	Unfenced plots						Fenced plots					
	Total		Natives		Aliens		Total		Natives		Aliens	
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Plant cover												
Time	13.07	***	8.07	***	13.83	***	14.56	***	8.56	***	15.33	***
Treatment	5.36	***	2.17	***	5.20	***	5.87	***	6.44	***	4.36	***
Time*Treatment	3.21	***	1.88	***	3.33	***	2.87	***	1.72	**	3.1	***
Species richness												
Time	13.07	***	8.07	***	13.83	***	14.56	***	8.56	***	15.79	***
Treatment	5.36	***	2.17	*	5.20	***	5.88	***	6.44	***	3.26	*
Time*Treatment	3.21	***	1.88	**	3.33	***	2.87	***	1.72	**	3.18	***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

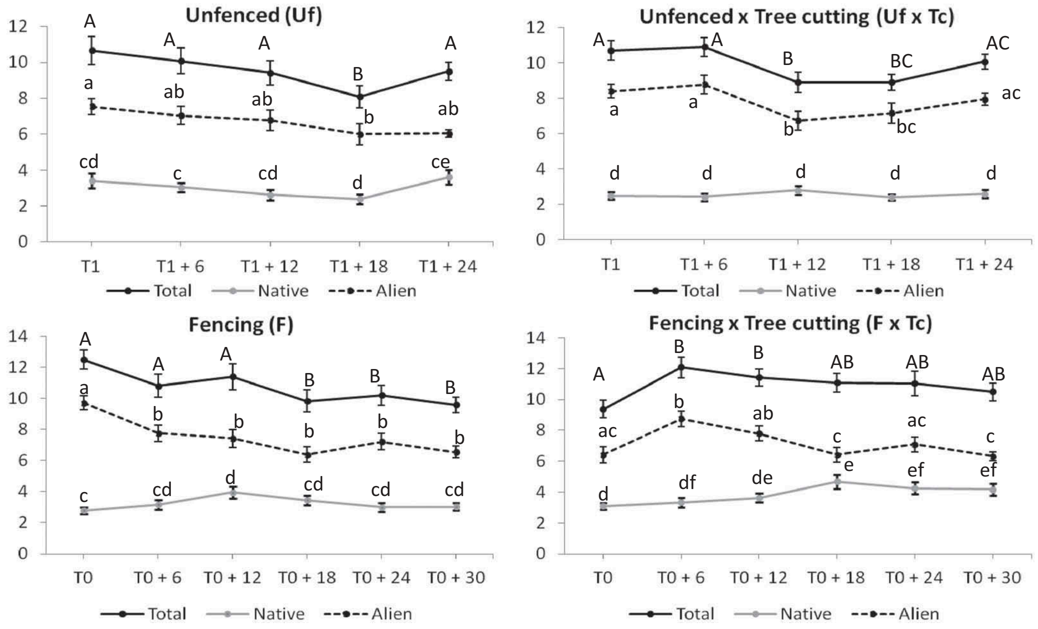

Figure 4. Comparison of species richness (mean ± SE; *n* = 24 quadrats) of understorey plants in the four treatments over 2 years.
A different letter or group of letters indicates significant differences between surveys in a given treatment (*post-hoc* pair-wise Wilcoxon-test).

significantly higher after 6 months, then decreased after 12 months with significant differences observed after 18 and 30 months. A significant decrease of alien species richness was observed in the F treatment at each monitoring period during the 30 months survey (Figure 4).

