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Restoring habitat for native and endemic plants through the introduction of a fungal pathogen to control the alien invasive tree *Miconia calvescens* in the island of Tahiti

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Abstract Success of biological control programs is commonly assessed by studying the direct negative impacts of released agents on the target invasive species. Very few quantitative studies have focused on the indirect positive effects on native biodiversity. In this study, we monitored the response of the plant community (both native and alien species) in permanent plots located in four different sites in montane rainforests of the tropical island of Tahiti (South Pacific) severely invaded over decades by the alien invasive tree *Miconia calvescens* DC (Melastomataceae), after the release of a defoliating fungal pathogen *Colletotrichum gloeosporioides* f. sp. *miconiae* Killgore & L. Sugiyama. Results of five years of monitoring showed that total native and endemic species richness and plant cover increased in all sites and plots. Partial defoliation of miconia canopy trees

(between 6% and 36%) led to significant recruitment of light-demanding pioneer species, but also to the appearance of some semi-shade and shade tolerant rare endemic species. Native ferns and angiosperms remained dominant (ca. 80%) in the forest understorey during the monitoring period. Colonization by a small number of alien plant species occurred in one permanent plot located at the lower elevation. We conclude that biological control may be considered a tool for partial habitat restoration and recovery of native and endemic species, but long-term monitoring is needed to confirm the stability and resilience of the “novel plant assemblage”.

Keywords *Colletotrichum gloeosporioides* · Native plants · Pathogen · Rainforest · Restoration · Plant succession

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Introduction

The majority of post-release evaluations of biological control programs have focused on the released agent establishment and performances (Morin et al. 2009). The assessment of their direct negative impacts on the target invasive species, such as the reduction in distribution (geographic and habitat range), demography (abundance, density, rate of spread, growth rate, percentage cover for weeds) or reproduction (fruit set, seed production, seed germination for weeds) are classically conducted (see e.g. Briese

2000; DeBach and Rosen 1991; Myers and Bazely 2003; Smith and DeBach 1942). In agro-systems, indirect positive effects are assessed through the recovery of economic plants, such as the increase of their density, biomass, plant growth or economic productivity (Culliney 2005; Huffaker and Kennett 1959). A very few but increasing number of quantitative studies have measured the recovery of native (or indigenous) plants associated with reduction in the density and/or impact of environmental weeds (Barton et al. 2007; Meyer and Fourdrigniez 2011; van Driesche et al. 2010). However, these examples of biological control benefits to conservation rarely deal with the process of vegetational changes in composition and structure during plant succession, and forest dynamics over time.

In this five-year study, we monitored the response of plant assemblages (native, endemic and alien species, ferns and angiosperms, herbaceous and woody species) in the understorey of tropical rainforests severely invaded by an introduced tree, *Miconia calvescens*, after the release of a defoliating fungal pathogen, *Colletotrichum gloeosporioides* f. sp. *miconiae*, used as a biological control agent. *Miconia calvescens* DC (Order Myrtales, Family Melastomataceae, hereafter miconia) is a small tree 6–12 m tall (up to 16 m), native to Central and South American rainforests, and introduced to the tropical oceanic island of Tahiti (French Polynesia, South Pacific) in 1937 as a garden ornamental. In less than 50 years, it spread over 70% of the island (about 80,000 ha) from sea-level (on the windward east coast, 400–600 m on the leeward coast) to 1,400 m in elevation (Fig. 1), forming dense almost monotypic stands including in species-rich montane cloud forests. Because of its closed-canopy and large leaves (up to 80 cm long), light availability in the forest understorey was dramatically reduced. Between 40 and 50 species endemic to Tahiti were considered to be on the verge of extinction due to miconia massive invasion, including many understorey herbs, shrubs and small trees, and biological control was viewed as the only potentially effective management option (Meyer and Florence 1996; Meyer 2010a).

