ORIGINAL ARTICLE

The biogeography of avian extinctions on oceanic islands

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ABSTRACT

Aim To test the influences of island area, island isolation, and human-introduced mammalian predators on avian extinctions that have occurred on oceanic islands worldwide.

Location The oceanic islands of the world.

Methods We augmented and re-examined an existing data set for 218 oceanic islands by means of causal modelling using path analysis (a form of structural equation modelling) and a null model.

Results The number of extinctions was not a simple function of the number of bird species on the various islands. Whereas introduced mammalian predators had an influence on the number of extinctions, island area (via indirect influences) and isolation (via direct influences) were equally or more important.

Main conclusions The multiple influences of physical and biotic factors on past extinctions can be revealed through modelling the causal influences of physical attributes of islands on biological characteristics, and the causal influences of both physical and biological characteristics on extinctions.

Keywords

Avifauna, extinction, island area, island isolation, path analysis, predators.

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INTRODUCTION

Island avifaunas have suffered a disproportionately high number and rate of extinctions (Manne *et al.*, 1999). In a study of extinctions on oceanic islands, Blackburn *et al.* (2004) found that the number of human-introduced mammalian predators was significantly associated with the proportion of native bird species that have become extinct during the period since European colonization of the islands. Such introductions may have produced an 'invasional meltdown' (*sensu* Simberloff & von Holle, 1997), in which further predator introductions are facilitated by those that have already occurred (Blackburn *et al.*, 2005). In addition, Blackburn *et al.* (2004) found that the number of introduced mammalian predator species influenced avifauna extinctions more strongly than island area or distance from the mainland – two important physical properties of islands.

The theory of island biogeography (MacArthur & Wilson, 1967) invokes the influence of island surface area and isolation from the mainland to explain naturally occurring diversity of species. Key processes in the theory are the colonization rate to

islands (assumed to be greater for islands close to the mainland) and the extinction rates of species on the islands (assumed to be greater for smaller islands). Whereas it is possible that both island area and the number of introduced mammalian predators influence avian extinctions, Blackburn *et al.* (2004) found that larger islands had more introduced mammalian predators and slightly greater extinction probabilities (i.e., proportions of original avifaunas that had gone extinct). Even though specific extinction rates were not calculated, these results seem contrary to the theory of island biogeography, which states that larger islands should have lower extinction rates.

Our purpose is to re-examine Blackburn *et al.*'s (2004) island extinction data using causal analyses of extinctions. The number of extinctions is an important parameter to study because it can be influenced by the size of the original avifauna. Avifauna size is thus a possible causal influence that can be tested along with other possible causal factors. In our model, we examined the number of extinctions during the period of recorded history. The structure of our causal model allowed us to evaluate

influences on the number and proportion of extinctions at the same time.

The present study is complementary to a previous analysis (Trevino *et al.*, 2007) of the same data set that investigated threats to extant avifauna on oceanic islands. Trevino *et al.* (2007) used causal modelling, as we do here, to show that island size and isolation are the most important influences on the number of threatened species. Their analyses also provided evidence that island avifauna have already gone through an extinction filter, leaving the most resilient species. Since our study is an analysis of extinction, it serves to test the hypothesis that factors associated with the threat of extinction are not the same as those that cause extinction.

METHODS

We augmented and re-examined an existing data set (Blackburn *et al.*, 2004) of biological and geographical factors that might influence avian extinctions on oceanic islands ($n = 197$) by adding data on island surface area and isolation measurements for an additional 21 islands (Environmental Systems Research Institute, 1995; United Nations Environment Programme, 1998). We ran analyses on both the original data set and on our augmented data set and found nearly identical results. We thus present only the more complete data. All variables were log-transformed to improve conformation to normal distributions and linear associations.

