AVIAN COMMUNITY STRUCTURE: LAND USE IMPACTS ON BETA DIVERSITY AND SPECIES RICHNESS IN THREE DISTINCT HABITATS ON MOOREA, FRENCH POLYNESIA

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Abstract.   Conservation efforts can be improved by considering the biological diversity in a region. Diversity, commonly divided into α, β, and γ types, describes the structure of one or more communities. β diversity is particularly helpful, as it allows for comparative analyses – such as comparing community structure in regions with active conservation efforts versus regions without those efforts. The island of Moorea, French Polynesia is a good model system for examining β diversity between different habitats, as most of the island falls within one of three habitat categories: forest, agricultural, and urban. The unusually low rate of avian endemism on Moorea is further motivation to examine the factors that shape bird community structure on that island. For this study, richness and abundance data for the birds of Moorea were collected at 12 sites in each habitat using a point-count method. β diversity was computed for each habitat, applying five widely-used diversity indices – Jaccard, Chao, Bray-Curtis, Manhattan, and Euclidean. The relative effect of native and invasive species on β diversity was examined by further subdividing the data to distinguish between native and invasive species and repeating the β diversity analysis for the Manhattan and Euclidean indices, which accommodate such a distinction. The β diversity results were supplemented by analyzing the α diversity of the communities, and by examining how species richness has changed over the past nine years. Five hypotheses were tested: (1) habitats have unique communities, (2) α and β diversity depend on habitat type, (3) β diversity is highest in the forest and lowest in urban areas, (4) invasive species account for most of the observed β diversity, and (5) species richness, percent native species, and number of endemic species rose from 2004 to 2013. Hypotheses (1), (2), and (4) were supported by the study, while (3) and (5) were not. Results suggest that conservation work should be guided by research into the roles native and invasive species play in determining the β diversity of habitats under consideration for conservation.

Key words: Aves; *beta diversity; Moorea, French Polynesia; alpha diversity; diversity index; dissimilarity value; conservation; native; invasive*

INTRODUCTION

Biodiversity (henceforth diversity) describes the biotic components of an ecosystem, is an indicator of the health of that system (Vora 1997), and can be used as an aid to guide conservation. However, diversity measurements are complicated by the fact that diversity is dependent on scale (Karp et al. 2012). As described by Simoes et al. (2013), diversity is defined at three relative scales, termed alpha (α), beta (β), and gamma (γ). α diversity refers to the diversity at one site, β diversity describes how communities vary between sites, and γ diversity describes the total diversity in a region containing those sites. The exact sizes of the region and sites depend on the purpose of the study, but β
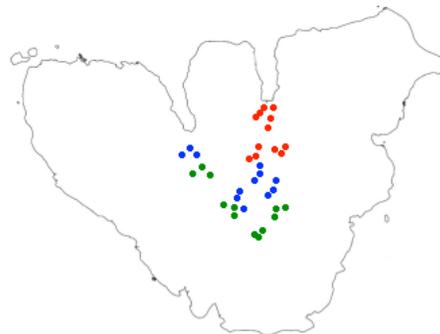
FIG. 1. Distribution of sites on Moorea, French Polynesia. Green is forest, blue is agricultural, and red is urban sites. (Base map courtesy of the Geospatial Innovation Facility, University of California, Berkeley.)

diversity is often the metric of choice, as it allows for comparative analyses.

The strength of β diversity lies in its ability to address questions of how and why communities in one location are more or less similar to communities in a different location (Anderson et al. 2011). The inherent complexity of comparing multiple locations has recently received much attention. As Anderson et al. (2011) described, β diversity can be defined in terms of community turnover along a gradient, or of community variation with geographic distance. While this adds a layer of complexity to any analysis of β diversity, Anderson et al. also showed that these metrics facilitate a variety of studies in ecology.

β diversity has been applied to a number of ecological questions. For example, Condit et al. (2002) demonstrated the importance of dispersal limitation from looking at the β diversity of tropical forests in Panama, Ecuador, and Peru. Diekotter and Crist (2013) established habitat-specific effects on insect diversity in agriculturally impacted ecosystems. These studies are similar in that neither was able to completely explain the mechanisms involved in structuring each system, citing that yet unknown processes are likely in play. This suggests that the ecosystems are overly complex for a study specific to β diversity, so a simpler system, such as an island, might be preferred (Boieiro et al. 2013).

Oceanic islands have long been a focus of ecologists, due in part to their high endemism (Durst 2004, Gillespie et al. 2013) and unique biogeography (Durst 2004). However, human development has broken up, altered, and destroyed native island habitats on most of Earth's oceanic islands (Florens et al. 2012). While patches of native biota often survive (Florens et al. 2012), and thereby bolster γ diversity, they are lost or replaced elsewhere in the same region with a more homogeneous biota, lowering the β diversity of those regions. Importantly, a positive correlation between β and γ diversity has been observed (McMullin et al. 2013, Murria et al. 2013, Qian and Song 2013). This suggests that β diversity may be an indicator for future trends in γ diversity. This correlation motivates further research into island-specific β diversity as it relates to human activity.

Florens et al. (2012) looked at the community structure of native woody plants on the island of Mauritius. Although β diversity was not examined in depth, it was shown to be lower than it would have been without human activity. Longo-Sanchez et al. (2009) studied aquatic insect assemblages on Gorgona Island. Defining β diversity with respect to the drainages of streams, they observed higher β diversity at the drainages farthest away from sources of human impact. Both of these studies indicate a negative relationship between human activity and β diversity.

The island of Moorea, French Polynesia, is well-suited for expanding on research relating β diversity to human disturbance. To date, a large portion of the literature has focused on plant community β diversity (see Condit et al. 2002, Florens et al. 2012, and Simoes et al. 2013), but as shown by Karp et al. (2012), birds are also feasible to study when looking at the β diversity of a system. Motivation to study birds on Moorea is furthered by the fact that unlike most islands, Moorea has low avian endemism and diversity (Durst 2004). It is thought this is due to human impact (Durst 2004), and I identified three possible in situ drivers of changes in diversity on Moorea: agricultural and urban land use, and alteration of native forest biota by introduction of invasive tree species. It has been shown that the β diversity of birds is directly affected by agricultural intensity (Karp et al. 2012), but the relative effects of urbanization and habitat invasion are largely unknown.