Colletotrichum gloeosporioides (Penz) Sacc. f. sp. *miconiae* Killgore & L. Sugiyama (Order Melanconiales, Class Coelomycetes, Subdivision Deuteromycetinae, hereafter Cgm), an imperfect fungus discovered in Brazil in 1997 and proven to be highly

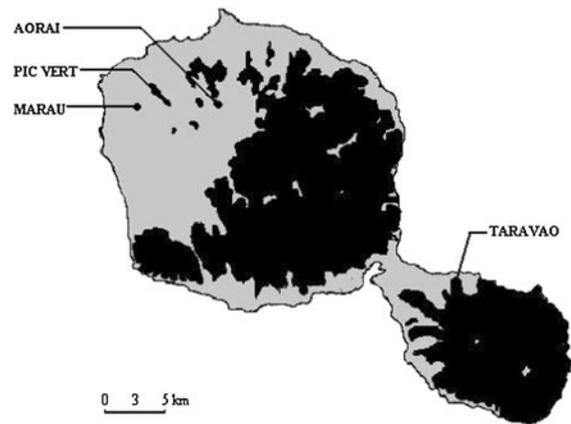


Fig. 1 Map of miconia distribution (in black) on the island of Tahiti, and location of the four study sites

specific to miconia (Killgore et al. 1999), was successfully released in Tahiti in 2000. Cgm causes leaf anthracnose and necrosis leading to the death of miconia young seedlings (up to 74% in laboratory conditions), and serious leaf damage on miconia saplings and reproductive trees in the field (over 90% of the leaves are infected). Necrotic spots (up to 90 per leaf) turn into lesions where plant tissue dies off completely and eventually becomes large holes, reducing leaf area and causing partial defoliation of miconia canopy trees (Meyer et al. 2008), thus increasing light reaching the understorey (Meyer et al. 2007).

Previous studies have demonstrated that the biological control agent has contributed to the recovery of rare threatened endemic plants in Tahiti, such as the small tree *Myrsine longifolia* (Meyer et al. 2007) and the subshrub *Ophiorrhiza subumbellata* (Meyer and Fourdrigniez 2011). These authors concluded that biological control may be considered an important management tool for the partial restoration of native forest severely invaded by weeds.

To further test that hypothesis, we studied vegetation changes at the plant community level by conducting a long-term survey of all vascular plant species (angiosperms—flowering plants and pteridophytes—ferns), both native, endemic and alien, in the understorey of miconia-invaded montane rainforests in Tahiti. The aims addressed for this monitoring program were to (1) study the indirect effects of biological control on native and alien plant

recruitment over time, (2) measure the changes in species composition and cover according to their light tolerance in the plant succession, and (3) assess the risk of colonization or reinvasion by other alien species.

Materials and methods

Four study sites were selected in the island of Tahiti according to their accessibility, three on the leeward coast (Aorai, Marau, Pic Vert) and one on the peninsula of Tahiti Iti (Taravao). A total of eleven 10 × 10 m permanent plots were set up in montane rainforests severely invaded by miconia (basal area between 20% and 100% of the total, except for one plot on Marau characterised by the presence of large remnant native and alien trees), located between 600 and 1,200 m a.s.l., and in areas with a mean annual rainfall ranging between 2,000 and 4000 mm (Table 1).

The patterns of miconia leaf damage caused by Cgm (necrotic spots, lesions and holes) are distinctive and easily recognized. Initial field trials were conducted in collaboration with a plant pathologist (E. Killgore,

Hawaii Department of Agriculture, Honolulu) to confirm accurate identification of Cgm damage (Meyer and Killgore 2000; Meyer et al. 2008). The percentage of leaf damage caused by the Cgm (%LD), a proxy measurement for partial defoliation, was assessed by cutting down ten miconia reproductive canopy trees around each permanent plot, with 25 canopy leaves collected from each tree. We used a grid mesh (2 × 2 cm) and calculate the %LD = number of squares with Cgm induced necrotic lesions and holes/leaf area (estimated number of squares covering the total leaf area). %LD was assessed each year between 2005 and 2009, and also in 2010 (Table 2).

