Native pioneer trees can be important phorophytes: Their control for biodiversity conservation on an oceanic island also harms native epiphytes and lianas (#119098)

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Native pioneer trees can be important phorophytes: Their control for biodiversity conservation on an oceanic island also harms native epiphytes and lianas

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Human activities generate multiple direct and indirect threats driving rapid biodiversity loss globally. Oceanic islands and tropical forests are most affected by this situation and within them, epiphytes and lianas are among the most threatened floristic components. Yet, they are often understudied and neglected particularly within restoration projects which instead typically favour planting trees and often overlook ecosystem dynamics and functional interactions. We compared native epiphytes and lianas growing on native pioneer trees (*Harungana madagascariensis* (Hypericaceae)) with those growing on other native trees of 1) similar trunk diameter; and 2) similar age, within wet native forests undergoing restoration after invasive alien plant control, on the volcanic oceanic island of Mauritius. We also investigated whether the different phorophytes had any differential influence on the fitness of epiphytes and lianas. We studied *H. madagascariensis* because it is the dominant native pioneer tree of the island's wet native vegetation and also because, since decades, it is often controlled by conservation managers. *Harungana madagascariensis* hosted more native epiphyte and liana species than adjacent native trees of similar ages. No significant difference in epiphyte and liana diversity was found on *H. madagascariensis* compared to other nearby native phorophyte of similar trunk diameter. Twice more epiphyte/liana species were closely associated with *H. madagascariensis*, compared to other phorophytes of similar diameter and none were closely associated with other phorophytes of similar age. *Harungana madagascariensis* hosted more reproducing orchids than phorophytes of similar age and size, and the orchid *Angraecum* spp. were larger on *H. madagascariensis* than on phorophytes of similar sizes. The sizes of lianas did not differ significantly across phorophytes. *Harungana madagascariensis* therefore benefit native epiphytes and lianas, promoting their rapid recovery after invasive alien plants are controlled, in contrast with other native

phorophytes. This contrast is in fact even larger because the cut *H. madagascariensis* are often many meters tall, often already hosting epiphytes, in contrast to seedlings that are planted in their place. On an oceanic island where biodiversity conservation is particularly urgent and where cutting *H. madagascariensis* for ecological restoration already lacks any evidence of benefits it brings, our study provides new evidence that the detrimental effects of this management extends beyond the destruction of the native pioneer trees, to also severely set back the restoration of the native epiphytes and lianas guilds. Our study underscores how native pioneer trees can help accelerate ecosystem recovery and foster the restoration of typically neglected native plant guilds. It also underscores the improbable need for stressing that evidence, and not hypotheses, should drive conservation policy.

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5

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Abstract

Human activities generate multiple direct and indirect threats driving rapid biodiversity loss globally. Oceanic islands and tropical forests are most affected by this situation and within them, epiphytes and lianas are among the most threatened floristic components. Yet, they are often understudied and neglected particularly within restoration projects which instead typically favour planting trees and often overlook ecosystem dynamics and functional interactions. We compared native epiphytes and lianas growing on native pioneer trees (*Harungana madagascariensis* (Hypericaceae)) with those growing on other native trees of 1) similar trunk diameter; and 2) similar age, within wet native forests undergoing restoration after invasive alien plant control, on the volcanic oceanic island of Mauritius. We also investigated whether the different phorophytes had any differential influence on the fitness of epiphytes and lianas. We studied *H. madagascariensis* because it is the dominant native pioneer tree of the island's wet native vegetation and also because, since decades, it is often controlled by conservation managers. *Harungana madagascariensis* hosted more native epiphytes and liana species than adjacent native trees of similar ages. No significant difference in epiphyte and liana diversity was found on *H. madagascariensis* compared to other nearby native phorophyte of similar trunk diameter. Twice more epiphyte/liana species were closely associated with *H. madagascariensis*, compared

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Introduction

Global biodiversity is declining rapidly, primarily driven by human activities and their associated impacts (Baillie, Hilton-Taylor & Stuart, 2004; Vie, Hilton-Taylor & Stuart, 2009; Barnosky et al., 2011). In the absence of intensified mitigation efforts, projections indicate that this downward trajectory will persist, potentially resulting in the extinction of up to 12% of species and a 63% reduction in wildlife population densities by the turn of the century (Leclère et al., 2020). Among the different regions of the globe, tropical oceanic islands suffered particularly from this situation as they host roughly half of the species recognized as threatened in any of the IUCN threat categories (IUCN, 2017), including 6,800 angiosperms species estimated to be highly threatened (Caujapé-Castells et al., 2010). Greater efforts of conservation, including of ecological restoration, should therefore be promoted, particularly given that habitat loss remains the most significant driver of biodiversity loss globally and on islands (Borges, Gabriel & Fattorini, 2019) and continues despite the creation of protected areas (Mora & Sale, 2011; Hill et al., 2015).

In response to this global biodiversity crisis, governments have committed to several international frameworks, such as the Convention on Biological Diversity (CBD) and the United Nations Sustainable Development Goals (SDGs) (CBD, 2011; UN, 2015). In 2022, the UN strengthened its commitment by introducing new targets under the Global Biodiversity Framework (e.g., Target 2), emphasizing the restoration of degraded terrestrial ecosystems (Global Biodiversity Framework (https://www.cbd.int/gbf)). Furthermore, large-scale initiatives like the Bonn Challenge (2011) and the UN Decade on Ecosystem Restoration (2021–2030) have been launched to drive coordinated global action. Overall however, planting tree seedlings has been highly favoured among restoration projects while the inclusion of other growth forms has commonly been disregarded (Ruiz-Jaen & Aide, 2005). Little attention has been paid to non-arborescent plant assemblage development in restoration areas (Garcia et al., 2014, 2015) as these plants rarely reach desirable diversity in restoration forests in a relatively short time (Shoo et al., 2016; Garcia et al., 2016). Yet these plants can make up a significant portion of biodiversity and play significant ecological functions in their ecosystems.

Epiphytic plants constitute an extremely species-rich guild, including over 27,000 recorded species which amount for almost 10% of global vascular plant diversity (Zotz, 2013), and comprise an essential part of the tropical and subtropical flora (Kreft et al., 2004; Krömer et al., 2005). Lianas also constitute a conspicuous feature in tropical forests, contributing up to 27.1% of their species diversity (Gentry, 1992; Zhu, 2008). Altogether, epiphytes and lianas provide important ecosystem functions, including primary productivity (Clark, Nadkarni & Gholz, 1998), food and habitat provisioning (Duellman, 1988; Nadkarni & Matelson, 1989; Yanoviak, 2015) as well as micro-habitat buffering (Scheffers et al., 2013) and canopy water storage (Campbell et al., 2015; Ah-Peng et al., 2017) among others. However, few studies investigated epiphyte colonization in secondary forests (Ceballos, 2020), and lianas have also been neglected in many conservation and research programs (Ashton et al., 2001; Nakamura, Proctor & Catterall, 2003; Vargas, Grombone-Guaratini & Morellato, 2020; Stone et al., 2020) despite their importance for ecosystem functioning (Schnitzer, 2015; Gotsch, Nadkarni & Amici, 2016) and their threatened status. Indeed, up to 1,700 liana species could be endangered worldwide (Song et al., 2022) and concerning epiphytes, with the Neotropics as example, 6,721 species (~60%) are threatened (Carmona-Higuita et al., 2024).

