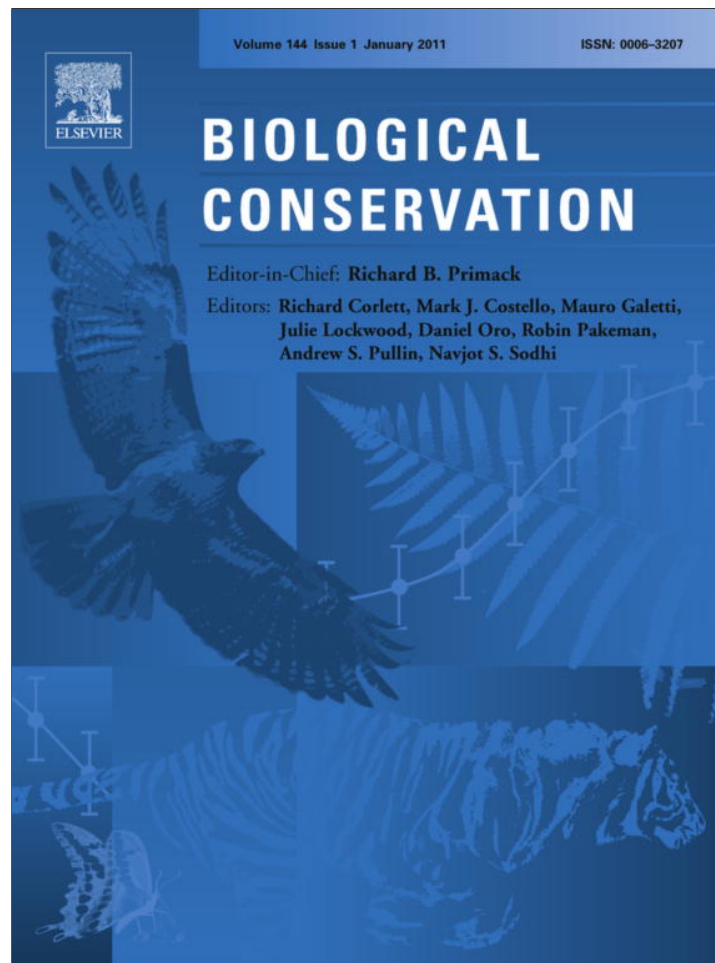


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Conservation benefits of biological control: The recovery of a threatened plant subsequent to the introduction of a pathogen to contain an invasive tree species

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ABSTRACT

Biological control using host-specific natural enemies is sometimes the only long-term and cost-effective option to contain dominant invasive alien species in natural ecosystems. To assess biocontrol success, most monitoring studies focus on the negative impacts of the released biocontrol agents on the target invasive species. Very few studies have shown the conservation benefits, i.e. their positive effects on the recovery of native species and habitats. A fungal pathogen (*Colletotrichum gloeosporioides* f. sp. *miconiae*) was successfully released on the island of Tahiti (South Pacific) to control the dominant invasive tree *Miconia calvescens* which forms dense monospecific stands in native rain- and cloud forests. The pathogen causes a leaf disease leading to partial (5–35%) defoliation of *Miconia* canopy trees. We studied the demographical parameters of the rare endemic sub-shrub *Ophiorrhiza subumbellata*, growing in the understorey of montane cloud forests invaded by *Miconia*. We compared *Ophiorrhiza* populations in 13 plots set up in two sites located between 950 and 1000 m elevation, having the same *Miconia* invasion degree but different levels of leaf damage. Our results showed that, whereas the total population density of *Ophiorrhiza* is not affected, plants' growth and fertility were significantly higher in more defoliated *Miconia* forests. A 3-year-long survey of *Ophiorrhiza* population at one study site indicated that the number of seedlings and juvenile plants increased, suggesting better recruitment and survival. This study demonstrates that biological control has contributed to the recovery of an endemic plant directly threatened by an invasive species, and may be considered as an important management tool for the partial restoration of native forests.

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1. Introduction

Classical biological control, using host-specific natural enemies, can be the only effective option to control widespread and dominant alien invasive species in natural ecosystems where other conventional methods (e.g. manual and chemical control) are costly and labour-intensive over the long-term (Waterhouse and Norris, 1987; Gardner, 1990; Myers and Bazely, 2003). Most of the tropical oceanic islands, such as Hawaii, Galápagos and French Polynesia in the Pacific Ocean, or the Mascarenes and Seychelles in the Indian Ocean, are characterized by a huge number of recently introduced plant species (>1000–2000+). Hundreds of these new introductions become naturalized (i.e. established in the wild) with the result that the number of exotic species can equal or exceed that of native vascular plants. Some (>50–100+) exotics have become dominant invasive species with large distribution ranges, high abundance, and important negative impacts on the native biota (Loope and

Mueller-Dombois, 1989; Meyer, 2004; Kueffer et al., 2010). For the species with long-distance seed dispersal capacities (e.g. anemochory and endo-ornithochory), the difficulty of their control is enhanced because of the mountainous island relief with very steep slopes and sometimes inaccessible high elevation ridges and peaks. A self-dispersing biological control agent can effectively locate target plants which are hidden or physically inaccessible and can enter sensitive areas which would otherwise suffer from disruption caused by the activities of a control team (Gardner et al., 1995).

To assess the success of a biological control program, most of the monitoring studies focus on the direct negative impacts of the released biocontrol agents on the target plant's: distribution (e.g. geographic and habitat ranges); demography (e.g. rate of spread, population density, abundance, and growth rate); reproduction (e.g. fruit set, seed production, and seed germination); or vigour (e.g. cover and biomass) (Briese, 2000; Syrett et al., 2000; Myers and Bazely, 2003). Even though the use of biological control in natural ecosystem has considerably increased, very few studies have dealt with the indirect positive effects on native species and the conservation benefits of biological control programs (Huffaker, 1951; Denslow and D'Antonio 2005; Barton et al., 2007).

