

Prehistoric species richness of birds on oceanic islands

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Abstract

Using data on prehistoric and modern birds from seven islands in the Kingdom of Tonga, we demonstrate that there is no positive relationship between species richness (S) and island area (A) over the observed range of A (1.8-259 km²). The uniform S-values occur across more than three orders of magnitude of A when prehistoric data are included, and the strongest predictor of S on any island is the level of fossil sampling (number of identified bones). Below a minimum value for A (in Tonga, <1.8 km²), S declines to zero as A does the same. Within the ranges of island elevation (E) and inter-island isolation (I) among the seven islands, neither E (11-312 m) nor I (0.6-38 km) has much if any effect on S. Under natural (pre-human) conditions, a positive species-area relationship may not be a valid generalization for birds on oceanic islands.

Species richness is one gauge of an area's ecological diversity. Obtaining high-quality data for this measurement can be challenging, however, even for organisms as conspicuous as birds (May 1988). This is especially true on oceanic islands, where human activities have extirpated so many species, thus necessitating the use of paleontological and archaeological techniques to recover evidence of the bird communities that existed at first human contact, which in most island groups was hundreds to thousands of years ago (Steadman 2006).

As reviewed by Connor and McCoy (1979), the generally observed positive relationship between number of species and area may have several theoretical causes. Larger areas have a greater diversity of habitats (reviewed in Lomolino and Weiser 2001), although an alternative explanation is that the positive species-area relationship is a consequence of passive sampling from a species pool, with larger areas receiving more input than smaller ones, and therefore having more species (Connor and McCoy 1979). That is, as the area surveyed (or number of bones identified, in this study) increases, the number of species encountered always will increase (Gleason 1922) because of the statistical chance of finding additional species, the so-called sampling effect. The third explanation, and one that has received considerable attention, is the "area effect per se"; the equilibrium theory of island biogeography predicts that islands that are larger, or closer to a source area, will support more species as a result of immigration and extinction processes, the dynamic equilibrium of species exchanges (Preston 1962, MacArthur and Wilson 1967). It is important to note that while adequate fit of this model to observed data has been seen as support of the equilibrium hypothesis, potential causes of a positive species-area relationship and the parameters that describe it cannot necessarily be distinguished on the basis of species-area data alone (Connor and McCoy 1979).

When using either prehistoric or modern data to estimate species richness, the effect of sampling must be taken into account. Ecologists and zooarchaeologists have used species-accumulation curves to gauge the adequacy of a sample to estimate total species richness, and rarefaction methods to estimate the true species richness in smaller samples, so that the richness in samples of different sizes can be compared (Kirch et al. 1987, Lyman and Ames 2007). Statistical methods also have been developed to estimate the asymptotic species richness from a sample (reviewed in Gotelli and Colwell 2001). Both approaches are used in this study – rarefaction to interpolate species richness to smaller samples, and nonparametric estimators to extrapolate the estimated total number of species.

We use modern and prehistoric data on the distribution of landbirds on seven islands in the Kingdom of Tonga, Oceania, to evaluate the relationships between species richness and

island area, elevation, and isolation. For decades, studies of species-area relationships (Simberloff 1970, Terborgh 1973) and the equilibrium theory (Preston 1962, MacArthur and Wilson 1967) have focused on modern bird distributions on islands. It is now well recognized, however, that essentially no species assemblages of island birds are unaffected by human activities (Steadman 1995). We must look to the past to estimate the sets of species that inhabited islands at first human contact.

Tonga is the only tropical Pacific archipelago with substantial prehistoric data from islands spanning more than three orders of magnitude of land area (Steadman 2006: Tables 6-10, 6-19-6-21; Table 1 herein). First we consider the relationships between species richness and island characteristics when prehistoric data (3033 bird bones identified to species-level) and sampling effects are not taken into account. We then examine the effects of sampling intensity (identified bones per island) on the prehistoric species richness of landbirds, leading to an estimate of the asymptotic number of species on these seven islands when people arrived.

