

Habitat Structure Affects Reproductive Success of the Rare Endemic Tree *Syzygium mamillatum* (Myrtaceae) in Restored and Unrestored Sites in Mauritius

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ABSTRACT

Invasive alien plants affect the functioning of ecosystems by altering plant–animal interactions, such as pollination, which may impede natural regeneration of native plant species. In Mauritius, we studied the reproductive traits and pollination ecology of the rare endemic cauliflorous tree *Syzygium mamillatum* in a restored forest (all alien plant species removed) and an adjacent unrestored area (degraded by alien plants). Flowers of *S. mamillatum* were only visited by generalist bird species. Although the initial number of flower buds per tree in the restored forest tended to be higher than that of trees in the unrestored area, final fruit set and the number of seeds per fruit were lower in the restored forest. This corresponded with lower bird visitation rates in the restored area. Additionally, during budding stage, most trees were severely attacked by lepidopteran larvae, and bud loss through herbivory was higher in the restored forest. Thus, the difference in reproductive performance of *S. mamillatum* between the two localities was caused by contrasting herbivore attack and bird visitation behavior in restored and unrestored areas. Our findings illustrate the importance of restoration efforts in mimicking the original physical structure of habitats and interaction structure of interspecific relationships, and the difficulty of doing so given the imperfect knowledge and the reality that many native species have become locally extinct and replaced by exotic species.

Key words: bird pollination; cauliflory; habitat restoration; herbivory; invasive species; *Zosterops mauritianus*.

ISLANDS ARE OFTEN DESCRIBED AS BIODIVERSITY HOTSPOTS due to their relatively high levels of endemism and their disproportional contribution to global species diversity (Whittaker 1998, Myers *et al.* 2000). Invasive alien species, however, threaten the extant native biological diversity of island ecosystems (Cheke 1987, Simberloff 1995, Valido *et al.* 2002). Introduced species may interact with native species in several ways: many introduced plant species compete with natives for resources (Callaway & Aschehoug 2000, Daehler 2003) or benefit from mutualistic interactions with resident species, often to the detriment of native mutualisms (Bond 1994, Simberloff & von Holle 1999, Richardson *et al.* 2000, Traveset & Richardson 2006). Although several studies have described the disruption of plant–animal interactions caused by competition for pollinators between alien and native plants (*e.g.*, Chittka & Schürkens 2001, Moragues & Traveset 2005), studies focusing on how mutualistic interactions are affected by a change in habitat structure associated with the spread of alien plant species are scarce. Native plant–animal interactions critical for plant reproduction can be disrupted by decreasing relative abundance or density of native plant populations (Ghazoul 2005, Ward & Johnson 2005) which consequently may alter pollinator behavior (Brown & Mitchell 2001, Ghazoul 2004). For example, Paton (2000) showed that the bird-pollinated plant *Astroloma conostephioides* native to southern Australia was severely pollinator limited in degraded and invaded habitats due to the absence of migratory nectarivorous birds from these areas. In addition, introduced herbivores, which consume vegetative or reproductive parts of a plant, can exert negative pressures on the reproduction of native plants and/or on their pollinators (see Traveset & Richardson 2006 and references therein). Where

populations are already compromised through habitat destruction, as is frequently the case on islands, such mechanisms might lead to localized extinction of plant or native pollinator populations.

The continuing decline of native plant and animal species in Mauritius, following the initial human-caused destruction of natural habitats, has been ascribed primarily to the spread of introduced species (Mauremootoo *et al.* in press a), which now dominate the remaining upland forests (Vaughan & Wiehe 1941, Lorence & Sussman 1986, Cheke 1987). Today, only about 2 percent of Mauritius is covered with some degree of native forest (Page & d'Argent 1997), and even these fragments are severely degraded in most areas. To restore patches of native habitat in Mauritius, several Conservation Management Areas (CMAs) have been established since 1969. These restored sites are remnants of the major original habitat types, and are fenced and regularly hand-weeded to eradicate introduced plant species. A survey in one of these restored areas (Brise Fér 'Old Plot,' 1.26 ha), 8 yr after the start of restoration work in 1987, showed an improvement in natural regeneration of native flora compared to adjacent unrestored areas (Mauremootoo *et al.* in press b). Thus, although there is evidence that the original plant community can regenerate following restoration, information on what actually limits regeneration of endemic plants in unrestored habitats is lacking. To improve current restoration strategies, it is necessary to understand the mechanistic basis of recruitment success of native plant species.

In addition to the direct impacts of invasive plants through competition for space, soil nutrients, light and water, the remaining populations of Mauritian plants are vulnerable to several threats. The original Mauritian fauna comprised a range of pollinating bird species, many of which are now locally or globally extinct. The loss of these native mutualists is thought to limit the natural regeneration of native plants that once were dependent on them (Kaiser 2006). The subsequent increasing abundance of introduced plants

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may have further disrupted native plant recruitment by modifying avian pollinator foraging behavior as a consequence of the change in density and distance between neighboring native plants. Removal of alien plants in restored areas may thus facilitate native plant recruitment through the recovery of associated pollination processes. Mauritius is therefore an ideal study system in which to explore the effects of such disruptions on the pollination of native plant species.