We studied native epiphyte and liana communities growing in tropical forest areas undergoing ecological restoration that follows the control of invasive alien plants (Baider & Florens, 2011) on the tropical volcanic oceanic island of Mauritius whose forests are known to sustain advanced invasion (Florens et al., 2016) that leaves fairly large gaps after invasive plants control (Florens & Baider, 2013). In particular, we compared the phorophyte potential of native pioneer trees that grow in those gaps with that of non-pioneer tree species. We focused on a widespread native pioneer tree species (*Harungana madagascariensis* Lam. (Hypericaceae)) (Bojer, 1837; Baker, 1877; Robson & Stevens, 1976; Botanic Gardens Conservation International (BGCI) & IUCN SSC Global Tree Specialist Group, 2019) that is commonly controlled by conservation managers who then plant other native tree species in its place (Florens & Baider 2013, F.M.M.P. Baguette, C. Baider, F.B.Vincent Florens pers. obs. 2023- 2025). More specifically, we investigated three questions: (a) How does *H. madagascariensis* compare as phorophyte with other naturally growing native trees of comparable sizes that belong to species that are commonly planted where *H. madagascariensis* is cut ('parallel host specificity')? (b) How does the phorophytic function of *H. madagascariensis* compare with that of other naturally growing trees of comparable age belonging to species that are typically planted after *H. madagascariensis* is removed? (c) Does the fitness of epiphytes and lianas vary depending on whether they grow on *H. madagascariensis* or other phorophytes of comparable age and size?

Materials & Methods:

Study sites

Mauritius (centred on 20°15' S and 57°35' E) is a tropical, volcanic island, situated about 900 km east of Madagascar, within the Madagascar and Indian Ocean Islands biodiversity hotspot (Myers et al., 2000). It covers 1,865 km^2 and culminates at 828 m elevation. The mean annual rainfall varies from 800 mm (leeward coast) to 4,000 mm (central uplands) and the mean annual temperature is 22° C (Staub, Stevens & Waylen, 2014). Following extensive degradation caused since human colonisation of the island in 1638, only 82.1 km^2 or 4.4% of the island's vegetation remains that still comprise a high percentage of native species (Hammond et al., 2015). This native vegetation, however, survived in highly fragmented forest patches (Florens, 2013) that are increasingly dominated by alien woody species, particularly in the understorey (Florens et al., 2016). Attempts to restore native vegetation communities have been implemented since the mid-1980s (Jones, 2008), comprising mainly of the control of invasive alien plants, and by 2021, ~700 ha of native forest is undergoing restoration on the island (Government of Mauritius, 2021).

Two of the forest areas undergoing ecological restoration for biodiversity conservation and known to host native epiphyte and liana communities (Figure 1) were surveyed between August 2023 and August 2024. The first one, Mount Camizard, (20°19'51" to 20°20'00"S and 57°42'52" to 57°43'02"E, 250–320 m asl) is located in the island's South-East within an area of Mountain Reserve inside the Bamboo Mountains forest block. The native forest at the site has been undergoing ecological restoration mainly through invasive alien plant control since 2005 and is close to the lower elevational range of *H. madagascariensis* on Mauritius. The second site is Brise-Fer in the South-West of Mauritius (20°22'10" to 20°22'30"S and 57°25'55" to 57°26'20"E, 560–600 m asl) within the Black River Gorges National Park. Different patches of the native forest at site sampled have been weeded of invasive alien plants for promoting ecological restoration since 1986, with the largest area weeded in 1996, which we chose for our sampling. Brise Fer occurs close to the higher elevational range of *H. madagascariensis*. Mount Camizard and Brise Fer receive comparable annual rainfall of respectively 2.5 and 2.4 m, and no permanent water sources, but some storm streams, cross the study areas.

Data collection

Naturally growing (non-planted) trees of *H. madagascariensis* (52 at Mount Camizard and 21 at Brise Fer) were randomly sampled along with the closest individual of another native tree species to each of them that was of (1) similar trunk diameter (measured at 1.3 m above ground, along the stem) and (2) similar age (Figure 2 and 3). Trees of similar age were chosen from within the ten most important species of each site (Florens et al., 2012) to ensure their nearby occurrence, their most comparable ecological importance to *H. madagascariensis* which itself is relatively common, and to also reflect the most commonly planted species by conservation practitioners after they cut *H. madagascariensis*. In all, 219 woody plants were sampled, including 73 trees of each category. For each of the 219 potential phorophyte, GPS coordinates were recorded (with GPSMap® 65, Garmin), the species identified, and its diameter at breast height (DBH) recorded. The reproductive status of each epiphyte and liana was recorded as either vegetating or reproducing (bearing flower buds, open flower, unripe fruit, ripe fruit or showing traces of fallen fruits for angiosperms and fertile fronds for pteridophytes). Furthermore, the number of leaves or fronds of each epiphyte, and the stem diameter of each liana were recorded to assess the influence of the phorophyte type on the fitness of epiphytes and lianas.

Vascular epiphytes and lianas were identified and counted on all sampled trees from the ground, with the aid of an 8x42 pair of binoculars when necessary. For larger trees (> 8 m height), we restricted our census up to the first section of the canopy (e.g. 1/3 of the branches length), equivalent to "Zone 3" (Johansson, 1974), to avoid observation bias due to the high probability of missing individuals higher up. Hemiepiphytes and hemiparasites were not considered due to their different ecology from epiphytes and lianas and also because of their rarity or absence in the study areas. We defined an individual epiphyte as an assemblage of rhizomes and leaves forming a clearly bounded stand (Sanford, 1968) due to the difficulty of delineating individual epiphytes when multiple shoots occur in close proximity. For species exhibiting a creeping growth form, individuals were considered separate if physically separated rhizome segments were growing on distinct branches or if no visible connection was discernible between them Finally, each clearly separated clump of epiphytic filmy ferns (Hymenophyllaceae) observed was defined as a single individual due to the impossibility to delimitate individuals otherwise in the field.