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The tropical oceanic island of Tahiti, French Polynesia (South Pacific) has been invaded by the invasive tree *Miconia calvescens* (hereafter *Miconia*) over two-thirds of the island including species-rich montane cloud forests. A host-specific plant pathogen biocontrol agent was released there in 2000 and monitored since. This has provided a good opportunity to assess the success of a biological control program in native island ecosystems and the indirect benefits to the endemic biota.

In this paper, we studied the population structure and life history traits of the rare endemic plant *Ophiorrhiza subumbellata* (hereafter *Ophiorrhiza*), growing in the understory of montane cloud forests directly threatened by *Miconia*'s massive invasion. The main aims were: (1) to assess the impact of the pathogenic fungus on *Miconia* canopy trees, (2) to measure the effects of *Miconia* partial defoliation on *Ophiorrhiza* density, growth and fertility, and (3) to monitor the demographic changes of *Ophiorrhiza* populations over a 3-year-period (between 2005 and 2008).

2. Study site and species

2.1. The island

Tahiti (17°38'S, 149°30'W) is the largest (1045 km²) and the highest island (2241 m) of French Polynesia (a French overseas territory) in the South Pacific Ocean. French Polynesia comprises 120 high volcanic islands, raised limestone atolls and low-lying atolls, and is located more than 5000 km away from the nearest continents. The island of Tahiti is formed by two ancient volcanoes, Tahiti Nui (ca. 30 km in diameter and between 800,000 years and 1.35 M years old) and Tahiti Iti (ca. 15 km in diameter and 400,000 years old). Climate is wet tropical oceanic (average temperature is between 25 and 28 °C at sea level), with a warm and wet season from November to April and a cooler and drier season from May to October. Because of a mountainous relief (with ten summits above 1500 m elevation and three above 2000 m) and the dominant Southeast tradewinds (called 'alizés' in French) there is a strong climatic contrast between the dry leeward West coast (mean annual rainfall <1500 mm/year) and the more humid windward East coast (>3000 mm/year). The island is characterized by deep V-shaped wet and warm valleys separated by knife-edged dry and windy ridges and colder summit peaks (0.6 °C temperature drop per 100 m). This topography provides a high diversity of native habitats which have allowed species radiation and high levels of endemism (Meyer and Salvat, 2009). The native vascular flora of Tahiti comprises more than 460 plant species of which 107 are strictly endemic to the island, and 86 are shared with one or more other islands of the Society archipelago (Florence et al., 2007). The lowland coastal forests, dry- and mesic forests, and valley rainforests have been disturbed by anthropogenic activities (mainly deforestation and fires for cultivation and housing development) since the arrival of the first Polynesians a thousand years ago. These activities accelerated after colonization by Europeans since the end of the 19th century compounded by the introduction of grazing mammals (pigs, goats, sheep, horses and cattle), urbanization, roads and the development of hydro-electricity. About 70% of the endemic flora is located in the montane cloud forest, starting at 600–800 m on the leeward coast, and 300–400 m on the windward coast, and in the subalpine vegetation above 1800 m elevation (Meyer, in press).

2.2. The invasive alien species

M. calvescens DC. (Melastomataceae) is a small tree 6–12 m tall (up to 16 m), native to tropical rainforests of Central and South America where it is described as an understory species in dense forest and a colonizer of small forest gaps. It was intentionally intro-

duced to a botanical garden in Tahiti in 1937 as a garden ornamental (under the horticultural name *Miconia magnifica* Triana) because of its strikingly large leaves with purple undersides. This species is a particularly aggressive colonizer in native forests and a competitor with indigenous and endemic plant species. Characteristics where it is invasive include: rapid vegetative growth (up to 1.5 m/year); early sexual maturity (after 4–5 years); self-pollination and independence from specific pollinators; three flowering and fruiting peaks per year; prolific fruit and seed production (up to 80 millions of tiny seeds produced per mature tree); active dispersal of the small fleshy berries by frugivorous native and alien birds over long-distances; high rates of seed germination even under very low light conditions; a large and persistent soil seed bank (up to 50,000 seeds/m² with a longevity of more than 16 years); and, shade-tolerance (Meyer, 1996, 1998). In less than 50 years, *Miconia* has successfully invaded all the mesic and wet forests of Tahiti and the nearby island of Moorea where the mean annual rainfall exceeds 2000 mm/year, from sea-level to 1400 m elevation on Tahiti, 1200 m on Moorea. It now covers more than 70% of Tahiti (i.e. about 80,000 ha) and 25% (about 3500 ha) of Moorea. *Miconia* forms dense almost monotypic stands (up to 3–6 individuals/m²) with a closed-canopy of large leaves, causing a dramatic decrease in the light availability in the understory (0.4–0.6% in a dense *Miconia* forest compared to 1–3% in native montane cloud forest, Meyer et al., 2007). Between 40 and 50 species of the 107 plants endemic to Tahiti, mostly herbs (e.g. terrestrial orchids), shrubs and small trees, were considered to be on the verge of extinction due to the massive invasion of *Miconia* (Meyer and Florence, 1996). *Miconia* is also invasive in the rainforests of Hawaii, New Caledonia, and far north Queensland in Australia, and remains a potential threat for many other wet tropical Pacific islands (Meyer, 2004; Loope et al., 2010).

