Research Article

Invasive alien plants elicit reduced production of flowers and fruits in various native forest species on the tropical island of Mauritius (Mascarenes, Indian Ocean).

M.L. Fabiola Monty[1*], F.B. Vincent Florens[1] and Cláudia Baider[2]

[1]Department of Biosciences, University of Mauritius, Réduit, Mauritius

[2]The Mauritius Herbarium, R. E. Vaughan Building, Agricultural Services, Ministry of Agro-Industry and Food Security, Réduit, Mauritius.

*Corresponding author, E-mail: fab.monty@gmail.com

Abstract

Biological invasions constitute a major threat to biodiversity. However, while the impact of invasive alien animals on native biota is often unambiguous, the impacts of invasive alien plants (IAP) appear to be considerably less severe and, at times, more debatable. Invasion by alien plants co-occur with other drivers of habitat change such that assessing impacts of IAP independently of these other factors may be difficult. Generalisations can be misleading, because studies reveal different responses of native plants to the presence of IAP. Therefore, there is a need to understand general trends and exceptions within a particular habitat. In the island of Mauritius, mechanical control of invasive alien plants has been implemented for decades in lowland wet forests. Weeded and non-weeded areas are very similar in all aspects, except for the control of IAP, providing an opportunity to study how IAP are affecting native plants. We monitored the reproductive output of 20-40 individuals each, of nine selected native species from different forest strata, in both weeded and adjacent non-weeded areas in a lowland wet forest, through direct count/estimation of the number of flower buds, flowers and fruits. Flower bud, flower and fruit production were greater in the weeded area. These results are consistent with previous findings that noted greater regeneration of native trees in these areas. This study also provides clues to reported decline of shade tolerant understory vegetation in alien invaded forest and further stresses the importance of removing alien plants to restore biodiversity and function and achieve conservation success.

Keywords: Conservation management, Invasive plants, Phenology, Native plants

Resumo

Invasões biológicas são uma ameaça séria à biodiversidade. Enquanto o impacto dos animais exóticos invasores na biodiversidade é considerado inequívoco, o das plantas exóticas invasoras (PEI) parece ser menos problemático e mais controversos. PEI atuam simultaneamente com outros elementos modificadores do ambiente e discernir os seus impactos únicos é uma tarefa difícil. Como estudos têm mostrado respostas diferentes das plantas nativas quando na presença de PEI, generalizações podem ser enganosas, pois é necessário que entenda-se primeiro as tendências gerais e depois as exceções de cada habitat. Na ilha Maurício, o controle mecânico de PEI têm sido feito nas florestas ombrófilas úmidas perenifólias de baixa altitude já há algumas décadas. Como áreas floristicamente similares onde PEI foram removidas são adjacentes às áreas que continuam invadidas, estudos podem determinar a influência das PEI nas plantas nativas. As fenofases de 20-40 indivíduos, de nove espécies nativas de diferentes estratos, foram inspecionadas em áreas adjacentes com e sem PEI, e quantificadas por meio de contagem direta e/ou estimativa do número de botões florais, flores e frutos. A produção de botões florais, flores e frutos foram maiores nas áreas sem PEI, o que corrobora estudos anteriores que mostraram uma maior regeneração de plantas nativas nessas florestas. Este estudo evidência o declínio de espécies do sub-bosque de florestas ombrófilas invadidas , e salienta a importância da remoção das PEI como uma ação importante para restaurar a biodiversidade e as funções ecológicas, atingindo-se conservação plena.

Palavras-chaves: Manejo da conservação, Plantas exóticas invasoras, Fenologia, Plantas nativas

Received: 9 September 2012; Accepted: 26 October 2012; Published: 18 March 2013.

Cite this paper as: Monty, M. L. F., Florens, F.B. V. and Baider, C. 2013. Invasive alien plants elicit reduced production of flowers and fruits in various native forest species on the tropical island of Mauritius (Mascarenes, Indian Ocean). *Tropical Conservation Science* Vol. 6(1):35-49. Available online: www.tropicalconservationscience.org

Introduction

Biological invasions constitute a major threat to biodiversity worldwide [1]. However, while the impact of invasive alien animals on native fauna and flora is often unambiguous, with profound changes and precipitous population declines [2-3], the impacts of invasive alien plants appear to be considerably less severe and, at times more debatable [4-5]. In particular, it can be challenging to disentangle the impacts of alien plants on native plants from the multitude of other impacting factors like habitat fragmentation, pathogens, browsers or seed predators, as these different threats typically operate concurrently. Examples clearly showing that invasive alien plants (IAP) can competitively replace native species without other simultaneous disturbances are rare [6]. Furthermore, examples exist where regeneration of certain native plants is good in forests invaded by alien plants [7-8]. This situation stresses the possible dangers of making generalisations on the impact of invasive alien plants on the flora of the regions they invade, and calls for further studies to disentangle the impact of alien plants from other simultaneously operating threats. Here we present the result of such an experimental study made *in-situ* in the lowland wet forests of the island of Mauritius.

Mauritius is a tropical oceanic island, part of the volcanic Mascarene archipelago, located in the south-western Indian Ocean. It is part of the Madagascar and Indian Ocean Islands biodiversity hotspot [9]. Of its 691 native species of flowering plants, 39.5 % are Mauritian endemic, of which 81.7 % are estimated to be endangered [10], highlighting the island's high conservation value and need for urgent conservation actions. Currently, only 5 % of Mauritius retains remnants of native vegetation [11], of which less than a third comprise 'good quality' vegetation (≥ 50 % native cover) [12]. These forest remnants constitute habitat for most of the remaining native biodiversity of the island. They are, however, under pressure from invasive alien species, such as the Strawberry guava (*Psidium cattleianum* Sabine) [13-14], a major plant invader on many other oceanic islands [15].

