INSIDIOUS ISLAND INVASION: AN EXPLORATION OF *FALCATARIA MOLUCCANA* STAND ECOLOGY

AMANDA J. MINNICH

Integrative Biology, University of California, Berkeley, California 94720 USA

Abstract. Mo'orea, French Polynesia of the Society Islands archipelago is a highly isolated volcanic Pacific Island. It is vulnerable to invasion by introduced species due to this isolation in conjunction with its small size and disharmonic native biota. *Falcataria moluccana* is one such invader; since its introduction in the 1960s to reforest burned and eroded ridges it has established monodominant stands throughout the island. I studied the effects of this species on vegetation ecology, specifically native and non-native understory diversity, tree community dynamics, and species spread potential. Contrary to expectations, I found that native understory was able to persist despite ecosystem modifications caused by *F. moluccana*. However, the majority of native species present were post-disturbance taxa. Tree community analysis revealed that *F. moluccana* trees are able to grow to large sizes where other trees cannot, which suggests either niche differentiation or resource monopolization. Seedling count results indicate that this species may be enabling its spread through ecosystem modification, specifically the infusion of nitrogen into the environment via leaf litter. Future studies on long-term dynamics of *F. moluccana* stands combined with germination studies, soil chemistry analyses, and resource availability surveys would be beneficial to future conservation efforts on Mo'orea.

Key words: invasive species; Falcataria moluccana; native plant diversity; Mo'orea; French Polynesia; global change ecology

INTRODUCTION

The introduction of alien species into a foreign environment is a known threat to native biodiversity and a source of major global environmental change (Vitousek 1997). Once introduced, a species can extirpate (go locally extinct), naturalize (reproduce freely but not spread outside of disturbed areas), or invade (spreads into neighboring native environments) (Richardson 1998). The most destructive of these invaders are those that not only monopolize the resources of an area through their growth patterns but also modify the ecosystem in which they grow, enabling them to edge out native vegetation and form monodominant stands (Vitousek 1997).

One type of invader that is becoming a large concern is introduced tree species. Introduced trees have historically been cultivated for lumber use and pulp production. In the past century alternate uses have emerged, particularly in the area of agroforestry. The term agroforestry refers to the use of trees in agriculture, whether as windbreaks or to help increase the nitrogen content of the soil. Alien tree species are often chosen over native species for their high growth rates; wide availability of seeds; and nitrogen fixing abilities, which help to restore degraded landscapes (Meyer 2002; Richardson 1998).

Initially only the benefits of these trees were noted, with little attention paid to negative long-term effects on natural habitats. While agroforestry can potentially increase crop yields and help decrease the degradation of soil, non-native tree species can spread to land previously occupied by native forest and cause great harm (McNeely 2004, Richardson 1998). Alien trees have the ability to completely transform a native forest, reducing structural diversity, disrupting prevailing vegetation dynamics, altering nutrient cycling, and affecting a myriad of other variables such as litterfall and decomposition rates, fire behavior, vegetation height, plant density, leaf area index, and energy balance (Richardson 1998, Versfeld & van Wilgen 1986).

Mo'orea, French Polynesia, is a Pacific volcanic island between 1.5 and 2.2 million years old. As an island, its ecosystem is particularly vulnerable to the effects of invasive species, due to its small size, isolated nature, and disharmonic native biota (Vitousek 1997). There are a number of plant species that are considered invasive threats on this island, including *Spathodea campanulata,* *Myconia calvescens*, and *F. moluccana* (Meyer 2004).

Falcataria moluccana is a textbook example of an aggressive invader. This species, which grows easily in disturbed habitats, was introduced by the Water and Forests Section of the Agricultural Service Department to reforest land that had been degraded by fires or erosion (FAO 2003). *Falcataria moluccana* trees affect the surrounding ecosystem in three main ways: they dump high levels of nitrogen via leaf litter into the environment; they fix nitrogen, increasing biologically available nitrogen levels; and they form a dense emergent canopy layer, significantly decreasing the amount of sunlight reaching the understory community (Hughes 2006). Their nitrogen dumping and fixing abilities lead to secondary ecosystem effects, including decreased fungal to bacterial ratios and increased abundance of extracellular enzymes that process carbon and nitrogen (Allison et al. 2006). By changing basic ecosystem processes, these trees drastically alter the environment in which neighboring biota live and reproduce. These changes can make it more difficult for native biota to grow, as well as potentially facilitate invasion by other non-native species (Hughes 2004; Sumida et al. 2005). In general, increased nutrient levels have been correlated with increased abundance and diversity of introduced plants (Hughes 2004).