In each permanent plot, 20 subplots (of a total of 64) were randomly selected (Fig. 2a) and species composition and abundance within the forest understorey stratum (less than or equal to 1.3 m in height) were analysed at three dates of the monitoring period (2005, 2007 and 2009) (Fig. 2b). In each subplot, the number of species was counted and the percentage cover of each species was visually assessed (Fig. 2b). Scientific name and biogeographical status of plant species (alien, native, endemic) in Tahiti were based on the Nadeaud botanical database (Florence et al. 2007). The light preference of plants, i.e. “light demanding” or early successional/secondary or pioneer species, “semi-shade”

Table 1 Characteristics of study sites and miconia invasion degree in the permanent plots (min–max value)

Sites (number of plots)	Elevation range (m)	Mean rainfall (mm year ⁻¹)	Miconia density (stems 100 m ⁻²)	Miconia basal area (cm ² m ⁻²)	% Total basal area
AORAI (<i>n</i> = 3)	630–1,200	2,000–2,500	62–206	17–40.49	25–91
MARAU (<i>n</i> = 2)	800	3,000	19*–42	3.31*–5.49	8*–100
PIC VERT (<i>n</i> = 3)	600–970	2,500–3,000	38–127	10.88–17.21	21–100
TARAVAO (<i>n</i> = 3)	600–1,020	3,500–4,000	144–402	27.06–32.48	94–100

Basal area is measured at 1.3 m off the ground

* Plot with other large alien and native trees

Table 2 Evolution of the partial defoliation of miconia canopy trees caused by the Cgm (mean % leaf damages and min–max value) with time in the permanent plots

%LD	Year 2005	Year 2007	Year 2008	Year 2009	Year 2010
AORAI	23.5 (13.3–33.7)	17.2 (11.1–20.6)	22.6 (13.2–35.1)	12.4 (6.3–16.3)	17.5 (6.3–28.2)
MARAU	12.9 (9.5–16.2)	17.2 (15.9–18.6)	18.8 (14.2–23.4)	11.6 (11.6–*)	18.8 (16.7–21.1)
PIC VERT	21.3 (13.7–28.9)	27.9 (21.9–36.4)	18.1 (8.9–26.1)	18.5 (11.4–23.9)	17.3 (10.2–22.2)
TARAVAO	23.9 (17.4–30.5)	17.3 (8.9–21.6)	21.6 (12.8–28.7)	16.8 (15.1–19.7)	27.5 (24.6–30.7)

