

1 **Biological Facilitation of the Giant Tree Fern *Angiopteris Evecta* in**  
2 **the Germination of the Invasive Velvet Tree *Miconia Calvescens***

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## 12 Abstract

13 **Background.** Biological facilitation is a type of relationship between two taxa that benefits at least  
14 one of the participants but harms neither. Although invasive species are widely known to compete  
15 with native taxa, recent studies suggest that invasive and native species can have positive  
16 relationships. This study aims to examine the biological facilitation of the germination of invasive  
17 *Miconia calvescens* by giant tree fern *Angiopteris evecta*, native to French Polynesia.

18 **Methods.** Field surveys were conducted to measure *A. evecta* and *M. calvescens* by applying the  
19  $10 \times 10 \text{ m}^2$  quadrat survey method. The density of seedlings, saplings, and matures plants of *M.*  
20 *calvescens* growing on the rhizomes of *A. evecta* and on bare soil was compared, and the  
21 correlation between the size of the rhizomes and the number of *M. calvescens* growing on them  
22 were checked. Comparative soil nutrient experiments were performed for the substrates of the  
23 rhizomes of *A. evecta*, soil under the rhizomes, and bare soils to determine whether the rhizomes  
24 are chemically different from other microenvironments. Also, chemical contents of the barks of *A.*  
25 *evecta* and five other dominant tree species that can provide potential microenvironments for  
26 seedlings and saplings of *M. calvescens* were analyzed. Leaf decomposition rates of five different  
27 species were compared to verify whether *A. evecta* has quickly decomposing leaves, and therefore  
28 induce the germination and recruitment of *M. calvescens* by enabling more sunlight to reach to the  
29 forest floor.

30 **Results.** Field surveys show that a greater number of seedlings and saplings of *M. calvescens* grow  
31 on the rhizomes of *A. evecta* than in bare soil. Furthermore, there is a positive correlation between  
32 the size of the rhizome and the number of *M. calvescens* growing on it. Substrates of *A. evecta* had  
33 higher potassium content compared to bare soil and the soil under the rhizomes. However, the  
34 chemical components of the rhizome of *A. evecta* were not distinct from those of barks of other  
35 five dominant tree species. The leaf decomposition rate of *A. evecta* is much higher than other  
36 species that are dominant in the forest.

37 **Discussion.** *Angiopteris evecta* facilitates the germination of *M. calvescens*, supported by the much  
38 higher number of seedlings and saplings growing on the rhizomes and the positive correlation  
39 between the size of the rhizome and the number of *M. calvescens* growing on it. Microslopes on  
40 the rhizomes of *A. evecta* prevent leaf litter from accumulating on the rhizomes, and enable more  
41 sunlight to reach and facilitate the germination of *M. calvescens* seeds. Also, field observation  
42 suggests that *A. evecta* has quickly decomposing leaves, which can induce the germination and the  
43 recruitment of *M. calvescens* in forest understories dominated by *A. evecta* by preventing the  
44 accumulation of leaf litter on the ground and enabling more sunlight to reach the seed bank. The  
45 germination of trees in tropical rainforests is often limited by the availability of potassium,  
46 suggesting that the rhizomes of *A. evecta* might be favored chemically. However, further studies  
47 are needed to verify whether potassium is a limiting factor in the germination of *M. calvescens*.  
48 Investigating biological facilitation of the germination of invasive *M. calvescens* by native *A.*  
49 *evecta* can yield a better understanding of invasion success and the relationship between native  
50 and invasive species. Invasion of *A. evecta* can induce and promote further invasion of *M.*

51 *calvescens*. Therefore, thorough management of the ongoing invasion of *A. evecta* is particularly  
52 necessary.

53

54 Keywords: Biological facilitation, Nurse plants, Biological invasions, *Miconia calvescens*,  
55 *Angiopteris evectas*

56

## 57 **Introduction**

58 Concerns about biological invasion have increased due to the role of invasion in degrading  
59 biological diversity worldwide (Usher et al., 1988). Even though only few introduced species  
60 become invasive (Smith, 1990; Meyer & Florence, 1996; Williamson & Fitter, 1996), they often  
61 significantly alter the native ecosystem and displace indigenous species. Native ecosystems on  
62 oceanic islands are especially vulnerable to biological invasion and displacement (Loope &  
63 Mueller-Dombois, 1989), due to reduced competitive ability by repeated founder effects, relative  
64 lack of natural disturbance in the evolutionary history of island biota, small population size and  
65 genetic variability (Wilson & Vitousek, 1988).

66 A considerable amount of research has been conducted to understand the characteristics of  
67 native communities that affect the success of invasions (Elton, 1958; Vitousek *et al.*, 1997; Tilman,  
68 1999). However, identifying general mechanisms for invasion success is challenging because of  
69 the conflict between landscape-scale patterns and smaller-scale experimental results, also known  
70 as invasion paradox (Fridley et al., 2007). Large-scale observations generally find a positive  
71 correlation between the diversity of native communities and invasion success (Lonsdale, 1999;  
72 Sax, Gaines & Brown, 2002; Brown & Peet, 2003; Davies et al., 2005). In contrast, the results of  
73 small-scale experiments consistently suggest competition between invasive and native species.  
74 Available niches are important for the introduction and the establishment of invasive species  
75 (Peterson, 2003); therefore a diverse native community and already occupied niches are not  
76 favorable for invasion success. This suggests that fundamental ecological factors other than  
77 competition play a role in the interactions between native and invasive species (Bulleri *et al.*,  
78 2008).

79 Invasive plants are known to suppress and eventually replace native forests via various  
80 mechanisms, including competition for resources and pollinators, shading the understory,  
81 restraining the recruitment of native vegetation by allelopathy, and disrupting underground fungal  
82 mutualisms (Thomas, 1980; Callaway & Aschehoug, 2000; Brown & Mitchell, 2001; Vilà &  
83 Weiner, 2004; Stinson *et al.*, 2006; Callaway *et al.*, 2008). *Miconia calvescens* is a major plant  
84 pest in the Pacific islands including Hawaii, Tahiti, Mo'orea, and other islands in French  
85 Polynesia. It shades the understory with its large leaves (> 1 m) and hinders the growth of native  
86 vegetation (Meyer, 1996). *Miconia calvescens* was introduced to Tahiti from Mexico, by retired  
87 Harvard physicist Harrison Smith at Papeari Botanical Garden in 1937 (Gaubert, 1992; Meyer,  
88 1994). It dominated the forest over 65% of the 1,045 km<sup>2</sup> island in 1996, 60 years after the first

89 introduction, and caused the decline of 70-100 native species, including 35-40 species endemic to  
90 French Polynesia (Meyer, 1996; Meyer & Florence, 1996). Also, after a small population of *M.*  
91 *calvescens* was first noted on Mount. Mouaputa on the island of Mo'orea in 1974 by an inhabitant  
92 of Afareiatu village, *M. calvescens* has spread throughout several other areas on the island  
93 (Schwartz, 1993; Meyer, 1996).

94 This study aims to provide insight on the role of *A. evecta* on the germination of *M.*  
95 *calvescens*, in order to understand biological facilitation in interspecific plants, and to suggest  
96 possible management techniques for plant invasions on Pacific islands. Schwartz (1933) noted that  
97 *M. calvescens* is often found on the caudices of the giant tree fern *Angiopteris evecta*. According  
98 to a pilot study, seedlings, juveniles, and occasionally mature plants (> 3 m) of *M. calvescens*  
99 inhabit and are present underneath *A. evecta* rhizomes with high frequency. Also, the abundance  
100 of *M. calvescens* tends to be greater in forests with an *A. evecta*-dominated understory. It is not  
101 known whether *A. evecta* facilitates the germination of *M. calvescens*; however, it is possible that  
102 the rhizome of *A. evecta* offers environments with higher light intensity, or provides chemically  
103 preferable substrates.

104

## 105 **Methods**

### 106 *Study Sites*

107 This study was conducted on the island of Mo'orea, French Polynesia (S 17.53° W 149.83°) during  
108 October and November of 2016. Mo'orea is part of the Society archipelago, which ranges from  
109 16° to 18° south latitude and from 148° to 155° west longitude, and is an island chain formed by  
110 hotspot volcanism.