The present study examined bird communities in forested, agricultural, and urban habitats on Moorea, with an emphasis on β diversity. This was done using multiple working hypotheses while looking at species distributions, α and β diversity, β diversity of native and invasive species, and changes in richness over time across all three habitat types. I sought to establish, first, if there was a difference in the species found in the bird communities in each habitat. Second, I asked if α diversity varied by habitat category. Third, I examined the dependence of β diversity on habitat category, and how the β diversity changed between habitats (increased or decreased). Fourth, I attempted to determine the relative effects of native and invasive species on the β diversity of each habitat. Lastly, I asked if community richness in each habitat has changed in the past nine years, as compared to a 2004 study on Moorea avifauna.

I hypothesized that species composition would be different for each habitat type, and that both α and β diversity would depend on habitat. Because urban habitats are arguably

the most impacted (Wang and Zhang 2013), I hypothesized that β diversity would be lowest in urban habitats and highest in forest habitats, with agricultural habitats having an intermediate diversity. I hypothesized that invasive species would play a greater role in defining community structure than native species. Finally, as there has been increased effort toward avian conservation on Moorea since 2004, I hypothesized that overall species richness, percent native species, and number of endemic species would rise in the forest habitats from 2004 to 2013.

<center>METHODS</center>

<center>*Study site*</center>

The study was conducted on the island of Moorea, French Polynesia (17°38′S 149°30′W and 17°32′S 149°50′W, Fig. 1). Located in the South Pacific, Moorea is a member of the Society Island Archipelago, and represents one of the major landforms west of Papua New Guinea. The study region was confined to the Opunohu and Pao Pao watersheds, spanning the center and northern portions of Moorea (see Fig. 1).

<center>*Point-Count Surveys*</center>

The study region was divided into three habitat categories: "forest", "agricultural", and "urban" (aided by maps from the Société d'Urbanisme de Polynésie Française). Due to time constraints of the study, the pelagic zone and coastal strands were excluded. Forest habitats were defined as any area with no buildings and where trees were spaced less than 10 meters apart. Agricultural habitats were defined as any area with either human-planted crops or human-maintained fields (for cattle) making up 90% or more of the area. Urban habitats were defined as areas where buildings were present and were less than 100 meters apart. Urban habitats often included a mix of small stands of trees and patches of grass interspersed between buildings, but those were included as part of the urban setting, as long as the surrounding buildings fit the aforementioned definition of less than 100 meters apart. Additionally, primary roads were avoided when sampling in forest and agricultural habitats, but not when sampling urban habitats, as roads were deemed part of the urban setting.

To choose sample sites for each habitat, a random GPS coordinate was chosen within the study region. This was repeated until four sites had been selected for each habitat category. A new site was selected only if it was at least 200 meters from any already-chosen site. Eight additional sites were chosen by walking in a random direction from each GPS-chosen site, for 100 meters, marking a site, returning to the GPS-chosen site, and walking in another random direction for 100 meters, and marking a second site. Combined, these methods designated 12 sites within each habitat (see Appendix C). The final location of each site was adjusted based on both accessibility of the selected coordinates and the feasibility of seeing 30 meters in all directions while standing at that site.

All sites were sampled three times, from November 6-28, 2013. Samplings were done in the style of a point-count survey, where richness (number and type of species) and abundance (number of individuals per species) data were recorded within a 30-meter radius of the site. Observations lasted 7 minutes. The length of the radius and duration of observation were based on a suggestion from Erica Spotswood (UC Berkeley, personal communication). While bird communities in temperate regions tend to be most active at very early and late times of day (e.g. 5am and 7pm), tropical communities exhibit a broader period of activity, spanning most of the day (Erica Spotswood, personal communication). These point-count surveys were made between 6am and 11am ("morning") and 3pm and 6pm ("evening"). Each site was sampled twice in the morning and once in the evening (with the exception of one forest site, which was sampled twice in the evening and once in the morning). Identification of birds was done both visually and by ear. This effort was aided by binoculars, photographs of the birds, and recordings of their calls and songs (stored on an MP3 player and used in the field) obtained from The Cornell Lab of Ornithology. This work conformed to the guidelines of UC Berkeley Animal Use Protocol T042-0814.

<center>*Data Analysis*</center>

The data were analyzed to understand species richness and α and β diversity in each habitat, the relative effects of native versus invasive species on β diversity, and how community richness has changed over time. All analyses were conducted in R (R Core Development Team 2013). The data were analyzed primarily with a two-way analysis of

variance (2- way ANOVA). For simplicity and to gather a stronger set of information about each community at each site, all replicates were pooled for all analyses (except for the discriminant analysis, which considered all 108 samples), leaving 12 independent samples per habitat.

To understand the species richness in each habitat, a discriminant analysis was done (Fig. 2). For this investigation, habitats were defined as the categories for "x", and number of species as the covariates for "y". Fig. 2 plots the data from each 108 point-count samplings as maximally separated by habitat type. The circles correspond to 95% confidence intervals – if the circles do not overlap, the two categories have a significantly different composition, with 95% confidence.

α diversity values were calculated using the Shannon-Weiner Diversity Index. To determine if α diversity changed from one habitat to another, three separate 2-way ANOVA's were done on the α diversity values for each possible pair of habitats (3 pairs: forest and agricultural, forest and urban, and agricultural and urban).

As β diversity analysis is a relatively new field, it is important to use multiple indices in any analysis of β diversity (see Appendix A for a description of each index used in this study). β diversity was expressed in terms of dissimilarity values. A dissimilarity value describes the difference in community structure between two sites. The formula used to calculate the dissimilarity value is defined by the respective diversity index. I applied five diversity indices – Jaccard, Chao, Bray-Curtis, Manhattan, and Euclidean – to richness and abundance data at each point in each habitat. The Jaccard, Chao, and Bray-Curtis indices were chosen because they are three of the most commonly applied β diversity indices. The Manhattan and Euclidean indices were selected because they were the only two indices that were useful for contrasting the native versus invasive data (see below).

I first sought to determine if β diversity depends on habitat. To answer this question, I performed a pairwise dissimilarity analysis for each of the three pairs of differing habitats. For each grouping of the data for two habitats, I computed the five diversity indices. This yielded an array of dissimilarity values, quantifying the difference between those two habitats, but ignoring the internal structure of each habitat. This is summarized by a distance matrix, divided by habitat. This process was applied to the same three pairs of habitats

used in the α diversity analysis, and repeated for all five diversity indices. I then performed a permutational multivariate analysis of variance (PERMANOVA) on these distance matrices, to see if the habitat pairs were significantly different. For brevity, this analysis will henceforth be referred to as "Pairwise β Analysis 1".