Plant cover after fencing and weeding

The species cover of understory plants varied according to treatments and over time. Indeed, there was a significant increase of the total cover after 6 months in the Uf and Uf × Tc treatments but a strong decrease for Uf and Uf × Tc after 12–24 months, and in F and F × Tc after 6–30 months (Figure 5). The cover of alien species, dominated by herbs (ca. 68%), was higher than native species cover, dominated by ferns (ca. 80%), in all treatments over time. The significant decrease in the cover of native plants cover observed in Uf after 12–18 months did not persist after 24 months. The Uf × Tc treatment did not change the native species cover at the end of the study whereas

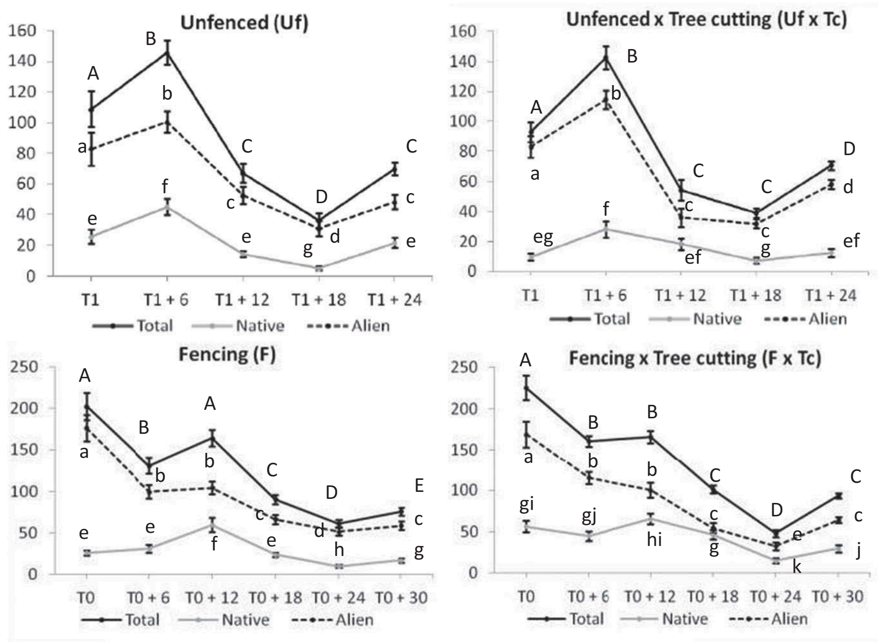

Figure 5. Comparison of species cover (mean% ± SE; *n* = 24 quadrats) of understorey plants in the four treatments over time, Rapa Iti, French Polynesia.
A different letter or group of letters indicates significant differences between surveys in a given treatment (*post-hoc* pair-wise Wilcoxon-test). Diagrams indicate means of proportion of life forms (*n* = 22 surveys) regardless of treatments and time of survey.

in F and F × Tc treatments, a significant reduction (*T*, $P < 0.001$) was observed after 30 months. Although alien cover was significantly higher in Uf × Tc after 6 months (*T*, $P < 0.01$), it significantly decreased (*T*, $P < 0.05$) after 12–24 months in Uf × Tc and Uf, as well as in F and F × Tc at all dates (*T*, $P < 0.0001$) (Figure 5).

Species turn-over after fencing and weeding

A rapid species turnover was observed during the study period, characterised by the recruitment of seedlings of many native or endemic trees such as *Pipturus australium* (Urticaceae), *Celtis pacifica* (Ulmaceae), *Sophora rapaensis*, and *Metrosideros collina* in the F × Tc plots after 30 months. Seedlings of *S. rapaensis* and the sedge *Carex stokesii* (Cyperaceae) were also recorded after 24 months in the untreated plots. The appearance of new alien species was lower in the fenced plots compared to unfenced plots. The alien grass *Melinis minutiflora* (Poaceae), which was present before the treatments but rather uncommon (mean cover of 5%), has disappeared from the fenced plots (Figure 6(a)). Recruitment of light-demanding species was higher in unfenced plots than in fenced plots, and new shade-tolerant species appeared only in the F × Tc plots. A larger number of light-demanding species disappeared in F whereas the higher disappearance of shade-tolerant species was observed in Uf × Tc (Figure 6(b) and Table S2).