111 Mo'orea is the second highest island in the Society Islands. Mo'orea is reported to be 1.49  
112 to 1.64 million years old (Duncan & McDougall, 1976). The island is about 18 km in width from  
113 east to west. Opunohu Valley is one of the two nearly identical bays on the northern side of the  
114 island. It extends 4 km southward to Mo'orea's north coast, and is surrounded by eroded caldera.

115 Research was conducted on two famous hiking trails in Opunohu Valley: Three Coconuts  
116 Trail and Three Pines Trail (Fig. 1). This study was conducted at sites along these two trails. The  
117 vegetation composition of the two trails is reported to be slightly different. Agnew (2014) noted  
118 that the study sites along Three Pines Trail were characterized by a high amount of *Inocarpus*  
119 *fagifer* and moderate presence of *Miconia calvescens*, and Three Coconuts Trail was characterized  
120 by *Hibiscus tiliaceus*, *Miconia calvescens*, and small ferns. According to a pilot study, the  
121 distribution of dominant trees in Opunohu Valley confirmed these earlier findings. The frequency  
122 of *H. tiliaceus*, *Neonauclea forsteri*, and *Falcataria moluccana* appears to be similar. *Barringtonia*  
123 *asiatica* was observed almost exclusively on Three Coconuts Trail. Three Pines Trail was mostly  
124 dominated by *I. fagifer*, and the frequency of *Miconia calvescens* was higher on Three Coconuts  
125 Trail. The density of *Angiopteris evecta* appeared to be highly dependent on the proximity of  
126 streams.

127

128 **Study Organisms**129 *Miconia calvescens*

130 *Miconia calvescens* is an arborescent species in family Melastomataceae, native to South and  
131 Central America. It grows in a monsoonal climate and tolerates fluctuating precipitation, sunlight,  
132 and shallow soil environments (Hurley, 1991). It grows on steep slopes on mountainous volcanic  
133 islands where leaf litter is limited and light is constantly available (Underwood, 1993). *M.*  
134 *calvescens* begins its life cycle as a small shrub but it can grow up to 15 m tall. It begins producing  
135 flowers and fruits at 4 to 5 years of age at 3 to 4 m in height, respectively. Each panicle on a tree  
136 produces hundreds of berries, each containing 120 to 230 seeds, enabling a mature tree to produce  
137 thousands of seeds per fruiting (Medeiros & Loope, 1997). Once seeds land on substrates, the plant  
138 can germinate in various environments including steep hillsides, the surface of rocks, and the bark  
139 of trees (Schwartz, 1993). Meyer (1994) has verified viable *M. calvescens* seed banks of more than  
140 2 years, and suggested seed life of at least 4 years. The plants can also germinate from fruits left  
141 in water for 3 months (Meyer & Malet, 1997), which suggests water as potential dispersal  
142 mechanism. Germination takes place in almost all light intensities down to 2 % of full sunlight  
143 (Meyer, 1996). Data from herbicidal defoliation incidents of Maui's main population claimed that  
144 *Miconia*'s seed banks stay largely dormant in the shade but become viable when the overhead  
145 canopy opens and more light is available (Medeiros & Loope, 1997).

146

147 *Angiopteris evecta*

148 *Angiopteris evecta*, commonly known as king fern, giant fern, oriental vessel fern, and mule's foot  
149 fern, is a large tree fern in family Marattiaceae. It is a robust pteridophyte with a globose upright  
150 rhizome and considerably thickened roots (Christenhusz & Toivonen, 2008). Its fronds are spirally  
151 arranged, bipinnate, and can grow up to 6 m long and 2.5-3 m broad. Its stout rhizomes can grow  
152 up to 150 cm in height and 100 cm in diameter, and have protruding leaf scars on the rhizomes.  
153 (Christenhusz & Toivonen, 2008). *A. evecta* inhabits tropical environments and thrives in wet  
154 forests and rainforests at low to middle elevations. The species is known to be native to the island  
155 of Samoa, Polynesia, Micronesia, and New Caledonia (Brownlie, 1969; Florence *et al.*, 2013;  
156 Fosberg *et al.*, 1982; Yuncker, 1945). However, it is cultivated worldwide as an ornamental plant,  
157 and appears to naturalize without restriction in wet valleys and on slopes in montane and lowland  
158 rainforests of Hawaii, Jamaica, and Costa Rica (Christenhusz & Toivonen, 2008).

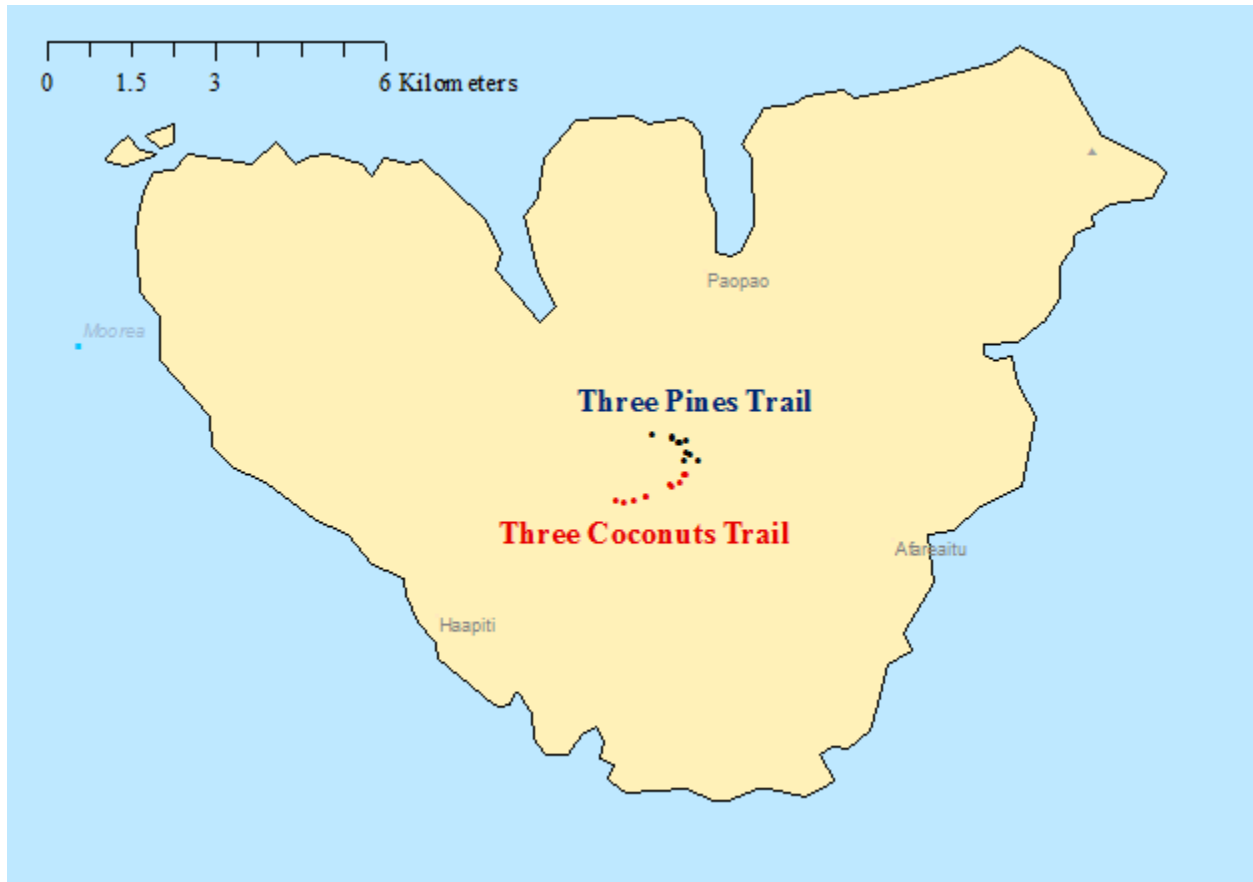
159 In the field, epiphytes are frequently observed on the rhizomes of *A. evecta*; including  
160 various bryophytes, pteridophytes, and several angiosperm seedlings and saplings. In Opunohu  
161 Valley, Mo'orea, less than 5 species of angiosperm seedlings and saplings inhabit rhizomes, and  
162 *M. calvescens* is the most frequently observed inhabitant.

