



# *Harungana madagascariensis* (Hypericaceae) is a key phorophyte for native epiphytes and lianas during ecological restoration: case study on an oceanic island

François M.M.P. Baguette<sup>1</sup>, Cláudia Baider<sup>2</sup> and François Benjamin Vincent Florens<sup>1</sup>

<sup>1</sup>Tropical Island Biodiversity, Ecology and Conservation Pole of Research, Department of Biosciences and Ocean Studies, Faculty of Science, University of Mauritius, Le Réduit, Mauritius  
<sup>2</sup>The Mauritius Herbarium, Agricultural Services, Ministry of Agro-Industry, Food Security, Blue Economy and Fisheries, Le Réduit, Mauritius

## ABSTRACT

Human activities generate multiple pressures on ecosystems, 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 in 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, in 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 reproductive status of epiphytes and their size. 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 native trees of similar age, but no difference was found with trees of similar diameter. Similarly, there was a higher abundance of epiphyte and liana on *H. madagascariensis* compared to other trees of similar age, but no difference with other trees of similar diameter. Twice more epiphyte/liana species were closely associated with *H. madagascariensis* (multipatt analysis, IndVal 0.31–0.92;  $p < 0.05$ ) compared to other phorophytes of similar diameter, and none were closely associated with other phorophytes of similar age. Finally, *Harungana madagascariensis* hosted more reproductive orchids than phorophytes of similar age and size, but the sizes of epiphytes and lianas did not differ significantly across phorophytes. *Harungana madagascariensis* therefore benefits native epiphytes and lianas, promoting their colonisation 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 native biodiversity is acutely threatened and where the benefits of cutting native pioneer trees like *H. madagascariensis* in

Submitted 11 July 2025  
Accepted 13 November 2025  
Published 19 December 2025

Corresponding author  
François M.M.P. Baguette,  
francois.baguette@umail.uom.ac.mu

Academic editor  
Alastair Potts

Additional Information and  
Declarations can be found on  
page 18

DOI 10.7717/peerj.20520

© Copyright  
2025 Baguette et al.

Distributed under  
Creative Commons CC-BY 4.0

## OPEN ACCESS

biodiversity conservation projects remain unproven, our study provides new evidence that the detrimental effects of this management extend beyond the destruction of the native pioneer trees, to also severely hinder the restoration of native epiphyte and liana species. Furthermore, our study underscores how native pioneer trees can help foster the conservation of typically neglected native plant guilds, and the improbable need for stressing that evidence, and not hypotheses, should drive conservation policy.

**Subjects** Conservation Biology, Ecology, Plant Science, Natural Resource Management, Forestry

**Keywords** Biodiversity conservation, Ecological restoration, Ecological succession, Ecosystem dynamic, Facilitation, Heliophyte, Mauritius, Orchids, Restoration policy

## 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 are particularly impacted by this situation as they host roughly half of the species recognized as threatened in any of the International Union for Conservation of Nature (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 (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; United Nations, 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 other growth forms have 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; Garcia et al., 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 have 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, epiphytes remain understudied (Zotz, 2016; Krömer & Batke, 2025; Sousa da Silva, Freitag Kramer & Zwiener, 2025), especially 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-Higueta et al., 2024).

We studied native epiphyte and liana communities growing in tropical forest areas that are currently undergoing ecological restoration for biodiversity conservation after 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 often leaves fairly large gaps after the control of invasive plants (Florens & Baider, 2013). In particular, we assessed the epiphyte and liana communities growing on a widespread native pioneer tree species (*Harungana madagascariensis* Lam. (Hypericaceae)) (Bojer, 1837; Baker, 1877; Robson & Stevens, 1980; Botanic Gardens Conservation International (BGCI) & IUCN SSC Global Tree Specialist Group, 2019) and other neighbouring native trees. We selected *H. madagascariensis* as focal species because this tree grows best following the control of woody invasive alien plants like the Strawberry guava (*Psidium cattleianum*), and is the main native tree species that grow in early stages of secondary ecological succession. However, it is commonly controlled by conservation managers who then typically plant other native species in its place (Florens & Baider, 2013; C. Baider, F.B. Vincent Florens, pers. obs., 2003–2025). More specifically, we compared the potential of *H. madagascariensis* to act as a phorophyte for native epiphytes and lianas relative to other native tree species of (1) comparable diameter, and (2) comparable age to the *H. madagascariensis* to gauge the wider effects of the policy of cutting back the native pioneer tree species from areas undergoing ecological restoration for biodiversity conservation. We investigated three questions in particular to explore the importance of *H. madagascariensis* for native epiphyte and liana communities: (a) How does *H. madagascariensis* compare as a phorophyte with other naturally growing native trees of comparable sizes that belong to species that are commonly planted where *H. madagascariensis* is cut? (b) How does the phorophytic function of *H. madagascariensis* compare with that of other naturally growing trees of comparable age belonging to species

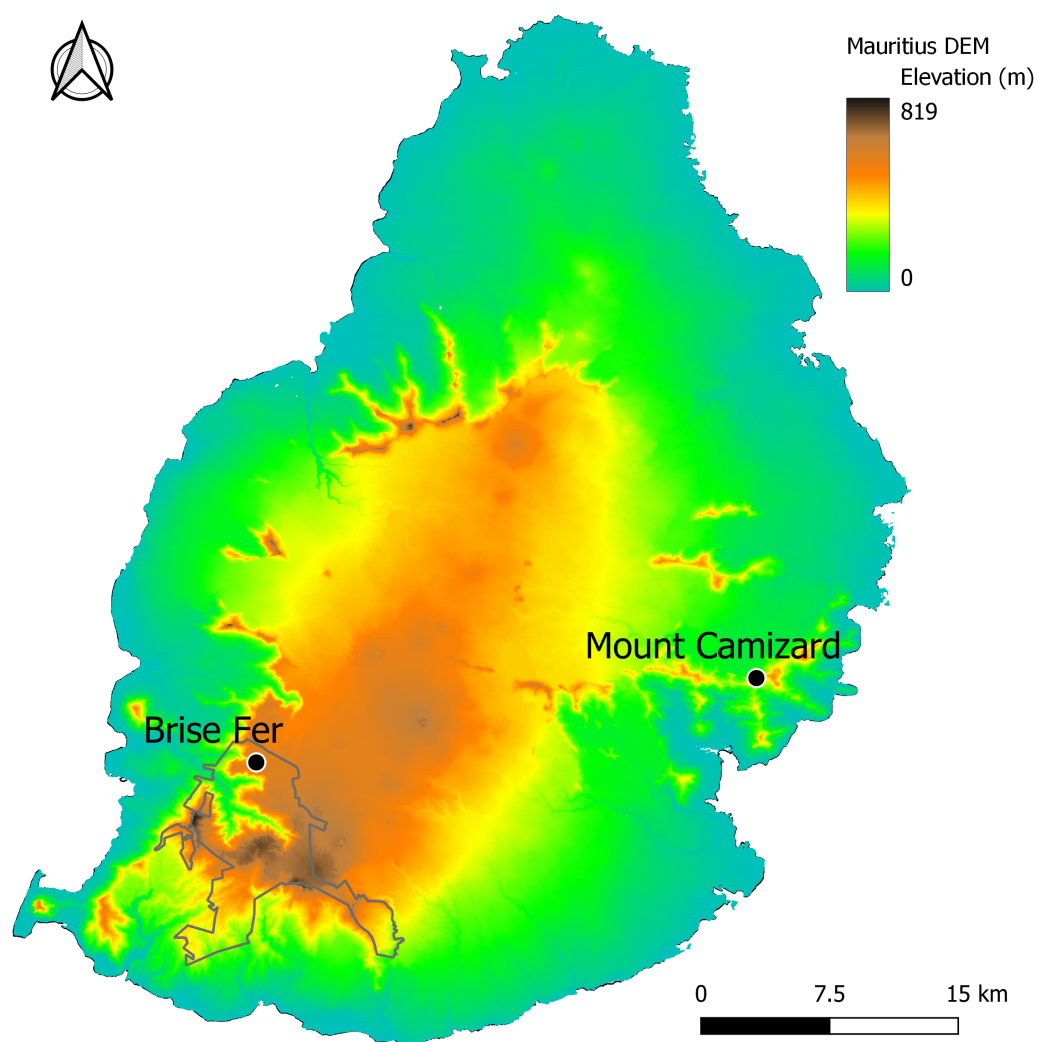
that are typically planted after *H. madagascariensis* is removed? (c) Do proxies of fitness of epiphytes and lianas vary depending on whether they grow on *H. madagascariensis* or other phorophytes of comparable ages and of comparable sizes?

## MATERIALS & METHODS

### Study sites

Mauritius is a tropical volcanic island located around 900 km east of Madagascar. Centred on 20°15'S and 57°35'E, it is part of the Mascarene Archipelago and falls within the Madagascar and Indian Ocean Islands biodiversity hotspot (Myers *et al.*, 2000). The island is about 1,865 km<sup>2</sup>, with a maximum elevation of 828 m. Mean annual rainfall ranges from 800 mm along the leeward coast to 4,000 mm in the central uplands, with an average annual temperature of 22 °C (Staub, Stevens & Waylen, 2014). Since human colonisation in 1638, extensive habitat transformation has reduced the island's native vegetation to ~82 km<sup>2</sup> or 4.4% of its original extent (Hammond *et al.*, 2015), which nevertheless continues to support a high proportion of native species (Florens *et al.*, 2012). This native vegetation, however, survives as highly fragmented patches (Florens, 2013) that are increasingly dominated by alien woody species, particularly in the understorey (Florens *et al.*, 2016). Although started in the first half of the 20th century (Vaughan & Wiehe, 1941; Baider & Florens, 2025), attempts to restore native vegetation communities by controlling invasive alien plants were upscaled from around the mid-1980s (Strahm, 1993; Jones, 2008), and as of 2024, ~700 ha of native vegetation (~8.5% of all native remnants) is undergoing restoration in that way on the island (Republic of Mauritius, 2024).

