Title
The aftermath of abandonment: Secondary succession in Cocos nucifera plantations on the island of Moorea, French Polynesia

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THE AFTERMATH OF ABANDONMENT: SECONDARY SUCCESSION IN *COCOS NUCIFERA* PLANTATIONS ON THE ISLAND OF MOOREA, FRENCH POLYNESIA

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Abstract. Islands systems are especially vulnerable to the possibility of introduced species becoming invasive and crowding out native flora. Human disturbances, such as clearing, development, grazing, and agriculture, have been known to facilitate the establishment of such disturbance-tolerant species. *Cocos nucifera* has been cultivated extensively on the lowland areas of the island of Moorea, French Polynesia, since the 1800s, and as coconut production became less profitable over time, plantations have been gradually abandoned as landowners look to more lucrative efforts. Plantations of varying ages of abandonment can be seen in different stages of succession around the island. Vegetation surveys were done of six sites (in three age classes) to assess the presence and abundance of native and invasive species, and to study the changes in community structure over time. Decrease in groundcover and increase in aerial cover seem to indicate the pattern of succession most accurately. The number of invasive versus non-invasive and native versus non-native species did not change significantly as plantations aged.

Key words: Cocos nucifera, abandoned plantation, plant community composition and structure, invasive species, secondary succession

INTRODUCTION

Introduced species can become invasive and have catastrophic effects on island ecosystems (Fritts & Rodda, 1998). In addition to altering fire regimes, nutrient cycling, and hydrology, invasive species can also reduce the abundance and survivability of native species (Mack, et. al., 2000). For example, on the island of Moorea, French Polynesia, *Miconia calvescens* is becoming increasingly problematic, creating dense monotypic stands in areas including native forests, posing a risk to the native flora (Meyer, 2000). There have been many studies on the role of anthropogenic disturbance in facilitating the establishment of invasive species, and disturbances can include clearing, development, grazing, and agriculture (Hill et al., 2005).

The conversion of forest to agriculture is widespread around the world, and it is important to understand the recovery process after agriculture in order to restore forests and conserve biodiversity (Howorth, 2006). Succession following the abandonment of agricultural land has been studied in areas that have been used for grazing (Alvarez-Yepiz et al., 2008), coffee plantations (Rivera, 1998), and agave (González-Iturbe et. al., 2002), among others.

The cultivation of Cocos nucifera has been an important part of French Polynesia, both culturally and economically. On the island of Moorea, *Cocos nucifera* has been cultivated extensively in lowland areas since the 1800's (L'orstom, 1993; H. Murphy, personal communication). Traditionally the plant has been utilized in many ways, from food, medicine, and building material, to toys, clothes, and other household items (H. Murphy, pers. comm.). The meat of the coconut was also harvested and dried to form copra, which was pressed to make coconut oil. In the 1850s the production of copra was very profitable, but shortly after World War II the operation became unprofitable and the majority of plantations were abandoned for more lucrative efforts (H. Murphy, pers. comm.). Although coconut production is still a major part of the economy in other parts of French Polynesia such as the Marquesas and the Tuamotus, there are only a few operating coconut plantations on the island of Moorea. Remnants of coconut production can be seen from the main road circumnavigating the island in the form of fragmented plots of plantations at various ages of abandonment. The nature of the varying ages of these sites is advantageous in setting up a chronosequence in which succession post-cultivation can be studied.

Previous student papers have looked at succession of epiphytes on coconut trees (Wallace, 2000) and fern fronds (Burke, 2005), but not much has been done on succession of vascular plant species. This study will utilize a series of abandoned plantations of different ages to study succession on a larger scale. Changes in species composition, as well as community structure, are analyzed to determine whether succession is observed in abandoned coconut plantations. Species composition will be analyzed to observe how diversity and abundance of native and non-native species, as well as invasive and non-invasive species, change over time. I expect to find abandoned coconut plantations do indeed experience succession over time. I hypothesize younger plots will have more ground cover, less woody species, and more invasive species, and older plots will have a higher species richness, more developed canopy, more native species, and less ground cover.

