Extinctions and threats to avifaunas on oceanic islands: Tests of influences of human populations and the filter effect

Heather Zimbler-DeLorenzo, Bertram Zinner, Ronald J Scheibel, F. Stephen Dobson

Extinctions and threats of extinctions in avifaunas on oceanic islands appear to be influenced by several island characteristics and introduced mammalian predators. These predators may have caused a “filter effect”; low numbers of threatened avian species on some islands might be due to high rates of past extinctions. Using path analysis, we examined these factors and the influence of human population size (as an indicator of human activity) on the number of species extinctions and threatened bird species on islands. Human population size had substantial influences on the number of extinctions (standardized partial regression coefficient $\rho = 0.315$, $N = 172$, $P = 0.0005$) but not on the number of threatened species on oceanic islands ($\rho = -0.061$, $P = 0.43$), independent of the number of introductions of predator species. The number of extinctions on islands produced a significant filter effect (viz., had a negative impact; $\rho = -0.186$, $P = 0.003$) on the number of currently threatened species. The activities of human populations, including mammalian predators they introduced, have likely resulted in a greater number of bird extinctions on these islands, and producing a significant filter effect, wherein islands with larger human populations now have fewer threatened species.

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Abstract. Extinctions and threats of extinctions in avifaunas on oceanic islands appear to be influenced by several island characteristics and introduced mammalian predators. These predators may have caused a "filter effect"; low numbers of threatened avian species on some islands might be due to high rates of past extinctions. Using path analysis, we examined these factors and the influence of human population size (as an indicator of human activity) on the number of species extinctions and threatened bird species on islands. Human population size had substantial influences on the number of extinctions (standardized partial regression coefficient ρ = 0.315, N = 172, P = 0.0005) but not on the number of threatened species on oceanic islands (ρ = -0.061, P = 0.43), independent of the number of introductions of predator species. The number of extinctions on islands produced a significant filter effect (viz., had a negative impact; ρ = -0.186, P = 0.003) on the number of currently threatened species. The activities of human populations, including mammalian predators they introduced, have likely resulted in a greater number of bird extinctions on these islands, and producing a significant filter effect, wherein islands with larger human populations now have fewer threatened species.

Keywords: avifauna, filter effect, human populations, mammalian predators, oceanic islands, path analysis

Introduction

Oceanic islands provide a model system for the study of species extinctions and of the number of species that are currently at conservation risk (Biber 2002, Blackburn et al. 2004, Trevino et al. 2007, Karels et al. 2008). Introduced mammalian predators have been found responsible for much of the extinction of bird species (Atkinson 1985, Johnson and Stattersfield 1990, Blackburn et al. 2004). Perhaps the most famous bird extinction on an island is the case of the dodo (*Raphus cucullatus*) of Mauritius, which has been attributed to human introduced mammalian predators (Olson 1989). At the same time that mammalian predators were introduced, however, birds were being exploited as a food resource and forests were being cleared. The human impacts of hunting and deforestation may have been just as important influences on this extinction as the introduction of mammalian predators. While it is difficult or impossible to separate the impacts of exotic introductions and direct human exploitation or habitat alteration on the extinction of the dodo, it may be possible to examine these factors as general influences on not only extinctions of bird faunas on oceanic islands, but on the number of bird species currently at conservation risk.

In particular, an "extinction filter" (Balmford 1996) would cause low numbers of threatened avian species on some islands due to high rates of past extinctions, in which islands with greater numbers of extinctions have fewer extant threatened species (Pimm et al. 1995, Biber 2002, Blackburn et al. 2004, Trevino et al. 2007, Bromham et al. 2012). The effect is produced when extinctions of some of the rare species on an island leaves fewer rare species extant. When the threatened species on the island are listed, we might see fewer of them than we expect, because so many rare species have already been lost to extinction. When we compare among islands, those that have the fewest extinctions will still have close to their full complement of threatened species. But those that have had a high number of extinctions will have fewer of their more rare (and thus threatened) species present. An indication of a filter effect is therefore a negative association of the number of extinct and threatened species, other things being equal.