2.3. The threatened endemic plant

Ophiorrhiza L. (Rubiaceae) is an Indo-Malesian genus comprising about 150 species (Mabberley, 2008), with its greatest diversity in New Guinea and Southeastern Asia (Van Balgooy, 1971). A total of 14 species is described in the South Pacific islands (Darwin, 1976), including nine species endemic to the Society archipelago (French Polynesia) which are restricted to the largest islands of Tahiti, Moorea, and Raiatea. All species are suffrutescent herbs to sub-shrubs, 0.2–2 m in height, growing in wet habitats, e.g. humid valleys along the banks of streams and wet cliffs, and they are found in the understory of low- to high elevation rainforests located between 40 and 1700 m elevation (Darwin, 1976; pers. obs., 1999–2009; Table 1). Although not listed in the IUCN Red Lists of threatened plants worldwide (Walter and Gillett, 1998), all nine species are rare, with small populations and a patchy distribution. Seven species were considered to be directly threatened by *Miconia*'s massive invasion (Meyer and Florence, 1996), and were declared legally protected in French Polynesia in 2007.

O. subumbellata (Seem.), the first Pacific species of this genus to be described by the botanist Georg A. Forster during the second voyage of James Cook in the Pacific (1772–1775), is a suffrutescent herb or sub-shrub reaching 1–1.8 m in height (Darwin, 1976; pers. obs.), with small opposite leaves (3–11 cm long × 1.2–2.8 cm wide). It is a procumbent or erect plant with slender stems, able to reproduce vegetatively from roots when damaged or broken, and exclusively found between 700 and 1200 m elevation (Darwin, 1976; Florence et al., 2007; pers. obs., 1999–2009). The most common natural habitats include steep slopes, ravines and river banks, and the species is never found in open habitats such as large tree-fall gaps, forest edges, roadsides or pasturelands.

Mature plants produce helicoid cymes comprising five to 18 (Darwin, 1976), sometimes up to 30+ (pers. obs.) tubular white to pinkish flowers. Fruits are small dry dehiscent subglobose

Table 1

List and status of the eight endemic *Ophiorrhiza* species present on the island of Tahiti (Society Islands, French Polynesia). Altitudinal range according to Darwin (1976), Florence et al. (2007) and pers. obs. (1999–2009). Habitat type: LRF = low elevation rainforest; MRF = mid-elevation rainforest; CF = high elevation or montane cloud forest. Abundance according to pers. obs. (1999–2009): er = extremely rare (<5 populations and <50 individuals currently known in the wild); vr = very rare (>5–10 populations and >50–100 plants); r = rare (>10–50 populations and >100–1000 plants); ? = unknown.

Scientific name	Islands	Altitudinal range (m)	Habitat type	Abundance
<i>Ophiorrhiza nelsonii</i> Drake	Tahiti	300–1170	MRF, CF	vr
<i>Ophiorrhiza orofenensis</i> Seemann	Tahiti	1700	CF	?
<i>Ophiorrhiza platycarpa</i> S. Darwin	Tahiti	40–240	LRF	er
<i>Ophiorrhiza scorpioidea</i> Nadeaud	Tahiti, Moorea	585–1000	MRF, CF	vr
<i>Ophiorrhiza setosa</i> S. Darwin	Tahiti, Moorea	400–500	MRF	er
<i>Ophiorrhiza solandri</i> Seemann	Tahiti	125; 1175	LRF, CF	er
<i>Ophiorrhiza subumbellata</i> J.G. Forster	Tahiti	330–1000	MRF, CF	r
<i>Ophiorrhiza tahitensis</i> Seemann	Tahiti	590–1405	MRF, CF	r

capsules containing 50–200 tiny seeds, ca. 0.5 mm in diameter (pers. obs.). In Tahiti, where extensive botanical surveys have recently been conducted, the distribution of *O. subumbellata* is completely sympatric with areas invaded by *Miconia*.

Only a very small number of populations are currently known in the wild (less than 50), each of them comprising between 1 and 67 individuals (pers. obs., 1999–2009), with an average of 7.4 ± 5.8 mature plants per population (unpub. data). We estimate the total number of plants to be less than 1000 on the island of Tahiti, with an estimated number of 100–500 reproductive individuals (Table 1). If IUCN Red List categories and criteria were used (IUCN 2001), the species might be classified as endangered (EN, more precisely EN B1; B2ab(i–iv); C2a(i)) as the total area of occupancy is estimated to be less than 100 km², is severely fragmented, with less than 2500 mature individuals, and with no subpopulation containing more than 250 mature plants.

2.4. The biocontrol pathogen agent

Due to the terrain, manual and chemical control methods have had limited success against *Miconia* in heavily invaded islands such as Tahiti and Moorea. Biological control, therefore, was viewed as the only effective alternative (Meyer, 2008). Exploratory trips to Central and South America were initiated in 1997 by the Hawaii Department of Agriculture in Honolulu (HDOA) to search for natural enemies of *Miconia*. A promising fungal pathogen, *Colletotrichum gloeosporioides* forma specialis *miconiae* Killgore and Sugiyama (Coelomycetes, Deuteromycetinae), hereafter *C. gloeosporioides miconiae*, was discovered in the State of Minas Gerais in Brazil. Host-specificity tests conducted at the quarantine facilities of HDOA showed that this pathogen was highly specific to *Miconia* (Killgore et al., 1999). It reproduces by asexual spores or conidia which are produced under high moisture conditions, and are disseminated by wind-driven rain. The pathogen causes foliar anthracnose and necrosis, and cankers on injured stems causing a dieback. In laboratory conditions, it attacks germinating *Miconia* seeds and kills emergent seedlings (up to 74% mortality, Meyer et al., 2008). After the final approval of the French Polynesian

Government, inoculum of *C. gloeosporioides miconiae* cultivated at HDOA was introduced to Tahiti and released in two permanent plots, in 2000 and 2002 respectively. Post-release monitoring surveys showed that the fungal pathogen successfully established and reproduced after three weeks, infecting 100% of the monitored plants at the release site. It then spread into all of the *Miconia* invaded areas of Tahiti and the neighbouring island of Moorea in less than 3 years. The pathogen caused 30% mortality of small seedlings less than 50 cm tall, and multiple damages were observed on about 25% of the surviving plants, including rotting stems. An unexpected impact was the damage caused by *C. gloeosporioides miconiae* on *Miconia* canopy leaves of mature trees leading to partial defoliation (Meyer et al., 2008).