Methods

The data on prehistoric distributions are based on bird bones from archaeological (cultural) and paleontological (non-cultural) sites meticulously excavated using standard methods from 1987 to 2001 (details in Steadman 1993, 2006, Burley et al. 2001, Steadman et al. 2002a, b). The bones were identified to the species level through direct comparisons with modern and prehistoric skeletal specimens using standard osteological techniques (e.g., Kirchman and Steadman 2005). The extirpated and extinct species disappeared after Polynesian people arrived in Tonga at 2800 to 2900 ybp (years before present); their loss was a direct or indirect result of prehistoric human occupation of these islands, with habitat loss, hunting, and predation by non-native vertebrates variously contributing to the extinction (Steadman 1993, 1995, 2006; Steadman et al. 2002a). The archaeological sites represent the first century of human presence on each island; within this geologically narrow window of time, we see no evidence of faunal turnover, nor do we find support for or against the existence of a dynamic equilibrium. We do not believe that the prehistoric bird communities were sampled more thoroughly in sites from small islands than in those from larger islands; each prehistoric site is within 1 km of the coast and within several km of each island's entire elevational range. The modern distribution of Tongan birds (Table 1) is based on point-counts and other surveys (Steadman 1998, 2006).

Generalized linear models (GLMs) and rank correlation coefficients were used to examine the relationships between modern species richness (S_m in Table 1; when a range is given the maximum was used) and island area (A), elevation (E), and isolation (I ; distance to the nearest island $>10 \text{ km}^2$; Table 1). The relationships between A and prehistoric species richness (S_p in Table 1) and total (prehistoric + modern) species richness (S_t in Table 1) also were examined using GLMs. The GLMs based on \log_{10} transformations of species number and/or area were Gaussian (e.g., simple linear regression), while those based on raw S -values were Poisson (e.g., Poisson regression; Venables and Ripley 1994). Our sample size was small (7) so we conducted a power analysis to determine the chance of finding a regression slope value to be statistically significant given the sample size and variance. We also compared estimated slopes to values from 100 published species-area studies (Connor and McCoy 1979).

We then evaluated the effect of sampling intensity on estimated S_p using the number of identified specimens (NISP) per taxon on each island as a measure of the number of individuals observed in the prehistoric data, or the sample size. A species accumulation curve was

constructed and examined. The correlation between S_p and NISP on each island was estimated, again using GLMs and rank correlation.

Rarefaction estimates the expected species richness in random subsamples of a given size (number of individuals or number of sample units) from the community (Heck et al. 1975). We used the function **rarefy** in the package **vegan** of the R open-source statistical software (R Development Core Team 2007). It is based on Hurlbert's (1971) formulation, and the standard errors on Heck et al. (1975), although of greater interest here was an estimate of the “true” (asymptotic) S_p in the entire sample. The species-area curve constructed in the PC-Ord software (McCune and Mefford 1999) is a sample unit-based (rather than individual-based) rarefaction curve, estimated by subsampling the data to determine the average number of species as a function of the number of observations in the subsample (in this case the number of islands, from 1 to 7). Subsampling was repeated 500 times for each subsample, yielding two nonparametric estimates of the true number of species in the entire sample (all seven islands), which were calculated using the method of Palmer (1990, 1991, 1995). In this approach, the greater the number of rare species in the dataset, the more likely it is that other species were present in the area but not recorded in the sample (Gotelli and Colwell 2001).

Results

The number of modern landbird species, S_m , appears to be related to island area (Figure 1a) based on a semi- \log_{10} model ($R^2 = 0.56$, $P = 0.031$). A \log_{10} - \log_{10} model yields similar results ($R^2 = 0.55$, $P = 0.035$), although the value of the slope coefficient, 0.069 (z in the species-area literature), is much lower than the canonical value of 0.26 (discussed in Lomolino and Weiser 2001) or the “typical range” of 0.15-0.35 (Rosenzweig 1995). When prehistorically sampled species S_p are considered, there is no relationship between S_p and A (Figure 1b) based on Poisson regression, i.e., the estimated coefficient for island area (0.000569) was not significantly different from zero ($P(>|z|) = 0.493$). The relationship also is not significant when a semi- \log_{10} ($R^2 = 0.26$, $P = 0.138$) or \log_{10} - \log_{10} ($R^2 = 0.29$, $P = 0.123$) species-area model was estimated using linear regression. Further, there was no relationship between S_t (modern + prehistoric species recorded on each island) and A based on either rank correlation (Kendall's $\tau = 0.488$; $P = 0.129$) or Poisson regression -- the coefficient for A was not significantly different from zero ($P(>|z|) = 0.288$) (Figure 1c). The power of these analyses to determine if the regression is significant (a slope significantly different than zero) is low owing to the small sample size -- 0.55 in the case of S_p versus A , and 0.53 for S_t versus A . However, when slope values for the \log_{10} - \log_{10} models of S_t (0.06119) and S_p (0.06410) were compared to 100 published slope values from the literature (Figure 2) using a one-sample t-test, they were significantly different from the sample mean of 0.66562 ($P \gg 0.001$ in both cases). This lends strength to the conclusion that there is no positive statistical relationship between total species number and island area in this dataset in spite of the small sample size.