A filter effect might be produced simply due to variation in the size or isolation of oceanic islands. The Theory of Island Biogeography explains the uneven distributions of species based on the balancing of colonization and extinction rates relative to the size of islands and their distance from the mainland (MacArthur and Wilson 1967). Smaller islands should have higher extinction rates due to smaller population sizes, and more isolated islands should have lower colonization rates that introduce or reintroduce species. The differences in colonization and extinction rates lead to the prediction that large islands close to a mainland should have relatively higher numbers of species. Island areas and degrees of isolation should thus have major influences on both the size of avifaunas and the numbers of species that have gone extinct during recorded history. We have already shown that island area has substantial positive indirect effects (though the size of the avifauna and introduction of mammalian predators) on the number of extinctions on oceanic islands, and that more isolated islands suffer greater extinctions (Karels et al. 2008, 2009). Also, islands more distant from a mainland have more threatened species and smaller numbers of extant avifauna (Trevino et al. 2007, 2008). Thus, island area and isolation appear to have strong influences on the number of extinctions and threatened bird species on islands.

However, Blackburn et al. (2004, see also Blackburn et al. 2005) concluded that the effect of introduced mammalian predators was more important than any geographical factor (e.g., island area, distance to a mainland) to the extinction of bird species on oceanic islands.

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These same extinctions have also been attributed to the anthropogenic habitat loss (Didham et al. 2005). Utilizing a causal model approach on the same dataset, Karels et al. (2008) showed that the strongest predictors of avian extinctions were island area and isolation from the mainland; with introductions of mammalian predators a secondary effect on extinctions. The factors that influence past extinctions, however, are not necessarily the same as those associated with current threat of extinction. Both Blackburn et al. (2004) and Trevino et al. (2007) found that introduced mammalian predators were not a significant influence on the current numbers or proportions of avian species considered threatened on oceanic islands. These studies both suggested that the difference between the significant influences of introduced mammalian predators on extinctions and currently threatened species reflect a filter effect.

The purpose of our study is to provide a preliminary examination of whether human activities influenced past extinctions and the abundance of currently threatened species among the island avifaunas. Anthropogenic activities, such as habitat destruction and introduction of exotic predators, are alternatives to biogeographic factors as possible influences on numbers of extinctions and threatened species. The most widely available indicator of human activities is the current human population size on the islands, and we used this as a crude index of anthropogenic influences on bird faunas.

We used standardized partial regression analyses, also called path analyses (Wright 1934, Li 1975, Shipley 2000, Kline 2005) to examine the influences of each environmental factor in the model, while holding other factors statistically invariant. Path analysis thus allows evaluation of human population size on both extinctions and threats to bird species, independent of the further influence of introduced mammalian predators. We examined direct and indirect influences of variables on avian extinctions and numbers of threatened species, an advantage of

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using path analyses. Thus, we hypothesized that anthropogenic factors influenced both extinctions and threats to extant species on oceanic islands, and predicted that such influences would be reflected by significant paths to the latter two variables from human population size.

We also tested for a filter effect on species of current conservation concern, something that has been suggested but not well quantified (Blackburn et al. 2004, Trevino et al. 2007). Any environmental factor might contribute to a filter effect, including anthropogenic and biogeographic factors. If a hypothesized filter effect were present, we predicted that there would be a significant negative influence of number of extinctions on the number of currently threatened bird species. Furthermore, if a filter effect was caused by anthropogenic activities, then we expected a negative indirect effect of our indices of human influences (viz., human population size and number of introduced mammalian predators) on the number of threatened species. Our predictions of anthropogenic influences on extinctions and threats to species, as well as the prediction of a filter effect, were tested independently of influences of direct effects from biogeographic influences (in fact, of all independent variables in the model).