The multiple regression models of Blackburn *et al.* (2004) assumed that physical and biological attributes of islands are independent of each other. Taking an alternative approach using causal modelling, we reasoned that the physical attributes of the islands might influence biological variables associated with the islands, but that biological variables are not likely to influence physical attributes. Physical attributes were island size and isolation of islands from the nearest mainland. Biological characteristics of islands were the number of species in the original (pre-extinction) avifaunas and the numbers of mammalian predators that were subsequently introduced to the islands. Assessment of kurtosis for each of the variables after transformation indicated that all conformed with the assumption of normality, where kurtosis is zero. The strongest kurtosis was shown in the distribution of the number of predators (-1.19), but its absolute value was much lower than what is considered a problematic skew (8–20; Kline, 2005). The model also met the most critical assumption of multivariate normality (kurtosis = 0.63).

Any of the physical or biological variables might be expected to have direct causal influences on the number of species that go extinct on the islands. We applied a path model to test our causal hypotheses of influences on extinctions in the island avifaunas (Wright, 1934; Li, 1975). We used structural equation modelling (SEM) to test the overall causal structure of our path model, as well as the individual hypotheses of causation (Shipley, 2000). Standardized partial regression coefficients were calculated for the number of extinctions regressed on each of the potential causal variables, while holding other independent variables in the model statistically invariant. Standardization was necessary because the variables were measured on different scales (i.e. area, counts and distances). Unlike other multiple regression techniques, path analysis allows a variable to be both influenced by other variables and a cause of variation in a dependent variable (Kline, 2005). Thus, for example, the number of introduced mammalian predators on islands can be a possible cause of extinctions of bird species, and the number of introduced predators can also be influenced by the area of islands.

We tested the critical assumption of multivariate normality in SEM using the program AMOS 6.0 (Arbuckle, 2005), as recommended by Byrne (2001). All further procedures were conducted in AMOS 6.0. All parameters in the model were estimated by means of maximum likelihood, and the overall goodness of fit of the model was performed with a likelihood ratio test. The maximum likelihood procedure minimizes the difference between the observed covariance matrix of variables included in the model and the predicted covariance matrix calculated from the model structure (Shipley, 2000). We further evaluated our model by performing a randomized permutation test in AMOS 6.0 to determine how many possible models are equal to or better than our hypothesized model.

Hypotheses of causal influences were tested by means of the significance of standardized path coefficients presented with 95% bias-corrected confidence intervals estimated with 1000 bootstrap samples. Path coefficients indicate the amount of change in the standard deviation of the dependent variable for every one standard deviation increase in the independent variable. Significance (given as *P*) in a path coefficient (indicated with a '*p*') was determined at the $\alpha = 0.05$ level when the maximum likelihood estimate of the parameter divided by its standard error (estimated with 1000 bootstrap estimates) exceeded 1.96 (Byrne, 2001).

Obviously, the number of bird species that go extinct on an island is dependent on the number of species in the original avifauna, but these variables need not be analysed as a composite variable (i.e., as the proportion of species that go extinct). This is because, in the path model, the influence of a particular independent variable on the number of extinctions (the dependent variable) can be evaluated while statistically 'controlling' variation in other independent variables (Li, 1975). So, the size of the original avifauna is controlled when the path coefficient is produced for, say, the direct influence of the number of introduced mammalian predators. The strength of the underlying proportion of species that have gone extinct among all the islands is evaluated by the path from the size of the avifauna to the number of extinct species. When causal factors influence both the numerator and the denominator of a calculated rate or proportion, path analysis can quantify confounding causal processes separately (Escudero *et al.*, 2000). We thus did not analyse proportions, rates, frequencies, or probabilities, but were able to take the size of the original avifauna into account when examining influences on the number of extinctions.