FIG. 1 Map of Moorea with study sites

TABLE 1. Age classes with site descriptions

Key	Age Class	Years of Abandonment	Site	Size (m^2)
A	1	0-<20 years	Tea Time	4800
B	1	0-<20 years	Teavaro	8000
C	2	20-<40 years	Maharepa	11,700
D	2	20-<40 years	Temae	5200
E	3	40=< years	Gump Station	5000
F	3	40=< years	Mari Mari	20,000

MATERIALS AND METHODS

Site selection

A total of six study sites were chosen based on the age of abandonment according to Hinano Murphy, a local expert on the history of the island. Plantations were separated into age classes, with plots of Age Class 1 abandoned from 0-<20 years, Age Class 2 from 20 to <40 years, and Age Class 3 40 years and older (Table 1). All sites were located in lowland and coastal areas, and were accessible from the main road circumnavigating the island (Fig. 1).

Vegetation survey

Beginning at the center of each plot, a 5x5m quadrat was laid down and all vegetation falling within that square was surveyed. Starting at the center of the first quadrat, a random direction and distance was chosen from a random number table to locate the starting point of the next quadrat; from that point, transect tape was laid out to the north for 5 meters, then west for 5 meters, and so forth to complete the square. This process was repeated so that for each site, 15 quadrats were surveyed, totaling a sample area of 375m² for each site. Sample specimens of each unknown plant species were taken back to the Gump station where they were identified to the species level whenever possible (Murdock, 2008; Whistler, 1995; Welsh, 1998). Voucher specimens were pressed and deposited at the University and Jepson Herbaria at the University of California, Berkeley.

Community Structure

Each quadrat was split into three levels: ground level, mid-level, and upper level. For ground level, total percent of ground cover was recorded using visual estimation, as well as the percent contributed by each species. Seedlings of woody species that were below knee height (~40cm) were considered ground cover. For mid-level, the total number of individual stems were counted for each woody species. For upper-level, total percent of aerial cover was recorded using a densiometer, as well as the percent contributed by each species. In this way, changes in the forest structure were assessed as the plots progressed in age. The software program JMP® 7.0.1 was used to run ANOVA to see if there was a correlation between the age of a plot and the amount of ground and aerial cover it had. It was also used to determine whether density of woody species increased as a plot aged, and also to see if these results were statistically significant. A Tukey-HSD test was used to see if age classes and sites were significantly different from each other.

Species Composition

Each species sampled were scored as a native or introduced species, and as an invasive or non-invasive species (PIER, 2008; Whistler, 1995; Whistler, 1992, Steele, 2002). In this paper, I define non-native species as one that has been introduced to the island in the last two hundred years. Simpson's index was used to look at species diversity, and ANOVA was used to see if there were significant differences between sites and age classes. A two-way contingency analysis was conducted to test the goodness of fit of the number of native and invasive species for each site and age class.

RESULTS

Community Structure

Figures 2 to 6 can be seen in Appendix 1. The sampling sites differed in the structure of their plant communities. Ground cover, aerial cover, and the total number of stems of woody species all differed significantly across sampling sites.

Ground cover ranged from 0 to 80% and was highest for Tea Time and Teavaro (both age class 1), about 50% for Mari Mari Kellum (age class 3), and lowest for Maharepa, Temae, and Gump Station (age class 2 and 3) (Figure 2, Appendix 1). Ground cover was found to be significantly different across sites of different age classes (ANOVA, DF=2, F ratio=49.4, $p<.0001$)(Figure 3, Appendix 1), and also sites of different age classes were significantly different ((Tukey-HSD, DF=5; F ratio=31.6; $p<.0001$) (Figure 2, Appendix 1).

Aerial cover ranged from 30% (age class 1) to 100% (Temae, age class 2), and also differed significantly across sites (ANOVA,

TABLE 3. Species richness and Simpson's diversity indices for woody and herbaceous species of each site.

Age Class	Site	Sp. Richness	D (woody)	E_D (woody)	D (herb.)	E_D (herb.)
1	Tea Time	11	2.56	0.85	1.73	0.217
1	Teavaro	11	1.24	0.62	3.095	0.387
2	Maharepa	12	2.99	0.748	1.77	0.221
2	Temae	4	2.74	0.68	0	0
3	Gump Station	6	4.3	0.717	0	0
3	Mari Mari K.	35	6.54	0.436	5.59	0.294

DF=5, Fratio=17.99, p<.0001) (Fig. 4, Appendix 1). Aerial cover differed significantly across age classes as well (ANOVA, DF=2, F ratio=35.7, p<.0001)(Fig. 5, Appendix 1).