A related question is how within-habitat variation of β diversity varies between habitats, which can be addressed by comparing the variance in β diversity between two habitats, rather than grouping data for pairs of habitats, as in Pairwise β Analysis 1. To do this, I kept the data subdivided by habitat, and applied each of the five diversity indices to the three habitats (in contrast to the 3 arrays for the 3 habitat pairs in Pairwise β Analysis 1). I then performed a 2-way ANOVA on each pair of habitats for each index, to determine if the variance in β diversity in one habitat was significantly different from another habitat. This analysis will henceforth be referred to as "Cross-Habitat β Analysis 2". For those habitat pairs that showed a significant difference from Cross-Habitat β Analysis 2, the mean dissimilarity values for each habitat were used to determine if β diversity was increasing or decreasing between the two habitats. For example, if forest and agricultural are significantly different, and forest has an average dissimilarity of 0.5 and agricultural an average of 0.25, β diversity would be described as decreasing from forest to agricultural habitats.

Because a majority of the birds on Moorea are invasive, I attempted to piece out the relative effects of native and invasive species on β diversity. To do this, I divided the data used for the α and β diversity analyses into native versus invasive species. I then ran the same tests of β diversity on each native and invasive data subset (henceforth "native" and "invasive").

To examine changes in community structure over time, I took my data and performed the same analyses Paul Durst did for his 2004 study on the avifauna of Moorea. The first step was an analysis of variance comparing average number of species by habitat. The second analysis of variance compared average percent native species by habitat. Finally, I compared average number of endemic species by habitat using a third ANOVA. These results were then compared to those reported for the 2004 study (see Discussion).

RESULTS

Discriminant Analysis

The discriminant analysis of the raw richness and abundance data, when grouped by habitat, show that all three habitats are significantly different from each other, with 95% confidence, as seen by the lack of overlap between the three circles (Fig. 2). In addition, the bi-plot of arrays describes the sign and magnitude of effect each species has in differentiating each habitat. Notable species include the Silvereye (species ID: ZOLA), which has a strong positive effect differentiating forest from agricultural habitats. Conversely, the Chestnut-breasted Mannikin (species ID: LOCA) has a strong but negative effect in differentiating forest and agricultural habitats (i.e. that species makes the two habitats appear more similar in their community structure).

α Diversity

α diversity was not identical between habitats (Fig. 3), but was not significantly different between any two habitats (see Table 1 for ANOVA values).

β Diversity – All Species

For Pairwise β Analysis 1, all β diversity indices applied (Jaccard, Chao, Bray-Curtis, Manhattan, Euclidean) showed that all habitats were significantly different from all other habitats (Table 2).

In Cross-Habitat β Analysis 2, when those habitats were run through each index independently, however, results were less clear (Fig. 4). The variances of β diversity in pairs of habitats were significantly different when derived from one index, but not when derived from another index (see Table 3 for ANOVA values). When the habitat pairs that were significantly different in any of the indices (Table 3) are compared to the

TABLE 1. ANOVA results for the Shannon-Weiner α diversity values between habitats.

		Diversity
	$F_{1, 10}$	p-value
Forest to Urban	4.47	0.061
Forest to Ag	0.26	0.62
Ag to Urban	0.56	0.47

corresponding mean dissimilarity values for that index for each habitat (Table 4), it can be inferred that β diversity increases from forest to urban habitats, forest to agricultural habitats, and agricultural to urban habitats.

β Diversity – Native Versus Invasive Effects

Because many sites did not contain any native species, and thus joint absences are high, only the Manhattan and Euclidean indices were applicable for those data (Manhattan and Euclidean indices include joint absences; Anderson et al. 2011). For consistency, only those two indices were run for the richness and abundance data on invasive species. When Pairwise β Analysis 1 was applied, all habitats were significantly different from all other habitats, as described by native and invasive species, separately.

When Cross-Habitat β Analysis 2 was applied to "native", the degree of significance differed between the two indices. At least one index showed there was a significant change in native species from forest to urban habitats, and from agricultural to urban habitats (see Table 5 for ANOVA values). When these are related to the mean dissimilarity value for each index (Table 6), β diversity for native species is inferred to increase from forest to urban habitats and from agricultural to urban habitats.

When Pairwise β Analysis 2 was applied to "invasive", significance varied between the two indices. For invasive species, a significant change was seen from forest to urban and forest to agricultural habitats, but not from agricultural to urban habitats (see Table 7 for ANOVA values). When these are related to the mean dissimilarity values for each index (Table 8), β diversity for native species is inferred to increase from forest to urban habitats and from forest to agricultural habitats.