Discussion

Plant succession and dynamics after restoration

This restoration experiment conducted in a dry-mesic remnant forest of the island of Rapa Iti shows that rapid changes may occur in plant cover, species composition and species diversity over a relative short period of time (between 6 and 30 months), following the exclusion of feral ungulates and/or the manual control of the invasive *Psidium cattleianum*. The time offset of 6 months for the initial surveys of the understorey vegetation in the fenced and unfenced plots, related to the strong logistic difficulties, might prevent direct comparisons and robust statistical analyses between the treatments, and thus alter the relevance of our results. However, as no major ecological change (e.g. local climate, feral animals pressure) occurred at the study site during this relative short period of time, we considered this time offset to be negligible.

Habitat restoration by controlling invasive plants has usually shown an increase of native species (Jäger and Kowarik 2010; Baider and Florens 2011). However, the increase of both alien species diversity and cover after excluding ungulates and/or controlling invasive plants has also been noticed (Cabin et al. 2000; Zavaleta et al. 2001; Cabin et al. 2002; Shimizu 2006; Jäger and Kowarik 2010; Weller et al. 2011; Cole and Litton 2014). The major increase of the invasive alien grass *Melinis minutiflora* after feral goat exclusion in Hawaii (Scowcroft and Hobdy 1987) or the vine

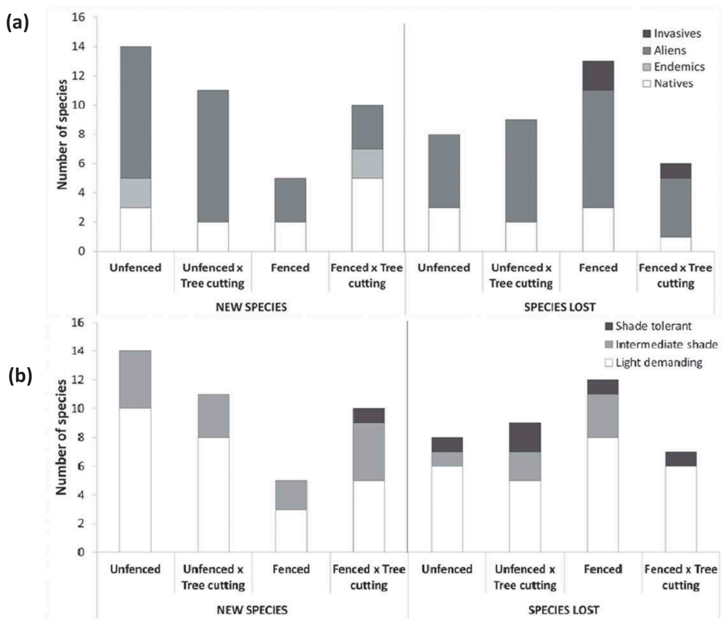

Figure 6. Recruitment and loss of species between the initial surveys (T1 and T0) and the last survey (24 months for Uf and Uf × Tc and 30 months for F and F × Tc) for each treatment, Rapa Iti, French Polynesia. Species were grouped by their biogeographic origin (a) and shade tolerance.

Operculina ventricosa after goat and pig eradication on Sarigan, Northern Mariana Islands (Kessler 2002) are striking examples of the complex effects of conservation management actions on plant species recruitment. Disturbances to soil and changes in the light regime caused by weeding can also enhance alien species dynamics (Cordell et al. 2009; Ostertag et al. 2009; Jäger and Kowarik 2010) and fencing may promote the release of invasive plants from grazing and browsing (Weller et al. 2011).

Our results showed that when *P. cattleianum* trees are removed without fencing, the abundance of both alien and native plants increased rapidly, probably associated with an increase of light in the understorey. It also reveals that the removal of invasive trees alone was not sufficient to promote native species recruitment in Rapa Iti contrarily to Mauritius where native rainforest regeneration was observed after controlling *P. cattleianum* (Baider and Florens 2011). This can be likely explained by the degree of invasion, the diversity of other alien plants and how they affect the native species (Zavaleta et al. 2001), but also microclimates, ungulates disturbance history, or site topography (Beltran et al. 2014) prior to the management actions.