Density of woody species significantly differed across sites (ANOVA, DF=5, Fratio=9.8, p<.0001), and also with age class (ANOVA, DF=2, Fratio=13.99, p<.0001; Tukey-HSD, DF=5, F ratio=9.8; p<.0001)(Fig.6 and 7, Appendix 1).

Species Composition

A total number of 57 species in 34 families were observed, and 46 were identified to the species level. 18 are considered native, 31are modern introductions, and 15 are considered invasive. There were no species that were observed in all sites, and only 11 were observed in more than one site (Table 2).

The species richness (S), Simpson index (D), and Equitability (E_D) of each site were calculated using the following equations (Fig. 8):

$$D = \frac{1}{\sum_{i=1}^{S} p_i^2}$$

$$E_D = \frac{D}{D_{max}} = \frac{1}{\sum_{i=1}^{S} p_i^2} \times \frac{1}{S}$$

FIG. 8. Equations used to compute Simpson index (D) and Equitability (E_D).

Species richness and diversity did not follow a pattern over time (Table 3). The diversity of woody species generally increased over age, but age classes were not significantly different (ANOVA, DF=2, F-ratio=5.82, p<.093). The diversity of herbaceous species did not significantly change across sites or age classes (ANOVA, DF=2, F-ratio=.338, p<.737).

There were no general trends seen in native and invasive species across sites (Fig. 9 and 10, Appendix 1). A two-way contingency analysis was conducted to observe differences in proportion of native species across sites (Likelihood ratio: DF=6, Chi square = 15.25, p<.018), and across age classes (likelihood ratio: DF=2, Chi square=1.18, p<.55). The same test was conducted for invasive species across sites (likelihood ratio: DF=6, Chi square=23.2, p<.007), and across age classes (likelihood ratio: DF=2, Chi square 2.27, p<.32).

TABLE 2. Species presence in each site (indicated by ‘X’). TT=Tea Time, TVO=Teavaro, MAH=Maharepa, TEM=Temae, GMP=Gump, MM=Mari Mari

FAMILY	Species	TT	TVO	MAH	TEM	GMP	MM
ANACARDIACEAE	*Mangifera indica*	_	_	_	_	X	_
ANNONACEAE	*Annona muricata*	_	_	_	_	_	X
ARACEAE	*Philodendron oxycardium*	_	_	_	_	_	X
ARECACEAE	*Cocos nucifera*	X	X	X	X	X	X
ASTERACEAE	*Elephantopus mollis*	_	_	_	_	_	X
	Mikania micrantha (H.B.K.)	_	_	_	_	_	X
	Wedelia trilobata (L.) Hitchc.	X	_	X	_	_	_
BIGNONIACEAE	*Spathodea campanulata* (P.Beauv.)	_	_	_	_	_	X
COMBRETACEAE	*Terminalia catappa*	X	_	_	_	_	_
COMMELINACEAE	*Commelina diffusa (*Burm.f.)	_	X	_	_	_	_
CONVOLVULACEAE	*Merremia umbellata (*L.) H. Hallier	X	X	_	_	_	_
CYPERACEAE	Grass' C	_	X	_	_	_	_
	Grass' E	_	X	_	_	_	_
DIOSCOREACEAE	*Dioscorea bulbifera* (L.)	_	_	_	_	_	X
EUPHORBIACEAE	*Aleurites moluccana* (L.) Willd	_	_	_	_	_	X
	ricinus cormmunis (L.)	X					
FABACEAE	*Albizia falcatoria*	_	_	_	_	_	X
	Centrosema virginianum (L.) Benth	_	X	_	_	_	_
	Inga feuillei	_	_	_	_	X	_
	Leucaena leucocephala (Lam.) de Wit	X	_	X	_	_	X
	Macroptilium atropurpureum (DC.) Urb.	X	_	_	_	_	_
	Macroptilium lathyroides (L.)	_	_	X	_	_	_
	Mimosa pudica (L.)	X	_	X	_	_	_
	Vigna marina	X	X	X	_	_	_
HELICONIACEAE	*Heliconia rostrata*	_	_	_	_	_	X
LAURACEAE	*Persea americana*	_	_	_	_	_	X
MALVACEAE	*Hibiscus tiliaceus ssp. hastatus*						
MELASTOMATACEAE	*Dissotis rotundifolia* (Sm.) Triana	_	_	_	_	_	X
	Miconia calvescens (DC.)	_	_	_	_	_	X
MELIACEAE	*Swietenia macrophylla*	_	_	_	_	_	X
MORACEAE	*Castilla elastica* (Sesse)	_	_	_	_	_	X
	Artocarpus altilis	_	_	_	_	_	X
MYRTACEAE	*Syzygium cuminii* (L.) Skeels	_	_	_	_	_	X
	Syzygium luehmannii (F.Muell.)	_	_	_	_	_	X
NEPHROLEPIDACEAE	*Nephrolepis exaltata*	_	_	_	_	_	X
ONAGRACEAE	*Ludwigia octovalvis* (Jacq.)	_	X	_	_	_	_
PAPILIONOIDEAE	*Inocarpus fagifer*	X	_	_	_	_	X
POACEAE	*Cyndon dactylon* (L.) Pers.	X	_	X	_	_	_
	Leptochloa virgata	_	_	_	_	_	X
	Grass B	X	_	X	_	_	_
	Grass D	_	X	_	_	_	_
POLYPODIACEAE	*Microsorum commutatum*	_	_	_	_	_	X
PTERIDACEAE	*Acrostichum aureum* (L.)	_	X	_	_	_	
RUBIACEAE	*Cyclophyllum barbatum (G.Forst.)*	_	_	_	_	X	X
	Geophila repens	_	_	_	_	_	X
	Morinda citrifolia	_	_	_	_	_	X