163

164 **Field Surveys**

165 Field surveys were performed in Opunohu Valley, Mo'orea (Fig 1). Schwartz (1993) reported that  
166 *M. calvescens* was observed in the elevation range of 20 to 898 m above sea level. *A. evecta* is  
167 known to be found in the range of 0 to 1,492 m (Christenhusz & Toivonen, 2008). In this study,  
168 surveys were conducted in accessible forests close to hiking trails, ranging from approximately  
169 100 to 400 m.

170



171

172 Figure 1. Map of Study Sites. The study was conducted at sites along two well-known hiking  
173 trails: Three Coconuts Trail and Three Pines Trail, in Moorea, French Polynesia.

174

175 Twenty different sites were chosen at random; ten from Three Pines Trail where *M.*  
176 *calvescens* is less dominant, and ten from Three Coconuts Trail where the population of *M.*  
177 *calvescens* is higher (for GPS coordinates see Table 1). The quadrat survey method was used to  
178 survey *M. calvescens* and *A. evecta*, at a scale of 10 x 10 m<sup>2</sup>.

179

180 Table 1. The GPS coordinates of the 20 field survey sites.

Site	Three Coconuts Trail	Three Pine Trail
1	S 17° 32.567' W 149° 49.738'	S 17° 32.120' W 149° 49.824'
2	S 17° 32.599' W 149° 49.803'	S 17° 32.131' W 149° 49.810'
3	S 17° 32.477' W 149° 49.698'	S 17° 32.172' W 149° 49.742'
4	S 17° 32.486' W 149° 49.673'	S 17° 32.161' W 149° 49.740'
5	S 17° 32.590' W 149° 49.830'	S 17° 32.143' W 149° 49.675'
6	S 17° 32.705' W 149° 50.065'	S 17° 32.352' W 149° 49.559'
7	S 17° 32.725' W 149° 50.173'	S 17° 32.102' W 149° 49.992'
8	S 17° 32.741' W 149° 50.268'	S 17° 32.266' W 149° 49.658'
9	S 17° 32.726' W 149° 50.349'	S 17° 32.299' W 149° 49.633'
10	S 17° 32.705' W 149° 50.063'	S 17° 32.351' W 149° 49.695'

181

182 Individual *Miconia calvescens* were categorized into three groups: seedlings, saplings,  
 183 and matures (Fig. 2). Individual plants were identified by noting the dark green adaxial side and  
 184 purple abaxial side of leaves which become distinctive after cotyledons. Prominent acrodromous  
 185 venation was used as a key characteristic for defining the sapling stage, which are not obvious in  
 186 the foliage leaves of seedlings. Individual plants over 3 m were considered to be mature.

187



188

189 Figure 2. Seedlings and saplings of *M. calvescens* (1<sup>st</sup> row: seedlings, 2<sup>nd</sup> row: saplings. Scale:  
190 1cm)

191

192 The height of all *M. calvescens* individual plants within the quadrat was measured. The  
193 number of each group (seedlings, saplings, and mature plants) of *M. calvescens* that grow on the  
194 rhizomes of *A. evecta* and the ground were compared. Density (individual plants per m<sup>2</sup>) of each  
195 group of *M. calvescens* on rhizomes of *A. evecta* and on bare soil was calculated. Different methods  
196 were applied to calculate density in different microenvironments because the rhizomes are three-  
197 dimensional. The rhizomes of *A. evecta* were considered to be perfectly globose, although they are  
198 not completely spherical. The surface area of rhizomes was calculated by substituting data into  
199 following equation:  $Surface\ Area_{Rhizomes} = 4\pi \sum (\frac{1}{2} Height)^2$ , and density was calculated by  
200 dividing the total number of *M. calvescens* on the rhizomes by surface area. The density of *M.*  
201 *calvescens* on bare soil was obtained in the same way, except that the surface area was calculated  
202 by substituting data into following equation:  $Surface\ Area_{Bare\ Soil} = 100 - \pi \sum (\frac{1}{2} Height)^2$ .  
203 This calculation can simplify and effectively show the difference between bare soil and the  
204 microenvironments created by the rhizomes of *A. evecta*. However, this calculation does not reflect  
205 the entire three-dimensional circumstances of the quadrat, such as three-dimensional surface area  
206 of rocks and fallen logs and area occupied by upright tree trunks. The density of each group  
207 (seedlings, saplings, and mature plants) on the rhizomes and in bare soil was calculated, and three



208 t-tests were applied for each group to compare the density in different microenvironments using R  
209 (R Core Development Team, 2013).

210 The sizes of *A. evecta* rhizomes was measured in order to assess the correlation between  
211 rhizome size and the number of *M. calvescens* growing on them. Girth and height were measured,  
212 and height was used to represent rhizome size, as they are correlated ( $y = 2.480x + 10.98$ ;  $R^2 =$   
213  $0.90$ ,  $F_{1/315} = 2913$ ,  $p < 0.00001$ ). For rhizomes with a perfect globose shape, the correlation  
214 equation would be  $y = 3.142x$ . Although the correlation shows that the rhizomes are not perfectly  
215 globose, height still represents the size of *A. evecta* well because the rhizomes tend to become  
216 spheroidal when they grow older and larger. The correlation between the height of rhizomes and  
217 the number of *M. calvescens* growing on them was verified using R (R Core Development Team,  
218 2013).

219

### 220 *Soil nutrient experiment*

221 Comparative soil nutrient experiments were conducted to determine whether substrates of the  
222 rhizome of *Angiopteris evecta* are chemically different from other soils or potential biotic  
223 microenvironments, and offer microenvironments with higher nutrient contents. Nitrogen,  
224 phosphorus, and potassium concentrations of different microenvironments were measured by  
225 using a LaMotte Soil Test Kit following the manufacturer's instructions (LaMotte Company, 2016).  
226 Two grams of each dried substrate and soil sample were reserved for the test. The LaMotte Soil  
227 Test Kit was used for the study in spite of its less accurate measurement method because the  
228 purpose of the study is to compare the nutrient contents of different microenvironments, not to  
229 measure their exact concentration.

230 Three different microenvironments were compared: substrates of the rhizomes of *A. evecta*,  
231 soil under the rhizomes, and bare soil. Three samples from each were collected from three  
232 respective microenvironments, and the mean value of each nutrient content was compared using  
233 an ANOVA test, followed by Tukey post hoc comparisons using R (R Core Development Team,  
234 2013).

235 A few tree species that are dominant in Opunohu Valley that could potentially offer habitat  
236 for *M. calvescens* to germinate and grow. *Hibiscus tiliaceus* trunks often lie almost parallel to the  
237 ground, and therefore have a less steep slope on their trunk than many other plants. *Inocarpus*  
238 *fagifer*, *Neonauclea forsteri*, and *Falcataria moluccana* have buttresses that support the trees,  
239 which lessen the precipitous angle of the trunks and provides a surface for small seeds to land on.  
240 *Barringtonia asiatica* is observed to have both buttresses at the base of its trunk and sometimes to  
241 have a horizontal trunk. However, none of these trees were observed to have *M. calvescens*  
242 growing on them with the exception of only a few saplings on the buttresses of *I. fagifer*. Therefore,  
243 nutrient contents of the bark of these five species and substrates of the rhizome of *A. evecta* were  
244 analyzed to determine whether the substrates of the rhizomes are chemically different than other  
245 possible biotic microenvironments. Three samples were collected for each species, and the mean

246 value of each nutrient was compared using an ANOVA test, followed by Tukey post hoc  
247 comparisons using R (R Core Development Team, 2013).

