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New Zealand’s native land birds: status and change on the mainland from estimates of occupancy for 1969–1979 and 1999–2004

New Zealand's native land birds: status and change on the mainland from estimates of occupancy for 1969–1979 and 1999–2004

Susan Walker, Adrian Monks

Landcare Research

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Parliamentary Commissioner for the Environment

PO Box 10-241
Wellington 6143
New Zealand

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Landcare Research, 764 Cumberland Street, Private Bag 1930, Dunedin 9054, New Zealand,
Ph +64 3 470 7200, Fax +64 3 470 7201, www.landcareresearch.co.nz

Reviewed by:	*Approved for release by:*
John Innes Senior Researcher Landcare Research	Gary Houliston Portfolio Leader – Enhancing Biodiversity Landcare Research

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Summary

Project and client

The Parliamentary Commissioner for the Environment is investigating what the future might hold for New Zealand's native birds, and contracted Landcare Research to use the occupancy data compiled for two bird atlases to give an overview of which New Zealand land birds are in trouble, which are safe, and where conservation effort is needed most.

Objectives

- To describe the method we devised to derive standardised estimates of native land-bird occupancy (the probability that a species occurs in a location) from the two Ornithological Society of New Zealand bird atlases.
- To use these estimates to provide, by way of summary statistics and analyses, an overview of which New Zealand land birds are in trouble, which are safe, and where conservation effort is needed most.

Methods

We fitted occupancy models for 64 native land bird taxa, which estimate the probabilities of occupancy in each of 2,155 10 × 10 km grid squares in two measurement periods (1969–1979 and 1999–2004). We analysed patterns of status and change between measurement periods in relation to the endemism levels and habitat groups of the bird taxa and a number of environmental variables.

Results

Level of endemism has had a major influence on the status of and changes in native land-bird occupancy. Endemic taxa tend to occupy small geographic ranges, which decreased between measurement periods. In contrast, non-endemic native species and self-introduced species that arrived since European settlement typically occupy larger areas than endemic taxa, and most increased their ranges between the measurement periods.

Range declines were greatest in two groups of endemic birds: forest and alpine birds (especially those endemic at high taxonomic levels, or 'deep endemics'), and wading birds, terns or gulls that breed mainly in the inland eastern South Island. These decreases were greatest in remote forested areas (forest birds) and inland South Island basins and braided riverbeds (wading birds, terns or gulls), which supported the largest remaining populations of these birds in the 1970s.

Most of the wading birds, terns and gulls that breed on the coast (and not inland), and most birds of coastal and freshwater wetlands and other open habitats, increased their ranges. Most of these species are non-endemic native or recently self-introduced, and their greatest range expansions were into areas characterised by farming, forestry, settlements and

coastal urban environments. Notable exceptions were the southern New Zealand dotterel (an endemic coastal-breeding wading bird), the Australasian bittern and reef heron (non-endemic freshwater and coastal wetland species), and the New Zealand pipit (an endemic species of open habitats). These species occupied smaller ranges in 1999–2004 than in 1969–1979.

Road density (our proxy for the degree of human transformation in the landscape) had greater negative effects on forest birds than on any other species' habitat group, and had greater effects on deep endemic forest birds.

Both intensive land use and predation contributed to declines in seven (six endemic and one non-endemic) inland-breeding wading bird, tern and gull species, which became less widespread across the inland South Island between the measurement periods**.**

Conclusions

The overall pattern of change in the New Zealand avifauna between 1969–1979 and 1999–2004 was one of continued range declines in birds of older endemic lineages (deep endemics) and a shift to a non-endemic avifauna dominated by bird species of non-forest, human-modified habitats.

Because there was little left to lose in the more settled parts of New Zealand by 1969–1979, most of the subsequent loss of endemic birds occurred in remote areas.

Native land birds in greatest need of conservation effort are forest and alpine birds (especially, but not only, deep endemics), and endemic wading birds, terns or gulls that breed in the inland eastern South Island.

We conclude that predation by introduced mammals is probably the primary cause of decline in endemic forest and alpine birds, because there was little habitat change in many remote natural areas where the declines were greatest. However, both habitat loss to intensive land use *and* predation are major causes of range declines in endemic inland-breeding wading birds, terns and gulls.

Factors associated with human occupation have additional negative effects on native forest bird species, especially deep endemics. This result means that even with predator control, populations of a number of endemic species may not recover substantially in settled landscapes, and the outcomes of conservation investment may be poorer than in large, continuous and remote forest tracts.

It is the forests and inland basins most remote from New Zealand's large human communities that still provide sufficient habitat for there to be a prospect of maintaining large, viable populations of endemic forest birds and inland-breeding wading birds, terns and gulls. Achieving this outcome would require large-scale management of multiple predators in forests and inland basins. For inland-breeding wading birds, terns and gulls, it would also require new action to effectively and permanently protect the remaining breeding habitats in inland South Island.

1 Introduction and background

The Parliamentary Commissioner for the Environment is investigating what the future might hold for New Zealand's native birds. Many of New Zealand's native land birds are extraordinary: they represent orders, families and genera that occur nowhere else in the world, and/or they have exceptional life-history traits which evolved in a distinctive oceanic island environment through an evolutionary history without predatory mammals.

Many native land-bird species are also highly vulnerable to both habitat change and the effects of invasive species (especially predatory mammals). New Zealand's record of avian extinctions since human settlement is unequalled, and the proportion of surviving species considered threatened is higher than in any other country (Bradshaw et al. 2010). Precise statistics depend on how birds are named, classified and counted, but here is one example. In 2013 the New Zealand Threat Classification List (Robertson et al. 2013) named 140 original land-bird species on the 'mainland' (by which we mean North, South and Stewart Islands). Of these, 44 species (32%) are now globally extinct: 13 passerines (of which seven were wrens), the little bittern, two species of snipe, a quail, six species of rail, six species of ducks or geese, an owlet nightjar and two owls, a large harrier, an enormous eagle, and 10 species of moa. Of the 96 remaining land-bird species, at least 16 are now either absent from the mainland or confined to a few small, intensively managed mainland sanctuaries. Only 26 mainland land-bird species were considered 'not threatened' (Robertson et al. 2013).

This situation makes bird conservation a major focus in New Zealand. Because of the size and urgency of the need for conservation intervention, it is important to understand which birds will benefit most from conservation effort and where, at a national scale. Research on and management of native birds in New Zealand has amassed considerable knowledge of bird species distributions and conservation ecology. The New Zealand Threat Classification List is updated every 3 to 4 years and draws together the principal national experts in the field to provide a high-level overview of how species are doing.

However, the only data sets that have recorded the spatial distributions of all bird species across the whole nation are two national atlases of bird distribution compiled by the Ornithological Society of New Zealand (OSNZ; Bull et al. 1985; Robertson et al. 2007). Field surveys for the atlases were undertaken from September 1969 to December 1979 and from December 1999 to November 2004. Therefore, the data potentially provide the only spatially explicit, nationally comprehensive, all-species, multi-decade (25-year) view of the status of and trends in New Zealand's avifauna.

This unique and valuable source of data on New Zealand birds has not been widely used to inform their strategic management. In part this may be because of two non-standard aspects of the data, which complicate comparisons between the two atlas measurement periods: the different spatial systems and locations of the sampling units in the atlases (imperial vs metric grid squares), and differences in the levels of effort applied across the nation between and within the two different surveys. To make robust comparisons between 1969–1979 and 1999–2004, it has been necessary to create a standardised set of data from the two atlases. This is what we have done, and present in this report, along with summary statistics and analyses.

This report describes the major patterns of status and change in occupancy in 64 taxa of extant native land birds that still occur on the New Zealand mainland. To assist this description, we group the 64 taxa according to their highest taxonomic level of endemism (seven levels), and by their use of habitats (we recognise six groups).

In an associated report (Walker et al. 2017), we focus solely on the native forest birds, investigating how much loss of indigenous forest cover has affected them and to what degree much colder forests have provided thermal refuge from decline.

2 Objectives

- To describe the method we devised to derive standardised estimates of native land bird occupancy (the probability that a species occurs in a location) from the two OSNZ bird atlases.
- To use these estimates to provide, by way of summary statistics and analyses, an overview of which New Zealand land birds are in trouble, which are safe, and where conservation effort is needed most.

3 Glossary of technical terms used

Deep endemic: a bird taxon that is endemic at the order, family, or subfamily level (see **Taxonomic level of endemism**).

Detection probability: the probability that a taxon will be detected at a site, if it is present. Detection probabilities are usually less than 1, so not accounting for detection probabilities will usually lead to occupancy probabilities being underestimated.

Endemic: a taxon is endemic if it is unique to a defined geographic location, in this case, New Zealand. Non-endemic native and recently introduced taxa are also found elsewhere in the world.

Geographic range occupancy (or range occupancy): the proportion of a given geographic range that is occupied by a bird taxon, calculated as the average of local occupancy probabilities across that range. The difference in average occupancy probability between measurement periods represents the net change in the proportion of the geographic range occupied.

Grid square or square: a square on the national grid. In this report we use a grid of 10,000 m (10 × 10 km) squares defined in the metric New Zealand Map Grid (NZMG) coordinate system.

Indigenous (or native): a taxon that occurs naturally in New Zealand but may or may not be **endemic.** Indigenous (or native) taxa may either have been present at the time of human settlement, or have introduced and established themselves without human assistance since that time.

Kriging: a method of interpolating between measures in space, used in this report to interpolate estimates of local occupancy probability from the centres of the two different spatial grids used in the two measurement periods to the centres of a common 10 × 10 km grid.

Local occupancy probability: the probability that a taxon is present in a particular grid square.

Local richness: the number of taxa likely to occupy a square, calculated as the sum of occupancy probabilities across taxa in that square. The most likely 'real' number of taxa is the sum rounded to the nearest integer.

Log range occupancy ratio (LROR): a measure that expresses changes in range occupancy relative to the previous measure. It is calculated as the natural log of the ratio of the proportion of geographic range occupied in 1999–2004 to the proportion of geographic range occupied in 1969–1979. Large negative LRORs indicate large decreases relative to occupancy in 1969–1979, and large positive LRORs indicate large relative increases.

Measurement period: the period of field survey for a national atlas of bird distribution compiled by the Ornithological Society of New Zealand (OSNZ; Bull et al. 1985; Robertson et al. 2007). Field surveys for the first atlas (the 'first measurement period') ran from September 1969 to December 1979 and for the second atlas (the 'second measurement period') from December 1999 to November 2004.

Occupancy: presence at a site.

Occupancy model: a model that combines estimates of probabilities of detection and occupancy at a site to estimate the probability that a taxon is actually present.

Occupancy probability (or probability of occupancy): the probability that a taxon uses, or is present at, a site. Occupancy probability is expressed as a proportion (i.e. between 0.0 and 1.0).

Taxon (plural taxa): a species or a combination of species, subspecies, forms or varieties for which we fitted an occupancy model (section 4.3). For example, in this report the taxon 'kiwi' on the North Island refers to all recognised forms of *Apteryx mantellii* ('North Island kiwi taxa') and on the South Island it refers to *A. rowi, A. haastii* and all recognised forms of *Apteryx australis* ('South Island kiwi taxa') together.

Taxonomic level of endemism (endemism level): the taxonomic level at which a taxon is endemic. High to low endemism levels in this report are represented by order, family, subfamily, genus, and species taxonomic levels. Order level of endemism means that the bird's order does not occur outside New Zealand. This is the case for kiwi, which belong to the endemic order Apterygiformes. In family-level endemics the family does not occur outside New Zealand. For example, rifleman and rock wren are family-level endemics because the New Zealand wren family (Acanthisittidae) does not occur outside New Zealand. High taxonomic levels of endemism indicate that the lineage of a species has probably been in New Zealand over a long geological time period, whereas non-endemic taxa are likely to have arrived more recently in geological time. We refer to taxa that are endemic at the order, family, or subfamily levels as 'deep endemics'.

4 Preparing the bird occupancy data set

4.1 The Ornithological Society of New Zealand's national atlases of bird distribution

We created a standardised set of data covering 64 taxa of native land birds (listed in Appendix 1) from the two national atlases of bird distribution compiled by the Ornithological Society of New Zealand (OSNZ; Bull et al. 1985; Robertson et al. 2007). Field surveys for the first atlas ran from September 1969 to December 1979 (1969–1979) and for the second Atlas from December 1999 to November 2004 (1999–2004). These two periods are referred to here as the first and second 'measurement periods'.

Observers for the first atlas recorded observations in 10,000 yard grid squares of the national grid in the imperial coordinate system. Observations in the second atlas were recorded in 10,000 m (10 × 10 km) squares on the national grid defined in the metric New Zealand Map Grid (NZMG) coordinate system. Some areas – including the Chatham Islands and many offshore islands – were not covered in one or both of the atlases, and are not considered here.

In each measurement period volunteer observers recorded and submitted observations of bird species on atlas record sheets. Each sheet covered one of the grid squares that had been observed over a stated time period. Observers could submit either a complete sheet (a 'full list') or an incomplete sheet (a 'part list'). In a complete sheet, the observer considered that they had recorded all of the species that actually occurred in the grid square (Robertson et al. 2007). These complete sheets are the only data we used.

There was no limit on how many sheets could be returned for a grid square. Accordingly, the numbers of complete sheets returned for the different grid squares across the country varied greatly within each measurement period and between measurement periods.

We used a two-stage modelling process to overcome the challenges presented, first by the different levels of observer effort across grid squares within each measurement period, and second by differences in the spatial locations of the grid squares between the two measurement periods.

4.2 Estimates of occupancy from atlas data

We fitted two occupancy models (one for each measurement period, 1969-1979 and 1999-2004) for each land-bird taxon, which provided estimates of the bird's probability of occupancy in each grid square that was sampled. These fitted estimates were then interpolated to a common 10 × 10 km grid. This two-stage process is summarised below and described in detail in Appendix 2 to this report.

4.2.1 Stage 1: Fitting occupancy models

In stage 1 we adopted an occupancy modelling approach to address differences in effort. Occupancy models recognise that the detection of species by observers is imperfect: often the probability of detecting a species that is actually present is much less than 1.0 (MacKenzie et al. 2002; Bailey et al. 2014). Non-detection of a species at a site does not mean that the species is truly absent, because it may be a false absence. Furthermore, detectability can vary not only among species but also across observers, and also as a result of other factors such as season. The probability of occupancy (the probability that a species was actually present at a site) is therefore explicitly estimated in models that combine probabilities of detection and occupancy allowing for unbiased estimates of occupancy.

We fitted two such models for each individual bird taxon: one for each of the two measurement periods. As noted above, in each model we considered only observations from complete sheets (those in which the observer considered they had recorded all species that actually occurred in the grid square). This means that absences should reflect a true failure to detect a bird, which is a prerequisite for estimating detection probabilities in occupancy models. We allowed probability of detection in each model to vary seasonally by including season (spring, summer, autumn or winter) as a covariate.

Each model was fitted using Bayesian inference with three Markov chain Monte Carlo (MCMC) chains (Appendix 2). Once the chains had converged, we drew 1,000 fitted estimates of occupancy probability from each chain for each grid square with data (i.e. squares with at least one complete sheet returned). These fitted estimates are of the probability that a bird was actually present in each grid square, and are expressed as proportions (i.e. between 0.0 and 1.0). We used only the median of the 3 (chains) x 1,000 estimates for each square in stage 2 (implications are discussed in section 4.2.3 below).

4.2.2 Stage 2: Interpolating estimates to a common grid

In stage 2 we addressed differences in the spatial location of observations. We did this by interpolating median estimates of occupancy for each species and measurement period from stage 1 from the centre of each original grid square to the centres of a common grid of 10 × 10 km squares using kriging (Appendix 2).

So as not to predict and compare probabilities of occupancy outside the range of the original data, the common grid excluded all locations not sampled by complete sheets in both atlases. It also excluded all squares overlying more than 75% water (i.e. some coastal grids overlying areas of sea and large lakes). These exclusions mean that our standardised data do not include all of the areas sampled in the atlases, but only the areas for which we can make robust comparisons between measurement periods.

4.2.3 Data used in subsequent analyses, and their limitations

The data set produced by this process contained estimates of the median probability of occupancy for each of 64 modelled indigenous bird taxa (Appendix 1), in each of 2,155 unique grid squares, in each of two measurement periods (1969–1979 and 1999–2004). All subsequent analyses were based on this standardised data set.

We assigned the 2,155 grid squares to either the North Island or the South Island. Nearshore islands were assigned to the nearer of the two major islands, so that Stewart

Island squares were assigned to the South Island. There are 1,083 North Island squares and 1,072 South Island squares, covering similar areas of land on each island (99,510 and 99,630 km^2, respectively). The data cover 88% of the land on the North Island and 66% of the land on the South Island and Stewart Island combined.

The database allows unbiased *median* probabilities of occupancy that are estimated on an identical basis to be compared at the same locations in two measurement periods. The variability in estimates of occupancy and in the estimates from kriging was not preserved. This variability in the median probabilities in the data set should be preserved and considered in subsequent analyses; for example, through bootstrapping. Although this is not impossible, it is very computationally intensive, and we have not been able to do it for the present analyses. As described in section 6.3, we were primarily concerned in fitting our models to take into account that squares adjacent to each other are less independent than those further apart ('spatial autocorrelation'), which has potential to bias parameter estimates. Taking spatial autocorrelation into account is itself a very computationally intensive process, which would prevent bootstrapping.

As a result, uncertainty in our estimates of occupancy (stage 1 above) is not represented in our summary statistics and models. Incorporating this uncertainty into our models may alter estimates of confidence intervals for the parameters of our models (results in sections 7.4 and 7.5, and Appendix 7), and therefore the inferred 'significance' or otherwise of effects.

4.3 Bird taxa included and excluded

We fitted occupancy models for as many of New Zealand's native land bird species as possible, which resulted in a data set covering 64 native land bird taxa (Appendix 1). We did not fit occupancy models for seabirds because coverage of the seas around New Zealand by the atlases was limited. Specifically, we omitted penguins (Sphenisciformes), albatrosses, fulmars, petrels, prions and shearwaters, storm petrels and diving petrels (Procellariformes), and tropicbirds (Phaethontiformes). We also omitted four of the five families of Pelecaniformes (pelicans, gannets and boobies, darters and frigate birds – Pelacidae, Sulidae, Anhingidae and Fregatidae), including only the cormorants and shags (Phalacrocoradicae) because a number of their species occur inland.

Some of New Zealand's extant indigenous land bird species were recorded too rarely in the atlases for occupancy to be estimated successfully. We were obliged to omit the following extant species or subspecies from our study: little-spotted kiwi (*Apteryx owenii*, in the order Apterygiformes); kākāpō (*Strigops habroptilus*, in the family Strigopidae); stitchbird (*Notiomystis cincta*, in the endemic family Notiomystidae; Driskell et al. 2007); and North Island saddleback and South Island saddleback (*Philesturnus carunculatus rufusater* and *P. carunculatus carunculatus,* both in the endemic family Callaeidae). We also excluded two species of New Zealand wrens (Ericson et al. 2002) that inhabited forest (North and South Island bush wrens *Xenicus longipes stokesii* and *X. longipes longipes*, in the family Acanthisittidae), which were extant and recorded in the first atlas (Bull et al. 1985), but are now considered to be globally extinct (Robertson et al. 2013). We excluded South Island kōkako (*Callaeas cinereus*), of which there has been only one accepted sighting since 1967 (in 2007; Miskelly et al. 2013). All the above taxa were recorded in fewer than 10 mainland squares in one or both atlases, and all are endemic to New Zealand at the order or family level.

Observations were too few for us to fit models for the cryptic freshwater wetland species marsh crake (*Porzana pusilla affinis*), spotless crake (*Porzana tabuensis tabuensis*) and banded rail (*Gallirallus philippensis assimilis*), and for brown teal (*Anas chlorotis*) in the South Island. We also omitted the grey duck (*Anas superciliosa*), which hybridises widely with exotic mallard and cannot reliably be distinguished from it in field observations.

We had to combine records of three species of parakeet (yellow-crowned, red-crowned and orange-fronted) into a single taxon, and all forms of weka (*Gallirallus australis*) into a single taxon, because a substantial proportion of atlas records were of unidentified species. Different 'kinds' of South Island kiwi (Innes et al. 2015) were not distinguished in the first atlas of bird distribution for New Zealand (Bull et al. 1985), so we treat all South Island kiwi (other than little spotted kiwi, *Apteryx owenii*, which was excluded) as a single taxon, which combines all subspecies of tokoeka (*Apteryx australis*; i.e. Haast, Fiordland and Rakiura tokoeka), rowi (*Apteryx rowi*) and great-spotted kiwi (*Apteryx haastii*). We also treat South Island and Stewart Island robin (*Petroica australis*) subspecies as a single South Island taxon.

Our models for North Island kōkako, whitehead, New Zealand dabchick and brown teal were fitted from and interpolated to squares only in the North Island. The New Zealand dabchick became extinct in the South Island as a breeding species in the 1940s, and records of brown teal were too few on the South Island to model. Our models for rock wren, brown creeper, kea, mohua, Australasian crested grebe, Stewart Island shag and black stilt were fitted from and interpolated to only South Island squares. For all other taxa, we fitted national models, which combined any recognised North Island, South Island and/or Stewart Island species (in the case of the robins *Petroica longipes* and *P. australis*), subspecies, forms or varieties.

5 Variables used in our analyses

5.1 Environmental characteristics of grid squares

We used publicly available GIS layers to calculate the following characteristics for each grid square (Figure 1):

- road density (RD): the length of all roads contained in the LINZ 25 m road centrelines data set, divided by land area in the square
- distance from the coast (DC): the shortest distance (in km) from the square centroid to the coastline, as defined in the LINZ New Zealand coastline 1:250,000 data layer
- crop, pasture or exotic forestry plantation (CPEF): the percentage of land in the square under cover of exotic crops (including horticulture), pasture or exotic forestry plantation, derived from the national land cover database (LCDB) cover classes 'Short-rotation Cropland', 'Orchard Vineyard and Other Perennial Crops',

'High Producing Exotic Grassland', 'Forest – Harvested' and 'Exotic Forest' (Appendix 3; LCRIT 2015)

- urbanisation (URB): percent of land in the square under the LCDB cover classes 'Built-up Area (settlement)', 'Urban Parkland / Open Space', 'Transport Infrastructure' and/or 'Surface Mines and Dumps' (Appendix 3).

For the analysis we transformed these variables so that they spanned similar scales and centred them on zero. Road density was transformed by first taking the square root, and then scaling by dividing by the standard deviation. We scaled the measure of distance from the coast by dividing by 10, and CPEF and urbanisation by dividing by the standard deviation.

We used road density as a proxy for the degree of human transformation in the landscape that is relevant to all bird groups. We preferred this measure over others such as deforestation or land cover class because, unlike these measures, road density is likely to reflect all forms of transformation and so be relevant to all bird groups. Distance from the coast was used to help differentiate spatial patterns of change in wading birds, gulls and terns, which forage on the coast but breed either inland (mainly in the South Island) or on the coast.

We used paired scatter plots and coefficients of correlation to examine relationships between the four grid square-level characteristics on each island (Figure 2). Road density and crop, pasture or plantation forestry cover were strongly positively correlated on both islands. Because they represent quite similar gradients, we avoid including both RD and CPEF as predictors in any model (see sections 6.4 and 6.5). Correlations between road density, distance to the coast and urbanisation were relatively weak (Figure 2).