In this study, we investigated the effect of habitat restoration on pollination interactions and fruit/seed set of the rare endemic tree *Syzygium mamillatum* Bosser & Guého (Myrtaceae) in a restored and an adjacent unrestored, heavily invaded area. Because preliminary observations indicated that flower buds were being attacked by herbivorous lepidopteran larvae, we also studied the impact of floral herbivory on the reproductive success of *S. mamillatum* in both areas.

Syzygium mamillatum is cauliflorous with flowers developing directly on the trunk. Cauliflory is a characteristic feature of many trees in Mauritius (Bossier *et al.* 1983) and elsewhere in the tropics (Endress 1994). No information is available on the pollination of *S. mamillatum*, but the congeneric *S. mauritianum* Guého & Scott with similar pink, showy flowers is primarily visited by nectarivorous birds (D. M. Hansen, pers. obs.). Based on these observations and the assumption that pollinator visitation may be negatively affected by invasives and restored by habitat management, we made three predictions: (1) host specificity of tropical herbivores is mostly found at genus or family level (Novotny & Basset 2005). Therefore, we expect a higher attack rate by the herbivore in the unrestored area where invasive Myrtaceae species are highly abundant and, thus, likely to sustain higher herbivore densities; (2) due to eradication of invasive plants and regular weeding in the restored area, the flowers of *S. mamillatum* trees will be more conspicuous to bird pollinators than those of trees in the unrestored area, and will therefore attract more pollinator visits; and (3) increased flower-visitation rate in the restored area will result in higher fruit and seed production in comparison with plants in the unrestored area.

METHODS

STUDY AREA AND SPECIES.—We conducted the study in the Black River Gorges National Park in Mauritius between July 2003 and January 2004. Our study site was Brise Fér CMA (24 ha; 20°22' S, 57°26' E; 570–600 m asl), established by the National Parks and Conservation Service in 1996. The native tree community in the restored (CMA) and adjacent unrestored area of Brise Fér consists mainly of canopy trees of the families Burseraceae, Ebenaceae, Celastraceae and Sapotaceae, and several subcanopy trees of the genera *Gaertnera* (Rubiaceae) and *Syzygium* (Myrtaceae) (Strahm 1994). In the unrestored area, invasive plants, primarily guava *Psidium cattleianum* Sabine (Myrtaceae), privet *Ligustrum robustum* (Rox.) Blume (Oleaceae), and several weedy Melastomataceae, form an impenetrable understorey with a canopy of ca 3–5 m in height. Native trees are found scattered within this site (see also Lorence & Sussman 1986).

We surveyed approximately 60 ha in Brise Fér forest, of which the restored area covered 24 ha. The actual area in which the *S. mamillatum* population occurred covered a total of 16 ha, approximately two-thirds of which were in the restored area, and one-third in the unrestored area. In total, we found 120 mature trees of *S. mamillatum*. *Syzygium mamillatum* is endemic to Mauritius and the recorded individuals represent the last large extant population, accounting for 87 percent of all the mature trees of this species. The remaining 18 trees are either isolated individuals or small stands located within the boundaries of the National Park (M. Allet and J.-C. Sevathian, pers. comm.). Eighty-two mature healthy trees in the restored and 38 in the unrestored area were labeled, mapped, and included in our study. Natural regeneration of *S. mamillatum* is very limited. The only seedlings are found within 1 m of the maternal trees—suggesting a lack of seed dispersal—and seedling survival is low close to maternal trees (D. M. Hansen, C. N. Kaiser and C. B. Müller, unpublished data). Since we worked with the only large extant population, replication across several sites was not possible. Nevertheless, we recognize the potential for within-site nonindependence of the data and tested for spatial autocorrelation using Mantel tests (see below).

Syzygium mamillatum is a subcanopy tree of 6–9 m in height, with a spectacular display of numerous, hermaphroditic flowers (calyx tube 8- to 10-mm long) on the trunk, located within 50 cm of the ground (Fig. 1A, B). The flowers contain nectar and are scentless. Each flower displays a hemispherical array of 80–90 anthers (filament length 8–10 mm), contains 15–20 ovules (Scott 1990), and produces a large and fleshy fruit. Preliminary experimental data suggested that *S. mamillatum* is largely self-incompatible (4% fruit set from 107 bagged flowers on seven plants; C. N. Kaiser, unpublished data), as is the case for many arborescent Myrtaceae species (Lack & Kevan 1984, Beardsell *et al.* 1993, Proenca & Gibbs 1994). In 2003, *S. mamillatum* flowered from November to December.