Estimation of tree age

We estimated tree age using long-term individual tree monitoring census data from 2005, 2010 and 2022 (only available from Brise Fer) supplied by the Mauritius Herbarium and comprising ~19,000 individual native woody plants belonging to ~100 species. First, using two segments of stem diameter monitoring (from 2005–2010 and from 2010-2023) we calculated the annual DBH increments of *Harungana madagascariensis* and of the ten most important species along which it grows. The ten most important species were determined following Importance Values from Florens et al., (2012). The changes in stem diameters were used to estimate the average annual growth rate of each species of interest. A growth rate ratio between *H. madagascariensis* and each of the other species was then computed to estimate the diameter of an individual of the ten other most important species that would be of similar age to the individual of *H. madagascariensis* being sampled (Supplementary Table S1). Finally, we sampled the nearest similar-aged plant to each *H. madagascariensis* studied. This indirect method was chosen as the census data used were the best available data for tree age estimation, and more reliable methods such as tree coring could not be performed due to the risk of damage (Florens, 2014; Tsen, Sitzia & Webber, 2016) which would not have been justifiable in our context.

Data analysis

Only native species were used in the data analysis, because introduced species encountered represented only individuals that were missed during invasive alien plant control campaigns and are therefore not characteristic of the study sites, and transient in nature until removed at a future weeding campaign. In all, 81% (1,805 of 2,229 individuals) of all epiphytes and lianas observed were identified to species level directly *in situ* or at the National Herbarium of Mauritius based on photographs taken *in-situ*. Beside these, Hymenophyllaceae were treated as a single group due to their small size and the difficulty to identify them to species level. Observations were grouped under morphospecies groups for species that were indistinguishable from each other either because of the lack of distinctive characters on immature individuals or due to the absence of visible distinctive characters. This was the case for *Angraecum calceolus*, *Angraecum caulescens* and *Angraecum multiflorum* which have been grouped under the "*Angraecum* spp. Group" (n = 383); *Bulbophyllum* spp. grouped under the "*Bulbophyllum* spp. Group" (n = 4); *Haplopteris* spp. in "*Haplopteris* spp. Group" (n = 3), and *Selaginella* spp. in "*Selaginella* spp. Group" (n = 19). Four observations of ferns could not be associated to any genus and those were excluded from the data analysis, on the basis that they could have been immature alien species. The final dataset used for analysis included the respective taxa classified as morphospecies.

We used RStudio version 2024.12.0.467 (R Core Team, 2024) to do all statistical analysis and graphs. Floristic diversity has been analysed using the Fisher α, Shannon-Weaver (H'), Simpson index (D), and Margalef Indices (Shannon & Weaver, 1949; Simpson, 1949; Margalef, 1958; Condit et al., 1998) calculated for all the tree categories (*H. madagascariensis* versus trees of similar diameter and similar age) in each site. Structural variables such as epiphyte density (N, epiphytes tree^{-1}), and species richness were also computed. Shapiro-Wilk Test was used to test the distribution of abundance and species richness data. Epiphyte abundance and species richness were compared between the different tree categories using Kruskal–Wallis rank sum tests with the post-hoc Dunn's tests of multiple comparisons with Bonferroni adjustment using the r packages rcompanion and dunn.test (Mangiafico, 2024; Dinno, 2024). Graphs were produced using the r package ggplot2 (Wickham, 2016).

Description of the epiphyte and liana communities in each tree category was made through its species composition and the relative importance value of all species. To this end, we carried out an indicator species analysis using the multipatt function in the indicspecies package (version 1.7.15) (De Cáceres, Legendre & Moretti, 2010) to identify species that are good indicators for one or several tree categories (Dufrêne & Legendre, 1997). Finally, we chose the Orchidaceae, the most abundant epiphyte family recorded (1,181 individuals), to compare the abundance of reproducing individuals on *H. madagascariensis* and other phorophytes of similar age and size. We also used the two most abundant orchid species or taxon recorded, namely *Angraecum pectinatum* and *Angraecum* spp. (respectively 523 and 386 individuals), and the most abundant species of liana recorded, namely *Piper borbonense* (226 individuals) to compare sizes of epiphyte and liana growing on the different phorophytes, as further proxies of fitness.

Results

Epiphyte or liana were observed on 116 of 219 (53%) sampled potential phorophytes, including very small ones (DBH ~1 cm). Trees devoid of epiphytes or lianas were mostly of relatively small sizes (median DBH: 5.5 cm), but also included six relatively large trees (DBH ≥ 15 cm). Plants sampled hosted 23 epiphyte species or morphospecies (1,973 individuals) and five liana species (256 individuals) (Supplementary Table S2). Overall, half (14) of the species occurred as < 10 individuals each, and the other half was represented by > 2,000 individuals (Supplementary Table S3). The most abundant species was the orchid *Angraecum pectinatum*, which accounted for 23.5% of all epiphytes. Other *Angraecum* species grouped into '*Angraecum* spp.' and the fern *Microsorum punctatum* were the other most frequent epiphytes (Supplementary Table S4). The Orchidaceae was the most important plant family, both in terms of abundance and species richness, including 36% of all species or taxa and 53% of all individuals (Supplementary Table S5).

Overall, *H. madagascariensis* hosted a higher diversity of epiphyte and liana than other native trees of similar age, and a slightly lower diversity than other trees of similar diameter (Table 1). A significant difference in species richness ($\chi^2 = 121.80$, df = 5, $p < 0.05$) and abundance ($\chi^2 = 107.59$, df = 5, $p < 0.05$) of epiphytes was found among phorophytes across both sites, with post hoc Dunn's tests revealing that *H. madagascariensis* hosted a significantly higher species richness ($p < 0.05$) and abundance ($p < 0.05$) of epiphyte communities than other native trees of similar age in both Brise Fer and Mount Camizard. However, no significant difference in epiphyte species richness existed on *H. madagascariensis* compared to other native trees of similar diameter ($p > 0.05$), and a similar result applied for abundance ($p > 0.05$) in both sites (Figure 4 and 5). In Brise Fer, six species were significantly associated with *H. madagascariensis* compared to only three with other trees of similar diameter (Table 2). Furthermore, five species were significantly associated with *H. madagascariensis* and trees of similar DBH compared to only one being associated with the combination of *H. madagascariensis* and trees of similar DBH and age (Table 2). No significant association were found in Mount Camizard.

