Life-history traits and extrinsic threats determine extinction risk in New Zealand lizards

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ABSTRACT

A species' vulnerability to extinction depends on extrinsic threats such as habitat loss, as well as its intrinsic ability to respond or adapt to such threats. Here we investigate the relative roles of extrinsic threats and intrinsic biological traits in determining extinction risk in the lizard fauna of New Zealand. Consistent with the results of previous studies on mammals and birds, we find that habitat specialization, body size and geographic range size are the strongest predictors of extinction risk. However, our analyses also reveal that lizards that occupy areas with high levels of annual rainfall and are exposed to exotic predators and high human population densities are at greater risk. Thus, while the intrinsic traits that render species prone to extinction appear largely congruent across vertebrate taxa, our findings illustrate that both extrinsic threats and intrinsic traits need to be considered in order to accurately predict, and hence prevent, future population declines.

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1. Introduction

There is an emerging consensus that we are in the midst of a mass extinction event that rivals those of the geological past (Pimm et al., 1995; Wake and Vredenburg, 2008; Maclean and Wilson, 2011). However, not all species are equally at risk of extinction (Bennett and Owens, 1997). Indeed, analyses of past and projected extinctions have frequently reported highly non-random patterns in extinction risk (McKinney, 1997; Purvis et al., 2000; Duncan et al., 2002; Olden et al., 2007; Anderson et al., 2011; Murray et al., 2011; Thuiller et al., 2011). Investigating the mechanisms that render species vulnerable to extinction can assist in the identification, and hence mitigation, of threatening processes and can ultimately lead to the development of better preventative approaches and more strategic allocation of conservation funds (Cardillo and Meijaard, 2012). For example, statistical relationships between threatening processes and extinction risk can allow conservation managers to assess the threat statuses of poorly understood species, or assist in the identification of stable species that are prone to future declines (Reed and Shine, 2002; Fisher and

Owens, 2004). In contrast to reactive management strategies, which are typically time-consuming and expensive, preventative approaches based on statistical models can provide a rapid, cost-effective means to assess the conservation statuses of large numbers of species (Anderson et al., 2011; Murray et al., 2011; Cardillo and Meijaard, 2012).

A species' vulnerability to extinction depends on extrinsic threats such as habitat loss and invasive species, as well as its intrinsic ability to respond or adapt to such threats (Fisher et al., 2003; Cardillo et al., 2004; Collen et al., 2011; Murray et al., 2011). Because the life-history, behavior, and ecology of a species dictates its demography (and thus its resilience to extrinsic threats: Olden et al., 2007), most previous studies of extinction risk have focused solely on intrinsic characteristics of species. These studies have frequently revealed that large-bodied, range-restricted, and ecologically specialized taxa are at greater risk (Fisher and Owens, 2004; O'Grady et al., 2004), although there is evidence that such relationships may be sensitive to taxonomic or spatial scale (Gage et al., 2004; Cardillo et al., 2008). Fewer studies of extinction risk have considered both intrinsic traits and extrinsic threats simultaneously. This is surprising, in that the impacts of extrinsic threats depend not only on a species' intrinsic characteristics, but also on the geographic distribution and severity of such threats (Collen et al., 2011; Murray et al., 2011). Accounting for both types of characteristics may therefore reveal spatial

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contingencies in extinction risk that are not apparent when either type of variable is considered in isolation.

