# Patterns of regional endemism among New Zealand invertebrates

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ABSTRACT

Biodiversity is unevenly distributed worldwide in terms of both species diversity and species endemism. Although centres of endemism are a conservation priority, both patterns and drivers of endemism are poorly understood in New Zealand. Here we explore whether invertebrate species distribution records in New Zealand represent the complete geographic range of species. We use distribution records of 2,322 invertebrate species to survey variation in range size and regional-endemism among 28 New Zealand regions, and explore the correlates of diversity and regional-endemism. Our data suggest patterns of regional-endemism in New Zealand invertebrates are not artefacts of sampling e

and low extinction rate for New Zealand. As species can only be viewed as endemic if they occur nowhere else both extinction of source populations and in situ speciation have a role in development of New Zealand's highly endemic biota.

The same factors may influence species diversity at a finer scale and can be revealed by recording regional variation in diversity within a land mass such as New Zealand (e.g. Heenan et al. 2017). Here we consider in particular regional endemism with a species regarded as a regional-endemic if it is restricted to an *a priori* area within the landscape. Thus, the term 'regional-endemism' is scale dependent. Our present focus on New Zealand invertebrates utilises published data where 'regions' are already defined (see methods). The number of species recorded within a region and the number of these species that are restricted to it can be compared to similar sized regions to better understand the distribu4.622ter

(3) Climate and habitat type influence endemism and species diversity in many ways. Slope, for example, may impact speciation rates because topographic heterogeneity results in habitat variation (Veech and Crist 2007) and more complex communities (Wollenberg et al. 2008), that may yield differential selection and high rates of speciation relative to extinction (species pump model, Moritz et al. 2000; Rahbek and Graves 2001). A complex environment with many biotic interactions might result in more species in the same geographic space compared to a simple community with few competitive interactions (species packing; MacArthur 1969). In Africa, endemism is concentrated in mountainous regions with low seasonality (Fjeldså et al. 1997; Jetz et al. 2004).

(4) Climatic/habitat stability is likely to suppress rates of extinction (Wallace 1876; Dowle et al. 2013). In some places the distribution of plants and animals appears to have been influenced by glaciation and aridification during Pleistocene glacial periods. For example, a gradient of European endemism suggests refugia in warmer climes were influential in preserving local diversity (Essl et al. 2013).

## Regional-endemism in New Zealand

Endemism appears to be unevenly graded across the New Zealand landscape (Wardle 1963; Rogers and Walker 2005; Millar et al. 2017) with three approximately coincidental regions of relatively high endemisms among vascular plants and insects (Figure 1; Wardle 1963; Trewick et al. 2011). It is also notable that some taxa have disjunct distributions in regions of high endemism and absence between (Trewick and Wallis 2001; Wallis and Trewick Endeical 1876r-38xima Tfnuneve coverage of New Zealand's natural history collection records might create arti taxon dataset. We investigate potential drivers of New Zealand's invertebrate regional-endemism by seeking correlations with environmental variables to infer the combination of environmental variables most associated with regional-endemism patterns. If the dominant influence on relative levels of regional-endemism in New Zealand is:

(1) the equilibrium between origin (arrival and speciation) and extinction we expect a positive correlation between land area and regional endemicity (measured by both the current and past size of the region).
(2) the ability of species to expand or shift their ranges we expect to see a correlation between land connectivity and regional endemicity.
(3) species-packing and ecological speciation we expect to see a positive correlation between regional diversity of topology and climate and regional endemicity.

Regional bias in extinction rates linked to environmental stability (e.g. climatic change and the extent of glaciers) is likely to be involved in determining relative levels of regional-endemism (4: habitat stability/longevity), but the size and heterogeneity of the 28 recognised regions considered in in our analyses preclude a test for this effect.

## Material and methods

### Invertebrate diversity

Table 1. Invertebrates used to study regional-endemism in New Zealand. FNZ = Fauna of New Zealand series published by Landcare Research (*or other reference).

| Class | Order | FNZ edition (common name) | Number of taxa |
|---|---|---|---|
| Insecta | Coleoptera | 2: Osoriinae (Staphylinidae) (rove beetles) | 37 |
| | | 3: Anthribidae (fungus weevils) | 35 |
| | | 6: Hydraenidae (aquatic ‘minute moss beetles’) | 32 |

evident when site sampling was abundant, we used two densely-sampled datasets for Simuliidae blackflies (Insecta: Diptera; Craig et al. 2012) and Lycosidae wolf spiders (Arachnida: Araneae; Vink 2002).