Two of the forest areas undergoing ecological restoration for biodiversity conservation and known to host native epiphyte and liana communities (Fig. 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, Brise-Fer, occurs close to the higher elevational range of *H. madagascariensis* 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. There, weeding of invasive alien plants has been done in different phases for conservation management since 1986. We selected the largest area, weeded in 1996, for our sampling. 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. Surveys in the Black River Gorges National Park and Mount Camizard were conducted with permission from The National Parks and Conservation Services of the Ministry of Agro-Industry, Food Security, Blue Economy and Fisheries, and Mr. Owen L. Griffiths and Mrs. Mary-Ann Griffiths respectively.



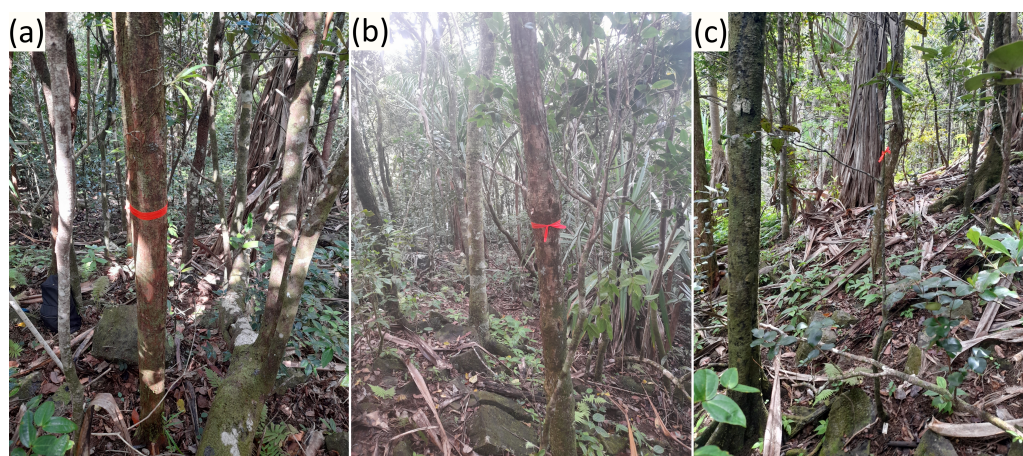
**Figure 1** The study sites of Brise Fer and Mount Camizard in Mauritius displayed on a digital elevation model (DEM) showing topographic variation. The Black River Gorges National Park is outlined. Mount Camizard is found within protected Mountain Reserves.

Full-size [DOI: 10.7717/peerj.20520/fig-1](https://doi.org/10.7717/peerj.20520/fig-1)

## Data collection

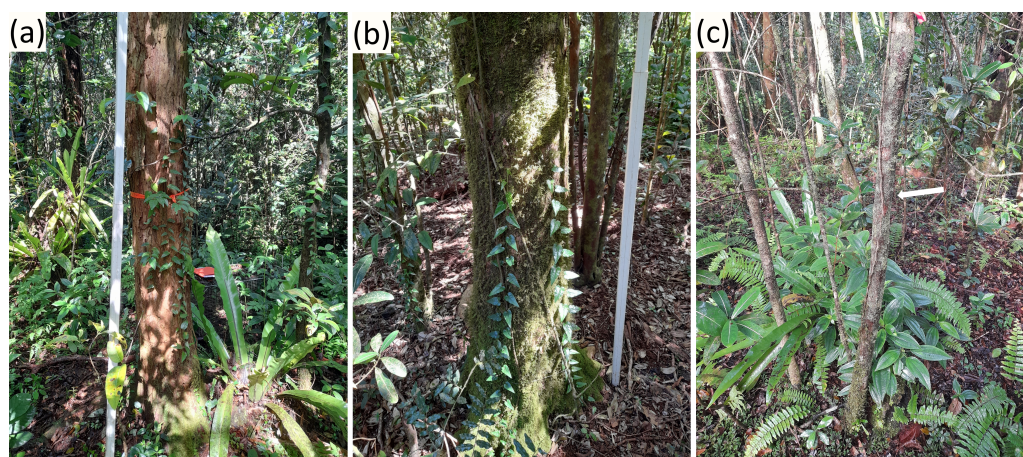
Naturally growing (non-planted) trees of *H. madagascariensis* (52 at Mount Camizard and 21 at Brise Fer) were randomly sampled along with the closest individual of another native tree species to each of them that was of (1) similar trunk diameter (measured at 1.3 m above ground, along the stem) and (2) similar age (Figs. 2 and 3). The decision to focus on individual trees rather than specific host species was in part guided by previous studies demonstrating that epiphyte assemblages are often more strongly influenced by tree-level structural attributes than by host identity (Zotz & Vollrath, 2003; Flores-Palacios & García-Franco, 2006; Komada et al., 2022), and that host specificity among vascular epiphytes and lianas is generally weak or absent (Garrido-Perez & Burnham, 2010; Wagner, Mendieta-Leiva & Zotz, 2015). The choice to include tree age in our analysis was guided





**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 distance) of another native species (*Euphorbia pyriformis*) 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 'Estimation of tree age' explains how similar ages were determined). Photos: François Baguette.

Full-size  DOI: 10.7717/peerj.20520/fig-2



**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 'Estimation of tree age' explains how similar ages were determined). Photos: François Baguette.

Full-size  DOI: 10.7717/peerj.20520/fig-3

by previous studies demonstrating the importance of including the dynamic of habitat-building trees in epiphyte studies (Merwin, Rentmeester & Nadkarni, 2003; Wagner & Zotz, 2020) and to ensure the validity of our comparisons between trees of different ecology and longevity. In Mount Camizard, each potential *H. madagascariensis* tree was selected using a coin-flip method, whereas at Brise Fer, trees were chosen from individuals previously recorded in a long-term monitoring plot of one hectare using random number attribution.

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, which served as the sampling units. For each of the 219 potential phorophytes, GPS coordinates were recorded (with GPSMap<sup>®</sup> 65, Garmin), the species identified, and its diameter at breast height (DBH) recorded. Plant reproductive status and size were used as proxies of epiphytes and lianas' fitness following Tremblay et al. (1998), Zhang, Nurvianto & Harrison (2010) and Wagner & Zott (2020). The reproductive status of each epiphyte and liana was recorded as either vegetative or reproductive (bearing flower buds, open flower, unripe fruit, ripe fruit or showing traces of fallen fruits for angiosperms and fertile fronds for pteridophytes). The number of leaves or fronds of each epiphyte, and the stem diameter of each liana, were recorded to assess plant size.

Vascular epiphytes and lianas were counted on all sampled trees from the ground, with the aid of an 8 × 42 pair of binoculars when necessary, and identified using identification keys from the regional Flora (Bossier et al., 1976–2023) and other relevant work (Hermans et al., 2025) (illustrations of selected species are provided in supplementary material (Fig. S1)). Identifications were validated by the second author, CB, and third author, FBVF, who are experts in Mauritius plant taxonomy. Sampled trees ranged from 1.3 m to 15.0 m in height, with *H. madagascariensis* reaching on average similar heights than other native trees of similar diameter (8.98 m and 8.36 m respectively). Trees of similar age were on average 3 m high. 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 the best long-term monitoring census data available for the island supplied by the Mauritius Herbarium and comprising ~19,000 individual native woody plants belonging to ~100 species from Brise Fer. It includes tree measurements from 2005, 2010 and 2022 (spanning a maximum of 17 years) collected in 3 ha permanent plots, which provided the most reliable results compared to the smaller datasets available (including from Mount Camizard) that were collected during a shorter time period and



that would therefore include a larger margin of error. Furthermore, the similarity in climate and forest structure and composition between the two sites and the extremely low growth rate of the studied species (0.15 cm/year on average, see [Table S1](#)) limits the potential bias that the lack of long-term data from Mount Camizard could have on our results. We calculated the annual DBH increments of *H. madagascariensis* and of the ten most important species along which it grows in both study sites using two segments of stem diameter monitoring (from 2005–2010 and from 2010–2023). The ten most important species were determined following Importance Values from [Florens et al. \(2012\)](#). 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 ([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 on the 219 sampled potential phorophytes 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” ( $n = 3$ ), *Polystachia mauritiana* and *Polystachia virescens* grouped in “*Polystachia mauritiana* s.l. Group” ( $n = 119$ ), 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 comprised the respective taxa classified as morphospecies, with 2,229 records of epiphytes and lianas collected from 219 sampled phorophytes.