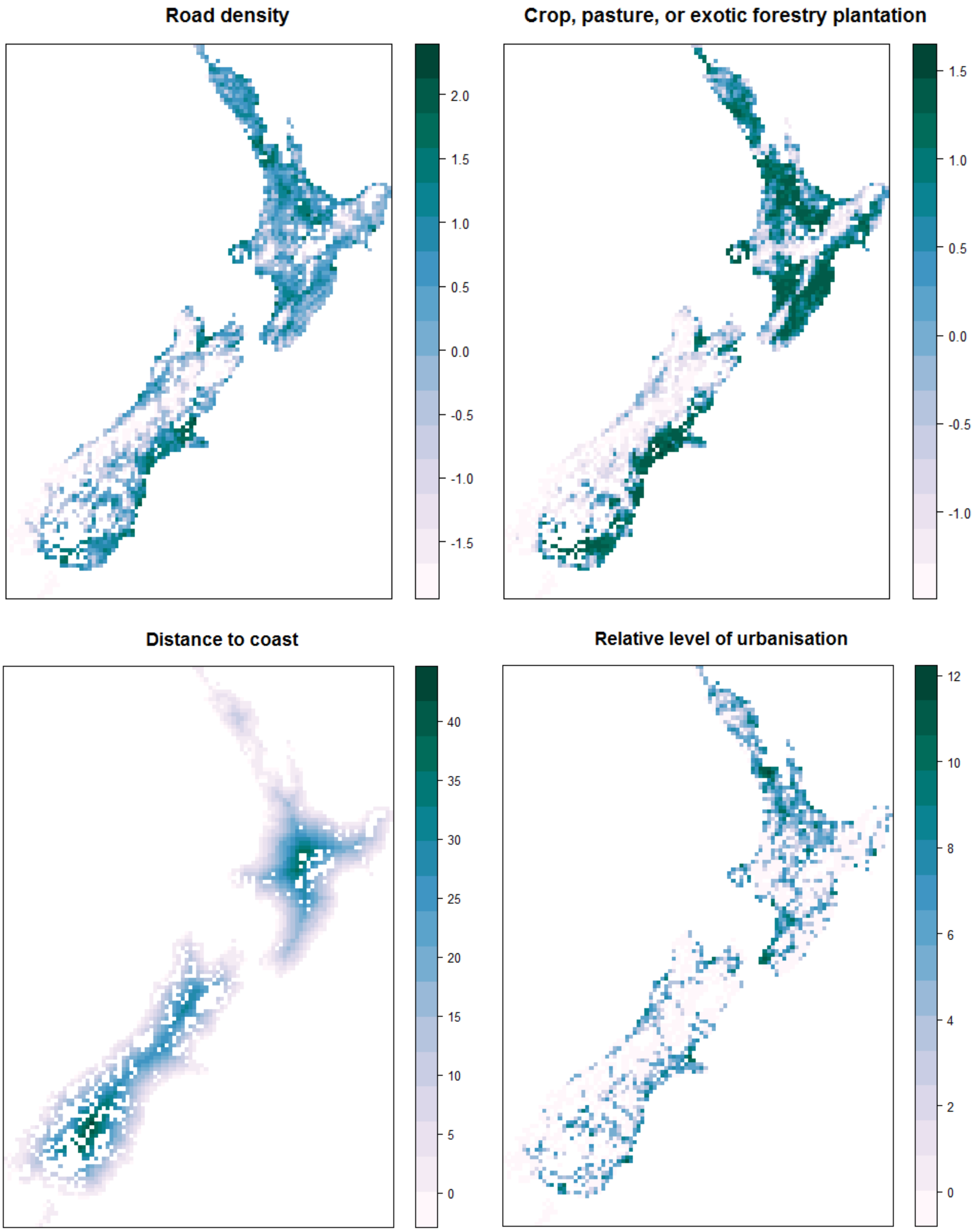

Figure 1 Environmental characteristics of the grid squares used in this report. Road density is the square root of road density (km/km$^{2)}$; crop, pasture or plantation forestry and levels of urbanisation are the percentage of the square under those cover types, scaled and centred (relative level of urbanisation was logged for display on this map); distance to coast is given in km/10.

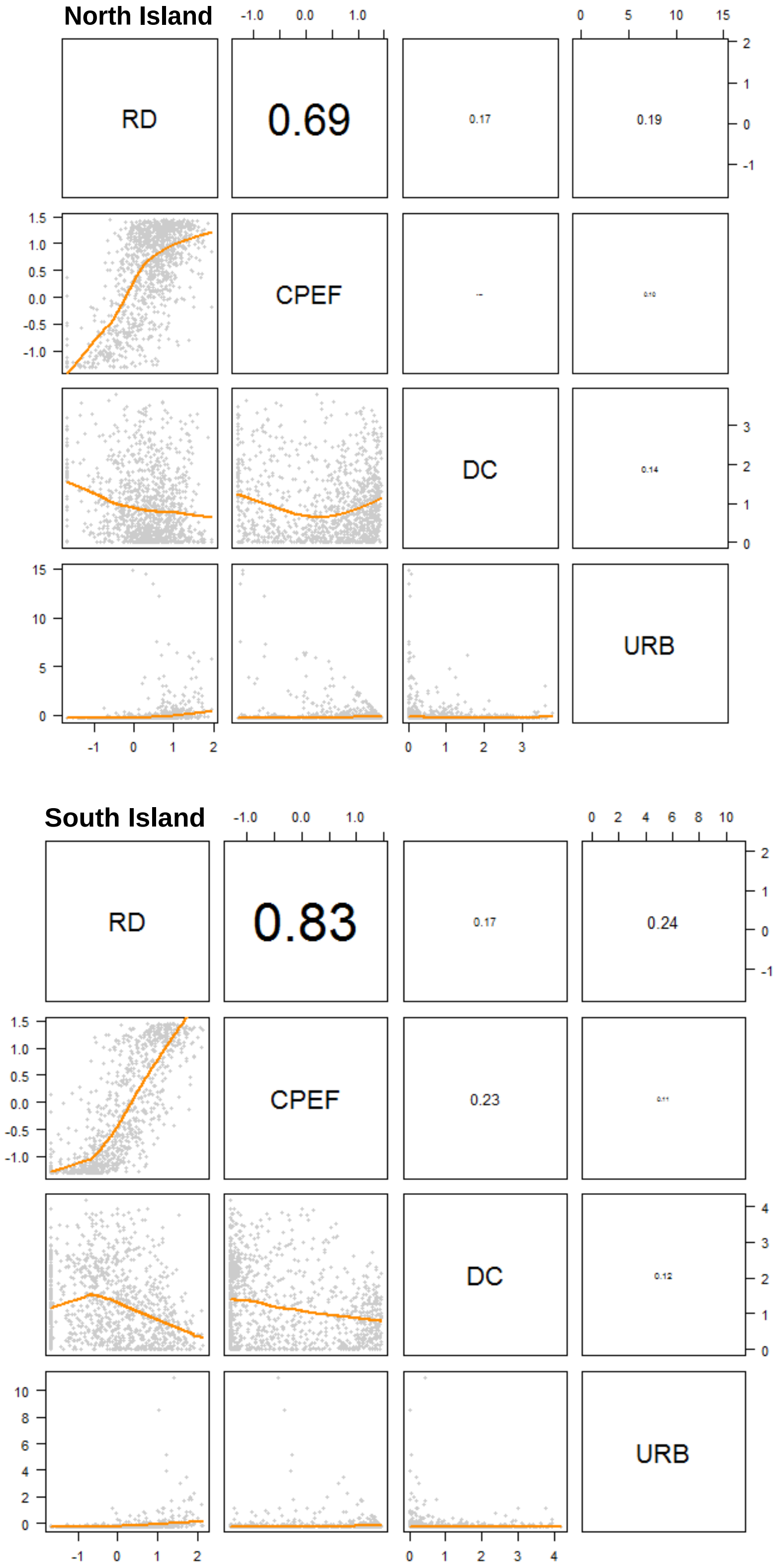

Figure 2 Relationships between environmental characteristics of the 2,155 grid squares in the North and South Islands. The characteristics compared on each island are labelled on the diagonal (RD = scaled and centred square root of road density; CPEF = crop, pasture or plantation forestry cover; DC = distance to coast in km/10), URB = relative level of urbanisation. In each set of subplots, plots below the diagonal show grid squares as points on scatter plots and their relationships (depicted using local regression curves, as orange lines). Subplots above the diagonal show the associated coefficients of correlation between pairs of characteristics; larger text indicates stronger correlation.

5.2 Endemism levels and habitats of the bird taxa

Endemic birds, especially deep endemics, evolved over long periods of time in New Zealand before human settlement. We recognised seven taxonomic levels of endemism and applied these as a proxy for the length of time a lineage has been isolated in New Zealand (Table 1). We refer to taxa that are endemic at levels 5, 6 and 7 (subfamily and higher) collectively as 'deep endemics'. In analyses we treat levels of endemism as a centred continuous integer predictor variable with equally spaced values of −3 (recently self-introduced) to 3 (endemic at the taxonomic level of order).

Table 1 The seven taxonomic levels of endemism recognised in this report, showing the higher-level division into endemic or non-endemic, and the number of taxa in this report that are assigned to each category

Endemism level	Endemic or non-endemic	Number of taxa
1. Recently self-introduced native	Non-endemic	8
2. Non-endemic native	Non-endemic	18
3. Endemic at the species level	Endemic	24
4. Endemic at the genus level	Endemic	4
5. Endemic at the subfamily level	Endemic	1 (blue duck/whio)
6. Endemic at the family level	Endemic	8
7. Endemic at the order level	Endemic	1 (kiwi species).

There are many valid ways to group bird taxa. In this report we recognise six groups based on their use of habitats (Table 2). We follow Innes et al. (2010) in defining native forest birds as those that breed and feed primarily in forest habitats. However, our list of 22 taxa differs from that of Innes et al. (2010) in including kea (*Nestor notabilis*), which feeds and breeds in forest (although not exclusively; Heather & Robertson 1996; O'Donnell & Dilks 1986).

Table 2 Seven groups of taxa recognised in our analyses based on their use of habitats

Habitat group	Number of taxa	Criteria
Forest	22	Birds that breed and feed primarily in forest habitats. Our list differs from that of Innes et al. (2010) by including kea (*Nestor notabilis*).
Inland-breeding wading bird, tern or gull	7	Birds in the order Charadriiformes ('shorebirds') that breed primarily in inland habitats.
Coastal-breeding wading bird, tern or gull	6	Birds in the order Charadriiformes ('shorebirds') that breed primarily in coastal habitats rather than inland.
Freshwater wetland	17	Birds that breed and feed primarily in freshwater wetland habitats.
Coastal wetlands and shores	5	Birds that breed and feed primarily on the coast, in wetlands and other habitats.
Open	7	Birds that breed and feed primarily in non-forest and non-wetland habitats that are not members of the order Charadriiformes.

The bird order Charadriiformes (also known as shorebirds) provides another natural grouping of birds. We refer to them in this report as 'wading birds, terns and gulls' because a number of New Zealand's native 'shorebirds' occur inland and seldom on shores. We divide the 13 wading bird, tern and gull species into two groups based on the location of their primary breeding habitats: inland (seven taxa) or coastal (six taxa). We divide 22 wetland birds into those of freshwater habitats (17 taxa) and coastal wetlands and shores (five taxa). The remaining seven taxa occur in other open habitats.

Endemism level is non-randomly distributed among land-bird taxa of different habitat types (Figure 3). Most of the deep endemic land birds that remain on New Zealand's three main islands are native forest birds. These 22 forest bird taxa include all but one of our 64 taxa that are endemic at the highest levels (order, family and subfamily levels) (Figure 3; Appendix 1), and three of the four that are endemic at the genus level. Just one bird species of open habitats (the alpine habitat specialist rock wren) is endemic at the family level.

The inland breeding wrybill (*Anarhynchus frontalis*) is the only non-forest taxon that is endemic at the genus level. Most (five of seven) inland-breeding wading bird, tern and gull taxa, and three of the seven taxa of open habitats (New Zealand pipit, New Zealand falcon, and paradise shelduck) are endemic at the level of species.

Four non-endemic native taxa and two species-level endemics (New Zealand dotterel and variable oystercatcher) make up the wading birds, terns and gulls that breed on the coast. Most birds of freshwater wetland habitats (12 of 17) and coastal wetlands and shores (three of five) are non-endemic native or recently self-introduced species. The New Zealand dabchick, fernbird, New Zealand scaup, little shag, brown teal, Stewart Island shag and spotted shag are wetland birds that are endemic at the species level.

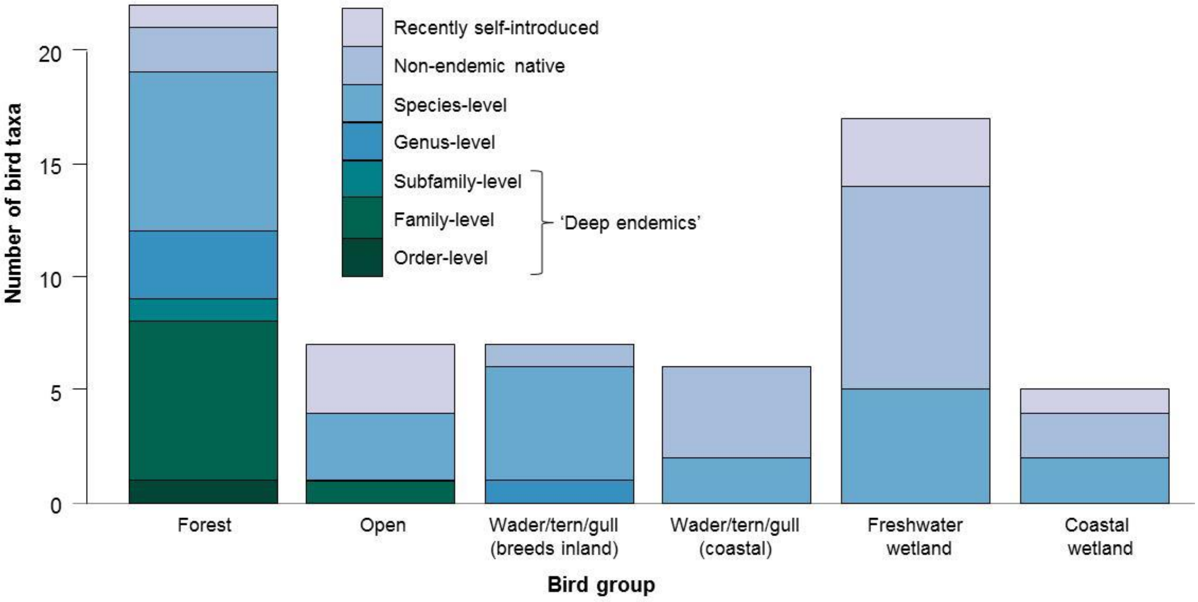

Figure 3 Distribution of endemism level among 64 taxa in six habitat groups.

6 Analyses

We used R version 3.2.2 (R Development Core Team 2016) to summarise the status of and changes in occupancy, and richness patterns (sections 6.1 to 6.3). Linear mixed effects models (sections 6.4 and 6.5) were fitted using the R package lme4 (Bates et al. 2015).

6.1 Summaries of status and change in occupancy

To summarise status of and change in taxa we calculated and plotted the average, the interquartile range (i.e. the middle 50% of estimates) and the 95% limits of (1) median probabilities of occupancy in the 1999–2004 measurement period ('status') and (2) differences in median probabilities of occupancy between 1999–2004 and 1969–1979 ('change') across all squares on each island.

We refer to the median occupancy probability in a particular square (derived in section 4.2) as 'local occupancy probability' (see Glossary, section 3). The average of median local occupancy probabilities across squares is used as an estimate of the proportion of the geographic range occupied by an individual bird taxon[1]. The difference in average occupancy probabilities between measurement periods is used to represent the net change in proportion of the geographic range occupied.

6.2 Relative changes (log range occupancy ratios, or LRORs)

When a taxon is rare (it occupies a small proportion of squares on an island), any change in the proportion of range occupied between measurement periods will often be small. However, small absolute changes can represent large and significant relative changes, such as a halving or doubling of the geographic range occupied in the first measurement period. We therefore use log range occupancy ratios (LRORs – equivalent to log response ratios; Hedges et al. 1999) to express and summarise relative changes in net range occupancy in a way that is independent of absolute magnitude and produces an approximately normal distribution. LRORs are calculated as the natural log of the ratio of the proportion of geographic range occupied in 1999–2004 to the proportion of geographic range occupied in 1969–1979. Large negative LRORs indicate large decreases relative to occupancy in 1969–1979, and large positive LRORs indicate large relative increases. Range contraction is an important signal of likely population decline (Caughley & Gunn 1996).

We plotted status, change and LRORs for bird taxa in each different habitat group. Within habitat groups we arranged taxa in order of decreasing level of endemism, and in order of low to high total range occupancy across both islands within each level of endemism.

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[1] Calculating geographic range occupied empirically requires drawing either zeros or ones at random from a binomial distribution with probability equal to the occupancy probability, and calculating the proportion of the draws that are ones. However if this process is repeated enough times, the estimate of proportion of range occupied is identical to the average occupancy probability across the squares of interest.

As a simple way of identifying whether certain groups have more- or fewer-than-expected taxa that declined or increased, we used chi-square tests to test whether the direction of range occupancy change between measurement periods on either island was independent of endemism level and of habitat group.

6.3 Local richness patterns

We summed median occupancy probabilities across taxa within squares to estimate the number of taxa likely to occupy a square ('local richness'). Change in local richness was derived by subtracting local richness estimates for squares in 1969–1979 from those for 1999–2004. For this purpose we combined taxa endemic at the levels of order, family and subfamily into a single group of 10 deep endemics.

To show spatial patterns of status and change, we plotted maps of local richness (numbers of taxa per square) and richness change across taxa aggregated by endemism level and habitat group. Summing occupancy probabilities (each between 0.0 and 1.0) results in non-integer estimates of the most likely number of taxa per square, when only whole numbers of species are possible in reality. We use scales on our map that round these estimates to the nearest integer (thus showing the most likely 'real' outcome). However, we plot the raw (non-integer) estimates in box plots to show their distribution and to enable comparisons between the islands.

6.4 Effects of time, endemism, habitat and environment on all land birds

We fitted models to test how time (i.e. measurement period), endemism level, habitat group and environmental factors affected median occupancy probabilities across the 64 native land birds. These models were fitted as linear mixed effects (lme) models using the R package lme4[2].

Occupancy probability was modelled as the logit $(x/(1 - x))$ of the proportion. Measurement period was a factor predictor variable, and we treated levels of endemism as a centred variable with seven equally spaced integers from −3 (recently self-introduced) to 3 (endemic at the taxonomic level of order). Responses of occupancy probability to our different environmental predictor variables (which we scaled and centred prior to model fitting) were fitted as linear terms.

In each model the taxon and family were included as random effects to account for non-independence of repeated measures on the same taxon and among taxa in the same bird

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[2] Our lme models don't take into account that squares adjacent to each other are less independent than those further apart ('spatial autocorrelation'), and models fitted without accounting for spatial autocorrelation can yield unreliable parameter estimates. To be confident that lme model results were robust, we therefore also attempted to fit all models as conditional autoregressive (CAR) mixed models using a Bayesian approach and the software Stan, interfaced through the R package RStan v. 2.14.1. We describe this process and compare its outputs to those from our lme models in Appendix 4.

family, and grid number was included to account for non-independence between repeated measures at the same location.

We expected that level of endemism in the birds and the geographic patterns of human settlement would be major drivers of occupancy and occupancy change in native land birds across all habitat groups. Specifically, we expected that:

- human settlement would more negatively affect deep endemic birds, which evolved for a longer period on a New Zealand land mass without mammals
- deep endemic birds would have shown the largest decreases between measurement periods
- recently self-introduced taxa would have shown the greatest increases, especially in more densely settled places
- non-endemic birds of non-forest habitats would be doing particularly well in densely settled places.

We tested our expectations by fitting two lme models for each island. The first, simpler model (Model 1) used a three-way interaction between measurement period, endemism level and our index of road density (a proxy for human settlement density) to predict occupancy probability. Model 2 included a fourth term (habitat group) in a full four-way interaction between measurement period, endemism level, road density and habitat group. To interpret these models we examined parameter estimates and plotted effects.

6.5 Effects of location and land use on inland-breeding wading birds, terns and gulls

We then focused on the seven wading birds, terns or gulls that breed mainly in the inland eastern South Island[3]. The primary breeding habitats of these species are braided riverbeds and outwash plains, which occur mainly in the interior of the South Island. These habitats provide negligible refuge from predators. Six of the inland-breeding species are endemic. Because they have undergone a period of evolution in isolation from mammal predators, they are less likely than non-endemic species to have retained or developed behaviours that enable them to avoid predation, especially in their breeding habitats, where they nest on the ground. In recent decades the breeding habitats of these birds have undergone loss and modification due to intensive agricultural development, afforestation and the spread of woody weeds.

For these reasons, we expected that

- occupancy probabilities would have decreased more between measurement periods in endemic taxa than in the non-endemic pied stilt

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[3] We investigate and describe the patterns of change in forest birds in detail in a companion report (Walker et al. 2017).

- occupancy probabilities would have decreased more in inland habitats than in their coastal feeding habitats
- occupancy probabilities would be lower in squares that have been more completely developed for exotic crops and pasture, or converted for forestry
- these effects would be greater in the South Island.

We compared inland and coastal range changes in the South Island by calculating and plotting LRORs (log ratios of range occupancy – our relative measure of range occupancy change) for the seven taxa in each range. Coastal squares were defined simply as those with centroid distance to the coast less than the mean distance across all squares (12.5 km).

We then fitted lme models of median occupancy probabilities for each island with a four-way interaction between measurement period, endemism level, distance to coast and our index of intensive agricultural and forestry land use (Model 3). A two-way interaction between measurement period and urbanisation was included in Model 3 to determine how much urbanisation was affecting the occupancy probabilities of these birds. We examined parameter estimates from the models for each island and plotted their effects.

7 Results

7.1 Status and change in occupancy

7.1.1 Native forest birds

Nineteen of the 22 native forest bird taxa in our occupancy data set occur in the North Island and 20 in the South Island. The most range-restricted forest taxa in both islands in 1999–2004 were endemic at the order, family and subfamily levels (blue duck/whio, kiwi species, kākā and long-tailed cuckoo on both islands, North Island kōkako and rifleman in the North Island, and yellowhead/mohua in the South Island), or at the species level (weka on both islands and parakeets and North Island robin on the North Island; Figure 4a, Appendix 5). Two species-level endemics (grey warbler and fantail) and the self-introduced silvereye occupied the largest geographic ranges on both islands.

Some taxa occupied very different ranges in the North and South Islands: rifleman, bellbird and tomtit occupied larger ranges in the South Island, while kererū, tūī, grey warbler, fantail, morepork, shining cuckoo and silvereye are more widespread in the North Island.

Just over half of the 22 native forest bird taxa became less widespread between measurement periods (10 taxa in the North Island and 11 in the South Island; Figure 4b). In those that occur on both islands, the direction of net range occupancy change between measurement periods was the same for most taxa on both islands. Exceptions were kererū and tūī: their ranges increased on the North Island and decreased on the South Island.