The exclusion of ungulates without the removal of invasive species, resulted in a significant decrease of native plant cover 30 months after treatment, as well as the reduction in the abundance and richness of alien species, including the invasive alien sub-shrub *Rubus rosifolius* was observed. However, occasional rockslides occurring just after the fencing treatment (T.L., pers. obs.) may have altered our results by creating soil disturbances and locally affecting species composition and abundance (e.g. by crushing plants or providing microsites for seed germination).

The efficiency of exclosures has been debated in other short-term studies showing the spread of alien plants after fencing (Cabin et al. 2000; Donlan et al. 2003; Cuevas and Quesne 2006). Despite the decrease of native species cover and the recruitment of some alien plants, when both treatments are combined, our results showed that the reduction of alien species cover and the regeneration of native species are strongly improved.

Resilience of a native forest and recovery of threatened endemic species

Seedling recruitment of several native and endemic woody species which were absent from our monitored quadrats before the treatments was observed during the study period. The newly recorded species include common native trees as well as rare threatened endemic taxa such as the shrub *Pipturus australium* (CR) which is not present in the surrounding areas of our study site. Whether their seedlings originated from the soil seed bank or from seed dispersal (by wind or frugivorous birds for the fleshy-fruited plants such as *Pipturus* and *Celtis*) has not been established. The Rapa fruit-dove *Ptilinopus huttoni*, an endemic forest bird feeding on fruits of many native and endemic tree species (Thibault and Varney 1991) is classified as EN because the population is very small (<250 mature individuals) and confined to undisturbed forest fragments. However, at present the population appears to be stable (BirdLife International 2018), and thus long-distance seed dispersal may be attributed to this species.

The appearance of *M. collina* is noteworthy, as it is a common widespread native tree in lowland mesic and montane rainforest of the high volcanic islands of French Polynesia and other South Pacific islands (Mueller-Dombois and Fosberg 1998), and considered as an umbrella species (Groom et al. 2006) for many other native and endemic plants (mainly epiphytes) and animals (nesting birds, arthropods, molluscs).

The relatively rapid colonisation by native and endemic species following fencing and weeding measures shows the relative resilience of the dry-mesic forest of Rapa Iti to initial recovery after threats are controlled or removed. Without restoration efforts on the island, some species apparently more palatable to ungulates and currently only found on cliffs, such as the island endemic *S. rapaensis*, may be driven to extinction in the near future. Indeed, the well-known *Sophora toromiro*, endemic to Rapa Nui (Easter Island) is probably extinct in the wild because of browsing and grazing by sheep (Maunder 1997). About 13 native or endemic plant species are considered critically endangered on Rapa Iti with less than 25 mature individuals in the wild (Motley et al. 2014), and *ex situ* conservation (i.e. seed collection, plant propagation in nurseries and reintroduction in the wild) associated with habitat restoration seem the best options for their recovery.

Logistical constraints meant that some aspects of the experimental design were not ideal. These issues, and their effects on the interpretations of the results, were considered at relevant points in this discussion.

Future management prospects

Long-term monitoring is needed to better understand vegetation dynamics and native forest ecosystem resilience to disturbances, and also to verify if our experimental management efforts have contributed to the partial restoration of degraded habitat and threatened plant populations. The 6 monthly surveys conducted during our study period of 30 months was crucial to observe changes in plant species composition and temporal and spatial variation in species cover, especially for the first year after fencing and weeding where local disturbances may occur.

In order to avoid reinvasion by *P. cattleianum* in the future, we recommend it to be cut every 2 years, and treat stumps with chemicals to avoid resprouting (Pratt et al. 1994) if permitted by local community, as well as removing the seedlings which were observed in the plots. Another potential effective control method is ring-barking and herbicide application for larger plants (see Cronk and Fuller 1995; Rocamora and Henriette 2015). The limited seed bank and high seed germination rate of *P. cattleianum* (Uowolo and Denslow 2008; Cordell et al. 2009) is an asset for the management success of this species over a long-term period. In addition, the hand-removal of the alien grass *Sporobolus indicus* which dominated alien cover in fenced plots at the end of the study might be important for the seedling recruitment of native species. The control of rodents (mainly rats *Rattus* spp.) in the fenced plots could also be a critical component of sustainable restoration and conservation efforts (Russell and Holmes 2015), especially for the recruitment of endangered woody tree species with large seeds (Meyer and Butaud 2009) which show no seedling recruitment on our study site, such as the threatened tree *Nesoluma* (syn. *Sideroxylon*) *polynesicum*.