Here we investigate how intrinsic traits and extrinsic threats influence extinction risk in the lizard fauna of New Zealand. To date, there have been comparatively few studies that have investigated correlates of extinction risk in reptiles (Fisher and Owens, 2004; but see Siliceo and Díaz, 2010; Mitchell and Janzen, 2010), despite the fact that reptile declines mirror those of other vertebrate groups in terms of severity and taxonomic and geographic breadth (Gibbons et al., 2000; Böhm et al., 2013). New Zealand has a diverse terrestrial lizard fauna consisting of ~100 species and undescribed entities (Chapple et al., 2009; Hay et al., 2010; Nielsen et al., 2011), but many of these taxa have experienced substantial range contractions in recent decades. In fact, ~75% of the New Zealand lizard fauna is either at risk or threatened with extinction (Hitchmough et al., 2010). Exotic mammals have been implicated as a major driver of lizard declines in New Zealand and many lizard taxa are now restricted to mammal-free offshore islands (Daugherty et al., 1994; Towns and Daugherty, 1994; Towns et al., 2001, 2003; Towns and Ferreira, 2001). In addition, New Zealand lizards are typically more abundant on predator-free islands (Whitaker, 1973) and previous studies have suggested that large, nocturnal taxa that overlap with the small mammal niche have undergone more substantial declines (Towns and Daugherty, 1994; Hitchmough et al., 2010). However, much of the evidence surrounding impacts of exotic mammals on New Zealand's lizard fauna remains correlative and circumstantial (Towns et al., 2003).

We use a comprehensive dataset on the life-history, ecology, and geographic distributions of New Zealand lizards to evaluate the effects of extrinsic threats suspected to have caused lizard declines in New Zealand (e.g., exotic mammals, habitat loss), as well as intrinsic traits that have been shown to influence endangerment in reptiles and other vertebrate taxa (e.g., range size, habitat specialization). We then use our model of extinction risk to predict the conservation statuses of data deficient lizards in New Zealand and to identify taxa which are currently listed as stable, but have the potential to become threatened due to their intrinsic traits and geographic distributions.

2. Methods

Data on the threat status of 99 described New Zealand reptile species and undescribed entities (hereafter 'species') were taken from a recent conservation assessment (Hitchmough et al., 2010). This assessment ranked species in one of five threat categories: (i) not evaluated, (ii) not threatened, (iii) at risk, (iv) threatened, and (v) extinct. We excluded marine species and those that were deemed extinct, introduced, or were not evaluated, leaving a total of three threat categories for our analysis (not threatened: $n = 21$; at risk: $n = 47$; and threatened: $n = 17$). We also excluded the tuatara (*Sphenodon punctatus*) from our analysis due to its unique life-history and large body size relative to the remainder of the New Zealand reptile fauna. The Chathams skink (*Oligosoma nigriplantare*) was also excluded, as this species is endemic to the Chatham Islands (~800 km east of New Zealand) and we lacked environmental data for this region. Our final dataset included 87 lizard species.

Data on the distribution of each species were taken from the New Zealand Department of Conservation's Herpetofauna Atlas, which collates all verified locality records collected by researchers, museums, government agencies and the general public in New Zealand (Department of Conservation, 2009). Fossils, translocations, and duplicate records were removed from the atlas database prior to conducting our analysis. We did not exclude historic records, as the majority of the atlas data are relatively recent. In fact,

the median date across all records is 1989, and less than 5% of all records are from earlier than 1965. Distribution data were used to calculate geographic range size and habitat specialization (see Section 2.1), and to estimate environmental parameters across each species' geographic range (see Section 2.2).

2.1. Intrinsic threats

We compiled a comparative dataset of the life-history and ecological traits of New Zealand lizards (Table A1) from the Landcare Research NZ Lizards Database (Bell, 2010) and recent molecular phylogenetic studies of the endemic skink (Chapple et al., 2009) and gecko faunas (Nielsen et al., 2011). Our dataset included mean body size (there is no substantial sexual size dimorphism in New Zealand lizards), habitat use, habitat specialization, activity phase, diet, maximum reproductive output, phylogenetic longevity (i.e., time since divergence [mya] from its most closely related extant species), reproductive mode, and biogeographic affinity. Occurrence records of each species were also used to calculate geographic range size. To reduce the effects of survey bias and georeferencing errors, range size was approximated as the number of occupied equal-area 1-km grid cells.