* Missing data

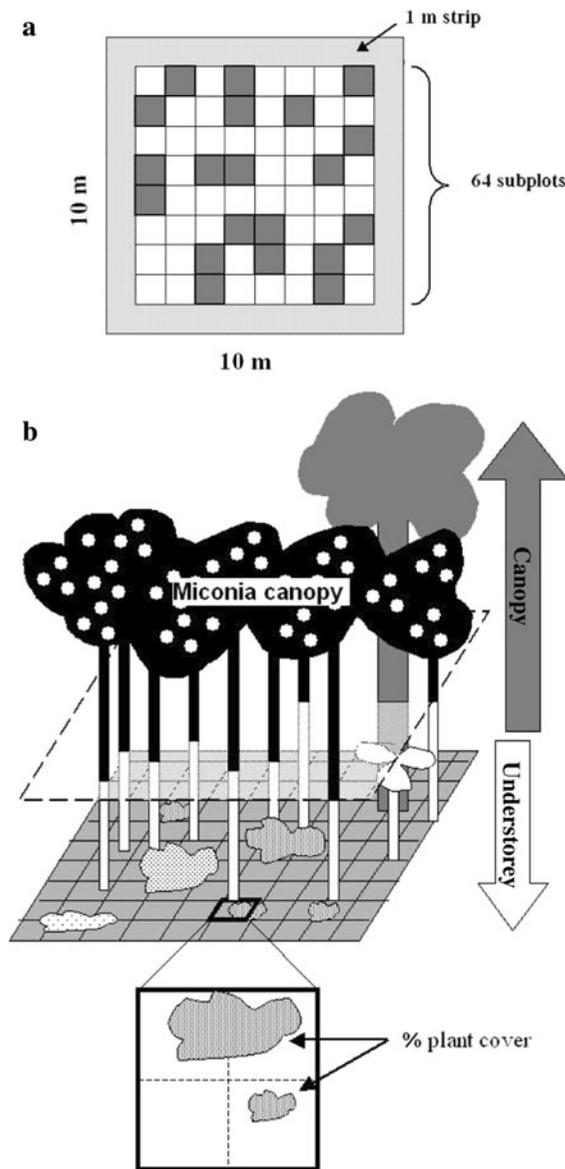


Fig. 2 **a** Permanent plots and selected subplots design. The shaded squares represent the random sampling of subplots that is conducted every year. **b** Diagram representing the method of basal area measurements of trees in the permanent plot and % understory plant cover in the subplots

or mid-successional/secondary species, and “shade tolerant” or late-successional/secondary species (Budowski 1965; Brokaw 1985), was determined according to personal field observations conducted in Tahiti and other French Polynesian and Pacific islands over the past two decades.

All data were analysed using non-parametric statistical tests with the SPSS software (SPSS

2005). For seven of our 11 plots where full data was available (two plots were set up after 2005, one was found deforested before 2007, and another one disturbed in 2009), a Friedman test was conducted to see if there is any statistical difference between our correlated samples ($n = 3$, the monitoring years of 2005, 2007 and 2009). Then, a Wilcoxon signed-rank test allowed us to compare all pairs (2005–2007, 2007–2009 and 2005–2009). When the test was statistically significant ($P < 0.05$), the multiple-comparison Bonferroni correction ($P/n < 0.016$), a more conservative approach classically used when several statistical tests are being performed simultaneously, was applied.

Results

The Cgm leaf damage (%LD) varies with elevation, ranging between 6% and 36% between 2005 and 2010 in our study sites (Table 2). This variation is explained by the fact that the Cgm seems more efficient at higher elevations where climate is cooler and wetter (Meyer et al. 2008). There is little or no change observed between sites and plots with time during the monitoring period (Table 2) which indicate that the fungal pathogen is still efficient, and that there is no increase of miconia canopy closure. Inter-annual variations of local weather conditions, such as a more pronounced dry season in 2009 (Météo-France, Direction inter-régionale de Polynésie française, pers. com. 2010) may affect the Cgm reproduction and disease development.

Changes in native and alien vegetation

A total of 61 species (or taxa) including 30 native plants, 18 endemic plants and 13 alien plants was recorded in ten of the permanent plots between 2005 and 2009. Total species number significantly increased between 2005 and 2007 ($P < 0.016$, Fig. 3a), varying from 24 species in 2005 to 39 in 2007 and 58 in 2009. An increase of the percentage of total plant cover was also observed, from ca. 30% in 2005 to ca. 60% in 2009 (Fig. 3b), but was not statistically significant between years. Species diversity had increased 2.5 fold and percent cover twofold after the five years of monitoring.

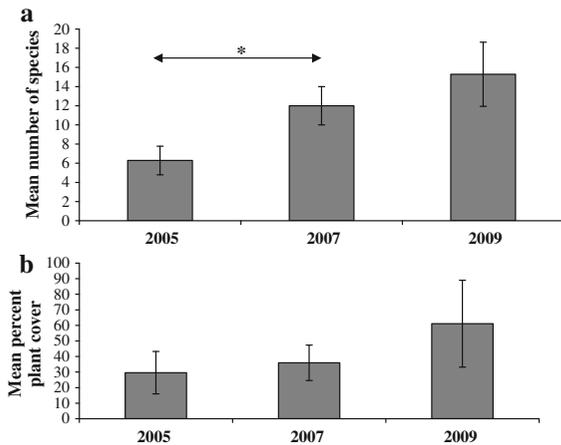


Fig. 3 Changes in species diversity (**a**) and plant cover (**b**) in all plots with time. Friedman test followed by a Wilcoxon signed rank test with Bonferroni correction ($*P < 0.016$): species diversity ($n = 7$; $\chi^2 = 12.074$; $df = 2$; $P < 0.01$); plant cover ($n = 7$; $\chi^2 = 4.571$; $df = 2$; $P = 0.102$); error bars represent SE