Conclusions

This experimental study conducted in a small remote island illustrates that rapid vegetation change may occur when a native forest remnant is fenced off to exclude feral ungulates and invasive tree species are controlled. Results demonstrate a significant increase of native plant species richness, and the recovery of both common native and rare threatened endemic plant species in fenced and weeded areas, indicating that species reintroduction is not necessarily required in forest restoration projects.

Acknowledgements

We are grateful to the To'ohitu (traditional council) of Rapa Iti for their agreement to fence the remnant dry-mesic forest in the Pariati Bay, as well as the mayor of the island and his council for their technical support. We thank the members of the local NGO Raumatariki for building the fence, especially Mahia Narii, Sebastien Narii, Eria Tamata for their help in the field, Tehiva Narii for his personal communication on the abundance of ungulates, Walter Teamotuaitau for the identification of some herbaceous plant species, Nicolas Loiseau and Gaëlle Legras (University of French Polynesia) for advice on statistical analyses. Vincent Florens (University of Mauritius) and Olivier Flores (University of La Réunion) provided relevant comments to early versions of this manuscript which considerably improved its quality.

Disclosure statement

No potential conflict of interest was reported by the authors.

Funding

This work was supported by a three-years grant from the Government of French Polynesia ('convention N°2459/MEJ/REC du 15 mai 2012') to the second author.

Notes on contributors

Jean-Yves Meyer is a research scientist working on conservation of terrestrial biodiversity in tropical islands with emphasis on the impact and management of invasive alien species.

Tiffany Laitame is a Ph.D. student whose research interest is focused on restoration ecology, particularly island forest dynamics.

Jean-Claude Gaertner is a research scientist, working on biodiversity monitoring in island ecosystems.

ORCID

Jean-Yves Meyer http://orcid.org/0000-0001-7968-9944
Jean-Claude Gaertner http://orcid.org/0000-0001-9248-6260

References

Anderson MJ. 2001. A new method for non-parametric multivariate analysis of variance. Austral Ecol. 26:32–46.

Aplet GH, Anderson SJ, Stone CP. 1991. Association between feral pig disturbance and the composition of some alien plant assemblages in Hawaii Volcanoes National Park. Vegetatio. 95:55–62.

Aronson J, Van Andel J. 2006. Challenges for ecological theory. In: Van Andel J, Aronson J, editors. Restoration ecology: the new frontier. Oxford (UK): Blackwell Publishing; p. 223–233.

Auld TD, Hutton I. 2004. Conservation issues for the vascular flora of Lord Howe Island. Cunninghamia. 8:490–500.

Baider C, Florens FBV. 2011. Control of invasive alien weeds averts imminent plant extinction. Biol Invasions. 13:2641–2646.

Baret S, Rouget M, Richardson DM, Lavergne C, Egoh B, Dupont J, Strasberg D. 2006. Current distribution and potential extent of the most invasive alien species in La Réunion (Indian Ocean, Mascarene islands). Austral Ecol. 31:747–758.

Beltran RS, Kreidler N, Van Vuren DH, Morrison SA, Zavaleta ES, Newton K, Tershy BR, Croll DA. 2014. Passive recovery of vegetation after herbivore eradication on Santa Cruz Island, California. Restor Ecol. 22:790–797.

BirdLife International. 2018. Species factsheet: *Ptilinopus huttoni* [accessed 2018 Sept 20]. http://www.birdlife.org.

Cabin RJ, Weller SG, Lorence DH, Cordell S, Hadway LJ. 2002. Effects of microsite, water, weeding, and direct seeding on the regeneration of native and alien species within a Hawaiian dry forest preserve. Biol Conserv. 104:181–190.

Cabin RJ, Weller SG, Lorence DH, Flynn TW, Sakai AK, Sandquist D, Hadway LJ. 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. Conserv Biol. 14:439–453.