3. Materials and methods

3.1. Direct negative impacts of *C. gloeosporioides miconiae* on *Miconia*

In 2008, we set up 15 *Miconia* study plots located at different elevations (between 400 and 1200 m) in four different sites (Fig. 1); three on Tahiti Nui (MAR with 2 plots, PIC with 3 plots, HAM with 5 plots) and one on the peninsula of Tahiti Iti (TAR with 5 plots). At each plot, ten tall (>6–12 m) reproductive *Miconia* trees were randomly selected and cut down. Twenty five canopy leaves per tree were collected, excluding the young small leaves on the tip of branches. Leaf damage was visually estimated in the laboratory, using a grid mesh of 2 × 2 cm squares placed over each leaf. The number of squares with *C. gloeosporioides miconiae* induced necrotic lesions and holes was divided by the total number of squares covering the total leaf area to obtain the '% C.g.m. leaf damage' index.

At the two sites where *Ophiorrhiza* demographical parameters were studied (see below), *C. gloeosporioides miconiae* defoliation of *Miconia* canopy leaves was also estimated in 2005.

3.2. Indirect positive effects of *C. gloeosporioides miconiae* on *Ophiorrhiza*

The effects of *C. gloeosporioides miconiae* on *Ophiorrhiza* populations was studied in 2005 and 2008 in two of the study sites (HAM and PIC), located between 950 and 1000 m. Thirteen 25 m² circular plots (radius = 2.8 m) were set up (7 at HAM and 6 at PIC). Each plot was centred on the tallest fertile *Ophiorrhiza* plant and encompassed almost all of the other individuals in a population. The number of *Ophiorrhiza* study plots reflected the rarity of this species and ease of site access as some populations were found on very steep slopes and cliffs in inaccessible habitats.

The number of 'juveniles' (size <5 cm tall, including seedlings), sterile and fertile adults were counted. For each monitored adult plant >5 cm height, diameter at base; the number of cymes (inflorescences and/or infructescences); and, the number of flowers and/or fruits (e.g. capsules) on the cymes was recorded.

Miconia invasion pressure was estimated in 2005 and 2008 by counting the number of *Miconia* plants (higher than 5 cm) in each *Ophiorrhiza* study plot and by calculating the basal area of stems for all *Miconia* plants at 1.3 m off the ground. Data were analysed using parametric and non-parametric statistical tests with the SPSS software (SPSS, 2005).

4. Results

4.1. *C. gloeosporioides miconiae* leaf damage on *Miconia*

The '% C.g.m. leaf damage' index ranged from 5–35% in our four study sites and 15 *Miconia* plots according to location and elevation