In an attempt to halt native biodiversity loss, previous small-scale, localized mechanical control of IAP was conducted for a couple of decades in Mauritius [10]. We investigated the impact of IAP control and its adequacy as a conservation measure on a decadal scale by comparing plant communities in weeded and adjacent non-weeded forest areas (Fig. 1A-B). With these two areas being in all aspects similar except for the presence or absence of IAP, improved regeneration of native plants in weeded areas can be attributed to the removal of alien plants, indicating that they are the main threat limiting population growth of the native flora. Previous studies in Mauritius have pointed in this direction. Species richness and density of native seedlings and adult woody plants as well as native butterflies are greater in areas where IAP are controlled [14, 16-17]. It also appears that over the last century or two, several Mauritian shade tolerant, understory native plants have declined more severely than taller species [18-21]. This supports findings that understory and herbaceous ground flora are among the species that recovered best when IAP are controlled [17], suggesting that alien plants may play a pivotal role in driving the long term decline of understory species.

However, the precise mechanisms behind this pattern remain to be investigated. For example, alien plants may be exerting detrimental effects on native plant fitness (as detectable in terms of survivorship, growth rate or reproductive output) at a variety of possible stages in the life history of native plants. Through direct or indirect pathways, these may include reduced survivorship or growth of adults, lowered reproductive output, lowered seedling growth and/or survival rate, etc. Enhanced flower and/or fruit production after weed removal has been found in two endemic canopy tree species in Mauritian lowland wet forest [22-23]. Such trends led to greater seed production and may ultimately improve regeneration of the native plants. However, because these two canopy species both have large seeds and overtop the invasive plants, their response to alien plant control may not be representative of the forest woody plant community as a whole.

Here we investigate the influence of IAP on the reproductive allocation of selected native woody species from various strata of the forest (understory, midstory and canopy), by comparing the production of flowers and fruits of individuals growing in both non-weeded areas and in immediately adjacent areas that were weeded of all invasive alien plants a decade or so earlier. The aims of the study were two-fold. First, we sought to determine if the impacts of alien plants on native plants' reproductive output were more generalised in the forest community than so far established. Second, we sought to investigate if smaller (understory) shade tolerant native plants are more at risk from invasive alien plants than larger ones.

A **B**

Fig.1. (A) Non-weeded forest with strawberry guava as dominant invasive plants (reddish-brown stems) and (B) Freshly weeded forest.

Methods

Study site

This study was conducted in Brise Fer, located within the Black River Gorges National Park in the southwest of Mauritius (Fig. 2A-C), at 550-600 m elevation, centred around latitude 20°22'50'' S and longitude 57°25'35'' E. The area has a mean annual rainfall of about 2,600 mm, with a mean temperature of 23 ^{0}C in summer and 17 ^{0}C in winter [24]. It is an evergreen, lowland wet forest with canopy trees reaching 14-18 m tall, consisting of relatively well preserved forest alternating with more degraded areas [13, 19]. The region supports at least 195 native vascular plant taxa, making it the currently most species-rich locality known in Mauritius [17]. It is also structurally the most well preserved lowland wet forest in Mauritius, with the highest density of native trees ≥ 10 cm diameter at breast height (dbh) per hectare (about 1,430 trees), and the highest basal area - of 49.1 m^2 - for native plants ≥ 1 cm dbh [25]. These characteristics make Brise Fer one of the most intact wet forests of the island, as defined by surveys in the 1930`s [26].

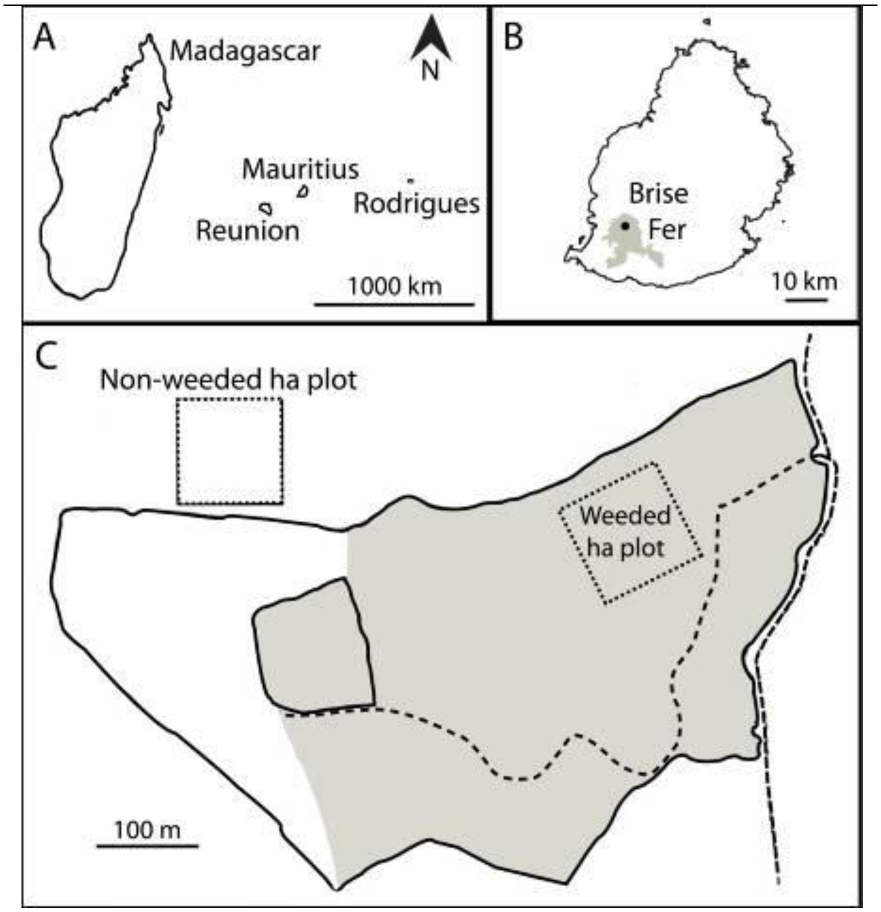

Fig.2. Geographic location of (A) Mauritius in the south western Indian Ocean, (B) Brise Fer forest in the Black River Gorges National Park (shaded) in southwest of Mauritius and (C) Weeded area of Brise Fer (shaded) and hectare plots (within doted lines) in weeded and non-weeded forest. Dashed line indicates vehicle track and solid lines the fences.