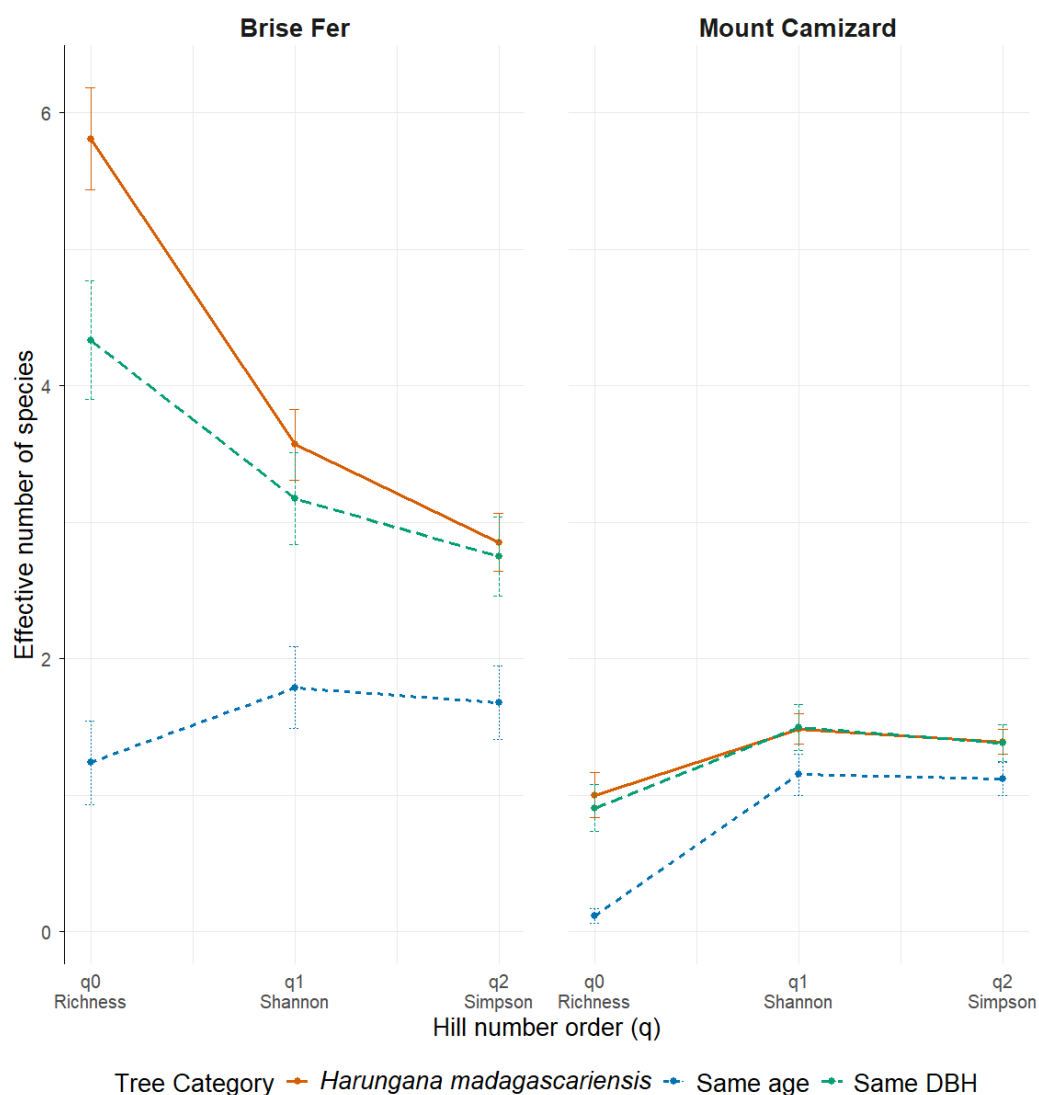
We used R version 4.4.1 ([R Core Team, 2024](#)) to do all statistical analysis and graphs. Hill numbers were calculated per tree across phorophyte category and site (orders  $q = 0, 1, 2$ ) using the R package ‘HillR’ ([Li, 2018](#)) to capture species richness, effective number of common species (Shannon), and dominant species (Simpson) ([Hill, 1973](#); [Chao, Chiu](#)

✂ Jost, 2014). Structural variables such as epiphyte abundance (N, epiphytes tree<sup>-1</sup>), and species richness were also computed. We assessed differences in epiphyte species richness and abundance among tree categories (defined by diameter at breast height) using generalized linear models (GLMs), with tree category as the main predictor, and site as a covariate. Counts of epiphytes were explored for overdispersion and excess zeros using residual diagnostics using ‘DHARMA’ package (Hartig, 2024). Species richness was analysed using Quasi-Poisson GLMs, while abundance was modelled using zero-inflated negative binomial (ZINB) GLMs to account for overdispersion and excess zeros. Model fit was evaluated using pseudo  $R^2$  ( $1 - \text{residual deviance}/\text{null deviance}$ ) (Zuur et al., 2009). *Post hoc* pairwise comparisons between tree categories were performed using estimated marginal means (EMMs) with Tukey adjustment via the ‘emmeans’ package (Lenth, 2025). To evaluate differences in phorophyte suitability for epiphytes, total abundance and total species richness of all epiphyte and liana individuals per tree were used as response variables. 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). In addition, we chose the Orchidaceae, the most abundant epiphyte family recorded (1,181 individuals), to compare the abundance of reproductive individuals (N, reproductive orchids tree<sup>-1</sup>) growing on *H. madagascariensis* and other phorophytes of similar age and size. The most abundant orchid species, namely *Angraecum pectinatum* (523 individuals), and the most abundant species of liana recorded, namely *Piper borbonense* (226 individuals) were used to compare the sizes of epiphytes and lianas growing on the different phorophytes. Extreme values of reproducing orchid abundance and plant size were removed prior to analysis to reduce the influence of extreme outliers. The distribution of reproductive status and plant size data was assessed using the Shapiro–Wilk test. As the data deviated from normality, non-parametric tests were applied in subsequent analyses. Reproductive orchid abundance and the size of epiphyte/liana 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).

## RESULTS

Epiphytes and lianas were recorded on 116 of 219 (53%) sampled potential phorophytes, including very small ones (DBH ~1cm). 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 (1,973 individuals) and five liana species (256 individuals) (Table S2). Overall, half (14) of the species occurred as <10 individuals each, and the other half was represented by >2,000 individuals (Table S3). The most abundant species was the orchid *Angraecum pectinatum*, which accounted for

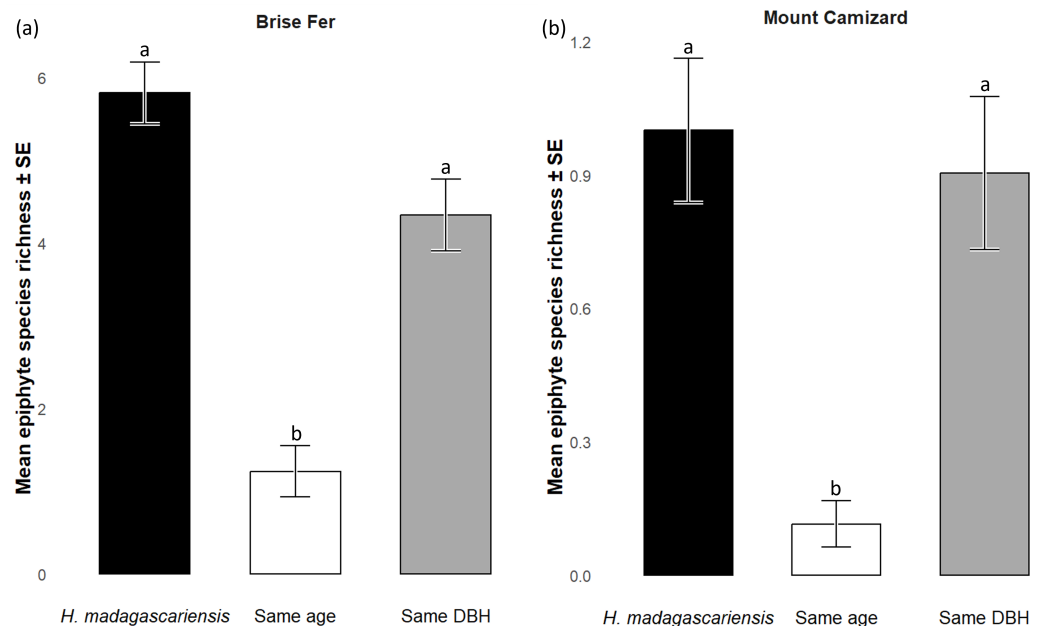


**Figure 4** Effective number of species (Hill numbers) per tree across phorophyte category and site. q0 represents the mean species richness, q1 the mean effective number of equally common species, and q2 the mean effective number of dominant species. 'Same DBH' stands for other potential native phorophytes 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.

Full-size [DOI: 10.7717/peerj.20520/fig-4](https://doi.org/10.7717/peerj.20520/fig-4)

23.5% of all epiphytes. Other *Angraecum* species grouped into '*Angraecum* spp.' and the fern *Microsorium punctatum* were the other most frequent epiphytes (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 (Table S5).

Generally, *H. madagascariensis* hosted a higher diversity of epiphyte and liana than other native trees of (1) similar age and (2) similar size, a situation more pronounced in Brise Fer than in Mount Camizard (Fig. 4). Tree category significantly affected epiphyte species

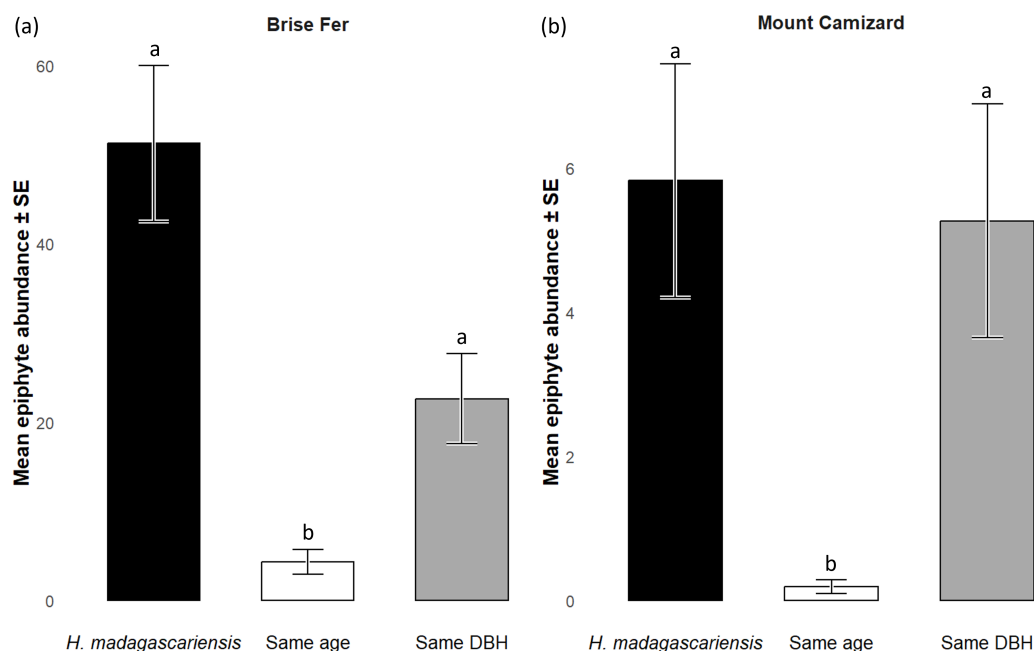


**Figure 5** Species richness ( $\pm$  SE) on *Harungana madagascariensis* and other potential phorophytes in (A) Brise Fer and (B) Mount Camizard where native forests are undergoing ecological restoration after weeding of invasive alien plants. ‘Same DBH’ stands for other potential native phorophytes 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. Different letters above bars indicate significant differences among categories, whereas bars sharing the same letter are not significantly different.