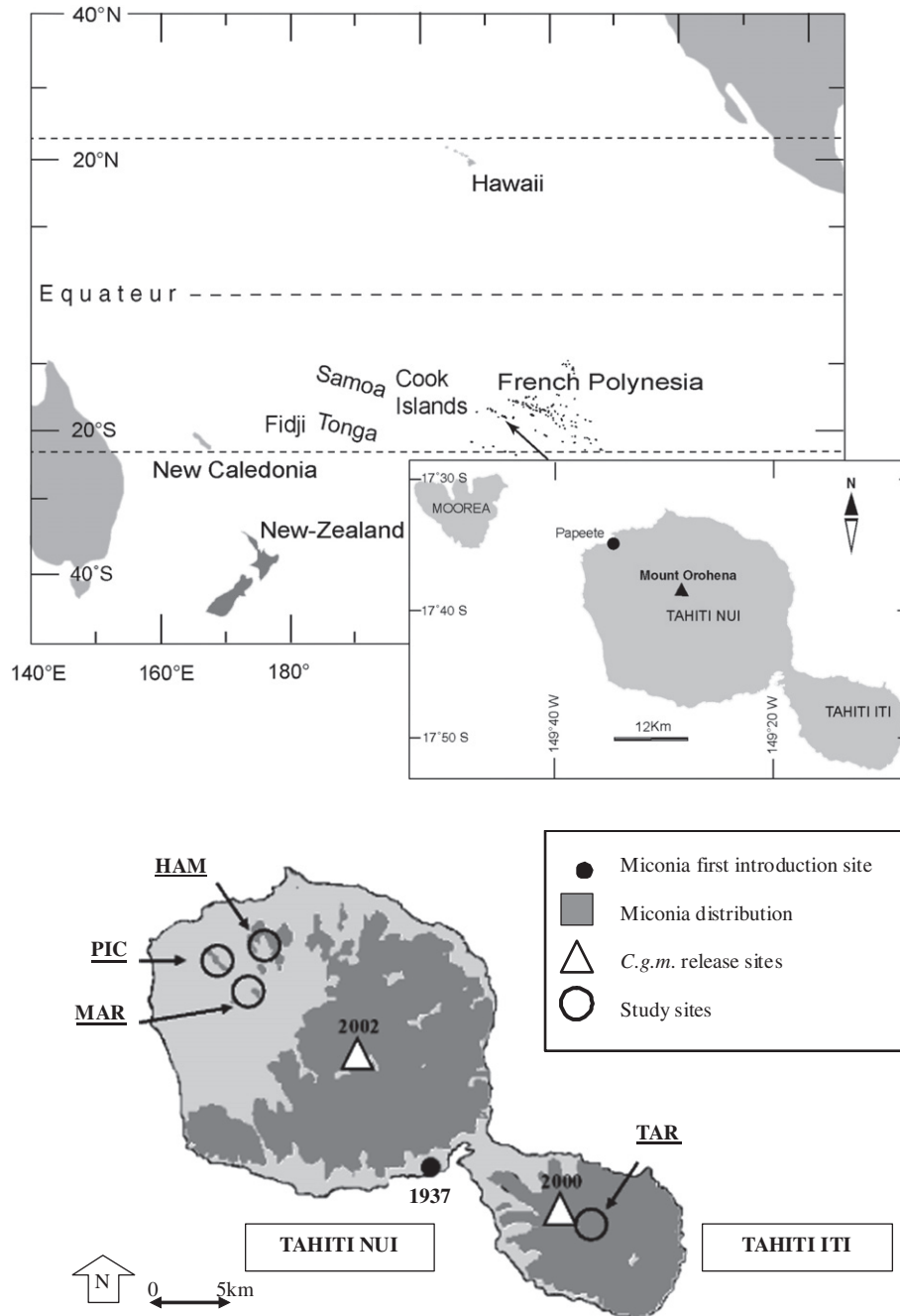


Fig. 1. Map of the island of Tahiti showing: *Miconia*'s first introduction site; its current distribution; release sites of the fungal pathogen; and, the location of the four study sites.

(Fig. 2). Partial defoliation of *Miconia* canopy leaves increases significantly with elevation ($R^2 = 0.78$; $p < 0.001$).

4.2. Effects of *Miconia* defoliation on *Ophiorrhiza*

The two *Ophiorrhiza* study sites (HAM and PIC) located at the same elevation were separated in two categories according to the damage index score: low damage (LD) areas where the *C.g.m.* leaf damage index was $<40\%$ (HAM, $N = 7$) and high damage (HD) areas with an index $>40\%$ (PIC, $N = 6$) (Table 2). The mean *Miconia* basal area measured in the two *Ophiorrhiza* sites was not statistically different (Mann–Whitney U test: $N = 13$, $U = 21.000$, $Z = 0.000$, $P = 1.000$), allowing us to study *Ophiorrhiza* demography independently to *Miconia*'s degree of invasion.

4.2.1. *Ophiorrhiza* density

A total of 615 *Ophiorrhiza* plants were counted in the 13 circular study plots: there were 324 individuals taller than 5 cm (of which 99 were fertile), and 291 juveniles smaller than 5 cm (Table 2). The total density of *Ophiorrhiza* plants was not significantly different between LD and HD sites (Mann–Whitney U test: $N = 13$, $U = 16.000$, $Z = -0.715$, $P = 0.535$), however the density of fertile adults was significantly higher in plots where *C.g.m.* leaf damage index is higher (Fig. 3, $N = 13$, $U = 3.500$, $Z = -2.517$, $P < 0.01$).

4.2.2. *Ophiorrhiza* growth

To determine the indirect effect of *C. gloeosporioides miconiae* on *Ophiorrhiza* growth, all the *Ophiorrhiza* individuals were separated into five diameter classes (less than 2 cm, 2–4 cm, 4–6 cm, 6–8 cm,

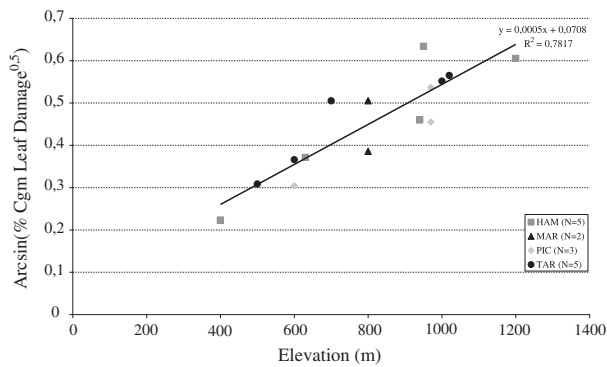


Fig. 2. Relationship between the mean *C.g.m.* leaf damage (Arcsine transformed data) on *Miconia* canopy and elevation in 2008 at the four study sites (Linear Regression: $N = 15$, $R^2 = 0.78$; $p < 0.001$).

and 8–15 cm). Results show that, for a same diameter class, *Ophiorrhiza* plants are taller when the *C.g.m.* leaf damage index is higher (Fig. 4). The difference is significant for juveniles plants belonging to small diameter classes (seedlings and saplings), but not for large adult plants.

4.2.3. *Ophiorrhiza* fertility

The mean number of *Ophiorrhiza* flowers and/or fruits per cyme was more than twice higher in HD plots (Fig. 5a, Mean = 19.54 ± 5.46 , $N = 69$) than in LD plots (Mean = 8.50 ± 3.28 , $N = 20$) (Mann–Whitney test: $U = 59,000$, $Z = -6204$, $P < 0.001$) and this was consistent across all height categories of fertile plants (Fig. 5b).