There was a significant difference in abundance of reproducing orchid ($\chi^2 = 63.93$, df = 5, $p < 0.05$) among phorophytes across both sites, with post hoc Dunn's tests revealing that *H. madagascariensis* hosted significantly more reproducing orchid than other native phorophyte of similar age and size in Brise Fer ($p < 0.05$ respectively) but no significant difference was observed in Mount Camizard (Figure 6). In addition, there was a significant difference of size (in terms of number of leaves) for *Angraecum* spp. ($\chi^2 = 24.78$, df = 5, $p < 0.05$) but not for *Angraecum pectinatum* ($\chi^2 = 3.35$, df = 5, $p > 0.05$) among phorophytes across both sites. Post hoc Dunn's tests revealed that individuals of *Angraecum* spp. on *H. madagascariensis* had significantly more leaves than individuals on other phorophytes of similar DBH ($p < 0.05$) in Brise Fer, and that the leafiness of these orchids was similar whether they grew on *H. madagascariensis* or on other phorophytes of similar age ($p > 0.05$) (Figure 7a). With regards to lianas, there was no significant difference of size (in terms of stem DBH) for *Piper borbonense* among phorophytes in Brise Fer ($\chi^2 = 0.69$, df = 5, $p > 0.05$) (Figure 7b).

Discussion

Ecological implications

The native pioneer tree *H. madagascariensis* which grows naturally best in disturbed areas, precisely therefore where other potential phorophytes are rare, constitute furthermore a relatively better phorophyte compared to other potential native phorophytes that grow alongside it in the Mauritian native forests. Furthermore, the epiphyte and liana communities that *H. madagascariensis* come to support in just two to three decades of its growth, is comparable to those assembling on often much-slower growing and much older, often multi-centennial trees of comparable size to *H. madagascariensis*, which further stresses the latter's importance for establishment and recovery of epiphytes and lianas following a disturbance. Our study also aligns with previous findings that tree age and sizes strongly influence phorophytic function in various ways that depend on tree species' ecology (pioneer versus later successional species) (Catling & Lefkovitch, 1989; Wolf, 1994; Annaselvam & Parthasarathy, 2001; Bernal, Valverde & Hernández-Rosas, 2005; José Válka Alves, Kolbek & Becker, 2008).

Moreover, we showed that, within two to three decades of a disturbance, the fitness of native epiphytes that establish on *H. madagascariensis* is substantially superior to that of epiphytes that establish on other potential phorophytes close by, as indicated by greater leafiness and greater proportion of mature individuals on *H. madagascariensis*. This superiority as phorophyte is apparent even when compared to much older other species of the same trunk diameter as the *H. madagascariensis*. This situation appears linked to the fact that the bark of *H. madagascariensis* is particularly thick and spongy relative to most other native phorophytes. Such a bark would retain moisture for longer periods and probably provide more nutrients, thereby promoting epiphyte establishment and their faster growth and maturation. Hence, *H. madagascariensis* can not only quickly provide large surface areas suitable for epiphyte establishment and maintenance, but also offer a suitable habitat for their relatively rapid growth and earlier maturation. Those results corroborate previous studies showing that pioneer trees can be suitable phorophytes for epiphytes (Callaway et al., 2002; Cascante Marín, 2008; Einzmann et al., 2015;

Besi et al., 2023; Pie et al., 2023; Wysocki et al., 2024), and lianas (Putz, 1984; Letcher, 2015; Schnitzer, 2015). However, it's important to note that site conditions modulate the benefits that pioneer trees like *H. madagascariensis* can bring, with greater positive impacts on boosting epiphytes and lianas in sites where greater species richness and abundance of epiphytes and lianas is found (e.g. Brise Fer compared to Mount Camizard).

Finally, the indicator analysis identified 21.4% of the epiphyte and liana species recorded in this study (N = 6) as significantly associated with *H. madagascariensis*, and 32.1% (N = 9) with *H. madagascariensis* and other trees of the same size, further stressing the key role that *H. madagascariensis* plays in supporting specific native epiphyte and liana species. Therefore, *H. madagascariensis* trees also constitute a real refugia for epiphytes and lianas relatively early following a disturbance. Importantly, those results obtained in Mauritius are likely to also apply more broadly within the vast native range, of about 13 M km^2, of *H. madagascariensis* (Baguette, Baider & Florens, 2025) whenever the tree grows within the natural range of epiphytic orchids, ferns and lianas, given the broad similarity of ecological niches and requirements of these guilds of plants.

Implications for ecological restoration and biodiversity conservation

The extreme invasion of Mauritius native forests by alien plants (Florens et al., 2016) has driven such a high rate of native tree mortality (Florens et al., 2017) including of some of the largest canopy species (Baider & Florens, 2006), that when alien plants are removed to foster ecological restoration, scanty native trees remain within the substantial gaps created in the forest canopy. These gaps form ideal habitat for *H. madagascariensis* which grows naturally from the seedbank to recreate a canopy reaching ~12 m high within four to six years (Swaine & Hall, 1983; Ndam & Healey, 2001; Manjaribe et al., 2013) before starting to decline after ~10 years (Hervé et al., 2015). Our results show that, where it grows, this pioneer tree is highly beneficial to native epiphytes species richness, abundance and fitness, more so than other species which grows alongside it. Yet, all major conservation practitioners of Mauritius cut back large numbers of *H. madagascariensis* in areas undergoing ecological restoration for biodiversity conservation (Figure 8), to create space where later successional woody native plants are often planted (Florens & Baider, 2013). Here, we show that by doing so, conservation managers not only reverse restoration progress of woody plant cover (Florens & Baider, 2013), but also set back ecosystem recovery by: 1) immediately destroying the many native structural epiphytes that have already established on *H. madagascariensis*; and 2) subsequently slowing down the recovery of structural epiphytes by leaving them poorer quality phorophytes than *H. madagascariensis* to grow on.

Among the species significantly associated specifically with *H. madagascariensis*, four are orchids. Orchids constitute a major group of the island flora as it is the island's most species-rich family of flowering plants, and is dominated by species endemic to the biodiversity hotspot region (80%), followed by species endemic to the Mascarene archipelago (41%), including those endemic to the island (10%) (Baider & Florens, 2022). The Orchidaceae is also the native angiosperm family that has sustained the highest extinction rate on Mauritius, with 22% of Mauritian native orchids driven extinct over the last 2.5 centuries or so (Baider & Florens, 2022) and many species are now extremely rare (e.g. Baider et al., 2012; Pailler et al., 2020a). Furthermore, known species have been found for the first time on the island relatively recently (Roberts et al., 2004) and new species are still being discovered even more recently (Fournel, Micheneau & Baider, 2015; Pailler & Baider, 2020; Pailler et al., 2020b). For all these reasons, conservation of native orchids in Mauritius should be a priority and our results show that *H. madagascariensis* can greatly help to enhance their conservation in wet forests by providing advantageous habitats for their colonisation and fast growth and maturation. It is thus particularly unfortunate that most conservation managers cut back *H. madagascariensis* from areas undergoing restoration. Importantly, *H. madagascariensis* germinates and grows naturally in wet forests undergoing restoration such that no additional investment after invasive plants weeding is required from conservation managers for its establishment.