My study sought to understand how variations in abiotic factors affect overall stand ecology. Specifically, I hoped to identify trends governing understory vegetation dynamics, to characterize the tree community, and to examine variables affecting seedling growth so as to learn more about the spread potential of this species.

METHODS

Study species

Falcataria moluccana is an invasive tree species introduced from Southeast Asia to French Polynesia in 1966 (FAO 2003). Growing up to 40m tall, it has a lateral branching pattern and a large spreading crown, both of which contribute to its distinctive silhouette (Wagner et al. 1999). This species has high growth rates, up to 4.5m a year, and has low-quality wood that is not suitable for timber. Its small seeds, contained in lightweight wind-dispersed pods, facilitate rapid dispersal (Little and Skolmen 1989). It grows mainly in dry lowland and mesic midland, although trees have been recorded at Mo'orea's full elevational range (Meyer 2000; Meyer 2004). It easily establishes itself in previously disturbed landscapes and can quickly spread to form large monodominant stands. Its high water consumption levels and large root systems contribute to transformation of the habitats where these stands form (Hughes 2006).

Study site

Ecological evaluations were conducted in Mo'orea, French Polynesia (17° 30'S, 149°50'W) between October 1 and November 14, 2009. Mo'orea is 134km^2 in area, with a maximum elevation of 1200m (ORSTOM 1993) and annual average rainfall of between 3000-4000mm per year (Pasturel 1993). Ecological data were taken from *F. moluccana* stands from around the island, ranging in elevation from 87m to 303m. The emergent canopy layer of *F. moluccana* trees is visible from long distances away, so stands were identified from sea level and then visited and assessed.

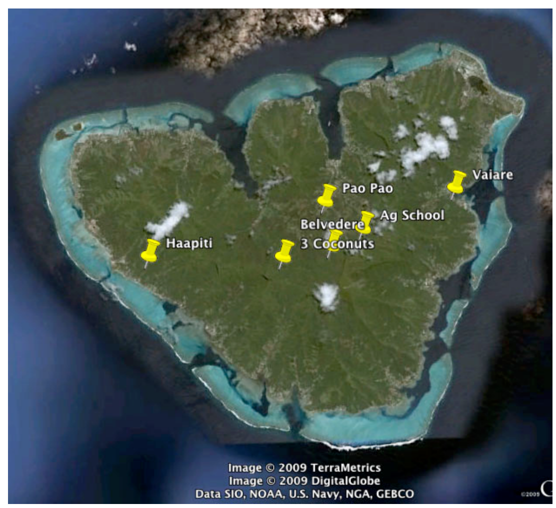

FIG. 1. Map of six study sites in Mo'orea, French Polynesia
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Ecological Assessment

Ecological surveys were taken in five 25m^2 quadrats per site. A representative sample of every species found in the understory vegetation was collected and catalogued at each plot. All trees had species identity taken, canopy level (emergent, canopy, or intermediate) assessed, and

TABLE 1. Further information about study sites with relevant characteristics

	Pao Pao Valley	Agriculture School	Haapiti	Vaiare	Belvedere	3 Coconuts
GPS Point	S 17°31'29.2 W149°49'41.3”	S 17°32'06.2 W149°50.1'14.5”	S 17°32'15.8" W149°53'32.0"	S 17°31'27.5" W149°46'50.9"	S 17°32'23.7" W149°49'38.9"	S 17°32'31.5" W149°50'41.3"
Elevation (m)	87	89	146	159	238	303
Dist. Level	High	High	med-high	high	med-high	low
Dist. Type	bordering pineapple plantation and dirt road	chainsawed, behind Ag. School, near dirt road	bordering farm/ houses	chainsawed	near major road	near trail
Dominant Tree Species	*Falcataria moluccana* **(56)** *Spathodea campanulata* **(76)**	*Falcataria moluccana* **(42)** *Spathodea campanulata* **(74)**	*Hibiscus tiliaceus* **(15)** *Mangifera indica* **(23)**	*Syzygium cumini* **(41)**	*Falcataria moluccana* **(40)** *Freycinetia arborea* **(29)**	*Angiopteris evecta* **(14)** *Falcataria moluccana* **(18)** *Pittosporum taitense* **(10)**

diameter at breast height (DBH) measured. (Note: *Angiopteris evecta* was measured as a tree even though it is actually a fern because of its large biomass and thus high potential to affect the surrounding ecosystem.) These measurements led to average DBH values, quantification of small stem and large stem species composition, and density measured in trees per hectare (tph). *Falcataria moluccana* seedling counts were also taken.