Brise Fer forest was also chosen because it contains the largest Conservation Management Area (CMA). CMAs are native habitat patches that have been weeded of IAP, mainly the Strawberry guava (*P. cattleianum*), which in wet lowland forests of Mauritius is virtually confined to the understory (>95% of all alien woody stems). In these forests, where canopy reaches 15-18 m in height, *P. cattleianum* typically grows as a slender small tree of up to eight m tall. About 4,000 individuals of *P. cattleianum* with diameter at breast height (dbh) ≥1 cm were recorded in 15 random plots of 100 m^2 of the best preserved forest remnants, giving a density of 26,607 per ha [14]. The larger woody alien plants were weeded at the study site in 1996 by cutting the stems followed immediately by uprooting of the stumps using axes and hoes. Smaller weeds were uprooted by hand pulling and thereafter regular maintenance weeding has been carried out to prevent re-invasion [27].

CMAs are also fenced off to try to exclude large alien mammals. The fencing is not effective, however, since equivalent levels of damage by large alien mammals were found inside and outside the fenced areas [14] by measuring the intensity of physical damage [28] caused by trampling by large mammals or uprooting by feral pigs. A number of gaps in the fencing caused by fallen trees, rusted fence, periodic rain storms or the pigs themselves digging their way underneath the fence appear to be responsible for the ineffectiveness of the fencing. The Brise Fer CMA is surrounded by non-managed forest of comparable quality, which enables comparative studies [17]. There is also one permanent one-hectare plot in each area (Fig. 2C), where the species identity, size (dbh), and spatial distribution of all native woody species and alien plants have been determined. The Brise Fer CMA covers ca. 20 ha; it was initially created in 1986-1987 with a patch of 1.26 ha and later expanded in 1992, 1995 and 1996. The non-managed forest of Brise Fer harbours at least seven alien woody plant species with a density of 27,287 individuals $ha^{-1}$for plants ≥ 1 cm dbh, of which 97.5 % are *P. cattleianum* [14].

Selection and monitoring of study species

Selection of the study species was based on the following criteria: a) they are known to flower or fruit during the sampling period (based on field observation, records from the regional Flora and herbarium samples); b) they are common enough in both the weeded and non-weeded areas to enable sampling of at least 20 individuals per site; and c) their adults belong to different guilds in the forest stratification (understory, midstory and canopy species). Nine native species were thus selected (Table 1).

Between 20 to 40 individuals of each selected species were randomly chosen in each hectare plot and monitored every two weeks for 5 months, from October 2007 to February 2008, during the season when the largest number of species is believed to be reproductive. For the shade tolerant understory shrub *Psathura borbonica* direct counts of all buds, flowers and fruits on each individual were feasible. For the other understory and midstory species, estimation of the number of flower buds, flowers and fruits was done using a pair of binoculars (10 x 42), except for *Gaertnera psychotrioides*. For the latter species inflorescences and infructescences were quantified in lieu of flowers and fruits, which were too closely packed to estimate from a distance. For the canopy species, with the crown obscured by understory vegetation, ground sampling was used to estimate the number of fallen flowers/corolla and fruits in four 1 m^2 quadrats arranged around the base of each tree, each sampled for one minute. For the canopy tree *Diospyros tessellaria*, only fallen flowers/corolla were sampled because the species is dioecious and distinguishing in the field between fruiting female trees and nonfruiting male trees was not always possible. For the canopy species, only individuals with > 10 cm dbh were sampled, because preliminary observations indicated that smaller trees may not always be mature. Similarly, only mature-sized plants of the non-canopy species were selected.

Table 1 Selected study species, their family, common name, range of height at maturity, forest stratum to which they belong and IUCN Red List Status. The Red List status of most species sampled has not yet been officially assessed. All species are insect pollinated. Apart from *T. persicariifolia* and *C. orientalis*, which are Mascarenes endemic, all species are endemic to Mauritius.

Family	Species	Common name	Height range (m)*	Forest stratum	IUCN Red List status
Rubiaceae	*Psathura borbonica* J. F. Gmelin	Bois cassant	small shrub	Understory	.
Rubiaceae	*Ixora parviflora* Lam.	N/A	0.6-5	Understory	.
Melastomataceae	*Memecylon ovatifolium* (Poiret) Wickens	Bois canne	1.5-5	Understory	.
Rubiaceae	*Gaertnera psychotrioides* (DC.) Baker	Bois banane	1.8- 12	Midstory	.
Apocynaceae	*Tabernaemontana persicariifolia* Jacq.	Bois de lait	1.5- 10	Midstory	EN
Achariaceae	*Erythrospermum monticolum* Thouars	Bois manioc	0.75- 10	Midstory	.
Myrtaceae	*Eugenia pollicina* Guého et A. J. Scott	Bois de clou	10-18	Canopy	.
Ebenaceae	*Diospyros tessellaria* Poiret	Bois d'ebene noir	12-20	Canopy	VU
Celastraceae	*Cassine orientalis* (Jacq.) Kuntze	Bois d'olive	8-20	Canopy	.

*Bosser *et al.* (1976-onwards) and pers. obs. (CB & FBVF)

Data analysis

Kolmogorov–Smirnov test of normality, frequency distribution graph and sample size of each data set were considered to choose appropriate non-parametric or parametric tests. Maximum reproductive output of every individual plant of each selected species in managed and non-managed forest was compared using the Wilcoxon rank-sum test. Peak production was used for comparison, as each individual plant was monitored several times, and total reproductive output could have included double counting of the same flower bud/flower or fruits. All tests were done using MINITAB v.14, and STATISTICA v.5 was used for the test of two percentages to compare the proportion of flowering and fruiting individuals in the weeded and non-weeded areas.

Results

Production of flower buds and flowers

Except for *Cassine orientalis*, all species studied were found flowering and/or fruiting. *Eugenia pollicina* and *D. tessellaria* were only fruiting while *Ixora parviflora* was only flowering. However, no analysis could be carried out for the latter species since only one individual flowered. For *D. tessellaria*, comparison of fruit production between weeded and non-weeded areas could not be confidently done since the absence of reproductive structures on many individuals rendered sexing of the trees impossible. Without fruits, it was impossible to distinguish a male plant from a female plant.