Methods

We began with a large published data set of the richness (i.e., number of species) of avifaunas of 220 oceanic islands (data supplemental to Blackburn et al. 2004, original data from Biber 2002), augmented with additional information for 18 (for extinctions) and 21 (for threatened species) of the islands (Trevino et al. 2007, Karels et al. 2008). Information in the dataset included the area of the islands (viz., island size), distance to a continental mainland, species richness of the original (pre-human colonization) avifaunas, number of human-introduced mammalian predators, years since historical human colonization of the islands, number of extinctions since historical colonization, and number of currently threatened species (updated from BirdLife International 2012). Islands were sampled from the Atlantic, Caribbean, Indian, and Pacific Oceans and found in relatively small chains or groups. Some archipelagos were extensively sampled (i.e. Cook Islands, Marianas, and Lesser Antilles). Islands ranged in size from 0.08 km^2 (Little Solander) to 587,713.3 km^2 (Madagascar) and varied in their distance from the mainland (San Salvador 80 km to Nuka Hiva 5800 km). Some islands were colonized by humans more recently (e.g., Wake Island ~100 years ago), compared to long ago (e.g., Prince Edward Island ~10,000 years ago).

We supplemented this information with human population size, to include human activity in our model (United Nations Environment Programme 2009), although economic indicators might provide a better index of human influences on environments (Schnaiberg 1980). While other variables may more accurately reflect the types of human activities on an island that reduce natural habitat area, such as urbanization associated with industrial production or agriculture, human population size was available for most of the islands. For smaller samples of islands, however, we examined the gross domestic products (125 islands) and number of agriculturalists on islands (117 islands). Analyses of these two variables were qualitatively similar to those of the larger sample of islands with human census data, except that these two variables had little influence on the number of extinctions. We examined and deleted latitude from our model, due to its lack of association with extinctions or threats (see also Blackburn et al. 2004). It would be desirable to account for historical population pressures, but records are lacking for many islands before European colonization, and certainly for those colonized before written records.

Two hundred ten islands had complete data for both extinctions and threatened species. However, of these, 38 had no known extinction and no threatened bird species. These cases

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were not appropriate for testing for a filter effect, since they provide no information about the relationship between extinctions and threats to species, and thus we retained 172 islands for analyses. We present this analysis with respect to species extinctions, as evaluation of the 210 islands yielded a very similar pattern of coefficients leading to extinctions and among other variables. All variables were augmented by 1 (to avoid zeros) and log transformed. We then constructed a single path diagram that reflected hypotheses of causal influences on the dependent variables number of extinctions and number of threatened species. Path analyses were conducted using the R (version 3.0.2) package SEM, with application of the CAR package for generating variance inflation factors. Significance of path coefficients was determined from the standard errors of the unstandardized regression coefficients. The data set and R script are available from Dryad and upon request from H.S.ZD. or F.S.D.

Our premise, with respect to avifaunas on oceanic islands, is one of directional cause and effect, in which physical properties such as island area and isolation may influence biological variables (Trevino et al. 2007, Karels et al. 2008), e.g. avifauna size, human population size, and number of human-introduced mammalian predator species (exotics such as rats, cats, etc.). These physical and biotic factors may in turn influence processes like extinction, and all of these previous factors may influence the production of characteristics that indicate conservation threat to species (such as rapid decline in numbers or low population size). This is a causal chain, and the reverse influences are unlikely, though, of course, human populations may make minor changes to island areas. Nonetheless, the use of a causal chain in path analyses increases both the analytical power and ease of interpretation of these correlative data sets, where establishing cause and effect can be difficult (Wright 1934, Li 1975). A further advantage of path analysis is that several regression analyses can be fitted together, so that we were able to examine influences

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on extinctions and threats to species simultaneously. The significance of indirect effects in a path model is indicated when both of the path coefficients that are multiplied together to estimate the indirect effect are themselves significant (Cohen and Cohen 1983, Kline 2005).

The original number of species in an avifauna on an island represents an upper limit on the possible number of extinctions and on the possible number of threatened species. Thus, an autocorrelation occurs between the number of species on islands and the latter two variables, and a positive association is expected (Trevino et al. 2008, Karels et al. 2009). To estimate expected path coefficients from the size of the original avifaunas to the number of extinctions and to the number of threatened species, we created null models by assigning random numbers of extinctions and number of threatened species to the islands. We used the mean proportion of extinctions on islands (= 0.127 of the original avifauna) and mean proportion of threatened species (= 0.083 of the original avifauna) to derive a binomial distribution rates of extinctio or threatened species. From these distributions, we selected random rates of extinctions or threats for each island. These rates were multiplied by the size of the avifaunas and assigned to islands to generate random expectations of extinctions and threats to avifaunas. Standardized partial regression analysis was then performed on the model containing the random expectations of number of extinct species or threatened species. All other variables were held to their actual values. This process was repeated 1000 times each and averaged to yield an expected influence of the size of the avifauna on the number of extinctions and the numbers of threatened bird species, respectively. Extinctions were analyzed first, in a path diagram in which extinctions were the independent variable. Then threatened species were examined in the full model, using the actual number of extinctions. We ran this program in R version 3.0.2, using the software