The environment was categorized by disturbance type and level. Disturbance level was rated between one and five with five being the most disturbed relative to the other sites. Disturbed was defined as visibly affected by recent human activity. Percent canopy cover was measured using a densitometer. Also, percent ground cover of various substrates was estimated. Substrate materials include understory vegetation, woody debris, *F. moluccana* litter, other leaf litter, palm fronds, bare soil, roots, and rocks.

Statistical Analysis

A variety of statistical tests were run to examine the possible relationships among the variables described above. A discriminant test was used to identify meaningful variables. Multivariate and paired correlation analyses were used to reveal significant relationships between these pairs of variables.

RESULTS

See Appendices A and B for a more detailed description of habitat evaluation data and understory species lists.

Understory Diversity

Native species were found in all six stands (Fig. 2).

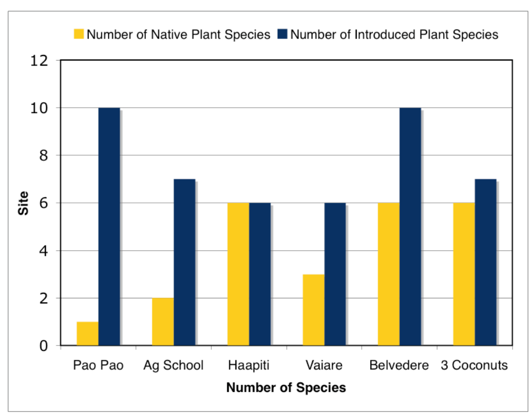

FIG. 2. Native and introduced understory diversity levels by site

TABLE 2. Paired correlation significance values for ecological variables in *F. moluccana* stands

Variable	Falcata DBH	Tree Density	Native diversity	Introduced diversity	Seedling count	Falcata litter	Bare Soil	Woody debris	Understory	Canopy Cover	Elevation
Falcata DBH											
Tree Density	0.0007										
Native Diversity	0.0077	0.0189									
Introduced Diversity	0.0052	0.0014	-								
Seedling count	-	0.0499	-	0.0040							
Falcata litter	-	-	-	-	0.0235						
Bare soil	-	-	-	-	<0.0001	0.0054					
Woody debris	0.0038	0.0055	-	-	-	-	-				
Under-story	-	-	-	-	-	-	0.0106	<0.0001			
Canopy Cover	-	-	-	-	0.0086	-	-	-	-		
Elevation	-	-	<0.0001	-	-	-	-	-	-	0.0083	
Disturbance Level	0.0028	0.0287	<0.0001	-	-	0.0351	-	-	-	<0.0098	<0.0001

= Significant Positive Correlation
= Significant Negative Correlation
= No Significant Correlation

I found that native understory diversity is positively correlated with elevation and *F. moluccana* DBH and negatively correlated with overall tree density and disturbance level (Table 2). Conversely, introduced diversity is positively correlated with tree density and negatively correlated with *F. moluccana* DBH (Table 2). Seven out of the ten native species collected are post-disturbance taxa (Appendix B), and none of the ten are particularly rare (Hembry pers. com.).

Tree Community

Elevation and percent canopy cover are significantly positively correlated. *Falcataria moluccana* DBH is negatively correlated with tree density, percent woody debris and disturbance. Tree density and percent woody debris are positively correlated (Table 2). Two tree species are currently unknown and have samples in the UC Berkeley Herbarium (Appendix B).

Falcataria moluccana has an overall average DBH of 32.1 cm, with a much higher DBH at Haapiti, Vaiare, and Three Coconuts than at the other sites (Fig. 3).

Defining large stem as DBH > 0.02 m, *F. moluccana* trees make up 89.4% of large stem trees (Fig. 4), but only 24.9% of the small stem tree population (Fig. 5). *F. moluccana* has the greatest overall abundance in two out of six sites. *Spathodea campanulata*, another highly invasive species, has the greatest abundance at the two lowest elevation sites (Table 1).

Spread Potential

Falcataria moluccana seedling count is negatively correlated with overall tree density, introduced plant diversity, and percent canopy cover (Table 2). Seedling count is positively correlated with percent bare soil and percent *F. moluccana* litter (Table 2). *Falcataria moluccana* litter is also positively correlated with disturbance level (Table 2).