2.2. Extrinsic threats

We calculated the mean value of seven variables within each species' geographic range: mean annual temperature, annual precipitation, temperature seasonality (standard deviation), precipitation seasonality (coefficient of variation), human population density, human influence, and extent of habitat loss. These variables were chosen because they characterize the main drivers of reptile declines worldwide (Foufopoulos and Ives, 1999; Reed and Shine, 2002; Whitfield et al., 2007; Sinervo et al., 2010; Böhm et al., 2013). Climate data were taken from the WorldClim database (~1-km resolution) (Hijmans et al., 2005). Data on human population density were taken from the GRUMP v1 dataset (based on United Nations-adjusted census data from 2000; ~1-km resolution; http://sedac.ciesin.columbia.edu/gpw, accessed 22/01/2012), whereas human influence data were extracted from the global human footprint v2 (~1-km resolution; http://ciesin.columbia.edu/wild_areas, accessed 22/01/2012). Extent of habitat loss within each species' range was based on the New Zealand Land Cover Database 2 (LCDB2), which is derived from satellite imagery taken from September 2001 to March 2002 (Terralink, 2004). Following Walker et al. (2008), we re-classified LCDB2 into indigenous and non-indigenous classes and calculated the proportion of all occurrence records in indigenous classes for each species as an estimate of habitat loss. We also determined whether species were represented on at least one offshore island that was free of introduced mammalian predators/competitors. Although several of these variables (e.g., climate, human influence and population density) are indirect measures of extrinsic threats, these variables correlate with extinction risk in other taxonomic groups (Cardillo et al., 2004; Davies et al., 2006; Sodhi et al., 2008), and represent the best data available at the national scale.

2.3. Statistical analyses

To facilitate interpretation and avoid overfitting our models, we used a subset of the life-history, ecological, and environmental variables described above to develop models of extinction risk: (i) geographic range size (ln-transformed), (ii) body size (quadratic relationship), (iii) habitat use (categorical: terrestrial, arboreal, or terrestrial-arboreal), (iv) habitat specialization (number of land-cover types occupied, corrected for range size), (v) activity phase (categorical: diurnal versus nocturnal), (vi) representation on at

least one predator-free offshore island (categorical: no predator-free island population versus at least one predator-free island population), (vii) mean annual temperature (quadratic relationship), (viii) annual precipitation (quadratic relationship), (ix) mean human population density (ln-transformed), and (x) extent of habitat loss (quadratic relationship). Because the number of habitat types that a species occupied was positively correlated with its geographic range size (Spearman's $\rho = 0.907$), we regressed range size on the number of habitat types occupied and used the residuals of this regression as an estimate of habitat specialization. The final set of explanatory variables used in our analysis was chosen on the basis of multicollinearity, data heterogeneity (e.g., only one species was oviparous), and the results of previous studies. Whenever possible, we avoided using variables with many missing values to reduce the probability of biasing our results (González-Suárez et al., 2012). If two variables with no missing data were correlated with each other, the variable with the highest explanatory power in a univariate model was retained.

We used cumulative link models with a logit link (i.e., proportional odds models) and the Bayesian Information Criterion adjusted for small sample sizes (BICc) to assess the strength of evidence for models containing all possible subsets of the ten variables outlined above. In all models, threat status was the response (coded as an ordinal variable: *not threatened* = 1, *at risk* = 2, *threatened* = 3), and intrinsic traits and extrinsic threats were included as fixed effects. BIC is similar to the more widely used Akaike's Information Criterion (AIC), but tends to fit fewer parameters than AIC, and is thus suitable for identifying main effects. The relative importance of each explanatory variable was estimated by summing the BIC weights across all models that contained a given variable. Nagelkerke's R^2 was used as a measure of the explanatory power of each model.

We initially included a taxonomic random effect in all models to account for clustering of species within genera; however, accounting for taxonomic dependence did not qualitatively influence variable importance and genus explained an insignificant amount of the variance in extinction risk (BICc was 4.47 units lower when genus was excluded from the global model). Furthermore, only two families of lizards are represented in New Zealand, and extinction risk does not vary between families (Hitchmough et al., 2010). We therefore present the results of our analysis using fixed-effects cumulative link models only. All statistical analyses were conducted in R© 2.15.1 using the *ordinal*, *rms*, and *MuMin* libraries (R Development Core Team, 2011).