Castro SA, Jaksic FM. 2008. Role of non-established plants in determining biotic homogenization patterns in Pacific oceanic islands. Biol Invasions. 10:1299–1309.

Caujapé-Castells J, Tye A, Crawford DJ, Santos-Guerra A, Sakai A, Beaver K, Lobin W, Florens FBV, Moura M, Jardim R. 2010. Conservation of oceanic island floras: present and future global challenges. Perspect Plant Ecol Evol Syst. 12:107–129.

Cole RJ, Litton CM. 2014. Vegetation response to removal of non-native feral pigs from Hawaiian tropical montane wet forest. Biol Invasions. 16:125–140.

Cole RJ, Litton CM, Koontz MJ, Loh RK. 2012. Vegetation recovery 16 years after feral pig removal from a wet Hawaiian forest. Biotropica. 44:463–471.

Cordell S, Ostertag R, Rowe B, Sweinhart L, Vasquez-Radonic L, Michaud J, Cole TC, Schulten JR. 2009. Evaluating barriers to native seedling establishment in an invaded Hawaiian lowland wet forest. Biol Conserv. 142:2997–3004.

Cowie RH. 2001. Decline, homogenization of Pacific faunas: the land snails of American Samoa. Biol Conserv. 99:207–222.

Cronk CB, Fuller JL. 1995. Plant invaders. The threat to natural ecosystems. London (UK): Chapman & Hall.

Cuevas JG, Quesne CL. 2006. Low vegetation recovery after short-term cattle exclusion on Robinson Crusoe Island. Plant Ecol. 183:105–124.

Davis MA. 2003. Biotic globalization: does competition from introduced species threaten biodiversity? BioScience. 53:481–489.

Donlan CJ, Croll DA, Tershy BR. 2003. Islands, exotic herbivores, and invasive plants: their roles in coastal California restoration. Restor Ecol. 11:524–530.

Eckhardt RC. 1972. Introduced plants and animals in the Galapagos Islands. BioScience. 22:585–590.

Florens FB, Baider C, Martin GMN, Seegoolam NB, Zmanay Z, Strasberg D. 2016. Invasive alien plants progress to dominate protected and best preserved wet forests of an oceanic island. J Nat Conserv. 34:93–100.

Florens FBV, Baider C. 2013. Ecological restoration in a developing island nation: how useful is the science? Restor Ecol. 21:1–5.

Florens FBV, Mauremootoo JR, Fowler SV, Winder L, Baider C. 2010. Recovery of indigenous butterfly community following control of invasive alien plants in a tropical island's wet forests. Biodivers Conserv. 19:3835–3848.

Gerlach J. 2004. A 10-year study of changes in forest vegetation on Silhouette Island, Seychelles. J Nat Conserv. 12:149–155.

Groom MJ, Meffe GK, Caroll CR. 2006. Principles of conservation biology. Sunderland (USA): Sinauer Associates.

Huenneke LF, Vitousek PM. 1990. Seedling and clonal recruitment of the invasive tree *Psidium cattleianum*: implications for management of native Hawaiian forests. Biol Conserv. 53:199–211.

Jäger H, Kowarik I. 2010. Resilience of native plant community following manual control of invasive *Cinchona pubescens* in Galápagos. Restor Ecol. 18:103–112.

Kessler CC. 2002. Eradication of feral goats and pigs and consequences for other biota on Sarigan Island, Commonwealth of the Northern Mariana Islands. In: Veitch CR, Clout MN, editors, p. 132-140. Turning the tide: the eradication of invasive species. Gland (Switzerland), Cambridge (UK): IUCN SSC Invasive Species Specialist Group.

Kraus F, Duffy DC. 2010. A successful model from Hawaii for rapid response to invasive species. J Nat Conserv. 18:135–141.

Kueffer C, Daehler CC, Torres-Santana CW, Lavergne C, Meyer JY, Otto R, Silva L. 2010. A global comparison of plant invasions on oceanic islands. Perspect Plant Ecol Evol Syst. 12:145–161.