Finally, it is important to stress that epiphyte support diverse ecological interactions with animals (Nadkarni & Matelson, 1989; Stuntz et al., 2002; Boechat, da Silva & Nunes-Freitas, 2019; Spicer & Woods, 2022), as lianas also do (Yanoviak, 2015; Odell, Stork & Kitching, 2019). In particular, *Piper borbonense*, the most abundant native liana growing on *H. madagascariensis*, produces many fruits eaten by native vertebrates (Heinen et al., 2023) including the threatened endemic Mauritius Bulbul (*Hypsipetes olivaceus*). Mauritius is the only place within *H. madagascariensis*' 13 M km^2 native range where conservationists cut the tree (Baguette, Baider & Florens, 2025), based on justifications contradicting best available evidence, including the unsubstantiated claim that it harms native biodiversity. Here, we show the opposite to be true regarding the neglected and threatened guilds of epiphytes and lianas. We hope that our findings may help practitioners shift scarce conservation resources away from management that harm native biodiversity, and above all that our results can trigger a paradigm shift in Mauritius where conservation policy is driven less by non-expert opinions and hypotheses and more by scientific evidence. This situation is not an isolated case; the mass-culling of a threatened Flying fox spearheaded by Mauritius' main conservation service was also based on non-expert opinions and hypotheses instead of evidence (Florens, 2015, 2016) and predictably led to failure (Florens & Baider, 2019). Concerning *H. madagascariensis*, while some encouraging signs have started appearing (Ferney Ltd., 2025) much remains to be done to meaningfully accomplish the paradigm shift (Figure 8).

Conclusion

Using the widely distributed *Harungana madagascariensis* as a model, we show that pioneer trees can serve as important and even superior phorophytes for native epiphytes and lianas compared to the rest of the woody plant community where it grows. This finding was made within tropical forest areas undergoing ecological restoration following the weeding of invasive alien plants and was already apparent within the early stages after the weeding. This is good news for conservation in a place like Mauritius where much of the biota is highly threatened with extinction, and where epiphytes and lianas remain a particularly diverse and also largely overlooked component of native plant diversity which has furthermore already sustained high extinction rates and comprise many rare and threatened species. However, the enduring practice of most major local conservation managers of cutting back native pioneer trees like *H. madagascariensis* from areas being restored for conservation of biodiversity remains a concern as it represents investment of scarce conservation resources in ways that setback biodiversity conservation objectives and undermine the reinstatement of natural functioning of the ecosystem being restored. A shift from the current hypothesis-based to an evidence-based conservation policy on that matter is warranted.

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Figure 1

The study sites of Brise Fer and Mount Camizard in Mauritius with 100 m contour lines indicated.

The Black River Gorges National Park is outlined. Mount Camizard is found within protected Mountain Reserves.

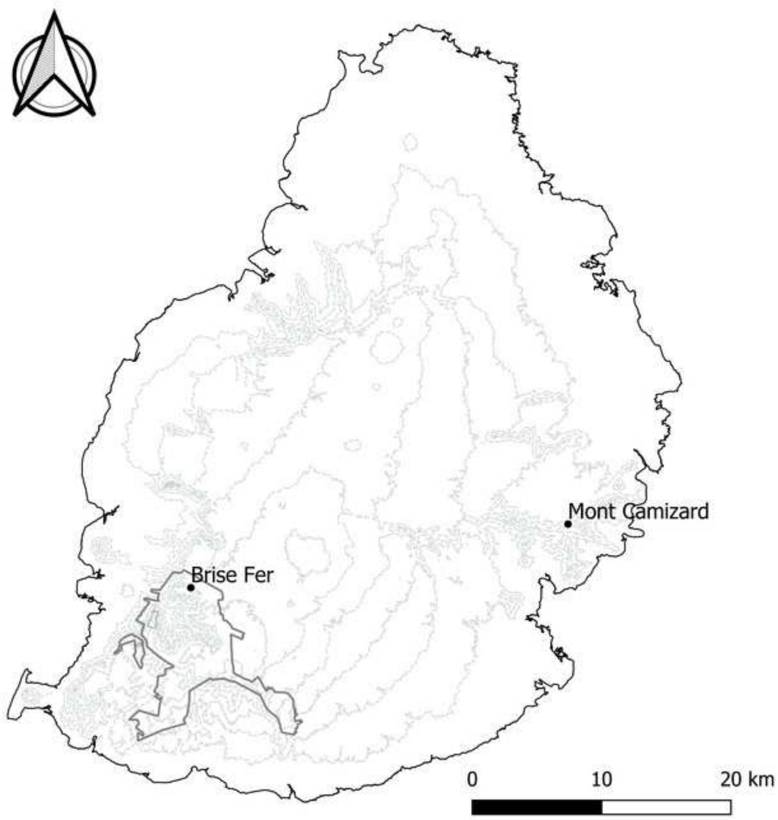

Figure 2

Illustration of phorophytes sampled in Mount Camizard .

(a) One *Harungana madagascariensis* of 9.5 cm, with (b) the closest individual (2.3 m) of another native species (*Euphorbia pyrifolia*) of similar diameter (9.5 cm), and (c) the closest individual (here at 1 m distance) of another native species (*Diospyros tessellaria*) of similar age (trunk diameter = 0.97 cm) (section 3.2.3 explains how similar ages were determined). Photos: François Baguette.

Figure 3

Illustration of phorophytes sampled in Brise Fer.

(a) One large *Harungana madagascariensis* of 30 cm trunk diameter, with (b) the closest individual (12 m away) of another native species (*Psiloxylon mauritianum*) of similar trunk diameter (31.9 cm), and (c) the closest individual (indicated by arrow) of another native species (*Eugenia kanakana*) of similar age (trunk diameter = 4.5 cm) (section 3.2.3 explains how similar ages were determined). Photos: François Baguette.

Figure 4

Species richness (± SE) on *Harungana madagascariensis* and other potential phorophytes in Brise Fer and Mount Camizard where native forests are undergoing ecological restoration after weeding.

'Same DBH' stands for other potential native phorophytes having comparable diameter at breast height and paired with each *H. madagascariensis* sampled; and 'Same age' refers to other potential native phorophytes having comparable age and paired with each *H. madagascariensis* sampled. "Epiphyte" refers to both epiphyte and liana species.