Full-size [DOI: 10.7717/peerj.20520/fig-5](https://doi.org/10.7717/peerj.20520/fig-5)

richness ( $\chi^2 = 90.403$ ,  $df = 2$ ,  $p < 0.05$ ), as well as site ( $\chi^2 = 192.156$ ,  $df = 1$ ,  $p < 0.05$ ). *Post-hoc* estimated marginal means (emmeans) indicated that *H. madagascariensis* hosted significantly more epiphyte species than trees of similar age ( $p < 0.05$ ), but differences with trees of similar diameter were not significant ( $p > 0.05$ ) (Fig. 5). Epiphyte abundance was also significantly affected by tree categories ( $\chi^2 = 92.243$ ,  $df = 2$ ,  $p < 0.05$ ), as well as site ( $\chi^2 = 65.177$ ,  $df = 1$ ,  $p < 0.05$ ). *Harungana madagascariensis* hosted significantly more epiphytes than trees of similar age ( $p < 0.05$ ) but differences with trees of similar diameter were not significant ( $p > 0.05$ ) (Fig. 6).

In Brise Fer, six out of 27 sampled species were significantly associated with *H. madagascariensis* compared to only three with other trees of similar diameter. Furthermore, five species were significantly associated with *H. madagascariensis* and trees of similar diameter compared to only one being associated with the combination of *H. madagascariensis*, trees of similar diameter, and trees of similar age (Table 1). No significant association were found in Mount Camizard. In terms of fitness, there was a significant difference in abundance of reproductive orchid ( $\chi^2 = 70.52$ ,  $df = 5$ ,  $p < 0.05$ ) among phorophytes across both sites, with *post hoc* Dunn’s tests revealing that *H. madagascariensis* hosted significantly more reproductive orchid than other native phorophyte of (1) similar age and (2) similar size in Brise Fer ( $p < 0.05$  respectively) but no



**Figure 6** Abundances of native epiphytes ( $\pm$  SE) on *Harungana madagascariensis* and other phorophytes in (A) Brise Fer and (B) Mount Camizard where native forests are under ecological restoration after weeding of invasive alien plants. ‘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. Different letters above bars indicate significant differences among categories, whereas bars sharing the same letter are not significantly different.

Full-size [DOI: 10.7717/peerj.20520/fig-6](https://doi.org/10.7717/peerj.20520/fig-6)

significant difference was observed in Mount Camizard (Fig. 7). There was no significant difference of size (in terms of number of leaves) for *Angraecum pectinatum* ( $\chi^2 = 4.43$ ,  $df = 4$ ,  $p > 0.05$ ) among phorophytes across both sites. With regards to lianas, there was no significant difference of size (in terms of stem DBH) for *Piper borbonense* among phorophytes in Brise Fer ( $\chi^2 = 1.11$ ,  $df = 2$ ,  $p > 0.05$ ).

## DISCUSSION

### Ecological implications

The native pioneer tree *H. madagascariensis* which grows naturally best in disturbed areas, precisely where other potential phorophytes are rare, constitutes a 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* can support in just two to three decades of its growth, are comparable to those assembling on often much-slower growing and much older, often multi-centennial trees of comparable size to *H. madagascariensis*. This further stresses the importance of *H. madagascariensis* for epiphytes and lianas establishment following a disturbance, reinforcing previous findings showing that tree age and size strongly influence phorophytic function in various ways

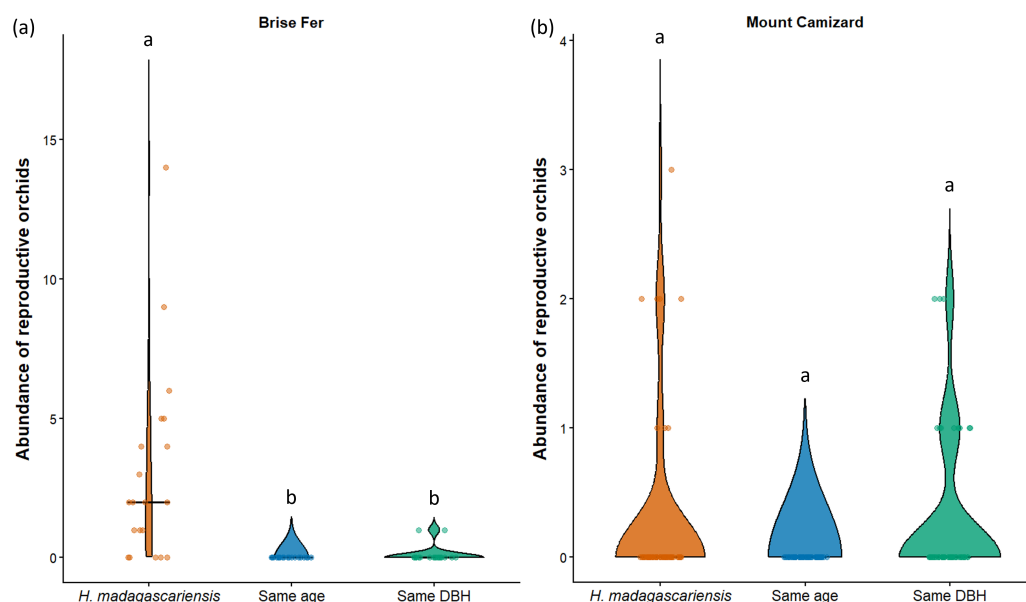


**Table 1** Native epiphytes and lianas significantly associated with potential phorophytes in Brise Fer where native forest is undergoing ecological restoration after weeding of invasive alien plants. ‘Harungana’ stands for *Harungana madagascariensis*; ‘Same DBH’ stands for other potential native phorophytes 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)	IndVal	pvalue
<i>Angraecum pectinatum</i>	Brise Fer	<i>Harungana</i>	0.919	<0.05
<i>Cnestis polyphylla</i>	Brise Fer	<i>Harungana</i>	0.612	<0.05
<i>Nephrolepis cordifolia</i>	Brise Fer	<i>Harungana</i>	0.593	<0.05
<i>Angraecum mauritianum</i>	Brise Fer	<i>Harungana</i>	0.504	<0.05
<i>Polystachia mauritiana</i> s.l.	Brise Fer	<i>Harungana</i>	0.430	<0.05
<i>Bulbophyllum</i> spp.	Brise Fer	<i>Harungana</i>	0.309	<0.05
<i>Asplenium nidus</i> var. <i>nidus</i>	Brise Fer	Same DBH	0.412	<0.05
<i>Urera acuminata</i>	Brise Fer	Same DBH	0.404	<0.05
Hymenophyllaceae	Brise Fer	Same DBH	0.378	<0.05
<i>Piper borbonense</i>	Brise Fer	<i>Harungana</i> + Same DBH	0.748	<0.05
<i>Microsorium punctatum</i>	Brise Fer	<i>Harungana</i> + Same DBH	0.614	<0.05
<i>Selaginella</i> spp.	Brise Fer	<i>Harungana</i> + Same DBH	0.488	<0.05
<i>Nephrolepis biserrata</i>	Brise Fer	<i>Harungana</i> + Same DBH	0.408	<0.05
<i>Rumohra adiantiformis</i>	Brise Fer	<i>Harungana</i> + Same DBH	0.345	<0.05
<i>Lepisorus spicata</i>	Brise Fer	<i>Harungana</i> + Same DBH + Same age	0.647	<0.05

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 (as assessed using commonly used proxies of fitness) can be substantially superior for those establishing on *H. madagascariensis* compared to other potential phorophytes close by. This double superiority as phorophyte (hosting greater diversity of epiphytes and fostering their higher fitness) 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 relatively thick and spongy compared to most other native phorophytes. Such a bark retains moisture for longer periods and probably provide more nutrients, thereby promoting epiphyte establishment and their faster growth and maturation compared to most other Mauritian native trees. 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 et al., 2008](#); [Einzmann et al., 2015](#); [Besl et al., 2023](#); [Pie et al., 2023](#); [Wysocki et al., 2024](#)), and lianas ([Putz, 1984](#); [Letcher, 2015](#); [Schnitzer, 2015](#)). However, it is 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



**Figure 7** Abundance of reproductive orchids on *Harungana madagascariensis* and other phorophytes at the two sampled sites: (A) Brise Fer and (B) Mount Camizard, where native forests are undergoing ecological restoration. Violin plots show the distribution density of orchid abundance per phorophyte category. The central horizontal lines indicate the medians, and individual observations are shown as jittered points. '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. Different letters above bars indicate significant differences among categories, whereas bars sharing the same letter are not significantly different.

Full-size [DOI: 10.7717/peerj.20520/fig-7](https://doi.org/10.7717/peerj.20520/fig-7)

greater species richness and abundance of epiphytes and lianas are 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*, compared with only 10.7% ( $N = 3$ ) with trees of the same size. These proportions are consistent with previous studies reporting that only a minority (15–30%) of epiphyte species show non-random host associations (Laube & Zotz, 2006; Wagner, Mendieta-Leiva & Zotz, 2015; Wagner, Wanek & Zotz, 2021), but further stress the important role that *H. madagascariensis* plays in supporting specific native epiphyte and liana species compared to other native trees that grow in conditions closest to those where *H. madagascariensis* grows. Therefore, *H. madagascariensis* trees provide a suitable habitat for epiphytes and lianas relatively early following a disturbance. Importantly, the patterns observed in Mauritius are likely applicable across the extensive native range of *H. madagascariensis* (over 12 million km<sup>2</sup>; Baguette, Baider & Florens, 2025), wherever the species occurs within the natural distribution of epiphytic orchids, ferns, and lianas, given the broad similarity in the ecological niches and requirements of these plant guilds.

