

# Does range-restricted evolutionary history predict extinction risk? A case study in lizards

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## ABSTRACT

**Aim** Conservation is often prioritized by identifying regional clusters of threatened or endemic species. Another approach is to assess the evolutionary distinctiveness of groups of taxa using phylodiversity measures. However, quantification of evolutionary history has traditionally not accounted for its uneven geographical distribution due to the variation in species ranges. We assess the efficacy of phylogenetic endemism (PE) to predict high extinction risk in comparison to estimates of species range restriction (weighted endemism, WE) and phylogenetic diversity (PD). PE measures the relative range restriction of evolutionary history (lineages), while WE concentrates on the tips of the tree of life, treating all such branches as being of equal length.

**Location/Methods** Using New Zealand's endemic skinks and geckos, we mapped the geographical variation in their extinction risk, PE, WE and PD and measured the extent to which extinction risk exhibited phylogenetic clustering for each group. Correlations between geographical concentrations of high skink and gecko extinction risk with PE, WE and PD were calculated.

**Results** PE was predictive of spatial clusters of high extinction risk for geckos ( $r^2 = 0.34$ ,  $P < 0.001$ ) while WE was markedly less so ( $r^2 = 0.19$ ,  $P < 0.001$ ). The reverse applied to skinks, with WE most predictive of high risk ( $r^2 = 0.26$ ,  $P < 0.001$ ). The phylogenetic signal of extinction risk was significantly conserved for geckos, but was weaker and non-significant for skinks. PE and WE were not predictive of low risk. PD was not predictive of risk.

**Main conclusions** PE and related measures may be predictive of extinction risk when risk is phylogenetically conserved. Mapping the geographical variation in PE could be a useful first assessment of extinction risk for many groups because phylogenies are increasingly available, while full risk status categories are not. These findings might apply to other groups and locations and warrant further investigation.

## Keywords

conservation, extinction risk, geckos, macroecology, New Zealand, phylogenetic endemism, skinks, spatial analysis, species range restriction, tree of life

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## INTRODUCTION

The unprecedented scale and rate of decline in Earth's biological diversity means that scarce conservation resources must be prioritized between multiple species and locations. Individual species, or the regions in which they occur, may be prioritized for conservation according to their risk of extinction—where risk is typically estimated using

demographic criteria such as population size, rate of decline and range restriction (e.g. IUCN, 2012). Another common approach is to prioritize conservation of endemic species, and geographical clusters of such species (Myers *et al.*, 2000; Mittermeier *et al.*, 2004), because a species' geographical range restriction is linked to elevated extinction risk (Lawton, 1993; Gaston & Fuller, 2009; Koester *et al.*, 2013). Prioritizing the conservation of taxa according to their

evolutionary distinctiveness is a third approach (Vane-Wright *et al.*, 1991). The evolutionary history embodied by a set of taxa may be a proxy for feature diversity (Forest *et al.*, 2007) and ecosystem function (Cadotte *et al.*, 2008). Thus, by focusing conservation effort on the branches of the tree of life rather than the tips (i.e. species), we might conserve a diverse set of taxa which collectively maximize the range of features which may provide the capacity to adapt to environmental change.

Phylogenetic diversity (PD, (Faith, 1992)) and related metrics (e.g. evolutionary distinctiveness, (ED, (Cadotte & Davies, 2010)) estimate the amount of unique evolutionary history embodied by a set of taxa by summing the branch lengths that connect a given subset of terminal taxa and the most recent common ancestor (i.e. the root) on a phylogenetic tree. Phylogenetic endemism (PE) is a range-weighted variation of PD in which the branch lengths are weighted according to their degree of geographical range restriction (Rosauer *et al.*, 2009), and can be used to identify locations across a landscape where species are both phylogenetically and spatially restricted. PD is the phylogenetic analogue of taxon richness, and similarly PE is the phylogenetic analogue of weighted endemism (WE) (Crisp *et al.*, 2001). Assuming that extinction risk is phylogenetically conserved for a particular species group, PE could be more predictive of extinction risk than using a measure that focuses on species geographical range restriction only, such as WE. Conversely, in cases where extinction risk has a weak phylogenetic signal, species-level geographical range restriction may be a more suitable predictor of extinction risk.

The nature of the relationship between range-restricted evolutionary history and extinction risk has not been previously investigated. Gudde *et al.* (2013) scaled phylogenetic tree branch lengths according to the extinction probability of portions of the tree and mapped the geographical variation in this composite metric. Other approaches such as EDGE (i.e. Evolutionarily Distinct and Globally Endangered) incorporate a species' threat status with the amount of unique evolutionary history it represents to create a composite index for setting conservation priorities (Isaac *et al.*, 2007). The EDGE index is a variant of the ED index. ED is calculated on a per-terminal branch (per-lineage) basis, but the sum of ED scores in a cell can be used as a measure of its uniqueness. However, ED approaches weight branches by the number of terminal branches that subtend them, meaning that they are sensitive to revisions that increase and decrease the numbers of terminal taxa. Furthermore, EDGE requires threat status estimates. These are often unavailable for many taxa, whereas the range estimates needed for PE are.