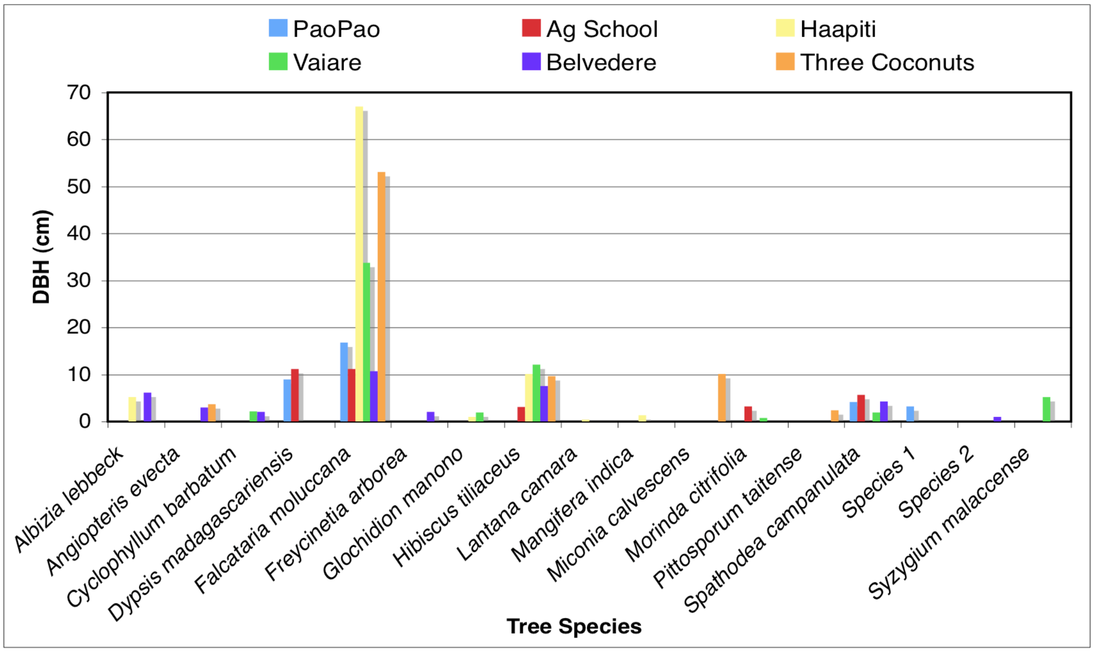

FIG. 3. Average species DBH by site

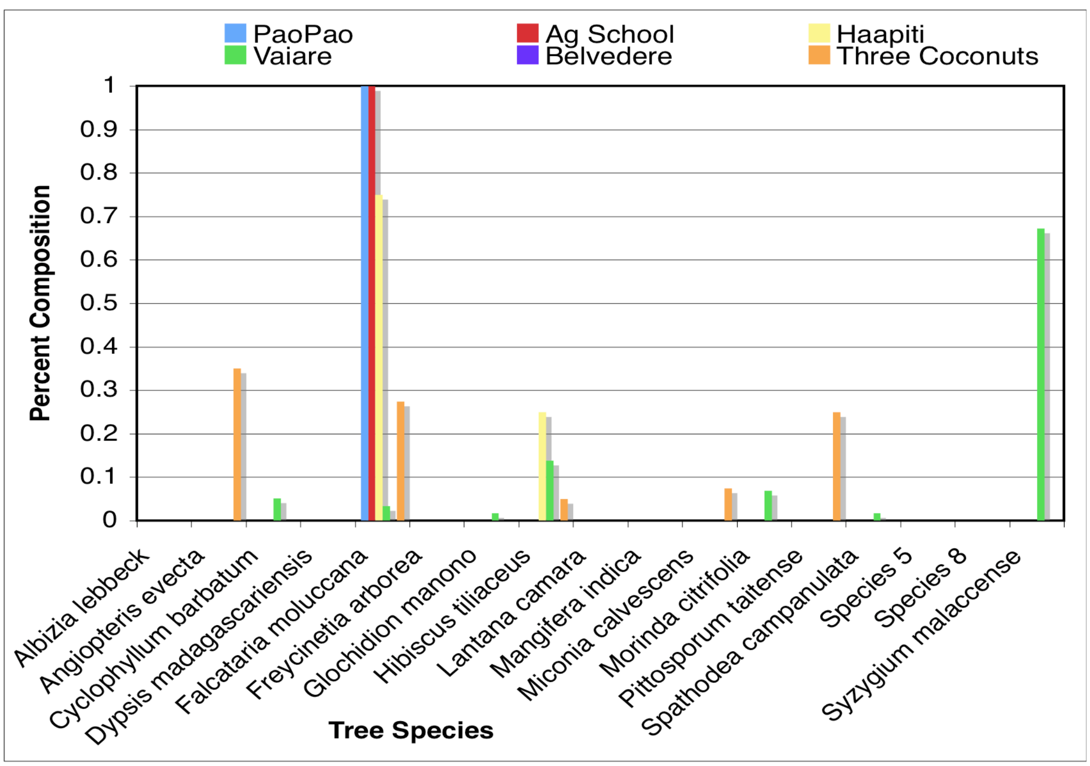

FIG. 4. Percent species composition of large-stem trees by site

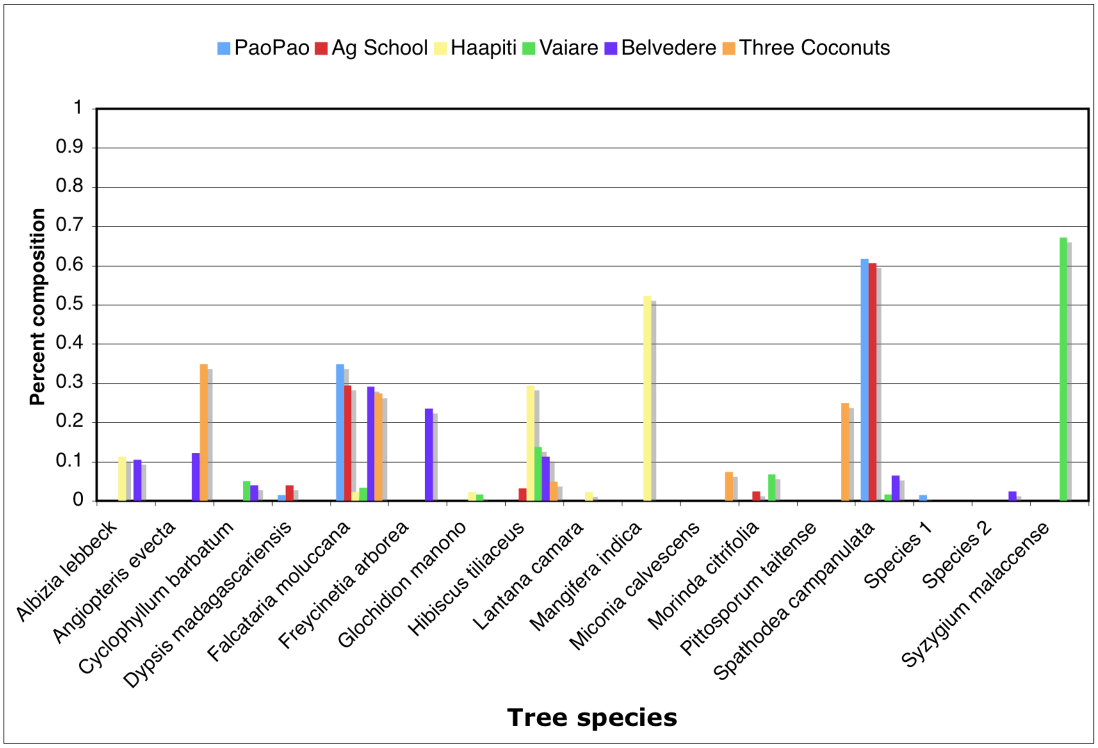

FIG. 5. Percent species composition of small-stem trees by site

DISCUSSION

Understory Diversity

The cohabitation of an ecosystem by native understory and *F. moluccana* trees indicates that at this time the trees are not modifying the ecosystem to such an extent that native plant growth is prevented. However, the prevalence of post-disturbance taxa at all sites emphasizes the fact that all the stands are disturbed to some extent, and that these stands do not represent an intact native forest. Currently native understory is present, but the long-term prognosis is unknown, so future studies examining these long-term dynamics are needed.

My results indicate that there is likely to be greater introduced understory diversity in a younger, more recently disturbed forest. Conversely, native understory diversity is greater in stands with less disturbance and larger trees. This indicates that disturbance negatively affects native plant species but positively affects introduced plant species, confirming the literature (Hughes 2005; Sumida et al. 2005). Furthermore, native plant diversity and elevation are correlated, so there is a greater variety of native plant species at higher elevations. This is a common finding on island habitats affected by human activity (Ricklefs 1999).

DBH is a proxy for age, so the Haapiti, Vaiare, and Three Coconuts sites are probably older than the Pao Pao, Agriculture School, and Belvedere sites (Fig. 3). However, this age difference does not mean that all these sites are a later successional stage of the highly disturbed low elevation forests, where there were a high density of small *F. moluccana* trees that got selected out. In particular, it is likely that the Three Coconuts environment was never as disturbed as the younger lower elevation sites. This stand was most likely formed either by invasion by a few *F. moluccana* trees, which were able to grow relatively undisturbed, or through human planting to reforest a burned or eroded ridge. If they were invaders, this indicates that natives can persist as understory in old stands, which is an important finding because it shows that native plants are not eradicated by the nitrogen dumping and canopy cover of the trees, and that some other factor is reducing their level in other *F. moluccana* stands. If trees were purposefully planted on an eroded ridge, this could mean that not only can native plants coexist with these trees, they were able to re-inhabit the ridge alongside the *F. moluccana* trees, which gives hope about native recolonization potential. Looking at old vegetation photos and planting records would help determine which scenario is correct.