## Implications for ecological restoration and biodiversity conservation

The extreme invasion of Mauritius native forests by alien plants (Florens *et al.*, 2016) has driven a high rate of native tree mortality (Florens *et al.*, 2017) including some of the largest canopy species (Baider & Florens, 2006). As a result, when alien plants are removed, scanty native trees often remain to foster ecological restoration 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 does not suppress native epiphytes and lianas but on the contrary, is highly beneficial to native epiphytes species richness, abundance and fitness, more so than other species that grow alongside it. Yet, all major conservation practitioners of Mauritius have been, at one point or another, cutting back large numbers of *H. madagascariensis* in areas undergoing ecological restoration for biodiversity conservation (Fig. 8), contra best available evidence of its benefits for ecological restoration (Florens & Baider, 2013; Baguette, Baider & Florens, 2025), and without evidence of its presumed negative impact on native biodiversity. Here, we show that in addition to such practices hindering restoration progress of woody plant cover and fostering re-invasion by invasive alien plants (Florens & Baider, 2013), it also slows broader ecosystem recovery by: (1) removing native structural epiphytes already established on *H. madagascariensis*; and (2) reducing future recruitment of structural epiphytes, as alternative phorophytes generally provide lower-quality habitat than *H. madagascariensis*.

Among the species significantly associated 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 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.



**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* (whose growth was being monitored – note metal tag) observed in a different restoration area managed by a different organization located in Ferney in Mauritius. Photos: François Baguette.

Full-size DOI: 10.7717/peerj.20520/fig-8

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 fleshy fruits eaten by and benefiting native vertebrates (Heinen et al., 2023) including the threatened endemic Mauritius Bulbul (*Hypsipetes olivaceus*), also recently found to be a key pollinator of a fast declining endemic plant (Bissessur et al., 2019), thereby stressing on the judiciousness of considering broader ecological interconnectivity when devising ecological restoration policy. Mauritius is the only place within *H. madagascariensis*' ~12 million km<sup>2</sup> 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 to reallocate scarce conservation resources away from management that harm native biodiversity, and provide them additional evidence of the benefits that pioneer species can bring for ecological restoration.

### Policy implications

Mauritius is globally well-known for some resounding conservation successes notably of birds (Sodhi et al., 2011) that were enabled by painstaking evidence-based approaches



(Jones & Swinnerton, 1997; Swinnerton et al., 2004; Jones, 2008). More recently, however, some management of threatened species by conservation practitioners were applied that contradicted best available evidence (Florens, 2015; Florens, 2016), failed to reach the intended objectives and instead worsened the situation for threatened native biodiversity (Florens & Baider, 2019). A similar situation also emerged concerning ecological restoration for biodiversity conservation of the island's most diverse native ecosystems whereby a policy of cutting back native plants was implemented. Indeed, following control of invasive alien plants, many native plants like woody lianas, strangler figs (FBV Florens, pers. obs., 2005 to present) and native pioneer trees like *H. madagascariensis* (Florens & Baider, 2013) that regenerated, were removed.

Mauritius was recently found to be the only place in the 12 or so million km<sup>2</sup> of native range of *H. madagascariensis* where such a policy is applied (Baguette, Baider & Florens, 2025). By cutting back *H. madagascariensis*, the policy, at a cost, sets back restoration progress of the native woody plant community and increases the re-invasion by alien plants, hence the costs of maintenance weeding (Florens & Baider, 2013). While this policy has been supported and/or implemented by government conservation services and most of the main local conservation NGOs for over three decades, its proponents have in that time not yet been able to present evidence that it somehow benefits native or threatened biodiversity. In this context, we now present novel evidence that the policy of conservation managers cutting back native pioneer trees from areas undergoing ecological restoration, is in fact harmful to the native biodiversity of epiphytes and lianas in addition to the native trees themselves in addition to diverting scarce conservation resources elsewhere from where it is proven to be impactful, such as the control of invasive alien plants (Monty Florens & Baider, 2013; Krivek et al., 2020). We therefore recommend that the enduring practice of cutting or lopping branches of *H. madagascariensis* be stopped and be replaced instead by planting of the species where it can grow but where seed bank or natural germination is lacking. Some encouraging signs have started appearing with the first conservation organisation shifting its policy in 2025 from cutting to planting the species (Ferney Ltd., 2025).

## CONCLUSION

Using the widely distributed *Harungana madagascariensis* as a model, we show that pioneer trees, although relatively short-lived, 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 constitute a particularly diverse but largely overlooked component of native plant diversity despite the fact that they comprise many rare and threatened species, and ecologically important ones too, notably for some endemic threatened frugivorous birds. We show that pioneer trees can greatly support conservation of native epiphytes and lianas, and



highlight concerns that local conservation efforts are being undermined when native pioneer species such as *H. madagascariensis* are actively removed from areas undergoing ecological restoration. A shift from the current hypothesis-based to an evidence-based conservation policy on that matter is therefore warranted, to promote faster and better ecological restoration, and optimize the use of conservation resources that in turn would enable a much needed upscaling of restoration efforts on the island.

## ACKNOWLEDGEMENTS

The authors are grateful to the University of Mauritius for its administrative support. We also thank Teesha Baboorun Baguette, Geetika Bhandra, Dr. Prishnee Bissessur, Yogishah Ashmi Bunsy, Raphaël Merven, and Ghanishta Seeburrun for their substantial assistance in data collection. We also thank Kenji Yip Tong and Dr. Peter Horchler for their assistance and advice with some data analyses. Finally, we are grateful for the particularly useful reviews from Dr. Jean M. Freitag Kramer, Dr. Edward Entalai Besi, and Dr. Jorge A. Meave, as well as the editorial work of Dr. Alastair Potts.

## ADDITIONAL INFORMATION AND DECLARATIONS

### Funding

This project was supported by the Agence Française de Développement (AFD) under the VARUNA Biodiversité programme (Project 22-SB3004) managed by Expertise France. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

### Grant Disclosures

The following grant information was disclosed by the authors:  
Agence Française de Développement (AFD) under the VARUNA Biodiversité programme: Project 22-SB3004.

### Competing Interests

The authors declare there are no competing interests.

### Author Contributions

- François M.M.P. Baguette conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the article, and approved the final draft.
- Cláudia Baidier conceived and designed the experiments, performed the experiments, analyzed the data, authored or reviewed drafts of the article, and approved the final draft.
- François Benjamin Vincent Florens conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the article, and approved the final draft.

### Data Availability

The following information was supplied regarding data availability:  
The data is available in the [Supplementary Files](#).

## Supplemental Information

Supplemental information for this article can be found online at <http://dx.doi.org/10.7717/peerj.20520#supplemental-information>.

## REFERENCES

- Ah-Peng C, Cardoso AW, Flores O, West A, Wilding N, Strasberg D, Hedderson TAJ. 2017. The role of epiphytic bryophytes in interception, storage, and the regulated release of atmospheric moisture in a tropical montane cloud forest. *Journal of Hydrology* 548:665–673 DOI 10.1016/j.jhydrol.2017.03.043.
- Annaselvam J, Parthasarathy N. 2001. Diversity and distribution of herbaceous vascular epiphytes in a tropical evergreen forest at Varagalaia, Western Ghats, India. *Biodiversity & Conservation* 10:317–329 DOI 10.1023/A:1016670621331.
- Ashton MS, Gunatilleke CVS, Singhakumara BMP, Gunatilleke IAUN. 2001. Restoration pathways for rain forest in southwest Sri Lanka: a review of concepts and models. *New Directions in Tropical Forest Research* 154:409–430 DOI 10.1016/S0378-1127(01)00512-6.
- Baguette FM, Baider C, Florens FBV. 2025. A scoping review of tropical pioneer trees' roles for restoration and conservation management: *Harungana madagascariensis* (Hypericaceae) a widespread African species as a model. *PeerJ* 13:e19458 DOI 10.7717/peerj.19458.
- Baider C, Florens FBV. 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: Laurance W, Peres C, eds. *Emerging threats to tropical forests*. Chicago: Chicago University Press, 199–214.
- Baider C, Florens FBV. 2011. Control of invasive alien weeds averts imminent plant extinction. *Biological Invasions* 13:2641–2646 DOI 10.1007/s10530-011-9980-3.
- Baider C, Florens FBV. 2022. Diversity, ecology, and conservation of Mauritius orchids. In: Mérillon J-M, Kodja H, eds. *Orchids phytochemistry, biology and horticulture: fundamentals and applications*. Cham: Springer International Publishing, 107–133 DOI 10.1007/978-3-030-38392-3\_29.
- Baider C, Florens FBV. 2025. Le botaniste et écologiste. In: *Octave wiehe—un mauricien visionnaire*. Mauritius: Precigraph, 65–82.
- Baider C, Florens F, Rakotoarivelo F, Bossier J, Paillet T. 2012. Two new records of *Jumellea* (Orchidaceae) for Mauritius (Mascarene Islands) and their conservation status. *Phytotaxa* 52:21–28 DOI 10.11646/phytotaxa.52.1.3.
- Baillie J, Hilton-Taylor C, Stuart SN. 2004. 2004 IUCN Red list of threatened species: a global species assessment. Gland, Switzerland and Cambridge: IUCN.
- Baker JG. 1877. *Flora of Mauritius and the Seychelles: a description of the flowering plants and ferns of those islands*. London: L. Reeve and Co.
- Barnosky AD, Matzke N, Tomiya S, Wogan GOU, Swartz B, Quental TB, Marshall C, McGuire JL, Lindsey EL, Maguire KC, Mersey B, Ferrer EA. 2011. Has the Earth's sixth mass extinction already arrived? *Nature* 471:51–57 DOI 10.1038/nature09678.