The abundance-weighted evolutionary distinctiveness (AED) index (Cadotte & Davies, 2010) is an extension of ED in which branches are weighted such that those with high abundances are down-weighted relative to rare ones. The AED<sub>t</sub> index is the sum of AED scores in a sample across all samples (e.g. cells), in essence weighting each branch in a sample by the fraction of its total abundance found across

the data set. AED<sub>t</sub> is therefore similar in principal to PE, except that PE is an endemism measure that uses range extents while AED<sub>t</sub> is a rarity measure based on abundances. Both PE and AED<sub>t</sub> are relatively robust to taxonomic lumping and splitting effects because the ranges and abundances of ancestral branches are a function of those corresponding to their terminals, and not a direct function of the number of terminals. However, while an abundance-weighted measure would often be highly relevant to conservation, good quality, direct estimates of abundance over regional (and broader) extents are uncommon.

We used an endemic radiation of New Zealand lizards (skinks and geckos) as a case study, and mapped locations in New Zealand where the proportion of threatened lizard species was higher than expected by chance. We determined whether these geographical clusters of high lizard extinction risk were better characterized by their respective PE scores, or by a measure quantifying species geographical range restriction only (WE). Although we focused principally on PE and WE, we also compared PD as a predictor of extinction risk. We achieved these aims by mapping the spatial clusters of high and low extinction risk for skinks and geckos and also mapping the geographical variation in their PE, WE and PD. We estimated the degree of taxonomic clustering of extinction risk in the gecko and skink phylogenies. Finally, we analysed the relationships between clusters of high and low extinction risk for skinks and geckos with respect to their individual PE, WE and PD scores.

## MATERIALS AND METHODS

### Study organisms

Skink (Scincidae) and gecko (Diplodactylidae) point locality data were derived from the New Zealand Department of Conservation Herpetofauna Database (Department of Conservation, 2012). This is New Zealand's official wildlife atlas for reptiles and amphibians (see <http://www.doc.govt.nz/our-work/reptiles-and-frogs-distribution/atlas/>). This is the data set from which all distribution maps of New Zealand lizard species are generated. Thus, the records provide comprehensive coverage of the known distribution of New Zealand lizard species. These data were updated by DGC to reflect the current taxonomy (Chapple *et al.*, 2009; Hay *et al.*, 2010; Nielsen *et al.*, 2011; Hitchmough *et al.*, 2013; Tingley *et al.*, 2013; Di Virgilio *et al.*, 2014). Records with multiple observations of the same species at the same location and date were treated as single observations. Spurious records were removed and each species record was checked to confirm that it matched currently recognized species distributions. The revised database contained 6397 skink observations across 54 species (genus *Oligosoma*), and 3959 gecko observations across 43 species and formally recognized operational taxonomic units (OTUs) (seven genera: *Dactylocnemis*, *Hoplodactylus*, *Mokopirirakau*, *Naultinus*, *Toropuku*, *Tukutuku* and *Woodworthia*). These monophyletic groups have

independent evolutionary and temporal origins in New Zealand, with close ties to Australia (geckos) and New Caledonia (skinks) (Chapple *et al.*, 2009; Nielsen *et al.*, 2011). Many of these species are cryptic and range restricted. In addition, the New Zealand herpetofauna database provides comprehensive distributional data for all species. Species with few records are generally those with very limited distributions (i.e. restricted to a particular mountain top or island), rather than being indicative of a limited knowledge of the distributions of a species.

