Island biogeography and the species richness of introduced mammals on New Zealand offshore islands

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ABSTRACT

Aim To investigate and establish the significance of various island biogeographic relationships (geographical, ecological and anthropological) with the species richness of introduced mammals on offshore islands.

Location The 297 offshore islands of the New Zealand archipelago (latitude: 34–47°S; longitude: 166–179°E).

Methods Data on New Zealand offshore islands and the introduced mammals on them were collated from published surveys and maps. The species richness of small and large introduced mammals were calculated for islands with complete censuses and regressed on island characteristics using a Poisson distributed error generalized linear model. To estimate the 'z-value' for introduced mammals on New Zealand islands, least-squares regression was used [$\log_{10} S$ vs. $\log_{10} A$].

Results High collinearity was found between the area, habitat diversity and elevation of islands. The island characteristics related to the species richness of introduced mammals differed predictably between large and small mammals. The species richness of introduced large mammals was mostly related to human activities on islands, whereas species richness of introduced small mammals was mostly related to island biogeographical parameters. The 'z-value' for total species richness is found to be expectedly low for introduced mammals.

Main conclusions Distance appears to have become ecologically trivial as a filter for introduced mammal presence on New Zealand offshore islands. There is strong evidence of a 'small island' effect on New Zealand offshore islands. The species richness of both small and large introduced mammals on these islands appears to be most predominantly related to human use, although there is some evidence of natural dispersal for smaller species. The ecological complexity of some islands appears to make them less invasible to introduced mammals. Some human activities have an interactive effect on species richness. A small number of islands have outlying species richness values above what the models predict, suggesting that the presence of some species may be related to events not accounted for in the models.

Keywords

Island biogeography, introduced mammals, linear modelling, New Zealand, offshore islands.

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INTRODUCTION

The patterns of species richness observed in insular systems have long fascinated biogeographers, but it is often difficult to disentangle the relationships between colonizing species, island topography and anthropogenic disturbance. Most island biogeographic studies have looked at native species, but the increasing phenomenon of island invasion by alien species now enables investigation of relationships using species whose arrival is relatively recent, and whose regional history is well

documented (Veltman *et al.*, 1996). The applicability of such an approach has already been demonstrated (Abbott, 1974; Lockwood *et al.*, 1999; Blackburn & Duncan, 2001; Sax, 2001). Of particular interest to biogeographers are those factors that determine species richness on islands.

MacArthur & Wilson (1963, 1967) first postulated what they considered to be good correlates of species richness on islands; these were primarily area and isolation (provided climate was held constant). Their inductive theory has been summarized and debated in the literature (see Gotelli & Graves, 1996; Brown & Lomolino, 1998) and apart from its recent division into a core deterministic model and elaborating stochastic model (see Whittaker, 1998), it has seen little change since its inception.

When investigating species richness on islands, it is important to consider variability between species and between islands. The factors affecting the distribution of species throughout an insular system will vary more widely as the taxonomic variety of species increases. It is, thus, sensible for investigations of species richness to limit themselves to a particular taxon, and the variables specific to that taxon. Most studies have taken this approach, although some have investigated multiple taxa (Abbott, 1983; Ricklefs & Lovette, 1999; Morand, 2000). It is also imperative to consider the scale at which the study is undertaken, and thus at which inferences can be made. At different scales, different island biogeographical relationships become apparent (Lomolino, 1999, 2000b; Whittaker, 2000). Because of the difficulties encountered in rigorously investigating ecological processes on a large spatial scale, the methodology used here aims to primarily examine pattern, with the goal of elucidating what processes merit further enquiry.

The New Zealand archipelago (Fig 1), comprising two main islands and 297 offshore islands larger than 5 ha, was geographically isolated from the Gondwanian landmass around 80 Ma (Stevens *et al.*, 1988). Because of early isolation, its native fauna lacked terrestrial mammals except bats (King, 1990). The advent of human colonization from the Pacific Islands (McGlone, 1989) *c.* 1000 years ago, followed by the arrival of Europeans around two centuries ago, saw the rapid influx of previously absent terrestrial mammals (Gibb & Flux, 1973). Due to these unique circumstances, the New Zealand archipelago is an excellent system for studying patterns in terrestrial mammal species richness on offshore islands, and on a relatively large scale. Such a study is also facilitated by the abundance of data of mammalian invaders on these islands, both from introduction records (Thomson, 1922) and recent surveys (Taylor, 1989; Atkinson & Taylor, 1991).

