Assessment of protected area coverage of threatened ground beetles (Coleoptera: Carabidae): a new analysis for New Zealand

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Abstract: Gap analysis is a tool that allows conservationists to quantify the effectiveness of protected areas at representing species diversity, but the lack of distribution maps for invertebrates has precluded its application to the world's most diverse animal groups. Here, we overcome this limitation and conduct a gap analysis, using niche modelling, on the Pterostichini (Coleoptera: Carabidae) of New Zealand, one of the most diverse and most threatened tribes of ground beetles in the nation. Niche modelling uses data on abiotic parameters to model predicted species ranges based on records of their known distribution, and is a useful tool for conservation planning. This method is widely applicable where there is good taxonomical knowledge of the group in question and distribution records are available. We obtained sample localities from museum records for 67 species of Pterostichini, including 10 species listed as threatened, and modelled their spatial distributions based on climate, landforms and soil properties. Most species had small spatial distributions, with 48–75% of species having ranges of less than 100 000 ha. We found the areas with highest species richness fell largely outside of the protected area network, as did the distribution of most individual species, with just 20–25% of species having more than 30% of their range falling within a protected area. In terms of percent land area, New Zealand has one of the world's largest protected area networks, but the spatial distribution of that network affords little protection to this group of invertebrates. This analysis provides support for the creation of new reserves to increase the value and efficacy of the protected areas network.

Keywords: Carabidae; Coleoptera; gap analysis; invertebrates; New Zealand; Pterostichini

Introduction

Invertebrates form the functional backbone of ecosystems around the world. They play globally important roles in processes as diverse as pollination (Ghazoul 2005), herbivory (Maron & Crone 2006), bioturbation (Meysman et al. 2006), water purification (Boulton et al. 2008), and regulation of insect populations (Kromp 1999). Moreover, they are the most speciose group of animals and yet are thought to be undergoing a mass extinction event (Fonseca 2009). The importance of invertebrates and their diversity raises a difficult proposition: we need to conserve these species, but how can we best conserve such species-rich groups? Their sheer diversity precludes the widespread use of species-specific management actions, suggesting that site-based conservation approaches are the most practical route forward (McGuinness 2007). This approach is the most commonly employed conservation tactic around the world (Rodrigues et al. 2004a, b). The degree to which protected areas represent species diversity can now be quantified using gap analysis (Rodrigues et al. 2004a, b). Gap analyses require data on the spatial distribution of species, which is available for all of the birds (Orme et al. 2006), mammals (Schipper et al. 2008) and amphibians (Stuart et al. 2004) of the world. However, such information is commonly unavailable for invertebrates, making gap analysis impractical and leaving it as a tool that is not routinely employed for assessing the conservation protection afforded to the world's most diverse taxon. Data are available now for a diverse group of invertebrates in New Zealand, allowing us to conduct the first national-scale gap analysis for invertebrates in one of the world's 25 biodiversity hotspots (Myers et al. 2000).

New Zealand is notable for its highly endemic biota, which has evolved in isolation from any other landmass for at least the last 25 million years. There is considerable discussion now as to whether isolation was longer due to the claims and rebuttals for the 'Oligocene inundation' (Goldberg et al. 2008; Giribet & Boyer 2010 and references therein). Following very extensive land extension and mountain building during the Pliocene and Pleistocene, the warmer climates of the interglacials and last 10 000 years in the South Island have led to a diversity of habitats and vegetation associations. On the lowlands dense wet forests dominated the west and dry forests and shrublands the east (Craig et al. 2000). However, the landscape suffered much modification from its natural state with the arrival of humans. New Zealand was one of the last countries in the world to be colonised by people and European settlers arrived less than 200 years ago (MfE 1997) with grazing animals and tillage practices. Since this time, forest-burning, agricultural land modification, hunting and the introduction of exotic species, both productive and pest, have had a significant impact on the natural habitats of New Zealand (McGlone 1989), causing the extinction of unique species and threatening many more (Fonseca 2009).

The family Carabidae is one of the New Zealand invertebrate taxa that are listed high on the priorities of conservationists (Larochelle & Larivière 2001; Johns 2003, 2005). However, information on relative abundance and distribution of rare species is incomplete and, as such, an

assessment of the true extent of threatened species is still lacking and most can be categorised as Data Deficient (Stringer & Hitchmough 2012). Carabidae is also species rich with a global estimate of more than 40 000 species, and its members occupy most terrestrial habitats (Erwin 1985). Carabids are not as diverse in New Zealand as on larger continents (Lovei 1991), although for the land area the species assemblage is by no means poor with an estimate of at least 600 species (Larochelle & Larivière 2001). Of those 600 estimated species, 461 species and 15 subspecies are recorded from 7 subfamilies, 21 tribes and 86 genera (Larochelle & Larivière 2007) with only a few being described since 2007. Ninety-two percent of described species are endemic (Larochelle & Larivière 2001), which is slightly higher than the 80–90% endemicity normally seen in New Zealand species assemblages (McGuinness 2007; Macfarlane et al. 2010).