The relationship between S_t and island elevation (E) was weakly positive but not significant based on Poisson regression (estimated coefficient for E was not significantly different from zero, $P(>|z|) = 0.124$) or rank correlation (Kendall's $\tau = 0.59$; $P = 0.068$). The relationship between S_t and isolation (I) also was not significant based on Poisson regression (estimated coefficient for I was not significantly different from zero, $P(>|z|) = 0.703$) or rank correlation (Kendall's $\tau = 0.21$; $P = 0.534$).

By contrast, the relationship between S_p and the sampling intensity (represented by NISP; Figure 1d) was highly significant. The results for linear regression ($R^2 = 0.93$, $P = 0.0003$) and Poisson regression ($D^2 = 0.91$) were concordant.

The species accumulation curve (Figure 3), based on NISP for species in the prehistoric record, shows how many new species are recorded when NISP values increase in the sample (seven islands). Visually, it appears that the line has not reached an asymptote, and thus the total cumulative number of prehistoric bird species on these Tongan islands at human contact was likely to have been >45 (the total number observed in the sample).

Individual-based rarefaction shows that if each island was sampled with equal intensity, for example the smallest number of NISP per island (147 for Ha'ano), the variation in S_p values across islands would be very low indeed (range = 19.3-23.6 species; Table 1). The species-sample area curve (Figure 4) estimated by sample-based rarefaction indicates a very flat accumulation curve (many species present even in the smallest sample). The estimated total number of prehistoric species on all seven islands combined is 52.6 or 56.1 (first- and second-order jackknife estimates), suggesting that the number of new species observed thus far in the prehistoric record for Tonga is beginning to level off, but has not yet reached an asymptote.

To summarize, when the intensity of fossil sampling (number of identified bones) is evaluated, potential increases in number of species (S) with island area (A), elevation (E), and isolation (I) are negligible.

Discussion

The line of best fit in a log-log plot of S vs. A has slope z , the value of which can change depending on spatial scale (McGuinness 1984, Brown & Lomolino 1998:376). We have shown that high-quality S -values for landbirds on true oceanic islands, derived from both prehistoric bones and rigorous modern surveys, yield z -values of essentially zero once a minimum island area is reached. As island area approaches zero, one after another resident species of landbird (and other organisms) must drop out as survival requirements are not met to sustain a population (Morse 1977, Lomolino and Weiser 2001, Steadman 2006). We have no evidence in Tonga of a steeper z for birds at large spatial scales, i.e., the largest islands. If all islands in Tonga were still largely forested and lacked non-native predators, the minimum land area required to sustain the complete avifauna may be as small as only 1-2 km². From the data analyzed in this paper, it seems that islands as small and low as Ha'afeva (1.8 km², 11 m elevation) had more or less the full range of species at human contact (Table 1, Figure 1).

None of the seven Tongan islands with fossil records is highly isolated (inter-island distances range from 0.6 to 38 km); within this range, we see no effects of isolation on S . In fact there is nothing special about the area, elevation, isolation, geological age, or human history of our seven islands that would make any one of them unusual in Tonga. Of course we wish that adequate fossils were available from more than seven islands. Given the geographic rarity of high-quality fossil records in general, and the extreme rarity of high-quality fossil records on multiple islands in a single island group, our Tongan sample of seven islands with bird fossils is the best there is, and represents many thousands of person-hours of excavation and sieving of sediments, and subsequent osteological comparisons.