The aims of the study were to investigate what factors are significantly correlated with the species richness of introduced terrestrial mammals on offshore islands and whether such effects might differ generally between larger and smaller species. The species–area relationship of New Zealand islands with respect to introduced terrestrial mammals is also interpreted, for comparison with other studies.
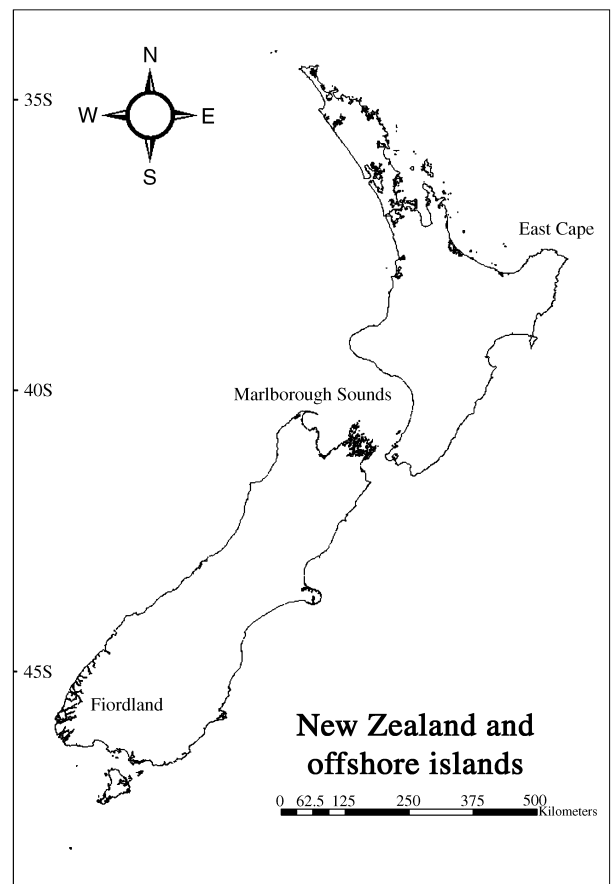
Figure 1 The New Zealand archipelago.

METHODS

Data sources

A combined matrix of variables by islands was collated from a number of different sources. The core data set was derived from the survey by Atkinson & Taylor (1991) of the distribution of alien mammals on New Zealand islands greater than 5 ha. The 5 ha limit was imposed because for most terrestrial mammals in the study, islands less than 5 ha have neither sufficient ecological diversity (Brown & Lomolino, 1998) nor a permanent supply of freshwater (Menard, 1986; Hugget, 1995) to sustain permanent mammal populations. Only the offshore islands, defined as those within 50 km of New Zealand's three main islands (North, South and Stewart), were considered in this study (*sensu* Atkinson & Bell, 1973). Beyond this distance the evolution of species endemism becomes a significant insular process (Williamson, 1981). The approximately 30 lacustrine islands within New Zealand were not considered. This was because being inland they are subject to different processes such as susceptibility to invasion from all directions and have significantly different climatic patterns.

The 17 major introduced mammal species of New Zealand were included, while those species of limited distribution were either discounted (e.g. weasels, *Mustela nivalis*) or included

Table 1 Symbol conversion from Atkinson & Taylor (1991) for introduced mammal status on offshore islands

Symbol	Interpretation	Conversion
+	Present	+
−	Not found during surveys or trapping	−
(no symbol)	Inadequate surveys or trapping to confirm absence	NA
E	Eradicated	+
?	Presence suspected, but not confirmed	NA
d	Deer not present, but island within swimming distance (c. 1 km)	−
s	Stoats not present, but island within swimming distance (1.2 km)	−
r	Rats not present, but island within swimming distance (c. 300 m)	−

within a larger taxonomic distinction (e.g. 'deer'). The combining of species into taxa does not violate the distinctiveness of the term 'species' because it was done only for species whose distributions are exclusive. Categories from Atkinson & Taylor (1991) were simplified to either 'presence', 'absence' or 'not available' (Table 1). Islands where species had recently been eradicated were reclassified to 'presence'.

In additional to the core data set was a summary of major habitats on New Zealand islands by Atkinson (1992). For those same islands listed in Atkinson & Taylor (1991), geographical and biological habitat and geological descriptions were listed. Locations of all offshore islands were taken from the Land Information New Zealand (LINZ) data base. These included Latitude, Longitude, land district code and the easting and northing for where the island's name appeared typeset on the map. For larger islands where multiple names appeared, triangulation was required to approximate island centrality. Updated island elevations and additional data on island distance from the mainland were measured from recent topographic maps (Table 2).

Diversity indices were calculated from counts of the number of distinct biological habitat and geological rock types present. For islands without censuses of some particular introduced mammal species, only conservative estimates of species richness could be constructed. To avoid biasing the data set with these, only islands with complete censuses were analysed. According to this criterion, 165 of the 297 islands had a relatively unbiased estimate of total introduced mammalian species richness.

Table 2 *A priori* variables of interest in the study

Variable	Description (units)
S	Total introduced mammal species richness
S_{large}	Large (> 10 kg) introduced mammal species richness
S_{small}	Small (< 10 kg) introduced mammal species richness
Latitude	Latitude (decimal)
Area	Area (ha)
Dist.Main	Distance from the mainland (m)
Elevation	Highest point (m)
BHDI	Biological habitat diversity index
GDI	Geological diversity index
Landing	Presence of a landing structure (wharf, etc.)
Settlement	European settlement history

Analysis of such a reduced data set requires that the subsample is still large enough to be statistically robust, and that it is a fair representation of the original sample (i.e. an unbiased subselection with regard to individual variables). The latter condition can be examined by comparison of the quantile distributions of the original and subsampled values of any variable, which highlights any anomalies between distributions (over-represented and under-represented values).

Statistical analysis

The distribution of observations in some variables was right-skewed, and was therefore $\log_{10}$ transformed to improve the linearity between the response and explanatory variables to meet the assumptions for linear modelling.

The species–area relationship is usually taken as the Arrhenius (1921) power model

$$S = cA^z$$

where S is the total species richness within the sample, A the total area sampled (island size) and c and z are mathematically determined coefficients unique to the sample. Taking the logarithm of both sides, this becomes

$$\log S = z \log A + \log c$$

This equation allows linear regression estimation of z (slope) and $\log c$ (intercept). This line can only be fitted for non-zero values of S (i.e. $S > 0$). The logarithm of 0 is undefined, and any transformation [such as $\log (S + 1)$] inappropriately biases z and c when comparing between studies (Williamson, 1981). Although removing observations is not favoured, it is the least obtrusive of solutions that have been suggested (Williams, 1996).