Community Structure Over Time

The results from the 2004 study are included as Appendix B. For the present study, although average species richness did vary between habitats (Fig. 5), species richness was not significantly dependent on habitat (ANOVA, $F_{2, 33} = 2.07$, p-value = 0.14). The percent of native species was dependent on habitat (ANOVA, $F_{2, 33} = 7.40$, p-value = 0.0022, Fig. 6). Lastly, the number of endemic species was dependent on habitat (ANOVA, $F_{2, 33} = 10.35$, p-value = 0.00032, Fig. 7).
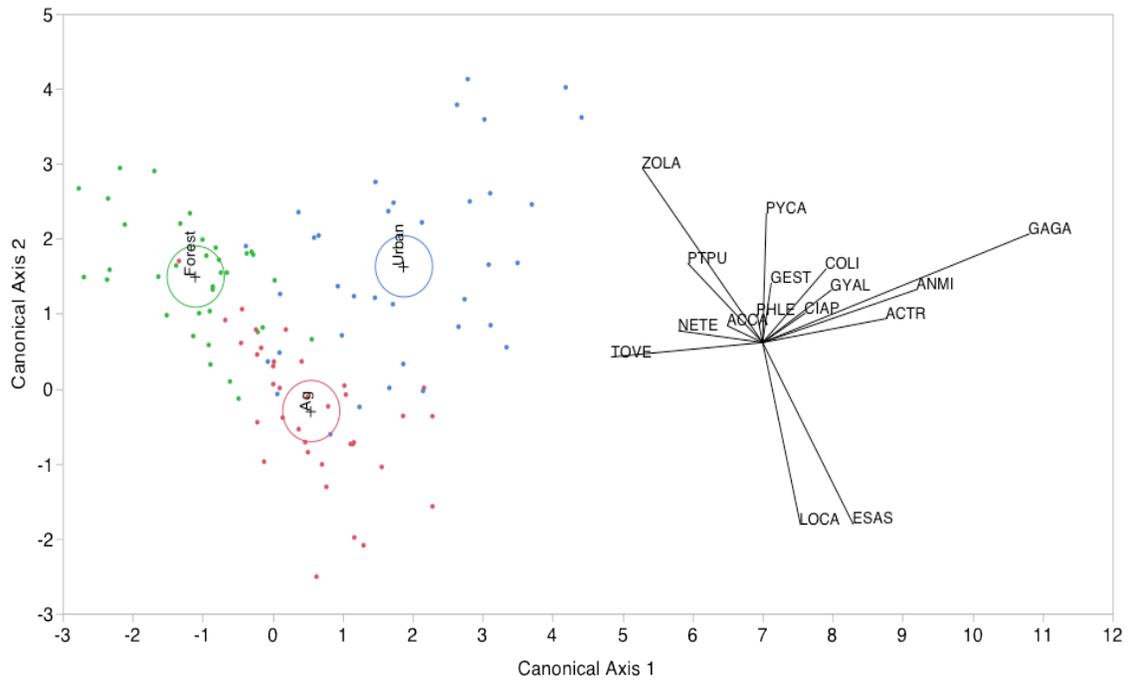
FIG. 2. Discriminant analysis of species abundance data. The points to the left represent each sampling, and are color coded by habitat. Green: Forest, Red: Ag, Blue: Urban. The three colored circles represent 95% confidence intervals. The bi-plot to the right represents the relative affect of each species in differentiating each habitat.
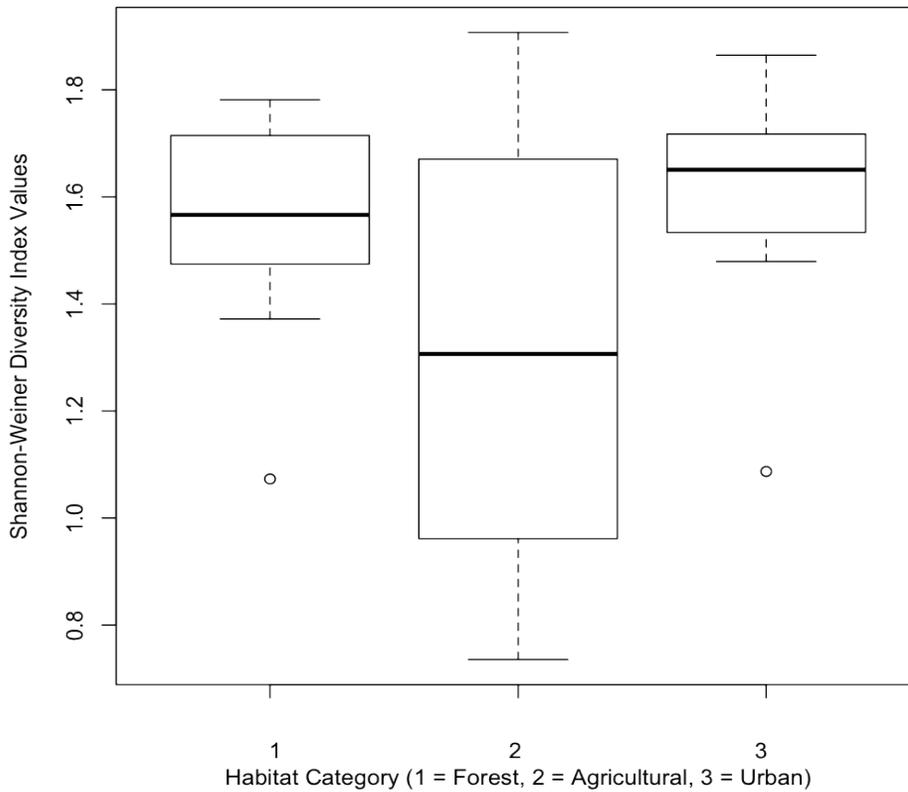

FIG. 3. Boxplot of α diversity values. Diversity values were calculated using the Shannon-Weiner diversity index. The thick black line is the average diversity, the top and bottom of the box are the 25% and 75% interquartiles, respectively. The Whiskers are the maximum and minimum values. The circle points are outliers.
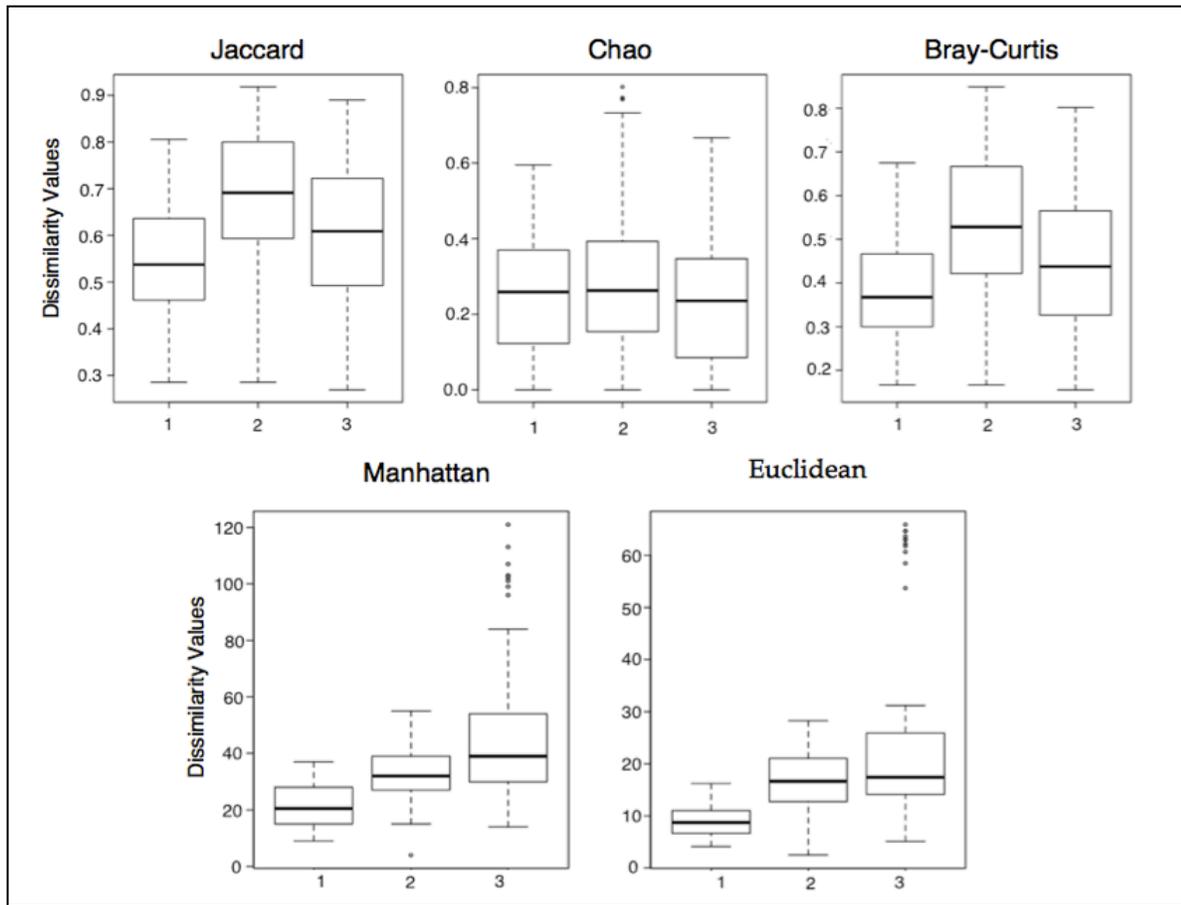
FIG. 4. Boxplots of β diversity values. Diversity values were calculated using the Jaccard, Chao, Bray-Curtis, Manhattan, and Euclidean diversity indices. Numbers on the x-axes correspond to habitats as 1 = Forest, 2 = Agricultural, and 3 = Urban.

