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 m^2 quadrat survey method. The density of seedlings, saplings, and matures 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 was checked. Comparative soil nutrient experiments were done for the substrates of the rhizomes of *A. evecta*, soil under the rhizomes, and bare soils to check whether the rhizomes are chemically different than other microenvironments.

Results. Field surveys show that there is a greater number of seedlings and saplings of *M. calvescens* growing on the rhizomes of *A. evecta* as compared to bare soil. Furthermore, there is a positive correlation between the size of rhizome and the number of *M. calvescens* growing on them. Substrates of *A. evecta* had higher phosphorus and potassium contents compared to other soil and substrates.

Discussion. *Angiopteris evecta* is facilitating 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 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 fast 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 the seed bank. The germination of trees in tropical rainforests is often limited by the availability for 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 of the germination of *M. calvescens*. Biological facilitation of the germination of invasive *M. calvescens* by native *A. evecta* can give better understanding on the invasion success and the relationship between the native and invasive species. Invasion of *A. evecta* can induce and promote further invasion of *M. calvescens*. Therefore, thorough management of ongoing invasion of *A. evecta* in some places is especially required.

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

Introduction

Concerns about biological invasions have been increased because of their role 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 the invasions (Elton, 1958; Vitousek *et al.*, 1997; Tilman, 1999). However, finding 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 community and the 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 the 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 the 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 by 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 Hawaii, 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 a retired Harvard physicist Harrison Smith at Papeari botanical garden in 1937 (Gaubert, 1992; Meyer, 1994). It dominated over 65% of the forest on the 1,045 km^2 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 to be threatened (Meyer, 1996; Meyer & Florence, 1996). Also, after a small population of *M. calvescens* was first noted on Mt. Mouaputa on the island of Mo’orea in 1974 by an inhabitant of village Afareiatu, *M. calvescens* has been spread throughout several other areas on the island (Schwartz, 1993; Meyer, 1996).

This study aims to give an insight on the role of *A. evecta* on the germination of *M. calvescens*, to understand the biological facilitation in interspecific plants and to suggest possible management of plant invasions on Pacific islands. Schwartz (1933) noted that *M. calvescens* are often found on the caudices of a giant tree fern *Angiopteris evecta*. According to a pilot study, seedlings, juveniles, and occasionally matures (> 3 m) of *M. calvescens* inhabit on and underneath rhizomes of *A. evecta* in high frequency. Also, the abundance of *M. calvescens* tends to be higher in forests with an *A. evecta*-dominated understory. It is unknown whether *A. evecta* is facilitating the germination of *M. calvescens*; however, it is possible that *A. evecta* is offering environments with higher intensity of light, or providing chemically preferred 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. The age of 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 the east to the west. Opunohu Valley is one of the two nearly identical bays on 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 in two famous hiking trails in Opunohu Valley: Three Coconuts Trail and Three Pines Trail (Fig. 1). This study was conducted on the sites along these two trails. The vegetation composition of two trails is reported to be slightly different. Agnew (2014) noted that the study sites along Three Pines Trail was characterized by high amount of *Inocarpus fagifer* and moderate *Miconia calvescens*, and Three Coconuts Trail by *Hibiscus tiliaceus*, *Miconia calvescens*, and small ferns. According to a pilot study, the distribution of dominant trees in Opunohu Valley confirmed these earlier finds. The frequency of *H. tiliaceus*, *Neonauclea forsteri*, and *Falcataria moluccana* seems to be similar. *Barringtonia asiatica* was observed almost exclusively on Three Coconuts Trail. Three Pines Trail was almost dominated by *I. fagifer*, and the frequency of *Miconia calvescens* was higher on Three Coconuts Trail. The density of *Angiopteris evecta* seems 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 starts to produce 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 barks of trees (Schwartz, 1993). Meyer (1994) has verified *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 is opened up 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 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 protruded 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, and also to 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 unrestrictedly naturalize 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 few angiosperm seedlings and saplings. In Opunohu Valley, Mo'orea, less than 5 species of angiosperm seedlings and saplings inhabit on the rhizomes, and *M. calvescens* is the most frequent one.