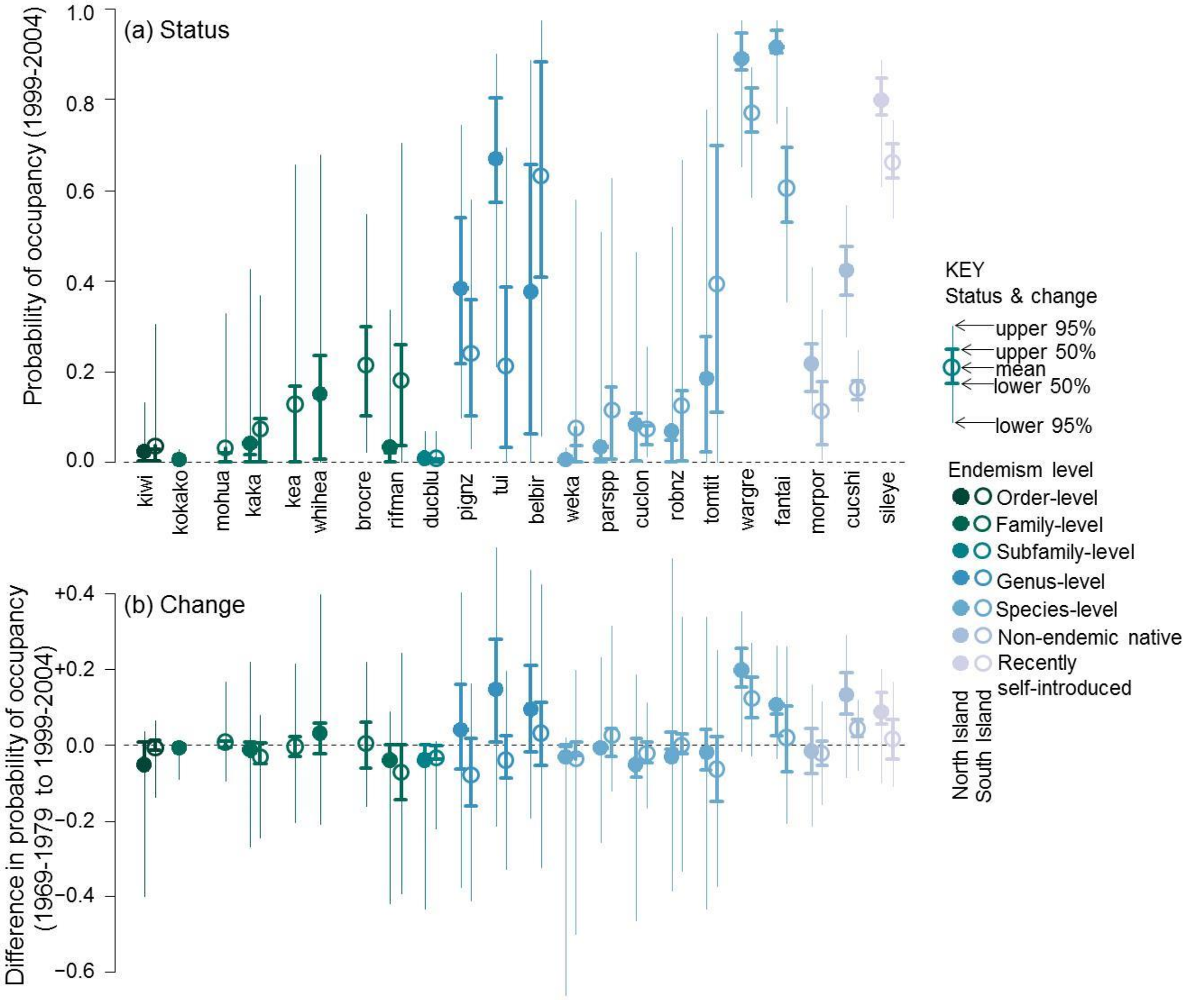

Figure 4 Occupancy in forest birds, showing (a) status in 1999–2004, and (b) change in occupancy between 1969–1979 and 1999–2004. Each plot shows the mean ('range occupancy') and upper and lower (50% and 95%) bounds of median-fitted estimates of occupancy in the North and South Islands (filled and hollow symbols, respectively). Taxa are arranged in order of decreasing level of endemism, and within endemism levels are arranged in order of increasing average occupancy across both islands. The taxa are: kiwi = kiwi species; kokako = North Island kōkako; mohua = yellowhead/mohua; kaka = kākā; kea = kea; whihea = whitehead; brocre = brown creeper; rifman = rifleman; ducblu = blue duck/whio; pignz = kererū; tui = tūī; belbir = bellbird; weka = weka species; parspp = parakeet species; cuclon = long-tailed cuckoo; robnz = New Zealand robin; tomtit = New Zealand tomtit; wargre = grey warbler; fantai = New Zealand fantail; morpor = morepork; cucshi = shining cuckoo; sileye = silvereye.

The largest absolute estimated net decreases in range occupancy among the native forest birds were in North Island brown kiwi, long-tailed cuckoo, blue duck, rifleman, North Island robin and weka in the North Island, and kererū, rifleman, tomtit, tūī, weka, blue duck and kākā in the South Island (Figure 4b). The largest estimated net range increases were in grey warbler, tūī, shining cuckoo, bellbird, silvereye, fantail and kererū in the North Island, and grey warbler, fantail and shining cuckoo in the South Island.

7.1.2 Wading birds, terns and gulls (Charadriiformes)

On both islands, wading birds, terns and gulls endemic at the genus or species levels occupied smaller ranges than non-endemic taxa (Figure 5a). Inland-breeding black stilts and wrybills and the coastal New Zealand dotterel were the most range restricted of the 13 taxa for which we have models (Appendix 5). The southern black-backed gull was the most widespread of the wading birds, terns and gulls on both islands.

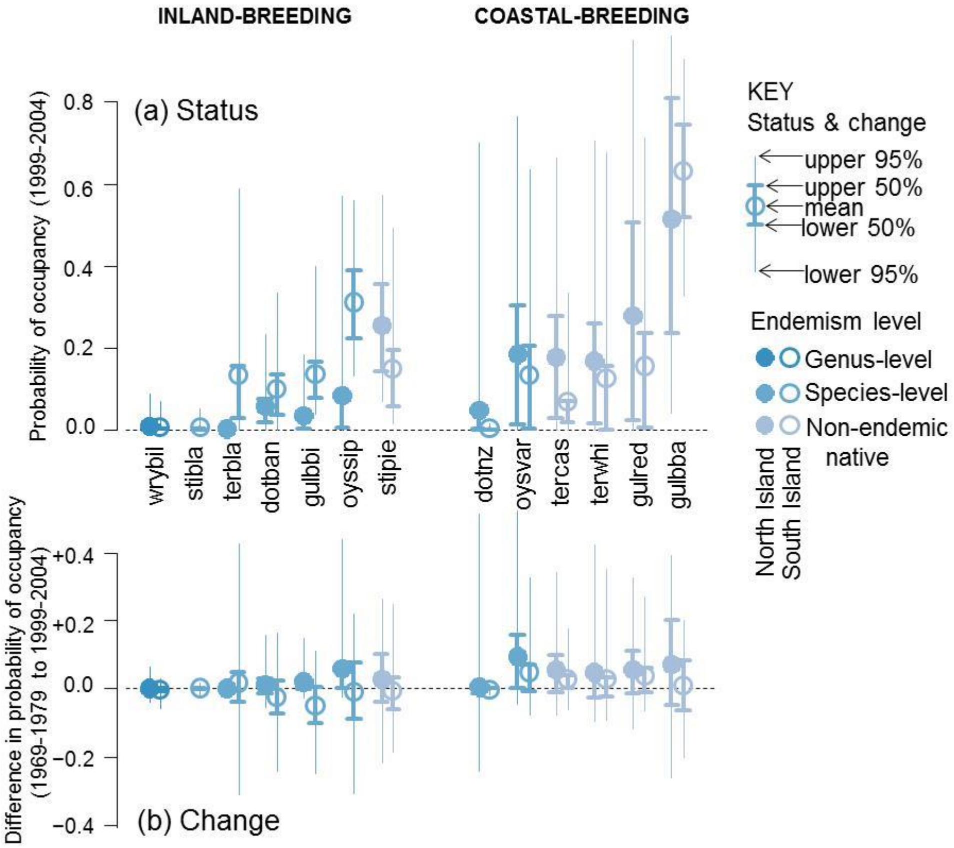

Figure 5 Occupancy in wading birds, terns and gulls (which share the order Charadriiformes), showing (a) status in 1999–2004, and (b) change in occupancy between 1969–1979 and 1999–2004. Each plot shows the mean ('range occupancy') and upper and lower (50% and 95%) bounds of median fitted estimates of occupancy in the North and South Islands (filled and hollow symbols, respectively). Taxa are arranged in order of decreasing level of endemism, and within endemism levels are arranged in order of increasing average occupancy across both islands. The taxa are: wrybil = wrybill; stibla = black stilt; terbla = black-fronted tern; dotban = banded dotterel; gulbbi = black billed gull; oyssip = South Island pied oystercatcher; stipie = Australasian pied stilt; dotnz = New Zealand dotterel; oysvar = variable oystercatcher; tercas = Caspian tern; terwhi = white-fronted tern; gulred = red billed gull; gulbba = southern black backed gull.

Six of the eight endemic taxa breed inland, principally in the inland South Island. The South Island provides both inland breeding and coastal feeding habitats for these species, which occupied larger ranges there than in the North Island, which offers mainly winter feeding habitat. The South Island ranges of endemic inland-breeding wading birds, terns and gulls decreased between 1969–1979 and 1999–2004 (Figure 5b; Appendix 5), although the range of the South Island pied oystercatcher increased on the North Island.

Most coastal-breeding taxa occupied larger ranges in the North Island than in the South Island (Figure 5a; Appendix 5). This may partly reflect the higher proportion of coastal grid squares that provide habitat there (16% of square centroids are within 1 km of the coast in the North Island, vs 12% in the South Island).

Five of the six coastal-breeding taxa became more widespread between 1969–1979 and 1999–2004. The largest average range increases were in the variable oystercatcher, red-billed gull and white-fronted tern on both islands, and the southern black-backed gull and Caspian tern in the North Island.

7.1.3 Birds of freshwater wetlands and coastal wetlands and shores

Most (15 of 22) of the taxa we were able to include in these two wetland habitat groups are non-endemic[4]. Many occupied relatively small ranges (i.e. <10% of squares) on both islands in 1999–2004 (Figure 6a; Appendix 5).

The most range-restricted freshwater wetland taxa on the South Island were Australasian bittern, Australasian crested grebe, white heron and fernbird; the brown teal was too restricted in distribution there to fit an occupancy model. White heron, brown teal, Australian coot and Australasian bittern were least widespread in the North Island. The most widespread taxa were kingfisher in the North Island, and pūkeko, white-faced heron, little shag and little black shag on both islands (Figure 6a; Appendix 5). Pied shag was the most widespread of the five species of coastal wetlands and shores.

Range occupancy estimates for most wetland birds were greater in 1999–2004 than in 1969–1979, especially across North Island squares (Figure 6b; Appendix 5). The exceptions were the Australasian bittern in the South Island, and the reef heron on both islands, which occupied smaller ranges in 1999–2004 than in 1969–1979. The largest average range increases were recorded in the North Island, especially in pūkeko, kingfisher, little black shag, white-faced heron and black swan, and in pied shag along the coast.

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[4] As noted in section 4.3, observations were too few for us to fit models for the cryptic freshwater wetland species marsh crake, spotless crake and banded rail, and for brown teal on the South Island. We also omitted grey duck (which hybridises widely with exotic mallard and cannot readily be distinguished from it in observations).

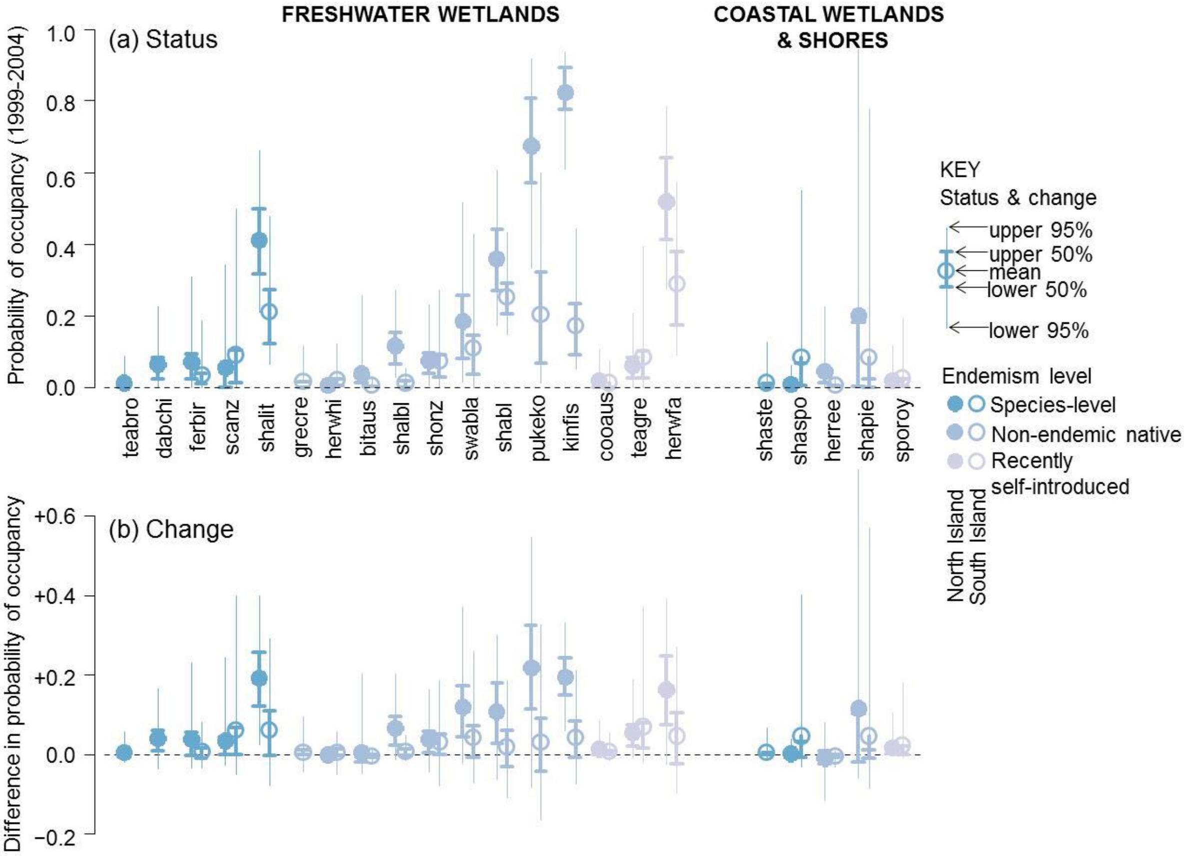


Figure 6 Occupancy of birds of freshwater wetlands and coastal wetlands and shores, showing (a) status in 1999–2004, and (b) change in occupancy between 1969–1979 and 1999–2004. Each plot shows the mean ('range occupancy') and upper and lower (50% and 95%) bounds of median fitted estimates of occupancy in the North and South Islands (filled and hollow symbols, respectively). Taxa are arranged in order of decreasing level of endemism, and within endemism levels are arranged in order of increasing average occupancy across both islands. The taxa are: teabro = brown teal; dabchi = New Zealand dabchick; ferbir = fernbird; scanz = New Zealand scaup; shalit = little shag; grecre = Australasian crested grebe; herwhi = white heron; bitaus = Australasian bittern; shalbl = little black shag; shonz = New Zealand shoveller; swabla = black swan; shabl = black shag; pukeko = pūkeko; kinfis = New Zealand kingfisher; cooaus = Australian coot; teagre = grey teal; herwfa = white-faced heron; shaspo = spotted shag; herree = reef heron; shapie = pied shag; sporoy = royal spoonbill.

7.1.4 Birds of other open habitats

Of the seven birds we categorised as open-habitat specialists, rock wren (endemic at the family level, confined to the South Island) and New Zealand falcon had the lowest range occupancies in 1999–2004 (Figure 7a). Paradise shelduck, welcome swallow, spurwing plover and Australasian harrier were very widespread, especially across North Island squares.

In the South Island, the ranges of the New Zealand pipit and rock wren decreased between 1999–2004 and 1969–1979, while the range of the New Zealand falcon increased somewhat (Figure 7b). Paradise shelduck, welcome swallow, spurwing plover and Australasian harrier ranges increased between measurement periods on both islands; increases were particularly large in the North Island.

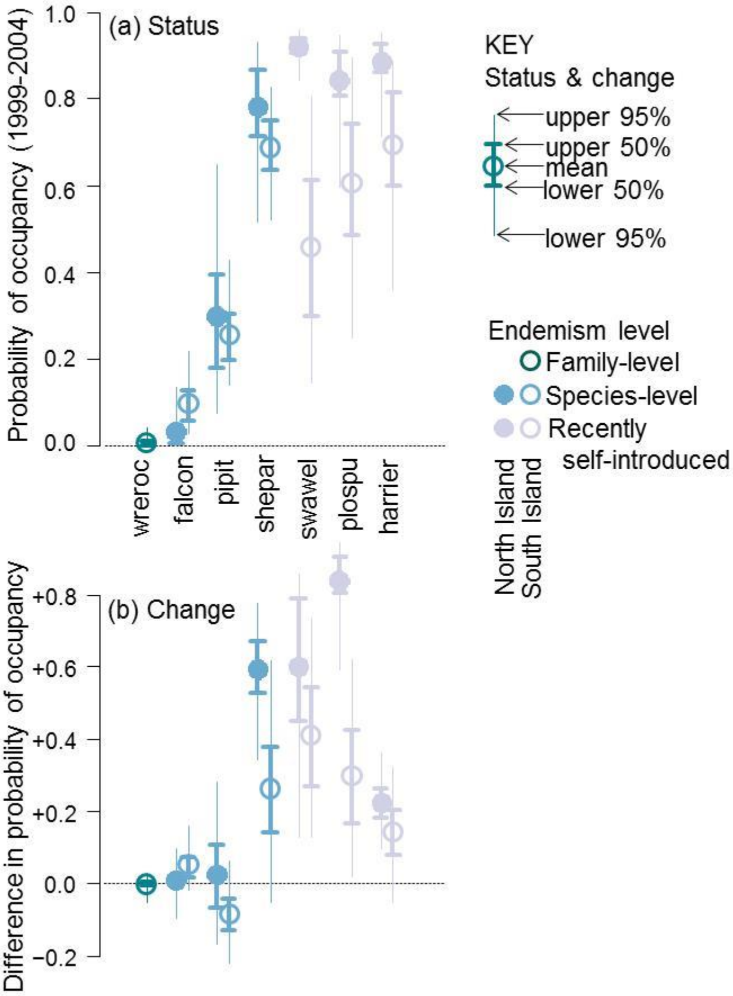


Figure 7 Occupancy of birds of open habitats (excluding Charadriiformes and wetland birds), showing (a) status in 1999–2004, and (b) change in occupancy between 1969–1979 and 1999–2004. Each plot shows the mean ('range occupancy') and upper and lower (50% and 95%) bounds of median fitted estimates of occupancy in the North and South Islands (filled and hollow symbols, respectively). Taxa are arranged in order of decreasing level of endemism, and within endemism levels are arranged in order of increasing average occupancy across both islands. The taxa are: wreroc = rock wren; falcon = New Zealand falcon; pipit = New Zealand pipit; shepar = paradise shelduck; swawel = welcome swallow; plospu = spurwing plover; harrier = Australasian harrier.

7.2 Relative changes (log range occupancy ratios, or LRORs)

Section 7.1 shows that species that occupied few squares generally also underwent small absolute net changes in range occupancy between measurement periods. The importance of these net changes relative to range occupancy in 1969–1979 is more readily appreciated when we use LRORs (section 6.2) to summarise and express them in a way that is independent of their absolute magnitude. When interpreting these ratios changes it is important to note the absence of estimates of confidence limits, which we have been unable to incorporate and which may be considerable in some taxa (see our discussion about incorporating uncertainty in occupancy estimates into our analyses in section 4.2.3).

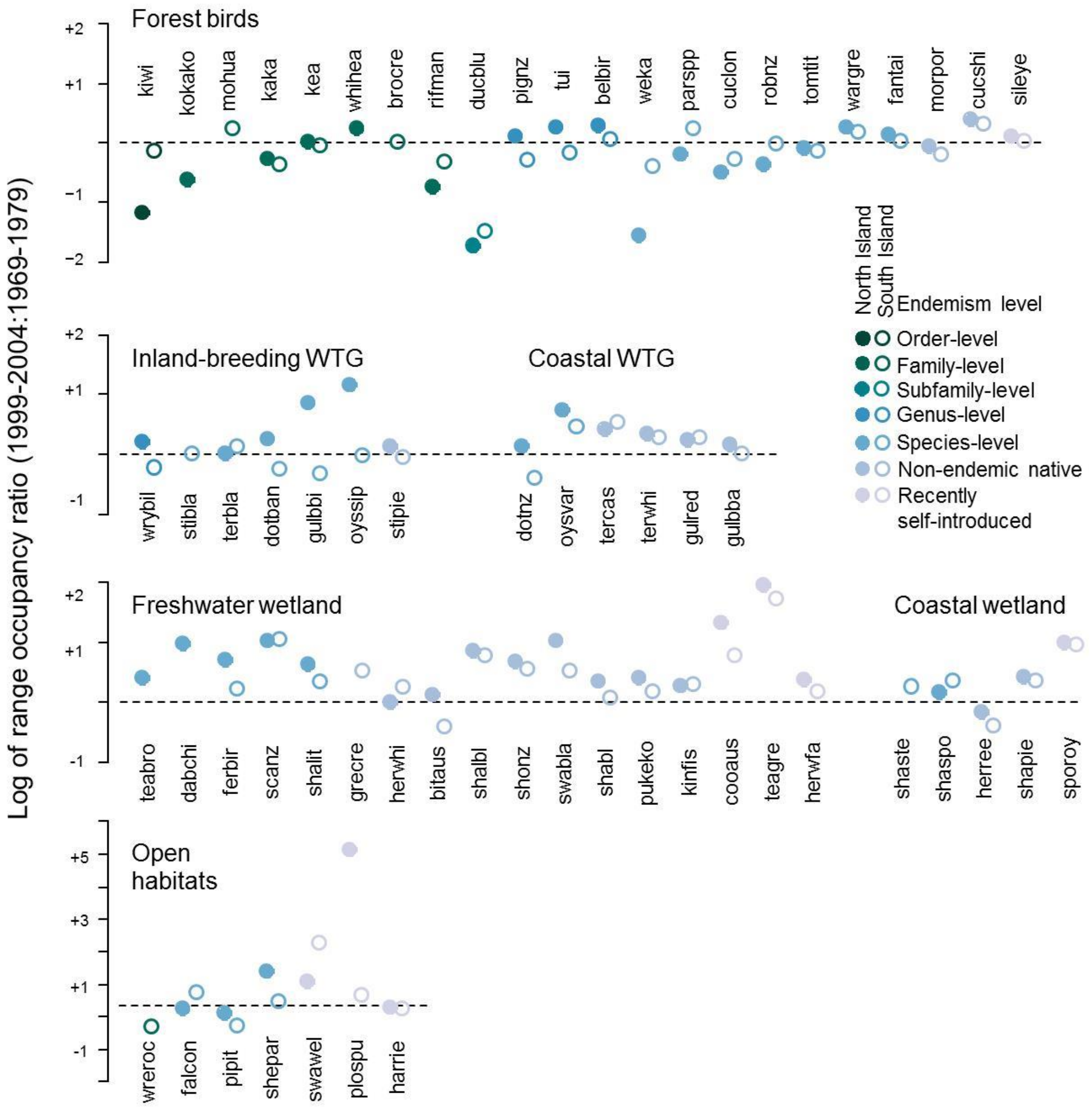


Figure 8 Relative net change in range occupancy between 1969–1979 and 1999–2004 for 64 native land-bird taxa in the North (solid symbols) and South I(hollow symbols) Islands, expressed as log range occupancy ratios (LRORs). Negative ratios indicate a net decrease and positive ratios indicate a net increase. Taxa are arranged in order of decreasing level of endemism, and within endemism levels are arranged in order of increasing range occupancy across both islands. **Native forest birds:** kiwi = kiwi species; kokako = North Island kōkako; mohua = yellowhead/mohua; kaka = kākā; kea = kea; whihea = whitehead; brocre = brown creeper; rifman = rifleman; ducblu = blue duck/whio; pignz = kererū; tui = tūī; belbir = bellbird; weka = weka species; parspp = parakeet species; cuclon = long-tailed cuckoo; robnz = New Zealand robin; tomtit = New Zealand tomtit; wargre = grey warbler; fantai = New Zealand fantail; morpor = morepork; cucshi = shining cuckoo; sileye = silvereye; **inland breeding WTG (wading bird, tern or gull):** wrybil = wrybill; stibla = black stilt; terbla = black-fronted tern; dotban = banded dotterel; gulbbi = black-billed gull; oyssip = South Island pied oystercatcher; stipie = Australasian pied stilt; **coastal WTG**: dotnz = New Zealand dotterel; oysvar = variable oystercatcher; tercas = Caspian tern; terwhi = white-fronted tern; gulred = red-billed gull; gulbba = southern black-backed gull; **freshwater wetland**: teabro = brown teal; dabchi = New Zealand dabchick; ferbir = fernbird; scanz = New Zealand scaup; shalit = little shag; grecre = Australasian crested grebe; herwhi = white heron; bitaus = Australasian bittern; shalbl = little black shag; shonz = New Zealand shoveller; swabla = black swan; shabl = black shag; pukeko = pūkeko; kinfis = New Zealand kingfisher; cooaus = Australian coot; teagre = grey teal; herwfa = white-faced heron; **coastal wetland and shores**: shaste = Stewart Island shag; shaspo = spotted shag; herree = reef heron; shapie = pied shag; sporoy = royal spoonbill; **other open habitats**: wreroc = rock wren; falcon = New Zealand falcon; pipit = New Zealand pipit; shepar = paradise shelduck; swawel = welcome swallow; plospu = spurwing plover; harrie = Australasian harrier.