HABITAT STRUCTURE.—Before restoration, Brise Fér CMA was as degraded as the unrestored area (Strahm 1994) but since weeding began in 1996, native plant species have been slowly regenerating. As a result of restoration, the forest understorey in the restored area is now very open and little vegetation obstructs the floral display on tree trunks. In contrast, flowers on trees in the adjacent unrestored area are hidden from a human observer's view by a dense understorey of invasive plants. To investigate and quantify the differences in habitat structure, we measured tree density around the focal trees. We counted the number of native and exotic trees (exceeding a diameter at breast height of 3 cm) within a radius of 3 m around the *S. mamillatum* trees that were used for pollinator observations in the restored and the unrestored area ($N = 9$ in each area).

HERBIVORY.—During flower bud development (October–November 2003) many *S. mamillatum* trees were attacked by the larvae of *Polyhymno* sp. (Lepidoptera, Gelechiidae, identified as an unknown species by K. Sattler, Natural History Museum London). Adult moths deposited their eggs in young flower buds and the developing larvae consumed the entire bud over a period of approximately one week. We assessed the impact of these attacks by

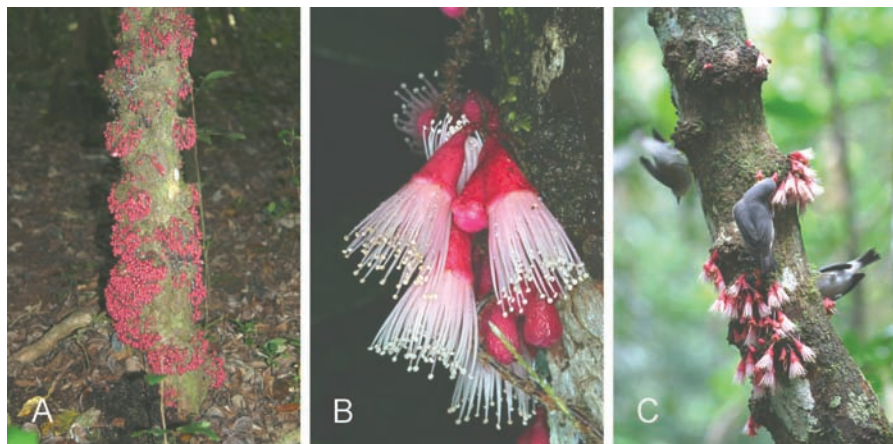


FIGURE 1. Floral characteristics of *Syzygium mamillatum*. (A) Buds are displayed on burrs along the stem, mainly at the base of the trunk. (B) Open flowers of *S. mamillatum* were visited by (C) gray white-eyes foraging for nectar.

counting affected trees in the population and the number of affected buds for all trees in the population. The proportion of attacked buds was the number of destroyed buds divided by the initial total number of buds per tree. The spread of the herbivore through the tree population was surveyed weekly during the budding time.

POLLINATOR OBSERVATIONS.—Between 12 November and 9 December 2003, pollinator observations were carried out on nine flowering trees in the restored and 10 trees in the unrestored area in 1-h ‘observation units’ for a total of 15 h in each area. Each tree was observed for 1–3 h. Flowers did not open before 0700 h and anthesis lasted for one day only, and thus all observations were carried out between 0700 h and 1900 h. We spatially stratified observation trees across the population to cover the center and the edges of the population evenly, and we selected those trees that had most flowers. Observations were carried out with binoculars (10 × 32 Trinovoid Leica, Germany) at a distance of > 6 m from the tree, which was considered far enough to avoid disturbing vertebrate flower visitors and sufficiently close to spot invertebrates. For each observed tree, we recorded the number of flowers observed, *i.e.*, visible on the trunk from our observation post (range: 18–450 flowers) and the total number of flowers displayed on the trunk. We recorded both visitation rate and bout length of flower visitors. Visitation rate is defined as the total number of visitors to the tree per hour divided by the number of visible flowers per tree. Bout length refers to the number of flowers probed per hour divided by the number of flowers observed.

To quantify the pollen load of avian flower visitors, we mist netted birds for 12 h close to 12 trees in full blossom in the restored area. We caught a total of 25 birds, which were ringed before release to avoid re-sampling the same individuals. Pollen samples were collected by sweeping the forehead, breast, and beak of each bird with a 25-mm² piece of basic fuchsin gel (Kearns & Inouye 1993). The sampled pollen grains were compared with a reference pollen collection (Kaiser 2006) and counted under a light microscope using a counting grid.

PLANT MORPHOMETRICS AND REPRODUCTIVE PERFORMANCE.—For 119 *S. mamillatum* trees, we measured diameter at breast height (dbh), tree height (H) ($N = 112$ trees), and mean distance to the nearest three conspecific neighbors (NND). We used Mantel statistics to investigate potential spatial autocorrelation for seed and fruit set ($N = 119$ trees), and visitation rate ($N = 19$ trees) (Sokal & Rohlf 1995). We calculated Euclidean distances as dissimilarity indices for seed set, fruit set, and visitation rate, and compared observed correlation coefficients with the reference distribution of correlation coefficients based on 1000 randomized permutations (Legendre & Legendre 1998).