Tree Community

Falcataria moluccana trees are the dominant large-stem trees at all sites but comprise only a quarter of small stem trees, which means they are able to effectively use the resources of an area to achieve high biomass levels. This could mean that this species is able to grow large in places where other species cannot, perhaps through niche differentiation, or that it is able to monopolize the resources – nutrients, water, space, or sunlight - of a habitat so as to outcompete other trees. Studies examining soil chemistry and resource availability could help to answer this question.

Spathodea campanulata's highly invasive nature is confirmed by its dominance of both highly disturbed low-elevation sites. While this species has not yet achieved large sizes in *F. moluccana* stands, the high density of its trees indicate that it may be a highly destructive invader (Meyer 2002).

Conversely, the presence of two dominant native species at the highest elevation site (Three Coconuts) and the absence of this dominance at the other sites (Table 1) adds strength to the positive correlation between elevation and native diversity described above.

Spread Potential

My results indicate that *F. moluccana* seedlings are more likely to be found in an environment with less invasive plants, less dense tree growth, and more light. Seedling count is positively correlated with percent bare soil, which confirms findings of past studies (Long 2007). This means that farmers and developers need to be particularly careful when clearing land because that is allowing for colonization by *F. moluccana* trees (Sumida et al. 2005).

Seedling count is also positively correlated with percent *F. moluccana* litter, which could potentially mean that these trees facilitate their spread through ecosystem modification, most likely through nitrogen dumping and fixing. This would mean that this species is modifying the ecosystem in a way that enables its spread, which is what characterizes the most destructive invaders (Asner 2008). Studies examining germination and growth rates of *F. moluccana* seeds under a variety of treatments could improve our understanding of this species' spread potential.

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APPENDIX A: Site Habitat Characterization Data