For both New Zealand skinks and geckos, the current taxonomy was derived from molecular and morphological studies (reviewed in Chapple & Patterson, 2007; Chapple *et al.*, 2008a,b, 2009, 2011; Patterson *et al.*, 2013; Chapple & Ritchie, 2013; Hitchmough *et al.*, 2013). For the geckos, many long-recognized and widely accepted species-level forms exist but currently await formal description (Nielsen *et al.*, 2011; Hitchmough *et al.*, unpub. data). For our purposes – and for simplicity – we here refer to them as ‘species’. The original phylogenetic studies on skinks (Chapple *et al.*, 2009) and geckos (Nielsen *et al.*, 2011) utilized both mitochondrial and nuclear DNA data. Not unexpectedly, the mtDNA data were more influential in reconstructing the species-level relationships (i.e. distal nodes), yet the authors observed no well-supported, mito-nuclear gene tree discordance. Because of this, we re-analysed only mtDNA phylogenetic data for geckos (~2000 bp of ND2, 16S rRNA; Nielsen *et al.*, 2011) and skinks (ND2; Greaves *et al.* (2007); Hare *et al.* (2008); Liggins *et al.* (2008); Chapple *et al.* (2009); Patterson & Bell (2009); Chapple *et al.* (2011)). The mtDNA data sets were also more taxonomically complete (39 of 42 extant gecko species, 52 of 54 extant gecko species; see Appendix S1 in Supporting Information) than the nuclear counterparts, allowing us to sample each species for both squamate groups. Phylogenetic trees were then generated for each data set as outlined in Chapple *et al.* (2009). In brief, we used MODELTEST (Posada & Crandall, 1998) to determine the most appropriate model of sequence evolution for our data set (which was GTR+I+G). MRBAYES 3.1.2 (Ronquist & Huelsenbeck, 2003) was used to complete Bayesian phylogenetic analyses. We ran the Bayesian analysis for five million generations, sampling every 100 generations (i.e. 50,000 sampled trees). We ran the analysis twice, using four heated chains per run. We discarded the first 25% of samples as burn-in and the remaining 37,500 trees were used to estimate posterior probabilities. The program TRACER 1.5 (Rambaut & Drummond, 2010) was used to check for chain convergence and mixing.

### Extinction risk categories

We used the conservation status categories assigned to skink and gecko species by Hitchmough *et al.* (2013) based on the New Zealand Threat Classification System (NZTCS) (Townsend *et al.*, 2008). Although IUCN risk categories are universal and updated regularly, only a small subset of New

Zealand lizard species have been assessed (16 of 54 skink species; 9 of 43 gecko species), whereas all species (including undescribed, but validated, ‘species’) were assessed as part of the NZTCS.

The NZTCS estimates the extinction risk of taxa according to one or more of the following criteria (depending upon the threat category): total number of mature individuals; ongoing or predicted population trend; total number of populations; number of mature individuals in the largest population; and area of occupancy of the total population. The numbers of skink and gecko observations (i.e. the number of distributional records) assigned to each threat status category by Hitchmough *et al.* (2013) are shown in Table 1. Reptiles assigned to the ‘Non-resident Native’ and ‘Introduced and Naturalized’ threat categories were excluded. We represented the rank of threat severity using a numeric rating scheme where 10 is the highest conservation risk (Extinct) and 1 is the lowest conservation risk (Not threatened) (Table 1). We assigned a high risk rating to the ‘Data deficient’ threat category because data deficient species are generally high priorities for conservation (Thiel-Egenter *et al.*, 2011), although this category included only six observations (of four species). For comparison, we also used a binary risk-rating scale. Under this rating scheme, skinks and geckos designated in categories between ‘extinct’ and ‘at risk – declining’ (4329 skink and gecko observations) were assigned to the ‘at risk group’. The remaining 6027 observations were allocated to the ‘not at risk’ group.

### Estimating geographical variation of extinction risk, PE, WE and PD

Uneven sampling effort is common in macroecological ‘atlas’ data. The effects of the unevenness of sampling effort were reduced by aggregating the skink and gecko point occurrences to separate grids (4.5 × 4.5 km cells) so that each

**Table 1** The number of New Zealand skink and gecko observations (i.e. the number of distributional records) assigned to each conservation threat status by Hitchmough *et al.*, (2013).

Threat classification	Threat rating	Skink observations	Gecko observations
Extinct	10	2	1
Data deficient	9	2	4
Threatened – nationally critical	8	17	0
Threatened – nationally endangered	7	314	16
Threatened – Nationally vulnerable	6	443	178
At risk – declining	5	1661	1691
At risk – recovering	4	92	22
At risk – relict	3	629	431
At risk – naturally uncommon	2	80	97
Not threatened	1	3157	1519
		<i>n</i> = 6397	<i>n</i> = 3959

species contributed only once to each cell, irrespective of the number of collection records. Aggregating the data to coarser cell sizes up to 10 km produced similar patterns of results, with consistent locations of high and low PE zones. Also, when data are aggregated to larger grid cells, the strength of correlations can sometimes artificially increase as data variability decreases (see O'Sullivan & Unwin, 2003, chapter 2). To gauge collection bias due to road surveys, we conducted the spatial analyses using all reptile occurrences and also a subset consisting of occurrences greater than 1 km from any surfaced or unsurfaced road. Around half of all records (49.8% of gecko and 55% of skink records) are > 1 km from any surfaced or unsurfaced road.