Field Surveys

Field surveys were done in Opunohu Valley, Mo'orea (Fig. 1). The study by 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 range of 0 to 1,492 m (Christenhusz & Toivonen, 2008). In this study, surveys were conducted in accessible forests close to hiking trails, approximately ranging from 100 to 400 m.

Twenty different sites were randomly chosen: ten from lower elevation where *M. calvescens* is less dominant, and ten from Three Coconut Trail where the population of *M.*

calvescens is higher (For GPS coordinates see Table 1). Quadrat survey method was applied to survey *M. calvescens* and *A. evecta*, and 10 x 10 m^2 quadrat was used.

Miconia calvescens individuals were categorized into three groups: seedlings, saplings, and matures (Fig. 2). Individuals were identified by noting their dark green adaxial side and purple abaxial side of leaves which become distinctive after cotyledons. Existence of obvious outer midribs along the leaf margin were used as a key feature for defining sapling stage, which are not prominent in the foliage leaves of seedlings. Individuals over 3 m were considered to be mature.

The heights of all *M. calvescens* individuals within the quadrat were measured. The number of each group (seedlings, saplings, and matures) of *M. calvescens* that grow on the rhizomes of *A. evecta* and the ground were compared. Densities (individuals per m^2) of each group of *M. calvescens* on the rhizomes of *A. evecta* and on bare soil were calculated. Different methods were applied to calculate density on different microenvironments because the rhizomes are three-dimensional. The rhizomes of *A. evecta* were considered as perfectly globose, although they are not completely spherical. The surface area of the rhizomes was calculated by substituting data into following equation: $Surface\ Area_{Rhizomes} = 4\pi \sum(\frac{1}{2}\ Height)^2$, and the 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 same way, except for that the surface area was calculated by substituting data into following equation; $Surface\ Area_{Bare\ Soil} = 100 - \pi \sum(\frac{1}{2}\ Height)^2$. The densities of each group (seedlings, saplings, and matures) on the rhizomes and bare soil were calculated respectively, and three respective t-tests were applied for each group to compare the density on different microenvironments by using R (R Core Development Team, 2013).

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

Soil nutrient experiment

Comparative soil nutrient experiments were conducted to check whether substrates of *A. evecta* are chemically different than other soils, hence offering microenvironments with higher nutrient contents. Nitrogen, phosphorus, and potassium contents of three different microenvironments, substrates of the rhizomes of *A. evecta*, soil under the rhizomes, and bare soil, were compared. Two grams of each dried substrate and soil sample were reserved to test the nutrient concentration using a LaMotte Soil Test Kit following the manufacturer's instructions (LaMotte Company, 2016).

Three samples were collected from three respective microenvironments, and the mean value of each nutrient content was compared with an ANOVA test, and then a Tukey post hoc comparisons by using R (R Core Development Team, 2013).

Results

Field Surveys

At sites along Three Coconuts Trail, the mean density of *M. calvescens* seedlings on the rhizome of *A. evecta* 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 that on bare soil, which was 0.174 m^{-2}. However, the density of matures did not differ between rhizomes and bare soil, which were 0.077 m^{-2} and 0.043 m^{-2}, respectively (Table 2; Fig. 3).

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 that on bare soil, which was 0.063 m^{-2}. In contrast, the density of matures was not statistically different, which were 0.063 m^{-2} and 0.004 m^{-2}, respectively (Table 2; Fig. 4).

At sites along Three Coconuts Trail where *M. calvescens* are abundant, the correlation between the heights of *A. evecta* rhizomes and the number *M. calvescens* growing on them of appeared to follow an exponential model ($R^2 = 0.63$, $F_{1/121} = 208.3$, $p < 0.00001$) (Fig. 5a). In 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).