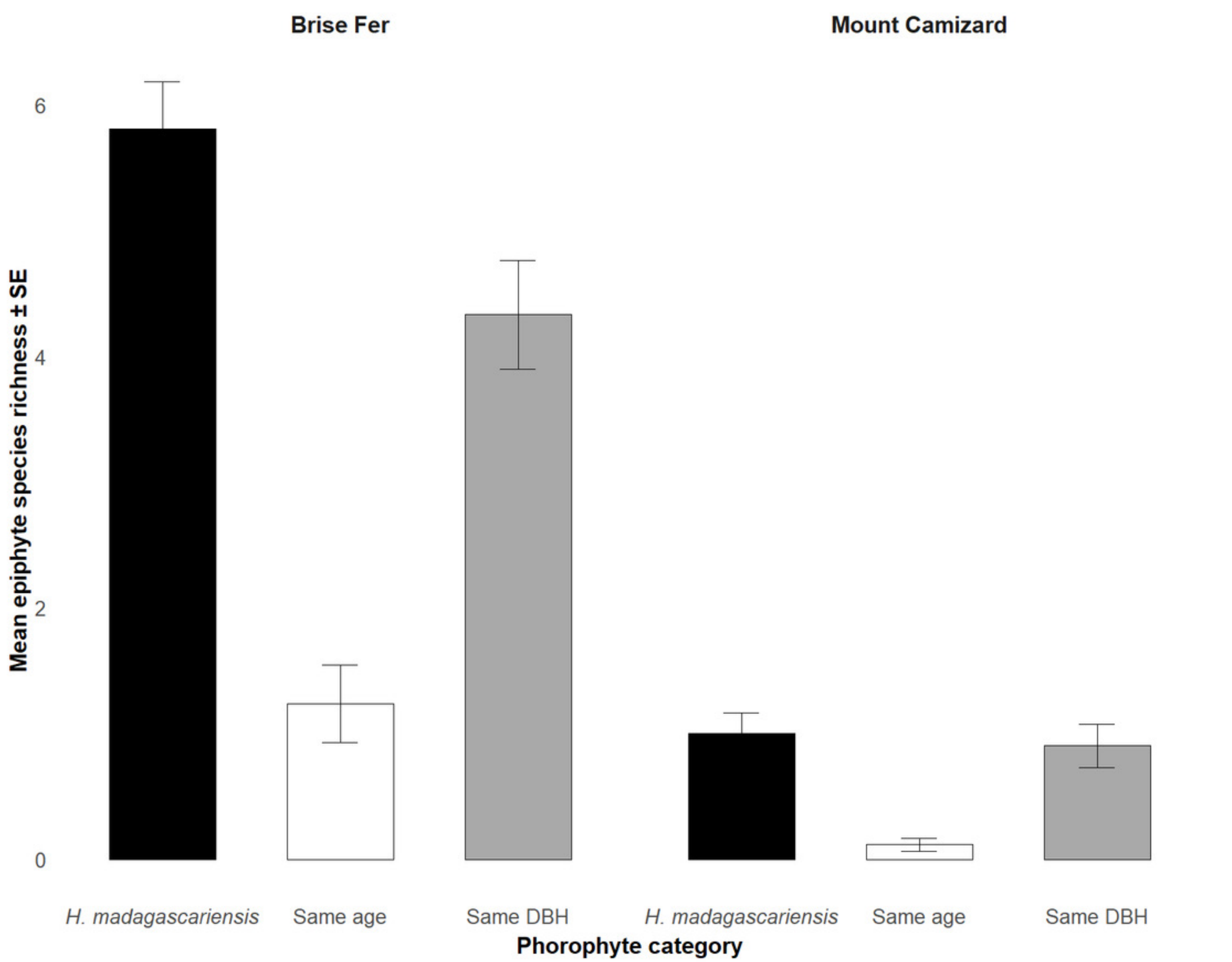

Figure 5

Abundances of native epiphytes (± SE) on *Harungana madagascariensis* and other phorophytes in Brise Fer and Mount Camizard where native forests are under ecological restoration after weeding.

'Same DBH' stands for other potential native phorophytes having comparable diameter at breast height and paired with each *H. madagascariensis* sampled; and 'Same age' refers to other potential native phorophytes having comparable age and paired with each *H. madagascariensis* sampled. "Epiphyte" refers to both epiphyte and liana species.