We separately estimated the variation in skink and gecko extinction risk, PE, WE and PD across New Zealand using moving neighbourhood analyses implemented using the BIO-DIVERSE software (version 0.19) (Laffan *et al.*, 2010). The moving neighbourhood was iterated over each cell location in turn throughout the study area. An extinction risk, PE, WE and PD score was calculated for each cell location based on the set of values within a circular neighbourhood of 18 km radius around it. Although not the main focus of this work, for completeness, we also applied AED<sub>t</sub> to the skink and gecko data using the same moving window specification.

To identify spatial clusters of high and low extinction risk, the Getis-Ord  $G_i^*$  statistic was used (Ord & Getis, 1995) (equation 1).  $G_i^*$  is a hotspot statistic that quantifies the degree of spatial clustering in a local sample of a particular variable, and the extent to which these values differ from the expected value if there were no clustering. For each target cell,  $G_i^*$  was calculated as the difference between the local sum of the threat ratings within the neighbouring cells that surround that cell, and the weighted mean global threat rating (of the whole data set), divided by its weighted standard deviation:

$$G_i^*(d) = \frac{\sum_j w_{ij}(d)x_j - W_i^* \bar{x}}{s^* \sqrt{\frac{(nS_{1i}^* - W_i^{*2})}{n-1}}} \quad (1)$$

where  $d$  is the window size;  $w_{ij}$  is the weight of cell  $j$  in the window around cell  $i$  (here  $w_{ij} = 1$  if a cell is within the window, 0 otherwise);  $n$  is the number of samples in the data set;  $W_i^*$  is the sum of the weights for the window around cell  $i$ ;  $S_{1i}^*$  is the sum of the squared weights for the window around cell  $i$ ;  $x_j$  is the threat status value at location  $j$ ;  $\bar{x}$  is the mean threat across all locations within the data set;  $s^*$  is the standard deviation across the full data set. The resulting value for each cell is a  $z$ -score, which is positive when the mean of the local sample of threat ratings is greater than the data set mean, and negative when less than the mean. The mean is the expected value if there is no spatial clustering. Cells with a significantly high  $z$ -score ( $z > 1.96$ ,  $P < 0.05$ ) suggest the presence of a cluster of high extinction risk. A  $z$ -score  $< -1.96$  is significantly lower than expected under a random spatial process and denotes an area of low extinction risk, perhaps where a low number of isolated samples of high risk are located near many samples of low risk.

PD (Faith, 1992) was measured as the set of branches in the minimum spanning path joining the species in the moving neighbourhood to the root of the tree. Evolutionary distinctiveness is an alternative measure of evolutionary history (Cadotte & Davies, 2010), but it is a per-taxon metric, whereas the focus here was on a lineage-based analysis. It is also abundance weighted, and our sampling does not adequately capture lizard abundances.

PE (Rosauer *et al.*, 2009) was calculated by multiplying each branch length by the fraction of its range that is found within the moving neighbourhood. Species-level geographical range restriction was measured using WE (Crisp *et al.*, 2001) which counts the number of species present in each grid cell, weighting each by the fraction of their geographical range found within the moving neighbourhood.

### Statistical analyses

For each reptile group, we calibrated separate, bivariate, generalized linear models (Nelder & Wedderburn, 1972) between the un-transformed high and low extinction risk surfaces, and square-root transformed PE, WE and PD surfaces. We assumed a Gaussian error distribution and used an identity link function.

As is often the case with spatial data, these data are spatially auto correlated. Therefore, we compared the results generated by the GLM analyses with results from a spatial statistical method. We used the *spdep* package (Bivand & Piras, 2015) for R statistical software (R Development Core Team, 2015) to conduct spatial autoregression (SAR) analyses using the high extinction threat areas identified for skinks and geckos and their respective standardized PD, PE, and WE surfaces. Creation of spatial weights is requisite for running the SAR. We defined a spatial weights matrix calibrated to find neighbours within a maximum inter-point distance of 18 km (matching the radius of the moving window used in the spatial analyses reported in the main text). For comparison, we also doubled this distance.

We investigated the extent to which the binary trait of extinction risk was phylogenetically conserved on the gecko and skink phylogenetic trees using the  $D$  statistic (Fritz & Purvis, 2010). This measures the strength of the phylogenetic signal of a binary trait, that is, the extent to which a trait such as extinction risk exhibits phylogenetic clustering. If  $D < 0$ , then the trait is highly conserved, whereas if  $D > 1$  it is over-dispersed. The significance of estimated  $D$  was tested by running 1000 simulations under two models: (1) phylogenetic randomness versus (2) phylogenetically conserved under a Brownian process.