Peak production of flower buds was significantly higher in the weeded area for all species (*P. borbonica* (W_{30} = 1257.5, $p < 0.001$), *Memecylon ovatifolium* (W_{30} = 1116.5, $p = 0.003$), *Tabernaemontana persicariifolia* (W_{30} = 1113.0, $p = 0.003$) and *Erythrospermum monticolum* (W_{40} = 2187.5, $p < 0.001$) (Fig. 3, Appendix 1). Peak production of flowers/inflorescences was also higher for all species in the weeded area (*P. borbonica* (W_{30} = 1281.0, $p < 0.001$), *M. ovatifolium* (W_{30} = 1025.5, $p = 0.0448$), *E. monticolum* (W_{40} = 2048.0, $p < 0.001$), *G.psychotrioides* (W_{30} = 1042.0, $p = 0.0497$)); except for one species *T. persicariifolia* (W_{30} = 889.0, $p = 0.628$) (Fig. 4, Appendix 1).

Production of fruits

Fruit production was also higher in the weeded area for all of the non-canopy species *P. borbonica* (W_{30} = 1314.0, $p < 0.001$), *M. ovatifolium* (W_{30} = 1063.5, $p = 0.024$), *T. persicariifolia* (W_{30} = 1079.0, $p = 0.009$) and *E. monticolum* (W_{40} = 1851.5, $p = 0.012$), except for *G. psychotrioides* (W_{30} = 892.5, $p = 0.702$) (Fig.5, Appendix 1). As for the canopy species, *E. pollicina*, no statistically significant difference was found , although mean fruit production per tree was 2.4 times greater in the weeded area (W_{20} = 480.0, p = 0.095).

Proportion of plants flowering and fruiting

The proportion of individual plants flowering and fruiting in the weeded forest during the time of monitoring was greater than in the non-weeded area for most species, except for *G. psychotrioides* (for fruiting only), with the most significant differences found for *P. borbonica* (Table 2).

Table 2 Proportion of individuals of the different species flowering and fruiting in the weeded and non-weeded areas, with respective p values (test of difference of two percentages). Significant p values are in bold.

Species	Proportion Flowering (%)			Proportion Fruiting (%)		
	weeded	non-weeded	p value*	weeded	non-weeded	p value*
Psathura borbonica	97	63	**0.017**	97	50	**0.001**
Memecylon ovatifolium	70	53	0.181	60	40	0.127
Gaertnera psychotrioides	50	37	0.314	23	30	0.541
Tabernaemontana persicariifolia	77	63	0.242	47	23	0.056
Erythrospermum monticolum	78	38	**0.027**	38	18	0.089
Eugenia pollicina	0	0	--	60	40	**0.020**

* two-tailed

Discussion

If IAP have negative impacts on the native flora, their control should ultimately elicit recovery of native plants' fitness (in terms of any one or more of survival, growth and reproduction) which can ultimately lead to community recovery. Responses of native trees to the removal of alien invasive woody species can be slow [29]. The situation on Mauritius provides a rare opportunity to investigate changes that occur from several years to a few decades after IAP control.

Flower bud and flower production in plants is generally limited by resources available [30], and direct competition for resources is one of the mechanisms by which IAP may affect native plant species [31]. In some cases, IAP can even utilize available resources more effectively than natives [32-33]. Depending on their ability to alter resource availability, IAP are likely to restrict the allocation of resources to reproduction in native plant species. For example, a direct negative relationship between the reproductive output of endemic species of *Psychotria* L. (Rubiaceae) and the density of the invasive *Miconia calvescens* DC. (Melastomataceae) has been found in Tahiti [34]. Therefore, removal of IAP is expected to release the native flora from shoot and root competition, resulting in enhanced flower and fruit production. Previous studies have shown enhanced reproductive output of the canopy trees *Sideroxylon grandiflorum* A. DC. (Sapotaceae) and *Canarium paniculatum* (Lam.) Benth. ex Engl. (Burseraceae) after control of IAP in Mauritius, probably as a result of reduced root competition following removal of alien plants [22-23].

Our present study shows that this benefit is more generalised, with the reproductive output of a suite of native species (belonging to different families and different strata of the forest) being enhanced after control of IAP. In Mauritius, several forest species regenerate better and achieve greater seedling densities following IAP control, which also results in a natural increase in species richness [17]. Our findings thus suggest a possible mechanism for the greater density and species richness of native seedlings, saplings and adults trees found in weeded Mauritian lowland wet forest [14, 17]. However, the greater number of flowers produced in the weeded areas does not always translate into more seeds being produced, due to other post-flower bud interactions like herbivory or pollination, as shown for *Syzygium mamillatum* Bosser & Guého (Myrtaceae) in Mauritius [35]. In our study, no signs of herbivory were found on flower buds/flowers of the selected species except in *G. psychotrioides,* which suffered light losses of flower buds that were chewed, suggesting herbivory of flower buds and flowers may not be very widespread.

Several processes operating at post flower production stages (e.g. pollination, seed predation and dispersal, germination, seedling survival etc.) may also contribute to the observed differences in species richness and plant density between weeded and non-weeded forests, which may exacerbate or attenuate the differences that we found. Disturbances such as the presence of invasive species can impact the behaviour and abundance of animal pollinators and reduce the reproductive output of tropical trees that depend on animals for pollination [36-37]. We did not study the contribution of pollination success to the differences in fruit production between weeded and non-weeded areas. However, in three of the species, the difference between proportions of plants bearing fruits in weeded and non-weeded areas increased relative to the equivalent difference in flower production of the same plants (Table 2). This suggests that pollination success may have a role in shaping the differences found In Mauritius, a study focusing on native butterflies, which are often considered as an indicator group for other insects [38], found more species and higher population densities in the weeded area [16]. Species that are mostly insect-pollinated may thus be expected to have greater fruit set in weeded areas. Concerning avian pollinators, the endemic grey-white eye (*Zosterops borbonicus mauritianus*), though more abundant in weeded areas, visited flowers of the small tree *S. mamillatum* more often in the non-weeded area [35]. This resulted in greater fruit set in this area, which the authors linked to differences in habitat structure and avoidance of predators. This finding demonstrates that measuring pollinator abundance may not suffice and that their behaviour can also be important.