248

### 249 *Leaf Decomposition experiment*

250 Molofsky and Augspurger (1992) suggested that smaller seeded species had fewer seedlings  
251 established under leaf litter than in bare soil in tropical forests. Species with a higher leaf  
252 decomposition rate contribute to shallow leaf litter on the forest floor, and enable more light to be  
253 available to reach the forest floor, thereby inducing germination. Seeds of *M. calvescens* are  
254 extremely small (< 1 mm), and they are known to stay dormant until more light becomes available.  
255 Therefore, a comparison study of leaf decomposition rates was conducted to determine whether  
256 the leaf decomposition rate of *A. evecta* was higher than others, and hence whether it facilitates  
257 the germination of *M. calvescens* indirectly.

258 A modified version of a method to measure leaf decomposition rate (Cornelissen, 1996)  
259 was developed to test decomposition in several common tree species. Five different species  
260 dominant in Opunohu Valley were selected: *I. fagifer*, *H. tiliaceus*, *B. asiatica*, *M. calvescens*, and  
261 *A. evecta*. Undecomposed leaves of five species were collected and dried for a week. Subsamples  
262 of leaves were weighed after air-drying and after 48 h in an oven at 60 °C to measure the initial  
263 oven-dry weight. Samples were sealed into 1 mm layer mesh nets, and buried under natural  
264 weather and soil conditions. Mesh bags were placed parallel to the ground at a depth of 50 cm.  
265 After 25 days, mesh nets were recollected from the burial sites, and adhering soils and extraneous  
266 materials were removed with a brush. Samples were dried for 48 h at 60 °C, and the decomposition  
267 rate was measured by calculating the percentage of dry weight loss after 25 days. Three mesh bags  
268 were buried for each species at three different sites in Opunohu Valley (GPS coordinates: S 17°  
269 32.567' W 149° 49.738', S 17° 32.552' W 149° 49.720', S 17° 32.143' W 149° 49.675'), and the  
270 mean decomposition rate from the five species was compared using an ANOVA test, followed by  
271 Tukey post hoc comparisons using R (R Core Development Team, 2013).

272

## 273 **Results**

### 274 *Field Surveys*

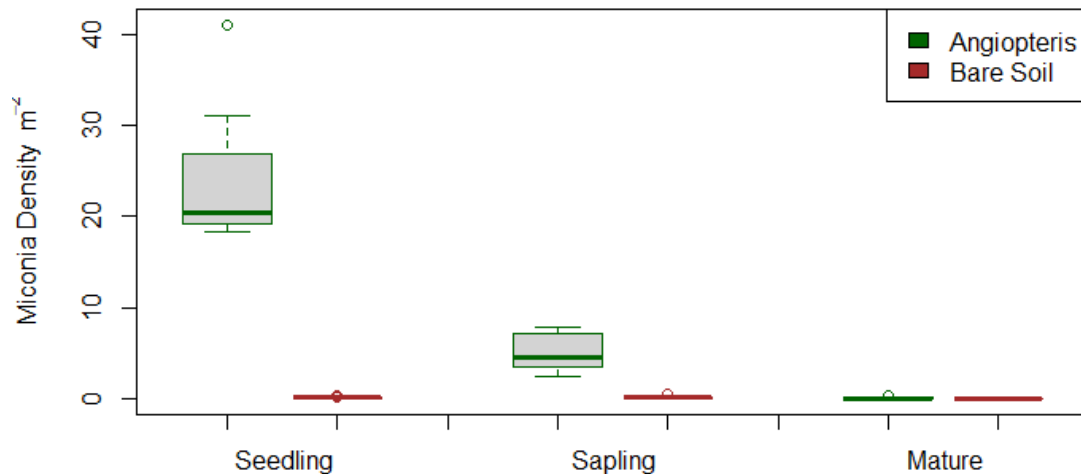
275 The mean density of *M. calvescens* seedlings on the rhizome of *A. evecta* at sites along Three  
276 Coconuts Trail was 23.73 m<sup>-2</sup>, much higher than the density on bare soil, which was 0.162 m<sup>-2</sup>.  
277 The mean density of saplings on the rhizome was 5.12 m<sup>-2</sup>, also higher than the density of 0.174  
278 m<sup>-2</sup> on bare soil. However, the density of mature plants did not differ between rhizomes and bare  
279 soil, measuring 0.077 m<sup>-2</sup> and 0.043 m<sup>-2</sup> respectively (Table 2; Fig. 3).

280

281 Table 2. T-test statistics comparing the density of *M. calvescens* on *A. evecta* rhizomes and bare  
282 soil.

Survey Site	Group	t-value	df	p-value
Three Coconuts Trail	Seedlings	10.175	9.004	3.085e-06
	Saplings	7.5219	9.099	3.4e-05
	Matures	0.8106	10.631	0.4354
Three Pines Trail	Seedlings	5.1741	9.007	5.825e-4
	Saplings	4.1657	9.0376	2.405e-3
	Matures	1.0957	9.0454	0.3015

283



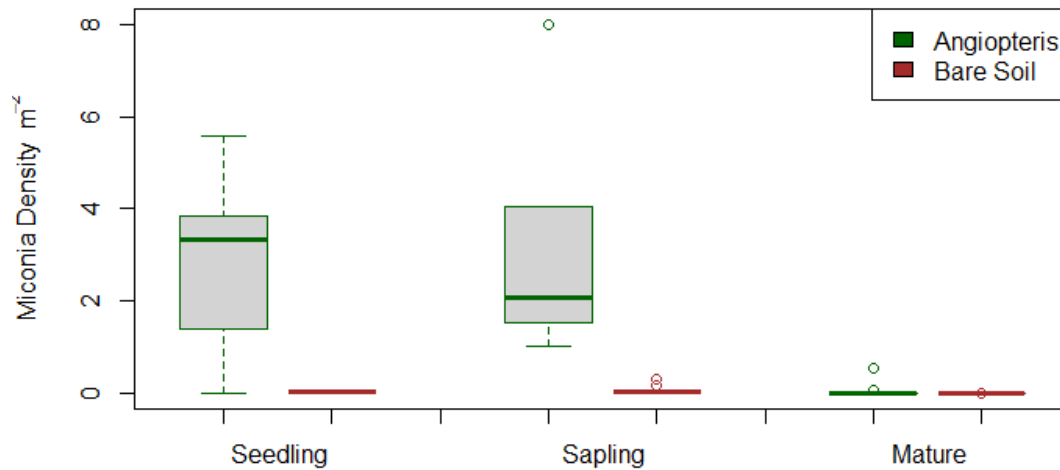
284

285 Figure 3. Density of seedlings, sapling, and mature plants of *M. calvescens* on *A. evecta*  
 286 rhizomes and bare soil. Data represents sites on the Three Coconuts Trail.

287

288 At sites along Three Pines Trail where *M. calvescens* is less dominant, the mean density of  
 289 seedlings on the rhizome of *A. evecta* was  $2.873 \text{ m}^{-2}$ , higher than the density on bare soil, which  
 290 was  $0.045 \text{ m}^{-2}$ . The mean density of saplings on the rhizome was  $2.843 \text{ m}^{-2}$ , also higher than the  
 291 density on bare soil of  $0.063 \text{ m}^{-2}$ . In contrast, the density of mature plants of  $0.063 \text{ m}^{-2}$  and  $0.004$   
 292  $\text{m}^{-2}$ , respectively, was not statistically different (Table 2; Fig. 4).