Soil Nutrients Experiment

Nitrogen content did not differ between three different microenvironments: on *A. evecta* rhizomes, soil under the rhizome, and bare soil. However, phosphorus concentration differed between microenvironments. Specifically, substrates on the rhizomes contained 58.9 ppm of phosphorus, much higher than the soil under rhizome and bare soil, which were 14.5 ppm and 11.8 ppm, respectively (TukeyHSD, $p < 0.005$, $p < 0.005$). Also, potassium concentration differed between microenvironments. Substrates on the rhizomes contained 344 ppm of potassium, higher than that of bare soil, which was 145 ppm. (TukeyHSD, $p < 0.05$) (Table 3; Fig. 6)

Discussion

Field surveys show that *A. evecta* is facilitating 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 the bare soil at the sites along the Three Coconuts Trail where *M. calvescens* is reported to be dominant. Especially for seedlings, 90.93% of total seedlings were growing on *A. evecta*. 57.32% of total saplings were growing on the rhizome, and 11.90% of matures were growing on or associated with the rhizome. At the sites along the Three Pines Trail where the population of *M. calvescens* is reported to be lower, still much larger amounts of seedlings and saplings were growing on the rhizome of *A. evecta*. 72.15% of seedlings, 62.50% of saplings, and 55.55% of matures 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 on each environment suggest that there is a much higher abundance of *M. calvescens* seedlings and saplings growing on the rhizome of *A. evecta*. This indicates that *A. evecta* is actually facilitating the germination of *M. calvescens*. Also, a positive correlation between the size of rhizomes and the number of *M. calvescens* growing on them supports that the existence of *M. calvescens* on the rhizomes is not a coincidence, but the rhizomes are actually preferable microenvironments. However, once they start their life on the rhizomes, only a few of them reach to the mature stages. This is possibly due to the scarce substrates on the rhizomes, or competition with *A. evecta* for resources.

There are three possible mechanisms for the establishment of seedlings and saplings of *M. calvescens* growing on the rhizomes of *A. evecta*. First, they can penetrate their roots into the spaces between the leaf scars on the rhizomes, reach to the soil under the rhizomes and supply nutrients and water for themselves (Fig. 7a). Second, they can grow horizontally towards the soil around the rhizomes, and then grow upward to the canopy after they root to the soil (Fig. 7b). *Miconia calvescens* has the ability to root from the middle of the stem where it is in contact with soil or water. Therefore, they can re-root when they reach the soil around the rhizome of *A. evecta*, and keep 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. 7c). Based on the field observations, rooting to the soil around the rhizome seems to be the most frequent way to establish.

Among the abiotic factors, light availability seems to mainly determine the germination of *M. calvescens* in the field. Even though a previous study reported that the germination happened when there was only 2% of full sunlight (Meyer, 1996), seedlings and saplings were mostly found on microenvironments where the canopy is less dense, or where leaf litter cannot be piled up and more light is available, such as steep slopes, surface of rocks, the buttresses of *I. fagifer*, soil under *I. fagifer* root or *H. taliaceus* stem, and the rhizome of *A. evecta* (Fig. 8). With a highly-covered canopy 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 a higher intensity of light can be highly favored. Schwartz (1993) also suggested that *M. calvescens* thrive on steep slopes because leaf litter cannot be accumulated on steep surfaces. The study also referred to the presence of *M. calvescens* on the rhizomes of *A. evecta*, and explained the presence by existence of the microslopes on the rhizomes. This is consistent with the study of Medeiros and Loope (1997) which reported that dormant seed banks of *M. calvescens* became viable when the overhead canopy was cleared up and more light was available. These synthetic studies suggest that availability for light is a crucial factor that determines the germination of *M. calvescens*, even though it is highly adapted to grow in low levels of light in the understory (Birnbaum, 1989).

Availability for light can also explain the inconsistency in the former studies (Underwood, 1993; Bock, 1997) which described water availability as the contributing factor for 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 litters are more likely to induce the germination of *M. calvescens* around the streams. Furthermore, leaf litters around the streams are regularly washed away during the rainy season, which enables more sunlight to reach to the soil around the streams.