The New Zealand Threatened Species List recognises about 8% of all New Zealand carabids as threatened (Hitchmough et al. 2007), though the present standards recognise different categories (Leschen et al. 2012; Table 1). The majority of these threatened carabids are heavily biased to two genera, suggesting that extinction threat to these species is phylogenetically clustered just as it is for vertebrates (Purvis et al. 2000). These genera are *Megadromus* (Harpalinae; Pterostichini) and *Mecodema* (Trechinae; Broscini) (McGuinness 2007), which together include the largest carabids in New Zealand. Their size is thought to leave them more susceptible to predation by introduced predators such as rats, mice, hedgehogs and mustelids (McGuinness 2007). Many species of these two genera are known to tolerate modified productive and urban areas, e.g. gardens, pastures and plantations. However, the population dynamics and distributions of most threatened New Zealand carabids are poorly understood (Larochelle & Lariviere 2001) and the loss of primary habitat is considered to be a key contributor to the decline in New Zealand carabids (McGuinness 2007). Another factor that likely influences their prominent inclusion on the threatened species list may be that their size makes them more noticeable to field biologists than smaller species, meaning that a decline in numbers is more likely to be noticed. A large proportion of other carabid species are adapted to live in either wet forest or tussock grassland (Larochelle & Larivière 2001), both of which habitats have undergone dramatic changes over the last century (Ewers et al. 2006; Walker et al. 2006). It has been argued that the historical impacts of habitat loss are no longer relevant to conservation issues in New Zealand because habitat loss has largely stopped (Ewers et al. 2006; Walker et al. 2006), and because the nation has a large network of protected natural areas (Craig et al. 2000). These protected areas form the Protected Areas Network (PAN-NZ) and are actively managed through weed control, pest and predator control, and ecosystem restoration projects (Department of Conservation 2009). Protected areas administered by the Department for Conservation total more than 8.6 million hectares; approximately one-third of New Zealand's land area (Statistics New Zealand 2002) and among the world's largest national networks in terms of percent land area (Convention on Biological Diversity 2009; UNEP-WCMC & IUCN WCPA 2010).

The large protected areas network in New Zealand reflects a concerted effort to conserve the nation's natural landscapes and endemic biodiversity. However, the geographic distribution of PAN-NZ is grossly uneven and being large is not enough, by itself, to guarantee an effective network (Norton 2000; Walker et al. 2006, 2008). For example, in the South Island the majority of protected areas are forests and alpine zones within and west of the main alpine ranges (rainfall c. 1500–10 000 mm) whereas the eastern forest, shrublands and tussocklands (rainfall c. 450–1500 mm), where most of these endangered species are found, are afforded much less protection. The spatial distribution of protected areas in New Zealand has, like most of the world, been predominantly determined by the spatial distribution of land values and potential land uses. Following colonisation, lowland areas were first to be converted to agricultural land and now native forest, shrubland and grassland are concentrated in mountainous regions and those of low agricultural value (Seabloom et al. 2002; Rodrigues et al. 2004b). Extensive areas of poor lowland soils with shrubby vegetation were planted with pines from 1904 to this day. Now wilding pines and spruces have been left to cover degraded areas of low agricultural value in the foothills, for example near Hanmer Springs, Craigieburn Valley and the Mackenzie Basin in Canterbury. Protected areas tend to be established primarily in locations where indigenous vegetation has survived, are scenically desirable, or are located in cooler, rugged, high-elevation environments with steep slopes and soils of relatively low quality for agriculture (McGlone 1989; Rutledge et al. 2004).

Whether the geographically biased PAN-NZ is able to protect species adequately in the present day depends on how species are distributed relative to the protected areas. Here, we generate environmental niche models for 67 species of New Zealand ground beetles, including 10 species listed as threatened, and project those niche models onto geographic space to estimate the spatial distribution of these species. We overlay those distributions onto PAN-NZ to estimate the ability of that large network to encompass and protect carabid species. This analysis represents the first national-scale gap analysis of invertebrates, and we use it to highlight an important conservation issue: having a large protected area alone is not enough to ensure species diversity is effectively protected.