Chi-square tests showed that on both islands the net direction of range occupancy change between measurement periods was not independent of either habitat group (forest vs non-forest, χ^2 = 21.6 (North Island), 11.8 (South Island), both $P < 0.001$ and df = 3); or endemism (endemics vs non-endemics, χ^2 = 47.3 (North Island), 18.5 (South Island), both $P < 0.001$, df = 3). The most conspicuous high-level patterns were:

- Of the bird taxa in which there was a net decrease in range occupancy between measurement periods, most (91% and 52% in the North and South Islands, respectively) were forest bird taxa and most (82% and 81%, respectively) were endemic at species or higher levels.
- Of the bird taxa in which there was a net increase in range, half or more were either non-endemic native or recently self-introduced taxa (50% and 58%, respectively) and most were non-forest taxa (80% and 76% in the North and South Islands, respectively).

The largest relative net decreases in range occupancy between measurement periods (the most negative LRORs) occurred in a suite of endemic forest birds (Figure 8): North Island brown kiwi, North Island kōkako and North Island robin in the North Island; and blue duck/whio, weka, rifleman, kākā and long-tailed cuckoo on both islands. Parakeet species in the North Island, and kiwi, kererū, tūī, tomtit and morepork also showed fairly large relative net range decreases in the South Island.

In non-forest birds, the largest relative net decreases in range in the South Island were in endemics of open habitats: the inland-breeding wrybill, banded dotterel and black-billed gull (see also below), and the coastal endemic New Zealand dotterel, rock wren and New Zealand pipit. Reef heron and Australasian bittern were the only non-endemic non-forest species with negative LRORs.

7.3 Local richness patterns

An important caveat when interpreting local richness patterns is that the median occupancy estimates and changes that are summed to estimate local richness (section 6.3) can be skewed. A square can be (relatively) 'rich' when a few birds have high median probabilities of occupancy but many are likely to be absent. Also, large changes in probabilities of occupancy of a few bird species can mask more subtle changes by many species in the opposite direction. For example, a moderate increase in the median occupancy probability of a single taxon (e.g. tūī, a genus-level endemic) can increase local richness even if there are smaller decreases in occupancy probabilities for other taxa in the same group (i.e. kererū and/or bellbird). Status and change in the local richness of any bird group is therefore best interpreted in conjunction with corresponding local occupancy and range occupancy plots for the individual taxa in each group.

There are clear latitudinal gradients and coastal-to-inland gradients in the number of native land-bird taxa present per square in 1999–2004 (Figure 9a). Local richness generally diminished from north to south and from the coast to inland, although some inland squares in and near the main axial ranges also had relatively high local richness. This pattern indicates that the diversity of native birds is generally higher where temperatures are higher, and that the occurrence of coastal-specialist birds supplements that of other land birds.

Richness patterns across different taxonomic levels of endemism

Few of New Zealand's deep-endemic land birds occur outside the main axial ranges and nearshore islands (Figure 9b). Taxa endemic at genus and species levels (Figures 9c & 9d) had wider ranges, but few occupied squares in the lowlands of Waikato, southern Taranaki, Manawatu, Hawke's Bay, Wairarapa, and the inland eastern South Island.

Non-endemic native and recently self-introduced taxa (Figures 9e and 9f) showed approximately inverse patterns of local richness compared to endemic birds (Figures 9a to 9d: see also Figure A6.1 in Appendix 6). Non-endemic native species were most numerous in squares around the coast, especially in the North Island and eastern and northern South Island, and fewest in squares on the southern and western coasts, and the main axial ranges (i.e. forests and mountains) of the South Island, and in inland South Island generally. Recently self-introduced taxa were most numerous in squares covering production and urban landscapes on both islands.

Overall, the local richness of native land birds increased between measurement periods across much of the North Island, especially around Auckland (Figure 10a). It increased along the coasts of the eastern and northern South Island, but not in the west and southwest. Local richness decreased most in the western South Island, some parts of the inland South Island, and in the central-western North Island.

Local richness of deep endemic birds decreased between measurement periods (Figure 10b) across much of their range. The number of genus-level endemics per square increased over many parts of the southern and eastern North Island, and around Auckland (Figure 10c). This is a relatively small group of taxa (n = 4) and much of the increase was due to higher occupancy probabilities in a single species (tūī). Local richness of genus-level endemics decreased widely across western South Island forests, in Northland, and in the western Waikato and King Country.

Local richness of species-level endemics (Figure 10d) and non-endemic native taxa (Figure 10e; see also Figure A6.2 in Appendix 6) increased in the North Island and eastern South Island, but decreased in the central western North Island, and in the western and inland South Island. Numbers of recently self-introduced taxa increased in most squares, but the biggest increases were in the North Island and coastal eastern South Island (Figure 10f).

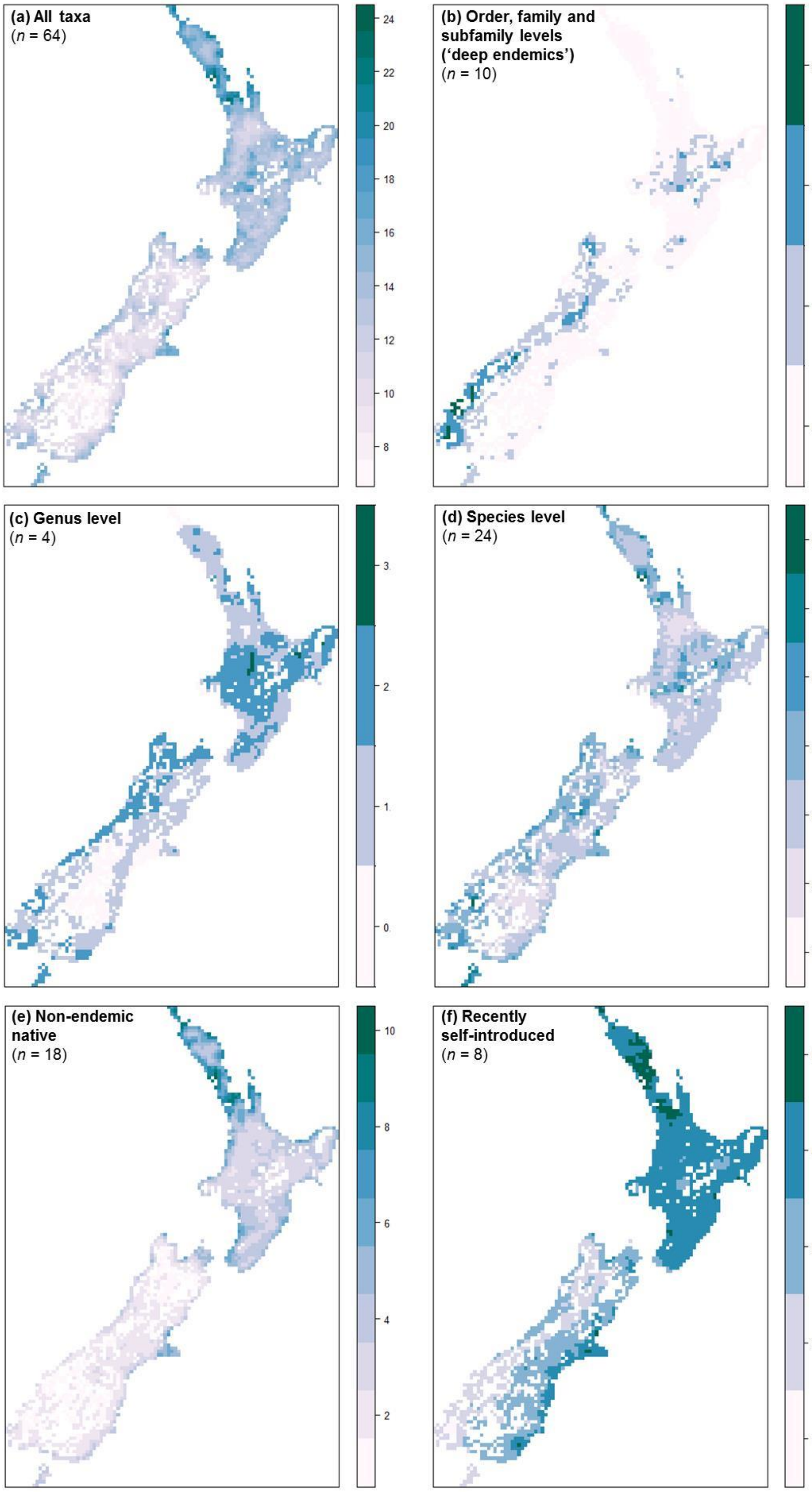


Figure 9 Local richness of taxa grouped into levels of endemism across the 2,155 grid squares in the 1999–2004 measurement period, rounded to the nearest integer. Note that the scales for the plots differ according to the maximum number of taxa per square in each group.

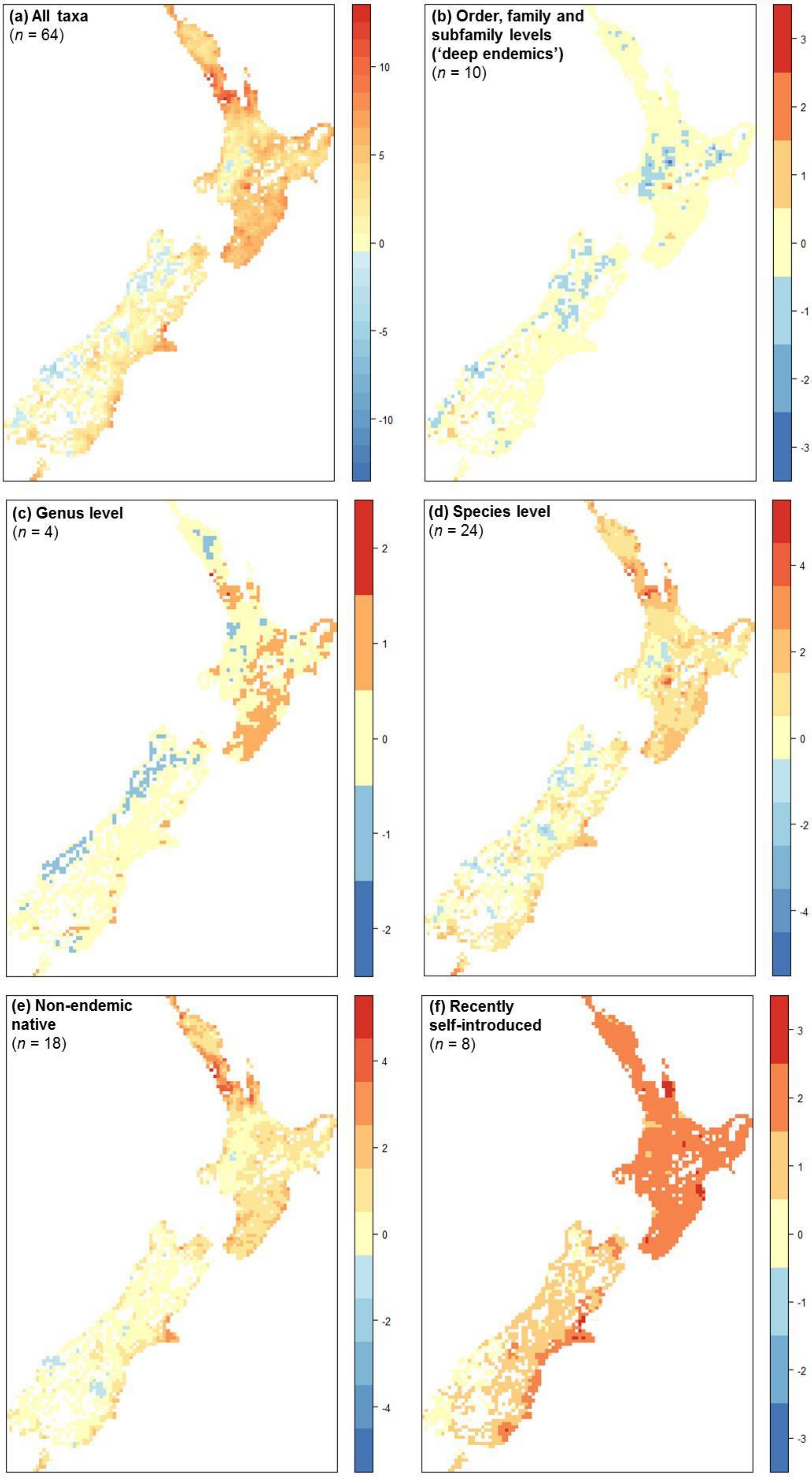
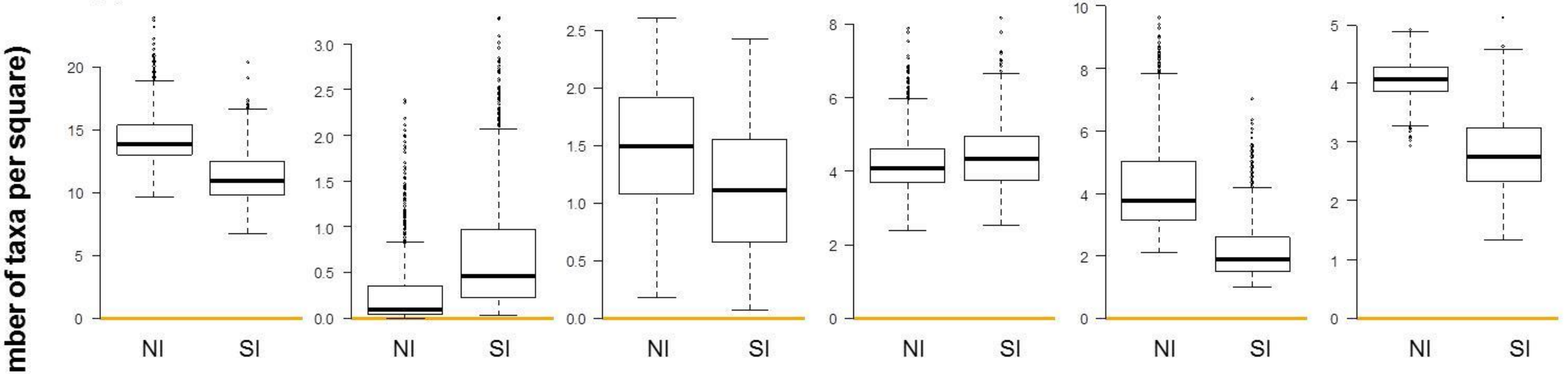


Figure 10 Change in local richness of taxa grouped into levels of endemism across the 2,155 grid squares, derived by subtracting local richness in the 1969–1979 measurement period from that in the 1999–2004 measurement period and rounding to the nearest integer. Note that the scales for the plots differ.

Figure 11 highlights some of the patterns in the maps, especially differences between islands.

- The numbers of native bird taxa per square, and increases in number, were larger in the North Island, mainly because the North Island supported more non-endemic taxa (Figure 11)
- The South Island remained the main stronghold for deep-endemic birds (Figure 11a). Changes in the number of deep endemics per square were generally small (<0.5 taxa per square, reflecting near absence from most squares by the 1970s) and negative, reflecting continued elimination of small residual populations (Figure 11b). However, there were also a few 'large' (one or two taxa) local positive and negative changes on both islands.

(a) Status: Local richness in 1999–2004



(b) Change in local richness 1969–1979 to 1999–2004

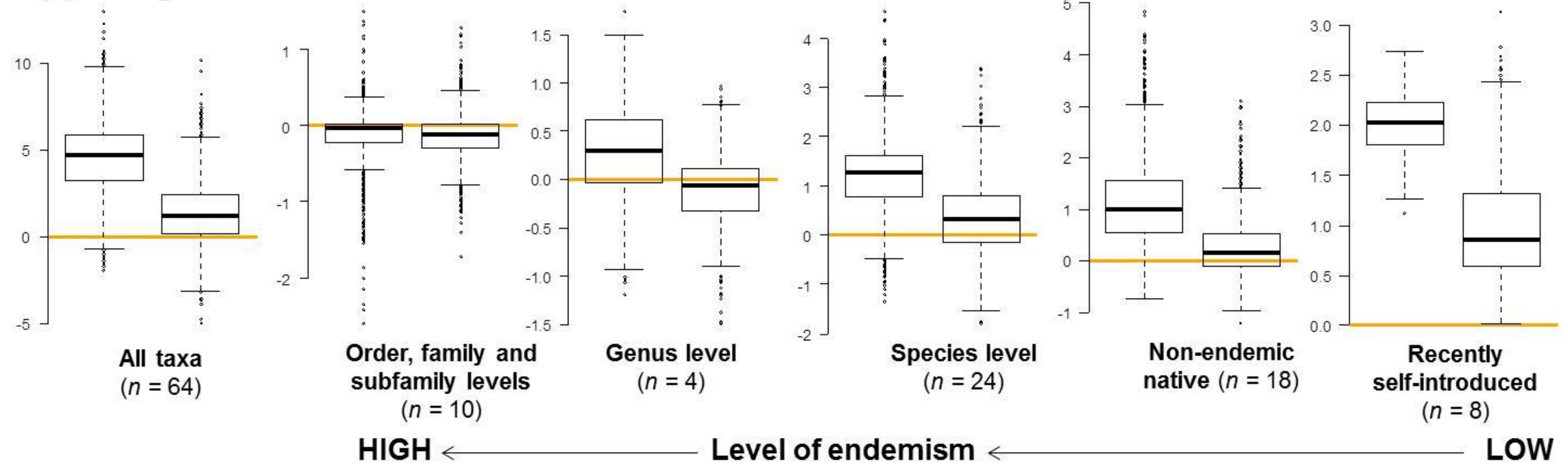


Figure 11 Local richness (1999–2004) and changes in local richness (1969–1979 to 1999–2004) in squares in the North and South Islands (NI and SI) for all native bird taxa ('all taxa') and native bird taxa, grouped according to level of endemism. The zero line is shown in orange, and vertical axis scales differ on each plot according to the number of taxa in each group. In each box, the bold horizontal line indicates the median, the box and whiskers bound the interquartile range and 95% interval respectively, and the points indicate values beyond the 95% interval.

Richness patterns in different habitat groups

Squares covering the remaining indigenous forests along the main axial ranges of the North and South Islands, and on Stewart Island, retained the highest local diversity of forest birds in 1999–2004 (Figure 12a). Few or no native forest birds occupied deforested squares in the inland South Island.

The number of native forest birds per square decreased across much of the South Island forest zone between measurement periods, although local richness did also increase locally in some places on Stewart Island and Fiordland (especially Waitutu) (Figure 13a). In the North Island there was a clear geographic pattern of loss. Local richness of forest birds decreased conspicuously in a swathe of partly and densely forested land between the western Waikato and eastern Taranaki. It also decreased in Northland, the western Bay of Plenty, and some parts of inland eastern North Island. Local richness of forest birds generally increased elsewhere across the North Island, with the biggest local increases in squares near the Central Plateau and in the axial ranges of the southern North Island.

Inland-breeding wading birds, terns and gulls were most numerous in squares covering inland South Island basins and riverbeds (their spring and early summer breeding habitats), and along the eastern and northern coasts of the South Island, and in some North Island coasts and harbours, especially those around Auckland (which represent their winter feeding habitats) (Figure 12b). Their local richness increased between measurement periods in some coastal squares, most notably around Auckland in the North Island, and decreased inland, most notably in the southern South Island (Figure 13b).

Squares covering North Island coasts and the northern, eastern and southern coasts of the South Island were richest in coastal-breeding wading birds, terns and gulls (Figure 12c) and in birds of coastal wetlands and shores (Figure 12d). Lowland North Island squares supported the most freshwater wetland birds (Figure 12e) and birds of open habitats (Figure 12f). In the South Island, open-habitat birds were most numerous in squares along the east coast and in the Marlborough Sounds (Figure 12f). Patterns of increase in coastal-breeding wading birds, terns and gulls, coastal and freshwater wetland birds, and birds of other open habitats generally mirror their patterns of local richness in 1999–2004 (Figures 13d–f). .

Boxplots in Figure 14 emphasise the following patterns.

- The numbers of forest bird taxa per square were similar in the North and South Islands. Native forest bird richness increased in most North Island squares between measurement periods, but there was no net change in the South Island.
- The South Island remains the main stronghold of inland-breeding wading birds, terns and gulls, and their local richness decreased more there between measurement periods.

North Island squares support higher numbers of freshwater wetland birds and birds of 'other' open habitats than the South Island. The local richness of these groups increased on both islands between measurement periods, but increases were greater in the North Island.

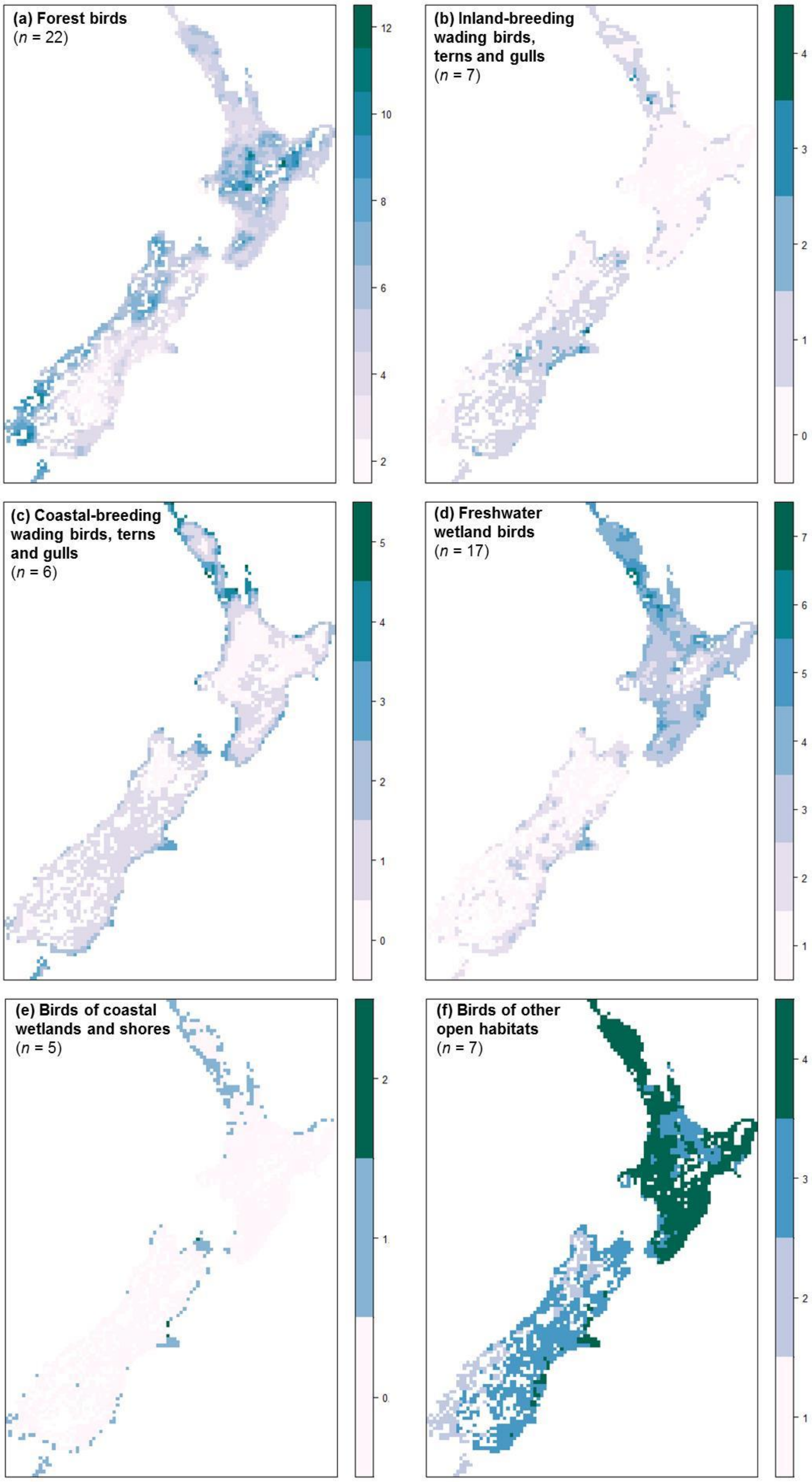


Figure 12 Local richness of taxa in the six different habitat groups across the 2,155 grid squares in the 1999–2004 measurement period, rounded to the nearest integer. Note that the scales for the plots differ according to the maximum number of taxa per square in each group.