Based on the field observations, *A. evecta* has fast decomposing leaves, supported by scarce leaf litter of *A. evecta* on the forest floor. In contrast, *Inocarpus fagifer* (Tahitian chestnut) has slowly decomposing leaves, supported by high abundance of dried leaves of *I. fagifer* that are barely decomposed. Different decomposition rates of different species can affect the germination and the recruitment of *M. calvescens* in the forest by modifying the amount of leaf litter on the ground, hence determining the amount of sunlight to reach to the soil and the seed bank. Fast decomposing leaves of *A. evecta* can facilitate the germination of *M. calvescens* in the forest with *A. evecta* dominated understory. In contrast, slowly decomposing leaves of *I. fagifer* can suppress the germination and the recruitment of *M. calvescens* in *I. fagifer* dominated forests. There was a significantly higher density of *M. calvescens* in some survey sites where *A. evecta* was dominant in the understory and *I. fagifer* leaf litters were small in quantity.

Different light availability caused by different leaf decomposition rates can explain the different patterns between the Three Coconuts Trail and the Three Pines Trail. Three Pines Trail is heavily dominated by *I. fagifer*, which produces long (> 30 cm) and slowly decomposing leaves. In Three Coconuts Trail, there are also high populations of *I. fagifer*, but the vegetation is more mixed. Long and narrow shaped leaves of *I. fagifer* can easily cover the rhizomes of *A. evecta*, and isolate the rhizomes from sunlight. 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 interpreted by low intensity of light that is caused by high abundance of *I. fagifer* in the sites.

Shallow roots of *M. calvescens* seem to be the important feature that enable them to grow on steep microenvironments. Loope (1997) suggested that *M. calvescens* have extremely shallow rooting system; therefore they can increase landslides subsequently. *Miconia calvescens* can thrive on steep microenvironments such as surfaces of rocks, buttresses, and rhizomes, because they have shallow roots and do not require to root into thick layer of soil. Other few angiosperms that inhabit the rhizomes of *A. evecta* also had shallow roots in common. 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 larger amount of phosphorus and potassium compared to the soil under the rhizomes and bare soil, it is still not clear whether *A. evecta* is chemically facilitating the germination of *M. calvescens*. According to former studies (Pasquini & Santiago, 2009; Wright et al., 2011; Santiago et al., 2012), potassium is the major limiting factor for growth of seedlings 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 on steep environments such as steep hillsides and rock surfaces where leaf litters are not accumulating; hence the nutrients cannot be constantly recruited and supplied. Therefore, availability for nutrients might not be the limiting factor for the germination and the growth of seedlings. Further study is needed to verify whether potassium is the limiting factor for the germination and growth of *M. calvescens*, hence *A. evecta* offers chemically preferred microenvironments.

Conclusion

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

Biological facilitation is a type of species interaction which benefits at least one of the participants and harms neither (Stachowicz, 2001). There are various examples of facilitation, such as offering refugee 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, therefore facilitating 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 are limiting 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 isn't well established in the tropical rainforest. 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 not many studies were conducted on native vegetation as nurse plants. Even though *A. evecta* is not only creating indirect microenvironments with adjusted abiotic features but also offering its caudex physically, it is also facilitating the germination and the establishment of the seedlings of *M. calvescens*, and can hence be considered as a nurse plant. Although it is similar to the concept of epiphyte because *M. calvescens* is physically attaching to *A. evecta*, it requires rooting into the soil around the rhizome in order to establish itself to a mature tree. Therefore, I suggest a broader concept for nurse plants that includes favored microenvironments with direct physical contacts with the target species.