Methods

Study taxa and data

We restricted our analysis to members of the tribe Pterostichini (Carabidae: Harpalinae) for which we had reliable data. Pterostichini is the most species rich tribe of New Zealand Carabidae, accounting for 18% of all described carabid species. Moreover, just over one-third of all carabid species named on the New Zealand threatened species list belong to the Pterostichini (Hitchmough et al. 2007). Eight of the 11 Pterostichini genera are endemic to New Zealand (Larochelle & Larivière 2001) and the following were chosen for this study: *Holcaspis* (31 species), *Megadromus* (26), *Neoferonia* (5), *Plocamostethus* (2), and *Zeopoecilus* (3). *Holcaspis* and *Megadromus* species are essentially eastern dryland genera, whereas the others are predominantly wet forest inhabitants. All these species are flightless, many are large, and all present localised distributions (Johns 2003). Unlike carabids elsewhere, some of these New Zealand species, and perhaps all species of *Megadromus*, are known to lay few eggs and to nurse them until a short time after hatching – a characteristic that makes them very sensitive to predation or habitat modification (Cartellieri & Lövei 2003).

We obtained location data for 5544 Pterostichini specimens held in New Zealand entomological collections up to 2010. Identifications were made or checked by Peter Johns and a georeference (New Zealand Map Grid) determined for those
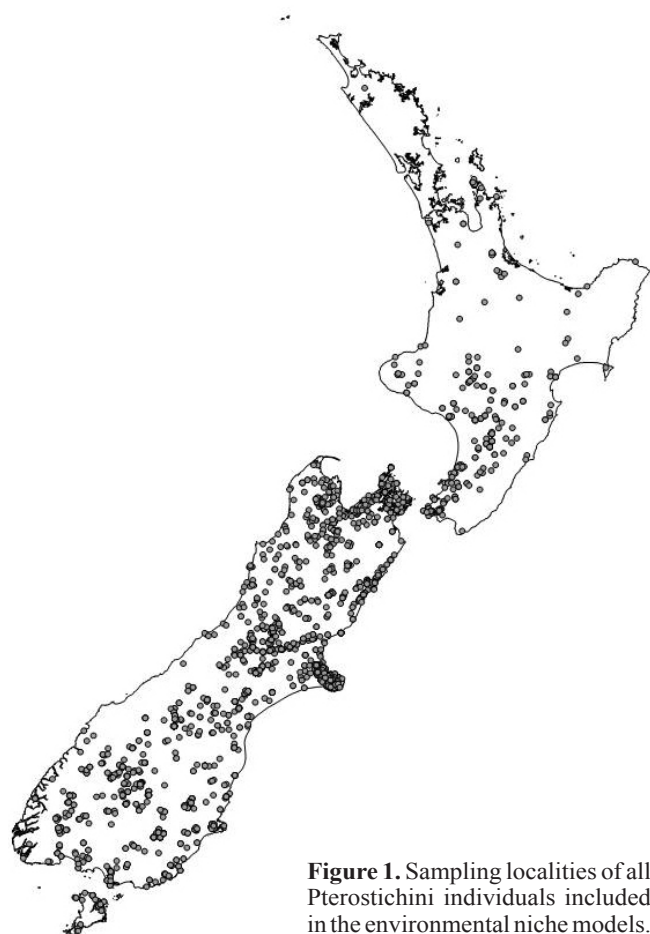
Figure 1. Sampling localities of all Pterostichini individuals included in the environmental niche models.

specimens whose labels presented adequate spatial information (Fig. 1). Most specimens collected over the last 30 years already had a grid reference made by the collector. For the rest, other textual information on site localities was converted to georeferences by searching for place names using local knowledge and online mapping resources such as GoogleMaps and Biogeomancer. We estimate that about 80% of all records are accurate to within 2 km or less, and none were included that could not be estimated to within 20 km. The geographic distribution of site localities was heavily biased to the South Island, especially Canterbury and Otago, reflecting the fact that approximately 68% of the total carabid fauna is known only from this island and it holds about 80% of the Pterostichini (Larochelle & Larivière 2007).

We chose not to model *Gourlayia regia*, a genus and species endemic to Three Kings Islands (off the northern tip of the North Island), and *Onawea pantomelas*, which is found only on Banks Peninsula (South Island). Both of these species are confined to a very small geographic area so including them in the models would not have provided additional information on potential ranges or habitat suitability for these species. Moreover, we omitted the genera *Prosopogmus* (1 species) and *Rhytisternus* (2) as they are introduced species and therefore have no conservation importance in New Zealand. Finally, we also excluded several described and over 20 undescribed or uncertain species, and those of the genera *Aulacopodus* (4 species) and *Psegmatopterus* (1), due to a paucity of records.