Implications for conservation

Islands have substantial conservation value due to their high level of endemism as well as to the elevated extinction risks that they face [39-41]. Disentangling the impact of invasive alien plants from other concurrent threats like habitat fragmentation or invasive alien animals is particularly important if conservation management resources are to be optimised. A poor understanding of such threats and of their relative importance can lead to well-intentioned but misguided conservation efforts [23]. The comparison of forest areas that are similar apart from being weeded or not of alien plants provides a useful way to isolate the impacts of IAP from other simultaneous threats. The greater production of flower buds, flowers and fruits among native species in the weeded forest compared to the adjacent non-weeded area demonstrates that IAP can hinder regeneration of native woody plants by causing a reduced production of viable seeds.

Our study thus provides an example of how control of IAP over the medium to long-term can be beneficial to the flora of an oceanic island's native forest, and by inference help restore a more natural setting that is favourable to reinstating interactions like pollination or frugivory. This is useful in a context where the ability of alien plants to pose major extinction threats is still debated [4-5,42]. We provide at least some basis for the observed patterns of long-term decline of native plants in the face of IAP, and for the improved regeneration and higher plant species richness found in weeded areas compared to adjacent non-weeded areas. Our work indicates that the impact of IAP on the reproductive output of native trees is more generalized than previously demonstrated [23], since it shows that understory species are also negatively impacted. Many of the most threatened endemic species of the island are understory species [14,18,21], which may also be the case elsewhere [43].

Although regeneration is not seed-limited for all species, reduction in seed production may have effects on overall population sizes [44]. This seems particularly relevant when considering the conservation of Mauritian understory plants, because studies on vegetation changes in the Mauritian lowland wet forests reported a greater decline for these plants compared to canopy species [19-20]. For example a survey of a plot in a lowland forest in 1986, which was initially sampled in the late 1930s when few IAP were present, found that the lowermost native plant strata of the forest had almost entirely disappeared, with a higher mortality rate for the shorter species compared to larger tree species [19]. One extreme case was the dominant understory shrub, *Chassalia capitata* DC. (Rubiaceae), which was reported to have gone from 284 individuals per 1,000 m^2 to being locally extinct. With timely removal of IAP, threatened understory and ground flora species appeared to show a stronger recovery compared to taller species [17]. As understory plants tend also to be generally shorter lived compared to the canopy species, the outcome of competitive interaction with IAP (including exclusion) can be reached quicker in this guild.

It is important to point out that our study likely underestimates the impact of IAP on the reproductive output of native species, since it measured flower buds, flowers and fruit production per plant. The density of native trees is known to increase after weeding [14], so that overall the reproductive output of native trees per unit area in the non-weeded forest may be even more depressed than recorded here, compared to weeded areas.

Removal of IAP (by mechanical weeding as in Mauritius or by biological control as in French Polynesia) has a positive impact on the regeneration potential of native species [17, 45-46]. However, in Mauritius, the weeding of alien plants is carried out over merely 1 % of the surviving habitat remnants [47]. Our study supports the need to expand areas over which IAP are controlled. This could be done at various scales, from highly localised weeding around very rare plants or clumps of plants in order to reduce their mortality or boost their reproductive output, (which would also increase native seedlings regeneration compared to alien ones [48]), to weeding large areas covering tens to hundreds of ha (for restoring whole ecosystems). The latter case would require precautions to minimise risks of secondary undesirable effects like erosion or re-invasion by other alien species. However, when controlling invasive alien plants, an evidence-based approach and best practice should be adopted to avoid wastage of resources and undue damage to non-target species [47]. With the need for recurrent mechanical control of *P. cattleianum* and the high cost associated, the use of biological control of this weed appears to be the most cost-effective long-term method [46,49]. Studies of natural enemies of *P.cattleianum* in its native habitats in Brazil have identified *Tectococcus oyatus* (Homoptera, Eriococcidae), which produces leaf gall, as the most promising biological control agent [50]. The insect has already been proposed for field release in Hawai`i [51]. However despite the insect`s high specificity, indirect impacts on non-targeted plants remain possible, calling for adequate testing using modern protocols [49] before such an approach can be implemented in Mauritius. In the meantime an eventual biological control programme is developed, mechanical weeding should be extended as much as possible owing to its strong benefits on native biodiversity in Mauritius.

Our study also suggests that IAP control may be beneficial to the restoration of ecological interactions like frugivory and seed dissemination. IAP can significantly decrease animal species richness and their abundance [52], thus native fauna can benefit both directly from the weeding and indirectly from the associated native flora recovery. Enhanced reproductive output of plants found in the managed areas also means that more food resources become available. The diverse food resources provided by plants (flower buds, flowers, nectar, pollen and fruits) support different guilds of faunal species including mammals, birds, reptiles and insects [53-54]. For example, the forest in southwest Mauritius where this study was conducted, harbours most of the threatened endemic bird, reptile and insect populations of high conservation value [55-56]. Increased availability of food resources due to habitat restoration should form a more important component of conservation efforts of the endangered extant fauna. Integrated conservation of both animal and plant species in the most natural setting possible is vital if functional ecosystems are to be restored and if risks of non-sustainability of conservation efforts is to be minimized.

Finally, it is true that the various post-flower bud processes (pollination, herbivory, seed dispersal, etc) that can affect the forest community are still not understood well enough to appreciate how important they are in their own right and how they are impacted by the presence or absence of IAP. The relative importance of post-flower bud processes in fostering or hindering population and community recovery thus remains to be quantified. It would be dauntingly difficult, if not impossible, to study the factors affecting each species with the level of detail found for example in Kaiser *et al.* [35] or the studies of Hansen and Müller [57-58], who showed that the critically threatened endemic plant *Roussea simplex* is pollinated and dispersed by endemic arboreal geckos and that alien ants can disrupt these mutualisms. Such detailed studies should, from a conservation standpoint, be undertaken on the most threatened species. But ultimately, it will also be important to determine the hierarchy of threat factors so as to address the strongest and most widespread impacts in priority. Given that the majority of native woody species studied so far tend to regenerate better in weeded areas [14, 17], the persistence and/or prevalence of the detrimental effect of IAP weeding described by Kaiser *et al.* [35] appear to be relatively unimportant for most species. As current knowledge stands, our study lends further support to the control of IAP as a conservation priority, given its positive impact on a variety of plant populations whose recovery will benefit other species through various interactions like pollination or frugivory. Further studies are warranted to determine which species are still not regenerating satisfactorily even after IAP control and why that is so, particularly given that they may, as in the case of *S. mamillatum*, be threatened with extinction, and hence require special conservation attention.