4.3. Changes in *Ophiorrhiza* populations with time

Four of the six plots in the HAM site were monitored both in April 2005 and May 2008. Although the leaf damages is slightly higher in 2008 compared to 2005, no significant difference in the *Miconia* degree of invasion was observed between the two dates on these selected plots (Table 3). In absence of any other anthropogenic or natural disturbance on the site, a change in the demographic parameters of *Ophiorrhiza* with time is likely to be related to the impact of *C. gloeosporioides miconiae* on *Miconia*.

4.3.1. Density changes

The number of *Ophiorrhiza* plants doubled in the study plots, from 1.05 ± 0.84 plants/m² in 2005 to 2.29 ± 1.75 plants/m² in 2008, but this difference is not statistically significant (Wilcoxon Signed-Rank test: $N = 4$, $Z = -1.095$, $P = 0.273$). When sorted by height class, *Ophiorrhiza* plants smaller than 5 cm (e.g. young seedlings) increased from 87 in 2005 to 137 in 2008, while plants 5–50 cm height increased 13-fold. Numbers did not increase between years, however, in the largest height class (50–200 cm). However, a

Table 2

Comparison of *Ophiorrhiza* density between the two sites (PIC, $N = 6$ plots and HAM, $N = 7$ plots).

	PIC	HAM	Mann–Whitney <i>U</i> test		
			<i>U</i>	<i>Z</i>	<i>P</i>
Mean <i>C.g.m.</i> leaf damages (%)	40.09 ± 6.12	28.67 ± 2.91	0.000	-1.964	-*
Mean <i>Miconia</i> basal area (cm ² /m ²)	14.90 ± 8.60	14.54 ± 8.49	23.000	-0.192	n.s.
Mean <i>Ophiorrhiza</i> density (ind./m ²)					
Total	1.07 ± 0.44	2.48 ± 2.72	19.000	-0.482	n.s.
Juveniles (<5 cm tall)	0.10 ± 0.11	1.49 ± 1.79	9.000	-1.996	-*
Sterile adults	0.53 ± 0.33	0.84 ± 0.86	21.500	-0.701	n.s.
Fertile adults	0.44 ± 0.21	0.15 ± 0.12	5.500	-2.441	-*

n.s. = no significant difference.
* $P < 0.05$.

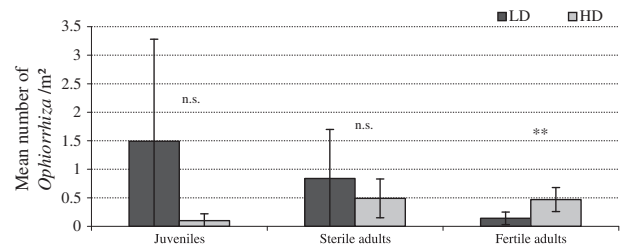


Fig. 3. Density of *Ophiorrhiza* plants according to height and reproductive status with *Miconia* defoliation (Mann–Whitney *U* test; n.s. = no significant difference, ** $P < 0.01$). LD = low damage, HD = high damage. Juveniles: $N = 13$, $U = 7.500$, $Z = -1.945$, $P = 0.510$; Sterile adults: $N = 13$, $U = 17.500$, $Z = -0.501$, $P = 0.628$; Fertile adults: $N = 13$, $U = 3.500$, $Z = -2.517$, $P < 0.01$.

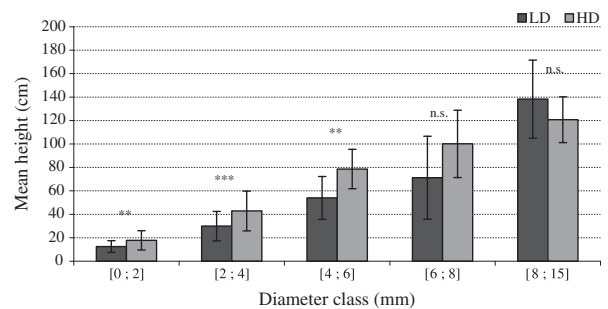


Fig. 4. Density of *Ophiorrhiza* in low (LD) and high (HD) defoliation sites according to diameter class. n.s. = no significant difference, ** $P < 0.01$, *** $P < 0.001$.

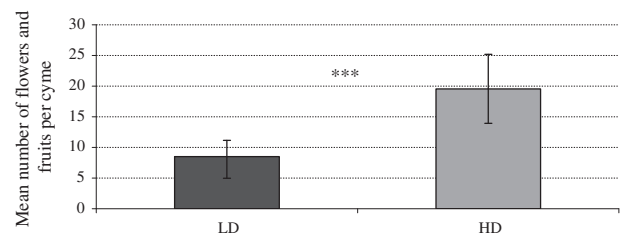


Fig. 5a. Fertility of adult *Ophiorrhiza* in low (LD) and high (HD) defoliation sites (*** $P < 0.001$).

χ^2 test shows that the distribution of *Ophiorrhiza* if all height classes are considered is significantly different between 2005 and 2008 (Fig. 6, $ddl = 2$, $\chi^2_{obs} = 35.8$, $P < 0.001$) suggesting that there is a notable change in the population structure. Results indicate that partial defoliation of *Miconia* enhances seedling recruitment (i.e. an increase of the seedlings with time) and survival (i.e. an increase of the juveniles), which could lead to an unambiguous increase in *Ophiorrhiza* population sizes.

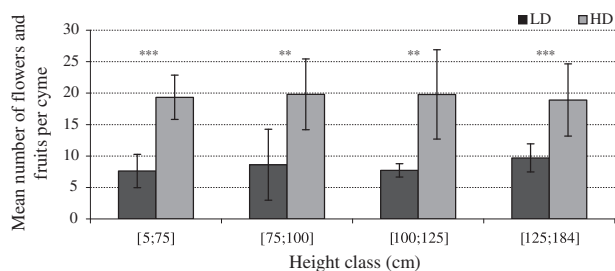


Fig. 5b. Fertility of adult *Ophiorrhiza* in low (LD) and high (HD) defoliation sites according to height class (** $P < 0.01$, *** $P < 0.001$).