Estimates of species richness can be approximated by the Poisson distribution, notwithstanding issues of independence (spatial autocorrelation). Thus, the generalized linear model family of linear models proposed by Nelder & Wedderburn (1972), using a natural logarithm link, was chosen to model species richness on islands (McCullagh & Nelder, 1994).

The model presented is thus:

$$E(y_i) = e^{\beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \cdots + \beta_n x_{in}}, \quad y_i \sim \text{Poisson}(E(y_i))$$

The partial correlation coefficients (β_n) are presented as the proportional change in the response variable (species richness)

for a change in one unit of the explanatory variable. Explanatory variables were not standardized before analysis. This means that comparisons of coefficients cannot be made between variables, as they remain scale dependent. A more liberal than usual significance level of 10% was chosen for this study, to support less apparent relationships. Lack of independence in observations of the response variable (spatial autocorrelation) was investigated using correlograms and semivariograms (Legendre, 1993). If detected, it could have been modelled in the covariance structure of the errors (*sensu* Selmi & Boulinier, 2001), but this was never necessary.

Explanatory variable selection was based on *a priori* hypotheses. This allows for meaningful interpretation of *P*-values (Philippi, 1993). It was hypothesized that the introduced mammalian species richness of New Zealand islands would be related to island latitude, $\log_{10}$ transformations of Area, Elevation, Distance to the mainland (Dist.Main), geological diversity indices (GDI) and biological habitat diversity indices (BHDI) and to the presence of landing structures (Landing) and their category of European settlement history (Settlement). It was also hypothesized that the interaction between landing structure type and European settlement history would affect introduced mammalian species richness. The corresponding null hypothesis is that species richness has no relationship to any of the aforementioned variables.

Statistically, these hypotheses are presented as:

H_0 : The coefficient for any particular variable in the regression model is equal to zero.

$$\beta_j = 0$$

H_1 : The coefficient for any particular variable in the regression model is not equal to zero.

$$\beta_j \neq 0$$

It was also hypothesized that any significance of the above variables would differ between small mammals (<10 kg) and large mammals ($\geq$ 10 kg) (Fig. 2). This *a priori* hypothesis arises from the general distinction in island biogeographic patterns observed between small and large mammals (Lomolino, 1982, 1984; Adler & Wilson, 1985; Sara & Morand, 2002). Such a result was suspected because small mammals are generally more able to self-disperse, while larger and more domesticated mammals typically require deliberate transportation to islands.

RESULTS

Reduced data set

Observation immediately shows that $n = 165$ islands is an adequate sample size for robust linear modelling (Chase & Bown, 1997). Missing values were present for only 19 of the 1815 observations (1%), 13 of which were in the variable BHDI. These missing values were negligible overall with regard to analysis and interpretation. Most variables in the reduced subset had a distribution similar to the complete data
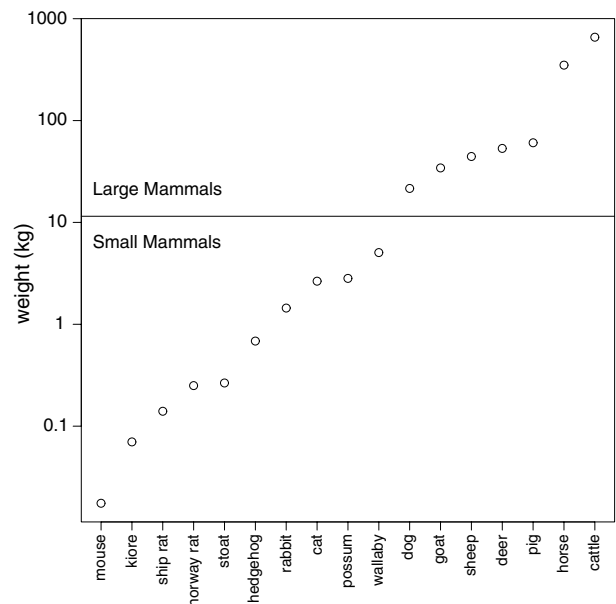

Figure 2 Body weight distribution of 17 introduced New Zealand mammals. Note the division at 10 kg into small and large mammals.

set, but some were under- and over-sampled for particular values. Islands with elevations less than 30 m were under-represented in the reduced data set. Similarly, islands closer than 300 m to the shore were severely under-represented, and this trend persisted until 10 km offshore, at which point the islands were fairly represented. Islands with GDI less than or equal to 2 were also under-represented.

The largest departure from distribution equality is in Latitude (Fig 3), which is under-sampled for values lying between $-45.00°$ and $-41.00°$, and correspondingly over-sampled for values lying between $-41.00°$ and $-38.00°$. Those latitudes under-represented are geographically located between the south of the Marlborough Sounds and the north of Fiordland in the South Island (Fig 1). Those over-represented lie around the central North Island south of the East Cape and north of the Marlborough Sounds. This reflects the geographical clustering of islands in New Zealand.