We were able to obtain enough data to model the environmental niche for 67 species from a total of 1144 sites. This represents 75% of all known species within the Pterostichini. Ten of the 67 species are on the New Zealand threatened species list under the former categories Sparse (3 species), Range Restricted (2), Nationally Endangered (2) or Nationally Critical (3) (Hitchmough et al. 2007). Leschen et al. (2012) recently revised these classifications and they are presented in Table 1.

Table 1. Present classifications of Pterostichini species (Leschen et al. 2012).

Classification	Species
Endangered: Nationally Critical (6 of 17 Carabidae)	*Holcaspis abdita* Johns, 2004 *Holcaspis bathana* Butcher, 1984 *Holcaspis bidentella* Johns, 2004 *Holcaspis brevicula* Butcher, 1984 [1]*Holcaspis* n. sp. 1 (Mackenzie Basin, Canterbury) [1]*Megadromus* n. sp. 8 "Omeo Hut" (Alexandra, Otago)
At Risk: Declining (1 of 6 Carabidae) Relict (5 of 7 Carabidae)	*Holcaspis falcis* Butcher, 1984 [2]*Megadromus antarcticus crassalis* (Broun, 1893) *Megadromus bucolicus* (Broun, 1903) *Megadromus compressus* (Sharp, 1886) *Megadromus omaramae* Johns, 2007 *Megadromus speciosus* Johns, 2007
Naturally Uncommon Data Deficient (5 of 13 Carabidae)	[1]*Megadromus fultoni* (Broun, 1882) [1]*Megadromus* sp. (Waiau River) [1]*Megadromus* sp. "Benmore" [1]*Megadromus* sp. "Millers Flat" [1]*Zeopoecilus* "D'Urville Island – Squally Cove" [1]*Zeopoecilus* "Stephens Island"

[1]Not included in present study because of rarity or single locality. *Megadromus* n. sp. 8 is 'Critically Endangered' as it has been searched for intensively without success. Attempts to ascertain the state of *Holcaspis* n. sp. 1 have been unsuccessful as access to the small (c. 2 ha) commercial site has been denied.
[2]Subspecies status used in Leschen et al. (2012).

Environmental niche modelling

We modelled the present-day environmental niche and consequent geographic distribution of pterostichines using the program MaxEnt (Elith et al. 2011). A comparative analysis of niche model performance by Elith et al. (2006) concluded that MaxEnt is one of the best performing niche models, providing consistently reliable outputs. Species niches were modelled as a function of up to 16 abiotic variables representing New Zealand climate, landforms and soil properties (Table 2), and using the default settings in MaxEnt. We are not aware of published studies that have directly demonstrated the relevance of these variables for limiting the distribution of carabids, and previous experiments have suggested that adult carabids are remarkably resilient to altered temperature conditions (Ewers 2008). However, we hypothesise that it is survival at the pre-adult life stages (egg and larval survival, and pupation success) that limits the distribution of the species, for which climatic features, such as temperature and humidity, and soil features, such as water logging and chemical composition, are likely to influence success. All variables were modelled at a fine spatial resolution of 100×100 m. We fitted two niche models for all species: the first mapped the species against just seven climate variables and the second mapped the species against all 16 climate, landform and soil variables (Table 2). The two models, hereafter referred to as the 'climate' and 'full' models, were generated because preliminary analysis indicated that

adding more environmental variables progressively reduced the predicted geographic range of a species. We interpret the climate model as representing an upper estimate for the geographic distribution for a species, and the full model as representing a lower estimate.

MaxEnt produces map outputs that assign each grid square a probability of the species being present in that grid square. To convert these probability maps into binary presence/absence maps, we considered a species to be present if the probability of presence was greater than 0.5. Probabilities less than 0.5 were deemed unsuitable for that species to occur. We overlaid the binary maps for all species to make a map of species richness based on the climate and full models.

Gap analysis

Species distribution maps were overlaid on a map of the Protected Areas Network (PAN-NZ) to investigate the degree to which protected areas encompassed the distributions of individual species. PAN-NZ includes all public conservation lands and covenants administered by the Department of Conservation, as well as local authority regional parks and private land under covenants such as held by the Queen Elizabeth II National Trust. We clipped the range of all 67 species in Arcmap to calculate the area that fitted inside PAN-NZ, under both the climate and full niche models. The proportion of range that fell inside the protected areas was

Table 2. Environmental variables used to model the niche of carabid species in New Zealand. All data were obtained from Leathwick et al. (2003), with the exception of altitude, which was obtained from the New Zealand National Digital Elevation Model (accessed May 2009 from http:www.nzdem.co.nz). Two models were constructed, one using just the seven climatic variables (climate model) and one using all data (full model).