The expected value of the path coefficient from the sizes of the bird faunas to the numbers of extinctions required a different null hypothesis from that of other paths, because smaller avifaunas cannot have more extinctions than the number of birds present on the islands. Thus, an autocorrelation occurs, and an additional procedure was needed to test the meaning and significance of this path. We created 500 simulated data sets of 218 islands, and used the average probability of extinction (= 11.4% of the avifaunas) and a binomial distribution to randomly assign extinct species to the islands from the actual sizes of the original avifaunas. If extinctions were completely random, the path coefficient from the size of avifauna to the number of extinctions would be $p = 0.88$. In our SEM analyses, we fixed the regression weight for this path at the random value, and this path model was rejected, indicating that this potential source of bias was not a major influence on the overall model. In addition, our path model was tested by goodness of fit, and refuting the model would not indicate that individual paths were statistically indistinguishable from zero.

In our path model, there are causal arrows from physical to biological variables, so that, in addition to the direct influence that each physical variable can have on the number of extinctions in the avifauna, the physical attributes can have indirect influences through their influence on biological variables. We chose island size and isolation as our physical attributes, in part because these are the influential parameters of the theory of island biogeography (MacArthur & Wilson, 1967). We chose not to include island elevation (a variable used by Blackburn *et al.*, 2004) for the following reasons. First, elevation was not reported for seven islands, which would mean reducing the sample size to 211. Second,

we compared path analyses for our path model and for another one in which elevation was included as a physical attribute of the islands, for the reduced sample of islands. Our model had a similar fit to the data and a lower Akaike information criterion (AIC) (owing to the additional variable) compared with the model with elevation included (without elevation, $\chi^2 = 0.01$, d.f. = 1, $P = 0.92$, AIC = 28.1; with elevation, $\chi^2 = 0.02$, d.f. = 1, $P = 0.89$, AIC = 40.0). Finally, island area and elevation were moderately correlated ($r = 0.57$), possibly creating bias arising from collinearity (Petraitis *et al.*, 1996). We thus used a simplified path model that assumed that elevation effects would be at least partly reflected by island area. Island area and isolation were also significantly correlated, but the association was much lower ($r = -0.28$).

We examined the total effect of each variable on extinction by examining its direct effect on extinction (path coefficients) and all possible indirect effects, which are the products of path coefficients (i.e. the product of paths from the variable of interest through mediator variables to extinction; after Schemske & Horvitz, 1988). Confidence intervals (95%) of the total direct effect, total indirect effect, and total effect of each variable on extinction were estimated using the bootstrap procedure (1000 samples) in AMOS 6.0.

RESULTS

The augmented data set was consistent with the structure of our path model (Fig. 1; $\chi^2 = 0.03$, d.f. = 1, $P = 0.88$). In the path model, the combined independent variables explained 30% of the variation in the number of extinctions. However,
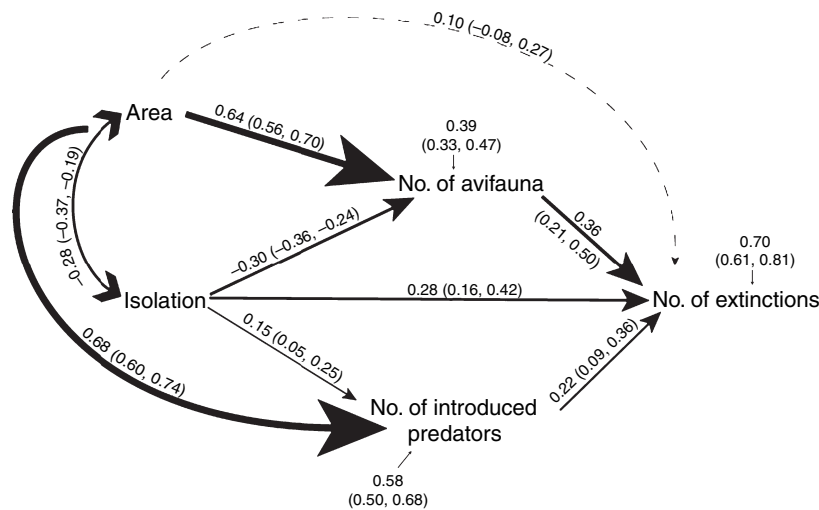