TABLE (continued).

FAMILY	*Species*	TT	TVO	MAH	TEM	GMP	MM
SAPOTACEAE	*Chrysophyllum cainito*	_	_	_	_	_	X
STERCULIACEAE	*Waltheria indica* (L.)	X	_	_	X	_	
VERBENACEAE	*Clerodendrom chinenses* (Osbeck) Mabb.	_	_	_	_	_	X
	Stachytarpheta urticifolia (Sims)	_	_	_	_	_	X
ZINGIBERACEAE	*Alpinia purpurata* (Vieill.) K.Schum.	_	_	_	_	_	X
UNKNOWNS	Fern A	_	_	_	_	_	X
	Fern C	_	_	_	_	_	X
	Fern D	_	_	_	_	_	X
	Fern E	_	_	_	_	_	X
	Fern F	_	_	_	_	_	X
	Bamboo vine	_	_	_	_	_	X

DISCUSSION

Community structure

I expected ground cover to decrease over time as the canopy is formed and less light is available to the understory, but this was not necessarily the case. Ground cover experiences a U-shaped trend over time, made more interesting by the discrepancy between the sites in the oldest age class: Gump has no ground cover at all, while Mari Mari has more than 50%. Since there are no other age class 3 sites, it is hard to tell which one is 'typical' of a plantation that has aged for more than 40 years. It would be interesting to find out what species of ferns (which comprised most of the groundcover) were present at Mari Mari's, and to see if they are shade-tolerant species. If there was a way to measure the age of a plantation more accurately, the presence of these ferns might indicate an older stage of succession where the understory develops after the canopy forms. Sites of age class 1 have significantly higher ground cover (80%), and this would make sense because the undergrowth is kept even while coconut production is still ongoing (H. Murphy, pers. comm.). Even if it was cleared using modern technologies such as lawnmowers that were introduced 30 or 40 years ago (F. Murphy, pers. comm.), this phenomenon of initial colonization by non-woody species is common and has been seen in other forest ecosystems (Howorth, 2006). Ground cover is high in the first age class and nonexistent in the second class, but it is difficult to say what the third class looks like due to the lack of replicates.

In the same way, I expected to see a linear increase in aerial cover as sites aged – the development of the upper canopy would progress as woody species grew with time. However, a Tukey-HSD test revealed aerial cover of age class 2 and 3 are not significantly different. This might suggest that there is a more drastic change in between age class 1 and 2, and that succession and formation of the upper canopy is occurring faster than previously thought. Future studies can narrow down age classes to encompass fine scale variations such as these.