293



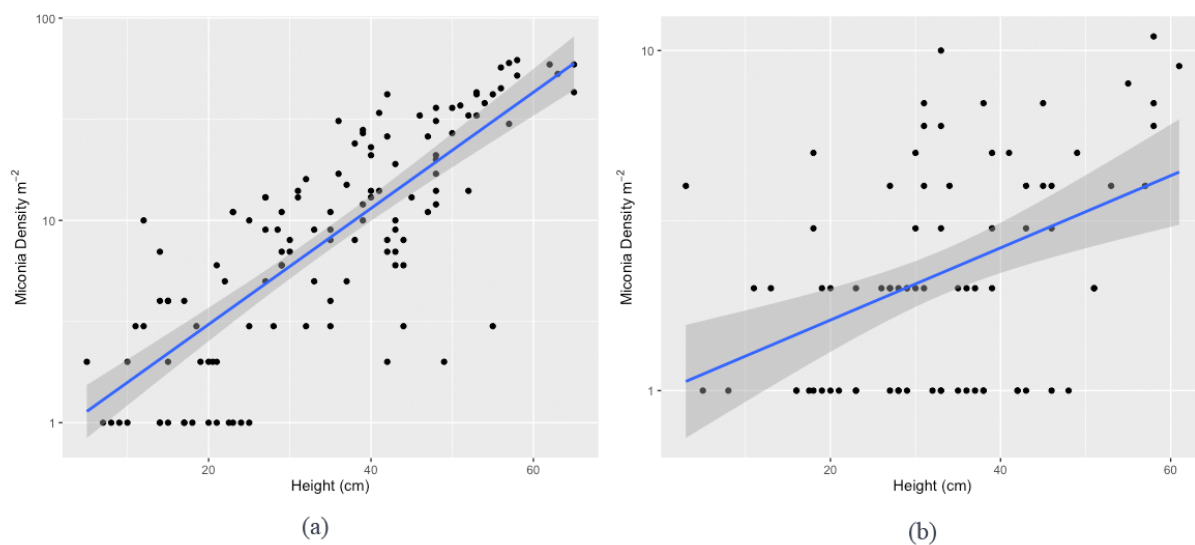
294

295 Figure 4. Density of seedlings, sapling, and mature plants of *M. calvescens* on *A. evecta*  
 296 rhizomes and bare soil. Data represents sites on the Three Pines Trail.

297

298 At sites along Three Coconuts Trail where *M. calvescens* are abundant, the correlation  
 299 between the height of *A. evecta* rhizomes and the number of *M. calvescens* growing on them  
 300 appeared to follow an exponential model ( $R^2 = 0.63$ ,  $F_{1/121} = 208.3$ ,  $p < 0.00001$ ) (Fig. 5a). On  
 301 Three Pines Trail where the population of *M. calvescens* is lower, data points are scattered and the  
 302 correlation is not significant ( $R^2 = 0.19$ ,  $F_{1/76} = 17.47$ ,  $p < 0.0001$ ) (Fig. 5b).

303



304

305 Figure 5. Correlation between the height of *A. evecta* rhizome and the number of *M. calvescens*  
 306 on them. Data represents sites on Three Coconuts Trail (a) and sites on Three Pines Trail (b).  
 307 Density values were log transformed prior to analyses.

308

309 ***Soil Nutrients Experiment***

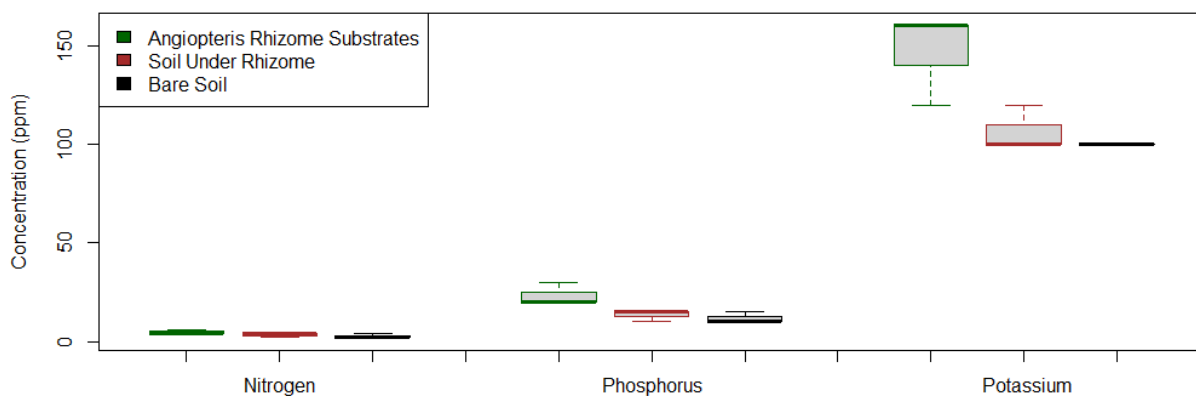
310 Nitrogen content did not differ between three different microenvironments: substrates of the *A.*  
 311 *evecta* rhizomes, soil under the rhizome, and bare soil (Table 3). However, phosphorus  
 312 concentration differed among microenvironments (Table 3). Specifically, substrates on the  
 313 rhizomes contained 23.33 ppm of phosphorus, higher than the concentration of 11,67 ppm in bare  
 314 soil (TukeyHSD,  $p < 0.05$ ). Also, potassium concentration differed among microenvironments  
 315 (Table 3). Substrates on the rhizomes contained 147 ppm of potassium, a much higher  
 316 concentration than both that of the soil under the rhizomes and bare soil (TukeyHSD,  $p < 0.05$ ,  $p$   
 317  $< 0.05$ ). Results are shown in Fig. 6.

318

319 Table 3. ANOVA statistics comparing nutrient contents among substrates and soils from three  
 320 different microenvironments: substrates of the rhizome of *A. evecta*, soil under the rhizome, and  
 321 bare soil.

	F value	p-value
Nitrogen	2.33	0.178
Phosphorus	7.17	0.0257
Potassium	8.6	0.0173

322



323

324 Figure 6. Soil nutrient comparison between three different microenvironments: substrates of the  
 325 rhizomes of *Angiopteris evecta*, soil under the rhizomes, and bare soil

326

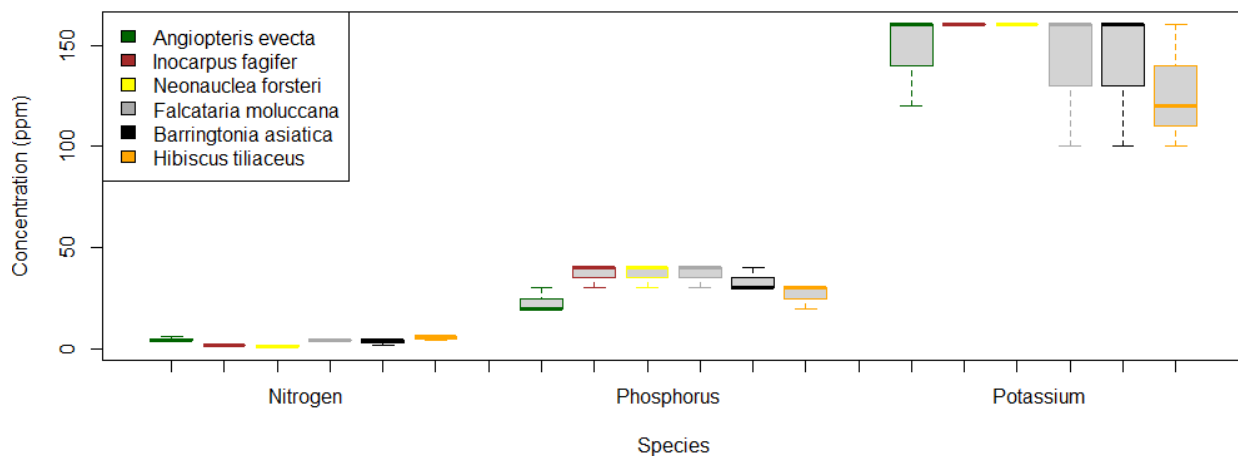
327 Nitrogen contents differed among six species: *Angiopteris evecta*, *Inocarpus fagifer*,  
 328 *Neonauclea forsteri*, *Falcataria moluccana*, *Barringtonia asiatica*, and *Hibiscus tiliaceus* (Table  
 329 4). However, the concentration of nitrogen in *A. evecta* did not significantly differ from other  
 330 species (TukeyHSD,  $p = 0.013$ ,  $p = 0.006$ ,  $p = 0.93$ ,  $p = 0.47$ ,  $p = 0.93$ ). Phosphorus and potassium  
 331 contents of the six species did not differ (Table 4). Results are shown in Fig. 7.