## RESULTS

### Mapped variation of extinction risk, PE, WE, PD

The variation in skink and gecko extinction risk across New Zealand was evident in discrete clusters of high and low

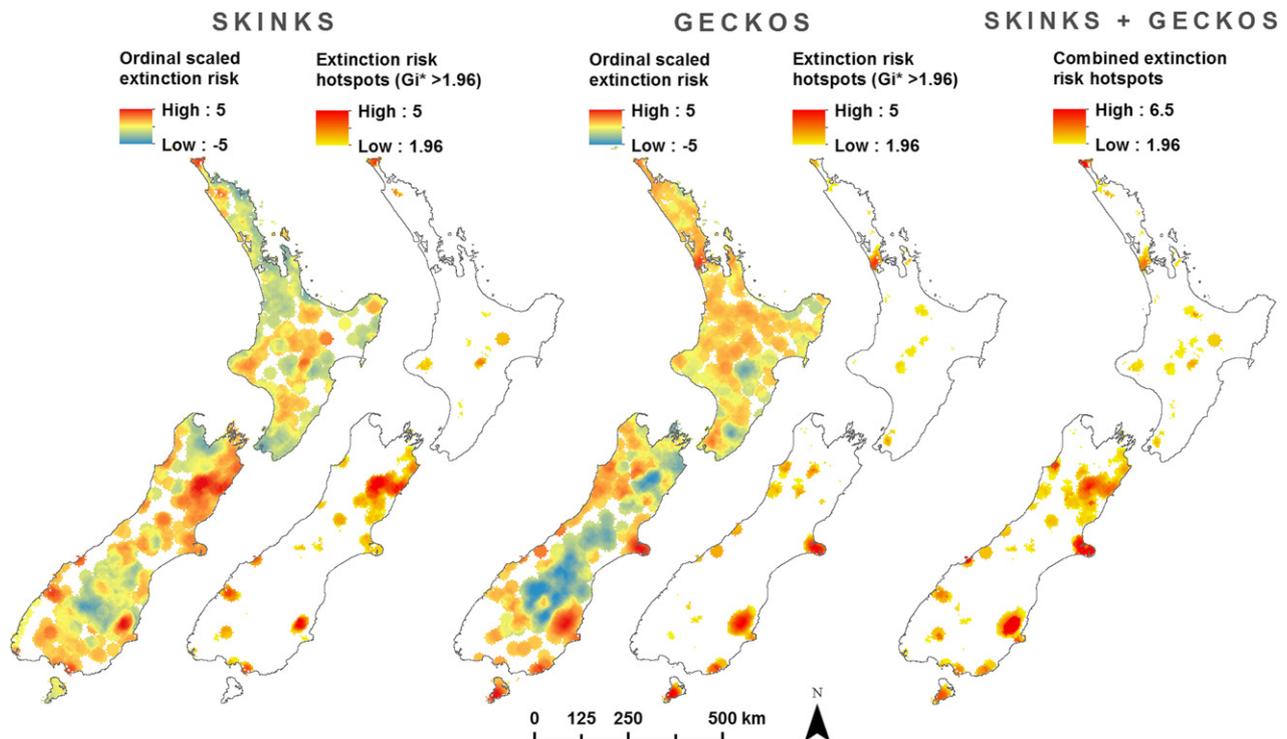
extinction risk across the country (Fig. 1), with each group generally showing differing spatial patterns of risk. For instance, there was intense clustering of high risk in Stewart Island (southern coast of the South Island) for geckos, but not for skinks. In contrast, parts of the north-eastern South Island showed clustering of extinction risk only for skinks. All of these areas are inhabited by both skinks and geckos. The spatial distribution and intensity of high and low extinction risk clusters for both groups was almost identical when the analyses were repeated using the binary risk-rating scheme (see Fig. S1, Appendix S2).

There was marked geographical variation in PE, WE and PD for both reptile groups (Fig. 2). Concentrations of high skink PE were geographically restricted. By comparison, gecko PE appeared comparatively lower with fewer PE hotspots, except for the small hotspot in northern Northland (the northernmost region of the North Island). There were areas of higher skink PD in the southern South Island, whereas gecko PD tended to be higher in parts of the northern South Island and across much of the North Island. In comparison to skinks, there are more areas of high PE for geckos in the northern region of the South Island and the southern region of the North Island. For skinks, PE and WE patterns appear quite different across New Zealand, whereas these patterns are more similar for geckos in the northern island and on Stewart Island. Patterns of PD and PE did not resemble one another for either group.