TABLE 2. Results from the PERMANOVA of habitat pairs resulting from Pairwise β Analysis 1 (see text). Degrees of freedom and residuals are given as subscripts to the F value, respectively. (*) denotes significance to 95% confidence.

		Jaccard	Chao	Bray	Manhattan	Euclidean
	$F_{4, 22}$	4.07	4.62	6.44	144.79	90.69
Forest to Urban	R^2	0.43	0.46	0.54	0.96	0.94
	p-value	0.001*	0.001*	0.001*	0.001*	0.001*
	$F_{4, 22}$	3.87	6.84	6.05	308.38	226.97
Forest to Ag	R^2	0.41	0.55	0.52	0.98	0.98
	p-value	0.001*	0.001*	0.001*	0.001*	0.001*
	$F_{4, 22}$	2.68	2.88	3.88	120.40	72.86
Ag to Urban	R^2	0.33	0.34	0.41	0.96	0.93
	p-value	0.037*	0.001*	0.001*	0.001*	0.001*
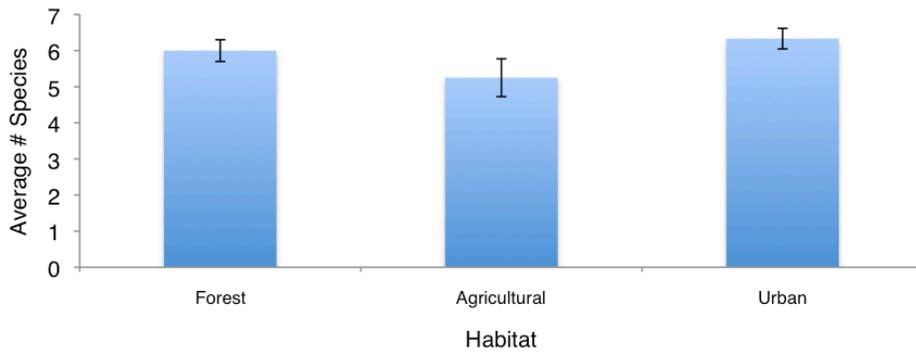
FIG. 5. Average species richness by habitat type. Error bars were computed using standard error.
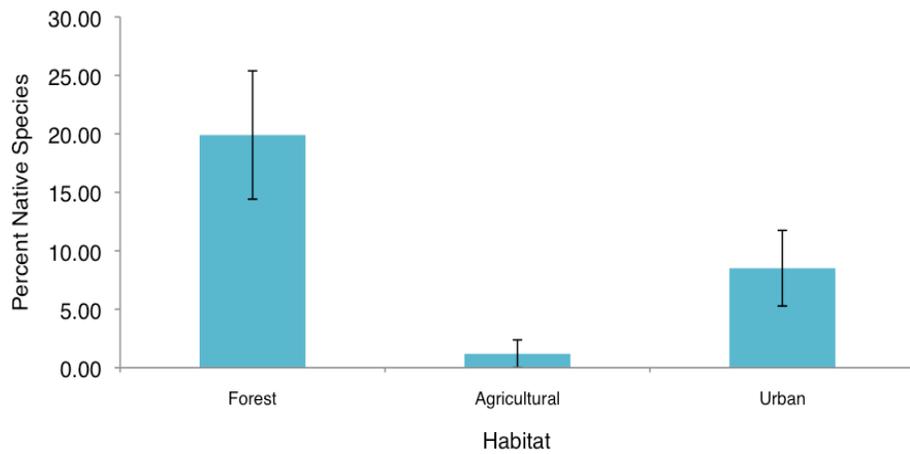

FIG. 6. Percent native species by habitat type. Error bars were computed using standard error.
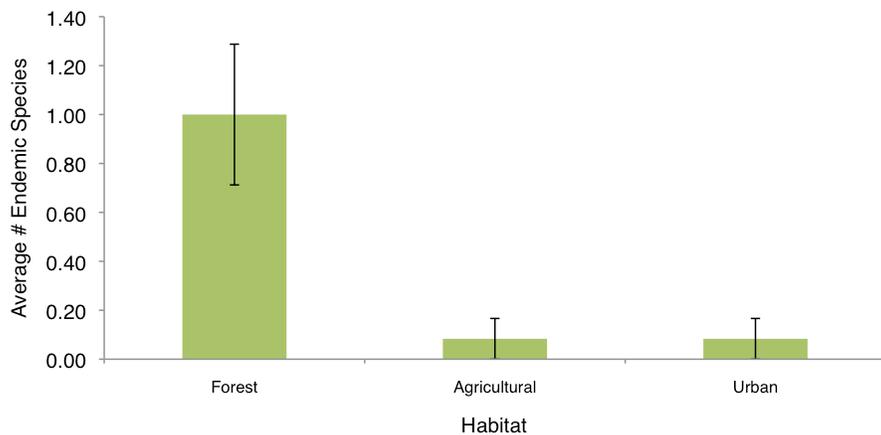

FIG. 7. Average number of endemic species by habitat type. Error bars were computed using standard error.

TABLE 3. Results from the ANOVA of habitat pairs resulting from Cross-Habitat β Analysis 2. Degrees of freedom and residuals are given as subscripts to the F value, respectively. (*) denotes significance to 95% confidence.

		Jaccard	Chao	Bray	Manhattan	Euclidean
Forest to Urban	$F_{1,64}$	1.79	0.64	2.62	5.44	4.30
	p-value	0.19	0.43	0.11	0.023*	0.042*
Forest to Ag	$F_{1,64}$	2.79	0.70	2.59	6.74	0.63
	p-value	0.10	0.41	0.11	0.012*	0.43
Ag to Urban	$F_{1,64}$	0.38	6.89	0.48	3.29	0.14
	p-value	0.54	0.011*	0.49	0.07	0.71

TABLE 4. Average dissimilarity values calculated in Cross-Habitat β Analysis 2.