332

333 Table 4. ANOVA statistics comparing nutrient contents among six dominant tree species in  
 334 Opunohu Valley: *Angiopteris evecta*, *Inocarpus fagifer*, *Neonauclea forsteri*, *Falcataria*  
 335 *moluccana*, *Barringtonia asiatica*, and *Hibiscus tiliaceus*

Nutrient	F value	p-value
Nitrogen	10.01	0.0006
Phosphorus	3.067	0.052
Potassium	0.779	0.58

336



337

338 Figure 7. Nutrient contents comparison between the substrates and the barks of six species:  
 339 *Angiopteris evecta*, *Inocarpus fagifer*, *Neonauclea forsteri*, *Falcataria moluccana*, *Barringtonia*  
 340 *asiatica* and *Hibiscus tiliaceus*

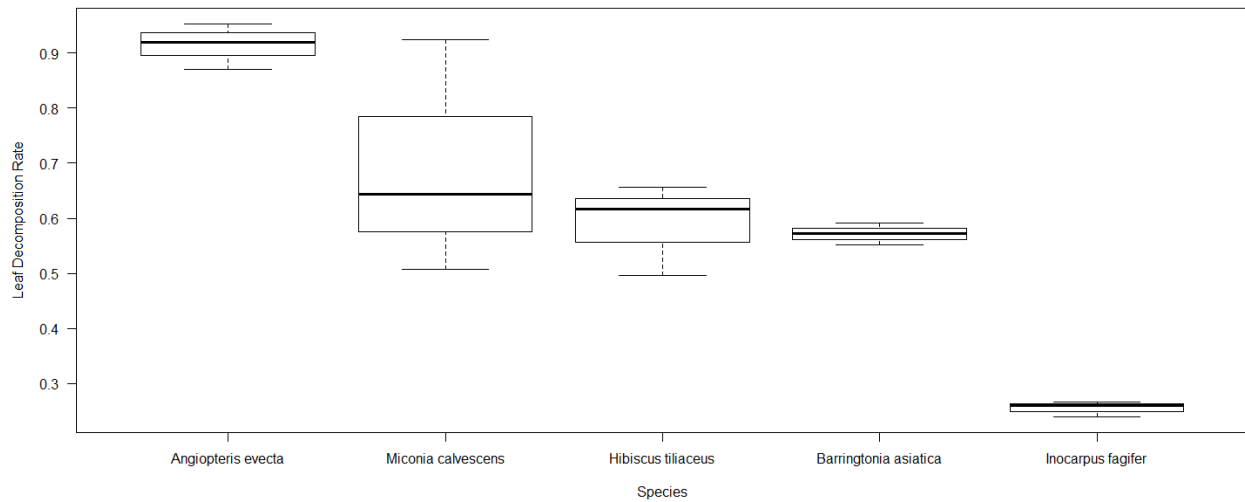
341

342

### 343 **Leaf Decomposition Experiment**

344 Mean leaf decomposition rates of the five species: *A. evecta*, *M. calvescens*, *H. tiliaceus*, *B.*  
 345 *asiatica* and *I. fagifer*, were 0.914 , 0.692, 0.590, 0.572 and 0.255, respectively (Fig. 8), and  
 346 differed from one another (ANOVA,  $F = 15.64$ ,  $p < 0.0005$  ). The decomposition rates of *A. evecta*,  
 347 *B. asiatica* and *I. fagifer* were uniform regardless of the burial site (standard deviation was 0.033,  
 348 0.016 and 0.012, respectively). However, the rates of *M. calvescens* and *H. tiliaceus* varied  
 349 depending on the burial site (standard deviation was 0.17 and 0.068, respectively). The  
 350 decomposition rate of *A. evecta* was significantly higher compared to the other species (Table 4).  
 351 In contrast, *I. fagifer* had a much lower rate than the other species (Table 4).

352



353

354 Figure 8. Leaf decomposition rate of five dominant tree species in Opunohu Valley, Mo'orea

355

356 Table 4. Summary of Tukey post-hoc comparisons among five dominant tree species in Opunohu  
 357 Valley: *Angiopteris evecta*, *Miconia calvescens*, *Hibiscus tiliaceus*, *Barringtonia asiatica* and  
 358 *Inocarpus fagifer*

	<i>A. evecta</i>	<i>M. calvescens</i>	<i>H. tiliaceus</i>	<i>B. asiatica</i>	<i>I. fagifer</i>
<i>A. evecta</i>		0.14	< 0.05	< 0.05	< 0.0005
<i>M. calvescens</i>			0.75	0.64	<0.005
<i>H. tiliaceus</i>				0.99	<0.05
<i>B. asiatica</i>					<0.05
<i>I. fagifer</i>					

359

360

### 361 Discussion

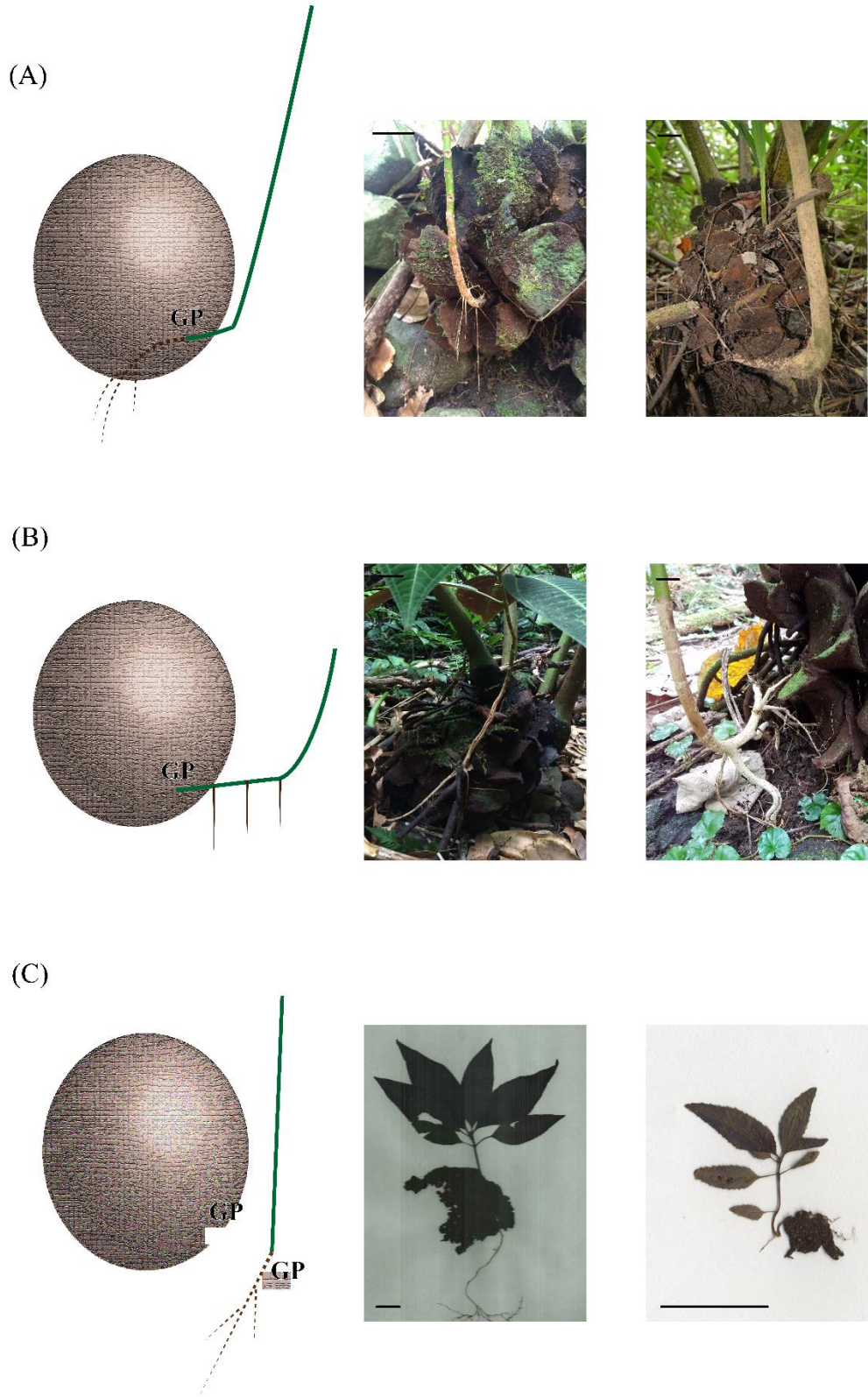
362 Field surveys show that *A. evecta* facilitates the germination of *M. calvescens*. There were  
 363 significantly higher numbers of seedlings and saplings of invasive *M. calvescens* growing on the  
 364 rhizomes of *A. evecta* compared to bare soil at the sites along the Three Coconuts Trail where *M.*  
 365 *calvescens* is reported to be dominant. 90.93% of total seedlings were growing on *A. evecta*, 57.32%  
 366 of total saplings were growing on the rhizome, and 11.90% of mature plants were growing on or  
 367 associated with the rhizome. At the sites along Three Pines Trail where the population of *M.*  
 368 *calvescens* is reported to be lower, much larger quantities of seedlings and saplings were growing  
 369 on the rhizome of *A. evecta*. 72.15% of seedlings, 62.50% of saplings, and 55.55% of mature plants  
 370 were found on the rhizome. Both the percentage of each group of *M. calvescens* growing on the  
 371 rhizome and the density of each group growing in each environment suggest that there is a much