I expected to see a direct relationship between the age of a site and the total number of stems of woody species. As sites aged, woody species should be able to establish and disperse, resulting in a higher proportion of woody species at different stages of development. However, Tukey HSD analysis showed that the density of woody species in age class 2 and 3 were not significantly different from each other. Again, this suggests succession of woody species occurs at a faster rate than hypothesized.

Species composition

On average, age class 3 had the highest species richness, followed by age class 1 and 2. Howorth (2006) and González-Iturbe (2002) also found that the oldest successional stage had the highest species richness, but they found a linear increase in species richness with age. Again, sites within age classes are significantly different (Maharepa had 12 while Temae had 4, and Gump had 6 while Mari Mari had 35), so it is difficult to determine which is 'typical'. Even on average, we find a U-shaped pattern, similar to the one found for ground cover – species richness decreases, then increases with age.

In general all sites were very different from each other. In some aspects sites of one age class would be more like sites from a different age class (ground cover for Gump looked more like ground cover for age class 2, for example), and sites within the same age class would be significantly different (such as the density of woody species in Maharepa and Temae, and the amount of ground cover in Gump and Mari Mari). These results are similar to a study done on abandoned agave plantations that found in general the floristic similarities are low between [successional] states and between sites (González-Iturbe, 2002). Because of these differences, it might be disadvantageous to lump these sites together based on a rough estimation of age – in future studies, sites should be assigned to age classes with narrower margins to account for changes that occur over shorter periods of time.

I hypothesized more invasive species would be found in newly abandoned plantations, but at both sites, there were in fact more non-invasive species. However, these results might be skewed due to the fact that grasses, which both sites had, were not counted because they were unidentifiable and unable to be scored as invasive or non-invasive. Again, the lack of replicates and the uniqueness of each site make it difficult to determine a pattern in the rate of colonization by invasive species across age classes. Similarly, there were no significant patterns in the abundance of native species across sites and age classes.

In general, it was difficult to discern patterns across age classes because sites within age classes were so different from each other. This might be due to differences in the size of the plot, environmental conditions, and the history of land use of plots adjacent to study sites. Species richness and diversity at Mari Mari might have been exceptionally high because the site was two to four times larger than the other sites, allowing the sampling area to encompass a larger number of species. It must also be noted that this study site was adjacent to areas that were still being used to cultivate other crops (lemons and dwarf coconuts). Compared to the other sites that are truly abandoned, this site might have been exposed to seeds and other propagules brought by people maintaining these crops. Indeed, there are a high number of introduced species in this site, including some crop species (breadfruit, star apple, ginger, nono, soursop, etc.), and many invasive and weedy species (notably African tulip tree and Miconia). On the other hand, it is also adjacent to undisturbed 'natural' areas, which might explain the presence of native species (such as Tahitian chestnut). In general, all sites were bordered to some extent by areas that were developed, which could influence the presence or absence of native or invasive species. The fact that all sites were in different physical environments could also be a confounding factor. Conditions such as soil type, precipitation, temperature, and the amount of exposure could influence the type of vegetation that can establish and thrive. A better project design would look at sites in which two age classes can be compared in the same location to control for these environmental variables.

Other limitations to this project include the fact that most of the lowland areas on the island have been developed, and there is very little 'natural' coastal area left. It would have been interesting to compare the oldest age classes with these natural areas to see how well these abandoned plantations have reintegrated back into the native environment. The lack of replicates also made it difficult to compare age classes – perhaps in a future study, more sites within the same age class can be sampled to account for the fact that sites may be different in size, history, and exposure to human activity. It must also be noted that some species were not identified and were not used to look at differences in native and invasive species. Even the ones that have been identified may not be correct, and for some species it is still contested whether they are native or non-native and invasive or non-invasive. All of these facts may explain some of the errors introduced to the study.

CONCLUSION

In this study I looked at six abandoned coconut plantations of varying ages to determine if and how community structure and species composition changed over time. There was a U-shaped trend in the amount of ground cover across age classes, and an increase in the density of woody species and aerial cover over time. In regards to species composition, sites within age classes were significantly different from each other, and the lack of replicates made it difficult to see general trends across age classes. From this preliminary study, I was not able to discern a pattern in the presence and number of native and invasive species over time, but changes in the qualitative characters in vegetation structure might be a better indicator of succession. Future studies could focus on age classes encompassing smaller increments of time, and more replicates within each age class to get a more accurate look at changes in species composition and community structure. A better understanding of the succession of native and invasive species within these abandoned plantations can give us more insight on how extensive coconut cultivation has had an impact on the island's vegetation.