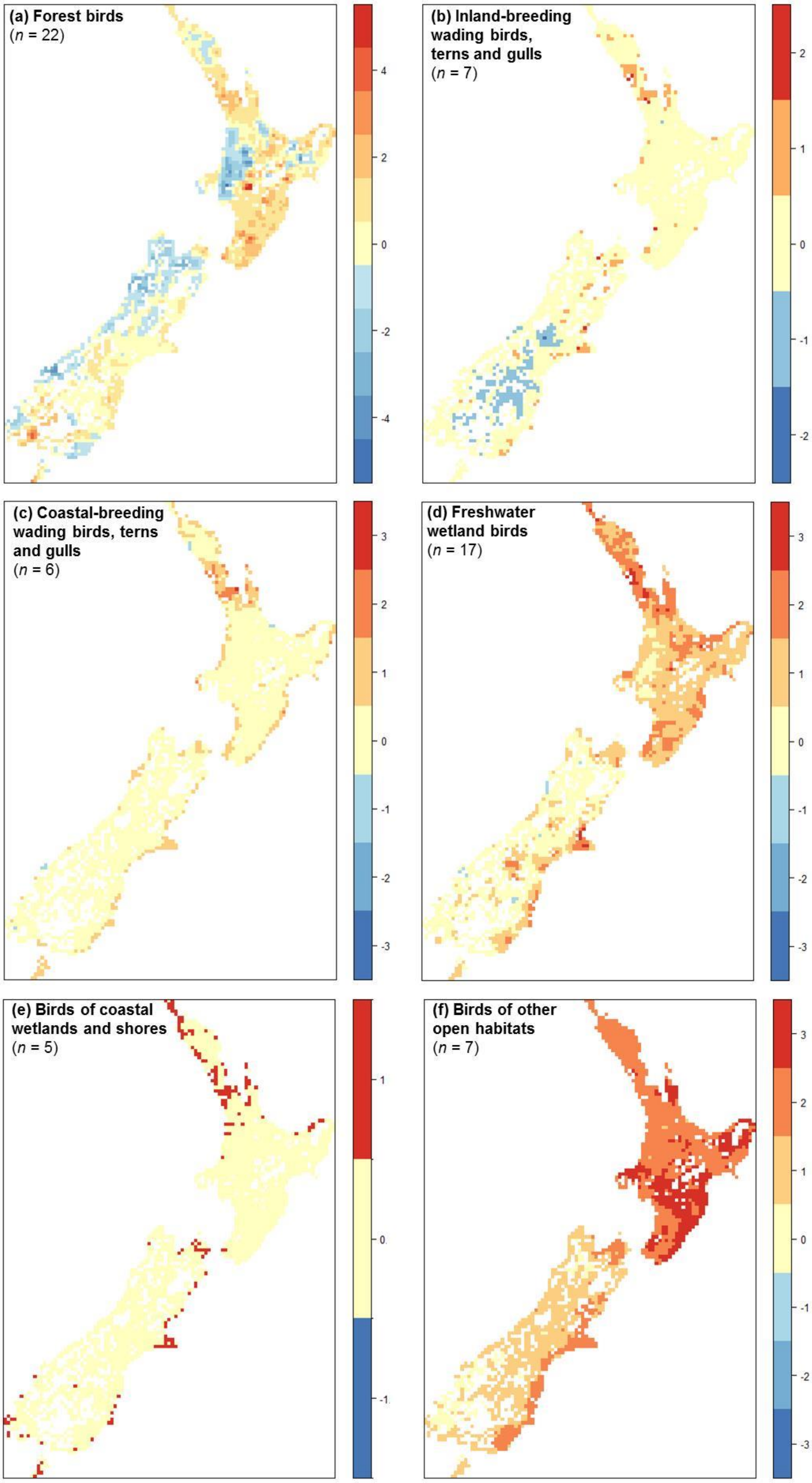


Figure 13 Change in local richness of taxa in the six different habitat groups across the 2,155 grid squares, derived by subtracting local richness in the 1969–1979 measurement period from that in the 1999–2004 measurement period and rounded to the nearest integer. Note that the scales for the plots differ according to the minimum or maximum richness change in each group.

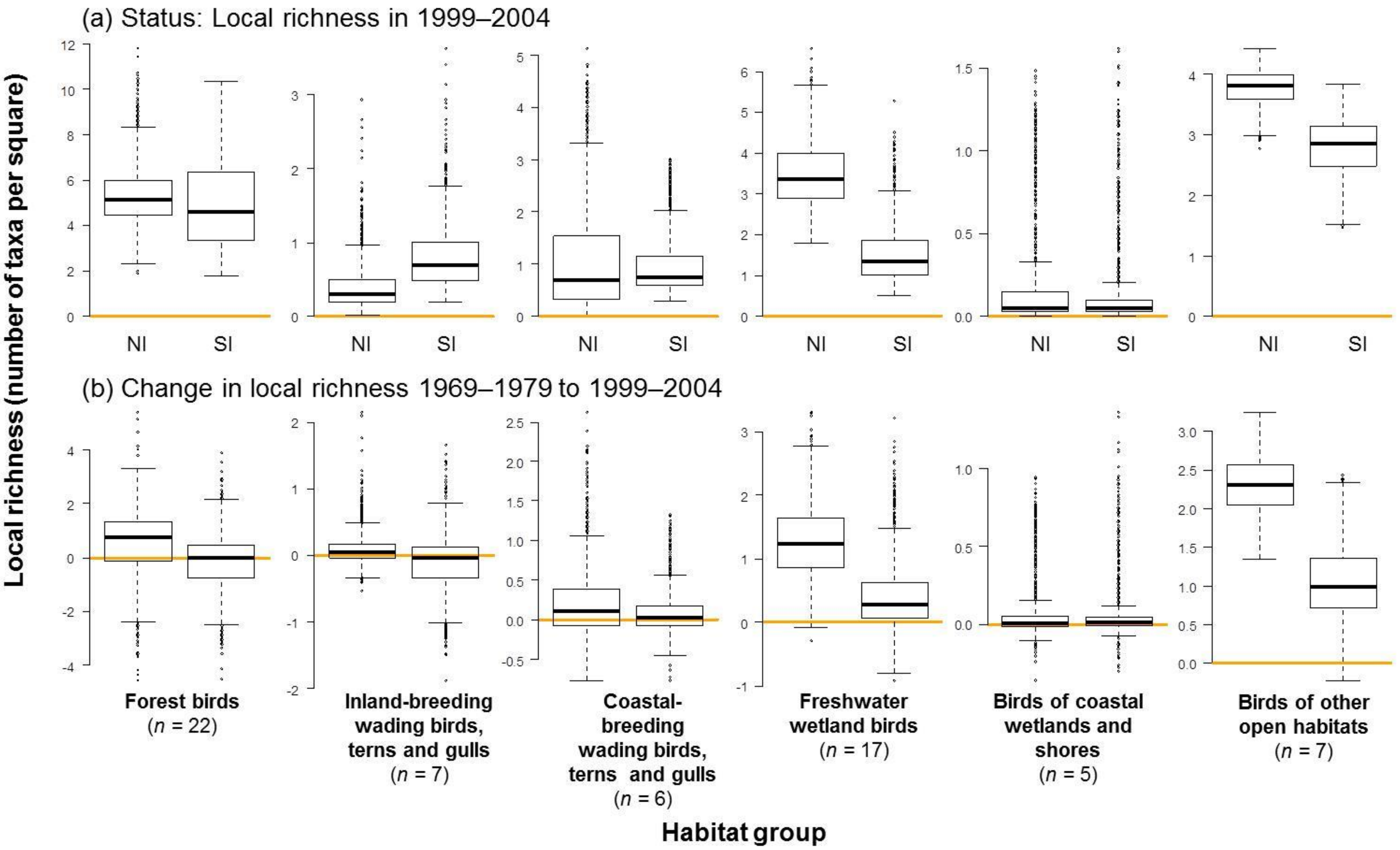


Figure 14 Local richness (1999–2004) and changes in local richness (1969–1979 to 1999–2004) in squares in the North and South Islands for taxa grouped by habitat. The zero line is shown in orange on each plot. In each box, the bold horizontal line indicates the median; the box and whiskers bound the interquartile range and 95% interval, respectively; and the points indicate values beyond the 95% interval. Note that the scales for the plots differ according to the number of taxa in each group.

7.4 Effects of time, endemism, habitat and environment on all land birds

Our models showed significant interacting effects of *measurement period*, *endemism level*, *road density* (our proxy for the degree of human transformation in the landscape) and *habitat group* on median probabilities of occupancy across the 64 bird taxa. Effects of these factors and their interactions in the simple model (which does not consider habitat group) are shown graphically in Figure 15, and the associated parameter estimates are tabulated in Table A7.1 in Appendix 6.

In these models we consider that there is strong support for an effect (i.e. it is statistically 'significant') when the 95% confidence intervals of parameter estimates in the table exclude zero.

Occupancy probabilities for native birds decreased between measurement periods and were lower in squares with high road density at the average (i.e. genus) level of endemism in both islands (Figure 15). This is supported by negative parameter estimates for *measurement period* and *road density* on both islands (Table A7.1). There were positive parameter estimates for the *measurement period:road density* interactions, indicating that occupancy probabilities decreased more in remote places than in settled places between measurement periods at the average endemism level (Table A7.1), perhaps because there was less left to lose in settled places (Figures 15a and 15b).

Very large parameter estimates for the interactions of *endemism level* with *measurement period* and with *road density* in models for both islands (Table A7.1) show that level of endemism had a profound effect on the direction of change in occupancy probabilities between measurement periods and on response to human settlement.

- Taxa that are endemic at higher levels decreased between measurement periods, while non-endemic taxa increased (negative *measurement period:endemism level* effects; Table A7.1). In Figure 15, blue lines (1999−2004) lie below grey lines (1969−1979) at higher levels of endemism, and lie above grey lines at low levels of endemism.
- Road density had a negative effect on occupancy probabilities in endemic birds and a positive effect on non-endemic taxa. Endemic birds were less likely to occupy squares with high road densities (Figures 15a and 15c) while non-endemic birds were less likely to occupy squares with low road densities (Figures 15b and 15d).

There were significant three-way interactions between *measurement period*, *endemism level* and *road density* (Table A7.1), but the sign of the parameter estimates differed (positive in the North Island, negative in the South Island). In the North Island the positive interaction means that the greater rate of decline between measurement periods for deeper endemics was more dramatic in remote squares. The opposite is true in the South Island, where deep-endemic birds decreased somewhat more in densely settled squares. This is consistent with deep endemic taxa being more completely extirpated from settled places in the North Island by 1969−1979 than in the South Island. Parameter estimates for the three-way interactions were relatively small, however, showing that they made only minor contributions to the overall patterns of occupancy change.

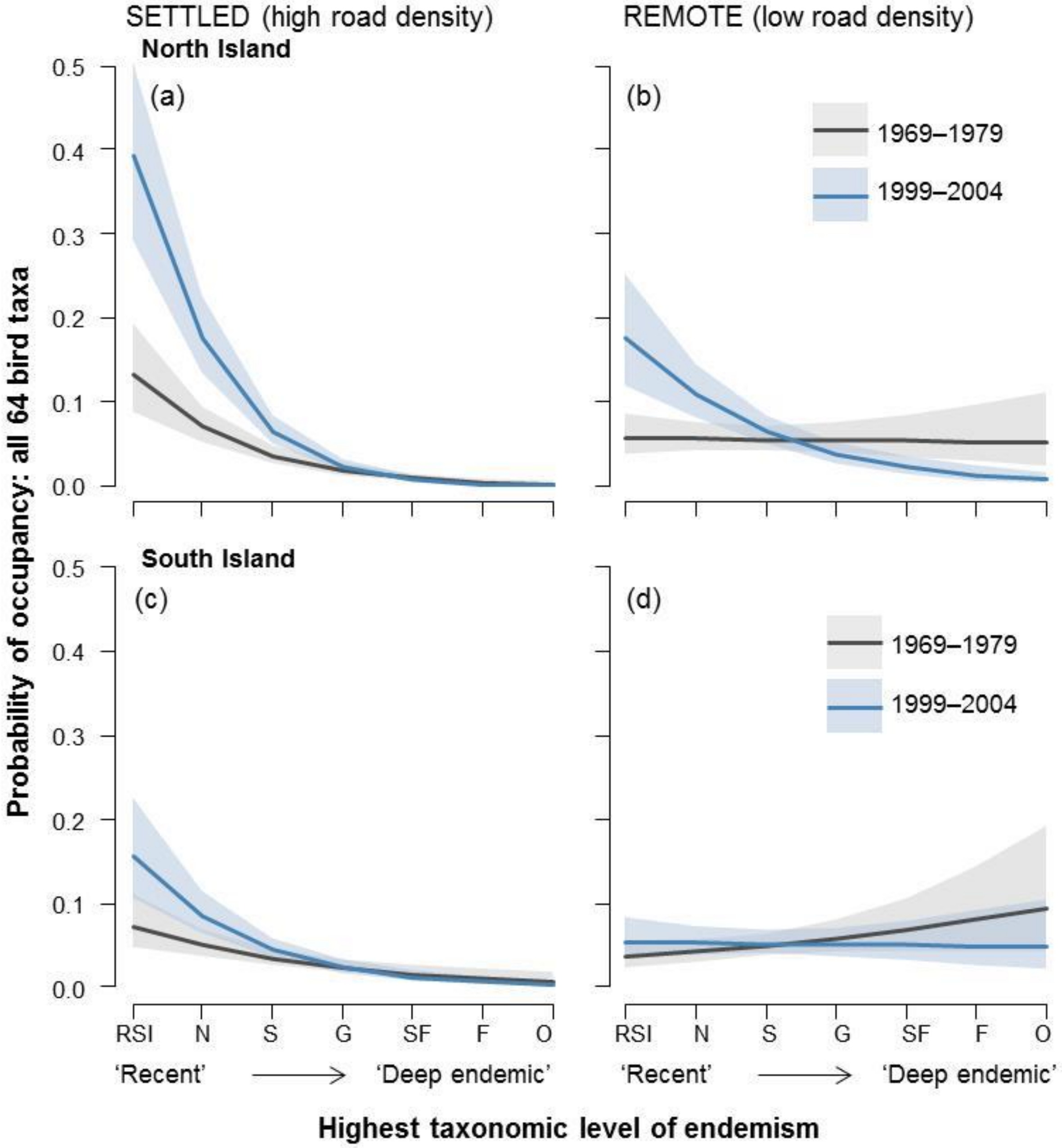


Figure 15 Fitted effects (and standard errors of effects) of endemism level (horizontal axes), measurement period (distinguished by grey and blue lines and shading), and road density (high in plots on the left and low in plots on the right) on fitted probabilities of occupancy in the 64 native land bird taxa on the North and South Islands (upper and lower row of plots, respectively). RSI = recently self-introduced, N = non-endemic native, S = species-level, G = genus-level, SF = subfamily-level, F = family-level, O = order-level. Effects are plotted at 1,025 km per 10 km^2 (high road density) and 3 km per 10 km^2 (low road density).

Our models that include habitat groups as a fixed effect (Figure 16) show that the very strong effect of endemism level on occupancy probability is common across our different habitat-based groups of birds. Regardless of habitat group, birds at higher taxonomic levels of endemism had lower occupancy probabilities and were more likely to decrease between measurement periods where there were still populations left to lose. Non-endemic birds in all habitat groups had higher occupancy probabilities, which were more likely to have increased between measurement periods.

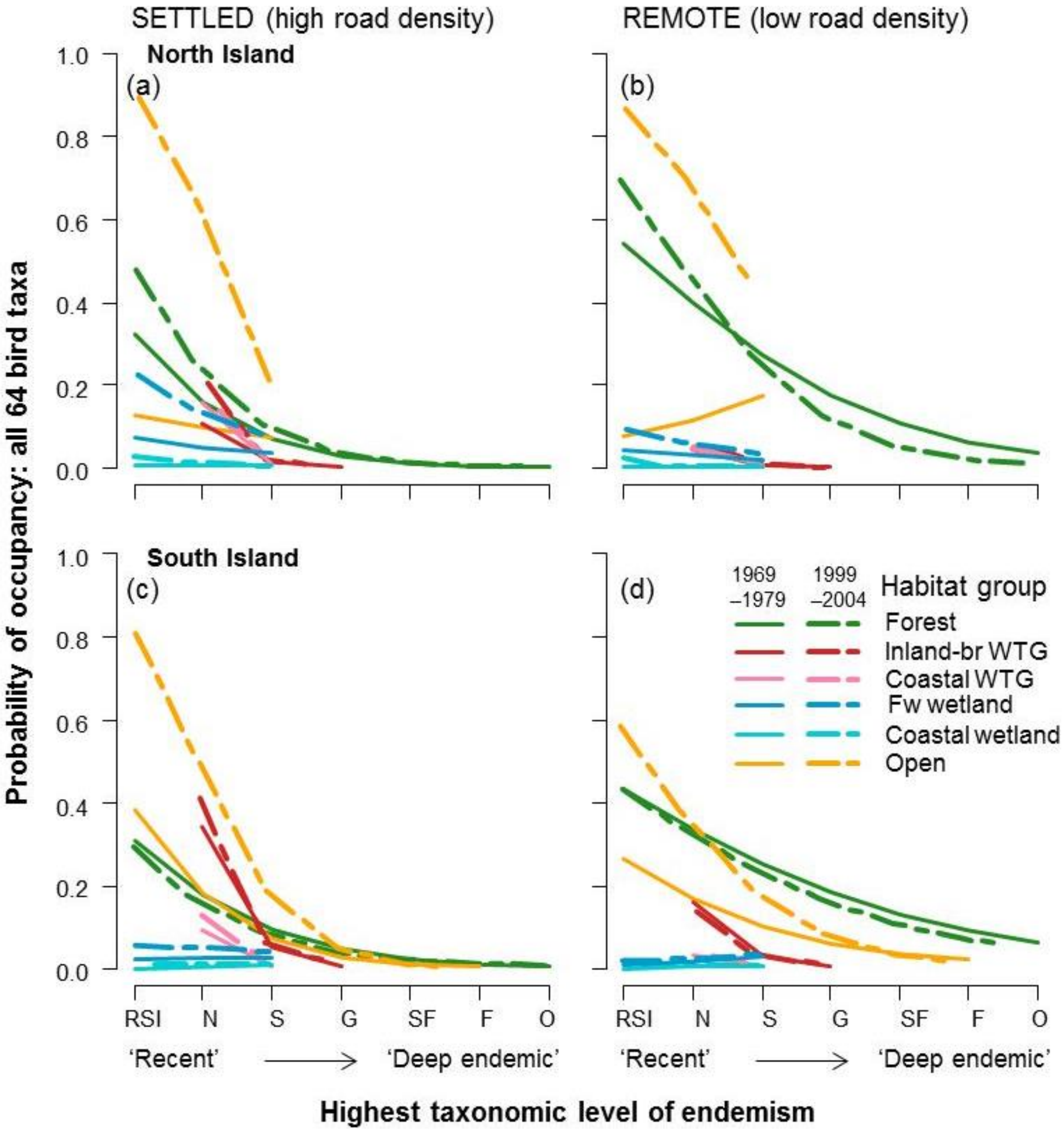


Figure 16 Fitted effects of endemism level (horizontal axes), bird habitat group (distinguished by different colours), measurement period (distinguished by solid and dashed line types), and road density (high in plots on the left and low in plots on the right) on fitted probabilities of occupancy in the 64 native land bird taxa in the North and South Islands (upper and lower row of plots, respectively). **Endemism levels:** RSI = recently self-introduced, N = non-endemic native, S = species-level, G = genus-level, SF = subfamily-level, F = family-level, O = order-level. **Habitat groups:** Forest = forest birds; Open = birds of other open habitats; Inland-br WTG = inland-breeding wading bird, terns and gulls; Coastal WTG = coastal-breeding wading bird, terns and gulls; Fw wetland = birds of freshwater wetlands; Coastal wetland = birds of coastal wetlands and shores. Effects are plotted at 1,025 km per 10 km^2 (high road density) and 3 km per 10 km^2 (low road density).

Effects of road density differed among habitat groups, however. Negative effects of road density on occupancy probability were greater on forest birds than on any other group (Figure 16). In most non-forest habitat groups, birds had higher occupancy probabilities in densely settled squares than in remote squares and/or showed greater increases in occupancy probabilities between measurement periods than forest birds in settled squares.

7.5 Effects of location and land use on inland-breeding wading birds, terns and gulls

Results in the preceding sections suggest that endemic wading birds, terns or gulls had decreased in local occupancy and range in their main breeding habitats in the inland eastern South Island. Figure 17 shows a geographic trend from a relatively wide distribution of inland squares supporting multiple inland breeding wading birds, terns and gull species across squares in the southern inland South Island, to a narrow inland distribution centred on the Upper Waitaki (Mackenzie) basin in the early 2000s. Increases in local richness are evident on some parts of the coast, especially around Auckland and the Coromandel peninsula in the North Island.

Our comparison of LRORs between the inland (breeding) and coastal (feeding) ranges in the South island (Figure 18) also indicated that relative decreases in range in this group of species were consistently greater in their South Island inland breeding habitats than in their coastal feeding habitats between measurement periods.

These summary statistics (Figures 18a−c) suggest that there were net decreases in range in all seven species of inland breeding Charadriiformes across inland South Island squares between measurement periods. The largest indicative relative net decreases in range occupancy were of wrybill (the only genus-level endemic), banded dotterel, black-billed gull, and South Island pied oystercatcher, followed by the Australasian pied stilt (the only non-endemic native species) (Figure 18c). In coastal squares, LRORs were marginally negative for two taxa (banded dotterel and black-billed gull) and were positive for the remaining five taxa, suggesting net increases in range occupancy.

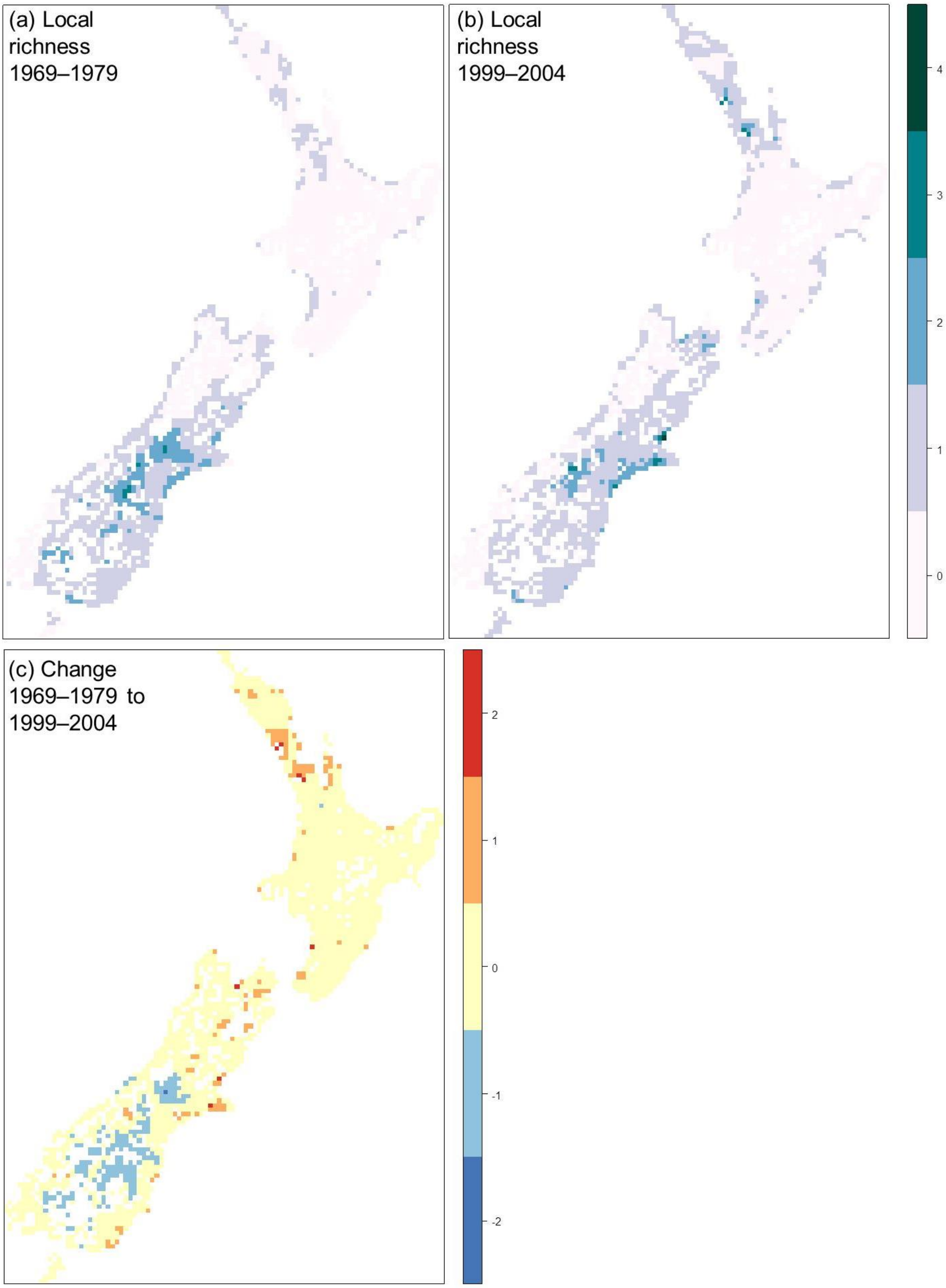


Figure 17 Local richness of seven inland-breeding wading birds, terns and gulls: (a) in 1969−1979, (b) in 1999−2004, and (c) change between those two measurement periods.