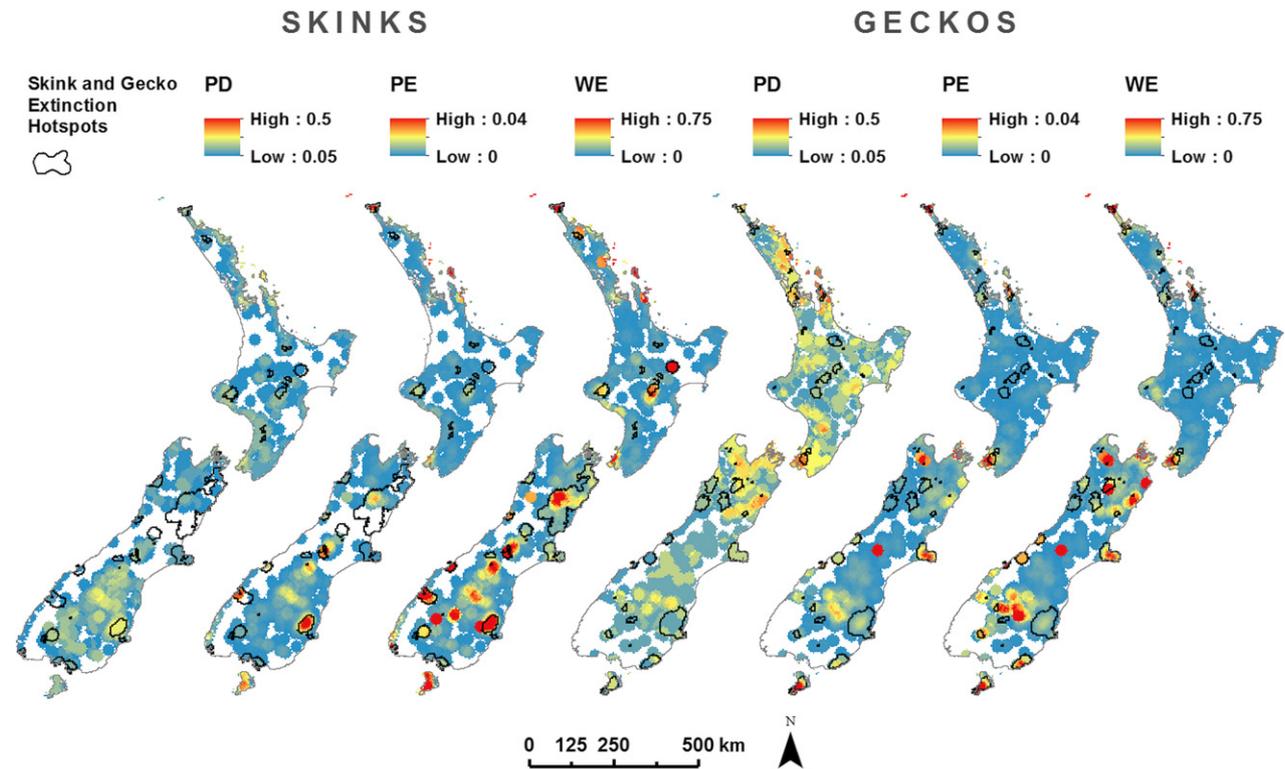
In some locations the intensity of PD, PE or WE appeared uniform and circular (i.e. matching the shape of the moving neighbourhood). In these instances there were relatively few or sparsely scattered observations, only a minority of which were strongly influencing the pattern in question. The analyses using the subset of sample data > 1 km from any road produced similar extinction risk, PE and WE results, see example for geckos (Fig. S2, Appendix S2). The intensity and spatial variation of AED<sub>t</sub> scores for skinks and geckos are very similar to their respective PE scores (Fig. S3, Appendix S2).

### Relationships of extinction risk with PE, WE and PD

The relationships of high and low extinction risk with PE, WE and PD differ considerably. In terms of high extinction risk clusters, PE was strongly predictive for geckos, while WE was markedly less so (PE explained 34% of the variation in high extinction risk areas, WE explained 16%; both  $P < 0.001$ ) (Table 2). The reverse situation applied to skinks: WE was most predictive of high extinction risk clusters ( $r^2 = 0.26$ ,  $P < 0.001$ ), contrasting with  $r^2 = 0.19$ ,  $P < 0.001$  for PE (Table 2). All of these relationships were positive. When the binary threat ratings were applied, these general relationships remain the same (Table S1, Appendix S3). None of the correlates was predictive of low extinction risk clusters (aside from WE for skinks; variation explained 12%)



**Figure 1** The distribution of  $G_i^*$  z-scores representing the variation in extinction risk for skinks and geckos across New Zealand. Z-scores > 1.96 are statistically significant, high values of elevated extinction risk. The rightmost panel shows a composite extinction threat map for both skinks and geckos (created by summing the individual high-risk maps for each group).



**Figure 2** The variation in skink and gecko weighted endemism (WE) phylogenetic diversity (PD) and phylogenetic endemism (PE) across New Zealand, overlaid with the outline of their respective extinction risk hotspots. To aid comparison, maximum and minimum PD, PE and WE values are standardized for both lizard groups.

and the regression coefficients were both negative and smaller in magnitude (Table 2). PD has a negligible, non-significant influence on high and low extinction threat for both lizard groups (e.g. gecko PD-high-threat  $r^2 = 0.003$ ).