Species classification and status

Native ferns were the dominant plant group in the understorey of miconia-invaded forest during all monitoring periods (Fig. 4), especially shade tolerant species such as *Bolbitis lonchophora* (Lomariopsidaceae), *Diplazium harpeodes* and *Tectaria lessonii* (Dryopteridaceae) (see appendix in electronic supplementary material) which are the most frequent, in 80–90% of the plots. There was a significant increase of native fern species diversity between 2005 and 2007 ($P < 0.016$), and an increase of native and endemic flowering plant diversity and plant cover, but also of alien plants, between 2005 and 2009 (Figs. 4, 5). The proportion of the aliens compared to natives and endemics remained low and stable, between 15% and 21%. The most frequent understorey alien plants beside miconia which is found in all plots were African tulip tree *Spathodea campanulata* (Bignoniaceae) and the thorny shrub *Rubus rosifolius* (Rosaceae), both in 80% of the plots (see appendix in electronic supplementary material). A small “burst” of non-native plants (five more species) was observed in one plot of the Taravao site located at 600 m elevation at the end of our monitoring period (2009).

Light preference

A significant increase of light-demanding pioneer (alien and native) species diversity was observed between

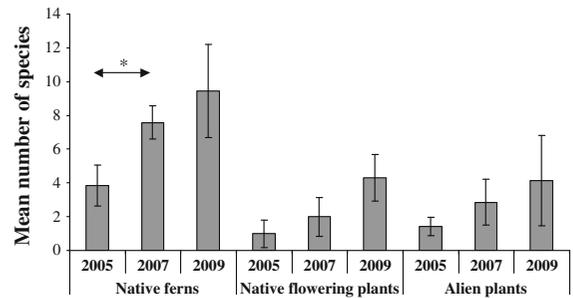


Fig. 4 Changes in species diversity according to taxonomical and biogeographical status. Friedman test followed by a Wilcoxon signed rank test with Bonferroni correction ($*P < 0.016$): native ferns ($n = 7$; $\chi^2 = 12.074$; $df = 2$; $P < 0.01$); native flowering plants ($n = 7$; $\chi^2 = 13.000$; $df = 2$; $P < 0.01$); alien plants ($n = 7$; $\chi^2 = 11.565$; $df = 2$; $P < 0.01$); error bars represent SE

2005 and 2007 ($P < 0.016$, Figs. 6, 7). The number of light-demanding species increased fivefold, and the cover tenfold during the monitoring period, resulting from the effects of partial defoliation of miconia canopy trees. The species diversity of semi-shade and shade tolerant plants, which were the most common early in the monitoring period, also increased. Seedlings of semi-shade tolerant species such as the endemic small tree *Coprosma taitensis* (Rubiaceae), the native tree fern *Cyathea* sp. (Cyatheaceae) or the rare endangered endemic *Ophiorrhiza* spp. (Rubiaceae) appeared in the plots in 2007 and 2009 as did several shade-tolerant endemics, including the shrubs *Cyrtandra* spp. (Gesneriaceae) and *Psychotria* sp. (Rubiaceae), both rare and threatened, and the trees *Myrsine* sp. (Myrsinaceae) and *Weinmannia parviflora* var. *parviflora* (Cunoniaceae), which are dominant trees in native cloud forests of Tahiti (Meyer 2010b) (see appendix in electronic supplementary material). Their appearance in the plant succession might be related to the increase of total plant cover in the understorey (from 30% to 60% in the five-year monitoring period) providing suitable micro-ecological (lower light and higher humidity) conditions for seed germination and seedling growth.