- Bernal R, Valverde T, Hernández-Rosas L. 2005.** Habitat preference of the epiphyte *Tillandsia recurvata* (Bromeliaceae) in a semi-desert environment in Central Mexico. *Canadian Journal of Botany* **83**:1238–1247 DOI [10.1139/b05-076](https://doi.org/10.1139/b05-076).
- Besi EE, Mustafa M, Yong CSY, Go R. 2023.** Habitat ecology, structure influence diversity, and host-species associations of wild orchids in undisturbed and disturbed forests in Peninsular Malaysia. *Forests* **14**:544 DOI [10.3390/f14030544](https://doi.org/10.3390/f14030544).
- Bissessur P, Bunsy Y, Baider C, Florens FBV. 2019.** Non-intrusive systematic study reveals mutualistic interactions between threatened island endemic species and points to more impactful conservation. *Journal for Nature Conservation* **49**:108–117 DOI [10.1016/j.jnc.2019.04.002](https://doi.org/10.1016/j.jnc.2019.04.002).
- Boechat RF, Da Silva BF, Nunes-Freitas AF. 2019.** Bird-epiphyte interactions in three Atlantic Forest environments in southeastern Brazil. *Revista Brasileira de Ornitologia* **27**:108–114 DOI [10.1007/BF03544454](https://doi.org/10.1007/BF03544454).
- Bojer W. 1837.** *Hortus Mauritianus, or, an enumeration of exotic and native plants that grow in Mauritius: arranged according to the natural method.* Mauritius: Printed by Aimé Mamarot and Company (In French).
- Borges PAV, Gabriel R, Fattorini S. 2019.** Biodiversity erosion: causes and consequences. In: Leal Filho W, Azul AM, Brandli L, Özuyar pg, Wall T, eds. *Life on land.* Cham: Springer International Publishing, 1–10 DOI [10.1007/978-3-319-71065-5\\_78-1](https://doi.org/10.1007/978-3-319-71065-5_78-1).
- Bosser J, Cadet T, Guého J, Julien HR, Marais W. 1976–2023.** *Flore des Mascareignes—La Réunion, Maurice, Rodrigues.* Port Louis, Mauritius: MSIRI/ORSTOM-IRD/Kew (In French).
- Botanic Gardens Conservation International (BGCI), IUCN SSC Global Tree Specialist Group. 2019.** *Harungana madagascariensis.* 2019: e.T62019179A146204258 DOI [10.2305/IUCN.UK.2019-2.RLTS.T62019179A146204258.en](https://doi.org/10.2305/IUCN.UK.2019-2.RLTS.T62019179A146204258.en).
- Callaway RM, Reinhart KO, Moore GW, Moore DJ, Pennings SC. 2002.** Epiphyte host preferences and host traits: mechanisms for species-specific interactions. *Oecologia* **132**:221–230 DOI [10.1007/s00442-002-0943-3](https://doi.org/10.1007/s00442-002-0943-3).
- Campbell MJ, Edwards W, Odell E, Mohandass D, Laurance WF. 2015.** Can lianas assist in rainforest restoration? *Tropical Conservation Science* **8**:257–273 DOI [10.1177/194008291500800119](https://doi.org/10.1177/194008291500800119).
- Carmona-Higueta MJ, Mendieta-Leiva G, Gómez-Díaz JA, Villalobos F, Ramos FN, Elias JPC, Jiménez-López DA, Zuluaga A, Holst B, Kessler M, Mathieu G, Zizka A, Zotz G, Krömer T. 2024.** Conservation status of vascular epiphytes in the neotropics. *Biodiversity and Conservation* **33**:51–71 DOI [10.1007/s10531-023-02730-8](https://doi.org/10.1007/s10531-023-02730-8).
- Cascante Marín A, Wolf JHD, Oostermeijer JGB, Den Nijs JCM. 2008.** Establishment of epiphytic bromeliads in successional tropical premontane forests in Costa Rica. *Biotropica* **40**:441–448 DOI [10.1111/j.1744-7429.2008.00403.x](https://doi.org/10.1111/j.1744-7429.2008.00403.x).
- Catling PM, Lefkovitch LP. 1989.** Associations of vascular epiphytes in a Guatemalan Cloud Forest. *Biotropica* **21**:35–40 DOI [10.2307/2388439](https://doi.org/10.2307/2388439).
- Caujapé-Castells J, Tye A, Crawford DJ, Santos-Guerra A, Sakai A, Beaver K, Lobin W, Florens FBV, Moura M, Jardim R, Gómes I, Kueffer C. 2010.** Conservation

- of oceanic island floras: present and future global challenges. *Perspectives in Plant Ecology, Evolution and Systematics* **12**:107–129 DOI [10.1016/j.ppees.2009.10.001](https://doi.org/10.1016/j.ppees.2009.10.001).
- CBD. 2011.** Conference of the parties decision X/2: strategic plan for biodiversity, 2011–2020. *Convention on Biological Diversity*.
- Ceballos SJ. 2020.** Vascular epiphyte communities in secondary and mature forests of a subtropical montane area. *Acta Oecologica* **105**:103571 DOI [10.1016/j.actao.2020.103571](https://doi.org/10.1016/j.actao.2020.103571).
- Chao A, Chiu C-H, Jost L. 2014.** Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through hill numbers. *Annual Review of Ecology, Evolution, and Systematics* **45**:297–324 DOI [10.1146/annurev-ecolsys-120213-091540](https://doi.org/10.1146/annurev-ecolsys-120213-091540).
- Clark KL, Nadkarni NM, Gholz HL. 1998.** Growth, net production, litter decomposition, and net nitrogen accumulation by epiphytic bryophytes in a tropical montane forest. *Biotropica* **30**:12–23 DOI [10.1111/j.1744-7429.1998.tb00365.x](https://doi.org/10.1111/j.1744-7429.1998.tb00365.x).
- De Cáceres M, Legendre P, Moretti M. 2010.** Improving indicator species analysis by combining groups of sites. *Oikos* **119**:1674–1684 DOI [10.1111/j.1600-0706.2010.18334.x](https://doi.org/10.1111/j.1600-0706.2010.18334.x).
- Dinno A. 2024.** Dunn’s test of multiple comparisons using rank sums.
- Duellman WE. 1988.** Patterns of species diversity in anuran amphibians in the American tropics. *Annals of the Missouri Botanical Garden* **75**:79–104 DOI [10.2307/2399467](https://doi.org/10.2307/2399467).
- Dufrène M, Legendre P. 1997.** Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* **67**:345–366 DOI [10.1890/0012-9615\(1997\)067\[0345:SAIST\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0345:SAIST]2.0.CO;2).
- Einzmann HJR, Beyschlag J, Hofhansl F, Wanek W, Zotz G. 2015.** Host tree phenology affects vascular epiphytes at the physiological, demographic and community level. *AoB PLANTS* **7**:plu073 DOI [10.1093/aobpla/plu073](https://doi.org/10.1093/aobpla/plu073).
- Ferney Ltd. 2025.** Building climate resilience in the Nyon river watershed. Mauritius: Ferney Ltd.
- Florens FBV. 2013.** Conservation in Mauritius and Rodrigues: challenges and achievements from two ecologically devastated oceanic islands. In: Raven PH, Sodhi NS, Gibson L, eds. *Conservation Biology. Voices from the tropics*. Oxford: John Wiley & Sons, Ltd., 40–50 DOI [10.1002/9781118679838.ch6](https://doi.org/10.1002/9781118679838.ch6).
- Florens FBV. 2014.** Research no matter the risks? A reply to Boura et al. *Trends in Ecology & Evolution* **29**:134–135 DOI [10.1016/j.tree.2014.01.006](https://doi.org/10.1016/j.tree.2014.01.006).
- Florens FBV. 2015.** Flying foxes face cull despite evidence. *Science* **350**:1325–1326 DOI [10.1126/science.350.6266.1325-a](https://doi.org/10.1126/science.350.6266.1325-a).
- Florens FBV. 2016.** Biodiversity law: mauritius culls threatened fruit bats. *Nature* **530**:33–33 DOI [10.1038/530033a](https://doi.org/10.1038/530033a).
- Florens FBV, Baider C. 2013.** 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](https://doi.org/10.1111/j.1526-100X.2012.00920.x).

- Florens FBV, Baider C. 2019.** Mass-culling of a threatened island flying fox species failed to increase fruit growers' profits and revealed gaps to be addressed for effective conservation. *Journal for Nature Conservation* 47:58–64 DOI 10.1016/j.jnc.2018.11.008.
- Florens FBV, Baider C, Martin GMN, Seegoolam NB, Zmanay Z, Strasberg D. 2016.** Invasive alien plants progress to dominate protected and best-preserved wet forests of an oceanic island. *Journal for Nature Conservation* 34:93–100 DOI 10.1016/j.jnc.2016.09.006.
- Florens FBV, Baider C, Martin G, 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 DOI 10.1007/s10531-012-0304-4.
- Florens FBV, Baider C, Seegoolam N, Zmanay Z, Strasberg D. 2017.** Long-term declines of native trees in an oceanic island's tropical forests invaded by alien plants. *Applied Vegetation Science* 20:94–105 DOI 10.1111/avsc.12273.
- Flores-Palacios A, García-Franco JG. 2006.** The relationship between tree size and epiphyte species richness: testing four different hypotheses. *Journal of Biogeography* 33:323–330 DOI 10.1111/j.1365-2699.2005.01382.x.
- Fournel J, Micheneau C, Baider C. 2015.** A new critically endangered species of *Angraecum* (Orchidaceae), endemic to the island of Mauritius, Indian Ocean. *Phytotaxa* 222:211–220.
- Garcia LC, Cianciaruso MV, Ribeiro DB, Dos Santos FAM, Rodrigues RR. 2015.** Flower functional trait responses to restoration time. *Applied Vegetation Science* 18:402–412 DOI 10.1111/avsc.12163.
- Garcia LC, Hobbs RJ, Mäesdos Santos FA, Rodrigues RR. 2014.** Flower and fruit availability along a forest restoration gradient. *Biotropica* 46:114–123 DOI 10.1111/btp.12080.
- Garcia LC, Hobbs RJ, Ribeiro DB, Tamashiro JY, Santos FAM, Rodrigues RR. 2016.** Restoration over time: is it possible to restore trees and non-trees in high-diversity forests? *Applied Vegetation Science* 19:655–666 DOI 10.1111/avsc.12264.
- Garrido-Perez EI, Burnham RJ. 2010.** The evolution of host specificity in liana-tree interactions. *Puente Biológico* 3:145–157.
- Gentry AH. 1992.** The distribution and evolution of climbing plants. In: Putz FE, Mooney HA, eds. *The biology of vines*. Cambridge: Cambridge University Press, 3–50 DOI 10.1017/CBO9780511897658.003.
- Gotsch SG, Nadkarni N, Amici A. 2016.** The functional roles of epiphytes and arboreal soils in tropical montane cloud forests. *Journal of Tropical Ecology* 32:455–468 DOI 10.1017/S026646741600033X.
- Hammond DS, Gond V, Baider C, Florens FBV, Persand S, Laurance SGW. 2015.** Threats to environmentally sensitive areas from peri-urban expansion in Mauritius. *Environmental Conservation* 42:256–267 DOI 10.1017/S0376892914000411.
- Hartig F. 2024.** DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.7. DOI 10.32614/CRAN.package.DHARMA.