Environmental variable	Range	Model
Annual rainfall deficit (mm)	0–412	Climate + Full
Average monthly ratio of rainfall to potential evaporation (ratio)	0.5–30.6	Climate + Full
June solar radiation (Mj m^{-2} day^{-1})	3.3–7.5	Climate + Full
Mean annual solar radiation (MJ m^{-2} day^{-1})	11.7–15.4	Climate + Full
Mean annual temperature (°C)	−5.1 to 16.3	Climate + Full
Mean July minimum temperature (°C)	−8.4 to 9.8	Climate + Full
Mean October vapour pressure deficit at 0900 hours (kPa)	0.00–0.64	Climate + Full
Acid-soluble phosphorus (mg per 100 g)	Five classes: 0–7, 7–15, 15–30, 30–60, 60+	Full
Age since last major topographical rejuvenation (years)	Three classes: <2000, 2000 to postglacial (c. 30 000), preglacial	Full
Altitude (m)	0–3754	Full
Chemical limitations to plant growth	Three classes: (1) nil–low limitations, (2) saline soils, (3) ultramafic soils	Full
Drainage	Five classes: very poor, poor, imperfect, moderate, good	Full
Exchangeable calcium (mg per 100 g)	Four classes: 0–1, 1–10, 10–40, 40+	Full
Induration	Five classes: none, very weakly, weakly, strongly, very strongly	Full
Particle size (mm)	Five classes: clay/silt (<0.06), sand (0.06–2), gravel (2–60), coarse gravel (60–200), boulders–massive (>200)	Full
Slope (degrees)	Seven classes: flat (0–3), undulating (4–7), rolling (8–15), strongly rolling (16–21), moderately steep (21–25), steep (26–35), very steep (>35)	Full

then calculated using the values before and after the clip. Rodrigues et al. (2004a) suggested that species with a range of less than 100 000 ha should have 100% of their range in a protected area to consider them at all protected by the network. However, their analysis was at global scale and at a much coarser spatial resolution than our analysis. Moreover, Rodrigues et al. (2004a) did not include in their analysis any terrestrial invertebrate species, which can maintain viable populations in much smaller areas. Consequently, we considered a species to be adequately covered by PAN-NZ if more than 30% of a species range was inside a protected area. We chose this arbitrary cut-off to reflect the fact that approximately one-third of the New Zealand land surface area is under some form of conservation protection. If protected areas were distributed at random, we might expect that c. 30% of all species ranges would be encompassed within PAN-NZ, so deviation from this expectation provides a meaningful basis for determining the relative effectiveness of PAN-NZ for ground beetles.

Statistical analysis

We estimated the fit of the environmental niche models using the Area Under the Receiver Operating Characteristic Curve (AUC). This statistic is not without controversy and it has been suggested that it is 'a misleading measure of the performance of predictive distribution models' (Lobo et al. 2008), nonetheless Lobo et al. acknowledged there is currently no other suitable alternative and thus it has been used extensively in the environmental niche modelling literature (Elith et al. 2006). It defines the ability of the fitted model to discriminate between sites where a species is present and those where the species is absent. Values of AUC are bounded between 0 and 1, with a value of 0.5 representing a model that does no better than random (Elith et al. 2006). Models with AUC values of 0.7 are considered useful and those with AUC values greater than 0.9

are considered strong evidence for a good model (Swets 1988).

We used a paired t-test to compare the range-size estimates emerging from the climate and full models. One-way ANOVA was used to compare range patterns among threatened and non-threatened species. Specifically, we tested for differences in the $\log_{10}$-transformed range size, and the arcsin-transformed proportion of a species' range that fell within protected areas. All analyses were conducted using the statistical software program R version 2.9.2 (R Development Core Team 2009).

Results

Across all species, we obtained very good niche model fits as assessed by AUC scores. Full models gave consistently higher AUC scores than the climate models (full model AUC scores: mean ± SD = 0.99 ± 0.01; climate model AUC scores: 0.97 ± 0.04). The small difference between climate and full models suggests that the added complexity of the full models did little to improve model fits, suggesting that the climate model is the more parsimonious of the two approaches.

Megadromus and *Holcaspis* are most species rich along the central and eastern South Island, a pattern that was consistent across the climate and full models (Fig. 2). However, the climate models predicted a larger geographic spread of climate suitability for the majority of species in comparison with the full models (Fig. 2). Overall, the most species rich areas tended to fall outside of the PAN-NZ network (Fig. 2).