Discussion

Post-release evaluations are an important yet often neglected component of biological control programs that are essential in assessing levels of success of biological control. This five-year monitoring study

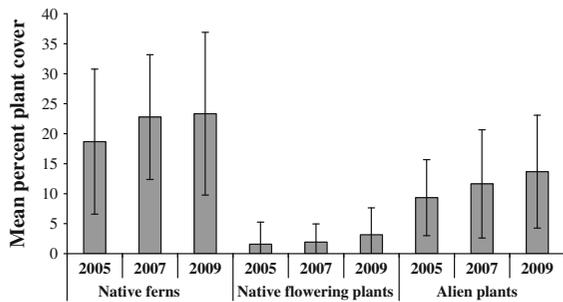


Fig. 5 Changes in plant cover according to taxonomical and biogeographical status. Friedman test followed by a Wilcoxon signed rank test with Bonferroni correction ($*P < 0.016$); native ferns ($n = 7$; $\chi^2 = 3.714$; $df = 2$; $P = 0.146$); native flowering plant ($n = 7$; $\chi^2 = 7.185$; $df = 2$; $P < 0.05$); alien plants ($n = 7$; $\chi^2 = 3.429$; $df = 2$; $P = 0.180$); error bars represent SE

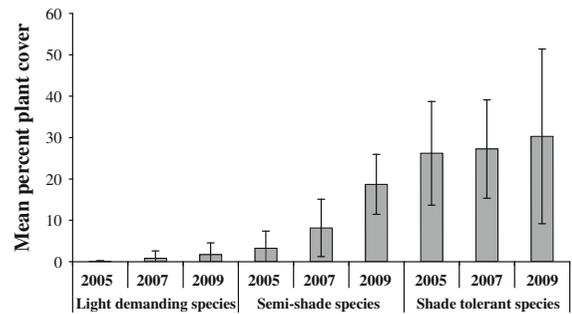


Fig. 7 Changes in plant cover according to species light preference. Friedman test followed by a Wilcoxon signed rank test with Bonferroni correction ($*P < 0.016$); light-demanding species ($n = 7$; $\chi^2 = 12.000$; $df = 2$; $P < 0.01$); semi-shade species ($n = 7$; $\chi^2 = 6.000$; $df = 2$; $P < 0.05$); shade-tolerant species ($n = 7$; $\chi^2 = 0.000$; $df = 2$; $P = 1.002$); error bars represent SE

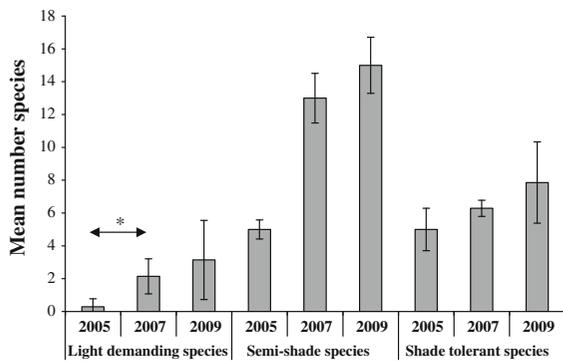


Fig. 6 Changes in species diversity according to their light preference. Friedman test followed by a Wilcoxon signed rank test with Bonferroni correction ($*P < 0.016$); light-demanding species ($n = 7$; $\chi^2 = 12.000$; $df = 2$; $P < 0.01$); semi-shade species ($n = 7$; $\chi^2 = 12.000$; $df = 2$; $P < 0.01$); shade-tolerant species ($n = 7$; $\chi^2 = 6.462$; $df = 2$; $P < 0.05$); error bars represent SE

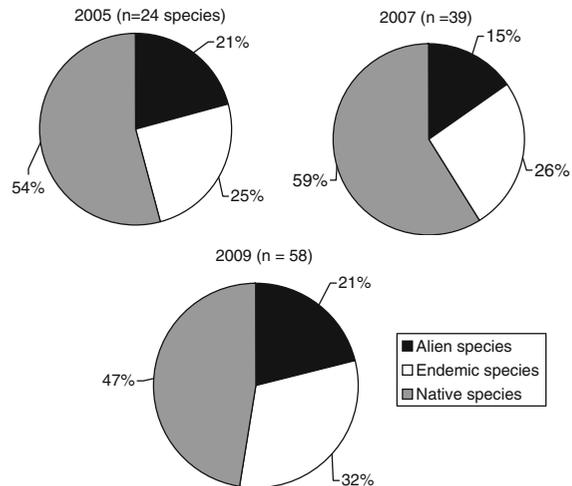


Fig. 8 Changes in species composition with time according to biogeographical status