Early in the season before larvae attacked the developing buds, we counted emerging buds (see Fig. 1A) to quantify initial flower bud production of all trees in the population. Fruit set was calculated for each tree as the number of developing fruits divided by the number of buds that developed into open flowers. Fruit counts were carried out for each individual tree at the end of December 2003, approximately 10 d after the trees had finished flowering. A second fruit count was conducted in mid February 2004 to investigate a potential reduction in fruit production that could be caused by maternal fruit abortion (Stephenson 1981), late-acting self-incompatibility (Proença & Gibbs 1994) or early inbreeding depression (Nic Lughadha 1998). The difference in number of fruits per tree between the two surveys divided by the initial number of developing fruits per tree is a measure of fruit loss. We collected a total of 1291 mature fruits (33% of total fruit crop) from 34 trees in the restored and 21 trees in the unrestored area and determined average fruit size (widest diameter), fruit weight, number of seeds, and seed weight.

DATA ANALYSIS.—We used parametric tests when assumptions of normality could be met by transformation and applied appropriate nonparametric tests otherwise. We cube-root transformed visitation rates and bout lengths, and log-transformed plant morphometrics and reproductive parameters. Means across trees \pm SE are given throughout unless otherwise noted.

To investigate the relationship between the amount of fruits lost between the two fruit counts and the initial number of fruits produced by each tree in both sites, we fitted a linear model with fruit loss as the response variable and the number of fruits per tree and site (restored/unrestored) as explanatory variables. Proportional data such as fruit set, bud, and fruit loss were arcsine transformed to meet the assumptions of normality and homoscedasticity (Quinn & Keough 2002).

To predict the patterns of fruit set, seed set, and bud loss in the restored and the unrestored site, we fitted three linear models. The response variables 'number of seeds per fruit' and 'proportion of buds per tree destroyed by herbivores' (bud loss) were fitted against the predictor variables 'mean number of buds per tree,' 'mean nearest neighbor distance' (NND, both log-transformed), and site (restored/unrestored). To test whether pollinator visitation could predict fruit set, we replaced the predictor variable NND with 'visitation rate' in the third regression analysis. All analyses were conducted with the statistical package R 2.1.1 (R Development Core Team 2005).

RESULTS

HABITAT STRUCTURE.—The density of native trees in the vicinity of *S. mamillatum* was not significantly different between the restored and the unrestored area ($F_{1,16} = 0.28$, $P = 0.61$). However, the number of introduced trees within a 3-m radius of *S. mamillatum* trees in the unrestored area exceeded the number of native trees by a factor of six (restored: 18.7 ± 1.6 trees, unrestored: 109 ± 7.3 trees; $F_{1,16} = 187$, $P < 0.001$).

HERBIVORY.—The first attacks of buds by *Polyhymno* sp. were recorded on 18 November 2003 (ca 2 weeks prior to first anthesis) in the restored area on only three trees located within 10 m of each

other. Three weeks later, approximately 50 percent of all trees were severely affected. Attacked trees lost on average 47.7 percent (± 3.5) of their buds, 60.5 percent (± 4.0) in the restored, and 28.4 percent (± 5.7) in the unrestored site. There was a significant positive correlation between the number of buds per tree and the proportion of destroyed buds per tree ($r = 0.27$, $N = 69$, $P = 0.026$). Both the total number of buds destroyed by *Polyhymno* sp. and the proportion of buds destroyed per tree were higher in the restored than in the unrestored area (number of buds destroyed: $F_{1,67} = 18.9$, $P < 0.001$, proportion of buds destroyed: $F_{1,67} = 14.8$, $P < 0.001$). Overall, the higher number of buds destroyed per tree in the restored area could be explained by management scheme, 'mean number of flowers' per tree and 'nearest neighbor distance' ($F_{3,65} = 5.9$, $P = 0.001$).

POLLINATOR OBSERVATIONS.—We observed a total of 89 interactions between flowering trees of *S. mamillatum* and three species of bird (Table 1). The endemic gray white-eye *Zosterops mauritianus* Gmelin (Zosteropidae) (Fig. 1C) was the most abundant flower visitor of *S. mamillatum* in the restored and the unrestored forest, but we observed fewer individual birds in the unrestored area (Table 1). The number of individuals of the introduced red-whiskered bulbul *Pycnonotus jocosus* L. (Pycnonotidae) was small and similar in both areas. The endemic Mauritius bulbul *Hypsipetes olivaceus* Jardine & Selby (Pycnonotidae) was only observed at trees in the restored area. Pollen swabs taken from one mist netted Madagascar fody *Foudia madagascariensis* L. (Passeridae) revealed that this species may be a pollen vector for *S. mamillatum* although it was not observed visiting flowers of *S. mamillatum*. Pollen from *S. mamillatum* was indistinguishable from pollen of other species in the genus using light microscopy. Thus, we could not assume that every pollen grain counted belonged to *S. mamillatum*. However, despite an extensive search we found no other flowering *Syzygium* species within our study area during the time of mist netting. Only a few pollen