	Jaccard	Chao	Bray	Manhattan	Euclidean
Forest	0.55	0.25	0.39	21.11	9.08
Ag	0.69	0.29	0.54	32.56	17.06
Urban	0.61	0.23	0.46	47.11	24.54

TABLE 5. Results from the ANOVA of habitat pairs resulting from Cross-Habitat β Analysis 2, including only native species. (*) denotes significance to 95% confidence.

		Manhattan	Euclidean
Forest to Urban	$F_{1,64}$	4.75	0.06
	p	0.033*	0.81
Forest to Ag	$F_{1,64}$	0.16	0.01
	p	0.69	0.95
Ag to Urban	$F_{1,64}$	88.19	122.20
	p	1.18E-13*	2.00E-16*

TABLE 6. Average Dissimilarity values calculated in Cross-Habitat β Analysis 2, including only native species.

	Manhattan	Euclidean
Forest	4.27	3.11
Agricultural	0.83	0.83
Urban	4.59	4.07

TABLE 7. Results from the ANOVA of habitat pairs resulting from Cross-Habitat β Analysis 2, including only invasive species. (*) denotes significance to 95% confidence.

		Manhattan	Euclidean
Forest to Urban	$F_{1,64}$	4.75	4.19
	p	0.033*	0.045*
Forest to Ag	$F_{1,64}$	8.09	0.42
	p	0.001*	0.52
Ag to Urban	$F_{1,64}$	2.12	0.06
	p	0.15	0.81

TABLE 8. Average dissimilarity values calculated in Cross-Habitat β Analysis 2, including only invasive species.

	Manhattan	Euclidean
Forest to Urban	16.83	8.35
Forest to Ag	31.73	16.91
Ag to Urban	42.52	23.53

Discriminant Analysis

Discriminant analysis provided a useful first look at the community structure in each habitat. That analysis (see Fig. 2) showed that habitats are significantly different from each other, lending motivation to analyze the components creating this difference: α and β diversity. It also allowed for a preliminary analysis of native versus invasive species effects on community structure. The bi-plot array shows that the four species with the greatest effect on habitat differences (length of the vector) are all invasive. This suggests that invasive species account for a large portion of observed differences in habitat communities. It also justified looking at the effect of native and invasive species on β diversity, as that analysis provided detail on how native and invasive species affect community structure, showing how the overall structure of communities in each habitat is different for native and invasive species (see below).

α Diversity

Although none of the pairs of habitats were significantly different when considering a 95% confidence interval (see Table 1), it is important to note that transitioning from forest to urban habitats yielded a far more significant change than any other pairing. Previous studies have found that α diversity decreases with increased urbanization (Meffert and Dziock 2013, Trentanovi et al. 2013). My data do not appear to support this relationship, as α diversity increases from forest to urban habitats.

β Diversity – All Species

This study showed that β diversity increases from forest to agricultural to urban habitats (see Tables 3 and 4). Overall, I inferred that β diversity increases as a function of these habitat categories. The habitats considered in this study can be thought of in two variables: modification and complexity. Modification describes the extent to which humans have modified the habitat and increases from forest to agricultural to urban habitats. Complexity describes the heterogeneity of a habitat and increases from agricultural to forest to urban habitats.

β diversity can be described as increasing as a function of modification. When complexity is considered instead of modification, β diversity first decreases (agricultural to forest habitats), then increases (forest to urban habitats).

β Diversity – Native Versus Invasive Effects

Although the β diversity data presented indicate a nearly equal effect of native and invasive species (as both were equally significant for β Analyses 1 and 2), those results are misleading. The Manhattan and Euclidean indices were used when analyzing "native" and "invasive" only because the large number of joint absences in "native" disallowed the use of another index. This was not the case for "invasive", which had few joint absences. As joint absences describe two sites both lacking a particular species, fewer joint absences in a dataset implies that dataset has more species. Therefore, "invasive" can be described as having more weight than "native" in the overall dataset. This means that invasive species account for more of the observed diversity than native species. This is not surprising, as it is known that Moorea, overall, has 38 bird species, only 9 of which are terrestrial and native (Société d'Ornithologie de Polynésie Française).

One explanation for this dominance of invasive species on Moorea might be that humans have disturbed two of the three major habitats identified in this study. Human disturbance creates habitats that are novel to native species, but that some invasive species are already adapted to (Sax and Brown 2000).

Community Structure Over Time

In the nine years between this study and the one by Paul Durst, the bird communities have changed only slightly (see Figures 5-7 and Appendix B). Overall richness values are very similar for the forests, agricultural, and urban habitats observed in the two studies – yielding an overall average of 6 species per habitat, with urban just above and agricultural just below the mean. This implies that, if the identities of the species are ignored, communities have remained the same from 2004 to 2013. However, when only native species are considered, the apparent trend is broken. Forest habitats have more than doubled in the average percent native species – rising from less than 8% in 2004 to 20% in 2013. Several sources of error exist for this difference in value (e.g. different sites were sampled then and now). However, the

consistency between the other values suggests that differences in how the studies were done were not important. Alternatively, the rise in percent native species in the forest may be a secondary effect of loss of non-native species. If this were the case, however, we would expect to see a decrease in the total species richness of the forest, and we do not. Lastly, the average number of endemic species per habitat remains relatively unchanged. The fact that percent native species, but not the number of endemic species, rose over the time period suggests that the additional species occupying the forest are native, but not endemic. This possible increase in native species richness is in contrast to findings on most other oceanic islands, where native species are continually being replaced by invasive species (Sax and Brown 2002).

Hypotheses

The hypothesis that species composition would vary by habitat was supported, as indicated by the discriminant analysis (Fig. 2). Similarly, the hypothesis that α and β diversity would be dependent on habitat type were supported. The hypothesis that β diversity would decrease with increased human activity was not supported. The exact opposite of this hypothesis was supported when habitats were considered in terms of modification, and a more varied relationship was observed when habitats were defined in terms of relative complexity. The hypothesis that invasive species would play a greater role than native species in determining β diversity was supported. The hypotheses that species richness and the number of endemic species would increase in forest habitats from 2004 to 2013 were not supported. The hypothesis that the percent native species would increase in forest habitats over that period was supported.