3. Results

Geographic range size, habitat specialization, body size, and annual precipitation were the strongest predictors of extinction risk in New Zealand lizards (Tables 1 and 2). Collectively, these four

variables explained ~65% of the variation in extinction risk. Extinction risk increased with decreasing geographic range size (Fig. 1a) and increasing habitat specialization (Fig. 1b), body size (Fig. 1c), and annual rainfall (Fig. 1d). We also found moderately strong evidence that diurnal species that were exposed to high human population densities were more prone to extinction. Finally, exotic mammalian predators and habitat affinities had relatively weak effects. Lizards that occupied at least one predator-free offshore island and that were terrestrial, or both terrestrial and arboreal, were less likely to be threatened (see Table 2 for relative variable importance weights).

Excluding species that were assigned a conservation ranking on the basis of their geographic range size (i.e., range-restricted species, and species with only one location; $n = 24$ species) changed model rankings and relative importance weights, but did not qualitatively change our conclusions (Tables B1 and B2). The most notable difference when range-restricted species were removed from our analysis was that the effect of annual precipitation was weaker, whereas habitat loss had a much stronger effect. Extinction risk increased with increasing habitat loss, but this relationship was non-linear (Table B2).

We then used our highest ranked model based on all species to predict the extinction risk of eight species of New Zealand lizards that were not assigned a conservation ranking due to insufficient data on threats and population trends. This exercise demonstrated that four of these data-deficient species could be *threatened*, whereas three could be *at risk* (Table 3). Our model also revealed that seven species that are currently listed as *not threatened* could be *at risk*, whereas five species that are *at risk* could be *threatened* (Table 4).

4. Discussion

Anthropogenic activities are the predominant driver of the modern extinction crisis, but not all species respond equally to these threats (Bennett and Owens, 1997; Cardillo et al., 2004). Indeed, our results clearly demonstrate that imperilled New Zealand lizards are a highly non-random subset of the New Zealand fauna with respect to their intrinsic biological traits. In particular, habitat specialists with large body sizes and small geographic ranges are more likely to be at risk of extinction.

Our findings regarding intrinsic biological traits accord with the results of previous studies on a wide array of vertebrate taxa (Duncan et al., 2002; Jones et al., 2003; Fisher and Owens, 2004; Olden et al., 2007; Sodhi et al., 2008; Davidson et al., 2009; Siliceo and Díaz, 2010; Murray et al., 2011). Compared to generalists, specialists should be less capable of dealing with novel environmental challenges (e.g., habitat loss, climate change) because they are often unable to persist outside of their narrow range of preferred habitats (Reed and Shine, 2002; Fisher et al., 2003; Fisher and

Table 1
Top-ranked models of extinction risk among New Zealand lizards.

Model	df	LL	ΔBIC	wBIC	R^2
Range + Rain^2 + Size^2 + Specialization	8	−50.52	0	0.21	0.65
Range + Rain^2 + Size^2	7	−53.18	0.86	0.14	0.61
Humans + Range + Rain^2 + Size^2 + Specialization	9	−49.13	1.68	0.09	0.66
Range + Size^2 + Specialization	6	−55.98	1.98	0.08	0.58
Activity + Range + Rain^2 + Size^2 + Specialization	9	−49.34	2.11	0.07	0.66
Range + Size^2	5	−58.51	2.58	0.06	0.54
Activity + Humans + Range + Rain^2 + Size^2 + Specialization	10	−47.45	2.79	0.05	0.68
Activity + Range + Rain^2 + Size^2	8	−52.47	3.89	0.03	0.62

Shown are the degrees of freedom (df), the log likelihood (LL), the difference in the Bayesian Information Criterion (BIC) between each model and the highest ranked model (ΔBIC), the model weights (wBIC), and Nagelkerke's R^2 for models with ΔBIC $\leqslant$ 4. Superscript numbers refer to quadratic fits. Range = geographic range size (ln-transformed); Rain = annual precipitation; Size = body size; Specialization = habitat specialization; Humans = mean human population density (ln-transformed); Activity: diurnal versus nocturnal activity.

