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

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Abstract

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

Methods. Field surveys were conducted to measure A. evecta and M. calvescens by applying the 10 × 10 m² quadrat survey method. The density of seedlings, saplings, and matures plants of M. calvescens growing on the rhizomes of A. evecta and on bare soil was compared, and the correlation between the size of the rhizomes and the number of M. calvescens growing on them were checked. Comparative soil nutrient experiments were performed for the substrates of the rhizomes of A. evecta, soil under the rhizomes, and bare soils to determine whether the rhizomes are chemically different from other microenvironments. Also, chemical contents of the barks of A. evecta and five other dominant tree species that can provide potential microenvironments for seedlings and saplings of M. calvescens were analyzed. Leaf decomposition rates of five different species were compared to verify whether A. evecta has quickly decomposing leaves, and therefore induce the germination and recruitment of M. calvescens by enabling more sunlight to reach to the forest floor.

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

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

Keywords: Biological facilitation, Nurse plants, Biological invasions, *Miconia calvescens*, *Angiopteris evecta*

**Introduction**

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

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

Invasive plants are known to suppress and eventually replace native forests via various mechanisms, including competition for resources and pollinators, shading the understory, restraining the recruitment of native vegetation by allelopathy, and disrupting underground fungal mutualisms (Thomas, 1980; Callaway & Aschehoug, 2000; Brown & Mitchell, 2001; Vilà & Weiner, 2004; Stinson *et al.*, 2006; Callaway *et al.*, 2008). *Miconia calvescens* is a major plant pest in the Pacific islands including Hawai‘i, Tahiti, Mo‘orea, and other islands in French Polynesia. It shades the understory with its large leaves (> 1 m) and hinders the growth of native vegetation (Meyer, 1996). *Miconia calvescens* was introduced to Tahiti from Mexico, by retired Harvard physicist Harrison Smith at Papeari Botanical Garden in 1937 (Gaubert, 1992; Meyer, 1994). It dominated the forest over 65% of the 1,045 km² island in 1996, 60 years after the first
introduction, and caused the decline of 70-100 native species, including 35-40 species endemic to French Polynesia (Meyer, 1996; Meyer & Florence, 1996). Also, after a small population of M. calvescens was first noted on Mount Mouaputa on the island of Mo’orea in 1974 by an inhabitant of Afareiatu village, M. calvescens has spread throughout several other areas on the island (Schwartz, 1993; Meyer, 1996).

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

Methods

Study Sites

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

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

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

*Miconia calvescens*

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

Angiopteris evecta

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

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

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

![Figure 1. Map of Study Sites](https://example.com/map.png)

The study was conducted at sites along two well-known hiking trails: Three Coconuts Trail and Three Pines Trail, in Moorea, French Polynesia.

Twenty different sites were chosen at random; ten from Three Pines Trail where *M. calvescens* is less dominant, and ten from Three Coconuts Trail where the population of *M. calvescens* is higher (for GPS coordinates see Table 1). The quadrat survey method was used to survey *M. calvescens* and *A. evecta*, at a scale of 10 x 10 m².
Table 1. The GPS coordinates of the 20 field survey sites.

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

Individual *Miconia calvescens* were categorized into three groups: seedlings, saplings, and matures (Fig. 2). Individual plants were identified by noting the dark green adaxial side and purple abaxial side of leaves which become distinctive after cotyledons. Prominent acrodromous venation was used as a key characteristic for defining the sapling stage, which are not obvious in the foliage leaves of seedlings. Individual plants over 3 m were considered to be mature.
Figure 2. Seedlings and saplings of *M. calvescens* (1st row: seedlings, 2nd row: saplings. Scale: 1cm)

The height of all *M. calvescens* individual plants within the quadrat was measured. The number of each group (seedlings, saplings, and mature plants) of *M. calvescens* that grow on the rhizomes of *A. evecta* and the ground were compared. Density (individual plants per m$^2$) of each group of *M. calvescens* on rhizomes of *A. evecta* and on bare soil was calculated. Different methods were applied to calculate density in different microenvironments because the rhizomes are three-dimensional. The rhizomes of *A. evecta* were considered to be perfectly globose, although they are not completely spherical. The surface area of rhizomes was calculated by substituting data into following equation: $Surface \ Area_{\text{Rhizomes}} = 4\pi \sum (\frac{1}{2} \text{Height})^2$, and density was calculated by dividing the total number of *M. calvescens* on the rhizomes by surface area. The density of *M. calvescens* on bare soil was obtained in the same way, except that the surface area was calculated by substituting data into following equation: $Surface \ Area_{\text{Bare Soil}} = 100 - \pi \sum (\frac{1}{2} \text{Height})^2$. This calculation can simplify and effectively show the difference between bare soil and the microenvironments created by the rhizomes of *A. evecta*. However, this calculation does not reflect the entire three-dimensional circumstances of the quadrat, such as three-dimensional surface area of rocks and fallen logs and area occupied by upright tree trunks. The density of each group (seedlings, saplings, and mature plants) on the rhizomes and in bare soil was calculated, and three
t-tests were applied for each group to compare the density in different microenvironments using R (R Core Development Team, 2013).