A null model for S - A relationships of landbirds in Oceania was proposed by Steadman (2006) on the premise that every species or allospecies known to inhabit an island group should occur on each high island (non-atoll) of a certain minimum land area (MLA) within that archipelago. The MLA may decrease on average in more isolated island groups. In remote parts

of Oceania, the MLA needed to sustain essentially the entire landbird fauna probably varies from as small as 1-2 km² (Tonga, Samoa, East Polynesia, Micronesia) to perhaps 10-30 km² (Fiji, Vanuatu). An island group with a landbird community conforming precisely to the MLA model would have a z-value of zero for the data from islands where $A \geq \text{MLA}$. We do not expect perfect fits for the MLA model, but it does provide a benchmark against which to evaluate species richness in any island group.

In Oceania, inter-island distances less than ca. 50-100 km tend to have little long-term influence on species richness of birds, whereas greater within-archipelago isolation probably reduces S-values for individual islands (Steadman 2006). Geological age influences species richness in a positive way; the longer that an island has existed, the more opportunities it has had for colonization and perhaps speciation. Two Pacific islands where S-values might be enhanced by old age are Grande Terre (New Caledonia) and Viti Levu (Fiji). On the other hand, islands with very young geological ages should have low S-values. This is why atolls do not fit the MLA model; most of them were inundated during the last interglacial (ca. 125,000 years ago) or even during the current interglacial (the past 10,000 years; Dickinson 2003, Steadman 2006). The MLA model applies to the majority of high islands in Oceania, which have geological ages of ca. >0.2 but <10 my. The ages of all seven Tongan islands probably are within this range (Dickinson and Burley 2007).

The MLA model can be evaluated and refined with fossils, as we have done here. The strength of the scrutiny will depend on completeness of fossil records, which can be assessed statistically. Most fossil data in hand from Oceania are limited in scope, although rarefaction analyses such as ours could be attempted as well in the Hawaiian Islands (James & Olson 1991, Olson & James 1991) or New Zealand (Worthy & Holdaway 2002).

The prehistoric data from Tonga, which are the first to evaluate the MLA model with statistical rigor, suggest a much more uniform, widespread distribution of landbird species at human contact than today. Much of the positive relationship between A and modern S-values is because it has been more difficult for people to extirpate populations of birds on large, steep islands than on smaller, typically flatter ones (Steadman 1995, 2006). This notion is reinforced by examining individual points relative to the fitted regression line in S-A plots; the points that lie farthest below the line of best fit (e.g., Steadman 2006: Figures 19-7, 19-11, 19-12b) represent highly disturbed islands, whereas the points most above the line are from islands with much native forest.

We restrict the generalization of our results to landbirds on tropical oceanic islands. Our results may be unlikely to apply to organisms that differ highly from birds in their regimes of dispersal, colonization, reproduction, and population dynamics. Almost certainly our results would not be applicable either to the rich but much less endemic biotas of continental islands or habitat patches on continents.

Finally, we note that species-area data based on minimal sampling yield artificially low S-values, which calls into question the analysis of large datasets based on uneven sampling methods and effort. Nearly 30 years ago, Connor and McCoy (1979) called for the publication of nonsignificant correlations between species number and area, positing that they would be as informative about species-area relationships as significant positive correlations, if not more so. Without standardized sampling, or at least statistical methods to account for uneven sampling, it is difficult to evaluate potential correlations between S and A. The quality of species richness data can be improved not only through more comprehensive modern surveys but also by gathering prehistoric data on the extent of anthropogenic impacts on diversity. More complete

survey data, whether modern or prehistoric, are likely to decrease the apparent influence of A on S on oceanic islands.

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Table 1. Prehistoric bones of landbirds from seven islands in Tonga. Numbers represent the number of identified prehistoric bones (NISP) from that island. ^e, species endemic to Tonga; ^{ef}, flightless species endemic to a single Tongan island; ^h, an island in the Ha`apai Group; M, modern record (within past 200 years); P, prehistoric record; † extinct species. Data from Steadman (1993, 1998, 2006, herein). Estimated number of prehistoric species (P) based on rarefaction to 147 NISP (sample size for Ha`ano).