Table 3

Changes in fertile adult plants of *Ophiorrhiza* ($N = 9$) in the HAM site (4 plots) between 2005 and 2008 (Mann–Whitney U test to compare % C.g.m. leaf damage and Wilcoxon Signed-Rank test to compare *Ophiorrhiza* fertility).

	2005	2008	Statistical tests		
Mean C.g.m. leaf damages (%)	33.67 ± 12.77	28.68 ± 2.91	4.000	-0.827	n.s.
Height (cm)	105.66 ± 35.60	140.55 ± 33.35	-2.668	-	**
Diameter (mm)	8.44 ± 2.87	11.55 ± 2.78	-2.552	-	*
Number of cymes per plant	6.77 ± 5.09	25.77 ± 24.70	-2.380	-	*
Number of flowers and/or fruits per plant	104.44 ± 103.30	236.55 ± 254.67	-1.955	-	n.s.

n.s. = no significant difference.

* $P < 0.05$

** $P < 0.01$

4.3.2. Changes in growth and fertility

The height and diameter of the monitored adult fertile *Ophiorrhiza* plants increased significantly between 2005 and 2008 (Table 3). The mean growth rate for plant size is 11.7 cm per year. The number of cymes were significantly higher in 2008 (Wilcoxon Signed-Rank test, $Z = -2.380$, $P < 0.01$), and the mean number of flower and fruit per plant increases but did not differ significantly ($Z = -1.955$, $P = 0.051$). Although fertility seems to be higher in 2008, our results suggest a significant decrease in the mean number of flowers and fruits per cyme (from an average of 15.4 in 2005 to 9.2 in 2008, $Z = -2.547$, $P < 0.05$). This could be related to a slight shift in the reproductive season between the 2 years, or more probably, a trade-off in favour of vegetative growth.

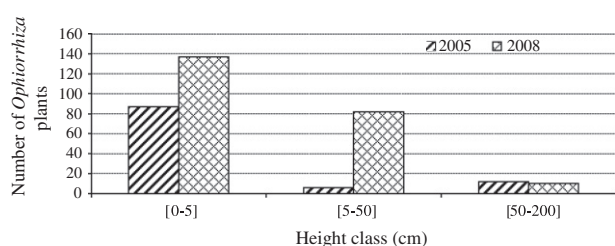


Fig. 6. Changes in *Ophiorrhiza* plant number between 2005 and 2008 according to height class (Pearson Chi-square test between 2005 and 2008: $\chi^2 = 35.8$, $ddl = 2$, $P < 0.001$).

5. Discussion

5.1. Conservation benefits of biological control programs

Biological control is often viewed as the only practical solution to contain dominant or widespread weeds both in agro-systems and in natural ecosystems. It is a cost-effective, long-range, control method with very few or no risk to non-target species if the natural enemies are proven to be highly host-specific (Gardner, 1990; McFayden, 1998). For the manager challenged with habitat conservation, the most important question is whether the impacts of introduced invasive species can ever be reversed (Myers and Bazely, 2003). The irreversibility of the modification of a plant community, despite removal of the factor which caused the disturbance, is becoming a key issue in ecology and conservation (Lindenmayer and Fischer, 2006). There are, however, very few quantitative studies evaluating the benefits of introduced biological control agents for the indigenous species and the restoration of native habitat. Studies on the ecological responses of invaded plant communities to target species reduction remain scarce (Denslow and D'Antonio, 2005).

Positive effects have been demonstrated in New Zealand from the introduction of agents to biologically control the herbaceous weed *Ageratina riparia* (Asteraceae). Barton et al. (2007) showed that species richness and mean percentage cover of native plants, but not of exotic (non-native) plants, increased after the agents were introduced. One of the few examples of biological control being initiated solely for conservation of native biodiversity is to be found in an arthropod pest control program. A predatory South American coccinellid beetle (*Hyperaspis pantherina*) was introduced to the island of St. Helena (South Atlantic Ocean) to control the scale insect *Orthezia insignis* (Homoptera: Ortheziidae). The scale was attacking a rare endemic plant (the gumwood *Commidendrum robustum*, Asteraceae), and this intervention probably saved field populations of the plant from extinction (Fowler, 2004).

5.2. The positive effects of the fungal pathogen *C. gloeosporioides miconiae*

Because of its large distribution and dominance on the island of Tahiti, and its enormous impacts on the native biota, invasion by the small tree *M. calvescens* represents one of the most dramatic and devastating cases of an exotic plant disrupting an island ecosystem ever documented (Whittaker and Fernandez-Palacios, 2007; Loope et al., 2010). By forming dense monotypic closed-canopy forests, the species was responsible for a dramatic decrease in light availability. Based on field observations, Meyer and Florence (1996) have emphasized how urgently the endemic flora endangered by the massive invasion need saving, especially the small trees, shrubs and sub-shrubs growing in the understory of the native rain- and cloud-forests. A decrease in the fertility of several endemic species of *Psychotria* (Rubiaceae) with an increasing degree of *Miconia* invasion was later demonstrated (Meyer et al., 2003). There was also lower seedling recruitment by the small endemic trees *Lepinia taitensis* (Apocynaceae) and *Myrsine longifolia* (Myrsinaceae) in more invaded areas (Meyer et al., 2007).