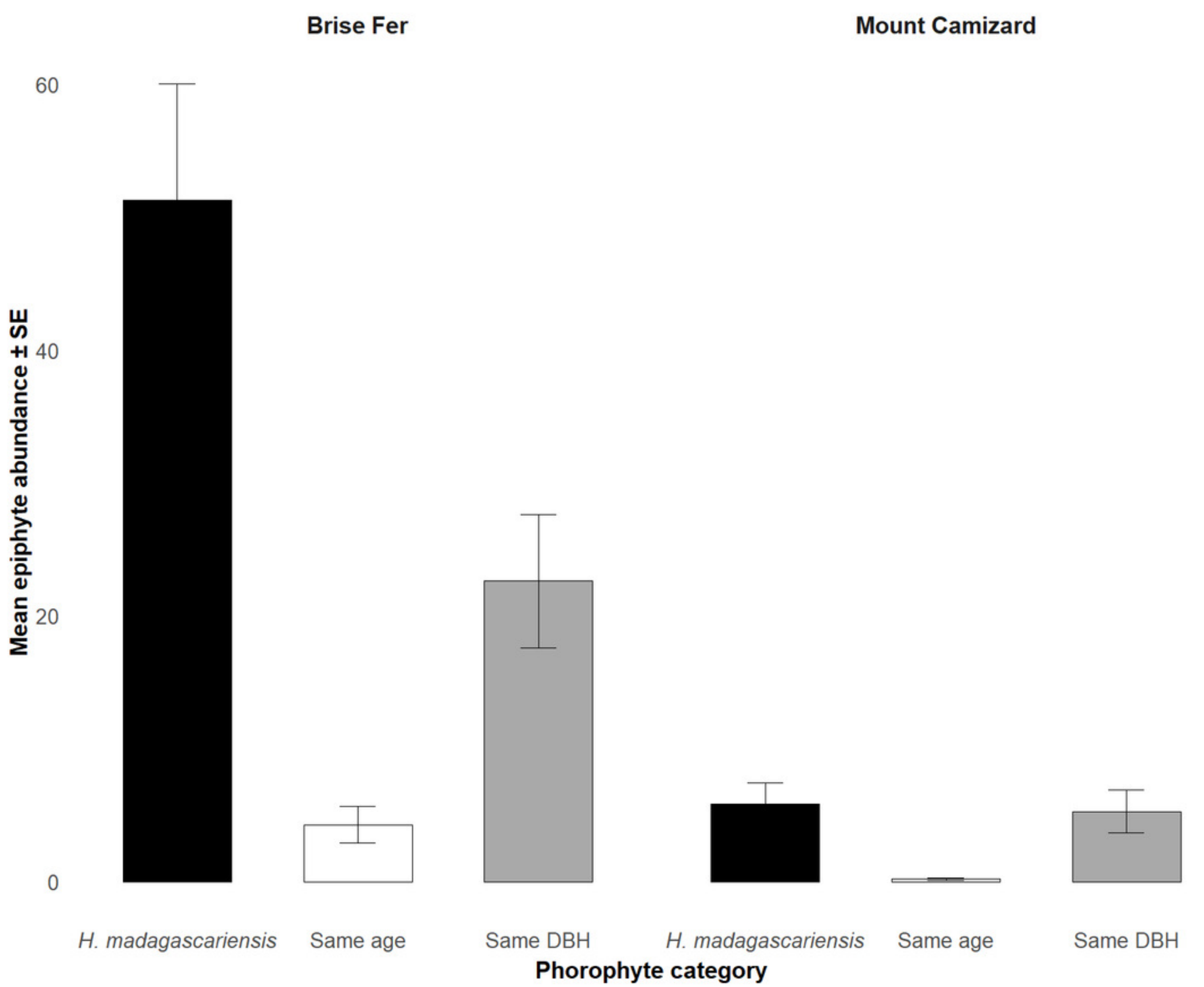

Figure 6

Abundance of reproducing orchids (± SE) on *Harungana madagascariensis* and other phorophytes in Brise Fer and Mount Camizard where native forests are under ecological restoration after weeding.

'Same DBH' stands for other potential native phorophytes having comparable diameter at breast height and paired with each *H. madagascariensis* sampled; and 'Same age' refers to other potential native phorophytes having comparable age and paired with each *H. madagascariensis* sampled.

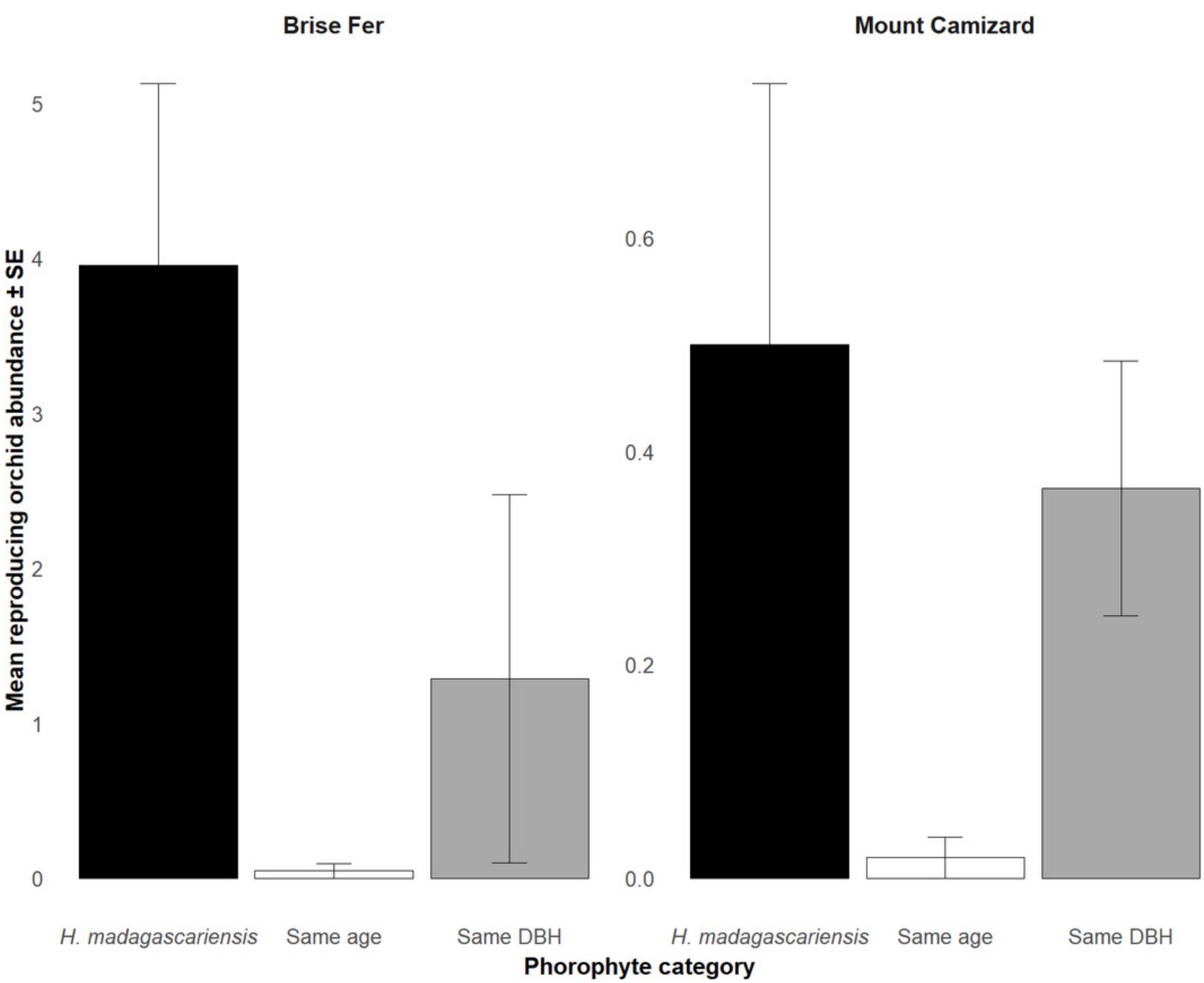

Figure 7

Size of selected epiphytes and lianas on *Harungana madagascariensis* and other phorophytes in Brise Fer and Mount Camizard where native forests are under ecological restoration after weeding.

(a) Mean number of leaves of *Angraecum pectinatum* and other *Angraecum* spp. (± SE). For Mount Camizard, no *A. pectinatum* were sampled on 'same age' phorophytes (white bars). (b) Mean stem diameter of *Piper borbonense* (± SE). Dark grey bars represent individuals growing on *H. madagascariensis* , lighter grey bars represent phorophytes of 'Same DBH', standing for other potential native phorophytes having comparable diameter at breast height and paired with each *H. madagascariensis* sampled; and white bars represent phorophytes of 'Same age' referring to other potential native phorophytes having comparable age and paired with each *H. madagascariensis* sampled on both graphs.