The SAR analysis results largely confirm the GLM results (Table S2, Appendix S4). For PE versus high extinction risk, the slope of the regression parameter is steeper for geckos than for skinks, whereas for WE-high-risk associations, the reverse applies. Comparing the AIC scores within each lizard

group, the differences between these are consistent with the above interpretation.

**Phylogenetic signal strength of extinction risk**

There was a significant phylogenetic signal of extinction risk for geckos ( $D$  significantly less than one; Table 3). Moreover,  $D$  was not significantly greater than zero, indicating a phylogenetic signal as strong as if extinction risk depended solely on an underlying continuous Brownian motion model. For skinks, extinction risk showed a weaker, non-significant phylogenetic signal.

**Table 2** Separate phylogenetic and weighted endemism surfaces for New Zealand skinks and geckos were correlated with corresponding areas of high extinction risk or low extinction risk identified for each species group. Values with asterisks are statistically significant ( $P < 0.001$ ).

Risk	Skinks		Geckos	
	$r^2$	$\beta_1$	$r^2$	$\beta_1$
<b>High-risk areas</b>				
Phylogenetic diversity	0.00	0.46	0.00	-0.57
Phylogenetic endemism	0.19*	7.47*	0.34*	9.81*
Weighted endemism	0.26*	1.52*	0.16*	1.26*
<b>Low risk areas</b>				
Phylogenetic diversity	0.04*	-1.42*	0.00	-0.09
Phylogenetic endemism	0.09*	-5.84*	0.08*	-6.17*
Weighted endemism	0.12*	-1.00*	0.04*	-0.64*

**DISCUSSION**

Using a spatially explicit analysis approach, we identified geographical concentrations of high species extinction risk which are potential areas of conservation concern. We then assessed

**Table 3** The phylogenetic signal for the binary trait of extinction risk (threatened or not threatened) for New Zealand geckos and skinks.

Phylogeny	$D$	$P (D > 0)$	$P (D < 1)$
Geckos	-0.48	n.s.	< 0.001
Skinks	-0.21	n.s.	n.s.

how well range-restricted evolutionary history (PE) predicted the elevated risk at these locations compared to a measure of relative species geographical range restriction (WE) and phylogenetic diversity (PD). This was illustrated using New Zealand skinks and geckos as example species groups.

The predictive capacity of PE for at-risk geckos was more than twice that of WE, but the reverse applied to skinks. These differences in the predictive capacities of PE and WE were reflected by the strength and significance of the phylogenetic signals of extinction risk (i.e. a strong, significant signal of risk for geckos, but not for skinks). While extinction risk is not an evolved trait, there are evolved attributes that are related to risk and thus related taxa may share similar vulnerabilities, that is, the loss of species to extinction may not be evenly distributed across a phylogeny (Fisher & Owens, 2004). Older lineages may be at greater risk (Gaston & Blackburn, 1997), as well as species-poor genera (Hughes, 1999; von Euler, 2001), those with higher genetic specialization (May, 1990), and species with small geographical range sizes and adapted to resource-limited environments (Leao *et al.*, 2014).

The differences observed between endemic geckos and skinks are mirrored in other aspects of their biology and evolution. New Zealand's geckos diverged from their Australian relatives > 40 million years ago (Ma) although most of the currently recognized species diversified in the early Miocene (Nielsen *et al.*, 2011; Skipwith *et al.*, 2016). Members of the different genera are easily distinguishable using morphology; however, many species-rich genera (e.g. *Woodworthia*) are comprised of numerous cryptic (i.e. morphologically similar) forms currently awaiting description. In contrast, skinks are more recent additions to the New Zealand fauna (16–23 Ma) and are contained within one species-rich genus that diversified in the late Miocene (Chapple *et al.*, 2009). Yet, like *Woodworthia* geckos, they are often hard to delimit morphologically and many cryptic taxa await description (Chapple & Ritchie, 2013).

Although more recent geological events (e.g. Pleistocene glacial cycles) have helped shape the current distributions of both radiations, the fact that these two groups differ is important to consider (Nielsen *et al.*, 2011). There are some general trait differences between New Zealand geckos and skinks which may provide insight into the phylogenetic signal of extinction risk for geckos but not skinks. For example, most New Zealand skinks are diurnal, terrestrial or saxicoline, active predators. While not all geckos neatly fit into Pianka's (1966) 'active forager versus sit-and-wait dichotomy' (e.g. *Mokopirirakau* 'Southern North Island' – Romijn *et al.* (2014)), the predominantly nocturnal foraging mode of geckos is generally much less active than that of skinks. New Zealand geckos are ecologically diverse, utilizing saxicoline (*Woodworthia*), terrestrial (*Dactylocnemis*), and arboreal (*Mokopirirakau*/*Naultinus*) habitats. One hypothesis warranting further study is that the lower activity rate of geckos may render them more vulnerable than skinks to predation by introduced, foraging mammals such as rats (*Rattus rattus*)

and stoats (*Mustela ermina*), which are adept climbers and present throughout New Zealand's two main islands.