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package LAVAAN. The significance of the actual path coefficients from the null expectation of the path coefficients was determined from the standard deviations of the coefficients.

Results

The path model that tested possible influences on extinctions was highly significant (R^2 = 0.320 ± 0.074 SD, N = 172, P < 0.0001). The path model for threatened species (Fig. 1) was also highly significant (R^2 = 0.535 ± 0.049 SD, N = 172, P < 0.0001). The variance inflation factor for the influence of area on the number of threatened species was high (at 3.7), but this coefficient was nonetheless highly significant (path from area to threat = 0.46, n = 172, P < 0.0001). All other variance inflation factors were less than 3 (Petraitis et al. 1996).

Human population size had a substantial and significant positive influence on the number of bird species that went extinct on oceanic islands (Figs. 1 and 2; ρ = 0.315, all N hereafter = 172, P = 0.0005). There was also an indirect effect, through the significant influence of human population size on the number of human-introduced mammalian predator species, yielding a slightly higher total effect for human population size on number of extinctions (total effect = 0.370; Table 1). Numbers of human-introduced mammalian predator species on the islands had a low to moderate influence the number of extinctions, as indicated by partial regression coefficient of about 0.18 (Table 1; approaches significance at P = 0.055). Island area had little direct influence on number of extinctions, but had a large indirect influence through the number of bird species originally on islands (indirect effect = 0.199), human population size (indirect effects = 0.186), and number of introduced mammalian predators (indirect effect = 0.090). Island isolation from the nearest mainland had a significant direct effect on number of extinctions of bird species and non-significant indirect effects. Time since human colonization

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of islands did not significantly influence numbers of extinctions. Finally, the number of bird species originally on islands had less influence on number of extinctions than expected from the null model (expected $\rho = 0.735 \pm 0.065$ SD, actual $\rho = 0.296 \pm 0.106$ SD, $P < 0.0001$).

Next, we analyzed the number of bird species that have been considered to be of conservation concern (viz., threatened species; those listed as Critically Endangered, Endangered, or Vulnerable by the IUCN [BirdLife International 2012]). Numbers of introduced mammalian predator species did not have a significant path to the number of threatened bird species (Table 1, Fig. 1). Island area had a significant direct influence on the number of threatened species, and a substantial indirect influence through the number of birds originally on islands (indirect effect = 0.337). Island isolation from a mainland had a significant positive direct influence on the number of threatened species and negative indirect effects through its influence on the number of bird species originally on the islands (indirect effect = -0.148). Human population size did not significantly influence the number of threatened bird species, nor did the number of introduced mammalian predators. Time since human colonization of the islands, however, significantly and negatively influenced the number of threatened species. The number of bird species originally on the islands had less influence on the number of threatened species than expected from the null model, though this was not statistically significant (expected $\rho = 0.645 \pm 0.078$ SD, actual $\rho = 0.496 \pm 0.088$ SD, $P = 0.07$).

Finally, when other variables were held statistically invariant, the number of species extinctions on islands had a significant negative effect on the number of threatened species (Fig. 1; $\rho = -0.186$, $P = 0.003$). Human population size did not have a significant direct influence on the number of threatened species on oceanic islands, but it had indirect negative effects through its influence on the number of species that had gone extinct and influence on the number of introduced mammalian predators. Human population size had a negative total influence on the number of threatened species (total direct and indirect effects = -0.153), similar to the direct effect of number of extinctions on the number of threatened species.