The size of predicted species ranges differed between the two models, with the climate model predominantly generating larger species ranges than the full model (paired t-test: $t_{66} = 4.95$, $P < 0.001$). Overall, the full model reduced the predicted range size of species by an average of 43% relative to the climate model, although there was considerable variation around
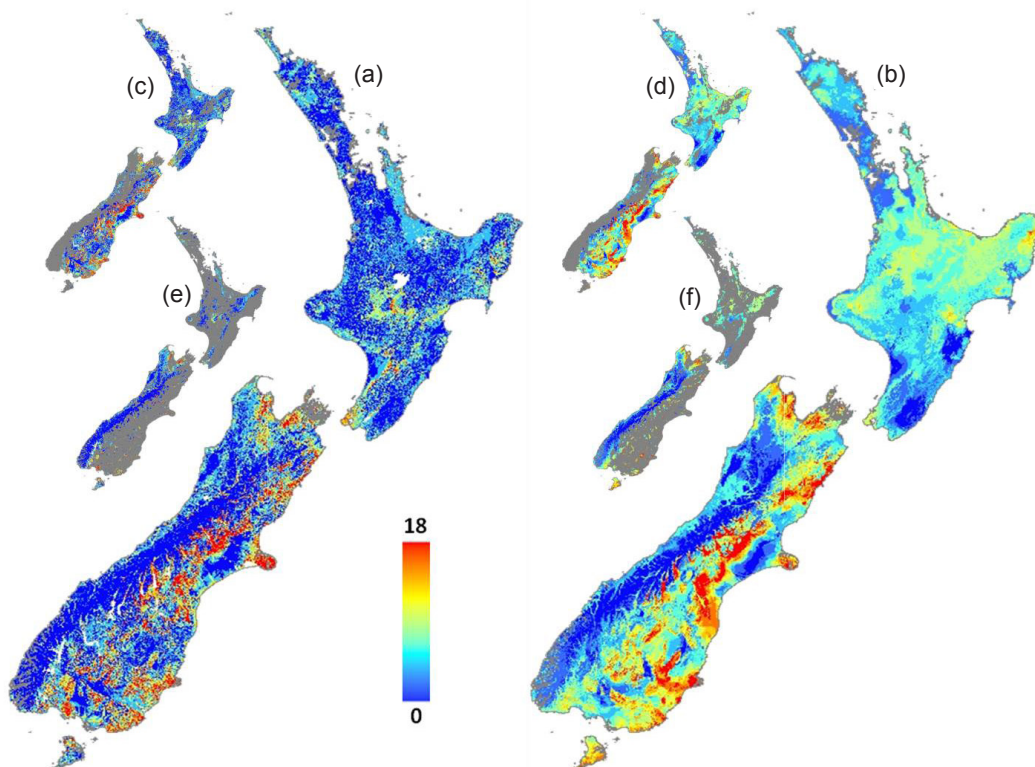

Figure 2. Species richness of Pterostichini ground beetles (Coleoptera: Carabidae: Harpalinae) in New Zealand as determined from a spatial projection of environmental niche models constructed under (a) the full model (climate, landform and soil property data) and (b) the climate model (climate data only). Insets show the patterns of species richness outside (c, d) and inside (e, f) protected areas for the full (c, e) and climate (d, f) models respectively. All figures are presented on the same linear colour scale from a minimum of 0 to a maximum of 18 species.

this value (Fig. 3). Species ranges were generally small and, across species, exhibited a log-normal distribution (Fig. 3). Median range size was 745 000 ha under the climate model (interquartile range 378 000 – 1 394 000), and just 442 000 ha under the full model (interquartile range 168 000 – 529 000 ha).

All species had at least a small part of their predicted range located within the PAN-NZ network. However, under the climate model, 12 of the 67 species (18%) had less than 5% of their range protected and 29 species (43%) had less than 10% protected (10 and 21 species respectively under the full model). Just 17 out of 67 modelled species (25%) had more than 30% of their range covered by protected land (14 species under the full model).