Intervals of the sampling proportions of both categorical variables for their levels (Table 3) included the average (total islands in subset/total islands), suggesting that the subsample of levels in the reduced data set is not particularly biased. In Settlement, both Abandoned and Ranger Station islands appear to be over-represented, with their respective lower-tails marginally above the average value.

Inspection of all inter-explanatory variable relationships revealed some collinearity between $\log_{10}$ Area, $\log_{10}$ Elevation and $\log_{10}$ BHDI. Only small islands (< 10 ha) appear relatively independent for values of each variable. Variance inflation factors were calculated for all numerical explanatory variables but none approached the threshold value of 10 (Glantz & Slinker, 2001). Correlograms and semivariograms showed no evidence of spatial autocorrelation in species richness.
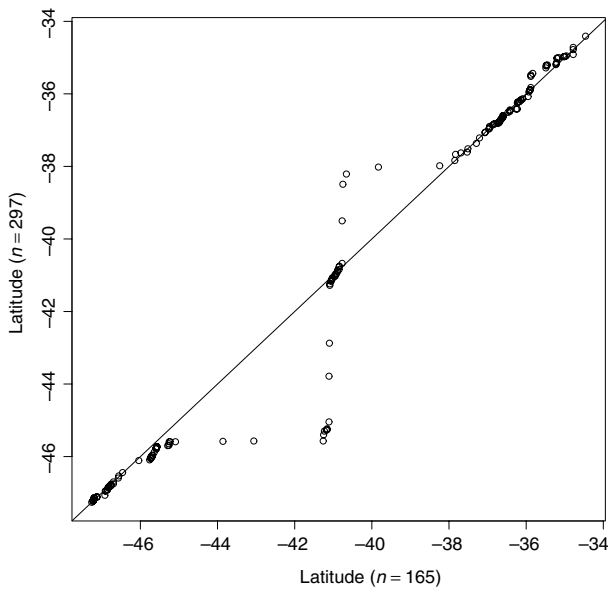
Figure 3 Quantile–quantile plot for Latitude subsample. Points below the line indicate under-sampling while points above the line indicate over-sampling of the parent Latitude variable. The significant departures represent the few islands sparsely distributed between island clusters.

Species–area relationship

Taking islands with values of S greater than zero meant that the sample size was reduced from 165 to 108 islands. Estimates and 95% confidence intervals ($n = 108$) for z and $\log_{10} c$ are (Fig 4):

$$z = 0.21 \; [0.16, 0.26]$$

$$\log_{10} c = -0.06 \; [-0.18, 0.06]$$

The intercept was not significant ($P = 0.325$), but the z-value was significant at the 5% level ($P < 0.001$). Residuals were normally distributed (Wilks–Shapiro test, $P = 0.140$).

When back-transformed, an insignificant intercept ($\log_{10} c$) means c is not significantly different from 1:

$$\log_{10} c = 0$$

$$\Rightarrow c = 1$$

Therefore, the original (multiplicative) species–area relationship is effectively defined by A^z.

Large mammals

Six terms were significant in the large mammal model (Table 4). For $\log_{10}$ terms, the proportional change is with respect to an order of magnitude ($\log_{10}$ unit) change in the variable, not a linear change. A chi-squared adequacy-of-fit test (χ^2, $P_{large} = 0.851$, d.f. $= 132$) failed to reject the null hypothesis that the large mammal model was adequate.

In the large mammal model, there were significant negative interaction terms between the presence of a wharf with both abandoned ($P = 0.020$) and inhabited ($P = 0.001$) European settlements (Fig 5). Different effects between levels of categorical variables are directly comparable because they are unitless.

When multiplying proportions together for interaction terms, the overall proportional effect of having an island with a wharf, which is currently inhabited is:

$$
\begin{aligned}
\text{Proportional change in } S_{large} &= \text{Wharf} \times \text{Inhabited} \\
&\quad \times \text{Wharf:Inhabited} \\
&= 5.48 \times 3.31 \times 0.11 \\
&= 2.00
\end{aligned}
$$

and for an island with a Wharf which was settled but subsequently abandoned:

$$
\begin{aligned}
\text{Proportional change in } S_{large} &= \text{Wharf} \times \text{Abandoned} \\
&\quad \times \text{Wharf:Abandoned} \\
&= 5.48 \times 2.18 \times 0.18 \\
&= 2.15
\end{aligned}
$$

Plotting indexed deviance residuals (McCullagh & Nelder, 1994) showed larger variation in random scatter above zero. Outliers were identified as values outside the range $[-2, 2]$. Plots of deviance residuals vs. explanatory variables revealed no abnormal, non-linear trends.

Four positive outliers were identified: RAKITU (ARID) I (2.48); NATIVE I, Paterson Inlet (2.37); CHETWODE IS, Nukuwaiata (2.08); MOKOHINAU IS, Burgess (Pokohinu) (2.08).