Discussion

Using the causal modeling approach, we found a significant direct positive influence of human population size on the numbers of extinctions of bird species on oceanic islands, and it was nearly twice as great at the statistically independent effect of introduced mammalian predators. The inclusion of human population size in the path model complimented previously published conclusions about extinctions (Karels et al. 2008, 2009). Island area had virtually no direct influence on extinctions, but a large indirect influence through the number of bird species in the original fauna, human population size, and number of introduced mammalian predator species. Large islands, through their substantial indirect influence via having large numbers of bird species in the original fauna and large human populations, have large numbers of extinctions. Isolated islands also have greater numbers of extinctions, though this pattern is weaker due to conflicting direct and indirect influences (e.g., a positive direct influence of isolation on numbers of extinctions, and negative influences on numbers of extinctions due to small numbers of bird species originally on the islands and low human populations). Surprisingly, the numbers of bird species originally on the islands had less influence on the numbers of extinctions than expected from a null model of bird extinctions. This may well indicate the importance of the other variables in the analysis.

While human population size did not have a significant influence on the number of threatened bird species on islands, its direct and indirect effects were negative, so that one might

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conclude that larger human populations result in fewer threatened species. This pattern was likely a result of the significant extinction filter (after Pimm et al. 1995, Balmford 1996). A filter effect occurs when islands that suffered more extinctions of species had fewer remaining rare species that would be listed as being under threat. Past studies have suggested that the numbers of introduced mammalian predators result in a filter effect on the number or proportion of threatened species (Blackburn et al. 2004, Trevino et al. 2007). Our results revealed the influences of anthropogenic activities on the number of threatened bird species on islands, through direct and indirect influences of human population size on past extinctions and the introduction of mammalian predators. Population size, however, may be a less accurate indicator of human influences on the environment than the amount of habitat in agriculture or gross domestic product of the islands (Schnaiberg 1980).

Influences of island area and isolation on the number of extinct and threatened species were similar to previous studies (Trevino et al. 2007, 2008, Karels et al. 2008, 2009): strong direct influences but also indirect effects of these classical geographical variables (Lomolino et al. 2010). The theory of island biogeography predicts greater extinction rates on small islands, due to their small populations (MacArthur and Wilson 1967). We found that when other variables were held statistically invariant, island area did not have a significant direct effect on the number of extinctions. In this analysis, the number of bird species initially on islands is held constant, and thus the direct influence of island area on the number of extinctions is independent of the size of the avifauna. Thus, our results do not support the premise of island biogeography that island size directly influences rate of extinctions. More distant islands had greater extinctions and extinction rates, independently of the size of the islands. This pattern is not predicted by the classical theory of island biogeography, and may be due to an interaction with

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colonization. Historical immigration may have more often replenished species that periodically went extinct on islands near mainlands (i.e., they had a greater "rescue effect" of Brown and Kodric-Brown 1977, Hanski 1982, Gotelli 1991), compared to the more isolated islands.

Our analyses suggested that historic human activities have led to extinctions. These human activities include the introduction of mammalian predators and other factors associated with human population size, such as habitat destruction and fragmentation, that have effects that are statistically independent of the number of introduced mammalian predators. In our analysis, the timing of colonizations did not have a significant direct impact on the number of extinctions, and only a minor indirect influence because more recently colonized islands had more introduced mammalian predators. In any case, human activities have produced extinctions that resulted in a significant filter effect that leaves some islands with fewer threatened species. This is likely because species lacking the ability to survive the early years of human invasion to an island go extinct, and the remaining species that were better able to cope with human induced environmental changes survive.

Human interactions with native species can be complex and contain feedbacks that cannot be analyzed in our relatively simple regression model (for examples of complexities, see Clausen and York 2008, McKinney et al. 2009, Boyer 2010, McKinney et al. 2010). For example, Boyer (2010) points to endemism, body size, taxon, dietary guild, and geographic region as important influences on likelihood of extinction of island birds. In addition, pre-historic and post-European waves of human invasion have occurred on islands (Pimm et al. 1995), though their impacts on extinction rates of bird species might be similar (Duncan et al. 2013). The characteristics of each oceanic island are unique, though some commonalities may occur. For example, although particular islands may have up to 23 introduced mammalian predator species (Blackburn et al. 2004), over 90% of islands have species of rats (*Rattus* sp.) that depredate bird nests (e.g., Towns et al. 2006, Tabak et al. 2013). Extinctions on islands have been attributed to competition and predation by exotic species (e.g., Walsh et al. 2013), habitat loss and fragmentation (Brooks et al. 2002, Didham et al. 2005), and even tourism (Steven and Castley 2013). Thus, specific patterns of extinctions and threats to bird species, as well as the conservation actions that should be taken on oceanic islands will likely be island-specific.