Of the threatened species modelled, only *Megadromus speciosus*, a 'relict' species, had more than 30% of its predicted range within the PAN-NZ network (54% under the climate model and 50% under the full model). Species of particular concern that had very little of their predicted range within the PAN-NZ network are *Holcaspis bidentella* and *H. brevicula*, which are classed as 'endangered' species and had only 2% of their predicted ranges protected under the climate model (4% and 1% respectively under the full model). Additionally *Holcaspis falcis*, an 'at risk' species, had only 3% of its predicted range protected under the climate model (2% under the full model). Two species classed as 'relict', *Megadromus compressus* and *M. omaramae*, had only 6% and 4% of their predicted ranges, respectively, protected under the climate model (13% and 7% respectively under the full model). These species' predicted ranges, like for many Pterostichini, were predominantly located to the east of the Southern Alps, which is afforded very little protection by the PAN-NZ network.
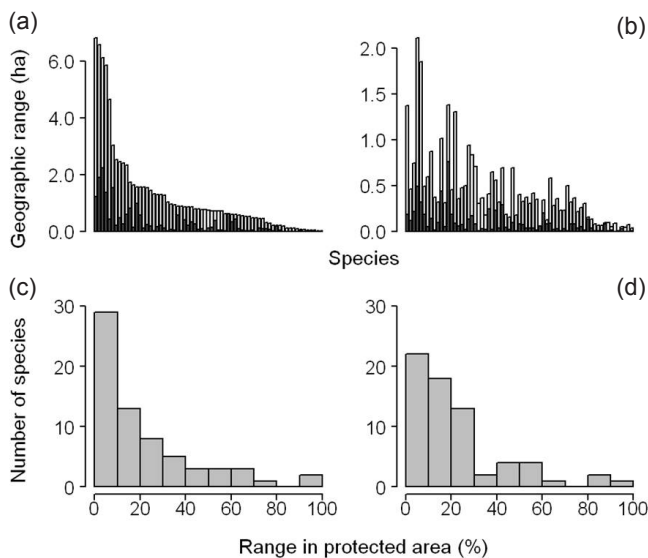
The climate model showed that the predicted geographic range size of threatened species did not differ significantly from non-threatened species (ANOVA on log-transformed data: $F_{1,65} = 1.80$, $P = 0.184$). Additionally, the proportion of threatened species' predicted geographic ranges within protected areas did not differ significantly from that of non-threatened species (ANOVA on arcsin-transformed data: $F_{1,65} = 0.0614$, $P = 0.805$).

Discussion

We found that most areas of high carabid species richness fell outside the New Zealand Protected Areas Network, and that few species had a large enough proportion of their range within PAN-NZ to consider them protected. It is not practical to manage every threatened invertebrate species individually and site-based conservation approaches are likely to be the most successful method for invertebrate conservation (McGuinness 2007). However, our data strongly suggest that the current spatial distribution of site-based conservation, as reflected by PAN-NZ, is inadequate to protect a highly endemic carabid fauna.

It is not immediately clear to what extent the results of our analysis can be extrapolated to invertebrates as a whole. For example, the distribution of the two most threatened carabid genera in New Zealand differ markedly. The genus *Mecodema* (Trechinae; Broscini) has more species distributed across the North Island and along the mountains of the South Island than the genus *Megadromus* (Harpalinae; Pterostichini), which was included in our models (Larochelle & Larivière 2007). The South Island's west coast is extensively protected, suggesting that our choice of the predominantly east coast dwelling Pterostichini has overstated the degree to which PAN-NZ fails to encompass carabid biodiversity as a whole. However, we chose to model the Pterostichini because they are one of the most diverse and threatened tribes of ground beetles in New Zealand and their apparent lack of protection is a cause for concern.

Our data allow for no inference on whether there is a cause-and-effect relationship between the threat status of the Pterostichini and their lack of coverage by protected areas. The New Zealand threatened species list provides little information on the specific threats facing these species, with the threat listed as 'Not known' or left blank for eight of the 10 threatened species we modelled (McGuinness 2001; Hitchmough et al. 2007). For two of these eight species, habitat loss and modification is suggested as a possible, but unconfirmed, cause of their threat status. The remaining two species with threat categories are listed as threatened because they occur in just one localised area. One of these species, *Holcaspis brevicula*, has been collected exclusively from exotic pine (*Pinus* spp.) plantations on the denuded Canterbury Plains (Brockerhoff et al. 2005; Berndt et al. 2008), indicating that the loss and modification of native habitats alone is not enough to explain the full patterns of threat to New Zealand carabids. An alternative cause of their threat status is predation by native and introduced species (McGuinness 2007). Carabids are preyed upon by native species such as the morepork owl (*Ninox novaeseelandiae*; Haw et al. 2001), and there is also no doubt that introduced predators consume carabid beetles (Daniel 1973; Jones et al. 2005), ensuring that active predator management, within PAN-NZ and on privately owned land, will also be required to effectively conserve endangered carabids.