	Tongatapu	`Eua	Foa ^h	Lifuka ^h	Ha`ano ^h	`Uiha ^h	Ha`afeva ^h
Island area (km²)	259	87	13.3	11.4	6.6	5.3	1.8
Elevation (m)	67	312	20	16	12	11	11
Isolation (km from nearest island ≥ 10 km²)	18	18	0.6	0.6	2.6	7.5	38
TOTAL SPECIES							
M (S_m)	19	14-15	13	13-14	10-12	10-13	11-14
P (S_p)	25	34	24	27	21	21	22
Estimated P per 147 NISP (rarefy)	20.6	23.6	21.9	21.0	21	19.7	19.3
M+P (S_t)	32	35-36	27	30-31	23-24	25-26	26-27
NISP	329	1258	212	607	147	184	296
HERONS							
<i>Egretta sacra</i>	M	M, 1	M	M, 1	M	M	M
^{e†} <i>Nycticorax</i> undescribed sp. B	---	3	1	2	1	---	3
DUCKS							
<i>Anas superciliosa</i>	M	M	M, 6	M	---	---	M, 5
OSPREY							
<i>Pandion haliaetus</i>	1	---	---	---	1	1	---
HAWKS							
<i>Circus approximans</i>	M	---	M	M?	M?	M?	M?

	Tongatapu	`Eua	Foa ^h	Lifuka ^h	Ha`ano ^h	`Uiha ^h	Ha`afeva ^h
<i>Accipiter rufitorques</i>	---	3	---	---	---	---	---
MEGAPODES							
<i>Megapodius pritchardii</i>	---	1	3	3	---	1	1
^e † <i>Megapodius alimentum</i>	5	43	2	194	5	35	93
† <i>Megapodius molistructor</i>	76	---	10	9	4	4	3
^e † <i>Megapodius</i> undescribed sp. F	---	2	---	---	---	---	---
†Genus uncertain	4	---	1	---	---	---	---
RAILS							
<i>Gallirallus philippensis</i>	M, 31	M, 18	M, 32	M, 77	M, 35	M, 19	M, 14
^{ef} † <i>Gallirallus</i> undescribed sp. F	---	---	---	---	---	---	2
^{ef} † <i>Gallirallus</i> undescribed sp. G	1	---	---	---	---	---	---
^{ef} † <i>Gallirallus vekamatolu</i>	---	90	---	---	---	---	---
<i>Porzana tabuensis</i>	M, 15	257	2	21	1	6	2
<i>Porphyrio porphyrio</i>	M, 14	M, 45	M, 41	M, 81	M, 24	M, 31	M, 15
PIGEONS, DOVES							
† <i>Caloenas canacorum</i>	---	---	---	10	1	---	4
<i>Gallicolumba stairi</i>	M, 8	60	2	19	1	3	40
^e † <i>Didunculus ngutulahi</i>	5	25	---	6	1	3	1
<i>Ptilinopus perousii</i>	M, 8	M, 9	6	M, 7	---	1	18
<i>Ptilinopus porphyraceus</i>	M, 1	M, 7	M, 2	M, 12	M, 3	M, 3	M, 8
<i>Ducula pacifica</i>	M, 21	M, 22	M, 3	M, 13	M?, 21	M?, 12	M?, 12
<i>Ducula latrans</i>	30	12	16	13	6	14	11

	Tongatapu	`Eua	Foa ^h	Lifuka ^h	Ha`ano ^h	`Uiha ^h	Ha`afeva ^h
°† <i>Ducula</i> undescribed sp.	---	9	3	8	---	---	14
°†Undescribed genus	39	9	7	26	---	5	3
PARROTS							
<i>Vini solitarius</i>	---	1	---	1	---	2	---
<i>Vini australis</i>	M	3	M	M	M	M	M
† <i>Ecleetus infectus</i>	---	10	---	9	---	1	---
CUCKOOS							
<i>Cacomantis flabelliformis</i>	1	---	---	1	---	1	---
BARN-OWLS							
<i>Tyto alba</i>	M	M, 25	M, 2	M	M, 1	M	M
SWIFTS							
<i>Collocalia spodiopygia</i>	M	M, 18	---	---	---	---	---
KINGFISHERS							
<i>Halcyon chloris</i>	M, 29	M, 58	M, 14	M, 33	M, 18	M, 17	M, 25
SWALLOWS							
<i>Hirundo tahitica</i>	M	M?	---	---	---	---	M
THRUSHES							
<i>Turdus poliocephalus</i>	3	36	---	1	---	---	---
WARBLERS							
°† cf. <i>Cettia</i> sp.	---	5	---	---	---	---	---
WHITE-EYES							
°†Genus unknown	1	3	---	---	---	---	---