Table 2
Drivers of extinction risk among New Zealand lizards.

Variable	Estimate	SE	Lower CI	Upper CI	Importance
Range	−1.06	0.26	−1.56	−0.55	1.00
Size	12.75	3.26	6.26	19.23	1.00
Size^2	−8.85	2.80	−14.42	−3.28	–
Rain	17.26	8.40	0.56	33.97	0.76
Rain^2	11.92	6.94	−1.90	25.74	–
Specialization	−0.19	0.09	−0.36	−0.02	0.69
Activity: nocturnal	−0.87	0.59	−2.05	0.31	0.26
Humans	0.29	0.21	−0.14	0.71	0.23
Presence on mammal-free island	−0.19	0.57	−1.32	0.94	0.09
Habitat use: terrestrial	−1.55	0.84	−3.23	0.12	0.08
Habitat use: terrestrial–arboreal	−0.69	1.04	−2.76	1.38	–

Shown are model-averaged coefficients and their unconditional standard errors and 95% confidence intervals across the models comprising >95% of wBIC. Also shown is the relative importance weight for each variable. Superscript numbers refer to quadratic fits. Range = geographic range size (ln-transformed); Rain = annual precipitation; Size = body size; Specialization = habitat specialization; Humans = mean human population density (ln-transformed); Activity = diurnal versus nocturnal activity; Habitat use = arboreal, terrestrial, or terrestrial-arboreal; Presence on mammal-free island = at least one population present on a mammal-free offshore island.
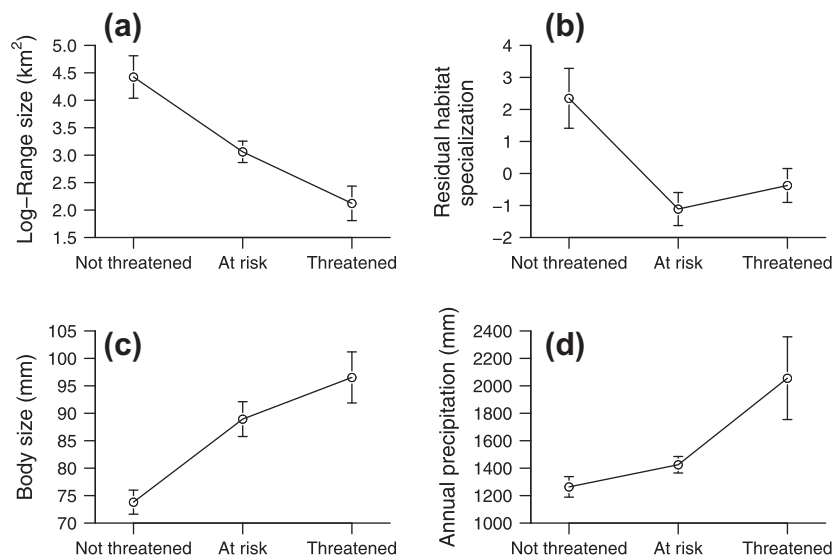
Fig. 1. Relationships between extinction risk and geographic range size (a), habitat specialization (residuals of range size versus number of habitat types used) (b), body size (c), and annual precipitation (d) within each species' range (mean ± SE) for 87 lizard species from New Zealand.

Table 3
Predicted conservation statuses of eight New Zealand lizards that were not evaluated by Hitchmough et al. (2010) due to insufficient data on threats and population trends. Predictions were based on the highest ranked model of extinction risk shown in Table 1.

