

Comment on “Avian Extinction and Mammalian Introductions on Oceanic Islands”

A key advance in conservation biology has been our ability to evaluate the relative importance of multiple drivers of extinction (1). Under this modern paradigm, species extinctions can no longer be explained solely by habitat loss, human hunting, climate change, disease, or species invasions operating alone, but rather by synergistic combinations of extrinsic factors operating on species with diverse sets of intrinsic traits (2–4). Nevertheless, Blackburn *et al.* (5) recently concluded that much of the variation in avian extinction rates across 220 oceanic islands could be explained by a strong positive correlation with the number of exotic predatory mammal species established since European arrival. Furthermore, this conclusion was made without explicitly quantifying the degree to which other potentially intercorrelated drivers of extinction risk (notably habitat conversion) covaried with introduction success. This is surprising, as these authors have independently assessed the importance of habitat conversion for global avian biodiversity loss (6).

Rolett and Diamond (7) estimated habitat loss rates for 69 Pacific islands, providing an opportunity to test whether avian extinctions also correlate with habitat loss across islands. For the 44 islands common to that study and the Blackburn *et al.* study (5), avian extinction rates are significantly positively correlated with pre-European deforestation scores (pre-European extinctions: Pearson's $r = 0.414$, $n = 44$, $P = 0.005$; total extinctions: $r = 0.395$, $n = 44$, $P = 0.008$) (Fig. 1A) (8, 9). There is likely to be spatial autocorrelation in extinction and deforestation rates among islands within archipelagos, but our conclusion still holds if the relation is analyzed at the archipelago level (total extinctions: $r = 0.573$, $n = 14$, $P = 0.033$). Furthermore, although total mammalian introductions are not significantly correlated with pre-European deforestation ($r = 0.161$, $n = 44$, $P = 0.296$), they are significantly correlated with the Rolett and Diamond forest replacement index (7) ($r = -0.621$, $n = 44$, $P < 0.0001$) (Fig. 1B). Again, the same conclusion holds at the archipelago level ($r = -0.744$, $n = 14$, $P < 0.002$). This suggests that the same environmental and biogeographic factors that control native

forest replacement (7) may also determine the success of mammalian introductions (5).

Unfortunately, the deforestation and forest replacement scores are coarse measures of habitat conversion and are available only for a small subset of islands. Thus, there is no statistical power to test the interaction between habitat conversion, species invasion, and biogeographic factors such as island area. However, our objective is not to dispute the importance of mammalian predators in causing some avian extinctions on islands or to discount the importance of island biogeographic factors, but rather to show that habitat conversion is strongly intercorrelated with both extinction and introduction rates, leaving absolute causality equivocal for avian extinctions in general. Given the strong intercorrelation between habitat conversion and species invasion (10), the relative importance of mammalian introductions cannot be determined without explicitly quantifying habitat loss rates across islands.

Although quantitative habitat loss rates are lacking for all 220 islands, previous studies using Pimm's species loss function (11) have shown that habitat loss is a remarkably accurate predictor of past extinction rates (11, 12) and current extinction threat (13) on 31 island archipelagos (12–14). In fact, whenever accurate habitat loss data are available, they are invariably so highly correlated with observed extinction rates that they confound any attempt to interpret extinctions in the light of species invasions alone. For example, habitat loss rates are sufficient to predict observed extinction rates within one island archipelago, New Zealand, for which comprehensive avian extinction and habitat loss data are available. Pimm's species loss function (11) predicts that New Zealand should have lost 31.5 to 41.1% of its original species following ~78% habitat conversion (12), yet the archipelago has lost only 28.6% (70 of 245 species) of breeding birds (including 37.9% of endemic species) (Table 1) (15, 16). Of course, extinction rates of the most severely affected terrestrial bird families, on the most heavily invaded islands, are almost twice as high as for the archipelago as a whole (Table 1). However, there has also been far greater habitat loss and fragmenta-

tion on large islands, such that extinction rates within islands are still only marginally (1 to 4%) higher than predicted from absolute forest loss (Table 1). This is not to say that habitat loss is the sole explanation for a high rate of bird extinctions in New Zealand, but it is certainly an important factor to quantify in addition to mammalian introductions.

Given unequivocal evidence that predation by introduced mammals has driven some island species to extinction (2, 5, 15, 17) and equally incontrovertible evidence that habitat loss causes population declines to