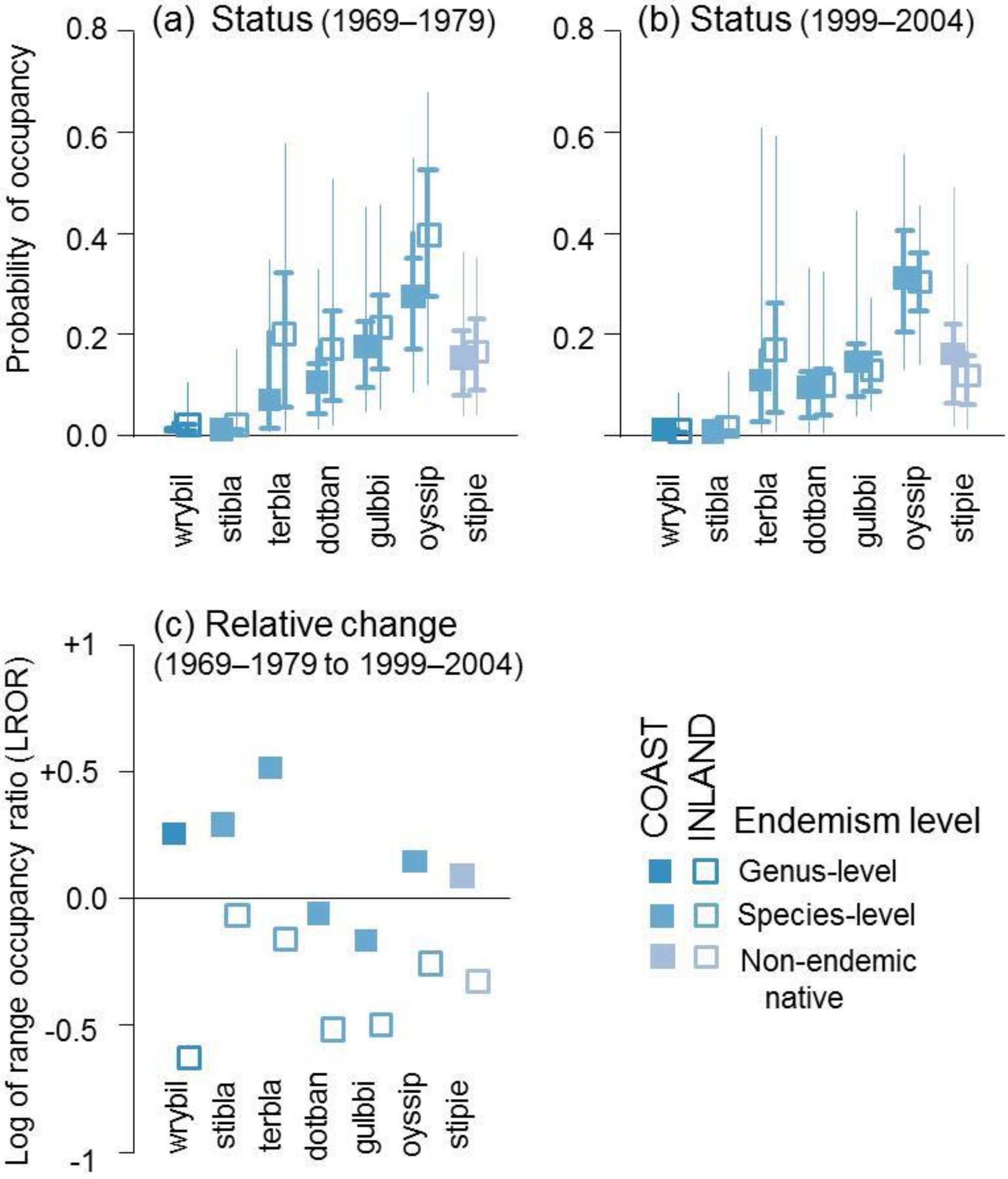


Figure 18 Occupancy of inland-breeding wading birds, terns and gulls across South Island squares near the coast and inland (filled and hollow symbols, respectively), showing (a) status in 1969−1979, (b) status in 1999−2004, and (c) relative net change in proportion of range occupied between 1969−1979 and 1999−2004, expressed as the range occupancy ratios (LRORs). Plots (a) and (b) show the mean and upper and lower 50% and 95% bounds of fitted estimates of occupancy. In (c) negative LRORs indicate a net decrease and positive ratios indicate a net increase. The 598 'coast' squares (solid symbols) have centroid distances to the coast less than the 12.5 km, and the 475 'inland' squares (hollow symbols) have centroid distances to the coast greater than 12.5 km. Taxa are arranged in order of decreasing level of endemism, and within endemism levels are arranged in order of increasing average occupancy across both islands. The species are: wrybil = wrybill; stibla = black stilt; terbla = black-fronted tern; dotban = banded dotterel; gulbbi = black-billed gull; oyssip = South Island pied oystercatcher; stipie = Australasian pied stilt.

Our models of inland breeding Charadriiformes show contrasting patterns of median occupancy probabilities with distance from the coast on the two main islands (Figure 19). In the North Island, occupancy probabilities were higher on the coast (Figures 19a & b) but in in the South Island they were higher inland (Figures 19c & d). This is indicated by negative and positive *distance from coast* parameter estimates, respectively, in the two models (Tables A7.2a & b in Appendix 7).

Our model for the South Island (Figures 19d−f; Table A7.2b in Appendix 7) confirmed that decreases in occupancy probability between measurement periods were greater inland (negative *measurement period:distance from coast* parameter estimate). Decreases were also greater in endemic species overall (negative *measurement period−endemism level* parameter estimate in Table A7.2).The model also showed that occupancy probabilities were lower, and recent decreases were greater, where there has been greater development for agriculture and forestry inland (negative parameter estimates for *distance from coast:agriculture and forestry*, and *measurement period:distance from coast:agriculture and forestry*). These effects can be seen in Figure 19e.

A positive four-way interaction in the South Island model (last row of Table A7.2b in Appendix 7) reflects greater decreases in less deeply endemic species than in endemic taxa in inland squares where there was greater development for agriculture and forestry. This greater decrease was possible because the Australasian pied stilt was still more widespread than the endemic species (on average) in 1969−1979 (Figure 19e). In less-developed squares, pied stilt occupancy probabilities remained similar to those in the 1970s.

There was no evidence that occupancy probabilities of inland-breeding wading bird, tern and gull species changed in their coastal feeding habitats in the South Island (Figure 19d).

Occupancy probabilities increased around the coast in the North Island (Figure 19a), at least in non-endemic taxa (represented by the Australasian pied stilt). This is reflected in a positive three-way interaction between *measurement period*, *endemism level*, and *distance from coast* (Table A7.2a).

Occupancy probabilities were higher, and increased between measurement periods, near North Island urban centres. This is shown by the positive interaction between *measurement period* and *urbanisation* in the North Island model (Table A7.2a). This parameter is shown in Figure 19c at the average level of endemism (i.e. species-level), because effects of urbanisation did not appear to vary with endemism level.

On the coasts of both islands, occupancy probabilities were higher in squares that were more developed with crops, horticulture, exotic pasture and/or afforestation (relatively large negative *distance from coast:agriculture and forestry* parameter estimates in both models; Table A7.2a,b). Because the difference was similar in the two measurement periods (Figures 18a & d), we suggest that any association may simply reflect the coincidence of these birds’ major late-summer and winter feeding grounds with New Zealand’s coasts, harbours and estuaries that have more agriculturally developed hinterlands.

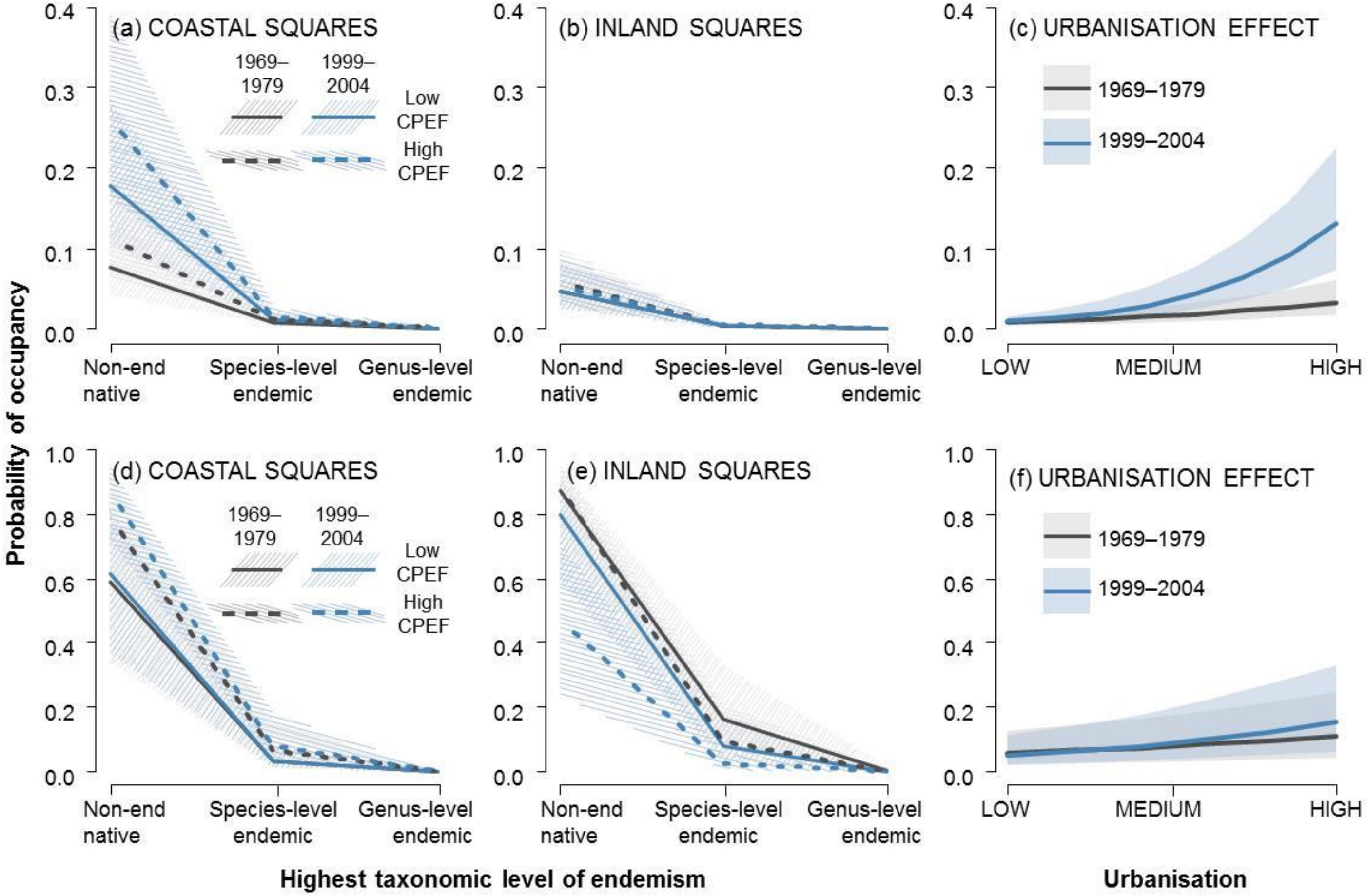


Figure 19 Fitted effects of endemism level (horizontal axes), measurement period (distinguished by grey and blue lines, see key), distance to coast (coastal squares in plots in first column and inland squares in plots in the centre column), and of measurement period and the level of urbanisation (third column), on fitted probabilities of occupancy in the seven inland-breeding native wading bird, tern or gull taxa in the North and South Islands (upper and lower row of plots, respectively). Note that the vertical scale in the North and South Island differ, reflecting generally lower occupancy probabilities in the North Island. Effects are plotted at 0 km from the coast ('COASTAL SQUARES') and 30 and 40 km inland in the North and South Islands, respectively ('INLAND SQUARES'). CPEF refers to our index of intensive agricultural and forestry land use: effects are plotted at 'High CPEF' (84% land cover was developed for exotic crops and pasture, or converted for forestry in 2001) and at 'Low CPEF' (10% of land cover was thus developed in 2001). In (f), LOW, MEDIUM and HIGH levels of urbanisation represent 0, 50 and 100% of square land cover.

8 Discussion

8.1 Homogenisation

Our results show a clear pattern of change in the New Zealand avifauna between the 1970s and the early 2000s, involving continued loss of species in endemic lineages, and a shift to dominance by non-endemic native species that arrived more recently (in geological time), and that are adapted to open, human-modified habitats. This is consistent with a global 'biotic homogenisation' trend: many species are declining as a result of human activities ('losers') and are being replaced by a much smaller number of expanding species that thrive in human-altered environments ('winners') (McKinney & Lockwood 1999; Ekroos et al. 2010; McCune & Vellend 2013). The result is a more homogenised biosphere with lower diversity at regional and global scales.

A very striking result of our study is that bird species that are endemic at higher taxonomic levels have been lost from New Zealand faster, both before the 1970s and between the 1970s and early 2000s. Most of the species we could not fit occupancy models for − because they are extinct globally, or were too rare on the three main islands − are endemic at high (order and family) levels. In the remaining birds, taxonomic level of endemism was by far the most influential factor determining species' probabilities of occupancy, and how they changed between the 1970s and early 2000s. These effects of endemism level were common to birds in all of the seven habitat groups in our data set.

This relationship between endemism level and extinction and endangerment in New Zealand land birds was first described by McDowall (1969). He noted that high taxonomic level of endemism indicates that the lineage of a species has been in New Zealand a long time. He concluded that extinction had not occurred randomly but was related 'in some way to evolutionary age. Species which have had a long evolutionary history in New Zealand seem now to be susceptible to extinction. This suggests some peculiarity in the evolutionary process … which in a time related manner affects the present viability of the species' (McDowall 1969, p. 8).

Why is vulnerability to loss related to the length of time of evolution on New Zealand? It is well known that island species develop a variety of 'insular' life-history traits that are associated with vulnerability to extinction and range declines following human settlement (Duncan & Blackburn 2004; Parlato et al. 2015). Our result, and McDowall's, suggests that lineages on islands not only acquire insular traits, but also progressively shed the ability to adapt to pressures that are characteristic of continents (including effects of humans and other mammals) over the period of time they are geographically or phylogenetically isolated from continental relatives and selection pressures.

Equally, lineages that have not been isolated on islands very long in geological time are more likely to retain traits that make them more resilient to continental selection pressures, and/or more capable of adapting to those pressures, because they have had less time to shed those traits and capabilities. This study shows that some New Zealand endemic bird species that diverged from overseas relatives quite recently have expanded their ranges in human occupied landscapes in recent decades. Among the forest birds, fantail and grey warbler (which are estimated to have diverged from overseas relatives c. 1.3 and 6.8 million years ago, respectively, B.J.M. Potter, unpublished data) are prominent examples. The endemic species of wetlands and other open habitats that increased in range diverged from their nearest overseas relatives in similarly recent times. However, most of the taxa that expanded their ranges between the 1970s and early 2000s are either non-endemic native or recently self-introduced species, which are now, or have recently been, exposed to continental conditions.

In sum, evolutionary isolation time seems to be an indicator of relative vulnerability to loss that is both (1) common across different groups of New Zealand's land birds and (2) persistent through time. The implication of McDowall's (1969) findings, and ours, is that taxonomic level of endemism is a proxy for isolation time, and this can be used as a simple rule of thumb for bird species' relative vulnerability to loss.

8.2 Bird groups and ecosystems in most trouble

New Zealand birds endemic at the genus or higher levels are almost exclusively forest birds. The single exception is the rock wren (*Xenicus gilviventris*), which is sister to all other New Zealand wrens (Acanthisittidae), which are forest-dwelling, and is likely to be a recent (Pleistocene) adaptation in the lineage. This reflects the fact that forest has been New Zealand's predominant land cover through avian evolutionary history (Lee et al. 2016). Extensive non-forest habitats are relatively new in geological time. They originated with mountain-building about 5 million years ago, and expanded and contracted again many times through the Pleistocene (Campbell & Hutching 2007).

This study (especially section 7.2) shows clearly that forest bird taxa endemic at the level of species or higher were the group that decreased most in range occupancy between 1969−1979 and 1999−2004. Their greatest range contractions were across remaining forests, where there were still populations left to lose in 1969−1979.

The declining forest birds included those classified as threatened or declining in the New Zealand Threat Classification System (Robertson et al. 2013) (mainland kiwi taxa, North Island kōkako, blue duck/whio, some subspecies of weka, North Island rifleman, and kākā on both islands). However, other species not considered threatened or declining were, apparently, in decline between 1969−1979 and 1999−2004. Some of these still had relatively large ranges in 1969−1979 (South Island rifleman, kererū, tūī, and morepork on the South Island and tomtit on both islands), but others already had restricted ranges, which decreased further (North Island robin and yellow-crowned parakeet on the North Island, and long-tailed cuckoo on both islands). We examine the patterns of forest bird occupancy changes in more detail in a companion report (Walker et al. 2017).

The second group in trouble is endemic inland breeding wading birds, terns and gulls. The wrybill (endemic at the genus level) and five species-level endemics (the black stilt, black-billed gull, black-fronted tern, banded dotterel and South Island pied oystercatcher) share an adaptation to breed mainly or solely inland, on sparsely vegetated inland habitats found on braided riverbeds and outwash terraces, which arose in the Pleistocene. All species are considered threatened or declining by Robertson et al. (2013), and our study shows that their inland South Island breeding ranges shrank markedly between measurement periods. In the 1970s many parts of inland southern South Island supported breeding populations of multiple inland-breeding wading bird, tern and gull species. By the early 2000s this range had contracted to a narrow distribution centred on the Upper Waitaki (Mackenzie) Basin.

These birds' ecological type is unique to New Zealand. Our braided riverbeds and outwash terraces occur in tectonically active landscapes on the eastern flanks of the Southern Alps, mainly in inland Canterbury, and are rare in the world. Most other unmodified examples occur in the extreme high-latitude parts of Canada, Alaska and Siberia. Braided river reaches in the Himalayas and Andes are typically highly modified (Gray & Harding 2007). The globally unusual habitat is combined in New Zealand with an absence of mammals throughout most of evolutionary time. This allowed the birds to evolve the habit of breeding on the ground where they were at little risk of predation, a situation that changed with the advent of mammal predators. More recently the habitats themselves have been transformed on a large scale by woody weed invasion (Caruso 2006) and by cultivation and irrigation (Innes & Saunders 2012; Grove et al. 2015; Peat et al. 2016).

8.3 Evidence of effects of predation

It is generally agreed that invasive mammal predators are probably the greatest threat to the continued survival of many of New Zealand's native birds (Innes et al. 2010; Wright 2011). Our results are consistent with this understanding for two reasons.

First, most of the greatest recent losses in native birds have occurred in remote areas that were the remaining strongholds for them in the 1970s and where disturbance, modification, and loss of habitat by human agency have been minimal. Largely protected forests, the alpine zone and many inland South Island basins and braided riverbeds apparently underwent little change in the extent, type or quality of habitat between the 1970s and early 2000s. Predation is the most likely explanation for bird declines in these places (Innes et al. 2010).

Second, as discussed above (8.1) it is the endemic species that have evolved longer in New Zealand – and therefore without mammalian predators – which occupy smaller ranges and underwent greater range declines between measurement periods.

It is possible that sustained depletion of food supply (in forests, from browsing by ungulates and arboreal omnivores) and diseases such as avian malaria (Niebuhr et al. 2016) have played additional roles in native bird declines. However, the magnitude of their roles (if any) is currently unclear.

8.4 Effects of human settlement and land use

Innes et al. (2010) described predation as the 'default explanation' for bird declines in New Zealand, but noted the importance of carefully evaluating other factors alone or in interaction.

This study shows very clear effects of road density (our proxy for degree of human transformation of the landscape) on the occupancy of native bird species, which varied strongly with species' habitat group and taxonomic level of endemism (section 7.4). Human occupation has been particularly detrimental to deep endemic forest birds, which were virtually absent from settled and deforested landscapes by the 1970s. However, most non-endemic forest birds were also less likely to occur in densely settled places than in remote areas.

Factors associated with human occupation[5] therefore have inhibiting effects even on those forest bird species that are most robust to predation. The strong negative effect of human settlement suggests that restoration of populations of many endemic forest bird species through predator control is likely to face far greater difficulties in settled landscapes than in large continuous and remote forest tracts.

We also found evidence of negative effects of intensive land use, in addition to predation, on inland-breeding wading birds, terns and gulls in their inland South Island breeding habitats. By the 1970s endemic species of inland-breeding wading birds, terns and gulls were less likely to occupy the parts of their inland South Island breeding ranges that had more intensive agricultural and/or forestry land use by the early 2000s. Between the 1970s and early 2000s, negative effects were seen on both endemic and non-endemic species, which declined significantly more in squares with more intensive agriculture or forestry than in little-developed squares.

In other native non-forest bird groups, dense human settlement clearly favours non-endemic species, especially those that are recently self-introduced to New Zealand, rather than endemic species. The pattern suggests that recently arrived non-forest bird species generally have traits that better enable them to 'get along' with humans in New Zealand's most human-transformed landscapes. This raises a question of whether efforts to enhance populations of endemic species in settled landscapes will mainly benefit the more successful non-endemic birds.

Coastal-breeding wading birds, terns and gulls, and coastal and shore wetland birds, increased on New Zealand's settled coastlines, especially near urban centres, between measurement periods. Simultaneously, freshwater wetland birds and birds of other open habitats expanded their ranges into many production landscapes. We are not sure what explains these effects in these predominantly non-endemic non-forest species, but there are a number of possibilities.

- Increased numbers of farming, coastal and city-dwelling human observers might account for these increases, but we think this unlikely because our occupancy models account for observer effort.

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[5] Density of human settlement in New Zealand is associated with (among other things) lower amounts of indigenous forest habitat for indigenous forest birds, with warmer temperatures, and with more intensive agricultural activity. We examine the effects of these variables on forest birds in more detail in an associated report (Walker et al. 2017).