Acknowledgements

We are grateful to the National Parks and Conservation Service (NPCS) of the Ministry of Agro-Industry and Food Security for permission to access and carry out fieldwork in the National Park and for extending its field camp facilities to MLFM. MLFM thanks Ms Lakhshmee Tengur for help and support in the field.

References

[1] Mooney, H. A., Mack, R. N., McNeely, J. A., Neville, L. E., Schei, P. and Waage, J. K. 2005. *Invasive alien species: a new synthesis*. Island Press, Washington, DC.

[2] Blackburn, T. M., Cassey, P., Duncan, R. P., Evans, K. L. and Gaston, K. J. 2004. Avian extinction and mammalian introductions on oceanic islands. *Science* 305:1955-1958.

[3] Clavero, M. and García-Berthou, E. 2005. Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution* 20(3):110.

[4] Gurevitch, J. and Padilla, D. K. 2004. Are invasive species a major cause of extinctions? *Trends in Ecology and Evolution* 19:470-474.

[5] Sax, D. F. and Gaines, S. D. 2008. Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academic of Science* 105:11490-11497.

[6] Caujapé-Castells, J., Tye, A., Crawford, D. J., Santos-Guerra, A., Sakai, A., Beaver, K., Lobin, W., Florens, F. B. V., Moura, M., Jardim, R., Gómes, I. and Kueffer, C. 2010. Conservation of oceanic island floras: present and future global challenges. *Perspectives in Plant Ecology, Evolution and Systematics* 12:107-129.

[7] Lugo, A. E. 2004. The outcome of alien tree invasions in Puerto Rico. *Frontiers in Ecology and the Environment* 2:265-273.

[8] Kueffer, C., Schumacher, E., Fleischmann, K., Edwards, P. J. and Dietz, H. 2007. Strong below ground competition shapes tree regeneration in invasive *Cinnamomum verum* forests. *Journal of Ecology* 95:273-282.

[9] Myers N., Mittermeier R. A., Mittermeier C. G., Da Fonseca, G. A. B. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.

[10] Baider, C., Florens, F. B. V., Baret, S., Beaver, K., Matatiken, D., Strasberg, D. and Kueffer, C. 2010. Status of plant conservation in oceanic islands of the Western Indian Ocean. *Proceedings of the 4th Global Botanic Gardens Congress.* 7 p. http://www.bgci.org/files/Dublin2010/papers/Baider–Claudia.pdf

[11] Safford, R. J. 1997. A survey on the occurrence of native vegetation remnants on Mauritius in 1993. *Biological Conservation* 80:181-188.

[12] Page, W. and D'Argent, G. 1997. A vegetation survey of Mauritius to identify priority rainforest areas for conservation management. Mauritian Wildlife Foundation. Unpublished report.

[13] Lorence, D. L. and Susmann, R. W. 1986. Exotic species invasion into Mauritius wet forest remnants. *Journal of Tropical Ecology* 2:147-162.

[14] Florens, F. B. V. 2008. *Ecologie des forêts tropicales de l'île Maurice et impact des espèces introduites envahissantes*. PhD thesis. Université de la Réunion, La Réunion, France.

[15] Kueffer, C., Daehler, C., Torres-Santana, C. W., Lavergne, C., Meyer, J.-Y., Otto, R. and Silva, L. 2010. A global comparison of plant invasions on oceanic islands. *Perspectives in Plant Ecology, Evolution and Systematics* 12:145-161.

[16] Florens F. B. V., Mauremootoo, J. R., Fowler S. V., Winder L. and Baider, C. 2010. Recovery of indigenous butterfly community following control of invasive alien plants in a tropical island's wet forests. *Biodiversity and Conservation* 19: 3835-3848.

[17] Baider, C. and Florens, F. B. V. 2011. Control of invasive alien weeds averts imminent plant extinction. *Biological Invasions* 13(12): 2641-2646.

[18] Bosser, J., Cadet, T., Guého, J. and Marais, W. 1976-ongoing. *Flore des Mascareignes: La Réunion Maurice, Rodrigues.* MSIRI/ORSTOM-IRD/Kew.

[19] Strahm, W. A. 1993. *The conservation and restoration of the flora of Mauritius and Rodrigues*. PhD thesis. University of Reading, UK.

[20] Virah-Sawmy, M., Mauremootoo, J., Marie, D., Motala, S. and Sevathian, J-C. 2009. Rapid degradation of a Mauritian rainforest following 60 years of plant invasion. *Oryx* 43(4): 599-607.

[21] Florens, F. B. V., Baider, C. and Bosser, J. M. 2008. On the Mauritian origin of *Badula ovalifolia* (*Myrsinaceae*), hitherto believed extinct, with complementary description. *Kew Bulletin* 63(3):481-483.

[22] Auchoybur, G. and Florens, F. B. V. 2005. Threats to the maintenance of *Canarium paniculatum* (Burseraceae) a Mauritian endemic canopy tree. *Frontiers in Tropical Biology and Conservation. The Annual Meeting of the Association of Tropical Biology and Conservation, 24-28th July 2005, University of Uberlândia, Brazil.* p. 164.

[23] Baider, C. and Florens, F. B. V. 2006. Current decline of the 'Dodo tree': a case of broken-down interactions with extinct species or the result of new interactions with alien invaders? In: *Emerging threats to tropical forests*. Laurance, W. F. and Peres, C. A. (Eds.), pp. 199-214. University of Chicago Press, Chicago.

[24] Padya, B. M. 1989. *Weather and Climate of Mauritius*. Mahatma Gandhi Institute, Mauritius.

[25] Florens F. B. V., Baider, C., Martin, G. M. N. and Strasberg, D. 2012. Surviving 370 years of human impact: what remains of tree diversity and structure of the lowland wet forests of oceanic island Mauritius? *Biodiversity and Conservation* 21:2139-2167.