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I

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APPENDIX A
Graphs of structural changes across sites and age classes.

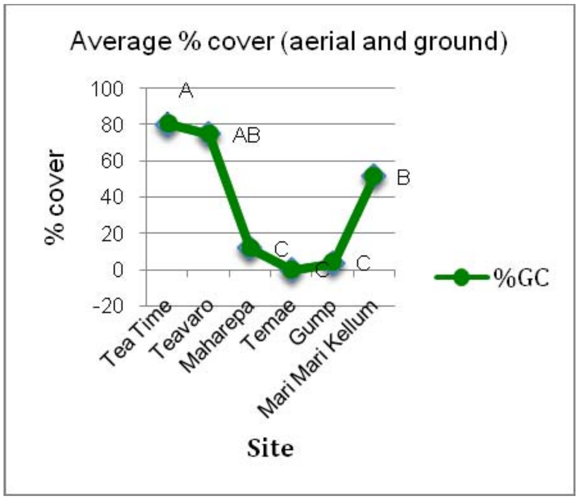

FIG. 2. Change in average percent ground cover (SE=6.68). Sites not connected by the same letter are significantly different (Tukey-Kramer, DF=5; F ratio=31.6; p<.0001)

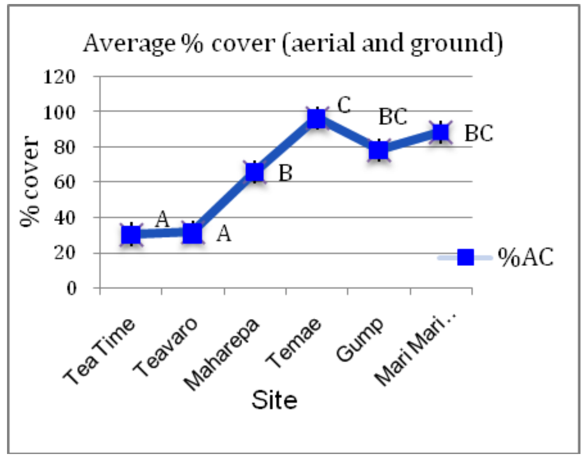

FIG. 4. Change in average percent aerial cover (SE=6.69). Sites not connected by the same letters are significantly different (Tukey-Kramer, DF=5; F ratio=17.99; p<.0001)

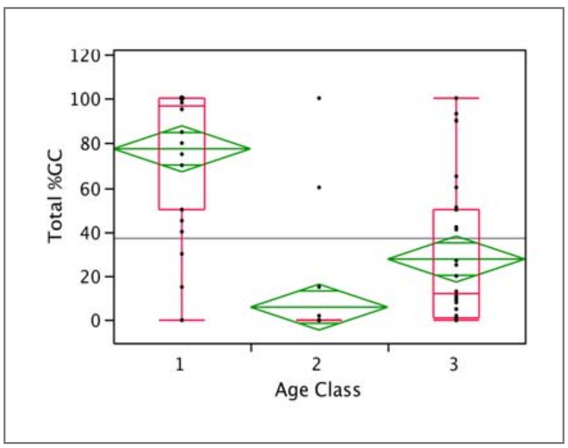

FIG. 3. Average total percent ground cover plotted against age class, displayed with 50 % quantiles (boxes) and means (diamonds) (ANOVA, DF=2, F ratio=49.4, p<.0001).