Although it has been widely known that invasive species compete with native species, recent studies reported that native species sometimes facilitate invasive species, and vice versa (Rodriguez, 2006; Leger & Espeland, 2010). Biological facilitation of the germination of *M. calvescens* by *A. evecta* is an example of this. These positive relationships between the native and invasive species can potentially explain the invasion paradox, the inconsistency between the large-scale observations that show a positive correlation between the native biodiversity and the invasion success and the small-scale experiments reveal competition between the native and invasive species. Better understanding for the relationship between the native and invasive species can potentially suggest more a practical management plan for biological invasions.

The growth of forest in Opunohu Valley is thought to be relatively recent (Descantes, 1993). There were no trees described in the painting of the artist Webber on Captain Cook's third Pacific voyage in 1777. However, there was a thick, wet forest noted by Tyerman and Bennet by 1821. Also, 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. Despite of the dominance of *I. fagifer* which has big, fast-decomposing leaves, the invasion of *M. calvescens* is still heavier in Opunohu Valley. This suggests that controlling the invasion of *M. calvescens* by manipulating vegetation would be extremely challenging.

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

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Tables & Figures

Table 1. The GPS coordinates of the 20 field survey sites. The surveys were conducted on the sites along two different hiking trails: Three Coconuts Trail and Three Pines Trail, in Opunohu Valley, Mo’orea.

Sites	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’

Table 2. T-test statistics between the density of *M. calvescens* on *A. evecta* rhizome and bare soil.

Survey Site	Group	t-value	df	p-value
Three Coconuts Trail	Seedlings	10.175	9.004	< 0.0001
	Saplings	7.5219	9.099	< 0.0001
	Matures	0.8106	10.631	0.4354
Three Pines Trail	Seedlings	5.1741	9.007	< 0.001
	Saplings	4.1657	9.0376	< 0.005
	Matures	1.0957	9.0454	0.3015

Table 3. ANOVA statistics of soil nutrients compared between three different microenvironments: substrates of the rhizomes of *A. evecta*, soil under the rhizomes, and bare soil

	F value	p-value
Nitrogen	0.13	0.88
Phosphorus	19	0.0024
Potassium	6.2	0.035

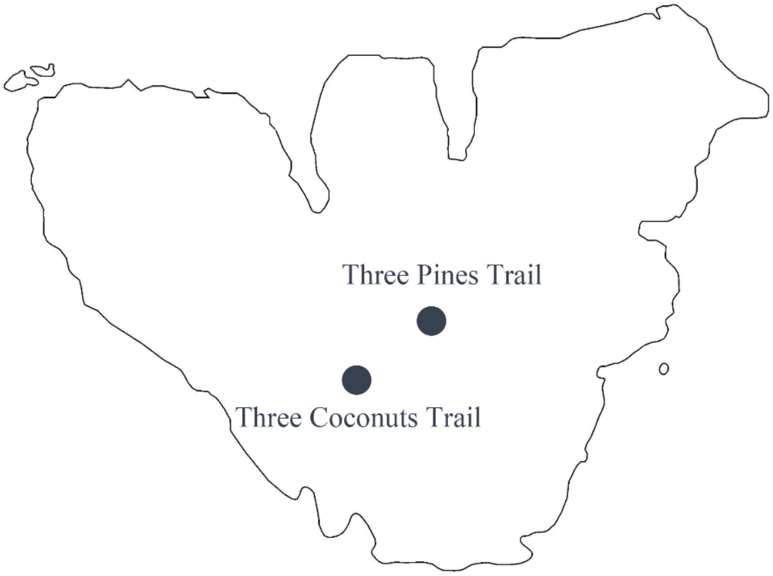


Figure 1. Map of Study Sites. This study was conducted on the sites along two hiking trails: Three Coconuts Trail and Three Pines Trail, in Opunohu Valley, Mo’orea.