Despite the strong phylogenetic signal of extinction risk on the gecko phylogeny, PD was not predictive of extinction risk because it does not identify locations where large amounts of evolutionary diversity are geographically restricted. This might suggest that estimates of evolutionary history can only predict extinction risk if they account for the uneven geographical distribution of evolutionary history due to the variation in species ranges. Restricted species ranges are also linked with narrower niche widths and lower tolerance and adaptability to environmental change (Brown, 1995; Thuiller *et al.*, 2005). It is also possible that species with fewer close relatives, that is, with higher genetic distinctness, are also more range restricted (Mooers & Redding, 2009), and therefore potentially at greater risk.

Clusters of high extinction risk, PE and WE were distributed across New Zealand and not only around main population centres. Repeating the analyses using a subset of the data (i.e. records > 1 km from roads – see Fig. S2, Appendix S2) showed the same general pattern of results. As with any macroecological data set covering a broad geographical area, our data have limitations such as an incomplete collection effort and by being presence-only data. Nonetheless, we used the best available data and its quality is consistent with other similar studies.

To some degree, PE and extinction risk ratings are related, (e.g. extinction risk assessments are influenced by geographical range sizes). However, PE uses the range of all terminal branches descending from each branch, so the correlation between PE and extinction risk will be a function of the range overlap among the high extinction risk terminal branches. Furthermore, related, at-risk species may share similar traits that make them more (or less) susceptible to a given threat (Tingley *et al.*, 2013). Thus, by using branches and lineages, not only the tips, such measures provide important additional information about biodiversity that may improve conservation outcomes (Laity *et al.*, 2015). This links to the wider debate in conservation science about conserving groups or lineages of organisms, as well as individual species (e.g. Vane-Wright *et al.*, 1991; Rissler *et al.*, 2006). That is, by focusing conservation effort on the branches of the tree of life rather than just the tips, we might conserve a diverse assemblage which collectively maximizes the range of features and attributes that facilitate adaptation to environmental change.

High extinction risk is concentrated in specific geographical locations in different parts of the study area. This suggests that, within these locations, lizard-specific vulnerability to extinction risk could also be a consequence of factors such as habitat alteration and climatic change. These locations may warrant consideration in conservation planning. Due to the faunal links and similarities between New Zealand, New Caledonia and Australia, including high rates of cryptic species discovery (Oliver *et al.*, 2009; Skipwith *et al.*, 2016),

future studies should be performed on those faunas to corroborate our findings.

## CONCLUSION

Phylogenetic endemism was a more effective predictor of extinction risk than species range restriction for geckos, a group which exhibited phylogenetically conserved extinction risk. Conversely, species geographical range restriction was more predictive for skinks, for which extinction risk was not phylogenetically conserved. PE may be predictive of risk in other groups elsewhere in the world if the traits linked to risk have a phylogenetic signal for those groups. PE may be a proxy for risk in such cases, meaning the need to assess risk status categories per se becomes less important for these purposes. While extinction risk can be mapped, it is resource-intensive to develop and maintain risk categories for large numbers of taxa. In contrast, well-sampled – and often time calibrated – species-level phylogenies are becoming increasingly available and can be linked with the also increasingly available geospatial data (e.g. via the Global Biodiversity Information Facility). The analyses used here can be applied to any species group, any location, and across spatial scales. More generally, we suggest that lineages with higher levels of PE may face a greater extinction risk; therefore conservation efforts may be more effective when focused on groups of taxa – the branches of the tree of life.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Conservation status of New Zealand lizards and GenBank numbers.

**Appendix S2** Skink and gecko high-threat areas in New Zealand.

**Appendix S3** Correlates versus high-threat areas using ordinal or binary threat ratings.

**Appendix S4** Bivariate spatial autoregression of correlates with high-threat areas.

## BIOSKETCH

**Giovanni Di Virgilio's** research interests are in GIS, remote sensing and spatial data analysis, with a focus on conservation and biogeography.

The interests of the co-authors are GIS and spatial ecology, invasion biology, phylogenetics, phylogeography and the evolutionary ecology of squamate reptiles.

Author contributions: G.D.V, S.W.L and D.G.C conceived the ideas; D.G.C and S.V.N. collected the data; G.D.V, S.W.L, D.G.C and S.V.N. analysed the data; and G.D.V led the writing.

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