- Freshwater wetland birds may be recovering from earlier, widespread wetland habitat loss (Ausseil et al. 2011), and coastal birds from earlier persecution (e.g. shags; Wilson 2006) and hunting (e.g. variable oystercatcher; Baker 1973).
- Some bird taxa were evidently still invading from points of self-introduction (e.g. spurwing plover and silvereye).
- It is also possible that habitat changes in coastal and harbour environments and farming districts have favoured some species; for example, through eutrophication increasing the productivity of feeding environments for some birds.
- Finally, some of these bird species may be adapting behaviourally to human disturbance of various kinds, or even to mammal predation. As discussed in section 8.1, non-endemics and 'recent' species-level endemics are more likely to retain traits that confer resilience to continental selection pressures, or the capability to adapt to them.

9 Conclusions

- The overall pattern of change in the New Zealand avifauna between 1969–1979 and 1999–2004 was one of continued range declines in birds of older endemic lineages (deep endemics) and a shift to a non-endemic avifauna dominated by bird species of non-forest, human-modified habitats.
- Because there was little left to lose in the more settled parts of New Zealand by 1969–1979, most of the subsequent loss of endemic birds occurred in remote areas.
- Native land birds in greatest need of conservation effort are forest and alpine birds (especially, but not only, deep endemics), and endemic wading birds, terns or gulls that breed in the inland eastern South Island.
- We conclude that predation by introduced mammals is probably the primary cause of decline in endemic forest and alpine birds, because there was little habitat change in many remote natural areas where the declines were greatest. However, both habitat loss to intensive land use *and* predation are major causes of range declines in endemic inland-breeding wading birds, terns and gulls.
- Factors associated with human occupation have additional negative effects on native forest bird species, especially deep endemics. This result means that even with predator control, populations of a number of endemic species may not recover substantially in settled landscapes, and the outcomes of conservation investment may be poorer than in large, continuous and remote forest tracts.
- It is the forests and inland basins most remote from New Zealand's large human communities that still provide sufficient habitat for there to be a prospect of maintaining large, viable populations of endemic forest birds and inland-breeding wading birds, terns and gulls. Achieving this outcome would require large-scale management of multiple predators in forests and inland basins. For inland-breeding wading birds, terns and gulls, it would also require new action to effectively and permanently protect the remaining breeding habitats in inland South Island.

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Appendix 1 The 64 land taxa

Table A1.1 The 64 native taxa included in our models and analyses. In the 'Islands' column, NI/SI means that different species or subspecies are recognised on the North and South Islands; NI means occurs only in the North Island; SI means occurs only on the South Island; and Both means the taxon occurs on both islands. Asterisks indicate that a single combined national model was fitted for all species or subspecies because of difficulty in distinguishing them from records in the atlases (e.g. all weka, and brown, tokoeka and great spotted kiwi were combined, all falcon 'forms', all robin species). Nomenclature follows Gill 2010. Within each habitat group (subheadings), birds are arranged in order of level of endemism, and then in alphabetical order of order, family and Latin name

Common name	Latin name	Family	Order	Endemism	Islands
Forest birds					
Kiwi species*	*Apteryx species*	Apterygidae	Apterygiformes	Order	NI/SI
Rifleman*	*Acanthisitta chloris chloris (SI)* or *A. c. granti (NI)*	Acanthisittidae	Passeriformes	Family	NI/SI
North island kōkako	*Callaeas wilsoni*	Callaeidae	Passeriformes	Family	NI
Kākā*	*Nestor meridionalis*	Nestoridae	Psittaciformes	Family	NI/SI
Kea	*Nestor notabilis*	Nestoridae	Psittaciformes	Family	SI
Whitehead	*Mohoua albicilla*	Pachycephalidae	Passeriformes	Family	NI
Brown creeper	*Mohoua novaeseelandiae*	Pachycephalidae	Passeriformes	Family	SI
Mohua/yellowhead	*Mohoua ochrocephala*	Pachycephalidae	Passeriformes	Family	SI
Blue duck/whio	*Hymenolaimus malacorhynchos*	Anatidae	Anseriformes	Subfamily	NI/SI
Kererū	*Hemiphaga novaeseelandiae*	Columbidae	Columbiformes	Genus	Both
Bellbird	*Anthornis melanura melanura*	Meliphagidae	Passeriformes	Genus	Both
Tūī	*Prosthemadera novaeseelandiae novaeseelandiae*	Meliphagidae	Passeriformes	Genus	Both
Grey warbler	*Gerygone igata*	Acanthizidae	Passeriformes	Species	Both
Long-tailed cuckoo	*Eudynamys taitensis*	Cuculidae	Cuculiformes	Species	Both
NZ falcon*	*Falco novaeseelandiae*	Falconidae	Falconiformes	Species	Both
NZ robin*	*Petroica longipes (NI)* or *P. australis (SI)*	Petroicidae	Passeriformes	Species	NI/SI
NZ tomtit*	*Petroica macrocephala*	Petroicidae	Passeriformes	Species	NI/SI
Parakeet (mainland species)*	*Cyanoramphus* spp	Psittacidae	Psittaciformes	Species	Both
Weka species*	*Gallirallus australis australis*	Rallidae	Gruiformes	Species	Both
NZ fantail*	*Rhipidura fuliginosa fuliginosa*	Rhipiduridae	Passeriformes	Species	NI/SI

Common name	Latin name	Family	Order	Endemism	Islands
Forest birds cont...					
Shining cuckoo	*Chrysococcyx lucidus lucidus*	Cuculidae	Cuculiformes	Native	Both
Morepork	*Ninox novaeseelandiae novaeseelandiae*	Strigidae	Strigiformes	Native	Both
Silvereye	*Zosterops lateralis lateralis*	Zosteropidae	Passeriformes	Native-Rec	Both
Coastal-breeding wading birds, terns or gulls					
NZ dotterel	*Charadrius obscurus aquilonius*	Charadriidae	Charadriiformes	Species	Both
Variable oystercatcher	*Haematopus unicolor*	Haematopodidae	Charadriiformes	Native	Both
Southern black-backed gull	*Larus dominicanus dominicanus*	Laridae	Charadriiformes	Native	Both
Red-billed gull	*Larus novaehollandiae scopulinus*	Laridae	Charadriiformes	Native	Both
Caspian tern	*Hydroprogne caspia*	Sternidae	Charadriiformes	Native	Both
White-fronted tern	*Sterna striata*	Sternidae	Charadriiformes	Native	Both
Inland-breeding wading birds, terns or gulls					
Wrybill	*Anarhynchus frontalis*	Charadriidae	Charadriiformes	Genus	Both
Banded dotterel	*Charadrius bicinctus bicinctus*	Charadriidae	Charadriiformes	Species	Both
South Island pied oystercatcher	*Haematopus finschi*	Haematopodidae	Charadriiformes	Species	Both
Black-billed gull	*Larus bulleri*	Laridae	Charadriiformes	Species	Both
Black stilt	*Himantopus novaezelandiae*	Recurvirostridae	Charadriiformes	Species	Both
Black-fronted tern	*Childonias albostriata*	Sternidae	Charadriiformes	Species	Both
Australasian pied stilt	*Himantopus himantopus leucocephalus*	Recurvirostridae	Charadriiformes	Native	Both
Coastal wetlands and shores					
Stewart Island shag	*Leucocarbo chalconotus*	Phalacrocoracidae	Pelecaniformes	Species	SI
Spotted shag	*Stictocarbo punctatus punctatus*	Phalacrocoracidae	Pelecaniformes	Species	Both
Reef heron	*Egretta sacra sacra*	Ardeidae	Ciconiiformes	Native	Both
Pied shag	*Phalacrocorax varius varius*	Phalacrocoracidae	Pelecaniformes	Native	Both
Royal spoonbill	*Platalea regia*	Threskiornithidae	Ciconiiformes	Native-Rec	Both

Common name	Latin name	Family	Order	Endemism	Islands
Freshwater wetlands					
Brown teal	*Anas chlorotis*	Anatidae	Anseriformes	Species	Both
NZ scaup	*Aythya novaeseelandiae*	Anatidae	Anseriformes	Species	Both
Fernbird	*Bowdleria punctata punctata*	Megaluridae	Passeriformes	Species	Both
Little shag	*Phalacrocorax melanoleucos brevirostris*	Phalacrocoracidae	Pelecaniformes	Species	Both
NZ dabchick	*Poliocephalus rufopectus*	Podicipedidae	Podicipediformes	Species	NI
NZ shoveller	*Anas rhynchotis*	Anatidae	Anseriformes	Native	Both
Black swan	*Cygnus atratus*	Anatidae	Anseriformes	Native	Both
White heron	*Ardea modesta*	Ardeidae	Ciconiiformes	Native	Both
Australasian bittern	*Botaurus poiciloptilus*	Ardeidae	Ciconiiformes	Native	Both
NZ kingfisher	*Todiramphus sanctus vagans*	Halcyonidae	Coraciiformes	Native	Both
Black shag	*Phalacrocorax carbo novaehollandiae*	Phalacrocoracidae	Pelecaniformes	Native	Both
Little black shag	*Phalacrocorax sulcirostris*	Phalacrocoracidae	Pelecaniformes	Native	Both
Australasian crested grebe	*Podiceps cristatus australis*	Podicipedidae	Podicipediformes	Native	SI
Pūkeko	*Porphyrio melanotus melanotus*	Rallidae	Gruiformes	Native	Both
Grey teal	*Anas gracilis*	Anatidae	Anseriformes	Native-Rec	Both
White-faced heron	*Egretta novaehollandiae novaehollandiae*	Ardeidae	Ciconiiformes	Native-Rec	Both
Australian coot	*Fulica atra australis*	Rallidae	Gruiformes	Native-Rec	Both
Birds of other open habitats					
Rock wren	*Xenicus gilviventris*	Acanthisittidae	Passeriformes	Family	SI
Paradise shelduck	*Tadorna variegata*	Anatidae	Anseriformes	Species	Both
NZ pipit	*Anthus novaeseelandiae novaeseelandiae*	Motacillidae	Passeriformes	Species	Both
Australasian harrier	*Circus approximans*	Accipitridae	Falconiformes	Native-Rec	Both
Spurwing plover	*Vanellus miles novaehollandiae*	Charadriidae	Charadriiformes	Native-Rec	Both
Welcome swallow	*Hirundo neoxena neoxena*	Hirundinidae	Passeriformes	Native-Rec	Both

Appendix 2 Data from the bird atlases

Our raw data were collated in two national atlases of bird distribution compiled by the Ornithological Society of New Zealand (OSNZ; Bull et al. 1985; Robertson et al. 2007), a citizen organisation. Field surveys for these atlases were undertaken from September 1969 to December 1979 (1969−1979) and from December 1999 to November 2004 (1999−2004) (in our study we refer to these survey periods as our two 'measurement periods').

As described by Scofield et al. (2012):

> *Following the lead of the British Trust for Ornithology landmark atlas (Sharrock 1976), the OSNZ (in association with the Ecology Division of the DSIR and the Wildlife Service of the Department of Internal Affairs) encouraged members to visit as many 10,000 yard squares of the (NZMS1) national grid as possible between 1969 and 1979, and record all birds seen onto a standardised card. By the end of the scheme 96% of all 10,000 yard squares had been visited, with an average of 5.3 cards per square … The data resulted in … a final atlas in 1985 (Bull et al. 1985).*

This atlas provided the data for our first measurement period in this study.

Surveys for the second atlas (1999−2004; Robertson et al. 2007) commenced 20 years after the first was published. As described by (Robertson 2007) it involved:

> *five years of fieldwork by over 850 voluntary observers (mostly members of OSNZ), who between them contributed 31,817 record sheets with a total of 1.5 million distribution records. For the survey, the country was divided into a grid of 10 km × 10 km squares. Record sheets were submitted from 96.4% of the 3192 grid squares in New Zealand.*

This atlas provided the data for our second measurement period in this study. On completing the publication of Atlas 2 in 2007, the OSNZ recreated electronic files of data collected for Atlas 1, which had been unwittingly destroyed in the early 1980s. They made the data from both atlases available for research on a cost-recovery basis.

Observers could return either complete or incomplete record sheets (referred to as 'cards' in the first atlas) for a square. Complete (full) sheets (or 'full lists') were those considered to be a complete record for the grid by the observer. In full sheets, absences (non-detections of a bird species) are expected to reflect a true failure to detect a bird in a given grid, while incomplete sheets (or 'part lists') represent partial geographic or fauna coverage of a square by the observer, so that absences are unreliable. We used only full sheets in our analyses.

Stage 1. Occupancy estimates for each surveyed grid square

In stage 1 we adopted an occupancy modelling approach. Occupancy models recognise that non-detection of a species at a site does not imply that the species is absent (it may be a 'false absence') and that detectability can vary not only among species but also with observer and other covariates such as season (McKenzie et al. 2002; Bailey et al. 2014).

Specifically, for each taxon by measurement period (1969−1979 and 1999−2004) combination we modelled the i^{th} occupancy observation (Y_{ijkm}) recorded in each of j grid squares, in k seasons, on m islands, as a finite mixture model comprising a probability process that described the occupancy state and another describing the observation process. The Y_{ijkm} were 1 for positive observations (sight or by sound) of a species and 0 otherwise. We only used full data sheets (i.e. those considered to be a complete record for the square by the observer) so that absences reflected a true failure to detect a bird taxon in a given square, rather than because of partial coverage of a square by the observer.

We modelled the Y_{ijkm} as:

$$Y_{ijkm} \sim \text{Bernoulli}(p_k \times z_{jm}) \qquad (1)$$

where p_k is the probability of detecting the taxon in season k and z_{jm} is a random variable describing the occupancy for the j^{th} square on island m (1 = occupied, 0 = not occupied). We accounted for seasonal differences in observability by including a separate fixed effect intercept for each of the k seasons (γ_{1k}).

$$\text{logit}(p_k) = \gamma_0 + \gamma_{1k} \qquad (2)$$

The occupancy state process was modelled as:

$$z_{jm} \sim \text{Bernoulli}(q_{jm}) \qquad (3)$$

where q_{jm} is the probability of occupancy of the j^{th} square on island m. We included a separate intercept for each island (β_{1m}) to allow the probability of occupancy to vary at this scale, and captured the variation in occupancy between grid squares using a random intercept for each square (α_{jm}):

$$\text{logit}(q_{jm}) = \beta_0 + \beta_{1m} + \alpha_{jm} \qquad (4)$$

Island was coded at two levels: 'North Island' and 'South Island'. While this grouping was at the level of the main islands of New Zealand, each classification also included any nearby offshore islands. Stewart Island/Rakiura was included with the South Island.

We assume diffuse priors throughout. For the β and γ terms we assume ~N(0, 10^3). The priors on the α_{jm} were assumed ~N(0, σ_m), with the island specific standard deviation σ_m assumed to be ~U(0, 100).

We fitted separate models for each taxon by measurement−period combination. For taxa that occur exclusively in only one island (whitehead, North Island kōkako, NZ dabchick and brown teal in the North Island, and kea, brown creeper, mohua, rock wren, black stilt, crested grebe and Stewart Island shag in the South Island), we modified the above model such that only squares from the one island were considered. We dropped the separate island intercept, such that the random intercept to capture variation in occupancy between grid squares became α_j, and Eq 4 became:

$$\text{logit}(q_j) = \beta_0 + \alpha_{1j} \qquad (5)$$

with the prior on the estimated standard deviation of the grid square-level random effects σ_{Grid} assumed to be ~U(0, 100).

For all other taxa, a single national model was fitted. Hence a single national model was fitted for the different species, subspecies and/or recognised forms of kiwi (excluding little spotted kiwi), falcon, weka, rifleman, blue duck/whio, tomtit, fantail, robin, fernbird and NZ dotterel that are recognised within and between islands.

The models were fitted using the Hamiltonian MCMC sampler Stan, accessed through the R package rstan (Stan 2.0; Stan Development Team 2015). Convergence was deemed to have been obtained when the Gelman-Rubin statistic R-hat was less than 1.05 for all parameter estimates (Gelman et al. 2004). All inference was based on 1,000 observations for each of three MCMC chains.

Stage 2. Kriging occupancy estimates to a common grid

The geospatial grid squares used for survey in the two national bird atlases differed. Square sides were 10-000 yards in the first atlas (our 1969−1979 measurement period) and 10,000 metres (i.e. 10 × 10 km) in the second atlas (our 1999−2004 measurement period), and different geospatial projections were used. Occupancy estimates derived from stage 1 were assigned the New Zealand Map Grid (NZMG) projection geographic coordinates of the centre of the relevant grid square and measurement period. We assumed that the areal extents of the grid squares (about 83.6 km^2 in 1969−1979 vs 100 km^2 in 1999−2004) were not materially different enough to affect either detection or occupancy probabilities, and therefore we did not apply any adjustments for square size.

To enable comparison of occupancy estimates between the two measurement periods at the same places, we created a common grid of 10 × 10 km squares in the NZMG projection, with the same centres as the grid used for the surveys for the second measurement period. To avoid prediction beyond the geographic range of our data, the common grid excluded any squares that were not sampled with at least one full sheet in the second measurement period.

We used simple kriging to interpolate the median probabilities of occupancy (q_{jm} and q_j described in Eqs 4 and 5 respectively) from the centres of the grid squares used in each measurement period to the centres of the squares of the common grid. In this process, functions in the R libraries gstat (Pebesma & Graeler 2015) were used for geostatistical analysis and libraries sp (Pebesma et al. 2015) and raster (Hijmans & van Etten 2015) for spatial data manipulation.

Kriging is based on the spatial variance of a variable, modelled using a variogram representing semi-variances with distance. Semi-variances were modelled with simple models describing how variance increases with distance from the centroids of the original squares. Different variogram models can be used, but we achieved best fits using Stein's parameterisation of the Matern model (Stein 1999) for most taxa. These models had four parameters (nugget, sill, range and kappa, defined in accordance with Cressie 1993, pp. 59, 67–68, 130–131).

In kriging our estimates of occupancy values to the common grid, we estimated 1,000 conditional simulations drawn from the normal distribution of parameters in the variogram model (Bivand et al. 2013), and retained the median value from simulations (Dungan 1999) at each common square centre as our estimate of occupancy for the square.

Appendix 3 Assignment of land cover classes

Table A3.1 Land cover classes from the national Land Cover Database (LCDB; LCRIT 2015) used in creating indices of land cover for grid squares. The 'Assignment' column indicates that the land cover class contributed to the percentage of land in a square that was considered to represent urbanisation or CPEF (crop, pasture, and/or exotic forestry)

Class No.	LCDB class name	Assignment
1	Built-up Area (settlement)	Urbanisation
2	Urban Parkland / Open Space	Urbanisation
5	Transport Infrastructure	Urbanisation
6	Surface Mines and Dumps	Urbanisation
30	Short-rotation Cropland	CPEF
33	Orchard Vineyard and Other Perennial Crops	CPEF
40	High Producing Exotic Grassland	CPEF
64	Forest – Harvested	CPEF
71	Exotic Forest	CPEF

Appendix 4 Conditional autoregressive (CAR) models

Aim

The linear mixed effects (lme) models used in this report to test how measurement period, endemism level and environmental factors affected indigenous birds (Methods, sections 6.4 and 6.5) don’t take into account that occupancy estimates from squares adjacent to each other are less independent than those further apart (‘spatial autocorrelation’). Models fitted without accounting for spatial autocorrelation can yield unreliable parameter estimates, but fitting models to these data that take account of it is computationally challenging where there are multiple observations for the same grid square (as in our two measurement periods). To be confident that lme model results were robust, we attempted to fit all models as conditional autoregressive (CAR) mixed models in a Bayesian modelling framework using the Hamiltonian MCMC sampler Stan (Stan 2.8.0; Stan Development Team 2015), accessed through the R package RStan v. 2.14.1 (Stan Development Team 2016).

Methods

All birds models: Two different CAR models were fitted for each island in turn to test our expectation that level of endemism in the birds, and the geographic patterns of human settlement, would be major drivers of occupancy and occupancy change in native land birds across all habitat groups. These are the CAR equivalents of our Models 1 and 2 in section 6.4. CAR Model 1 fitted a three-way interaction between measurement period, endemism level, and our index of road density (a proxy for human settlement density). CAR Model 2 included a fourth term (habitat group) and a full four-way interaction between measurement period, endemism level, road density and habitat group.

Inland-breeding wading birds, terns and gulls (Charadriiformes) models**:** A third model (CAR Model 3) was fitted for each island to look at effects on the occupancy probabilities of the seven wading birds, terns or gulls that breed mainly in the inland eastern South Island. Fixed effects were a four-way interaction between measurement period, endemism level, distance to coast and our index of the intensive agricultural and forestry land use, and a two-way interaction between measurement period and urbanisation (equivalent to Model 3 described in Methods section 6.5).

All CAR models assumed that occupancy in adjacent neighbouring grid squares was correlated (i.e. had similar occupancies), but that occupancy in non-adjacent grid squares was not correlated. We initially attempted to fit a random effect parameter controlling spatial dependence for each taxon to allow the spatial variance to vary between taxa, but it became clear that the computational demands were such that none of these models would converge in a timely manner. We then tried an alternative random effect, which allowed spatial variance to vary in each measurement period; again, no model would converge. Our third and final attempt to fit each model therefore included a single random effect controlling spatial dependence that did not vary across taxa or measurement periods.

For probability of occupancy estimates p_{ij} from the i^{th} location and the j^{th} species (from the first stage of occupancy modelling, Appendix 2) we modelled

$$\operatorname{logit}(p_{ij}) \sim \mathrm{N}(X_{ij}\beta + \varphi_i + \alpha_{1j} + \alpha_{2j}, \sigma) \tag{6}$$

where X_{ij} is a design vector (the i^{th} row for the j^{th} species from a design array), β is a vector of fixed-effect coefficients (which varied by model, as described above), φ_i is a spatial adjustment term for the i^{th} location, α_{1j} and α_{2j} are random effects for species and family respectively and assumed to be normally distributed with a mean of 0 and with corresponding standard deviations of σ_{species} and σ_{family}, and σ is the error standard deviation.

We modelled the φ_i as:

$$\varphi_i \sim \mathrm{MVN}(0, [\tau(D-\rho W)]^{-1}) \tag{7}$$

where W is the adjacency matrix, D is diag(m_i) an $n \times n$ diagonal matrix where m_i is the number of neighbours for location i and ρ is a parameter controlling spatial dependence ($\rho = 0$ implies spatial independence and $\rho = 1$ implies an intrinsic conditional autoregressive specification). We assumed uninformative priors throughout. All standard deviations (σ, σ_{species} and σ_{family}) were assumed to have U(0, 20) priors. Finally, ρ was assumed ~U(0,1) and τ ~U(0,20). Priors on all β terms were ~ N(0, 10^3).

We coded the CAR terms by adapting the sparse CAR code provided for Stan by Max Joseph (http://mc-stan.org/documentation/case-studies/mbjoseph-CARStan.html; accessed 10 May 2017). Models were run for variable lengths of time until convergence was obtained. Convergence was assessed via visual inspection of trace plots and calculation of the r-hat statistic (Gelman et al. 2004).

Results

Our CAR models for the North Island data set converged more readily than those using the South Island data. The greater difficulty in fitting the South Island models may be due to less spatial contiguity in the data. In the North Island the great majority of squares with data have all eight neighbours, and few have only one or two neighbours. In the South Island the most frequent numbers of neighbours were five and six, and there were many more squares with only one or two neighbours.

CAR Model 1 and CAR Model 2 for the North and South Island failed to converge. CAR Model 3 (effects on occupancy of inland breeding Charadriiformes) for the North and South Islands converged. Parameter estimates and the significance of effects were generally similar to those in the lme models, and are reported in Table A4.1. Fitted effects from the fixed effects in these models are plotted in Figure A4.1, and can be compared with Figure 19 (which they closely resemble).