Figure 2. Seedlings and Saplings of *Miconia calvescens* (1st raw: seedlings, 2nd raw: saplings. Scale: 1cm)

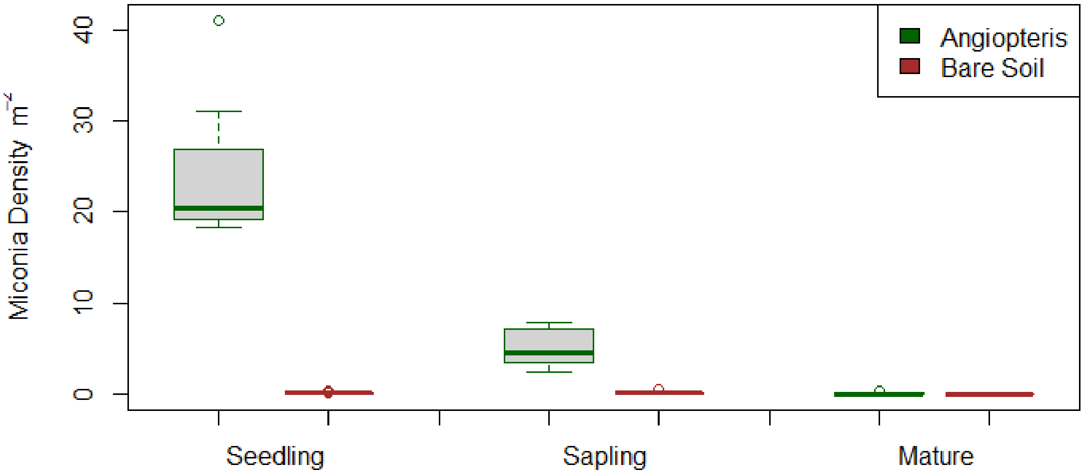


Figure 3. Density of seedlings, sapling, and matures of *M. calvescens* on *A. evecta* rhizome and bare soil. Data represents sites on the Three Coconuts Trail (t-tests, $p < 0.0001$, $p < 0.0001$, $p > 0.1$)

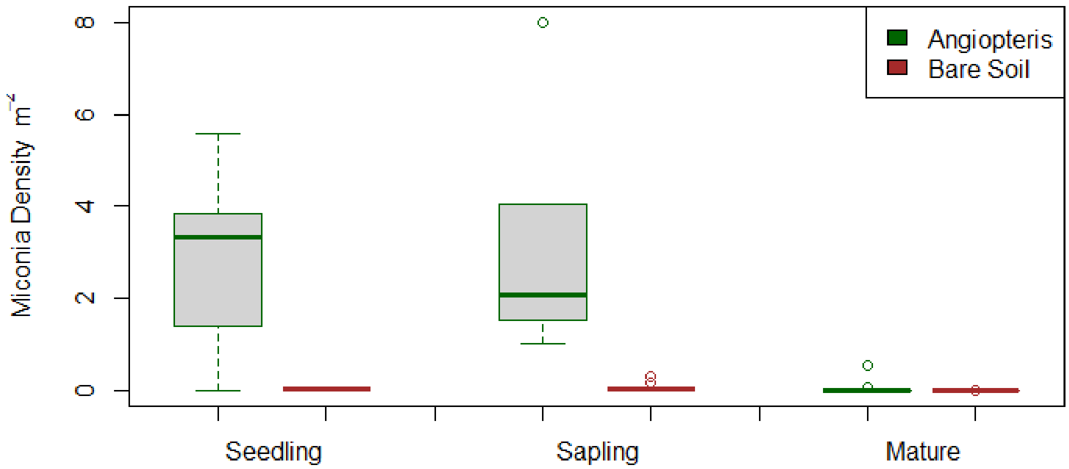
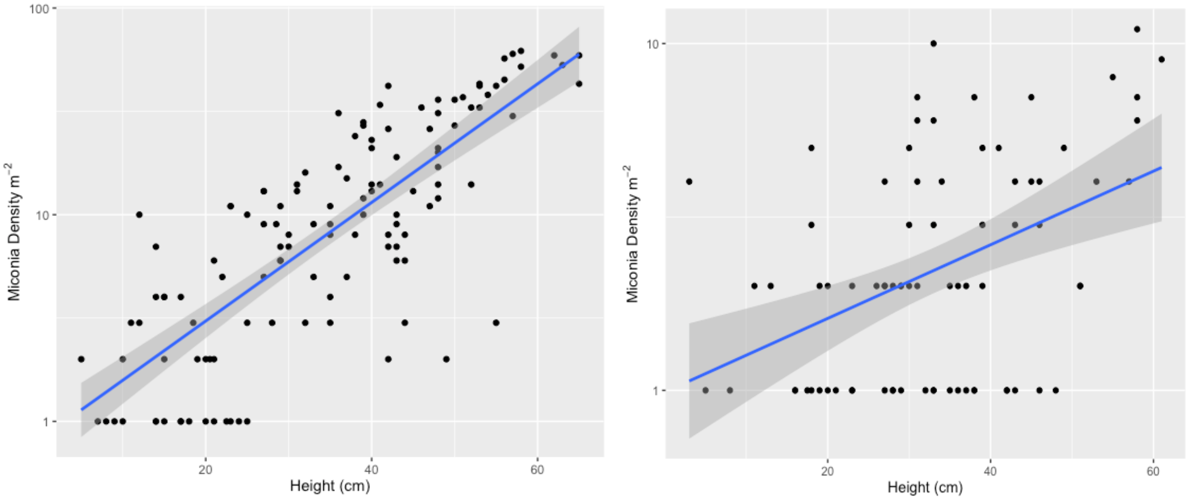