	Tongatapu	`Eua	Foa ^h	Lifuka ^h	Ha`ano ^h	`Uiha ^h	Ha`afeva ^h
STARLINGS							
<i>Aplonis tabuensis</i>	M, 21	M, 164	M, 41	M, 34	M, 16	M, 22	M, 19
CUCKOO-SHRIKES							
<i>Lalage maculosa</i>	M, 2	M, 31	M, 1	M, 2	M, 2	M	M?, 1
†cf. <i>Lalage</i> sp.	1	2	---	---	---	---	---
ROBINS, WHISTLERS							
<i>Petroica</i> cf. <i>multicolor</i>	---	---	1	---	---	---	---
<i>Pachycephala jacquinoti</i>	4	---	1	3	1	---	---
MONARCHS							
<i>Clytorhynchus vitiensis</i>	M, 2	M, 74	8	7	2	M?, 1	---
<i>Myiagra</i> sp.	---	5	---	---	---	---	---
HONEYEATERS							
<i>Myzomela cardinalis/jugularis</i>	---	14	---	---	1	---	---
<i>Foulehaio carunculata</i>	M, 6	M, 173	M, 7	M, 14	M, 2	M, 2	M, 2

Figure 1. Species number versus area and number of individuals for seven islands in Tonga: a) number of modern species (S_m) versus \log_{10} (island area; km^2); b) number of species from prehistoric record (S_p) versus \log_{10} (island area; km^2); c) modern plus prehistoric (S_i) versus island area (km^2); d) number of identified specimens (NISP; bones) per island versus number of species from prehistoric record.

Figure 2. Boxplot showing the distribution of 100 published species-area slope coefficients (z) from \log_{10} - \log_{10} regression models (from Connor and May 1979). Mean = 0.66562, 95% confidence interval = (0.43567, 0.8955). Maximum = 3.695, minimum = -4.402.

Figure 3. Species accumulation curve showing the increase in number of species observed versus prehistoric sampling (numbers of identified specimens) per island.

Figure 4. Species-sample area curve estimated by sample-based rarefaction showing the estimated number of prehistoric species (S_p) per sample size (number of subplots = number of islands) based on random resampling of the prehistoric species data.

Figure 1.