Table 3 Subsampling proportions and confidence intervals for levels of the categorical variables Landing and Settlement. No irregularities are apparent

	Landing			
	Total	–	Wharf	Not available
Proportion	165/297	148/256	16/35	1/6
95% Interval	0.56	(0.52, 0.64)	(0.29, 0.63)	(−0.21, 0.55)
	Settlement					
	Total	–	Abandoned	Unmanned farm	Inhabited	Ranger station	Not available
Proportion	165/297	130/230	11/14	2/4	13/29	7/8	2/12
95% Interval	0.56	(0.50, 0.63)	(0.56, 1.02)	(−0.19, 1.19)	(0.26, 0.64)	(0.62, 1.14)	(−0.07, 0.41)
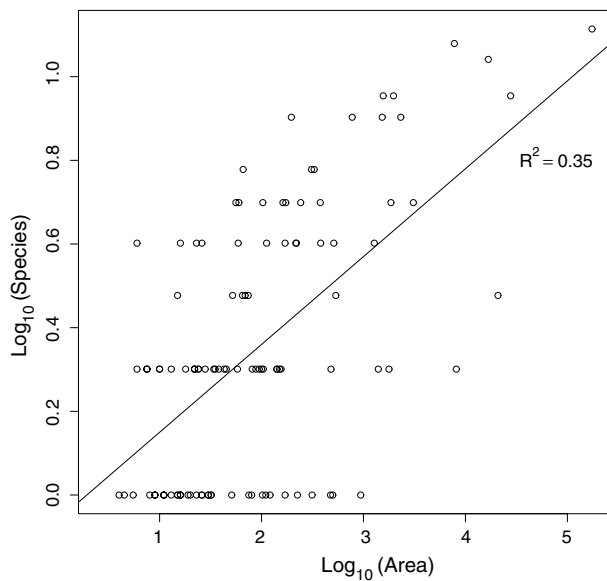
Figure 4 Linear regression of $\log_{10} S$ on $\log_{10} A$ for introduced mammals on New Zealand offshore islands.

Table 4 Significant model terms and their proportional changes in species richness for the large mammal model

Term	Coefficient	SE	*P*-value	Signif.	Proportional change in S_{large}
Wharf	1.70	0.49	0.001	***	5.48
Wharf:inhabited	−2.18	0.68	0.001	**	0.11
Inhabited	1.20	0.43	0.006	**	3.31
Wharf:abandoned	−1.71	0.74	0.020	*	0.18
Abandoned	0.78	0.40	0.052	(*)	2.18
$\log_{10}$ Area	0.51	0.30	0.094	(*)	1.66

Small mammals

Five terms were significant in the small mammal model (Table 5). As earlier, for $\log_{10}$ terms the proportional change is with respect to an order of magnitude ($\log_{10}$ unit) change in the variable. A chi-squared adequacy-of-fit test (χ^2, $P_{\text{small}} = 0.832$, d.f. = 132) failed to reject the null hypothesis that the small mammal model was adequate.

There were no significant interactions between levels of Landing and Settlement in the small mammal model.

Plotting indexed deviance residuals showed larger variation in random scatter above zero. Outliers were identified as values outside the range [−2, 2]. Plots of deviance residuals vs. explanatory variables revealed no abnormal, non-linear trends.

One positive outlier was identified: NATIVE I, Paterson Inlet (2.24).

DISCUSSION

The bias in the reduced data set with respect to Latitude is an artefact of the geographical distribution of New Zealand
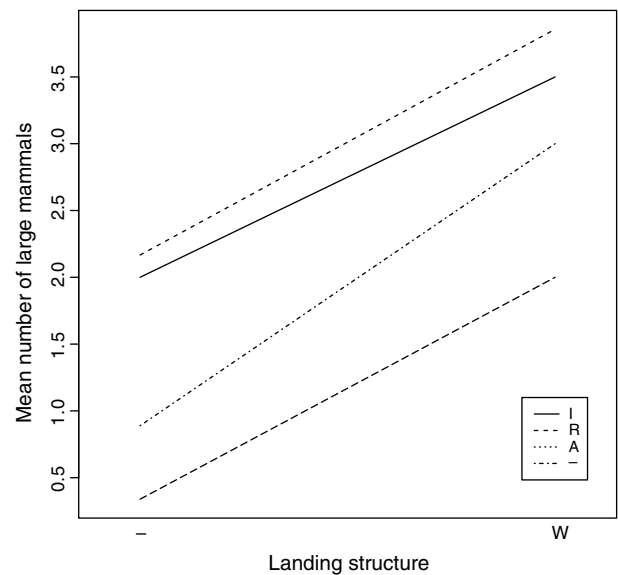
Figure 5 Interaction plot for the categorical variables Landing and Settlement. Parallel lines indicate no interaction. Note the two parallel groups; Inhabited (I)/Abandoned (A) and Ranger Station (R)/Never Settled (−). There is no line for Unmanned Farm (F) as those islands had no landing structures.

Table 5 Significant model terms and their proportional changes in species richness for the small mammal model

Term	Coefficient	SE	*P*-value	Signif.	Proportional change in S_{small}
$\log_{10}$ Area	0.93	0.24	< 0.001	***	2.53
Latitude	0.07	0.02	0.001	***	1.07
(Intercept)	3.87	1.17	0.001	***	N/A
$\log_{10}$ Elevation	−0.84	0.41	0.042	*	0.43
$\log_{10}$ Dist.Main	−0.21	0.12	0.080	(*)	0.81
$\log_{10}$ GDI	−0.84	0.49	0.087	(*)	0.43

islands. These form three main groups (Atkinson & Bell 1973), with two 'gaps' of relatively few islands. Consequently, islands are not linearly distributed with respect to Latitude. It is within these gaps lying off the central North and central South Islands that the bias lies. The total bias is minimal, and for the three main groups the reduced data set is representative. No significant collinearity was detected using variance inflation factors (Glantz & Slinker, 2001). Overall, the reduced data set is an accurate subsample of the original data set, and so inferences should be applicable to the entire archipelago.