Taxa	Predicted conservation status
Mokopirirakau aff. granulatus 'Cupola'	Threatened
Mokopirirakau aff. granulatus 'Okarito'	Threatened
Oligosoma aff. inconspicuum 'Okuru'	Threatened
Oligosoma pikitanga	Threatened
Oligosoma toka	At risk
Oligosoma 'Whirinaki'	At risk
Toropuku aff. stephensi 'Coromandel'	At risk
Oligosoma levidensum	Not threatened

Owens, 2004; Murray et al., 2011). Large-bodied species may also be particularly vulnerable to anthropogenic threats, as they typically possess characteristics that make them slow to recover from rapid environmental perturbations (Owens and Bennett, 2000; Reed and Shine, 2002). Fossil and extinct reptile species on islands have larger body sizes than their extant relatives (Case and Bolger, 1991; Case et al., 1992, 1998), and in New Zealand, two reptile species have gone extinct (one gecko and one skink), and both have been the largest representatives of their family on the archipelago

(Bauer and Russell, 1986; Worthy, 1987). Additionally, species with small geographic ranges are typically at greater risk of extinction because they have small population sizes, rendering them particularly susceptible to demographic stochasticity, inbreeding, and localized threats and catastrophes (Allendorf and Luikart, 2007).

New Zealand is home to a wide array of exotic mammals that prey on lizards and previous studies have implicated exotic mammals in lizard declines (Whitaker, 1973; Towns and Daugherty, 1994; Hitchmough et al., 2010). Our finding that large lizards were more vulnerable to extinction may therefore reflect the inability of large-bodied species to overcome high rates of predation by exotic mammals (e.g., Polynesian rats Rattus exulans: Whitaker, 1973). In New Zealand specifically, smaller lizards can escape predation while inactive or torpid by choosing retreat sites that are too narrow for small predators such as mice and weasels to enter. In contrast, larger lizards that overlap in body diameter with the smaller mammalian predators are extremely vulnerable to predation while immobile in retreats. Most of the largest New Zealand lizards now have distributions that have contracted to islands where mammals are absent, having been extirpated over the majority of their former ranges. Our analyses revealed some support for the notion that lizards that occupy at least one predator-free offshore island were less prone to extinction, but counter to previous studies, we did not find that nocturnal and ground-dwelling species that overlap with

Table 4
New Zealand lizards that are predicted to have a higher risk of extinction on the basis of their geographic distributions and intrinsic characteristics. Predictions were based on the highest ranked model of extinction risk shown in Table 1.