The partial opening of *Miconia* canopy following the introduction of the pathogen *C.g.m.* has reversed this situation. The recovery of *Lepinia taitensis* and *Myrsine longifolia*, measured as an increase of the density of seedlings, was observed in dense *Miconia* stands highly defoliated by *C. gloeosporioides miconiae*. There were no natural factors (e.g. cyclones, floods, and treefall gaps) or anthropogenic disturbances (deforestation, feral pig activity, etc.) that would have explained this recovery.

5.3. Population dynamics of *Ophiorrhiza* before and after biocontrol

Most of the *Ophiorrhiza* species found on the island of Tahiti are endemics limited to one or two-islands (Tahiti and Moorea) with apparently restricted ranges and small populations. They were described as naturally rare during the last century, before *Miconia*'s introduction and invasion, according to labels on herbarium specimens of botanists Nadeaud (1873) and M.L. Grant (1930–31). All of them are small herbs or sub-shrubs, described by botanist Darwin (1976) as growing in: “moist shaded forest” (for *O. nelsonii*); “humid shaded environments” (*O. tahitensis*); “wet shaded areas along the banks of streams” (*O. longituba*); “on wet cliffs and in the deep shade of wet forests” (*O. solandri*); “shaded fern forests or more open habitats” (*O. subumbellata*); and, “moist shaded habitats” (*O. orofensis*). However, it must be emphasized that island forests in the Society Islands and in the Southeastern Polynesian biogeographical subregion are characterized by the short stature of the canopy: the canopy does not exceed 20 m in height in lowland valleys and is more often between 5 and 10 m on slopes, ridges, and peaks. These island forests have trees with small crowns and small leaves, and an overall simplified vertical structure (Meyer and Lavergne, 2001). This peculiar forest physiognomy allows a relatively high light intensity to reach the ground (e.g. 1–3% in native montane cloud forest in Tahiti, Meyer et al., 2007) compared to lowland rainforests in continents or large continental islands. The Society Islands endemic *Ophiorrhiza* are thus not shade-tolerant *per se*, but should be rather considered as semi-sciaphilous species which require, or benefit from, light in order to flower and set fruit. This is also been observed for several species of Tahitian endemic *Psychotria* (Meyer et al., 2003).

Six of the seven the endemic *Ophiorrhiza* species present on the island of Tahiti are currently found between 40 m and 1400 m elevation in low-, mid- and high elevation rainforest and montane cloud forest. Only *O. orofensis* was observed at 1700 m, which is the upper limit of forest and lower limit of subalpine vegetation in Tahiti. The known populations of the former six species are now totally included into *Miconia*'s invaded area. We assumed that the dramatic decrease on the light availability in the understory of dense *Miconia* forest (e.g. 0.4–0.6%) has caused the observed decline of the endemic *Ophiorrhiza* species. *Miconia* partial defoliation following the introduction of the fungal pathogen ranges from 5% to 35% in our study plots set up in 2008, and between 13% and 36% in other sites located between 900 and 1100 m in Tahiti (unpub. data), leading to more favourable light environment conditions. Leaf damages are higher with increasing elevation, both in Tahiti (this study) and Moorea (Chen, 2009).

The increase of the fertility of mature plants and of the number of seedling and juvenile plants of *O. subumbellata* observed over time during this study suggests a better recruitment and survival of this threatened species. Our results also show that the largest *O. subumbellata* may survive in the shaded understory of closed-canopy *Miconia* forest. It is noteworthy that *O. tahitensis*, a species found in more shaded habitats and at higher elevation (above 1400 m), seems less sensitive to *Miconia*'s defoliation than *O. subumbellata* (unpub. data). Other endemic species threatened by *Miconia*'s invasion, especially the more shade-tolerant ones, may show differential responses to the effects of *C. gloeosporioides miconiae*.

6. Conclusions

Despite more than one century of biological control programs, there are few documented examples of the conservation value of biocontrol agents in natural ecosystems. In agro-systems, success is often measured primarily in terms of increased production, eco-

nomical gain or economic loss prevented (Hokkanen and Lynch, 1995; Culliney, 2005); assessing the benefits provided to natural systems is more difficult. Moreover, the harm that introduced biocontrol agents can do to indigenous species (the “unpredictability and irreversibility” of biological control, Simberloff and Stiling, 1996), and the fact that new biological interactions are created (Louda and Stiling, 2004) has been recently highlighted.

Another common criticism of biological control of weeds is the risk of re-invasion by another alien species (Syrett et al., 2000), or the potential creation of bare ground (Syrett et al., 2004). It is thus important to document vegetation change and dynamics associated with successful control of the target species, especially in natural areas in island ecosystems in which native vegetation types are particularly vulnerable, with native species considered to be less competitive, and under invasive species pressure from numerous alien species which are available to recolonize open or cleared habitats.

To assess the effects of the fungal pathogen at the community level rather than at the species level, we are currently monitoring the recruitment of native and non-native plants in the forest understory in permanent plots set up since 2005 in Tahiti. Our preliminary results showed that species diversity and plant cover of native species increases with time, an effect which is most pronounced for light-demanding native species, with little re-invasions by other alien plants (unpub. data). Long-term monitoring and scientific investigations will still be necessary to ensure that the fungal pathogen introduced to control *M. calvescens* on Tahiti can be considered as an effective tool for partial restoration of native forests, and that biological control “is destined to play an increasingly prominent role in the management of natural systems” as predicted by Gardner et al. (1995). Managers and scientists need to be conscious that the return to intact pristine conditions of the native forest ecosystems invaded by weeds is an unrealistic and unachievable goal, and that we will have to deal with “novel ecosystems” (Hobbs et al., 2009) with new (native and alien) species assemblages and interactions in a world of biological globalization.

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