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

**Soil nutrient experiment**

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

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

A few tree species that are dominant in Opunohu Valley that could potentially offer habitat for *M. calvescens* to germinate and grow. *Hibiscus tiliaceus* trunks often lie almost parallel to the ground, and therefore have a less steep slope on their trunk than many other plants. *Inocarpus fagifer*, *Neonauclea forsteri*, and *Falcatoria moluccana* have buttresses that support the trees, which lessen the precipitous angle of the trunks and provides a surface for small seeds to land on. *Barringtonia asiatica* is observed to have both buttresses at the base of its trunk and sometimes to have a horizontal trunk. However, none of these trees were observed to have *M. calvescens* growing on them with the exception of only a few saplings on the buttresses of *I. fagifer*. Therefore, nutrient contents of the bark of these five species and substrates of the rhizome of *A. evecta* were analyzed to determine whether the substrates of the rhizomes are chemically different than other possible biotic microenvironments. Three samples were collected for each species, and the mean
value of each nutrient was compared using an ANOVA test, followed by Tukey post hoc comparisons using R (R Core Development Team, 2013).

Leaf Decomposition experiment

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

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

Results

Field Surveys

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

Table 2. T-test statistics comparing the density of *M. calvescens* on *A. evecta* rhizomes and bare soil.
<table>
<thead>
<tr>
<th>Survey Site</th>
<th>Group</th>
<th>t-value</th>
<th>df</th>
<th>p-value</th>
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<tbody>
<tr>
<td>Three Coconuts Trail</td>
<td>Seedlings</td>
<td>10.175</td>
<td>9.004</td>
<td>3.085e-06</td>
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<tr>
<td></td>
<td>Saplings</td>
<td>7.5219</td>
<td>9.099</td>
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<td></td>
<td>Matures</td>
<td>0.8106</td>
<td>10.631</td>
<td>0.4354</td>
</tr>
<tr>
<td>Three Pines Trail</td>
<td>Seedlings</td>
<td>5.1741</td>
<td>9.007</td>
<td>5.825e-4</td>
</tr>
<tr>
<td></td>
<td>Saplings</td>
<td>4.1657</td>
<td>9.0376</td>
<td>2.405e-3</td>
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<tr>
<td></td>
<td>Matures</td>
<td>1.0957</td>
<td>9.0454</td>
<td>0.3015</td>
</tr>
</tbody>
</table>

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

At sites along Three Pines Trail where *M. calvescens* is less dominant, the mean density of seedlings on the rhizome of *A. evecta* was 2.873 m⁻², higher than the density on bare soil, which was 0.045 m⁻². The mean density of saplings on the rhizome was 2.843 m⁻², also higher than the density on bare soil of 0.063 m⁻². In contrast, the density of mature plants of 0.063 m⁻² and 0.004 m⁻², respectively, was not statistically different (Table 2; Fig. 4).
Figure 4. Density of seedlings, sapling, and mature plants of *M. calvescens* on *A. evecta* rhizomes and bare soil. Data represents sites on the Three Pines Trail.

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

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

Nitrogen content did not differ between three different microenvironments: substrates of the *A. evecta* rhizomes, soil under the rhizome, and bare soil (Table 3). However, phosphorus concentration differed among microenvironments (Table 3). Specifically, substrates on the rhizomes contained 23.33 ppm of phosphorus, higher than the concentration of 11.67 ppm in bare soil (TukeyHSD, p < 0.05). Also, potassium concentration differed among microenvironments (Table 3). Substrates on the rhizomes contained 147 ppm of potassium, a much higher concentration than both that of the soil under the rhizomes and bare soil (TukeyHSD, p < 0.05, p < 0.05). Results are shown in Fig. 6.

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

<table>
<thead>
<tr>
<th></th>
<th>F value</th>
<th>p-value</th>
</tr>
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<tbody>
<tr>
<td>Nitrogen</td>
<td>2.33</td>
<td>0.178</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>7.17</td>
<td>0.0257</td>
</tr>
<tr>
<td>Potassium</td>
<td>8.6</td>
<td>0.0173</td>
</tr>
</tbody>
</table>