Taxa	Observed threat status	Predicted threat status
Mokopirirakau aff. granulatus 'southern North Island'	Not threatened	At risk
Oligosoma aff. polychroma Clade 2	Not threatened	At risk
Oligosoma aff. polychroma Clade 4	Not threatened	At risk
Oligosoma notosaurus	Not threatened	At risk
Oligosoma repens	Not threatened	At risk
Woodworthia aff. maculata 'Central Otago'	Not threatened	At risk
Woodworthia aff. maculata 'Cromwell'	Not threatened	At risk
Dactylocnemis aff. pacificus 'Three Kings'	At risk	Threatened
Oligosoma acrinasum	At risk	Threatened
Oligosoma fallai	At risk	Threatened
Oligosoma macgregori	At risk	Threatened
Oligosoma oliveri	At risk	Threatened
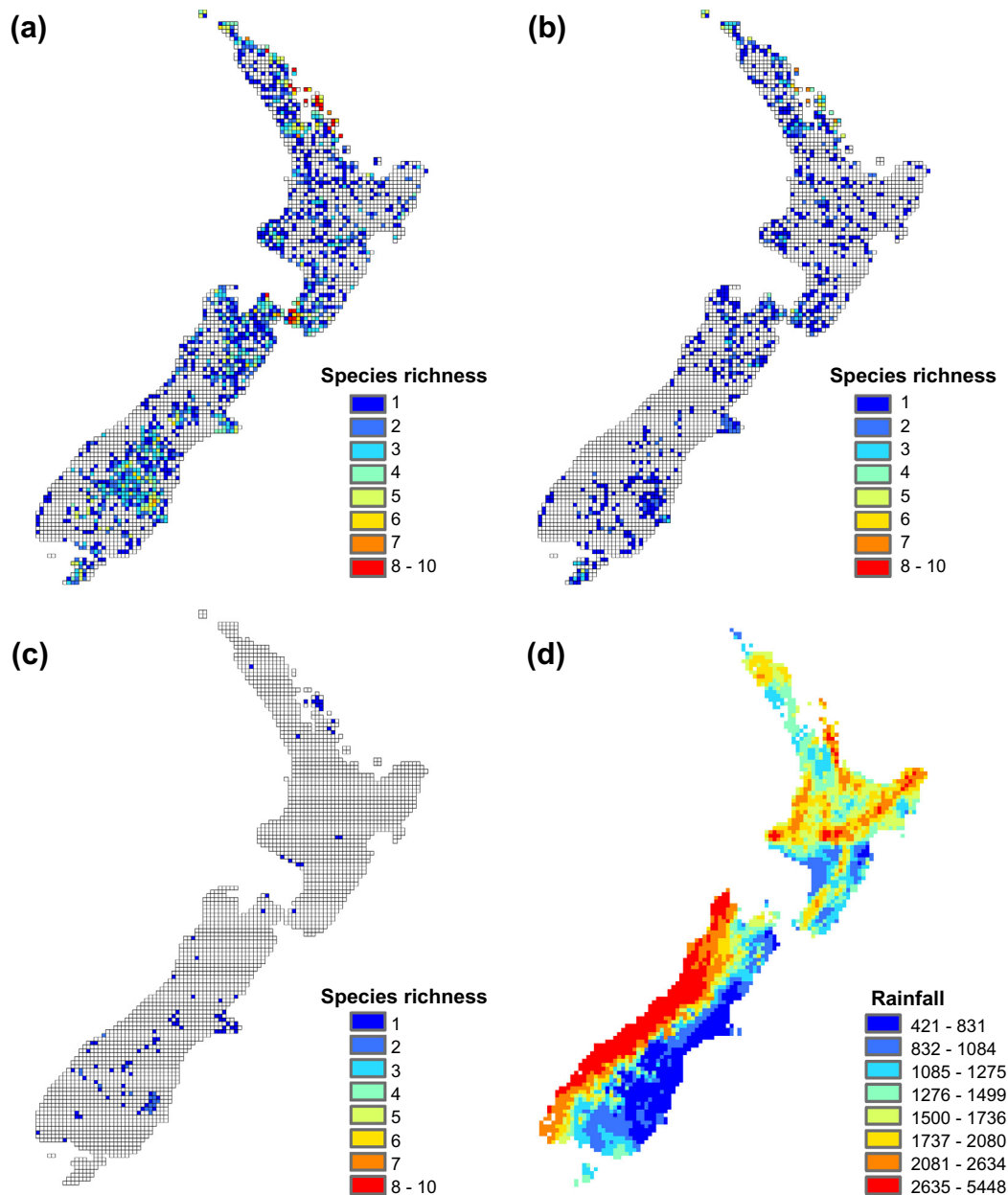
Fig. 2. Geographic distribution of New Zealand lizard richness and mean annual precipitation (10 km resolution). (a) Total number of lizard species. (b) Number of *at risk* lizard species. (c) Number of *threatened* lizard species. (d) Mean annual precipitation (1950–2000).

the small mammal niche were currently disproportionately at risk (Towns and Daugherty, 1994; Hitchmough et al., 2010). In fact, after controlling for additional confounding traits, we found that diurnal and arboreal species were more prone to extinction. Future studies should seek to clarify the mechanism responsible for the relationship between body size and extinction risk by investigating more causal intrinsic variables (e.g., abundance, population size and growth rate) and more direct measures of threats imposed by exotic species (e.g., range overlap or predator abundance) (Fisher et al., 2003; Murray et al., 2011).