Diversity and Conservation

The results from this study present implications for conservation on Moorea. The apparent increase in native species presence in the forests suggests that current efforts are at least somewhat effective. The fact that all other values for richness remained constant from 2004 to 2013 hints that those conservation efforts, while marginally successful in increasing native species presence, are fighting mostly just to keep the ratio of native to invasive species constant.

Expansion of these efforts into new areas could help move forward a goal of restoration, rather than simply conservation. For example, the endemic Tahiti Kingfisher was only in areas that had a running stream, so maintenance and repair of stream systems could expand the range of the Tahiti Kingfisher. Overall richness from 2004 to 2013 was also nearly constant, so simpler endeavors could try to increase species richness, especially in agricultural habitats, where it was lowest in 2013. For example, agricultural habitats that had a few trees interspersed had noticeably more species, so planting as few as a dozen trees in every five acres of agricultural land could bolster richness. Whatever action is taken, though, increased focus on conservation of the bird communities on Moorea cannot come too soon.

Avian communities on oceanic islands are often less diverse than their mainland counterparts (Sax and Brown 2002). In developing regions, such as Moorea, this already-low diversity is being altered by invasive species that are filling the niches created by human disturbance (Durst 2004). While this may not lower diversity locally (it may even increase it), if all the habitats in a region are replaced with the same invasive species, then both β and γ diversity will be dramatically reduced.

Diversity, whether applied to a system on an island or the mainland, is the best metric for understanding the effectiveness of conservation efforts, as it is a direct measurement of the health of a system (Vora 1997). Therefore, understanding the diversity in any region actively being impacted by humans is a good idea. The first step is to census all the species present in that region. Care must be given when describing the habitats, and a continuous variable of human impact is the most powerful. After that, diversity values for each habitat can be calculated and applied to questions of conservation.

The goal of conservation, in general, is to maintain the abundance of *in situ* species. When diversity values decrease despite increased conservation, there are two options: (1) diversity is not being measured correctly, or (2) conservation efforts are ill placed. When diversity values are inconsistent or cannot be obtained, the method of conservation must be considered. Conservation of a particular sea turtle species focused on fecundity and the survival of offspring for decades, until it was

discovered that sea turtle species was more dependent on adult survival (Ennenson and Litzgus 2008). While this example concerns population and not community ecology, the lesson remains the same: the problem with conservation is often not in the amount of effort given, but where that effort is focused. The efficiency of conservation is maximized when this lesson is considered alongside accurate diversity measurements. Hopefully studies such as this one will help to provide those diversity values and aid present and future conservation efforts.

While this study attempted to describe effect of human disturbance on the birds of Moorea using a multi-faceted approach, it only begins to portray the complete mosaic of avian ecology on Moorea. A more thorough analysis of α diversity in disturbed and non-disturbed habitats, utilizing a sampling scheme designed for an α diversity analysis, and application of additional α diversity indices (e.g. Simpson) would help to further establish how disturbance affects diversity at small scale. It would be useful to apply a quantitative definition of habitat modification and habitat complexity, to yield a continuous gradient to compare α and β diversity against. Lastly, inclusion of shorebirds and pelagic birds would give future studies a more complete description of Moorea avifauna. Also, those data could be compared to Durst's 2004 study, which included shorebirds and pelagic birds to provide a continued analysis of bird community structure on Moorea over time.

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APPENDIX A
DESCRIPTION OF β DIVERSITY INDICES

Index	Formula	Variables
Jaccard	2B/(1+B)	B = Bray-Curtis dissimilarity
Chao	U[j]*U[k]/(U[j] + U[k] - U[j]*U[k])	U[j,k] = C[j,k]/N[j,k] + (N[k] - 1)/N[k] * a1/(2*a2) * S[j,k]/N[j,k]
		C(j) = number of species in site j shared with species in site k
		N(j) = total number of species at site j
		a1 = number of species in site j with only 1 individual in site k
		a2 = number of species in site j with only 2 individuals in site k
		S(j) = total number of individuals in the species that correspond to a1
Bray-Curtis	(A+B-2*J)/(A+B)	A = number of species in site A
		B = number of species in site B
		J = number of species in both sites
Manhattan	A+B-2*J	A = number of species in site A
		B = number of species in site B
		J = number of species in both sites
Euclidean	sqrt(A+B-2*J)	A = number of species in site A
		B = number of species in site B
		J = number of species in both sites

(Information obtained from Oksanen 2013)
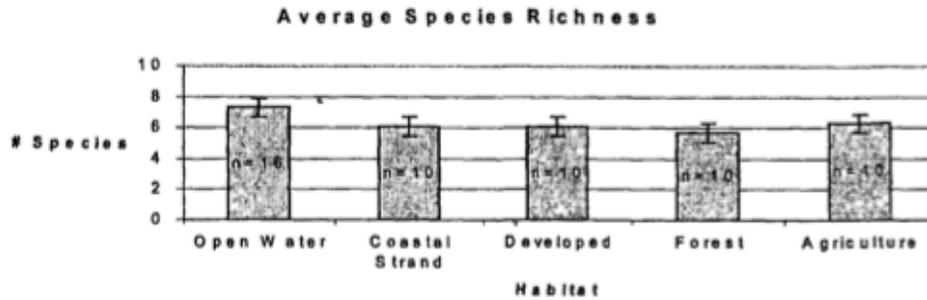
FIG. 2. The average species richness for each habitat.
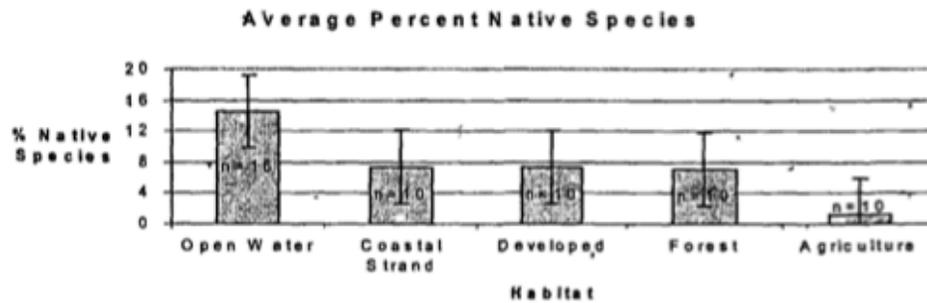
FIG. 3. The average percent of native species for each habitat.
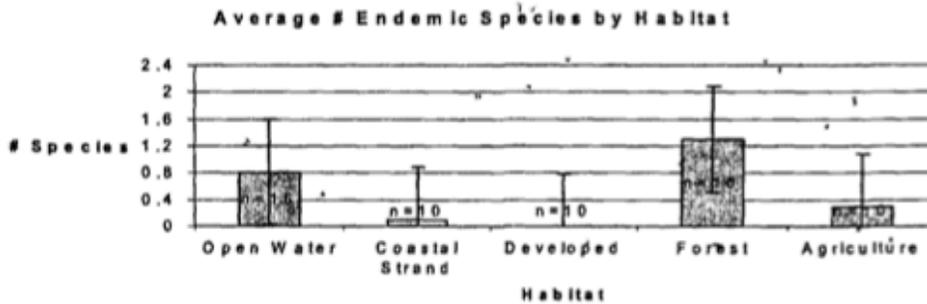
FIG. 4. The average number of endemic species by habitat.