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Table 1. Direct and indirect path contributions for physical and biotic influences on the number of bird species that have gone extinct during the historical period and the number of bird species currently threatened with extinction on oceanic islands. Significant direct effects (viz., path coefficients for Fig. 1) are: *P <0.01, **P < 0.001, ***P < 0.0001). The direct effect of introduced mammalian predators only approached significance: □P = 0.055.

	Influences on Species Extinctions			Influences on Threatened Species		
Variable	Direct	Indirect	Total	Direct	Indirect	Total
Island area	-0.057	0.498	0.441	0.459***	0.211	0.671
Island Isolation	0.359***	-0.128	0.231	0.502***	-0.109	0.393
Avifauna	0.296*	0.000	0.296	0.501***	-0.056	0.445
Human Population	0.315**	0.055	0.370	-0.061	-0.093	-0.153
Introduced mammalian predators	0.176□	0.000	0.176	-0.071	-0.060	-0.130
Time since colonization	-0.015	-0.050	-0.064	-0.273***	0.032	-0.241

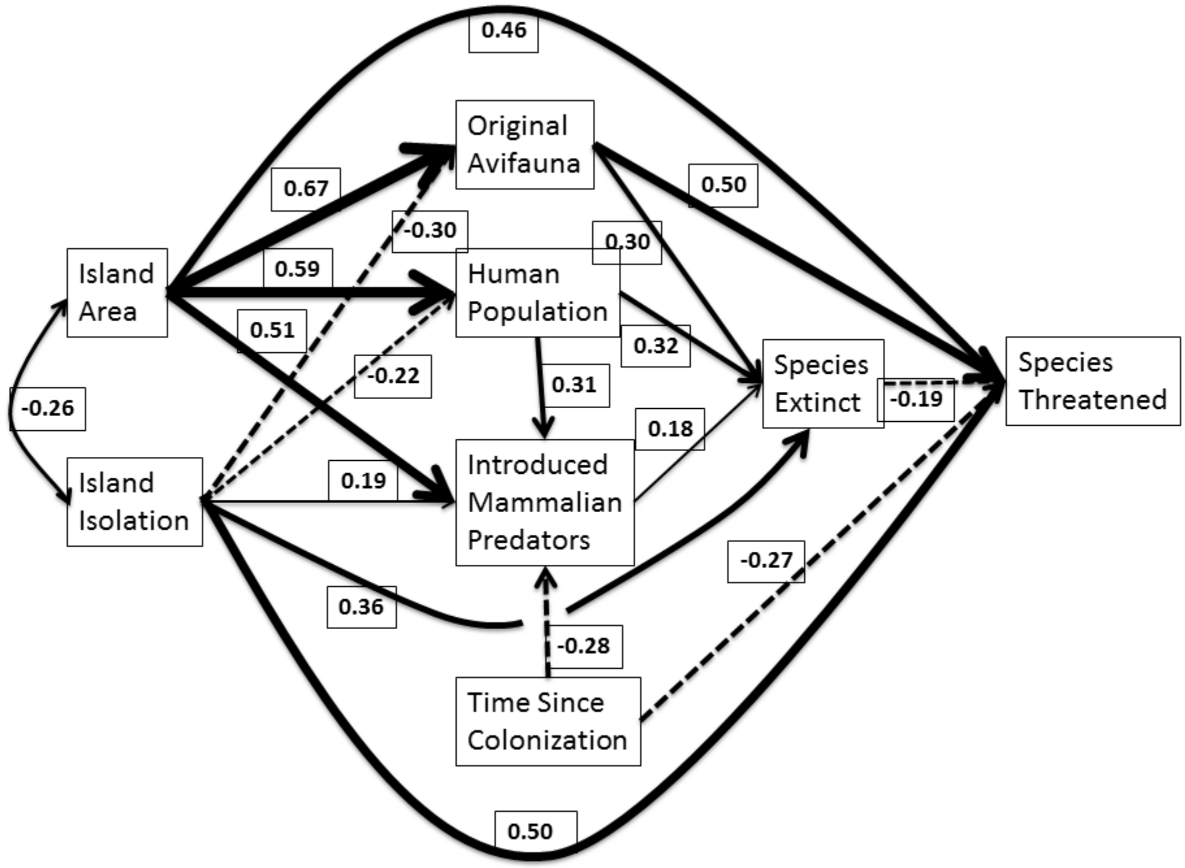