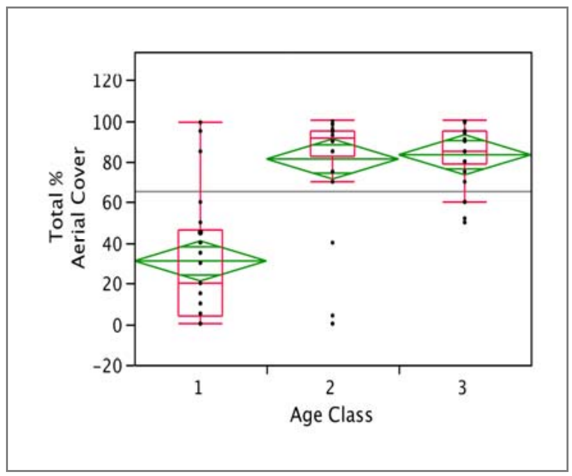

FIG. 5. Average total percent aerial cover plotted against age class, displayed with 50 % quantiles (boxes) and means (diamonds) (ANOVA, DF=2, F ratio=35.7, p<.0001).

APPENDIX A (continued).

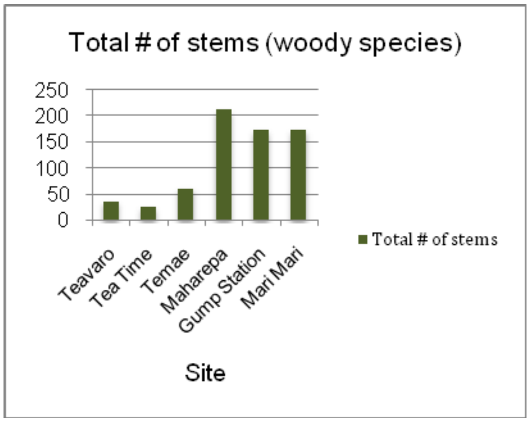

FIG. 6 Relative density of woody species plotted as total number of stems across sites. Teavaro, Tea Time, and Temae are significantly different from Maharepa, Gump station, and Mari Mari (Tukey-Kramer, DF=5; F ratio=9.8; p<.0001).

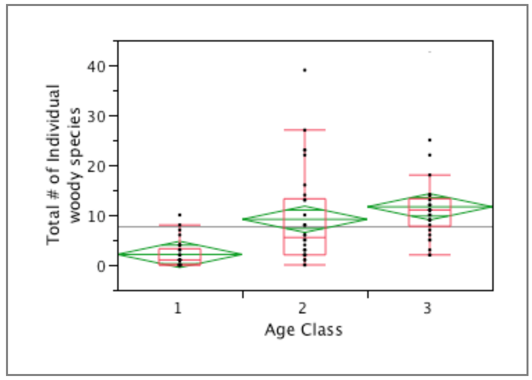

FIG. 7. Relative density of woody species plotted against age class, displayed with 50 % quantiles (boxes) and means (diamonds)

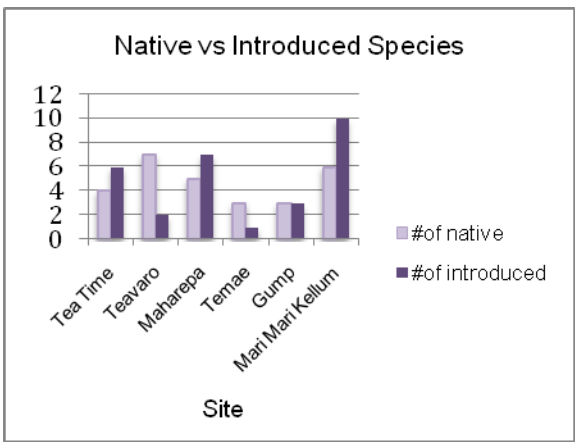

FIG. 9. Number of native vs. introduced species in each site.

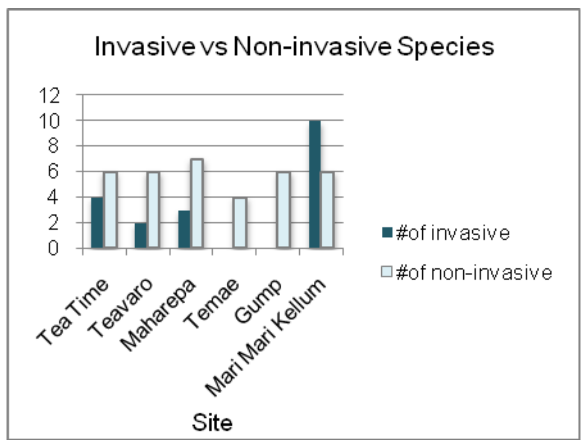

FIG. 10. Number of invasive vs. non-invasive species in each site.