- Heinen JH, Florens FBV, Baider C, Hume JP, Kissling WD, Whittaker RJ, Rahbek C, Borregaard MK. 2023.** Novel plant–frugivore network on Mauritius is unlikely to compensate for the extinction of seed dispersers. *Nature Communications* **14**:1019 DOI [10.1038/s41467-023-36669-9](https://doi.org/10.1038/s41467-023-36669-9).
- Hermans J, Schuiteman A, Rajaovelona L, Hervouet J-M, Cribb P. 2025.** A revision of Polystachyinae (Orchidaceae) in Madagascar, the Mascarenes, Seychelles and Comoro Islands. *Kew Bulletin* **80**:435–572 DOI [10.1007/s12225-025-10285-w](https://doi.org/10.1007/s12225-025-10285-w).
- Hervé D, Razanaka S, Rakotondraompiana S, Rafamantanantsoa F, Carrière S. 2015.** Transitions agraires au sud de Madagascar. In: *Résilience et viabilité, deux facettes de la conservation*. Antananarivo, Madagascar: IRD-SCAC/ PARRUR.
- Hill M. 1973.** Diversity and evenness: a unifying notation and its consequences. *Ecology* **54**:427–432 DOI [10.2307/1934352](https://doi.org/10.2307/1934352).
- Hill R, Miller C, Newell B, Dunlop M, Gordon IJ. 2015.** Why biodiversity declines as protected areas increase: the effect of the power of governance regimes on sustainable landscapes. *Sustainability Science* **10**:357–369 DOI [10.1007/s11625-015-0288-6](https://doi.org/10.1007/s11625-015-0288-6).
- IUCN. 2017.** International Union for Conservation of Nature annual report 2017. Gland, Switzerland: IUCN.
- Johansson D. 1974.** *Ecology of vascular epiphytes in West African rain forest*. Uppsala: Svenska Västgeografiska Sällskapet.
- Jones CG. 2008.** Practical conservation on Mauritius and Rodrigues, steps towards the restoration of devastated ecosystems. In: Cheke AS, Hume JP, eds. *Lost land of the dodo*. London: T & AD Poyser, 256–259.
- Jones CG, Swinnerton KJ. 1997.** A summary of conservation status and research for the Mauritius kestrel *Falco punctatus*, pink pigeon *Columba mayeri* and echo parakeet *Psittacula eques*. *Dodo-Journal of the Wildlife Preservation Trusts* **33**:72–75.
- José Válka Alves R, Kolbek J, Becker J. 2008.** Vascular epiphyte vegetation in rocky savannas of southeastern Brazil. *Nordic Journal of Botany* **26**:101–117 DOI [10.1111/j.0107-055X.2008.00190.x](https://doi.org/10.1111/j.0107-055X.2008.00190.x).
- Komada N, Itioka T, Nakanishi A, Tagane S, Shimizu-kaya U, Nakagawa M, Meleng P, Pungga RS, Kanzaki M. 2022.** Effects of host tree size on the species richness and abundance of epiphyte assemblages in a Bornean lowland tropical forest. *Tropics* **30**:53–61 DOI [10.3759/tropics.MS21-12](https://doi.org/10.3759/tropics.MS21-12).
- Kreft H, Köster N, Küper W, Nieder J, Barthlott W. 2004.** Diversity and biogeography of vascular epiphytes in Western Amazonia, Yasuní, Ecuador. *Journal of Biogeography* **31**:1463–1476 DOI [10.1111/j.1365-2699.2004.01083.x](https://doi.org/10.1111/j.1365-2699.2004.01083.x).
- Krivek G, Florens FBV, Baider C, Seegobin VO, Haugaasen T. 2020.** Invasive alien plant control improves foraging habitat quality of a threatened island flying fox. *Journal for Nature Conservation* **54**:125805 DOI [10.1016/j.jnc.2020.125805](https://doi.org/10.1016/j.jnc.2020.125805).
- Krömer T, Batke SP. 2025.** Epiphytic plants: perspective on their diversity, distribution, systematics and conservation in the changing environment. *Plants* **14**:2265 DOI [10.3390/plants14152265](https://doi.org/10.3390/plants14152265).

- Krömer T, Kessler M, Robbert Gradstein S, Acebey A. 2005. Diversity patterns of vascular epiphytes along an elevational gradient in the Andes. *Journal of Biogeography* 32:1799–1809 DOI 10.1111/j.1365-2699.2005.01318.x.
- Laube S, Zotz G. 2006. Neither host-specific nor random: vascular epiphytes on three tree species in a Panamanian lowland forest. *Annals of Botany* 97:1103–1114 DOI 10.1093/aob/mcl067.
- Leclère D, Obersteiner M, Barrett M, Butchart SHM, Chaudhary A, De Palma A, De Clerck FAJ, Di Marco M, Doelman JC, Dürauer M, Freeman R, Harfoot M, Hasegawa T, Hellweg S, Hilbers JP, Hill SLL, Humpenöder F, Jennings N, Krisztin T, Mace GM, Ohashi H, Popp A, Purvis A, Schipper AM, Tabeau A, Valin H, Van Meijl H, Van Zeist W-J, Visconti P, Alkemade R, Almond R, Bunting G, Burgess ND, Cornell SE, Di Fulvio F, Ferrier S, Fritz S, Fujimori S, Grooten M, Harwood T, Havlík P, Herrero M, Hoskins AJ, Jung M, Kram T, Lotze-Campen H, Matsui T, Meyer C, Nel D, Newbold T, Schmidt-Traub G, Stehfest E, Strassburg BBN, Van Vuuren DP, Ware C, Watson JEM, Wu W, Young L. 2020. Bending the curve of terrestrial biodiversity needs an integrated strategy. *Nature* 585:551–556 DOI 10.1038/s41586-020-2705-y.
- Lenth RV. 2025. emmeans: estimated marginal means, aka least-squares means. R package version 1.10.6. DOI 10.32614/CRAN.package.emmeans.
- Letcher S. 2015. Patterns of liana succession in tropical forests. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE, eds. *Ecology of lianas*. Oxford: John Wiley & Sons Ltd, 116–130.
- Li D. 2018. hillR: taxonomic, functional, and phylogenetic diversity and similarity through Hill Numbers. *Journal of Open Source Software* 3:1041 DOI 10.21105/joss.01041.
- Mangiafico SS. 2024. rcompanion: functions to support extension education program evaluation. New Brunswick: Rutgers Cooperative Extension.
- Manjaribe C, Frasier CL, Rakouth B, Louis EE. 2013. Ecological restoration and reforestation of fragmented forests in Kianjavato, Madagascar. *International Journal of Ecology* 2013:726275 DOI 10.1155/2013/726275.
- Merwin MC, Rentmeester SA, Nadkarni NM. 2003. The influence of host tree species on the distribution of epiphytic bromeliads in experimental monospecific plantations, La Selva, Costa Rica. *Biotropica* 35:37–47.
- Monty MLF, Florens FBV, 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* 6:35–49 DOI 10.1177/194008291300600107.
- Mora C, Sale P. 2011. Ongoing global biodiversity loss and the need to move beyond protected areas: a review of the technical and practical shortcomings of protected areas on land and sea. *Marine Ecology Progress Series* 434:251–266 DOI 10.3354/meps09214.
- Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853–858 DOI 10.1038/35002501.