A number of hypotheses have been postulated for the observed relationship between area and the number of species on an island (Williamson, 1981; Rosenzweig, 1995; Gotelli & Graves, 1996; Whittaker, 1998). The most popular means by which to distinguish between these competing hypotheses has usually been multiple regression (Rosenzweig, 1995). For terrestrial species these hypotheses are essentially:

1 Random placement – if individuals are distributed at random, a larger sample area will contain more species.

2 Habitat diversity – larger islands have more habitats supporting more species.

3 Equilibrium – total species number is a dynamic equilibrium between immigration and extinction.

The relationship between area and habitat diversity has long been recognized (Williams, 1943; Lack, 1969, 1976; Williamson, 1981; Rosenzweig, 1995; Gotelli & Graves, 1996; Whittaker, 1998) and investigated (Harner & Harper, 1976; Ricklefs & Lovette, 1999; Welter-Schultes & Williams, 1999). Although the area–habitat diversity hypothesis is popular, it is also the most difficult to assess (Gotelli & Graves, 1996). A relationship with population densities has also been investigated (Wright, 1981), but Connor et al. (2000) found no correlation for mammals. Elevation has also been investigated to a lesser extent (Abbott, 1978; Lomolino, 1984; Burbidge et al., 1997), although only recently has it received attention as a further correlate of area, habitat and the number of individuals (Rahbek, 1995). Measurements of the number of individuals, habitats and extinction rate are all correlated with area, and thus all explain very similar variability within species richness models. It is yet unclear which, if any, is the true manifestation of the underlying process controlling the species–area relationship (Whittaker, 1998).

Following past discrediting of strict inference from z-values (Connor & McCoy, 1979; Lomolino, 1989; Gotelli & Graves, 1996), they are now used as an exploratory means to investigate 'insularity' (Sara & Morand, 2002). Calculations of z-values have usually been made with large, well-established native taxa (Lomolino, 1982, 1984; Abbott, 1983), where S is greater than zero. In this study, only islands with $S > 0$ were considered, which is similar to arbitrarily selecting a minimum island size whereby S is always greater than zero. This predisposes the z-value to suggest more frequent mammal occurrence than is the case, and this bias should be considered. MacArthur & Wilson (1967) originally stated that the range of insular z-values lies between 0.20 and 0.35, although this has subsequently become a more conservative 0.25–0.33 range (Rosenzweig, 1995). The z-value of 0.21 obtained here lies outside the generally accepted literature values for islands, although for large vertebrates z-values do tend to be lower, at around 0.25 (Lomolino, 1984; Sara & Morand, 2002). Some convex curvature upwards can be seen in Fig. 4. Fitting a regression line in Gleason's semi-log space (Gleason, 1922) provides a better fit ($r^2 = 0.44$). Following Connor & McCoy (1979), however, the difference of less than 5% would not be significant, though it has been noted that this significance level is entirely arbitrary (Gotelli & Graves, 1996). There are also no generally accepted 'canonical' values for parameters of the Gleasonian model (Lomolino, 2000a). Lomolino (2000a) advocates a hypothetical sigmoidal shaped species–area curve based on a unimodal species distribution as originally proposed by Schoener (1976) and Gilpin & Diamond (1976). However, if 'small' islands are not sampled, as may be the case in this study, the 'small-island' effect (Lomolino & Weiser,

2001) depicted by the shallower left-hand tail of the sigmoidal curve would be neglected. The remaining segment of the curve would then appear convex as it does in Fig. 4. Furthermore, such an effect may be scale-specific (Blackburn & Gaston, 2002); only apparent on smaller scales, as compared to larger scales where it may not be apparent (Williamson et al., 2001). These consequences warrant further investigation.

Lomolino (1982) states that large z-values are the result of distant archipelagos, thus correspondingly low values, as was found in this study, suggest an adjacent archipelago. That is clearly not the case when distances of islands were quite appropriately (Lomolino, 1999) measured across three orders of magnitude (0.1–100 km), whereas the swimming distance of most New Zealand introduced mammals is only in the order of 0.1–1 km (Atkinson & Taylor, 1991). Abbot (1983) cautions against the interpretation of low z-values; they could suggest the effect of area on dispersal is minimal, but exclude any effect of distance. Species could be poor colonizers, not reaching any islands irrespective of area, or good colonizers, able to live on any island irrespective of area. In the light of the widespread distribution of mammals throughout the New Zealand archipelago, the most likely explanation is the latter. This suggests that the human-facilitated dispersal of mammals throughout the New Zealand landscape has effectively rendered the archipelago smaller within an ecological context, with area playing less of an interactive role, since distance to the mainland is now ecologically trivial. Because the distribution of introduced mammals in New Zealand was mediated by human-facilitated dispersal (King, 1990), barriers to natural dispersal became negligible. Distance has been found similarly insignificant in other studies of insular mammal species richness (Burbidge et al., 1997; Sara & Morand, 2002), although in those cases it more likely reflects the poor dispersal ability of endemic mammals, rather than their human-mediated dispersal. Mammalian species richness on New Zealand offshore islands appears to have a similar relationship to area as found on overseas land-bridge islands (similar z-values are presented in Lomolino, 1986; Millien-Parra & Jaeger, 1999), suggesting that over-water dispersal is not as significant a barrier in New Zealand as it is elsewhere. This suggests that anthropological variables might be better predictors of introduced mammal dispersal to New Zealand offshore islands.