[26] Vaughan, R. E., and Wiehe, P. O. 1937. Studies on the vegetation of Mauritius I. A preliminary survey of the plant communities. *Journal of Ecology* 25:289-343.

[27] Dulloo, M. E., Kell, S. P. and Jones. C. G. 2002. Conservation of endemic forest species and the threat of invasive species. *International Forestry Review* 4:277-285.

[28] Clark, D. B. and Clark, D. A. 1989. The role of physical damage in the seedling mortality regime of a Neotropical rain forest. *Oikos* 55:225-230.

[29] Ostertag, R., Cordell, S., Michaud, J., Cole, T. C., Schulten, J. R., Publico, K. M. and Enoka, J. H. 2009. Ecosystem and restoration consequences of invasive woody species removal in Hawaiian lowland wet forest. *Ecosystems* 12:503-515.

[30] Herrera, C. M. 1991. Dissecting factors responsible for individual variation in plant fecundity. *Ecology* 72(4):1436-1448.

[31] Levine, J. M., Vilà, M., D'Antonio, C. M., Dukes, J. S., Grigulis, K. and Lavorel, S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceeding of the Royal Society of London Series B* 270:775-781.

[32] Stratton, L. C. and Goldstein, G. 2001. Carbon uptake, growth and resource-use efficiency in one invasive and six native Hawaiian dry forest tree specie. *Tree Physiology* 21:1327-1334.

[33] Funk, J. L. and Vitousek, P. M. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446:1079-1081.

[34] Meyer, J.-Y., Florence, J. and Tchung, V. 2003. The endemic *Psychotria* of Tahiti (French Polynesia) threatened by the invasive *Miconia calvescens* (Melastomataceae): status, distribution, ecology, phenology and conservation. *Revue d'Ecologie (La Terre et Vie)* 58(2):161-185.

[35] Kaiser, C. N., Hansen, D. M and Müller, C. B. 2008. Habitat structure affects reproductive success of the rare endemic tree *Syzygium mamillatum* (Myrtaceae) in restored and unrestored sites in Mauritius. *Biotropica* 40(1):86-94.

[36] Ghazoul, J. 2004. Alien abduction: disruption of native plant-pollinator interactions by invasive species. *Biotropica* 36(2):156-164.

[37] Morales, C. L. and Traveset, A. 2009. A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters* 12:716-728.

[38] Kremen, C. 1994. Biological inventory using target taxa: a case study of the butterflies of Madagascar. *Ecological Applications* 4:407-422.

[39] Frankham, R. 1998. Inbreeding and extinction: island populations. *Conservation Biology* 12(3):665-675.

[40] Pauley, G. 1994. Biodiversity on oceanic islands: its origin and extinction. *American Zoology* 34(1):134-144.

[41] Kier, G., Kreft, H., Lee, T. M., Jetz, W., Ibisch, P.L., Norwich, C., Mutke, J. and Barthlott, W. 2009. A global assessment of endemism and species richness across island and mainland regions. *Proceedings of the National Academy of Science* 106(23):9322-9327.

[42] Moles, A. T., Flores-Moreno, H., Bonser, S. P., Warton, D. I., Helm, A., Warman, L., Eldridge, D. J., Jurado, E., Hemmings, F. A., Reich, P. B, Cavender-Bares, J., Seabloom, E. W., Margaret, M., Mayfield, M. M., Sheil, D., Djietror, J. C., Peri, P. L., Enrico, L., Cabido, M. R., Setterfield, S. A, Lehmann, C. E. R. and Thomson, F. J. 2012. Invasions: the trail behind, the path ahead, and a test of a disturbing idea. *Journal of Ecology* 100:116-127.

[43] Meyer J-Y. and Florence, J. 1996 . Tahiti's native flora endangered by the invasion of *Miconia calvescens* DC. (Melastomataceae). *Journal of Biogeography* 23(6):775-781.

[44] Knight, T. M., Steets, J. A., Vamosi, J. C., Mazer, S. J., Burd, M., Campbell, D. R., Dudash, M. R., Johnston, M. O., Mitchell, R. J. and Ashman, T. 2005. Pollen limitation of plants reproduction. *Annual Review of Ecology*, *Evolution and Systematics* 36:467-97.

[45] Lavergne, C., Florens, F. B. V., Strasberg, D. 2004. Eradication of invasive alien plants has consequences on biodiversity: the case study of *Hedychium gardnerianumin* Réunion Island - INVABIO Programme. *Proceedings of Workshop on Biodiversity in La Réunion Island*, p. 35-36.

[46] Meyer, J.-Y. and Fourdrigniez, M. 2011.Conservation benefits of biological control: the recovery of a threatened plant subsequent to the introduction of a pathogen to contain an invasive tree species. *Biological Conservation* 144: 106-113.

[47] Florens F. B. V. & Baider, C. 2012. Ecological restoration in a developing island nation: how useful is the science? *Restoration Ecology 21:1-5.* doi:10.1111/j.1526-100X.2012.00920.x

[48] Kueffer, C., Schumacher, E. Dietz, H. Fleischmann, K. and Edwards, P. J. 2010. Managing successional trajectories in alien-dominated, novel ecosystems by facilitating seedling regeneration: a case study. *Biological Conservation* 143:1792-1802.

[49] GISP. 2001. *Invasive alien species: A toolkit of best prevention and management practices*. CABInternational, Wallingford, Oxon, UK.

[50] Wikler, C., Pedrosa-Macedo, J.H., Vitorino, M.D., Caxambu, M.G. and Smith, C.W. 1999. Strawberry guava (*Psidium cattleianum*) – Prospects for biological control. *Program and abstracts of the X International Symposium on Biological Control of Weeds.* Montana State University, Bozeman, Montana, USA., p. 659-665.

[51] USDA. 2008. Field release of *Tectococcus oyatus* (Homoptera, Eriococcidae) for biological control of strawberry guava, *Psidium cattleianum* Sabine, Myrtaceae, in Hawai'i. Environmental Assessment. United States Department of Agriculture.

[52] Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y. and Pyšek, P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters* 14:702-708.

[53] Jordano, P. 2000. Fruits and frugivory. In: *Seeds: the ecology of regeneration in plant communities*. Fenner, M. (Ed.), pp.125-166. CABI Publ., Wallingford, UK.