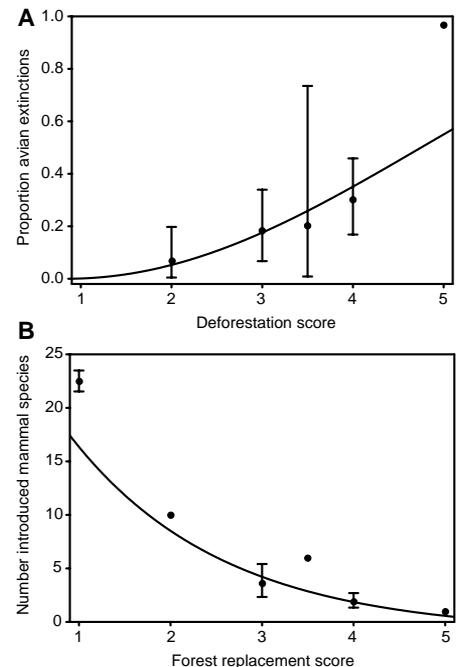


Fig. 1. Relation between pre-European habitat conversion (7), mammalian introductions, and avian extinctions (5) on 44 Pacific Ocean islands. (A) Total avian extinctions are significantly positively correlated with qualitative pre-European deforestation scores, although a categorized regression analysis (9) is marginally nonsignificant ($F_{1,3} = 8.195$, $r^2 = 0.156$, $P = 0.064$) because of the small number of scored categories. A score of 1 represents no deforestation, whereas a score of 5 represents almost complete deforestation. Means and 95% confidence intervals are back-transformed from arcsin square-root transformed variates. (B) Total mammalian introductions are significantly negatively correlated with the Rolett and Diamond forest replacement index (categorized regression $F_{1,4} = 42.775$, $r^2 = 0.386$, $P = 0.003$). A score of 1 indicates that introduced tree species comprised less than 10% of all tree individuals prior to European settlement, whereas a score of 5 indicates that there were few trees and that forest was mostly replaced by grasses and shrubs (7). Means and 95% confidence intervals are back-transformed from $\ln(x + 1)$ transformed variates.

Table 1. Habitat loss and avian extinction rates in New Zealand. Predictions use estimates of habitat conversion and the species (S)–area (A) relation $[S_{t+1}/S_t = (A_{t+1}/A_t)^z]$, with slope z varying from 0.25 to 0.35 (17). The predicted extinction of 77 to 101 species from the total avifauna uses a total habitat conversion estimate of 78% (12) and greatly exceeds the observed extinction rate of 70 species (15). For terrestrial and

freshwater bird species (excluding the families Diomedidae, Procellariidae, Hydrobatidae, Spheniscidae, Phaethontidae, Sulidae, Stercorariidae, and Laridae), observed extinction rates are similar to SA predictions based on a quantitative geographic information systems analysis of forest loss using the 1:50,000 digital topographic database created in 1989 (www.linz.govt.nz).

	South Island		North Island		New Zealand archipelago	
	Prehuman	Present	Prehuman	Present	Prehuman	Present
Land area (km ²)		150,437		113,733		267,304
Native forest cover (km ²)	127,871	37,246	112,027	27,172	240,574	67,746
Forest loss (%)		70.9		75.7		71.8
Number remnants		37,800		81,715		121,025
Mean remnant size (ha)		98.5		33.3		53.9
Edge (km):area (km ²) ratio		3.256		4.776		3.897
		Total bird species				
Observed number	113	66	100	49	245	175
Observed % extinct		41.6		51.0		28.6
Predicted % extinct						31.5–41.1
		Nonmarine bird species				
Observed number	88	56	81	46	161	96
Observed % extinct		36.4		43.2		40.4
Predicted % extinct		26.6–35.1		29.8–39.1		27.1–35.8

extinction (2, 6, 11–13), the difficulty is in reconciling how two very different drivers of extinction might operate nonadditively. Comparative analyses leave little doubt that multiple agents of decline should interact complementarily or synergistically across phylogenetic lineages (2), but, surprisingly, this does not appear to be the case. Mammalian invasions or habitat loss, each in its own right, appear sufficient to explain the observed avian extinction rates. Whatever the relation between extrinsic drivers of extinction risk, there is growing recognition that they are strongly intercorrelated and that different mechanisms are important in determining the fate of different species (1–3). Fortunately, conservation biology is very much cognizant of this fact and is moving on from single-factor explanations for extinction threat. For example, of the 170 World Conservation Union red-listed species in Oceania and the Caribbean Islands identified as threatened by habitat loss and/or invasive alien species, 50% (84 species) are listed as threatened by both factors acting in concert. We caution against the tendency of many studies to focus on single-factor

explanations for extinction threat without explicitly considering the full complexity of synergies between habitat conversion, invasion, climate change, disease, and a host of other extrinsic drivers of population decline (4, 10).

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References and Notes

- O. E. Sala et al., *Science* **287**, 1770 (2000).
- I. P. F. Owens, P. M. Bennett, *Proc. Natl. Acad. Sci. U.S.A.* **97**, 12144 (2000).
- A. Purvis, K. E. Jones, G. M. Mace, *BioEssays* **22**, 1123 (2000).

- W. F. Laurance, M. A. Cochrane, *Conserv. Biol.* **15**, 1488 (2001).
- T. M. Blackburn, P. Cassey, R. P. Duncan, K. L. Evans, K. J. Gaston, *Science* **305**, 1955 (2004).
- K. J. Gaston, T. M. Blackburn, K. Klein Goldewijk, *Proc. R. Soc. London Ser. B Biol.* **270**, 1293 (2003).
- B. Rolett, J. M. Diamond, *Nature* **431**, 443 (2004).
- Pre-European deforestation and forest replacement scores are based on historic observational records and paleoecological studies in (7). Detailed materials and methods are available from R.K.D. on request.
- R. R. Sokal, F. J. Rohlf, *Biometry* (W. H. Freeman, New York, ed. 3, 1995).
- J. Gurevitch, D. K. Padilla, *Trends Ecol. Evol.* **19**, 470 (2004).
- S. L. Pimm, R. A. Askins, *Proc. Natl. Acad. Sci. U.S.A.* **92**, 9343 (1995).
- T. M. Brooks et al., *Conserv. Biol.* **16**, 909 (2002).
- T. M. Brooks, S. L. Pimm, N. J. Collar, *Conserv. Biol.* **11**, 382 (1997).
- An informal meta-analysis of published studies is available from R.K.D. on request.
- R. N. Holdaway, T. H. Worthy, A. J. D. Tennyson, *N.Z. J. Zool.* **28**, 119 (2001).
- Detailed materials and methods are available on request from R.K.D.
- F. Courchamp, J.-L. Chapuis, M. Pascal, *Biol. Rev.* **78**, 347 (2003).
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