Figure 1 Path model of influences on the number of extinctions of birds on oceanic islands, with standardized path coefficients (single-headed arrows). One correlation (−0.28) is given, that for area and isolation of islands. Solid arrows represent significant paths ($P < 0.05$), and their effect strength is visually represented by the thickness of the arrows. Small single-headed arrows pointing towards dependent variables are labelled with the proportion of unexplained variance not accounted for by the causal effects of independent variables. Lower and upper 95% confidence limits of path coefficients and of the proportion of unexplained variance of dependent variables are shown in brackets. The sample size for all variables was 218.

Table 1 Influences of physical and biological variables on numbers of extinctions of bird species on islands. Standardized path coefficients are listed for the direct effects for each causal variable. Standardized indirect effects are the products of the path coefficients for the biogeographical variables. Standardized total effects are the sum of direct and indirect effects. Bias-corrected 95% confidence limits and *P*-values were estimated from 1000 bootstrap samples.

Causal variable	Direct effects	Indirect effects	Total effect
Area*	0.10 (−0.08, 0.27)	0.38 (0.27, 0.50)**	0.48 (0.37, 0.60)**
No. of avifauna	0.36 (0.21, 0.50)**	–	0.36 (0.21, 0.50)**
Introduced predators	0.22 (0.09, 0.36)**	–	0.22 (0.09, 0.36)**
Isolation*	0.28 (0.16, 0.42)**	−0.07 (−0.14, −0.11)	0.21 (0.12, 0.31)**

*Indirect effects are summed paths through the number of avifauna and number of introduced predators.
**$P < 0.01$.

while the model explained less than the majority of the variation in extinctions, the variation explained was substantial and highly significant. Our path model was chosen *a priori* for the realism of its causal structure (see Methods). There was little evidence of other causal structures that would fit better than that for the one we proposed. Less than 7% ($n = 8$) of all possible permutations ($n = 120$) of paths among the variables were equal to or better fitting than ours.

Larger islands had larger avifaunas, and this indirectly produced a greater number of extinctions ($p = 0.64 \times 0.36 = 0.23$; Fig. 1). This result is not surprising, but it would not be quantifiable with a standard multivariate analysis (e.g. Blackburn *et al.*, 2004; Table 1). In addition, the random expectation for the path coefficient from the size of avifauna to the number of extinct species ($p = 0.88$, see Methods) was significantly greater than the coefficient that actually occurred (i.e. $p = 0.36$; $p < 0.001$). There was a direct effect of island isolation on bird extinctions ($p = 0.28$), with more isolated islands having more extinctions. Distance to the nearest mainland was not an influential factor on the probability of extinction in Blackburn *et al.*'s (2004) analyses.

The number of introduced mammalian predators had a positive influence on the number of bird extinctions ($p = 0.22$; Fig. 1). There was a moderately positive indirect effect of island area on the number of extinctions, through the influence of island area on the number of mammalian predators ($p = 0.68 \times 0.22 = 0.16$). Surprisingly, more isolated islands had significantly more introduced mammalian predators, although this pattern was relatively weak.

Although island area influenced the number of bird extinctions through its substantial influences on avifauna size and number of introduced mammalian predators, it had a small positive but statistically non-significant direct influence on the number of extinctions ($p = 0.10$). Direct and indirect effects can be summed to indicate total effect (Table 1). Island area had the greatest total influence on the number of birds that have gone extinct on islands, primarily through indirect effects. Island isolation and the number of introduced predators had secondary influences on bird extinctions, through direct effects.