372 higher abundance of *M. calvenscens* seedlings and saplings growing on the rhizome of *A. evecta*  
373 compared to in bare soil. This indicates that *A. evecta* facilitates the germination of *M. calvenscens*.  
374 Also, a positive correlation between the size of rhizomes and the number of *M. calvenscens* growing  
375 on them supports the theory that the existence of *M. calvenscens* on the rhizomes is not a  
376 coincidence, but that the rhizomes are actually preferable microenvironments. However, only a  
377 few *M. calvenscens* that start life on the rhizome reach maturity. This may be due to the scarce  
378 substrates on the rhizomes, or to competition with *A. evecta* for resources.

379         There are three possible mechanisms for the establishment of seedlings and saplings of *M.*  
380 *calvenscens* on the rhizomes of *A. evecta*. First, they can penetrate their roots into the spaces  
381 between the leaf scars on the rhizomes, reaching to the soil under the rhizomes and supplying  
382 nutrients and water for themselves (Fig. 9a). Second, they can grow horizontally towards the soil  
383 around the rhizomes, and then grow upward to the canopy after they root in the soil (Fig. 9b).  
384 *Miconia calvenscens* has the ability to root from the middle of the stem where it has contact with  
385 soil or water (Fig. 10). Therefore, they can re-root when they reach the soil around the rhizome of  
386 *A. evecta*, and maintain their growth around the rhizomes even though their germination point and  
387 the initial roots are still on the rhizomes. Lastly, seedlings and saplings growing on the substrates  
388 on the rhizomes or on the margin of leaf scars can fall to the ground easily, and then can keep  
389 growing on the soil around the rhizomes. Some of the seedlings and saplings growing around the  
390 rhizomes were still attached to the substrates and pieces of rhizomes of *A. evecta* (Fig. 9c). Based  
391 on field observations, rooting in the soil around the rhizome seems to be the most frequent  
392 mechanism of establishment.

393





395 Figure 9. Three possible mechanisms for the establishment of seedlings and saplings of *Miconia*  
396 *calvescens* growing on the rhizome of *Angiopteris evecta*. The rhizome is represented as spheroid,  
397 and the initial germination point of *M. calvescens* is indicated as GP. (A) Penetration into the  
398 spaces between leaf scars. (B) Rooting in the soil around the rhizomes. (C) Growth around the  
399 rhizomes after gravity causes seedlings or saplings to fall off (Scale: 1 cm).

400



401

402 Figure 10. Rooting ability of *M. calvescens*. The figure depicts an individual plant that is re-  
403 rooting from the middle of the mature trunk (> 3 m) after the trunk has fallen across a creek.

404

405 Among the abiotic factors, light availability seems to be the main determinant of the  
406 germination of *M. calvescens* in the field. Although a previous study reported that germination  
407 occurred when there was only 2 % of full sunlight (Meyer, 1996), seedlings and saplings were  
408 mostly found in microenvironments where the canopy is less dense, or leaf litter cannot be piled  
409 up and more light is available. Such microenvironments include steep slopes, the surface of rocks,  
410 the buttresses of *I. fagifer*, soil under *I. fagifer* roots or *H. taliaceus* stems, and the rhizome of *A.*  
411 *evecta* (Fig. 11). With high canopy coverage and a thick layer of leaf litter on the forest floor, the  
412 germination of small seeded species can be suppressed (Molofsky & Augspurger, 1992), such as  
413 *M. calvescens* which has extremely small seeds (< 1 mm). Therefore, microenvironments with  
414 higher intensity of light can be highly favored. Schwartz (1993) also suggested that *M. calvescens*  
415 thrives on steep slopes because leaf litter cannot accumulate on steep surfaces. The study also  
416 referred to the presence of *M. calvescens* on the rhizomes of *A. evecta*, and explained this presence  
417 by the existence of microslopes on the rhizomes. This is consistent with a study by Medeiros and  
418 Loope (1997), which reported that dormant seed banks of *M. calvescens* became viable when the  
419 overhead canopy cleared and more light was available. These synthetic studies suggest that light

420 availability is a crucial factor that determines the germination of *M. calvescens*, even though this  
421 species is highly adapted to grow in low levels of light in the understory (Birnbaum, 1989).

422



423

424 Figure 11. *Miconia calvescens* growing in microenvironments (on steep hill, on rock, on  
425 buttresses of *I. fagifer*, under stem of *H. taliaceus*)

426

427 Light availability also can explain the inconsistency in the former studies (Underwood,  
428 1993; Bock, 1997) which described water availability as the contributing factor in the distribution  
429 of *M. calvescens* supported by the proximity of *M. calvescens* downstream of the dense hill area,  
430 but it does not explain the large invasion into the pasture area. Considering the amount of  
431 precipitation in the tropical rainforest, the availability of water is not likely to be the limiting factor  
432 for the germination and consequent distribution of *M. calvescens*. Rather, steep slopes around the  
433 streams, which prevent the accumulation of leaf litter, are more likely to induce the germination  
434 of *M. calvescens* around the streams. Furthermore, leaf litter around the streams is regularly  
435 washed away during the rainy season, which enables more sunlight to reach the soil around the  
436 streams.

437 Different decomposition rates of different species can affect the germination and  
438 recruitment of *M. calvescens* in the forest by modifying the amount of leaf litter on the ground,  
439 and therefore determining the amount of sunlight to reach the soil and the seed bank. Although  
440 other factors such as the dominance of the species in an area, the life span of the leaves, and the  
441 average number of leaves dropped by an individual plant in a certain period of time can also  
442 determine the amount of leaf litter on the ground, the decomposition rate is decisive for  
443 determining the thickness of the leaf litter. The leaf decomposition rate of *A. evecta* was much  
444 higher than other species, which is consistent with field observations that leaf litter of *A. evecta* is  
445 extremely scarce on the forest floor. The rapidly decomposing leaves of *A. evecta* can facilitate the  
446 germination of *M. calvescens* in forests with an *A. evecta* dominated understory. In contrast, slowly  
447 decomposing leaves of *Inocarpus fagifer* (Tahitian chestnut) can suppress the germination and  
448 recruitment of *M. calvescens* in *I. fagifer* dominated forests. A significantly higher density of *M.*  
449 *calvescens* was observed in some survey sites where *A. evecta* was dominant in the understory and  
450 *I. fagifer* leaf litter was small in quantity. Also, the leaf decomposition rate of *M. calvescens*  
451 differed significantly depending on burial site (0.507 to 0.924), indicating that rapid decomposition  
452 of *M. calvescens* in some sites can facilitate further recruitment and invasion of their own species  
453 in *M. calvescens* dominated forests.