Figure 4. Density of seedlings, sapling, and matures of *M. calvescens* on *A. evecta* rhizomes and bare soil. Data represents sites on the Three Pines Trail. (t-tests, $p < 0.001$, $p < 0.005$, $p > 0.1$)



(a) (b)

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

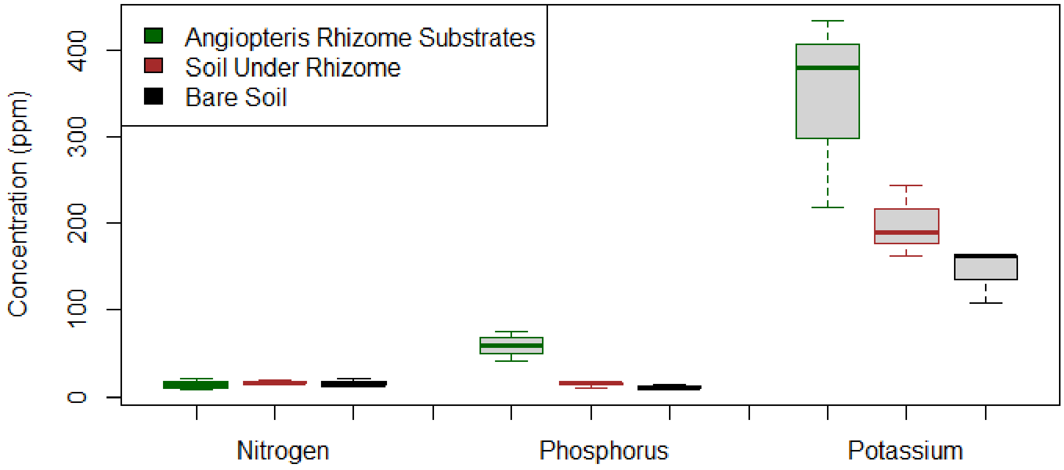


Figure 6. Soil nutrient comparison between three different microenvironments: substrates of the rhizomes of *A. evecta*, soil under the rhizomes, and bare soil