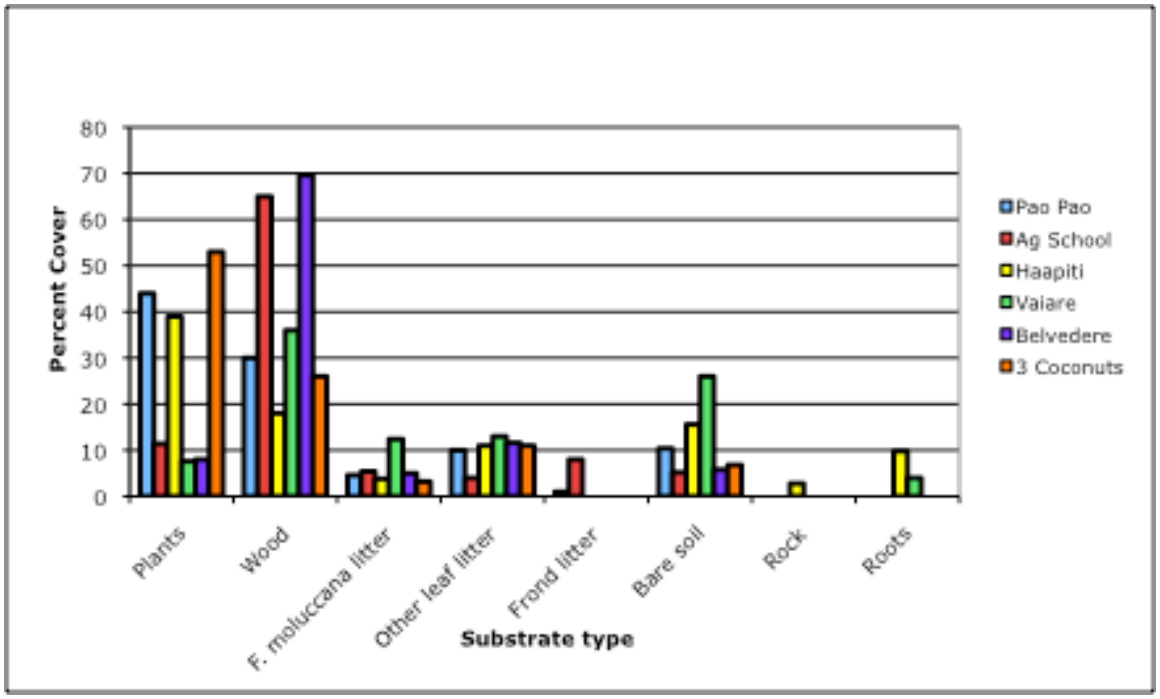

FIG. 6. Substrate percent cover by site

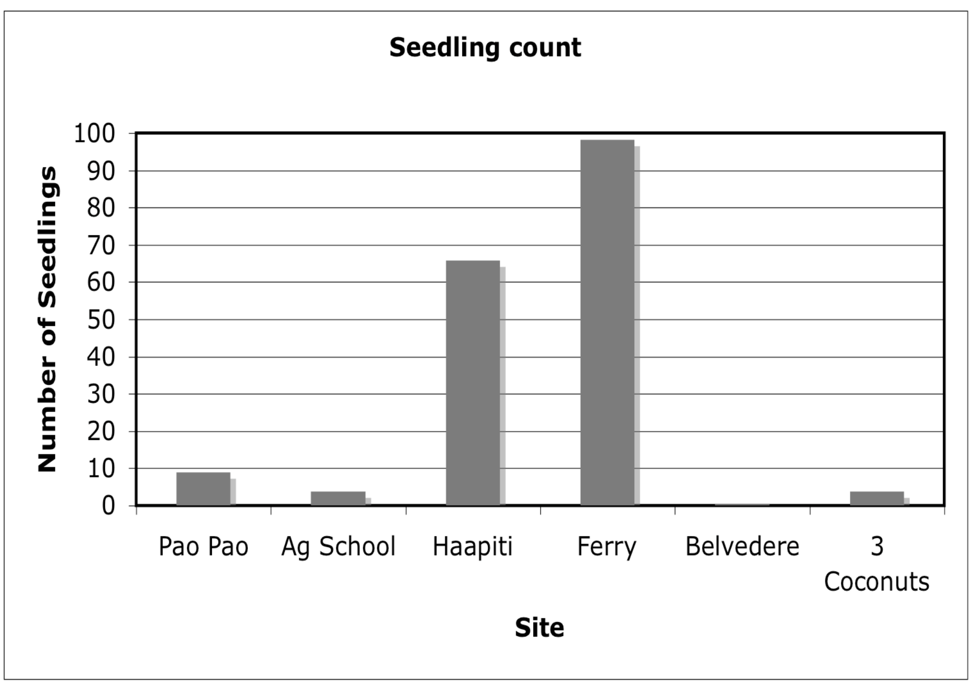

FIG. 7. *Falcataria moluccana* seedling count by site

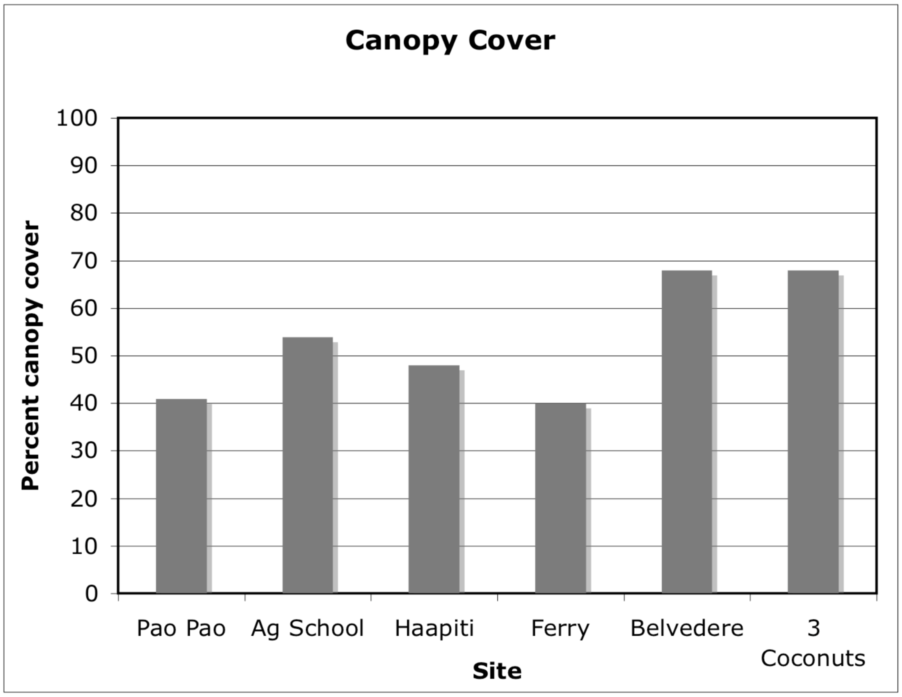

FIG. 8. Percent canopy cover by site

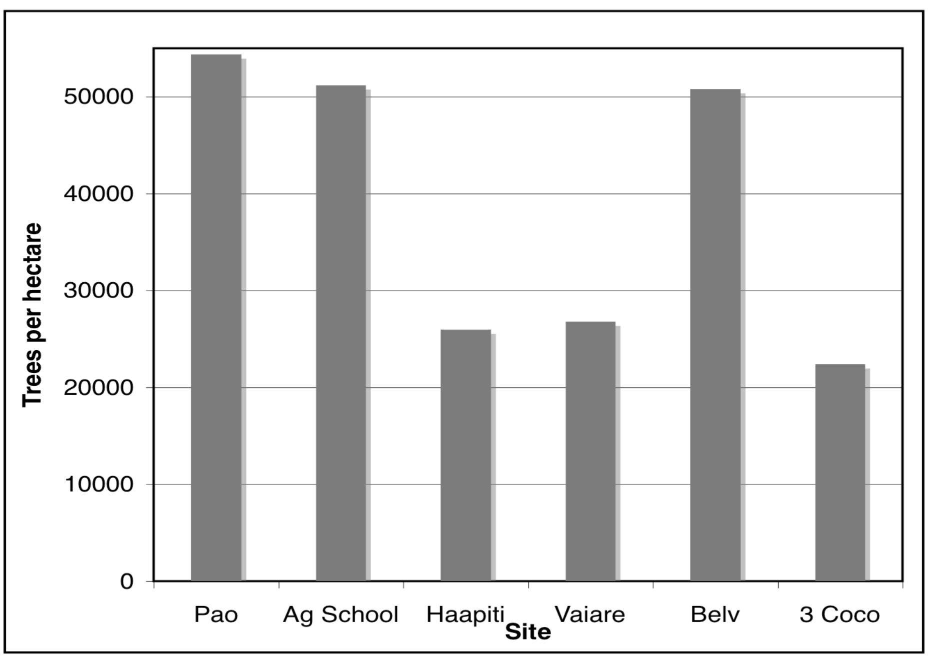

FIG. 9. Tree density in trees per hectare (tph) by site

APPENDIX B: Understory Vegetation Species List

TABLE 3. Native vegetation species list by site and family, with post-disturbance species in **bold**

	Location	Pao Pao Valley (87m)	Ag School (89m)	Haapiti (146m)	Ferry (159m)	Belvedere (238m)	Three Coconuts (303m)
Family	Species (Native)						
Davalliaceae	*Davallia fejeensis*			X		X	
Dryopteridaceae	***Nephrolepis biserrata***		X	X		X	X
Glechniaceae	***Dicranopteris linearis***			X			
Malvaceae	***Hibiscus tiliaceus***	X	X	X	X	X	X
Marattiaceae							X
Marattiaceae	*Angiopteris evecta*					X	X
Pandanaceae	***Pandanus tectorius***					X	
Phyllanthaceae	***Glochidion manono***				X		X
Phyllanthaceae	***Glochidion cf.myrtifolium***			X			
Pittosporaceae	*Pittosporum taitense*						X