DISCUSSION

Island area appeared to have the strongest influence on bird extinctions on islands, primarily through indirect influences; that is, through its positive influence on the size of the avifauna and its positive influence on the number of introduced mammalian predators (Table 1). The influence of island area on extinctions would have been even stronger, however, if extinctions had been a random draw from the starting avifauna (the predicted indirect influence = 0.57, compared with the 0.23 indirect influence reported above; difference $P < 0.001$). This suggests that island extinctions were not a random draw from the avifaunas, and this is a new insight. Our ability to predict extinctions on islands was significantly poorer than if species were randomly taken from avifaunas, indicating that some islands have been particularly hard-hit, whereas others have escaped relatively unscathed. In their study of island species that are currently listed as threatened with extinction, Trevino *et al.* (2007) also found substantial influences of island area, although in that study a significant direct influence was evident.

Island isolation appeared to have a significant direct influence on the number of extinctions on islands, with more extinctions occurring under very isolated conditions (Fig. 1), perhaps owing to the lack of a rescue effect (Brown & Kodric-Brown, 1977). This result differed from Blackburn *et al.*'s (2004) conclusion that distance from the mainland was unimportant as an influence on extinction probability. The difference occurred as a result of our focus on causal modelling of the number of extinctions, rather than on an analysis of the probability of extinction (see Methods in Blackburn *et al.*, 2004). In subsequent exhaustive univariate and multivariate analyses of the same data, parsed in different ways, Blackburn & Gaston (2005) found island isolation to be a significant influence on extinctions in every case, in contrast to their earlier analyses (although they did not analyse introduced mammalian predators in that study). Our path model properly quantifies these conflicting results and indicates the importance of island isolation as an influence on extinctions. In their study of species on islands that are currently threatened with extinction, Trevino *et al.* (2007) also found substantial influences of island isolation, primarily through a direct influence.

Island area and isolation, variables used in the theory of island biogeography (MacArthur & Wilson, 1967), have an exceptionally important influence on bird extinctions on islands, owing to both direct and indirect influences. Like Blackburn *et al.* (2004), we think that the number of introduced predators is an important parameter when considering the causes of bird extinctions on islands, but in contrast to Blackburn *et al.* (2004), we think that the physical attributes of the islands themselves and the size of the original avifauna are likely to be as or even more important. For example, it appeared that the greatest number of extinctions occurred on large isolated islands, a very different conclusion from that reached by Blackburn *et al.* (2004). This may be because larger islands support larger human populations and more agriculture, and because human communities on islands far from the mainland need to more fully exploit natural resources for self-sufficiency (see also Didham *et al.*, 2005). Larger islands are more likely to be farmed, which in turn increases the persistence of introduced species (Duncan & Forsyth, 2006). The likely result of these factors could be greater loss of pristine native habitats and their associated avifaunas. The environmental factors underlying area effects on oceanic islands (e.g. agriculture, habitat loss, land-use changes) are poorly understood at present, but could be explicitly factored into SEMs (e.g. Harrison *et al.*, 2006; Seabloom *et al.*, 2006).

Past extinctions and present threats to avifaunas exhibited different patterns of causal influence with respect to introduced mammalian predators. While predators had a significant influence on past extinctions of birds on oceanic islands (Fig. 1), they had little or no influence on currently threatened bird species (Blackburn *et al.*, 2004; Trevino *et al.*, 2007). This important result, together with the above-mentioned significant direct influence of island area on the number of threatened species (Trevino *et al.*, 2007), suggests that past extinctions and currently threatened species result from different combinations of causal abiotic and biotic environmental influences. Thus, there may be limitations on what past extinctions can teach us about current threats of extinction in oceanic bird faunas.

Blackburn *et al.* (2004) emphasized the importance of the number of introduced mammalian predator species on extinction probability, over all other variables. The more complete analyses of Blackburn & Gaston (2005) might have cast doubt on the relative importance of mammalian predators over all other possible influences on extinctions, but those analyses did not include the number of predator species. Our path analysis revealed that island area, isolation, and the number of introduced mammalian predators were all very important influences on island avifauna extinctions, and revealed a complex pattern of direct and indirect influences (Table 1). For this reason, we consider path analysis and structural equation modelling particularly promising for analysing important patterns of extinctions, such as those of bird species on oceanic islands.