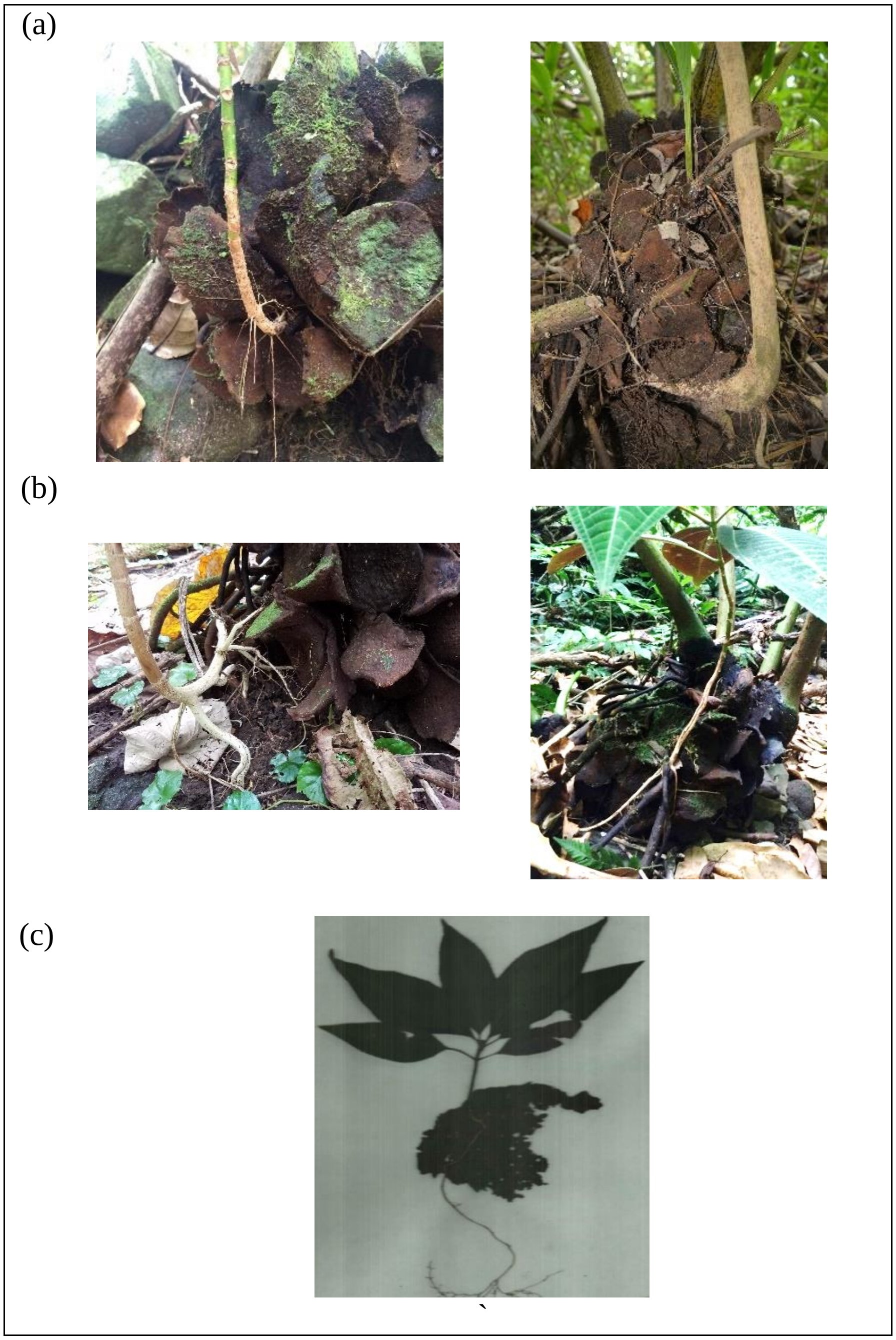


Figure 7. Three possible mechanisms for the establishment of seedlings and saplings growing on the rhizome of *A. evecta*. (a) Penetration into the spaces between leaf scars. (b) Rooting to the soil around the rhizomes. (c) Grow around the rhizomes after being fallen off the rhizomes by gravity.

Figure 8. *Miconia calvescens* growing on microenvironments (on rock, on buttresses of *Inocarpus fagifer*, under stem of *Hibiscus taliaceus*