### Comparison of endemism with geography/environment

excluding low-lying land and marginal-marine deposition (Figure 2B) (Trewick and Bland 2012). As a proxy for the extent of connectivity/isolation of each region we used the number of neighbouring regions currently sharing a boundary. For each region, measures of slope and elevation were included as proxies for habitat heterogeneity. Mean annual temperature and mean annual solar radiation were included because these variables might conceivably influence underlying mutation rates and speciation rate (Dowle et al. 2013). Mean monthly water balance ratio (MMWBR; the average of the monthly ratios of rainfall to potential evaporation) was used as a measure of water availability since aridity may have effects on patterns of regional-endemism, as observed for Madagascan fauna (Wilmé et al. 2006). This information was derived from the Ministry for the Environment data service website. The mean and variance of each region for each variable was calculated in ArcMap from ArcGIS 10.1 (ESRI, CA) using geographic regions (LENZ layer ‘NZ Area Codes for recording specimen localities’). As a measure of habitat availability, we included prehuman forest cover, calculated from McGlone (1989) and an estimate of current forest cover in each region (as a measure of the recent impact of human arrival). We used the relative human population size of each region and the presence of a relevant research institution in the region (a binary variable) as a proxy for sampling bias, because there might be a tendency for more thorough description of local versus more distant fauna. The relative population size of each region was calculated based on 2006 census data using the ‘populated places’ polygon (by Peter Scott, from Koordinates.com).

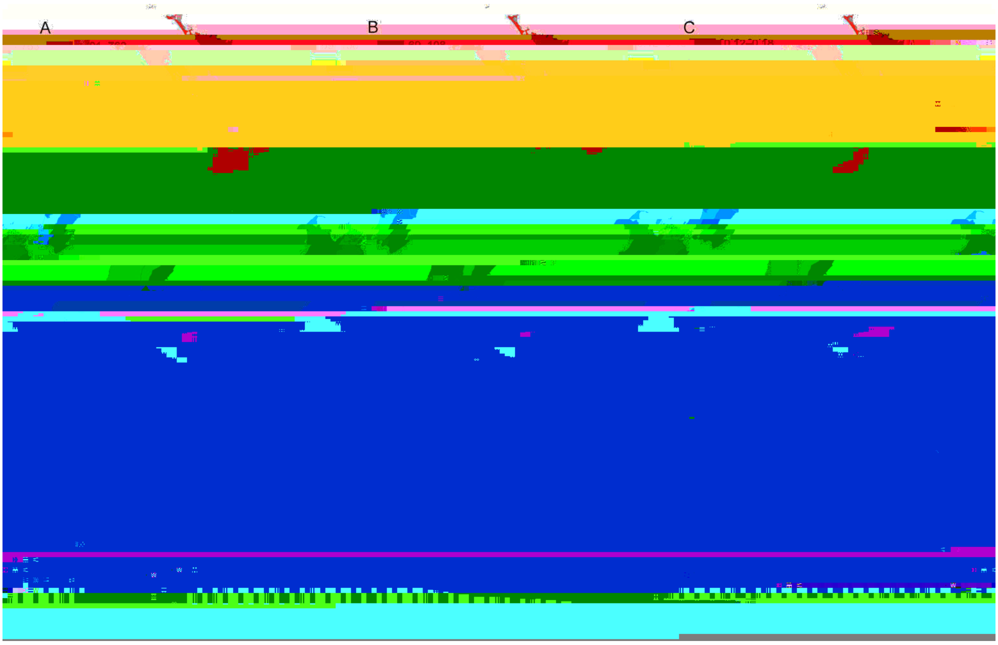

Figure 3. Endemism and diversity levels of invertebrate species are not homogeneous among regions of New Zealand. Four colours represent discretized (binned) numbers per region out of a sample of 2322 taxa. (A) Total invertebrate diversity. (B) Number of endemic invertebrates. (C) Endemism score using the average level of endemism for each taxon. Bar plots illustrate ranked regional total diversity (D) and ranked regional total number of endemic taxa (E).

regional-endemic taxa, but only 8.8% of the total land area of mainland New Zealand. In contrast, Hawke's Bay (HB), Gisborne (GB), Wanganui (WI), Rangitikei (RI), Wairarapa (WA), Kaikoura (KA), north Canterbury (NC) and south Canterbury (SC) accounted for 23% of total land area but only 5% of all endemic taxa. No spatial autocorrelation was detected within the endemism and diversity indices ($P > 0.05$).

## Sampling effort

To explore whether the data were dominated by sampling effort we excluded taxa recorded from only one site and that had poor overall sampling of the group. This reduced the number of regional-endemic taxa from 734 to 152 species. The strong relationship between the number of endemic taxa in each region and the number of well-sampled endemic taxa ($R^2 = 0.87$; $P < 0.001$; Figure 4B), suggests that overall sampling is representative of actual levels of endemism within regions.

We explored further the influence of variation in sampling effort using patterns of endemism in two intensely sampled families; Simuliidae flies and Lycosidae spiders (Table 2). Within each region, every collection site provided independent presence/absence records for each of the 11 Simuliidae and 18 Lycosidae species endemic to North Island and/or South Island New Zealand. In both families, most species were recorded from few regions while few species were widespread, in keeping with the predominant pattern of range restriction seen in the larger invertebrate dataset (Figure 5).