Fig. 1. A path diagram showing potential influences of the physical (island area and isolation from a mainland) and biotic (original number of bird species, the size of the current human population, number of introduced exotic mammalian predators, and time since human colonization) environmental factors on the number of bird species that have gone extinct and those that are currently threatened with extinction on 172 oceanic islands. Only significant ($P < 0.005$) path coefficients are shown, except for the influence of number of introduced mammalian predator species on number of extinct bird species ($P = 0.055$). The thickness of each line is proportional to the value of the path coefficient. Negative path coefficients are given dashed.

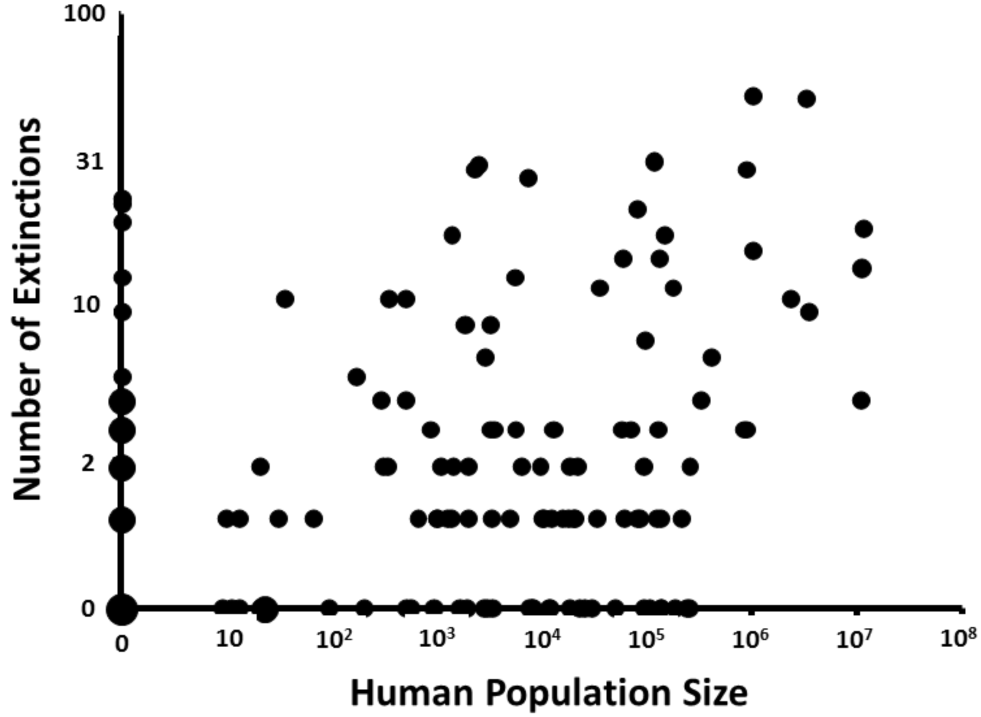

Fig. 2. Associations of number of extinctions and human population size (variables log transformed, r = 0.377, n = 172, P < 0.0001). There were 36 islands for which human population size and number of bird species extinctions were both zero (largest dot). Seventeen other islands shared values among 2-5 islands (5 medium sized dots). Data is plotted on log scales, although axes labels indicate actual population size and extinction numbers