- Nadkarni NM, Matelson TJ. 1989. Bird use of epiphyte resources in Neotropical trees. *The Condor* 91:891–907 DOI 10.2307/1368074.
- Nakamura A, Proctor H, Catterall CP. 2003. Using soil and litter arthropods to assess the state of rainforest restoration. *Ecological Management & Restoration* 4:20–28 DOI 10.1046/j.1442-8903.4.s.3.x.
- Ndam N, Healey J. 2001. Woody plants recovery in abandoned farms of different ages in the Mount Cameroon region. *Systematics and Geography of Plants* 71:817–826 DOI 10.2307/3668720.
- Odell EH, Stork NE, Kitching RL. 2019. Lianas as a food resource for herbivorous insects: a comparison with trees. *Biological Reviews* 94:1416–1429 DOI 10.1111/brv.12508.
- Pailler T, Baider C. 2020. *Bulbophyllum mascarenense* Pailler and Baider sp nov.: a new endemic orchid species from the Mascarenes. *Botany Letters* 167:417–423 DOI 10.1080/23818107.2020.1817145.
- Pailler T, Rakotoarivelo F, Razafimandimbison S, Bytebier B, Florens F, Martos F, Baider C. 2020a. Taxonomic revision of *Jumellea* (Orchidaceae, Angraecinae) in the Mascarenes. *Phytotaxa* 477:1–34 DOI 10.11646/phytotaxa.477.1.1.
- Pailler T, Verlynde S, Bytebier B, Florens FBV, Baider C. 2020b. Revision of *Angraecum* sect. *Perrierangraecum* (Orchidaceae; Epidendroideae; Vandeae) for the Mascarenes, with a description of a new endemic species for Mauritius. *Phytotaxa* 442:183–195 DOI 10.11646/phytotaxa.442.3.4.
- Pie MR, Caron FS, Dallimore T, Einzmann H, Hietz P, Kessler M, Ramos FN, Elias JPC, Kreft H, Krömer T, Higuera MJC, Zuleta D, Machado G, De Gasper AL, Zotz G, Mendieta Leiva G, Jimenez-Lopez DA, Mendes AF, Brancalion P, Mortara S, Blum CT, Irupe MV, Martínez-Meléndez Nayely N, Benavides AM, Boelter CR, Batke S. 2023. Phylogenetic diversity and the structure of host-epiphyte interactions across the Neotropics. *PeerJ* 11:e15500 DOI 10.7717/peerj.15500.
- Putz FE. 1984. How trees avoid and shed lianas. *Biotropica* 16:19–23 DOI 10.2307/2387889.
- R Core Team. 2024. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.
- Republic of Mauritius. 2024. *Voluntary national review*. Port Louis, Republic of Mauritius: Ministry of Foreign Affairs, Regional Integration and International Trade.
- Roberts DL, Florens VF, Baider C, Bosser J. 2004. *Taeniophyllum coxii* (Summerh.) Summerh.(Orchidaceae): a new record for Mauritius, Indian Ocean. *Kew Bulletin* 59:493–494 DOI 10.2307/4110957.
- Robson NKB, Stevens P. 1980. 49. Guttiferae. In: Bosser J, Cadet T, Guého J, Marais W, eds. *Flore des Mascareignes: La Réunion, Maurice, Rodrigues*. Port Louis, Mauritius: MSIRI/ORSTOM-IRD/Kew.
- Ruiz-Jaen MC, Aide TM. 2005. Restoration success: how is it being measured? *Restoration Ecology* 13:569–577 DOI 10.1111/j.1526-100X.2005.00072.x.
- Sanford WW. 1968. Distribution of epiphytic orchids in semi-deciduous tropical forest in southern Nigeria. *Journal of Ecology* 56:697–705 DOI 10.2307/2258101.

- Scheffers B, Brunner R, Ramirez S, Shoo L, Diesmos A, Williams S. 2013.** Thermal buffering of microhabitats is a critical factor mediating warming vulnerability of frogs in the Philippine Biodiversity Hotspot. *Biotropica* 45:628–635 DOI 10.1111/btp.12042.
- Schnitzer SA. 2015.** The contribution of lianas to forest ecology, diversity, and dynamics. In: Parthasarathy N, ed. *Biodiversity of lianas*. Cham, Switzerland: Springer, 149–160.
- Shoo LP, Freebody K, Kanowski J, Catterall CP. 2016.** Slow recovery of tropical old-field rainforest regrowth and the value and limitations of active restoration. *Conservation Biology* 30:121–132 DOI 10.1111/cobi.12606.
- Sousa da Silva AT, Freitag Kramer JM, Zwiener VP. 2025.** Diversity patterns and knowledge gaps of Atlantic Forest epiphyllous bryophytes: a highly neglected group. *Annals of Botany* 135:1047–1058 DOI 10.1093/aob/mcaf007.
- Sodhi NS, Butler R, Laurance WF, Gibson L. 2011.** Conservation successes at micro-, meso- and macroscales. *Trends in Ecology & Evolution* 26:585–594 DOI 10.1016/j.tree.2011.07.002.
- Song S, Shen J, Zhou S, Guo X, Zhao J, Shi X, Yu Z, Gong Q, You S, Landrein S. 2022.** Highlighting the plight of threatened lianas: distribution, dynamics, and potential habitat areas of a critically endangered species. *Global Ecology and Conservation* 36:e02130 DOI 10.1016/j.gecco.2022.e02130.
- Spicer ME, Woods CL. 2022.** A case for studying biotic interactions in epiphyte ecology and evolution. *Perspectives in Plant Ecology, Evolution and Systematics* 54:125658 DOI 10.1016/j.ppees.2021.125658.
- Staub CG, Stevens FR, Waylen PR. 2014.** The geography of rainfall in Mauritius: modelling the relationship between annual and monthly rainfall and landscape characteristics on a small volcanic island. *Applied Geography* 54:222–234 DOI 10.1016/j.apgeog.2014.08.008.
- Stone MJ, Shoo L, Stork NE, Sheldon F, Catterall CP. 2020.** Recovery of decomposition rates and decomposer invertebrates during rain forest restoration on disused pasture. *Biotropica* 52:230–241 DOI 10.1111/btp.12682.
- Strahm. 1993.** The conservation and restoration of the flora of Mauritius and Rodrigues. PhD Thesis, University of Reading.
- Stuntz S, Ziegler C, Simon U, Zotz G. 2002.** Diversity and structure of the arthropod fauna within three canopy epiphyte species in central Panama. *Journal of Tropical Ecology* 18:161–176 DOI 10.1017/S0266467402002110.
- Swaine MD, Hall JB. 1983.** Early succession on cleared forest land in Ghana. *The Journal of Ecology* 71:601–627 DOI 10.2307/2259737.
- Swinnerton KJ, Groombridge JJ, Jones CG, Burn RW, Mungroo Y. 2004.** Inbreeding depression and founder diversity among captive and free-living populations of the endangered pink pigeon *Columba mayeri*. *Animal Conservation* 7:353–364 DOI 10.1017/S1367943004001556.
- Tremblay RL, Zimmerman JK, Lebrón L, Bayman P, Sastre I, Axelrod F, Alers-García J. 1998.** Host specificity and low reproductive success in the rare endemic

- Puerto Rican orchid *Lepanthes caritensis*. *Biological Conservation* **85**:297–304 DOI [10.1016/S0006-3207\(97\)00163-8](https://doi.org/10.1016/S0006-3207(97)00163-8).
- Tsen EWJ, Sitzia T, Webber BL. 2016. To core, or not to core: the impact of coring on tree health and a best-practice framework for collecting dendrochronological information from living trees. *Biological Reviews* **91**:899–924 DOI [10.1111/brv.12200](https://doi.org/10.1111/brv.12200).
- United Nations. 2015. *Transforming our world: the 2030 agenda for sustainable development*. New York: UN General Assembly.
- Vargas BDC, Grombone-Guaratini MT, Morellato LPC. 2020. Lianas research in the Neotropics: overview, interaction with trees, and future perspectives. *Trees: Structure and Function* **35**:333–345 DOI [10.1007/s00468-020-02056-w](https://doi.org/10.1007/s00468-020-02056-w).
- Vaughan RE, Wiehe PO. 1941. Studies on the vegetation of Mauritius: III. The structure and development of the upland climax forest. *Journal of Ecology* **29**:127 DOI [10.2307/2256223](https://doi.org/10.2307/2256223).
- Vie J-C, Hilton-Taylor C, Stuart SN. 2009. *Wildlife in a changing world: an analysis of the 2008 IUCN Red list of threatened species*. Gland, Switzerland: IUCN.
- Wagner K, Mendieta-Leiva G, Zotz G. 2015. Host specificity in vascular epiphytes: a review of methodology, empirical evidence and potential mechanisms. *AoB PLANTS* **7**:plu092 DOI [10.1093/aobpla/plu092](https://doi.org/10.1093/aobpla/plu092).
- Wagner K, Wanek W, Zotz G. 2021. Functional traits of a rainforest vascular epiphyte community: trait covariation and indications for host specificity. *Diversity* **13**:97 DOI [10.3390/d13020097](https://doi.org/10.3390/d13020097).
- Wagner K, Zotz G. 2020. Including dynamics in the equation: tree growth rates and host specificity of vascular epiphytes. *Journal of Ecology* **108**:761–773 DOI [10.1111/1365-2745.13333](https://doi.org/10.1111/1365-2745.13333).
- Wickham H. 2016. *ggplot2: elegant graphics for data analysis*. New York: Springer. Available at <https://ggplot2.tidyverse.org>.
- Wolf JHD. 1994. Factors controlling the distribution of vascular and non-vascular epiphytes in the northern Andes. *Vegetatio* **112**:15–28 DOI [10.1007/BF00045096](https://doi.org/10.1007/BF00045096).
- Wysocki A, Wierzcholska S, Proćków J, Konowalik K. 2024. Host tree availability shapes potential distribution of a target epiphytic moss species more than direct climate effects. *Scientific Reports* **14**:18388 DOI [10.1038/s41598-024-69041-y](https://doi.org/10.1038/s41598-024-69041-y).
- Yanoviak SP. 2015. Effects of lianas on canopy arthropod community structure. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE, eds. *Ecology of lianas*. Oxford: Wiley-Blackwell Publishing, 343–361 DOI [10.1002/9781118392409.ch24](https://doi.org/10.1002/9781118392409.ch24).
- Zhang L, Nurvianto S, Harrison R. 2010. Factors affecting the distribution and abundance of *Asplenium nidus* L. in a tropical lowland rain forest in Peninsular Malaysia. *Biotropica* **42**:464–469 DOI [10.1111/j.1744-7429.2009.00607.x](https://doi.org/10.1111/j.1744-7429.2009.00607.x).
- Zhu H. 2008. Species composition and diversity of lianas in tropical forests of Southern Yunnan (Xishuangbanna), South-Western China. *Journal of Tropical Forest Science* **20**:111–122.
- Zotz G. 2013. The systematic distribution of vascular epiphytes—a critical update. *Botanical Journal of the Linnean Society* **171**:453–481 DOI [10.1111/boj.12010](https://doi.org/10.1111/boj.12010).



- Zotz G. 2016.** Epiphyte taxonomy and evolutionary trends. In: *Plants on plants—the biology of vascular epiphytes*. Cham, Switzerland: Springer, 13–49.
- Zotz G, Vollrath B. 2003.** The epiphyte vegetation of the palm *Socratea exorrhiza*—correlations with tree size, tree age and bryophyte cover. *Journal of Tropical Ecology* 19:81–90 DOI [10.1017/S0266467403003092](https://doi.org/10.1017/S0266467403003092).
- Zuur AF, Ieno EN, Walker N, Saveliev AA, Smith GM. 2009.** *Mixed effects models and extensions in ecology with R*. New York: Springer.