TABLE 1. Visitation rate and pollen load of four different species of birds visiting *Syzygium mamillatum* in the restored and the unrestored area. Ten trees in each area were observed for a total of 30 h. Visitation rate is defined as the number of visitors divided by the total number of flowers observed per hour. One bird species *F. madagascariensis* was not observed visiting our trees but caught in the mist net. Pollen swabs revealed that this species was carrying pollen of *S. mamillatum*. Pollen load is given as mean \pm SE number of pollen grains and N refers to the number of birds captured by mist nets. Annotations show pairs for analysis. E = endemic, I = introduced

Visitor species	Common name	Status	Restored			Unrestored			Pollen load	N
			No. of individuals observed	No. of flowers probed	Visitation rate	No. of individuals observed	No. of flowers probed	Visitation rate		
<i>Zosterops mauritianus</i>	Gray white-eye	E	52	518	0.032 ^a	25	188	0.22 ^a	949 \pm 422 ^c	16
<i>Pycnonotus jocosus</i>	Red-whiskered bulbul	I	5	93	0.0005 ^b	4	16	0.01 ^b	2357 \pm 761 ^c	7
<i>Hypsipetes olivaceus</i>	Mauritius bulbul	E	3	83	n/a	0	0	n/a	272	1
<i>Foudia madagascariensis</i>	Madagascar fody	I	0	0	n/a	0	0	n/a	8308	1

^aStudent's *t*-test $t = -2.57$, $df = 17$, $P = 0.020$.

^bStudent's *t*-test $t = -0.81$, $df = 17$, $P = 0.43$.

^cWilcoxon-Mann-Whitney $U = 23.0$, $N = 22$, $P = 0.027$.

grains from other plant families were found in the samples, which suggested that birds visited mainly *S. mamillatum*.

In contrast to our prediction, the overall mean visitation rate (*i.e.*, the number of visitors per tree divided by the number of flowers observed) was lower in the restored than in the unrestored area ($t = -2.65$, $df = 17$, $P = 0.017$; Fig. 2A). Although mean bout length was not statistically different between areas ($t = -1.67$, $df = 17$, $P = 0.12$), birds in the unrestored area probed almost twice as many flowers per visit than those in restored areas (Fig. 2B). No significant spatial autocorrelation was found for visitation rate ($r = -0.12$, $P = 0.72$), hence our sampled trees can be considered as statistically independent within-site replicates. Trees with many flowers attracted more birds than trees with fewer flowers ($r = 0.48$, $N = 19$, $P = 0.036$), and birds that visited trees with many flowers probed, on average, more flowers than those on trees with fewer flowers ($r = 0.59$, $N = 19$, $P = 0.004$). Visitation rate of the gray white-eye was higher in the unrestored than in the restored area although the total number of gray white-eyes observed was twice as high in the restored area (Table 1). There was no significant difference in visitation rate of red-whiskered bulbuls between sites. The gray white-eye, despite being the most abundant flower visitor, carried significantly fewer *Syzygium* pollen grains than the red-whiskered bulbul, the second most abundant visitor (Table 1).

PLANT MORPHOMETRICS AND REPRODUCTIVE PERFORMANCE.—Trees in the restored and the unrestored area were of similar height ($F_{1,110} = 0.02$, $P = 0.90$), although trees at the restored site had a larger dbh (6.5 ± 0.19 cm) than trees in the unrestored area (5.6 ± 0.18 cm; $F_{1,116} = 4.6$, $P = 0.035$). We found a positive relationship between dbh and the number of buds per tree ($r = 0.37$, $N = 118$, $P < 0.001$), indicating that bigger trees were more abundant in the restored area and produced more buds.

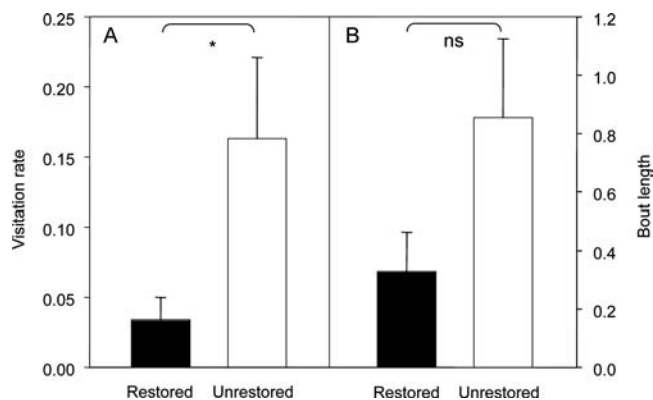


FIGURE 2. Differences in mean (\pm SE) (A) visitation rate and (B) bout length per tree in restored ($N = 9$ trees) and unrestored areas ($N = 10$ trees). * = $P < 0.05$, ns = not significant. Visitation rate is the number of birds visiting during one observation unit (=per tree) divided by the number of observed flowers. Bout length refers to the number of probed flowers per tree per observation unit divided by the number of observed flowers.