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

Nitrogen contents differed among six species: *Angiopteris evecta*, *Inocarpus fagifer*, *Neonauclea forsteri*, *Falcataria moluccana*, *Barringtonia asiatica*, and *Hibiscus tiliaceus* (Table 4). However, the concentration of nitrogen in *A. evecta* did not significantly differ from other species (TukeyHSD, p = 0.013, p = 0.006, p = 0.93, p = 0.47, p = 0.93). Phosphorus and potassium contents of the six species did not differ (Table 4). Results are shown in Fig. 7.
Table 4. ANOVA statistics comparing nutrient contents among six dominant tree species in Opunohu Valley: \textit{Angiopteris evecta, Inocarpus fagifer, Neonauclea forsteri, Falcataria moluccana, Barringtonia asiatica, and Hibiscus tiliaceus}

<table>
<thead>
<tr>
<th>Nutrient</th>
<th>F value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nitrogen</td>
<td>10.01</td>
<td>0.0006</td>
</tr>
<tr>
<td>Phosphorus</td>
<td>3.067</td>
<td>0.052</td>
</tr>
<tr>
<td>Potassium</td>
<td>0.779</td>
<td>0.58</td>
</tr>
</tbody>
</table>

Figure 7. Nutrient contents comparison between the substrates and the barks of six species: \textit{Angiopteris evecta, Inocarpus fagifer, Neonauclea forsteri, Falcataria moluccana, Barringtonia asiatica} and \textit{Hibiscus tiliaceus}

\textbf{Leaf Decomposition Experiment}

Mean leaf decomposition rates of the five species: \textit{A. evecta, M. calvescens, H. tiliaceus, B. asiatica} and \textit{I. fagifer}, were 0.914, 0.692, 0.590, 0.572 and 0.255, respectively (Fig. 8), and differed from one another (ANOVA, $F = 15.64, p < 0.0005$). The decomposition rates of \textit{A. evecta, B. asiatica} and \textit{I. fagifer} were uniform regardless of the burial site (standard deviation was 0.033, 0.016 and 0.012, respectively). However, the rates of \textit{M. calvescens} and \textit{H. tiliaceus} varied depending on the burial site (standard deviation was 0.17 and 0.068, respectively). The decomposition rate of \textit{A. evecta} was significantly higher compared to the other species (Table 4). In contrast, \textit{I. fagifer} had a much lower rate than the other species (Table 4).
Figure 8. Leaf decomposition rate of five dominant tree species in Opunohu Valley, Mo’orea

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

<table>
<thead>
<tr>
<th></th>
<th>A. evecta</th>
<th>M. calvescens</th>
<th>H. tiliaceus</th>
<th>B. asiatica</th>
<th>I. fagifer</th>
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<td></td>
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<td>&lt; 0.05</td>
<td>&lt; 0.05</td>
<td>&lt; 0.0005</td>
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<td>B. asiatica</td>
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<td>I. fagifer</td>
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Discussion

Field surveys show that A. evecta facilitates the germination of M. calvescens. There were significantly higher numbers of seedlings and saplings of invasive M. calvescens growing on the rhizomes of A. evecta compared to bare soil at the sites along the Three Coconuts Trail where M. calvescens is reported to be dominant. 90.93% of total seedlings were growing on A. evecta, 57.32% of total saplings were growing on the rhizome, and 11.90% of mature plants were growing on or associated with the rhizome. At the sites along Three Pines Trail where the population of M. calvescens is reported to be lower, much larger quantities of seedlings and saplings were growing on the rhizome of A. evecta. 72.15% of seedlings, 62.50% of saplings, and 55.55% of mature plants were found on the rhizome. Both the percentage of each group of M. calvescens growing on the rhizome and the density of each group growing in each environment suggest that there is a much
higher abundance of *M. calvescens* seedlings and saplings growing on the rhizome of *A. evecta* compared to in bare soil. This indicates that *A. evecta* facilitates the germination of *M. calvescens*. Also, a positive correlation between the size of rhizomes and the number of *M. calvescens* growing on them supports the theory that the existence of *M. calvescens* on the rhizomes is not a coincidence, but that the rhizomes are actually preferable microenvironments. However, only a few *M. calvescens* that start life on the rhizome reach maturity. This may be due to the scarce substrates on the rhizomes, or to competition with *A. evecta* for resources.

There are three possible mechanisms for the establishment of seedlings and saplings of *M. calvescens* on the rhizomes of *A. evecta*. First, they can penetrate their roots into the spaces between the leaf scars on the rhizomes, reaching to the soil under the rhizomes and supplying nutrients and water for themselves (Fig. 9a). Second, they can grow horizontally towards the soil around the rhizomes, and then grow upward to the canopy after they root in the soil (Fig. 9b). *Miconia calvescens* has the ability to root from the middle of the stem where it has contact with soil or water (Fig. 10). Therefore, they can re-root when they reach the soil around the rhizome of *A. evecta*, and maintain their growth around the rhizomes even though their germination point and the initial roots are still on the rhizomes. Lastly, seedlings and saplings growing on the substrates on the rhizomes or on the margin of leaf scars can fall to the ground easily, and then can keep growing on the soil around the rhizomes. Some of the seedlings and saplings growing around the rhizomes were still attached to the substrates and pieces of rhizomes of *A. evecta* (Fig. 9c). Based on field observations, rooting in the soil around the rhizome seems to be the most frequent mechanism of establishment.
Figure 9. Three possible mechanisms for the establishment of seedlings and saplings of *Miconia calvescens* growing on the rhizome of *Angiopteris evecta*. The rhizome is represented as spheroid, and the initial germination point of *M. calvescens* is indicated as GP. (A) Penetration into the spaces between leaf scars. (B) Rooting in the soil around the rhizomes. (C) Growth around the rhizomes after gravity causes seedlings or saplings to fall off (Scale: 1 cm).