[54] Wäckers, F. L., Van Rijn, P. C. J. and Bruin, J. Eds. 2005. *Plant-provided food for carnivorous insects: A protective mutualism and its applications*. Cambridge University Press, UK.

[55] Jones, C. G. and Hartley, J. 1995. A conservation project on Mauritius and Rodrigues: an overview and bibliography. *Dodo: Journal of the Jersey Wildlife Preservation Trust* 31:40-65.

[56] Motala, S. M., Krell, F. T., Mungroo, Y. and Donovan, S. E. 2007. The terrestrial arthropods of Mauritius: a neglected conservation target. *Biodiversity and Conservation* 16:2867-2881.

[57] Hansen, D. M. and Müller, C. B. 2009. Reproductive ecology of the endangered enigmatic Mauritian endemic *Roussea simplex* (Rousseaceae). *International Journal of Plant Sciences* 170(1):42-52.

[58] Hansen, D. M. and Müller, C. B. 2009. Invasive ants disrupt gecko pollination and seed dispersal of the endangered plant *Roussea simplex* in Mauritius. *Biotropica* 41(2):202-208.

Appendix 1

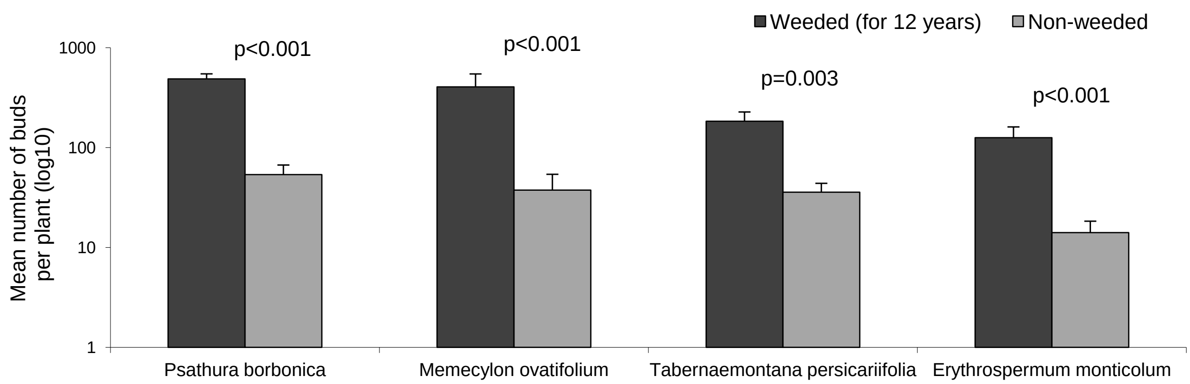

Fig.3. Differences in mean (+SE) number of buds (log_{10}) produced per plant per species at peak production in weeded and non-weeded areas

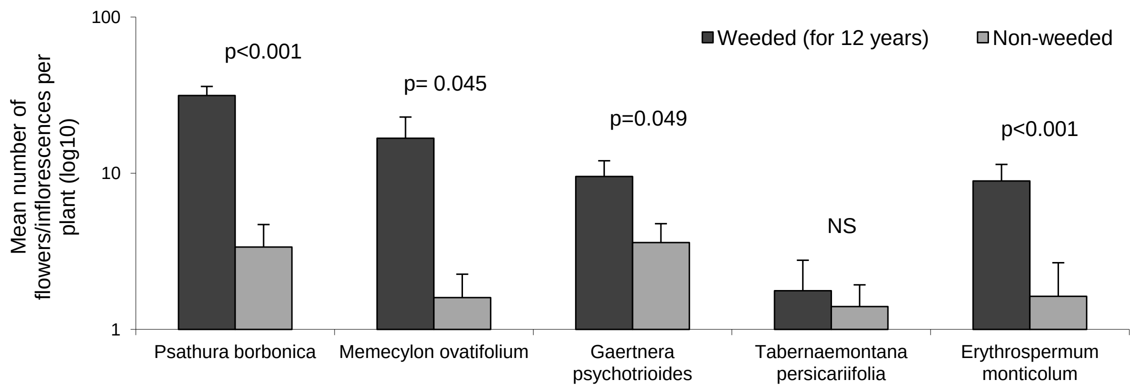

Fig.4. Differences in mean (+SE) number of flowers/inflorescences (log_{10}) produced per plant per species at peak production in weeded and non-weeded forest areas.

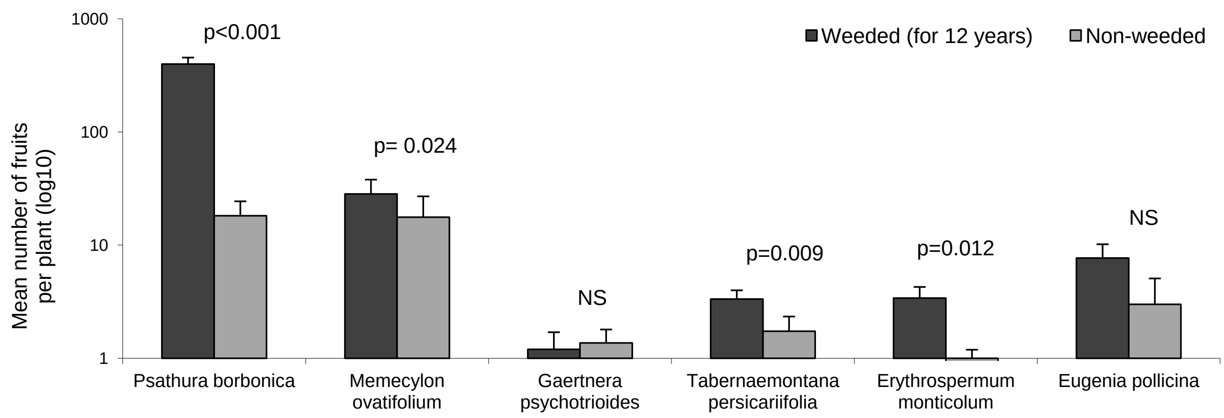

Fig.5. Differences in mean (+SE) number of fruits (log10) produced per plant per species at peak production in the weeded and non-weeded areas.