demonstrates that biological control may contribute to partial habitat restoration severely invaded by an alien tree, with indirect positive effects on native and endemic plant recruitment, including some rare and endangered species (*Cyrtandra*, *Ophiorrhiza*, *Psychotria*). The successful miconia biological control program in Tahiti also provides an opportunity to determine the impact of an invasive plant on native biodiversity, like classical weed control experiments (Baider and Florens 2011; Barton et al. 2007).

Miconia canopy leaf damage caused by Cgm (ranging between 6% and 36% in our study sites) increases light availability in the forest understorey invaded by miconia and explains the significant

increase of plant diversity, especially for light-demanding species. The continuous increase in understorey diversity despite a stable degree of leaf damage is likely due to a lag time in plant recruitment and growth following introduction of Cgm.

A slight increase of alien plant diversity was observed, but their proportion remains still low and stable (15–20%) compared to the number of native flowering plants and ferns (Fig. 8), indicating some kind of “resilience” in the community structure and composition. However, in the lower elevation permanent plots (600–630 m) located near cultivated and ranching areas, there was colonization by other light-demanding weeds such as the herbs *Ageratum*

conyzoides and *Erechtites valerianifolia* (Asteraceae), trees *Cecropia peltata* (Cecropiaceae) and *S. campanulata*, the thorny shrubs *Lantana camara* (Verbenaceae) and *R. rosifolius*, and the climbing vine *Passiflora suberosa* (Passifloraceae). Seedlings of the bird-dispersed shade-tolerant strawberry guava *Psidium cattleianum* (Myrtaceae) and wind-dispersed quinine tree *Cinchona pubescens* (Rubiaceae), both highly invasive in the Taravao site were observed.

Reinvasion or recolonization by other undesirable alien plants is indeed an important issue for weed management (Barton et al. 2007; Denslow and D'Antonio 2005; Syrett et al. 2000). In the case of mistflower *Ageratina riparia* (Asteraceae) biological control program in New Zealand using a pathogen, a “weak replacement weed effect” was observed. The potentially serious invader African club moss *Selaginella kraussiana* reinvaded some areas in which mistflower declined (Barton et al. 2007; S. Fowler, Landcare Research, New Zealand, pers. com. 2010). On the island of La Réunion, large areas formerly invaded by the bramble *Rubus alceifolius* (Rosaceae) were re-colonized by different alien invasive plants such as the shrubs *Solanum mauritianum* (Solanaceae) and *Clidemia hirta* (Melastomataceae) after the release of the leaf-eating insect *Cibdela janthina* (S. Baret, Parc National de La Réunion, pers. com. 2010).

The major cyclone that hit Tahiti in February 2010, with maximum wind gusts of 120 km h⁻¹, a rare natural disturbance in Eastern Polynesia, has caused massive defoliation of dense miconia forests in some areas of the island interior. Large tree fall gaps now occurred in some of our permanent plots. It is probable that plant succession will be shifted towards fast growing, light demanding pioneers—mainly aliens—in these highly disturbed areas.

Our study illustrates that biological control may be considered as a tool for habitat restoration and ecosystem management (Headrick and Goeden 2001). However, the stability and composition of plant communities that replace the target weed may differ (Tisdale 1976). The “novel plant assemblage” is certainly not the same as the pre-invaded species composition, which is difficult to assess in Tahiti as miconia has invaded almost all areas of similar ecological conditions. Native biodiversity will not necessarily return after the reduction of the density and/or impact of miconia, and it is unlikely that any

ecosystem that has been heavily infested with a weed species will ever return to the pre-infestation state (Paterson et al. 2011). Potential beneficial effects of the biological control agent on forest ecosystem functions and services (e.g. soil erosion and fertility, nutrient cycles, water regime, etc.) will require a longer monitoring period of time (>ten years) and/or the use of more high-tech monitoring tools (e.g. biosensors).

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