Among the abiotic factors, light availability seems to be the main determinant of the germination of *M. calvescens* in the field. Although a previous study reported that germination occurred when there was only 2% of full sunlight (Meyer, 1996), seedlings and saplings were mostly found in microenvironments where the canopy is less dense, or leaf litter cannot be piled up and more light is available. Such microenvironments include steep slopes, the surface of rocks, the buttresses of *I. fagifer*, soil under *I. fagifer* roots or *H. taliaceus* stems, and the rhizome of *A. evecta* (Fig. 11). With high canopy coverage and a thick layer of leaf litter on the forest floor, the germination of small seeded species can be suppressed (Molofsky & Augspurger, 1992), such as *M. calvescens* which has extremely small seeds (<1 mm). Therefore, microenvironments with higher intensity of light can be highly favored. Schwartz (1993) also suggested that *M. calvescens* thrives on steep slopes because leaf litter cannot accumulate on steep surfaces. The study also referred to the presence of *M. calvescens* on the rhizomes of *A. evecta*, and explained this presence by the existence of microslopes on the rhizomes. This is consistent with a study by Medeiros and Loope (1997), which reported that dormant seed banks of *M. calvescens* became viable when the overhead canopy cleared and more light was available. These synthetic studies suggest that light...
availability is a crucial factor that determines the germination of *M. calvescens*, even though this species is highly adapted to grow in low levels of light in the understory (Birnbaum, 1989).

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

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

Figure 11. *Miconia calvescens* growing in microenvironments (on steep hill, on rock, on buttresses of *I. fagifer*, under stem of *H. taliaceus*)
Different light availability caused by different leaf decomposition rates can explain the different patterns of the distribution of *M. calvescens* observed in the Three Coconuts Trail and the Three Pines Trail. Three Pines Trail is heavily dominated by *Inocarpus fagifer*, which produces long (> 30 cm) and slowly decomposing leaves. Three Coconuts Trail has high populations of *I. fagifer* as well, but the vegetation is more mixed. The long and narrow leaves of *I. fagifer* can easily cover the rhizomes of *A. evecta*, isolating the rhizomes from sunlight. The much lower density of *M. calvescens* and weaker correlation between the height of *A. evecta* rhizomes and the number of *M. calvescens* growing on them in the sites along Three Pines Trail can be explained by the low light intensity caused by the high abundance of *I. fagifer* in the sites.

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

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

**Conclusion**

Competition has been suggested as a dominant ecological principle by the most influential ecologists since Darwin. Considerable work has been done on models of competition, including the interspecific competition model by Lotka (1925) and Volterra (1931), the competitive exclusion principle (Gause, 1934; Hardin, 1960), and niche differentiation (Hutchinson, 1959; Leibold, 1995). However, the importance of positive facilitation to species, population, and
community level variables has been emphasized for the last few decades (Haunter & Aarssen, 1988; Callaway, 1991).

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

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

Although it is widely known that invasive species compete with native species, recent studies report that native species sometimes facilitate invasive species, and vice versa (Rodriguez, 2006; Leger & Espeland, 2010). Biological facilitation of M. calvescens germination by A. evecta is an example of this. These positive relationships between native and invasive species can potentially explain the invasion paradox, the inconsistency between large-scale observations that show a positive correlation between the native biodiversity and invasion success and small-scale experiments that reveal competition between native and invasive species. A better understanding of the relationship between the native and invasive species could lead to an improved practical management plan for biological invasion.
The growth of forest in Opunohu Valley is thought to be relatively recent (Descantes, 1993). No trees were depicted in the painting by the artist Webber on Captain Cook’s third Pacific voyage in 1777. However, thick, wet forest was described by Tyerman and Bennet by 1821. Furthermore, the valley is mostly dominated by the introduced species *I. fagifer* (Tahitian chestnut). This suggests that the vegetation in Opunohu Valley was highly manipulated by Tahitians. In spite of the dominance of *I. fagifer* which has big, slowly-decomposing leaves, the invasion of *M. calvescens* is still significant in Opunohu Valley. This suggests that controlling the invasion of *M. calvescens* by manipulating other vegetation would be extremely challenging.

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

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