454 Different light availability caused by different leaf decomposition rates can explain the  
455 different patterns of the distribution of *M. calvescens* observed in the Three Coconuts Trail and  
456 the Three Pines Trail. Three Pines Trail is heavily dominated by *Inocarpus fagifer*, which produces  
457 long (> 30 cm) and slowly decomposing leaves. Three Coconuts Trail has high populations of *I.*  
458 *fagifer* as well, but the vegetation is more mixed. The long and narrow leaves of *I. fagifer* can  
459 easily cover the rhizomes of *A. evecta*, isolating the rhizomes from sunlight. The much lower  
460 density of *M. calvescens* and weaker correlation between the height of *A. evecta* rhizomes and the  
461 number of *M. calvescens* growing on them in the sites along Three Pines Trail can be explained  
462 by the low light intensity caused by the high abundance of *I. fagifer* in the sites.

463 The shallow roots of *M. calvescens* seem to be an important characteristic that enables it  
464 to grow in steep microenvironments. Loope (1997) suggested that *M. calvescens* has an extremely  
465 shallow rooting system; subsequently leading to an increase in landslides. *Miconia calvescens* can  
466 thrive in steep microenvironments such as rock surfaces, buttresses, and rhizomes, because it has  
467 shallow roots and does not need to root in a thick layer of soil. Therefore, the germination and the  
468 establishment of the seedlings of *M. calvescens* can be facilitated by *A. evecta* because it has  
469 shallow roots.

470 Although substrates of the rhizomes of *A. evecta* had significantly more phosphorus and  
471 potassium than the soil under the rhizomes and bare soil, it is still not clear whether *A. evecta*  
472 chemically facilitates the germination of *M. calvescens*. According to several studies (Pasquini &  
473 Santiago, 2009; Wright et al., 2011; Santiago et al., 2012), potassium is the major limiting factor  
474 for seedling growth in tropical forests. Therefore, *A. evecta* might offer microenvironments with a  
475 higher concentration of potassium and assist further growth of seedlings and saplings of *M.*  
476 *calvescens*. However, a high number of the seedlings and saplings are still found in steep  
477 environments such as steep hillsides and rock surfaces where leaf litter does not accumulate; hence  
478 nutrients cannot be constantly recruited and supplied. Therefore, availability of nutrients might not  
479 be the limiting factor for the germination and growth of seedlings. Furthermore, nutrient contents  
480 of the *A. evecta* rhizome were not markedly higher than those of the bark of five dominant tree  
481 species that can potentially offer microenvironments for germination and growth of the seedlings  
482 of *M. calvescens*. Therefore, it is not certain whether the *A. evecta* rhizome chemically facilitates  
483 the germination of *M. calvescens*, or whether other aspects of the rhizome, such as its shape, enable  
484 the facilitation. Further study is needed to verify the mechanism of the facilitation of the *A. evecta*  
485 rhizome on the germination of *M. calvescens*.

486

## 487 **Conclusion**

488 Competition has been suggested as a dominant ecological principle by the most influential  
489 ecologists since Darwin. Considerable work has been done on models of competition, including  
490 the interspecific competition model by Lotka (1925) and Volterra (1931), the competitive  
491 exclusion principle (Gause, 1934; Hardin, 1960), and niche differentiation (Hutchinson, 1959;  
492 Leibold, 1995). However, the importance of positive facilitation to species, population, and

493 community level variables has been emphasized for the last few decades (Haunter & Aarssen,  
494 1988; Callaway, 1991).

495 Biological facilitation is a type of species interaction that benefits at least one of the  
496 participants and harms neither (Stachowicz, 2001). There are various examples of facilitation, such  
497 as offering refuge from physical stress, competition, and predation (Boucher *et al.*, 1982;  
498 Callaway, 1995; Bruno *et al.*, 2003; Tirado & Pugnaire, 2005). Facilitation is either mutual or  
499 commensal, but there are some exceptions with more complex interactions, such as between  
500 seedlings and nurse plants in deserts. A nurse plant is one with an established canopy, that provides  
501 increased shade, moisture, nutrients, and protection from herbivores to new plants growing under  
502 it (Holmgren *et al.*, 1966). Initially, the relationship is commensal. Later, however, as nursed plants  
503 grow and become established, they are likely to compete with nurse plants for resources (Callaway,  
504 1991; Valiente-Banuet & Ezcurra, 1991).

505 The concept of nurse plants is widely used in arid and semi-arid environments (Flores &  
506 Jurado, 2003). Nurse plants offer adjusted light, moisture, nutrients, as well as reduced herbivory  
507 to the seedlings of different species growing under them, and therefore facilitate the establishment  
508 of seedlings in harsh, barren environments. This is more common in environments such as arid or  
509 alpine environments where abiotic or other biotic factors limit the performance of seedlings (Flores  
510 & Jurado, 2003; Cavieres *et al.*, 2006). The relationships between nurse plants and target species  
511 have been studied in various environments such as desert, savannah, alpine habitat, swamp,  
512 tropical dry forest and tropical sub-humid forest (Weltzin & McPherson, 1999; Callaway *et al.*,  
513 2002; Egerova *et al.*, 2003; Flores & Jurado, 2003; Castro *et al.*, 2004; Cavieres *et al.*, 2006; Padilla  
514 & Pugnaire, 2006). However, the idea of nurse plants is not well established in the context of  
515 tropical rainforests. Former studies (Ashton *et al.*, 1997; Feyera *et al.*, 2002) examined the use of  
516 introduced species for the restoration of native vegetation in tropical forests. But few studies have  
517 been conducted on native vegetation as nurse plants. Even though *A. evecta* not only creates  
518 indirect microenvironments with adjusted abiotic features but also offers its caudex physically, it  
519 also facilitates the germination and the establishment of the seedlings of *M. calvescens*, and can  
520 hence be considered a nurse plant. Although it is similar to the concept of epiphyte because *M.*  
521 *calvescens* is physically attached to *A. evecta*, it must root in the soil around the rhizome in order  
522 to establish itself as a mature tree. Therefore, I propose a broader conceptualization of nurse plants  
523 that includes favored microenvironments with direct physical contact with the target species.

524 Although it is widely known that invasive species compete with native species, recent  
525 studies report that native species sometimes facilitate invasive species, and vice versa (Rodriguez,  
526 2006; Leger & Espeland, 2010). Biological facilitation of *M. calvescens* germination by *A. evecta*  
527 is an example of this. These positive relationships between native and invasive species can  
528 potentially explain the invasion paradox, the inconsistency between large-scale observations that  
529 show a positive correlation between the native biodiversity and invasion success and small-scale  
530 experiments that reveal competition between native and invasive species. A better understanding  
531 of the relationship between the native and invasive species could lead to an improved practical  
532 management plan for biological invasion.

533           The growth of forest in Opunohu Valley is thought to be relatively recent (Descantes, 1993).  
534 No trees were depicted in the painting by the artist Webber on Captain Cook's third Pacific voyage  
535 in 1777. However, thick, wet forest was described by Tyerman and Bennet by 1821. Furthermore,  
536 the valley is mostly dominated by the introduced species *I. fagifer* (Tahitian chestnut). This  
537 suggests that the vegetation in Opunohu Valley was highly manipulated by Tahitians. In spite of  
538 the dominance of *I. fagifer* which has big, slowly-decomposing leaves, the invasion of *M.*  
539 *calvescens* is still significant in Opunohu Valley. This suggests that controlling the invasion of *M.*  
540 *calvescens* by manipulating other vegetation would be extremely challenging.

541           The extent of the biological facilitation of *M. calvescens* by *A. evecta* can vary depending  
542 on the other vegetation present. However, it is obvious that *A. evecta* rhizomes can offer favored  
543 microenvironments for *M. calvescens* to germinate, especially when the forest is dominated by  
544 trees that have relatively rapidly decomposing leaves. Therefore, invasion of *A. evecta* in Hawaii,  
545 Costa Rica, and Jamaica (Christenhusz & Toivonen, 2008) can accelerate further invasion of *M.*  
546 *calvescens* in these places. Especially in Hawaii, both *A. evecta* and *M. calvescens* are invasive,  
547 which implies the need for a better management plan to prevent the further invasion of both plant  
548 pests. Thorough surveys of the native vegetation and current degree of invasion are needed to plan  
549 better management action.

550

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