The fact that habitat specialization, body size, and geographic range size were such strong predictors of extinction risk suggests that species' intrinsic traits mediate the impacts of extrinsic threats imposed by human activities. However, variables describing direct human impacts (e.g., habitat loss, human population density) were of secondary importance compared to intrinsic biological traits in our analyses. One plausible explanation for this finding is that populations of threatened species may have already been extirpated from the most disturbed habitats (Cardillo et al., 2004). For example, several species of New Zealand lizards in the *at risk* category have very small but stable ranges confined to predator-free offshore islands following extinction over the majority of their pre-human ranges (Worthy and Holdaway, 2002). Unfortunately, we lack detailed data on the distributions of New Zealand lizards prior to European settlement, and thus we were not able to disentangle the effects of current and historic threats. Conversely, temporal lags between disturbance and ensuing population declines may obscure the relationship between measures of human impact and extinction risk (Davies et al., 2006).

We also found strong evidence that species that experienced high levels of annual precipitation across their ranges were more vulnerable to extinction. Importantly, this finding is not simply a result of geographic biases in the origins of *at risk* and *threatened* species (Fig. 2), or due to the fact that many species with restricted ranges occur on the wet west coast (correlation between geographic range size and precipitation = −0.18). Instead, contemporary precipitation patterns may serve as a proxy for historical land-use change. Lowland habitat modification in wetter regions has been both more recent and more uniformly severe than in the drier rain-shadow regions east of the main mountain ranges. Alternatively, the observed relationship between rainfall and extinction risk may be due to different predator dynamics in wet and dry forests. Podocarp-broadleaf forests, which typically dominate wetter regions of the country, support consistently high predator numbers, whereas mast seeding in dry beech forests creates more intermittent predation pressure. These differences in predation pressure have resulted in more severe declines in a number of New Zealand bird species in podocarp-broadleaf forests (Gaze, 1985; Elliott, 1996; Kearvell et al., 2002). We suggest a similar difference in predator impacts may be a driver of extinction vulnerability in the lizard fauna. Regardless of the precise mechanism underlying the relationship between rainfall and extinction risk in New Zealand lizards, this finding demonstrates the need to consider environmental characteristics in order to identify spatial biases in the probability of extinction.

Our results not only reveal novel insights into the factors that lead to a high risk of extinction in New Zealand lizards, but also provide a cost-effective framework for making quantitative predictions regarding the likelihood of future population declines. For example, our model predicted that nearly all of the species that were ranked as data-deficient (Hitchmough et al., 2010) are either *at risk* or *threatened*, suggesting that these species require urgent conservation assessment. Additionally, our model identified 12 species that could be at greater risk than their current statuses suggest. These species may be prone to extinction, but understudied or not declining rapidly enough to capture the attention of researchers (Reed

and Shine, 2002). Thus, our analysis can help focus future research and conservation efforts by prioritizing species that deviate from model expectations.

4.1. Conclusions

Our finding that habitat specialization, body size, and geographic range size were the most important biological correlates of extinction risk in New Zealand lizards accords with the results of previous studies conducted on a wide range of vertebrate taxa (Duncan et al., 2002; Fisher and Owens, 2004; Olden et al., 2007; Davidson et al., 2009; Murray et al., 2011), suggesting that the intrinsic traits that render species vulnerable to extinction are largely consistent across different taxonomic groups. These traits may therefore serve as useful proxies for extinction risk in the absence of species-specific data on population trends. However, our analyses also revealed that species that occupied areas with high levels of annual rainfall and were exposed to exotic predators and high human population densities were at greater risk of extinction. Thus, future studies of extinction risk will need to simultaneously consider both intrinsic traits and extrinsic threats in order to accurately predict (and thus prevent) future population declines. Integrated approaches that account for both types of threats will become increasingly important as novel selection pressures imposed by habitat loss, climate change, and species introductions further create spatial heterogeneity in extinction risk.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.05.028.

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