Figure 4. (A)

Although intensely sampled, neither the Simuliidae nor Lycosidae comprised sufficient species diversity to test for significant heterogeneity among regions.

## Endemism and environment

The relationship between endemism and the environment was tested using a set of environmental variables (Table S1). There were no simple correlations between endemism or diversity and the environmental variables, however, a significant positive correlation (after Bonferroni correction) was observed between endemism-score (which is a measure that corrects for species diversity) and land area 3 million years ago ($R = 0.34$; $P = 0.001$; Figure 2D). Variation in levels of regional-endemism among the regions was best explained by multiple variables in the general linear model (Table 3). Total species diversity ($t = 6.20$; $P = 0.00001$), land area 3 Ma ($t = 7.45$; $P < 0.00001$) and the presence of a research institution ($t = 7.32$; $P < 0.00001$) each improved the model, having a significant positive impact on regional-endemism. Climatic variables (represented in this model by the ratio of rainfall to evaporation and seasonal sunshine variation) also contributed to regional-endemicity, and each correlated with other environmental variables not in the model (Table 3 and S2). Interestingly, variance in solar radiation and water availability

(MMWBR) interacted to have a significant negative effect ($t = -3.49$; $P = 0.003$). The effect of total species diversity and number of neighbouring regions interacted with one another to negatively affect regional-endemism ($t = -3.11$; $P = 0.007$). Two other variables included in the model, mean slope and current forest cover, did not have a significant effect ($t < 1.25$; $P > 0.05$).

## Discussion

### The patterns

The same pattern of regional variation was apparent in our dataset of endemic invertsampled families of New Zealand invertebrates, Lycosidae spiders and Simuliidae black flies, provided information on absences and were not biased by sampling. Within these families, species distributions were heterogeneous with few widespread and many restricted species, as seen in the larger invertebrate dataset (Figure 5). We are confident that the distributions of invertebrate species, as recorded in the Fauna of New Zealand series, do contribute meaningful data for analysing patterns of New Zealand regional-endemism.

As observed in plants (Wardle 1963; McGlone et al. 2001; Heenan et al. 2017), levels of invertebrate endemism are not homogeneous among New Zealand regions. Rather, some regions have high endemism while others had few or no endemic invertebrate taxa in our sample (Figure 3 invertebrate species diversity was positively correlated with endemism in New Zealand (Figure 4A). However, species diversity interacted with number of connecting (neighbouret al. 2018). Although we have evidence that climate and habitat may influence relative levels of invertebrate species endemicity the correlation of variables and heterogeneity of regions makes isolation of the relevant drivers difficult.

## Climatic and habitat stability

The distribution of plants and animals appears to have been influenced in some places by glaciation and aridification during Pleistocene glacial periods. For example, a gradient in levels of European endemism suggests refugia in warmer climes were influential in preserving local diversity (Essl et al. 2013). During New Zealand's LGM (Williams et al. 2015

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## Conclusions

Small-ranged species are a conservation priority, therefore, understanding current patterns of regional-endemism in New Zealand is important for protection of biodiversity. We investigated regional-endemism using a rich invertebrate dataset and found that although variation in sampling effort does influence the data, most species are range restricted and endemism levels are not evenly distributed across the country. High invertebrate species diversity and high endemism can both be conserved if Northland and Nelson are provided with resources to protect their natural habitats. No single variable appears to drive variation in regional-endemism. Those variables that were important appear to be related to differences in geologically recent land availability, and connectivity between regions. High levels of endemism in some regions are not simply a product of the accumulation of species over time, rather regional-endemism depends on the ability of a region to retain local species. Regions with fewer neighbours have lower migration rates, whereas those with many neighbours are less able to retain endemic taxa. The absence of land in southern North Island until recent geological time shows that tectonic activity in New Zealand continues to have a significant influence on current endemism levels.

## Acknowledgements

Matt Irwin, Lesley Essen and Jean Sanderson helped organise data. The research was aided by a Massey University Research Fund grant to M.M.R. and scholarships to B.T.S. from Massey University, the Brian Mason Scientific & Technical Trust, and the NZ Entomological Society. We appreciate the support of the Phoenix group (www.evolves.massey.ac.nz). The manuscript was improved by constructive criticism from Matt McGlone and two anonymous reviewers.

## Disclosure statement

No potential conflict of interest was reported by the authors.

## Funding

This work was supported by Massey University under Grant MURF 2014 & Doctoral scholarship to BTS; Brian Mason Scientific & Technical Trust and New Zealand Entomological Society.

## Data availability statement

Data associated with the paper from Fauna of New Zealand series https://www.landcareresearch.co.nz/publications/books/fauna-of-nz-series

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