Large mammals

Although there is some correlation with other geographical and ecological variables, the significant levels of the categorical variables can generally be interpreted as surrogates for different human activities. This supports the notion that the species richness of large introduced mammals on New Zealand offshore islands primarily reflects the level of anthropogenic activity that has occurred on them (King, 1990), a common theme in patterns of global invasion (Vitousek et al., 1997).

The effect of log_{10} Area is barely significant in the model. For large mammals it is most likely that the role of area is

related to human activity, such as available farming land, or more generally to human settlement habits. The average area of islands that are considered permanently inhabited is over 1000 ha.

Very few studies of mammalian species richness appear to have investigated possible interactions between explanatory variables (although see Lomolino, 1986). This might be because effects beyond the main terms in statistical analyses are considered ecologically irrelevant. Whereas this would be true for independent and non-interactive variables, as hypothesized *a priori* here, interaction between anthropogenic historical factors should reasonably be expected. The interaction plot (Fig. 5) shows two groups each with parallel slopes. The slopes may be interpreted as the rate of change in species richness on islands when a wharf is added. It is evident that the group with the gentler slope (where addition of a wharf does not have so great an effect) is islands that have never been inhabited, or only had a ranger station on them. The other group, comprising abandoned and inhabited islands, has a slope that increases much more rapidly upon addition of a wharf. This clearly reflects the consequences of adding a wharf to an island that has at some stage served as a settlement – where domesticated mammals are intentionally introduced. Interestingly, the value of both interaction terms was negative. This means that the combined interactive effect of the categorical variable levels on an island is less than would be expected if the levels were independently additive. In other words, should one of the categorical variable levels be present, then species richness increases markedly. The addition of the other categorical variable level has less effect thereafter, as most of the few species available from the source pool of seven large mammals will already be present, and fewer are available to be subsequently added to the island's pool of species.

We should expect the distribution of large mammals, being particularly commensal with humans, to be highly correlated with human activity. It has always been assumed that the distribution of introduced mammals across the New Zealand landscape, including its offshore islands, is regulated by human factors (King, 1990; C. Veitch pers. comm.). The results presented here are quantitative evidence supporting such a relationship, at least for the large introduced mammals of New Zealand.

Small mammals

Five variables and the intercept were all significant predictors of small mammal species richness. The intercept is the value for species richness should all other variables be zero, and in this case has little biological relevance (Glantz & Slinker, 2001). Recalling that for $\log_{10}$ transformed variables proportional changes are for a change of one magnitude, it can be seen that a change in one magnitude of area results in a 2.53-fold increase in small mammal species richness. This is not surprising, regardless of the underlying process. The evidence supporting this effect is also very strong. The effect of latitude is similarly significant, although for a change of 1° in latitude,

only a small proportional increase of 1.07 is seen in small mammal species richness. The gradient of increase in latitude is northwards. The total proportional variation in small mammal species richness from the southern most (Big South Cape) to the northern most (Motuopao) island of New Zealand, holding all other variables constant, is 2.38 ($1.07^{12.8}$). Similar trends in latitude for species have been found in other studies (Pianka, 1966; Brown & Lomolino, 1998; Sax, 2001; Duncan & Forsyth, unpubl. data).

$\log_{10}$ Dist.Main and $\log_{10}$ GDI were only marginally significant at the 10% level. Both coefficients were negative, suggesting the further an island is from the mainland, or as its geological diversity increases, it tends to have a lower small mammal species richness. The negative relationship between distance and species richness is well documented (MacArthur & Wilson, 1963, 1967; Lomolino, 1982, 1984, 1990, 1999; Adler & Wilson, 1985; Rosenzweig, 1995; Whittaker, 1998), and is probably related to lower immigration. The relationship between abiotic–biotic complexity and species richness is less well understood. Although it would follow that geological diversity might be correlated with biological habitat diversity, this was not the case here. Habitat diversity is known to be positively correlated with species richness – greater habitat heterogeneity allows a greater diversity of species to establish (Lack, 1969, 1976; Adler & Wilson, 1985; Ricklefs & Lovette, 1999; Davidar *et al.*, 2001). Geological diversity was included as a surrogate for floral diversity (Johnson & Raven, 1970; Wardle, 1984) to investigate any relationship between ecological complexity and introduced species richness. The hypothesized diversity–stability relationship predicts that diverse ecosystems are less susceptible to invasion by exotic species (Pimm, 1991; Rosenzweig, 1995). Thus, although superficially similar, biological and geological habitat diversity, in fact, characterize different relationships with species richness. Abbot (1980) discusses the differences between plant diversity and habitat diversity as predictors. In this study, there was only a weak negative correlation between geological diversity and small mammal species richness that does not provide credible evidence either way for the presumption that more complex systems are less invasible. The relationship between geological diversity and floral complexity was also only assumed, not tested.