REFERENCES

Arbuckle, J.L. (2005) *Amos 6.0 user's guide*. Amos Development Corporation, Spring House, PA.

Blackburn, T.M. & Gaston, K.J. (2005) Biological invasions and the loss of birds on islands. *Species invasions: insights into ecology, evolution, and biogeography* (ed. by D.F. Sax, J.J. Stachowicz and S.D. Gaines), pp. 85–110. Sinauer Associates, Sunderland, MA.

Blackburn, T.M., Cassey, P.C., Duncan, R.P., Evans, K.L. & Gaston, K.J. (2004) Avian extinction and mammalian introductions on oceanic islands. *Science*, **305,** 1955–1958.

Blackburn, T.M., Petchey, O.L., Cassey, P. & Gaston, K.J. (2005) Functional diversity of mammalian predators and extinction in island birds. *Ecology*, **86,** 2916–2923.

Brown, J.H. & Kodric-Brown, A. (1977) Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58,** 445–449.

Byrne, B. (2001) *Structural equation modeling with AMOS: basic concepts, applications, and programming*. Lawrence Erlbaum Associates, Mahwah, NJ.

Didham, R.K., Ewers, R.M. & Gemmell, N.J. (2005) Comment on ''Avian and mammalian introduction on oceanic islands''. *Science*, **307,** 1412a.

Duncan, R. P. & Forsyth, D. M. (2006) Modelling population persistence on islands: mammal introductions in the New Zealand archipelago. *Proceedings of the Royal Society B: Biological Sciences*, **273,** 2969–2975.

Environmental Systems Research Institute (1995) *Geography Network* (http://www.geographynetwork.com), accessed December 2004.

Escudero, A., Iriondo, J.M., Olano, J.M., Rubio, A. & Somolinos, R.C. (2000) Factors affecting establishment of a gypsophyte: the case of *Lepidium subulatum* (Brassicaceae). *American Journal of Botany*, **87,** 861–871.

Harrison, S., Grace, J.B., Davies, K.F., Safford, H.D. & Viers, J.H. (2006) Invasion in a diversity hotspot: exotic cover and native richness in the California serpentine flora. *Ecology*, **87,** 695–703.

Kline, R.B. (2005) *Principles and practice of structural equation modeling*. Guilford Press, New York, NY.

Li, C.C. (1975) *Path analysis: a primer*. Boxwood Press, Pacific Grove, CA.

MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

Manne, L.L., Brooks, T.M. & Pimm, S.L. (1999) Relative risk of extinction of passerine birds on continents and islands. *Nature*, **399**, 258–261.

Petraitis, P.S., Dunham, A.E. & Niewiarowski, P.H. (1996) Inferring multiple causality: the limitations of path analysis. *Functional Ecology*, **10**, 421–431.

Schemske, D.W. & Horvitz, C.C. (1988) Plant animal interaction and fruit production in a neotropical herb: a path analysis. *Ecology*, **69**, 1128–1137.

Seabloom, E.W., Williams, J.W., Slayback, D., Stoms, D.M., Viers, J.H. & Dobson, A.P. (2006) Human impacts, plant invasion, and imperiled plant species in California. *Ecological Applications*, **16**, 1338–1350.

Shipley, B. (2000) *Cause and correlation in biology: a user's guide to path analysis, structural equations and causal inference*. Cambridge University Press, Cambridge.

Simberloff, D. & von Holle, B. (1997) Positive interaction of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21–32.

Trevino, H.S, Skibiel, A.M., Karels, T.J. & Dobson, F.S. (2007) Threats to avifauna on oceanic islands. *Conservation Biology*, **21**, 125–132.

United Nations Environment Programme (1998) *Islands* (http://islands.unep.ch), accessed December 2004.

Wright, S. (1934) The method of path coefficients. *The Annals of Mathematical Statistics*, **5**, 161–215.

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