Several trees in the restored site produced a high number of buds ($14.6\% > 2000$ buds, 691 ± 1295 SD) in contrast to trees in the unrestored area ($3.1\% > 2000$ buds, 338 ± 597 SD). However, we found no statistically significant differences in mean number of buds and flowers per tree between the two areas presumably due to a greater variance in the restored area (Fig. 3A). Similarly, mean fruit production per tree was not significantly higher in the restored than in the unrestored area (Fig. 3B). Since the majority of *S. mamillatum* trees grow in the restored area, we recorded an overall 4.5-fold difference in total number of fruits (8343 vs. 1816) and a 3.5-fold difference in the total number of seeds (18,772 vs. 4907) between the restored and the unrestored area. During the second fruit count in February 2004, we counted a total of 2744 fruits in the restored and 974 fruits in the unrestored site. The number of fruits per tree was not related to the proportion of fruits lost (only trees with > 10 fruits; $F_{1,63} = 0.93$, $P = 0.34$), and the latter did not differ between sites ($F_{1,63} = 1.4$, $P = 0.24$).

Average fruit set per tree was lower in the restored than in the unrestored area (overall fruit set: 0.248 ± 0.019), and mean number of seeds per fruit (overall 2.14 ± 0.39) showed a trend ($P = 0.057$) toward fewer seeds per fruit in the restored area (Fig. 3C). Neither fruit nor seed set data were spatially autocorrelated (fruits: $r = -0.05$, $P = 0.92$; seeds: $r = 0.03$, $P = 0.26$). Fruit set increased significantly with increasing visitation rate ($r = 0.53$, $N = 19$, $P = 0.020$). Fruit set and the number of seeds per fruit could not be sufficiently explained by management scheme, 'mean number of flowers' per tree and 'visitation rate' (fruit set: adj. $R^2 = 0.23$, $F_{3,14} = 2.7$, $P = 0.087$) or nearest neighbor distance, respectively (seeds/fruit: adj. $R^2 = 0.05$, $F_{3,51} = 1.9$, $P = 0.15$).

Mean fruit size per tree in the restored area was 17.4 ± 0.32 mm, while it was larger in the unrestored areas, measuring 18.4 ± 0.33 mm ($F_{1,53} = 4.6$, $P = 0.037$). Although there was a strong positive correlation between fruit size and weight ($r = 0.86$, $P < 0.001$), we found no significant difference in fruit weight between sites (restored: 5.60 ± 0.28 g, unrestored: 6.25 ± 0.33 g, $F_{1,53} = 2.2$, $P = 0.146$). Interestingly, 73 percent of fruits overall developed at a height of < 30 cm on the trunk.

DISCUSSION

HERBIVORY LIMITS FRUIT PRODUCTION.—A substantial proportion (48%) of *S. mamillatum* buds in the population was destroyed by *Polyhyhmo* larvae. Little is known about the genus *Polyhyhmo* and host-plant records for only four *Polyhyhmo* species exist for Fabaceae in the Nearctic, India, and the African tropics (Robinson *et al.* 2001). Given the natural distribution of other *Polyhyhmo* species and the high attack rate on *S. mamillatum*, *Polyhyhmo* sp. may be introduced to Mauritius. The rate of bud destruction was higher inside the restored area than outside ($\sim 61\%$ vs. $\sim 28\%$), which may be explained by lepidopteran herbivores relying primarily on visual and olfactory cues for host-plant selection (Finch & Collier 2000). Host trees in the restored area may simply be more visible or smell more conspicuously than host trees in the unrestored area, which are obscured by the dense undergrowth (Wiklund 1984). A