The relationship between $\log_{10}$ Elevation and small mammal species richness was negative. The $\log_{10}$ Area term in the model has a positive relationship with species richness, which would suggest that $\log_{10}$ Elevation should do so as well, because $\log_{10}$ Area and $\log_{10}$ Elevation are positively correlated. However, when the effect of $\log_{10}$ Area alone on species richness is taken out, $\log_{10}$ Elevation then has a negative relationship with species richness. The negative relationship of $\log_{10}$ Elevation with small mammal species richness might suggest that islands with higher elevation have been less invaded by small mammals, though $\log_{10}$ Elevation may be a surrogate for some other, perhaps more abstract, variable not included in the model, such as ecological complexity. Mueller-Dombois (1999) promotes incorporating a vertical component,

measured as elevation, into general island biogeography theory, reasoning that elevation is a good approximation of water flow from upland to lowland areas, and thus causing increased habitat heterogeneity. The strong correlation between area and elevation quite likely confounds the interpretation of real elevation effects in many studies. Few studies appear to have investigated the effect of elevation on mammals that have a much lower dependency on suitable habitat availability, although Lomolino (1990) suggests elevation is a good predictor for active mammal dispersers to islands (which can see their destination). Such a result should promote a positive relationship with elevation although that is not the case here. More work is clearly necessary to identify the unique effect of elevation on species richness.

Overall, the five significant variables appear to be surrogates for underlying natural processes that relate to the dispersal of species to offshore islands, and the potential for an island to be invaded based on its area and ecological complexity. These match those factors suggested by island equilibrium theory (MacArthur & Wilson, 1963, 1967) and subsequent studies (Lomolino, 1982, 1990; Ceballos & Brown, 1995; Burbidge et al., 1997; Millien-Parra & Jaeger, 1999).

CONCLUSIONS

Between both models, four islands were identified as outliers, though only with values one or two species over that predicted. When working with small species, richness counts, the stochastic variation that may cause an increase of only one more species may be common enough to permit four islands (in the case of the large mammal model) to be outliers. However, all of the large mammal model outliers were for more species than predicted (i.e. the model under-predicted). This suggests that these islands may be relatively over-saturated by large mammals, possibly because of idiosyncratic colonization events (or motives) not included in the model.

When considering these findings, the importance of scale must be considered (Whittaker et al., 2001). Spatial autocorrelation was investigated and not detected. Had any been present, the geographic variable latitude would have accounted for most of it (Augustin et al., 1998; Selmi & Boulinier, 2001). Selmi & Boulinier (2001) found little spatial autocorrelation for taxa with poor dispersal opportunities (such as mammals or introduced species). Following their work, this suggests in this study that the species pool of introduced mammals able to colonize New Zealand offshore islands is constant across the country, and hence island characteristics alone determine species richness. Lomolino (1999, 2000b) presents a graphical model that illustrates how, at different spatial scales, different variables can appear to take precedence. It is thus important that an appropriate diversity of islands be sampled from throughout an archipelago, at the appropriate scales of the variables, before inferences are applied to the entire archipelago (Lomolino, 1999; Lomolino & Weiser, 2001). For smaller studies of fewer islands (such as Conroy et al., 1999; Palmer et al., 1999), Lomolino & Weiser (2001) cite this as a possible

reason for conflicting results when interpreted in the light of the equilibrium theory of island biogeography. Whittaker (2000) asserts that the effects of area, isolation, altitude and habitat diversity are all proportional to the scale at which they are measured, a sentiment shared by Blackburn & Gaston (2002). Because the data set for this study was all islands larger than 5 ha in New Zealand, it is hoped that the relative importance of each explanatory variable has been established within the context of the entire archipelago. As human activity is positively correlated with island area, by restricting the study to 'larger' islands, the results are predisposed to emphasize human effects. However, for islands less than 5 ha, mammal species richness is usually zero, and (as specified earlier) some arbitrary lower limit for island size was necessary.

The results may be difficult to place within the context of the MacArthur and Wilson's equilibrium theory of island biogeography because the theory only occupies one corner of Whittaker's (1998, 2000) conceptual representation of island species turnovers. Because introduced mammals are only now completing range expansion since their arrival in New Zealand, we cannot be sure if they have yet, or still are attaining an equilibrium or non-equilibrium state (Gibb & Flux, 1973). Patterson (1999) suggests that historical influences drive islands towards non-equilibrium. We also do not know whether the final state will be dynamic or static, but Brown & Lomolino (1998) note that new equilibrium states can be achieved following non-equilibrium conditions. Holland (2000) suggested that the New Zealand biota was impoverished before introductions began, at a sub-equilibrium biodiversity state, and that subsequent introductions have so far only served to approach equilibrium. However, this seems absurd when considering the geological timescales over which New Zealand's biota has evolved, and the intense predatory interactions that have been generated by the recently invading fauna (King, 1984). The models presented here suggest that explaining the patterns of mammalian species richness on New Zealand offshore islands is a relatively deterministic process, governed by a few major variables acting as surrogates for general underlying processes. The results suggest that the introduction of mammals to New Zealand offshore islands has driven insular ecosystems into a state of non-equilibrium, in a manner similar to non-equilibrium results found for Japanese terrestrial mammal assemblages on offshore islands (Millien-Parra & Jaeger, 1999). Only time will tell if New Zealand's introduced mammals will conform to island biogeographic theory principles (dynamic equilibrium) or to some alternative principle.

Overall species richness relationships to island characteristics can be complex and subtly masked by more easily measured variables, even when the system itself can appear to be readily simplified. Interactive effects between variables can also play a significant role in determining insular species richness. Introduced species are an excellent model for investigating insular systems, and results are directly applicable both in preventing further expansion within an archipelago, and to other archipelagos where similar species may potentially

become a problem. For mammals on New Zealand islands, the species richness of the introduced taxa was found to be almost entirely attributable to anthropological events, which emphasizes the need to prevent and mitigate the adverse effects of humans in sensitive insular systems.

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