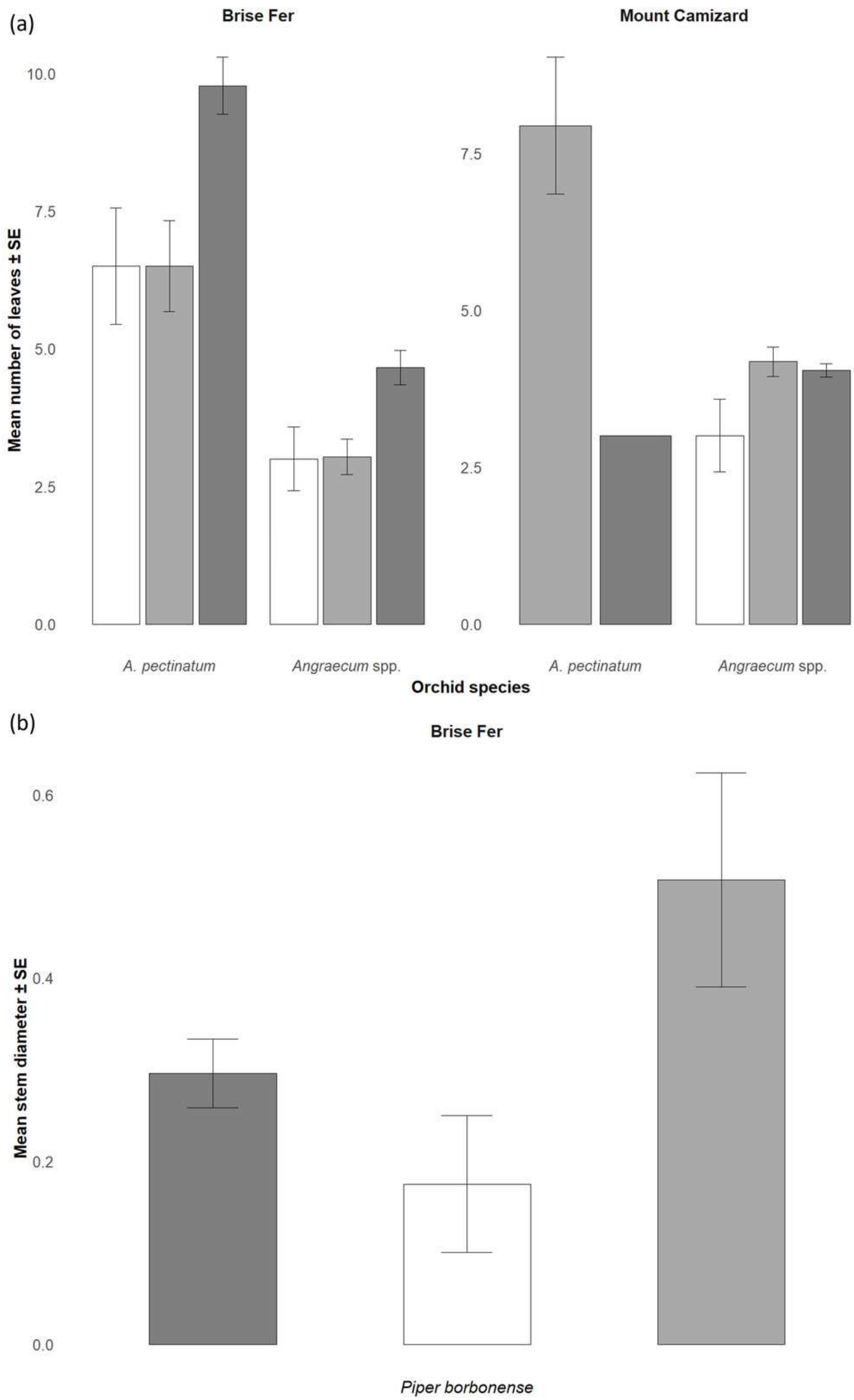
(a)
Brise Fer
Mount Camizard
Mean number of leaves ± SE
10.0
7.5
5.0
2.5
0.0
A. pectinatum
Angraecum spp.
Orchid species
(b)
Brise Fer
Mean stem diameter ± SE
0.6
0.4
0.2
0.0
Piper borbonense

Figure 8

Control of *Harungana madagascariensis* within native forests undergoing restoration for conservation of biodiversity done alongside maintenance weeding of invasive alien plant species.

(a) Ring-barked *H. madagascariensis* observed at Mount Camizard during data collection for this study. (b) Cut stem of *H. madagascariensis* observed in a different restoration area managed by a different organization located in Ferney valley in Mauritius.

Table 1(on next page)

Diversity indices of native epiphytes and lianas on potential phorophytes in Brise Fer and Mount Camizard where native forests are undergoing ecological restoration after weeding.

‘*Harungana*’ stands for *Harungana madagascariensis* ; ‘Same DBH’ stands for other potential native phorophytes having comparable diameter at breast height and paired with each *H. madagascariensis* sampled; and ‘Same age’ refers to other potential native phorophytes having comparable age and paired with each *H. madagascariensis* sampled.

	Brise Fer			Mount Camizard		
Diversity_Index	***Harungana***	**Same DBH**	**Same age**	***Harungana***	**Same DBH**	**Same age**
Fisher α	3.41	4.02	2.78	1.30	1.53	1.50
Simpson (D)	0.69	0.71	0.65	0.64	0.68	0.64
Shannon and Weaver (H')	1.64	1.84	1.37	1.23	1.44	1.14
Margalef (K)	2.74	3.06	1.93	1.09	1.27	1.00

Table 2(on next page)

Native epiphytes and lianas significantly associated with potential phorophytes in Brise Fer where native forest is undergoing ecological restoration after weeding of invasive alien plants.

'*Harungana*' stands for *Harungana madagascariensis*; 'Same DBH' stands for other potential native phorophytes having comparable diameter at breast height and paired with each *H. madagascariensis* sampled; and 'Same age' refers to other potential native phorophytes having comparable age and paired with each *H. madagascariensis* sampled.

Species	**Site**	**Associated phorophyte(s)**	**Chi-square (χ^2)**	**p value**
Angraecum pectinatum	Brise Fer	*Harungana*	0.919	< 0.05
Cnestis glabra	Brise Fer	*Harungana*	0.612	< 0.05
Nephrolepis cordifolia	Brise Fer	*Harungana*	0.593	< 0.05
Angraecum mauritianum	Brise Fer	*Harungana*	0.504	< 0.05
Polystachia concreta	Brise Fer	*Harungana*	0.430	< 0.05
Bulbophyllum sp.	Brise Fer	*Harungana*	0.309	< 0.05
Asplenium nidus var. *nidus*	Brise Fer	Similar DBH	0.412	< 0.05
Urera acuminata	Brise Fer	Similar DBH	0.404	< 0.05
Hymenophyllaceae	Brise Fer	Similar DBH	0.378	< 0.05
Piper borbonense	Brise Fer	*Harungana* + Similar DBH	0.748	< 0.05
Microsorum punctatum	Brise Fer	*Harungana* + Similar DBH	0.614	< 0.05
Selaginella sp.	Brise Fer	*Harungana* + Similar DBH	0.488	< 0.05
Nephrolepis biserrata	Brise Fer	*Harungana* + Similar DBH	0.408	< 0.05
Rumohra adiantiformis	Brise Fer	*Harungana* + Similar DBH	0.345	< 0.05
Lepisorus spicata	Brise Fer	*Harungana* + Similar DBH + Similar age	0.647	< 0.05