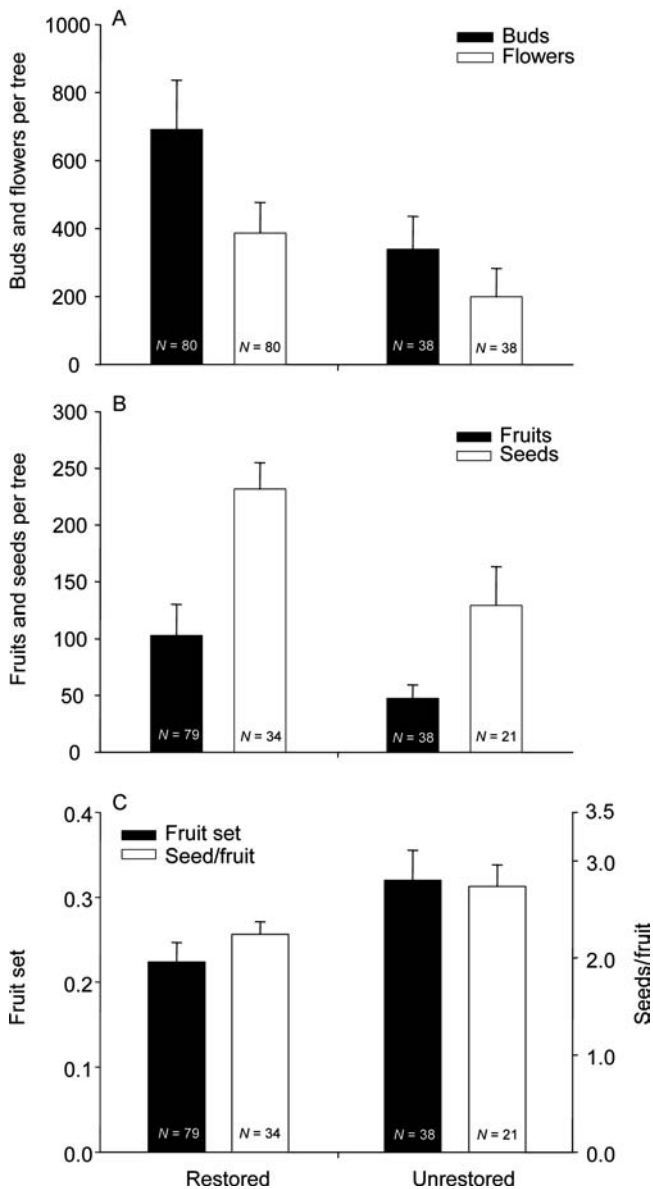


FIGURE 3. Differences in mean (+ SE) (A) number of buds (initial) and flowers (after herbivore attack) per tree, (B) number of fruits and total number of seeds/fruit per tree, and (C) fruit set and number of seeds/fruit per tree in restored and unrestored areas. Fruit set is defined as number of fruits divided by number of flowers per tree. Total number of seeds per fruit was calculated for each tree based either on mean seeds/fruit from individual counts of trees or from the overall mean. In (A) both number of buds and flowers per tree were not significantly different between management schemes (buds: $t = -1.21$, $df = 117$, $P = 0.23$, flowers: $t = -0.18$, $df = 117$, $P = 0.86$). (B) Number of fruits ($t = 0.58$, $df = 115$, $P = 0.57$) and seed/fruit per tree ($t = 1.18$, $df = 115$, $P = 0.24$) were not different between sites. (C) Fruit set was significantly different between sites ($t = -2.72$, $df = 115$, $P = 0.007$) and number of seeds per fruit per tree showed a trend toward more seeds in fruits from the unrestored area than fruits from the restored area ($t = -1.95$, $df = 53$, $P = 0.056$). For the analysis of number of seeds per fruits, fruits were collected from 55 trees in total.

trade-off between maximizing floral display to attract pollinators and minimizing visibility to herbivores has been stressed by other authors (e.g., Fenner *et al.* 2002, Juenger *et al.* 2005) and may play a role in our system. The positive correlation between the attack rates and number of buds per tree suggests positive density dependence. The negative impact of herbivorous larvae on the reproduction of endangered endemic trees in Mauritius can be substantial and warrants further research.

POLLINATION BIOLOGY.—The endemic gray white-eye was the most abundant visitor to *S. mamillatum* flowers, followed by the endemic Mauritius bulbul and the introduced red-whiskered bulbul. Bird pollination of *S. mamillatum* fits in well with the overall generalized pollination system of the Myrtaceae with a wide range of vertebrate and invertebrate floral visitors (e.g., Hopper 1980, Lack & Kevan 1984, Boulter *et al.* 2005). Nocturnal flower visitors, such as hawk-moths, cannot be excluded with certainty, but their contribution to pollination is likely to be minimal because flowers opened early in the morning and anthesis lasted for one day only.

Total fruit and seed production and pollinator abundance were greater in the restored area. However, visitation rate (*i.e.*, number of visits per flower) was higher in the unrestored area, resulting in higher fruit set and a trend toward more seeds per fruit, and fruits were larger but not heavier in the unrestored area. Thus, why do trees, with respect to pollination, appear to perform better in the unrestored area? Gross fruit and seed production is largely dependent on the number of trees in each area. There are at least two possible explanations for the discrepancy in visitation rates and fruit-to-flower ratios between sites.

First, avian foraging behavior may differ with habitat structure. Trees surrounded by dense undergrowth may offer better protection from predators, resulting in longer stays and potentially greater pollen transfer in such patches. Bird visitation behavior may also explain differences in seed set. We showed a positive correlation between floral abundance and bout length, which could have resulted in a higher proportion of intratree pollen transfer in the restored area and consequently in lower seed set due to self-incompatibility. Klinkhamer and de Jong (1993) proposed that optimal plant fitness is obtained by displaying an intermediate number of flowers. Trees in the restored area, which bear many flowers may therefore experience more self-pollination, resulting in lower fruit set and number of seeds per fruit than trees in the unrestored habitat, where floral abundance was low. Proença and Gibbs (1994) described late-acting self-incompatibility for several Brazilian Myrtaceae species, which might also be the case for *S. mamillatum*. Our study showed that the flower-to-fruit ratio in *S. mamillatum* decreased between December 2003 and February 2004, particularly in the restored site (see also Nic Lughadha 1998).