Rubiaceae	***Cyclophyllum barbatum***			X	X	X	-

TABLE 4. Introduced vegetation species list by site and family

	Location	Pao Pao Valley (87m)	Ag School (89m)	Haapiti (146m)	Ferry (159m)	Belvedere (238m)	Three Coconuts (303m)
Family	Species (Introduced)						
Anacardiaceae	*Mangifera indica*			X			
Arecaceae	*Dypsis madagascariensis*	X	X				
Asteraceae	*Sphagneticola trilobata*	X	X				
Bignoniaceae	*Spathodea campanulata*	X	X		X	X	
Bromeliaceae	*Ananas comosus*	X					
Commelinaceae	*Commelina Diffusa*	X	X	X		X	X
Compositae	*Elephantopus mollis*			X	X		X
Fabaceae	*Adenanthera pavonina*					X	
Fabaceae	*Albizia lebbeck*			X		X	
Melastome	*Miconia calvescens*						X
Myrtaceae	*Psidium Guajava*			X		X	
Myrtaceae	*Syzygium malaccense*		X		X		
Passifl oraceae	*Passiflora suberosa*	X				X	
Passifl oraceae	*Passiflora maliformis*	X			X		X
Polypodiaceae	*Microsorum commutatum*						X
Rosaceae	*Rubus rosifolius*					X	X
Rubiaceae	*Coffea arabica*					X	
Rubiaceae	*Morinda citrifolia (noni)*	X	X		X	X	
Verbenaceae	*Lantana camara*			X	X	X	X
Verbenaceae	*Stachytarpheta urticifolia*	X					
Zingiberaceae		X	X				