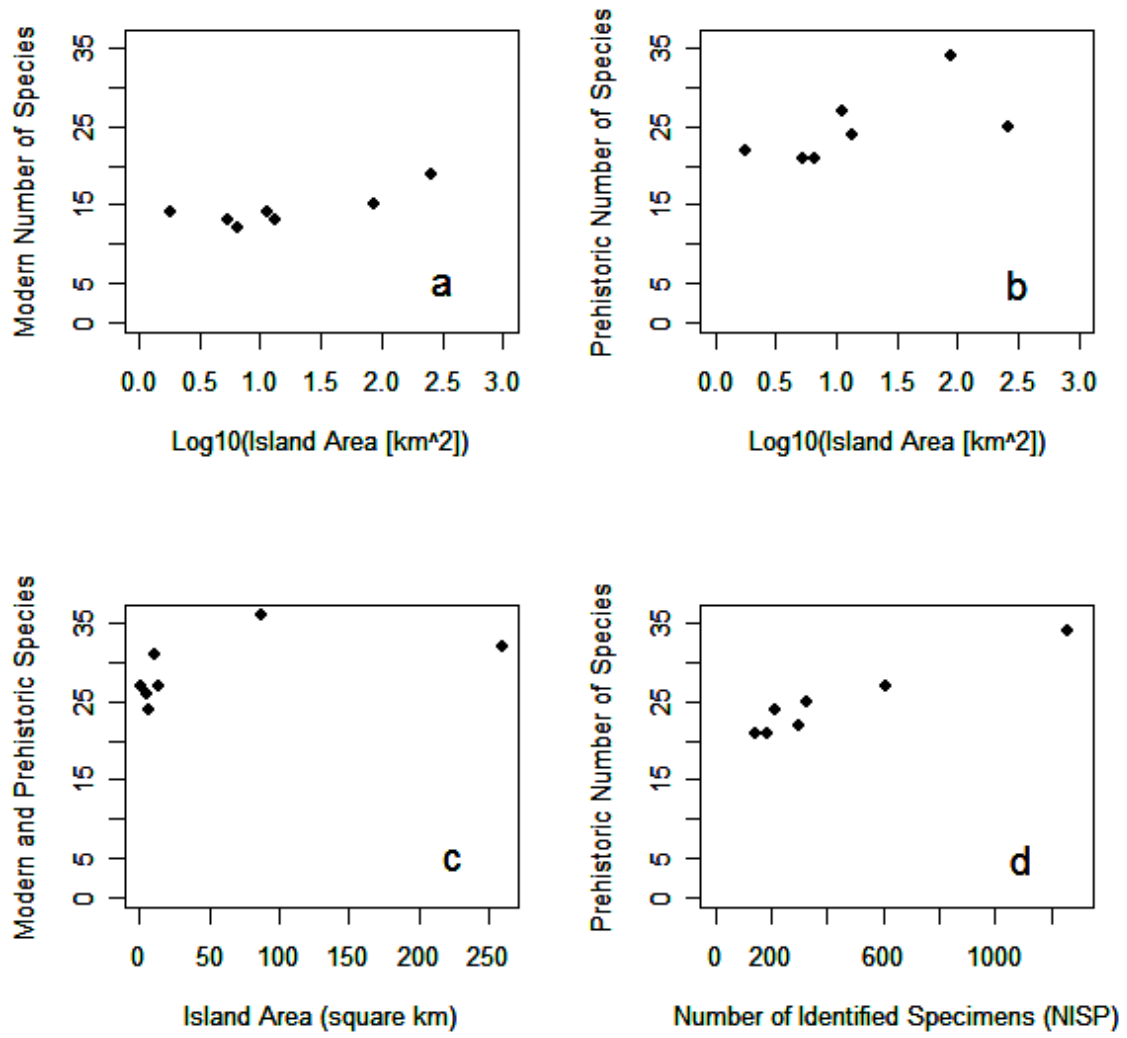


Figure 2.

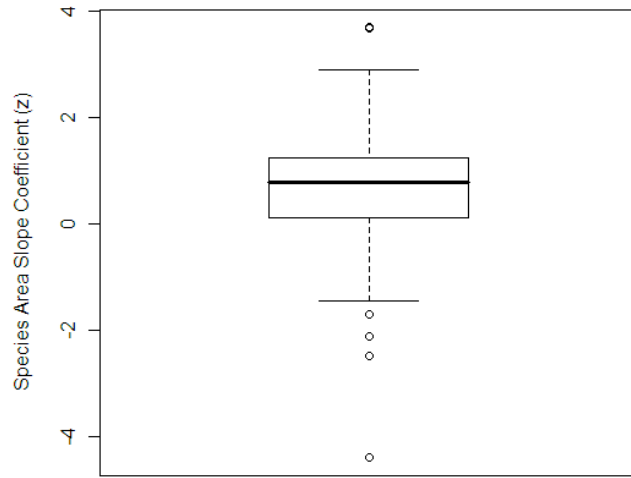


Figure 3

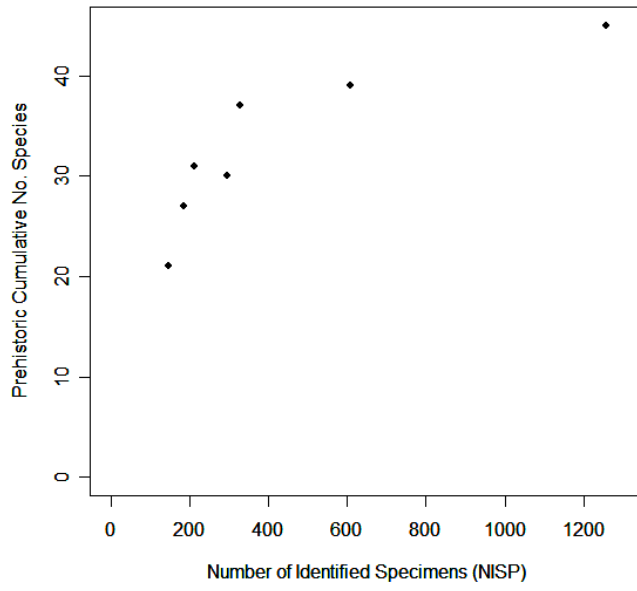


Figure 4.