Second, hermaphroditic flowering plants often produce an initial excess of flowers that does not contribute to female fitness through fruit or seed production (Sutherland 1987). Several different mechanisms have been proposed to explain how floral excess production elevates female fitness (Burd 1998). Larger floral displays may attract more pollinators (Conner & Rush 1996), may allow higher fruit set in resource-rich years and thereby increase

lifetime fitness (Lloyd 1980), or may provide a 'reproductive assurance' against losses to, for example, herbivores or fungi (Ehrlén 1991, Hingston & Potts 2005). Another female function mechanism is selective abortion of fruits. Floral overproduction provides a larger pool from which higher quality fruits can be selectively matured (Janzen 1977, Stephenson 1981), provided there is variation in quality, such as in number of seeds per fruit (e.g., Waser *et al.* 1995) or paternity patterns (Charnov 1979, Niesenbaum 1999). In *S. mamillatum* trees in the restored area, these mechanisms may act in concert or individually. Overproduction and fruit maturation is likely to be dependent on these effects and they appear to be stronger in the restored area.

To summarize, subtle changes in bird behavior through habitat structure could explain higher reproductive performance of trees in the unrestored area. It is, however, encouraging that fruit and seed production in the restored area is high, which is the first requirement for habitat restoration to be successful. Even if the unrestored, relatively dense area may be better for pollinators, it is likely that high competition for nutrients and light has a negative effect on seedling recruitment and reproductive success was actually higher in the restored area. At population level, successful conservation of *S. mamillatum* is therefore closely linked to the removal of invasive plants from relatively small confined areas.

POLLINATOR IDENTITY.—Since specialized nectar-feeding birds are locally extinct in Brise Fér, the pollination service to *S. mamillatum* must be fulfilled by generalist extant native and introduced bird species. The gray white-eye was the most numerous visitor, but it may not be the most efficient pollinator of *S. mamillatum*. Despite having a shorter beak and, therefore, having to probe flowers of *S. mamillatum* more deeply to obtain nectar, gray white-eyes carried only half as many pollen grains as red-whiskered bulbuls. When red-whiskered bulbuls forage for nectar, the prominent feather-crest often touches the anthers. Therefore, the red-whiskered bulbul is most likely the more efficient pollinator of *S. mamillatum*, but its role as a major seed disperser of invasive plant species may overall hamper habitat restoration (Linnebjerg 2006). The large amount of *S. mamillatum* pollen found on the introduced Madagascar fody is intriguing: owing to its short beak, this species must probe the flowers deeply to reach the nectar. This may suggest that the locally extinct Mauritian fody *Foudia rubra* (Gmelin) was once an efficient pollinator of *S. mamillatum*.

PLANT RECRUITMENT.—Successful and sustainable reproduction of plant populations depends firstly on intact plant–pollinator interactions and subsequently on seed dispersal and seedling recruitment. Physiological and evolutionary theories have been proposed to explain the occurrence of cauliflory and caulicarp (fruits on the trunk) (Haberlandt 1893, cited in Richards 1996), but few studies have focused on their ecological significance. It may be that caulicarp, rather than being seen simply as the inevitable consequence of cauliflory, is the more significant trait with respect to selective forces acting on the reproductive display of *S. mamillatum* (see also van der Pijl 1957). As a result, this peculiar flower presentation low on the

stem may occur primarily to ease access for ground-dwelling seed dispersers to the fruits (Hopper 1980, Beardsell *et al.* 1993, Warren *et al.* 1997, Kaiser 2006). Likely ground-dwelling candidates among the many extinct frugivores in Mauritius are the two giant tortoises *Cylindraspis triserrata* and *C. inepta* or the giant skink *Leiolopisma mauritiana*. The absence of seed dispersers may explain the lack of natural regeneration of *S. mamillatum* in Brise Fér. Indeed, in another study, we show how extant giant Aldabra tortoises can be used as ecological analogue seed dispersers of *S. mamillatum* (D. M. Hansen, C. N. Kaiser and C. B. Müller, unpublished data).

IMPLICATIONS FOR CONSERVATION.—Although the degradation of the native Mauritian flora and the subsequent restoration programs have been well described (Vaughan & Wiehe 1941, Page & d'Argent 1997, Mauremootoo *et al.* in press (b)), little is known about the rate of regeneration in restored areas and, therefore, the success of these management strategies.

Our finding that trees in unrestored area perform slightly better overall, presumably due to the denser understory, indicates that the current management strategy—at least in the short term—may be missing a crucial factor. Paradoxically, the restoration process of weeding exotic plants creates a disturbance that may affect the behavior of invertebrate pest insects and bird pollinators. As a practical recommendation, we suggest that weeding in restored areas should be conducted with a minimum of disturbance and perhaps as a temporally more gradual removal of exotic plants, which would promote structural habitat heterogeneity (see Hobbs & Huenneke 1992, D'Antonio & Meyerson 2002).

In conclusion, for the management of rare declining species it is important to acknowledge mutualistic and antagonistic interactions and to consider that these interactions may be 'provided' by exotic and/or generalist species since formerly widespread specialists or generalists are now locally extinct. Our study highlights the futility in reconstructing original habitat conditions without incorporating information on ecosystem functions. On tropical oceanic islands, little is known about the original network of interactions among native plant and animal species. Although it will be impossible to consider the full community background, restoration should focus at least on the functionally most important interactions and on structural habitat traits, taking steps toward a broader understanding of ecosystem functioning.

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