APPENDIX C
LOCATIONS OF ALL SITES SAMPLED

Site	Habitat	Latitude	Longitude
F1	Forest	17°32'12.00"S	149°49'46.55"W
F1.1	Forest	17°32'7.60"S	149°49'44.79"W
F1.2	Forest	17°32'11.98"S	149°49'43.90"W
F2	Forest	17°31'56.35"S	149°49'40.67"W
F2.1	Forest	17°32'0.24"S	149°49'42.12"W
F2.2	Forest	17°31'56.14"S	149°49'36.71"W
F3	Forest	17°31'31.04"S	149°50'43.57"W
F3.1	Forest	17°31'31.26"S	149°50'46.47"W
F3.2	Forest	17°31'30.67"S	149°50'41.33"W
F4	Forest	17°32'2.40"S	149°50'16.80"W
F4.1	Forest	17°31'58.80"S	149°50'20.40"W
F4.2	Forest	17°31'58.80"S	149°50'16.80"W
A1	Agricultural	17°31'43.10"S	149°49'40.49"W
A1.1	Agricultural	17°31'39.09"S	149°49'36.55"W
A1.2	Agricultural	17°31'36.51"S	149°49'34.96"W
A2	Agricultural	17°31'25.09"S	149°49'38.75"W
A2.1	Agricultural	17°31'29.74"S	149°49'41.06"W
A2.2	Agricultural	17°31'19.58"S	149°49'38.79"W
A3	Agricultural	17°31'54.32"S	149°50'11.91"W
A3.1	Agricultural	17°31'50.19"S	149°50'12.90"W
A3.2	Agricultural	17°31'52.89"S	149°50'14.81"W
A4	Agricultural	17°31'20.38"S	149°50'56.16"W
A4.1	Agricultural	17°31'22.83"S	149°50'51.27"W
A4.2	Agricultural	17°31'17.28"S	149°50'53.68"W
U1	Urban	17°30'33.10"S	149°49'18.09"W
U1.1	Urban	17°30'38.19"S	149°49'20.78"W
U1.2	Urban	17°30'27.43"S	149°49'14.72"W
U2	Urban	17°30'27.92"S	149°49'23.72"W
U2.1	Urban	17°30'25.09"S	149°49'20.24"W
U2.2	Urban	17°30'30.38"S	149°49'27.02"W
U3	Urban	17°30'58.12"S	149°49'17.36"W
U3.1	Urban	17°30'54.51"S	149°49'14.95"W
U3.2	Urban	17°30'56.16"S	149°49'20.95"W
U4	Urban	17°31'1.48"S	149°49'28.44"W
U4.1	Urban	17°30'56.86"S	149°49'26.27"W
U4.2	Urban	17°31'1.60"S	149°49'32.92"W

APPENDIX D
COMPLETE LIST OF THE BIRDS OF MOOREA

(*) denotes species that were included in the study

(**) denotes species that were included in the study, but not oberserved

Scientific Name	Common Name	Habitat/Status
Macronectes giganteus	Giant Petrel	Pelagic/Native
Pseudobulweria rostrata	Tahiti Petrel	Pelagic/Native
Puffinus pacificus	Wedge-tailed Shearwater	Pelagic/Native
Puffinus lherminieri	Audubon's Shearwater	Pelagic/Native
Phaethon lepturus*	White-tailed Tropicbird	Terrestrial/Native
Sula leucogaster	Brown Booby	Pelagic/Native
Sula sula	Red-footed Booby	Pelagic/Native
Fregata minor	Great Frigatebird	Pelagic/Native
Fregata ariel	Lesser Frigatebird	Pelagic/Native
Egretta sacra	Pacific Reef Heron	Pelagic/Native
Anas superciliosa	Pacific Black Duck	Shorebird/Native
Circus approximans*	Swamp Harrier	Terrestrial/Introduced
Gallus gallus*	Junglefowl	Terrestrial/Introduced
Porzana tabuensis**	Spotless Crake	Terrestrial/Native
Pluvialis fulva	Pacific Golden Plover	Shorebird/Native
Numenius tahitiensis	Bristle-thighed Curlew	Shorebird/Native
Heteroscelus incanus	Wandering Tattler	Shorebird/Native
Onychoprion bergii	Great Crested Tern	Pelagic/Native
Onychoprion fuscatus	Sooty Tern	Pelagic/Native
Onychoprion lunata	Gray-backed Tern	Pelagic/Native
Anous stolidus*	Brown Noddy	Pelagic/Native
Anous minutus**	Black Noddy	Pelagic/Native
Gygis alba*	White Tern	Pelagic/Native
Columba livia*	Rock Dove	Terrestrial/Introduced
Geopelia striata*	Zebra Dove	Terrestrial/Introduced
Ptilinopus purpuratus*	Gray-green Fruit-dove	Terrestrial/Native
Eudynamys taitensis**	Long-tailed Koel	Terrestrial/Native
Aerodramus leucophaeus**	Tahiti Swiflet	Terrestrial/Native
Todiramphus tutus**	Chattering Kingfisher	Terrestrial/Native
Todiramphus veneratus*	Tahiti Kingfisher	Terrestrial/Native
Hirundo tahitica**	Pacific Swallow	Terrestrial/Introduced
Pycnonotus cafer*	Red-vented Bulbul	Terrestrial/Introduced
Acrocephalus caffer*	Tahiti Reed Warbler	Terrestrial/Native
Acridotheres tristis*	Common Myna	Terrestrial/Introduced
Zosterops lateralis*	Silvereye	Terrestrial/Introduced
Estrilda astrild*	Common Waxbill	Terrestrial/Introduced
Lonchura castaneothorax*	Chestnut-breasted Mannikin	Terrestrial/Introduced
Neochmia temporalis*	Red-browed Firetail	Terrestrial/Introduced

(Information obtained from the Société d'Ornithologie de Polynésie Française: www.manu.pf/E_MOOREA.html)