Figure 3. (a, b) Geographic range size of Pterostichini ground beetles (Coleoptera: Carabidae: Harpalinae) in New Zealand as determined from a spatial projection of environmental niche models constructed under (a) the climate model (climate data only) and (b) the full model (climate, landform and soil property data). Range sizes are presented in millions of hectares. Species are ordered left to right according to range size as estimated from the climate model; the ordering of species is the same in panels (a) and (b). Dark shading shows the proportion of the range that falls within a protected area. (c, d) Frequency histograms showing the percentage of the geographic ranges that fall within the New Zealand Protected Area Network for ranges generated from the (c) climate model and (d) full model.

Pterostichini were most species rich along the eastern side of the Southern Alps that divide the South Island. Pterostichini diversity was comparatively low in the North Island, although it should be noted that this analysis excluded the predominantly North Island genus *Aulacopodus* (three of the four species are known only from the North Island) for lack of data (Crosby et al. 1998). The most species rich regions fall almost entirely outside the New Zealand protected area network. The Canterbury Plains on the eastern South Island have very little protected land in comparison to the west, and have suffered the heaviest levels of deforestation of any New Zealand region (Ewers et al. 2006)), although there are significant protected areas in the Canterbury high country. Today, the extensive Canterbury Plains region is dominated by intensive agriculture with only tiny vestiges of native forest and shrubland remaining on the coastal Banks Peninsula and inland along the foothills of the Southern Alps (Ewers et al. 2005). Between these two extremes less than 0.5% of the original natural vegetation remains (Leathwick 2001).

Our estimates of geographic range size varied greatly between the climate and full models. The two models predict generally consistent spatial patterns of individual species ranges and for species richness as a whole, but the full model tended to predict very localised, scattered distributions. This pattern reflects the additional level of detail that is absent from models based on climatic variables alone, and potentially indicates an important set of restrictions on the occupancy patterns of species within their wider geographical range. In some cases, predicted ranges under the full model included single one-hectare grid squares with no adjacent suitable land, whereas the climate models tended to predict larger, contiguous geographic ranges. Many of the small remnant patches of natural habitat that exist across New Zealand likely exist on private rather than public land, suggesting that, at this spatial scale, it is important to encourage private landowners to undertake site-based conservation. Within New Zealand, there is evidence that this is taking place. Institutions such as the Queen Elizabeth II National Trust help private landowners to protect natural features of their land in perpetuity (Queen Elizabeth II Trust 1984). However, covenants such as these provide only legal protection for the land and do not address the specific management needed to ensure the conservation of species inhabiting these areas. The New Zealand government recognises the importance of encouraging private landowners to contribute towards the maintenance of biodiversity (MfE 2000), and many regional councils are actively working with landowners to conserve and restore biodiversity (MfE et al. 2004). Nonetheless, the PAN-NZ dataset includes private lands under covenant for biodiversity values and still fails to encompass significant portions of the geographic ranges for some of New Zealand's threatened ground beetles. Therefore it is vital that the processes by which land is identified as requiring protection, assigned protected status, and actively managed for conservation, are addressed.

Conclusions

Gap analysis is an established method for determining the effectiveness of protected area networks at representing species diversity and for determining priority areas for conservation (Rodrigues et al. 2004a, b). We conducted the first gap analysis for invertebrates in New Zealand and focused that analysis on a diverse and highly threatened subset of the invertebrate fauna. Our results showed that the spatial distribution of the New Zealand protected area network fails to provide adequate protection for these endemic species. This analysis supports a review of the processes that assign land with protected status and the addition of new reserves to the protected areas network, to represent a range of habitats. Areas that could be considered are those in the east of the South Island, where little protection is provided for the threatened species there. Additionally, the future conservation of ground beetles in New Zealand will depend on the degree to which conservation goals, such as predator control, can be promoted on private land; a process that New Zealand is actively working towards. Much previous work has been conducted to gain knowledge of the fauna at the basic level of species recognition and description. It is imperative that distribution and population data are now sought and considered, in order to define more closely the association between soil, vegetation and climate for the poorly known 'Data Deficient' species (Stringer & Hitchmough 2012) of all families that contribute to New Zealand's diverse invertebrate fauna.

Supplementary Material

Additional supporting information may be found in the online version of this article:

Table S1. List of the 67 Pterostichini species modelled and the distribution of specimens among six museum collections.

The *New Zealand Journal of Ecology* provides online supporting information supplied by the authors where this may assist readers. Such materials are peer-reviewed and copy-edited but any issues relating to this information (other than missing files) should be addressed to the authors.

Acknowledgements

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