Laurent V, Maamaatuaiahutapu K, Maiau J, Varney P. 2004. Atlas climatologique de la Polynésie française. Papeete (Polynésie française): Météo France Délégation inter-régionale de Polynésie française.

Loope L, Medeiros A. 1994. Impacts of biological invasions on the management and recovery of rare plants in Haleakala National Park, Maui, Hawaiian Islands. In: Bowles ML, Whelan CJ, editors. Restoration of endangered species. Cambridge (UK): Cambridge University Press; p. 143–158.

Lorence DH, Sussman RW. 1986. Exotic species invasion into Mauritius wet forest remnants. J Trop Ecol. 2:147–162.

Mack RN, Simberloff D, Lonsdale WM, Evans H, Clout M, Bazzaz FA. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol Appl. 10:689–710.

Maunder M. 1997. Conservation of the extinct Toromiro tree, *Sophora toromiro*. Curtis's Botanical Magazine. 14:226–231.

McDonald IAM, Thébaud C, Strahm WA, Strasberg D. 1991. Effects of alien plant invasions on native vegetation remnants on La Réunion (Mascarene Islands, Indian Ocean). Environ Conserv. 18:51–61.

Medeiros AC, von Allmen EI, Chimera CG. 2014. Dry forest restoration and unassisted native tree seedling recruitment at Auwahi, Maui. Pacific Sci. 68:33–45.

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

Meyer J-Y. 2011. Guide floristique de Rapa. Papeete (Polynésie française): Direction de l'Environnement, Délégation à la Recherche.

Meyer J-Y, 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? Biol Invasions. 11:1569–1585.

Meyer J-Y, Claridge EM, editors. 2014. Terrestrial biodiversity of the Austral Islands, French Polynesia. Paris (France): Muséum national d'Histoire naturelle. Collection Patrimoines Naturels 72.

Meyer J-Y, Pouteau R, Spotswood E, Taputuarai R, Fourdrigniez M. 2014. The importance of novel and hybrid habitats for plant conservation on islands: a case study from Moorea (South Pacific). Biodivers Conserv. 24:83–101.

Meyerson LA, Mooney HA. 2007. Invasive alien species in an era of globalization. Front Ecol Environ. 5:199–208.

Motley TJ, Luongo A, Meyer J-Y. 2014. Vegetation types and map of Rapa. In: Meyer J-Y, Claridge EM, editors. Terrestrial biodiversity of the Austral Islands, French Polynesia. Paris (France): Muséum national d'Histoire naturelle; p. 133–147. Collection Patrimoines Naturels 72.

Mueller-Dombois D, Fosberg FR. 1998. Vegetation of the tropical Pacific islands. New York (US): Springer.

Ostertag R, Cordell S, Michaud J, Cole TC, Schulten JR, Publico KM, Enoka JH. 2009. Ecosystem and restoration consequences of invasive woody species removal in Hawaiian lowland wet forest. Ecosystems. 12:503–515.

Paulay G. 1994. Biodiversity on oceanic islands: its origin and extinction. Am Zool. 34:134–144.

Perrings CS, Dalmazzone S, Williamson M. 2005. The economics of biological invasions. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage JK, editors. Invasive alien species: a new synthesis. Washington (US): Island press; p. 16–35.

Pratt LW, Santos GL, Stone CP 1994. A test of four herbicides for use on Strawberry guava in Kipahulu Valley, Haleakala National Park. Technical Report 90. Honolulu (US): University of Hawaii Cooperative National Park Resources Studies Unit.

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner U, Vilà M. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species traits and environment. Glob Chang Biol. 18:1725–1737.

Rocamora G, Henriette E. 2015. Invasive alien species in Seychelles. Why and how to eliminate them? Identification and management of priority species. Mèze (Paris, France): Biotope, Muséum national d'Histoire naturelle.

Russell JC, Holmes ND. 2015. Tropical island conservation: rat eradication for species recovery. Biol Conserv. 185:1–7.

Sax DF, Gaines SD. 2008. Species invasions and extinction: the future of native biodiversity on islands. Proc Nat Acad Sci USA. 105:11490–11497.

Scowcroft P, Conrad C. 1992. Alien and native plant response to release from feral sheep browsing on Mauna Kea. In: Stone CP, Smith CW, Tunison JT, editors. Alien plant invasions in native ecosystems of Hawai'i: management and research. Honolulu (US): University of Hawaii Cooperative National Park Resources Studies Unit; p. 625–665.

Scowcroft PG, Hobdy R. 1987. Recovery of goat-damaged vegetation in an insular tropical montane forest. Biotropica. 19:208–215.

Shimizu Y. 2006. Population dynamics of an invasive plant (*Psidium cattleianum*) after two continuous disturbances in the *Pinus-Schima* secondary forest on Chichijima in the Ogasawara (Bonin) Islands. Reg Views. 19:1–15.

Soulé ME. 1990. The onslaught of alien species and other challenges in the coming decades. Conserv Biol. 4:233–239.

Steadman DW. 2006. Extinction and biogeography of tropical pacific birds. Chicago (US): University of Chicago Press.

Suding KN. 2011. Toward an era of restoration in ecology: successes, failures, and opportunities ahead. Annu Rev Ecol Evol Syst. 42:465–487.

Thaxton JM, Cole TC, Cordell S, Cabin RJ, Sandquist DR, Litton CM. 2010. Native species regeneration following ungulate exclusion and nonnative grass removal in a remnant Hawaiian dry forest. Pacific Sci. 64:533–544.

Thibault J-C, Varney A. 1991. Numbers and habitat of the Rapa fruit-dove *Ptilinopus huttoni*. Bird Conserv Int. 1:75–81.

Towns DR, Ballantine WJ. 1993. Conservation and restoration of New Zealand island ecosystems. Trends Ecol Evol. 8:452–457.

Tunison JT, Loh RK, Pratt LW, Kageler DW 1994. Early succession in pig-disturbed mountain parkland: Hawai'i Volcanoes National Park. Technical Report 89. Honolulu (USA): University of Hawaii Cooperative National Park Resources Studies Unit.

UICN France, MNHN, & DIREN Polynésie française 2015. La Liste Rouge des espèces menacées en France. Chapitre flore vasculaire endémique de Polynésie française [accessed 2017 Jan 30]. http://uicn-france.fr/wp-content/uploads/2015/12/Liste_rouge_Flore_vasculaire_endemique_de_Polynesie_francaise.pdf.

Uowolo AL, Denslow JS. 2008. Characteristics of the *Psidium cattleianum* (Myrtaceae) seed bank in Hawaiian lowland wet forests. Pacific Sci. 62:129–135.

Vilà M, Espinar JL, Hejda M, Hulme PE, Jarošík V, Maron JL, Pergl J, Schaffner U, Sun Y, Pyšek P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol Lett. 14:702–708.

Walker LR, Walker J, Del Moral R. 2007. Forging a new alliance between succession and restoration. In: Walker LR, Walker J, Hobbs RJ, editors. Linking restoration and ecological succession. New York (US): Springer; p. 1–18.

Weller SG, Cabin RJ, Lorence DH, Perlman S, Wood K, Flynn T, Sakai AK. 2011. Alien plant invasions, introduced ungulates, and alternative states in a mesic forest in Hawaii. Restor Ecol. 19:671–680.

Wessels FJ, Cuda JP, Johnson MT, Pedrosa-Macedo JH. 2007. Host specificity of *Tectococcus ovatus* (Hemiptera: Eriococcidae), a potential biological control agent of the invasive strawberry guava, *Psidium cattleianum* (Myrtales: Myrtaceae), in Florida. BioControl. 52:439–449.

Wilson EO. 1992. The diversity of life. Cambridge (UK): Belknap Press of Harvard University Press.

Zavaleta ES, Hobbs RJ, Mooney HA. 2001. Viewing invasive species removal in a whole-ecosystem context. Trends Ecol Evol. 16:454–459.