Table A4.1 Comparison of parameter estimates (on the logit scale of the response variable) from the lme and CAR models of probabilities of occupancy in inland-breeding wading bird, tern and gulls on the North and South Islands (Model 3). 95% lme CL are the lower and upper bounds of 95% higher posterior density intervals (HPDI), and 95% CAR CL are the lower and upper bounds of 95% Bayesian credible intervals

(a) North Island Model	**lme estimate**	**95% lme CL**	**CAR estimate**	**95% CAR CL**
Intercept	−4.86	[−5.96, −3.73]	−6.65	[−10.34, −1.97]
Measurement period	0.12	[0.07, 0.16]	−0.42	[−0.56, −0.29]
Endemism level	−1.37	[−1.41, −1.32]	−2.28	[−5.35, 1.26]
Distance from coast	−0.27	[−0.32, −0.24]	−0.48	[−0.59, −0.38]
Agriculture and forestry	0.09	[0.04, 0.14]	0.09	[−0.04, 0.21]
Urbanisation	0.10	[0.07, 0.14]	0.03	[0.00, 0.07]
Measurement period:Endemism level	−0.30	[−0.35, −0.26]	−0.72	[−0.84, −0.60]
Measurement period:Distance from coast	−0.17	[−0.21, −0.12]	0.02	[−0.08, 0.11]
Endemism level:Distance from coast	−0.03	[−0.06, 0.00]	−0.07	[−0.13, −0.01]
Measurement period:Agriculture and forestry	0.00	[−0.05, 0.05]	−0.07	[−0.22, 0.08]
Endemism level:Agriculture and forestry	−0.05	[−0.08, −0.01]	−0.03	[−0.13, 0.06]
Distance from coast:Agriculture and forestry	−0.08	[−0.12, −0.03]	−0.10	[−0.19, −0.02]
Measurement period:Urbanisation	0.10	[0.06, 0.14]	0.10	[0.06, 0.14]
Measurement period:Endemism level:Distance from coast	0.10	[0.06, 0.15]	0.20	[0.12, 0.29]
Measurement period:Endemism level:Agriculture and forestry	−0.01	[−0.05, 0.04]	−0.06	[−0.18, 0.07]
Measurement period:Distance from coast:Agriculture and forestry	0.01	[−0.03, 0.05]	0.06	[−0.04, 0.16]
Endemism level:Distance from coast: Agriculture and forestry	−0.02	[−0.06, 0.01]	−0.05	[−0.11, 0.01]
Measurement period:Endemism level: Distance from coast:Agriculture and forestry	0.02	[−0.02, 0.07]	0.04	[−0.05, 0.13]

(b) South Island Model	**lme estimate**	**95% lme CL**	**CAR estimate**	**95% CAR CL**
Intercept	−2.74	[−4.39, −0.74]	−6.53	[−10.38, −2.24]
Measurement period	−0.17	[−0.21, −0.14]	−0.04	[−0.16, 0.08]
Endemism level	−2.08	[−2.49, −1.59]	−3.60	[−6.36, 0.28]
Distance from coast	0.28	[0.23, 0.33]	0.18	[0.08, 0.27]
Agriculture and forestry	0.21	[0.17, 0.25]	0.11	[0.01, 0.22]
Urbanisation	0.07	[−0.01, 0.14]	0.03	[−0.02, 0.09]
Measurement period:Endemism level	−0.07	[−0.10, −0.02]	−0.26	[−0.38, −0.17]
Measurement period:Distance from coast	−0.33	[−0.37, −0.28]	−0.22	[−0.30, −0.12]
Endemism level:Distance from coast	−0.01	[−0.04, 0.02]	−0.02	[−0.07, 0.04]
Measurement period:Agriculture and forestry	−0.04	[−0.08, 0.00]	−0.15	[−0.27, −0.04]
Endemism level:Agriculture and forestry	−0.10	[−0.12, −0.07]	−0.09	[−0.16, −0.01]
Distance from coast:Agriculture and forestry	−0.17	[−0.22, −0.12]	−0.15	[−0.22, −0.07]
Measurement period:Urbanisation	0.06	[0.00, 0.11]	0.06	[−0.01, 0.12]
Measurement period:Endemism level:Distance from coast	0.06	[0.02, 0.10]	0.11	[0.03, 0.19]
Measurement period:Endemism level:Agriculture and forestry	−0.01	[−0.05, 0.02]	−0.24	[−0.34, −0.13]
Measurement period:Distance from coast:Agriculture and forestry	−0.10	[−0.14, −0.05]	0.08	[−0.01, 0.16]
Endemism level:Distance from coast: Agriculture and forestry	−0.04	[−0.07, −0.01]	−0.08	[−0.13, −0.02]
Measurement period:Endemism level: Distance from coast:Agriculture and forestry	0.10	[0.06, 0.14]	0.17	[0.10, 0.25]

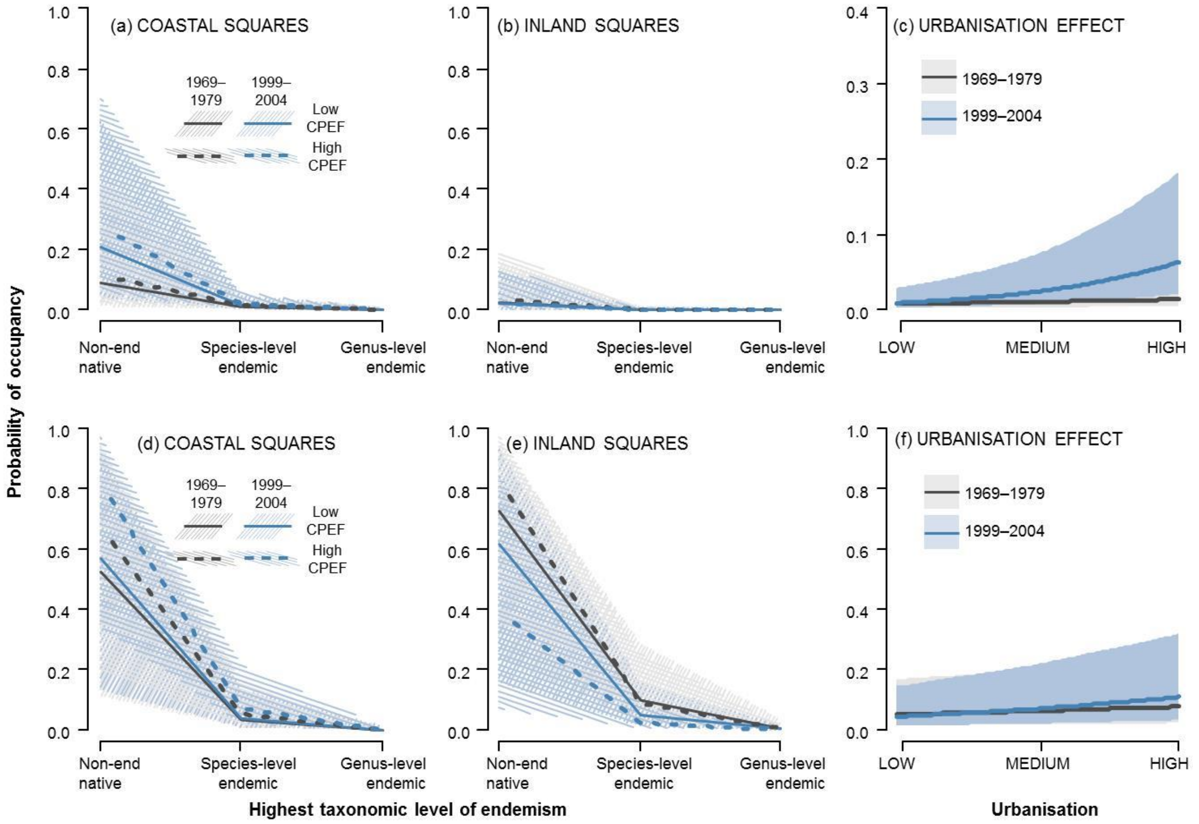

Figure A4 Fitted effects (from our **CAR models)** of endemism level (horizontal axes), measurement period (distinguished by grey and blue lines, see key), distance to coast (coastal squares in plots in first column and inland squares in plots in the centre column), and of measurement period and the level of urbanisation (third column), on fitted probabilities of occupancy in the seven inland-breeding native wading bird, tern or gull taxa on the North and South Islands (upper and lower row of plots, respectively). Note that the vertical scale in the North and South Island differ, reflecting generally lower occupancy probabilities in the North Island. Effects are plotted at 0 km from the coast ('COASTAL SQUARES') and 30 and 40 km inland in the North and South Islands, respectively ('INLAND SQUARES'). CPEF refers to our index of intensive agricultural and forestry land use: effects are plotted at 'High CPEF' (84% land cover was developed for exotic crops and pasture, or converted for forestry in 2001) and at 'Low CPEF' (10% of land cover was thus developed in 2001). In (f), LOW, MEDIUM and HIGH levels of urbanisation represent 0, 50 and 100% of square land cover. **This figure can be compared with Figure 19 in the main body of this report, which is closely resembles.**

Differences between the CAR and lme Model 3 for North Island were that the main effect of *measurement period* switched from positive to negative in the CAR model (Table A7.3 in Appendix 7), and the 95% credible intervals of the main effects of *endemism level* and *agriculture and forestry*, and of the *endemism level:agriculture and forestry* interaction included zero. The positive effect of urbanisation was weaker in the CAR model (the lower 95% credible interval was almost zero) but the *measurement period:urbanisation* interaction term remained positive and highly significant.

The South Island CAR model for inland breeding Charadriiformes differed from the South Island lme model in that

- the 95% credible interval of parameters for *measurement period* and the interaction between *measurement period, distance from coast* and *agriculture and forestry*, included zero in the CAR model
- there was a negative interaction between *measurement period, endemism level* and *agriculture and forestry* in the CAR model.

Discussion

As we expected, including a term to account for spatial autocorrelation slightly altered parameter estimates and fitted values in our mixed effects models (Model 3) because it took into account the non-independence of occupancy estimates from adjacent squares. However, both the parameter estimates and fitted effects were similar overall, and led to similar interpretations. The same is true for CAR models of forest birds reported in our associated report (Walker et al. 2017). We would be more satisfied if more of our CAR models had converged. However, on the basis of those that have converged, we consider that our lme models (and conclusions based on them) in the main body of this report are likely to be generally robust.

In the North Island the differences in Model 3 parameter estimates suggest that failing to account for spatial autocorrelation meant that positive associations of some inland breeding wading birds, terns and gulls with more developed and urbanised squares in the North Island were somewhat overemphasised. However, the differences do not affect our conclusion that any association may merely reflect the coincidence of these birds' major late-summer and winter feeding grounds with New Zealand's coasts, harbours and estuaries that have more agriculturally developed hinterlands, rather than an ecological effect of agricultural or forestry development. Our finding that occupancy probabilities increased between measurement periods near North Island urban centres was supported and confirmed.

The CAR model suggested that in the South Island decreases in occupancy probabilities of inland breeding wading birds, terns and gulls between atlases were greater in endemic species and in squares that were more developed for agriculture or forestry, regardless of distance from the coast. In contrast, our lme models suggested that decreases between atlases were greater in squares that were both distant from the coast and more developed for agriculture or forestry, at the average level of endemism. These differences do not alter our interpretation (based on the lme model) that there is evidence of negative effects of intensive land use, in addition to predation, on inland-breeding wading birds, terns and gulls in the South Island.

Appendix 5 Native land-bird taxa

Table A5 The 64 native land-bird taxa, showing their range occupancy (mean median occupancy probability) across North and South Island squares, 95% intervals of median occupancy probabilities in each measurement period (in square parentheses), change in range occupancy (mean and 95% intervals of occupancy probability change), and the log of the range occupancy ratio (LROR). Asterisks indicate that a single combined national model was fit for all species or subspecies because of difficulty in distinguishing them from records in the atlases (e.g. brown, tokoeka and great spotted kiwi were combined, as were all weka, all falcon 'forms', all robin species)

	North Island				South Island			
Common name	**1969–1979**	**1999–2004**	**Change**	**LROR**	**1969–1979**	**1999–2004**	**Change**	**LROR**
Forest birds								
Kiwi species*	0.08 [0.00, 0.02]	0.02 [0.00, 0.14]	−0.06 [−0.41, 0.03]	−1.17	0.04 [0.00, 0.39]	0.04 [0.00, 0.32]	−0.01 [−0.15, 0.06]	-0.15
Rifleman	0.08 [0.00, 0.04]	0.04 [0.00, 0.35]	−0.04 [−0.43, 0.09]	−0.75	0.26 [0.02, 0.73]	0.19 [0.00, 0.71]	−0.07 [−0.41, 0.24]	-0.33
North island kōkako	0.01 [0.00, 0.01]	0.01 [0.00, 0.03]	−0.01 [−0.10, 0.01]	−0.63				
Kākā	0.05 [0.00, 0.03]	0.03 [0.00, 0.34]	−0.02 [−0.29, 0.18]	−0.28	0.11 [0.00, 0.48]	0.08 [0.00, 0.38]	−0.03 [−0.26, 0.08]	-0.37
Kea					0.14 [0.00, 0.66]	0.14 [0.00, 0.66]	0.00 [−0.21, 0.22]	-0.03
Brown creeper					0.21 [0.07, 0.44]	0.22 [0.02, 0.55]	0.00 [−0.16, 0.22]	0.01
Whitehead	0.13 [0.00, 0.16]	0.16 [0.00, 0.69]	0.03 [−0.22, 0.41]	0.24				
Yellowhead					0.03 [0.00, 0.23]	0.03 [0.00, 0.34]	0.01 [−0.10, 0.21]	0.25
Blue duck/whio	0.05 [0.00, 0.01]	0.01 [0.00, 0.10]	−0.04 [−0.44, 0.00]	−1.73	0.05 [0.00, 0.27]	0.01 [0.00, 0.07]	−0.04 [−0.25, 0.01]	−1.48
Kererū	0.36 [0.05, 0.39]	0.39 [0.10, 0.74]	0.04 [−0.40, 0.41]	0.11	0.32 [0.03, 0.79]	0.24 [0.03, 0.57]	−0.08 [−0.41, 0.15]	-0.28
Bellbird	0.29 [0.01, 0.39]	0.39 [0.00, 0.89]	0.10 [−0.19, 0.45]	0.29	0.60 [0.03, 0.99]	0.64 [0.06, 0.97]	0.04 [−0.29, 0.43]	0.05
Tūī	0.54 [0.09, 0.68]	0.68 [0.25, 0.89]	0.15 [−0.23, 0.54]	0.25	0.25 [0.00, 0.79]	0.21 [0.00, 0.68]	−0.04 [−0.34, 0.19]	-0.17
Grey warbler	0.70 [0.55, 0.90]	0.90 [0.72, 0.98]	0.20 [0.00, 0.35]	0.25	0.65 [0.49, 0.78]	0.77 [0.60, 0.87]	0.13 [−0.03, 0.27]	0.18
Long−tailed cuckoo	0.15 [0.00, 0.09]	0.09 [0.00, 0.48]	−0.06 [−0.48, 0.18]	−0.49	0.10 [0.02, 0.26]	0.07 [0.01, 0.26]	−0.02 [−0.18, 0.12]	−0.27
NZ robin*	0.11 [0.00, 0.07]	0.07 [0.00, 0.52]	−0.04 [−0.58, 0.23]	−0.38	0.14 [0.00, 0.83]	0.13 [0.00, 0.69]	0.00 [−0.34, 0.35]	−0.02
NZ tomtit	0.22 [0.00, 0.20]	0.20 [0.00, 0.78]	−0.02 [−0.48, 0.34]	−0.10	0.47 [0.04, 0.95]	0.41 [0.00, 0.95]	−0.07 [−0.38, 0.25]	−0.15
Parakeet (mainland species)	0.03 [0.00, 0.02]	0.02 [0.00, 0.33]	−0.01 [−0.22, 0.13]	−0.19	0.09 [0.00, 0.36]	0.12 [0.00, 0.60]	0.03 [−0.12, 0.32]	0.23
Weka species*	0.03 [0.00, 0.01]	0.01 [0.00, 0.02]	−0.03 [−0.69, 0.02]	−1.56	0.11 [0.00, 0.71]	0.07 [0.00, 0.58]	−0.04 [−0.48, 0.18]	−0.4
NZ fantail	0.82 [0.62, 0.92]	0.92 [0.79, 0.97]	0.11 [−0.01, 0.27]	0.12	0.59 [0.26, 0.83]	0.60 [0.34, 0.78]	0.02 [−0.21, 0.26]	0.03
Shining cuckoo	0.30 [0.18, 0.43]	0.43 [0.29, 0.57]	0.14 [−0.09, 0.30]	0.37	0.12 [0.06, 0.23]	0.16 [0.11, 0.25]	0.04 [−0.06, 0.12]	0.31
Morepork	0.24 [0.09, 0.22]	0.22 [0.11, 0.44]	−0.02 [−0.22, 0.16]	−0.07	0.14 [0.03, 0.34]	0.11 [0.01, 0.33]	−0.02 [−0.16, 0.12]	−0.18
Silvereye	0.71 [0.60, 0.80]	0.80 [0.64, 0.89]	0.09 [−0.08, 0.21]	0.12	0.64 [0.48, 0.78]	0.66 [0.53, 0.75]	0.02 [−0.11, 0.17]	0.03
Inland−breeding wading birds, terns and gulls								
Wrybill	0.01 [0.00, 0.01]	0.01 [0.00, 0.05]	0.00 [−0.03, 0.03]	0.20	0.01 [0.00, 0.07]	0.01 [0.00, 0.07]	0.00 [−0.06, 0.02]	−0.22
Banded dotterel	0.04 [0.00, 0.05]	0.05 [0.00, 0.19]	0.01 [−0.05, 0.13]	0.25	0.13 [0.01, 0.44]	0.09 [0.00, 0.32]	−0.03 [−0.25, 0.14]	−0.23

	North Island				South Island			
Common name	**1969–1979**	**1999–2004**	**Change**	**LROR**	**1969–1979**	**1999–2004**	**Change**	**LROR**
Inland–breeding wading birds, terns and gulls cont…								
South Island pied oystercatcher	0.02 [0.00, 0.07]	0.07 [0.00, 0.56]	0.05 [−0.02, 0.44]	1.16	0.32 [0.09, 0.63]	0.30 [0.13, 0.53]	−0.02 [−0.32, 0.20]	−0.03
Black-billed gull	0.01 [0.00, 0.03]	0.03 [0.00, 0.17]	0.02 [−0.02, 0.13]	0.85	0.18 [0.04, 0.44]	0.13 [0.04, 0.38]	−0.05 [−0.25, 0.11]	−0.31
Black stilt					0.01 [0.00, 0.07]	0.01 [0.00, 0.05]	0.00 [−0.03, 0.01]	0.00
Black-fronted tern	0.00 [0.00, 0.00]	0.00 [0.00, 0.01]	0.00 [0.00, 0.01]	0.00	0.12 [0.00, 0.52]	0.13 [0.00, 0.59]	0.01 [−0.32, 0.41]	0.13
Australasian pied stilt	0.22 [0.08, 0.25]	0.25 [0.07, 0.57]	0.03 [−0.22, 0.27]	0.12	0.15 [0.03, 0.35]	0.14 [0.01, 0.44]	−0.01 [−0.20, 0.23]	−0.04
Coastal wading birds, terns and gulls								
NZ dotterel	0.03 [0.00, 0.02]	0.02 [0.00, 0.43]	0.00 [−0.14, 0.29]	0.13	0.00 [0.00, 0.00]	0.00 [0.00, 0.00]	0.00 [0.00, 0.00]	−0.41
Variable oystercatcher	0.06 [0.00, 0.13]	0.13 [0.00, 0.67]	0.07 [−0.05, 0.43]	0.72	0.07 [0.00, 0.40]	0.10 [0.00, 0.55]	0.04 [−0.07, 0.30]	0.45
Southern black-backed gull	0.4 [0.10, 0.45]	0.45 [0.04, 0.94]	0.05 [−0.26, 0.37]	0.15	0.62 [0.34, 0.80]	0.62 [0.32, 0.91]	0.00 [−0.20, 0.20]	0.01
Red-billed gull	0.17 [0.00, 0.21]	0.21 [0.00, 0.89]	0.04 [−0.11, 0.31]	0.22	0.09 [0.00, 0.49]	0.12 [0.00, 0.64]	0.03 [−0.06, 0.25]	0.28
Caspian tern	0.10 [0.00, 0.14]	0.14 [0.00, 0.64]	0.05 [−0.06, 0.32]	0.39	0.03 [0.00, 0.20]	0.06 [0.00, 0.29]	0.02 [−0.05, 0.15]	0.52
White-fronted tern	0.09 [0.00, 0.12]	0.12 [0.00, 0.65]	0.03 [−0.09, 0.37]	0.33	0.08 [0.00, 0.39]	0.09 [0.00, 0.58]	0.01 [−0.10, 0.29]	0.27
Coastal wetlands and shores								
Spotted shag	0.00 [0.00, 0.01]	0.01 [0.00, 0.06]	0.00 [−0.01, 0.03]	0.41	0.03 [0.00, 0.18]	0.06 [0.00, 0.44]	0.03 [−0.03, 0.31]	0.77
Stewart island shag					0.01 [0.00, 0.03]	0.01 [0.00, 0.07]	0.00 [−0.01, 0.04]	0.56
Reef heron	0.04 [0.00, 0.03]	0.03 [0.00, 0.18]	−0.01 [−0.1, 0.05]	−0.20	0.01 [0.00, 0.03]	0.00 [0.00, 0.02]	0.00 [−0.02, 0.01]	−0.61
Pied shag	0.06 [0.00, 0.14]	0.14 [0.00, 0.92]	0.08 [−0.06, 0.68]	0.85	0.03 [0.00, 0.26]	0.06 [0.00, 0.70]	0.03 [−0.07, 0.53]	0.74
Royal spoonbill	0.00 [0.00, 0.02]	0.02 [0.00, 0.10]	0.02 [0.00, 0.09]	1.90	0 [0.00, 0.01]	0.02 [0.00, 0.14]	0.02 [0.00, 0.13]	1.87
Freshwater wetland								
NZ scaup	0.02 [0.00, 0.06]	0.06 [0.00, 0.36]	0.04 [−0.02, 0.25]	1.01	0.03 [0.00, 0.19]	0.10 0.00, 0.52]	0.06 [−0.05, 0.42]	1.06
Brown teal	0.01 [0.00, 0.01]	0.01 [0.00, 0.03]	0.00 [−0.02, 0.03]	0.41				
Fernbird	0.03 [0.00, 0.07]	0.07 [0.00, 0.31]	0.04 [−0.04, 0.23]	0.71	0.03 [0.00, 0.13]	0.03 [0.00, 0.18]	0.01 [−0.03, 0.08]	0.22
Little shag	0.21 [0.11, 0.40]	0.40 [0.21, 0.65]	0.19 [0.03, 0.39]	0.63	0.14 [0.07, 0.28]	0.20 [0.06, 0.46]	0.05 [−0.08, 0.28]	0.33
NZ dabchick	0.02 [0.00, 0.06]	0.06 [0.00, 0.23]	0.04 [−0.04, 0.17]	0.98				
NZ shoveller	0.04 [0.00, 0.08]	0.08 [0.00, 0.23]	0.04 [−0.04, 0.16]	0.68	0.04 [0.00, 0.18]	0.07 [0.00, 0.26]	0.03 [−0.08, 0.18]	0.54
Black swan	0.07 [0.00, 0.19]	0.19 [0.01, 0.51]	0.12 [−0.02, 0.37]	1.02	0.06 [0.00, 0.23]	0.1 [0.00, 0.39]	0.04 [−0.07, 0.25]	0.51
Australasian bittern	0.03 [0.01, 0.04]	0.04 [0.00, 0.26]	0.00 [−0.05, 0.20]	0.11	0.01 [0.00, 0.03]	0.00 [0.00, 0.02]	0.00 [−0.02, 0.01]	−0.41
White heron	0.01 [0.00, 0.01]	0.01 [0.00, 0.02]	0.00 [−0.02, 0.01]	0.00	0.01 [0.00, 0.10]	0.02 0.00, 0.10]	0.00 [−0.04, 0.06]	0.26
NZ kingfisher	0.63 [0.42, 0.83]	0.83 [0.61, 0.94]	0.20 [0.07, 0.33]	0.27	0.12 [0.05, 0.26]	0.16 [0.05, 0.42]	0.04 [−0.07, 0.21]	0.29
Black shag	0.25 [0.17, 0.36]	0.36 [0.18, 0.60]	0.11 [−0.06, 0.30]	0.36	0.23 [0.16, 0.37]	0.25 [0.15, 0.43]	0.02 [−0.11, 0.19]	0.08
Little black shag	0.05 [0.02, 0.11]	0.11 [0.03, 0.27]	0.06 [−0.01, 0.20]	0.84	0.01 [0.00, 0.02]	0.01 [0.00, 0.05]	0.01 [−0.02, 0.05]	0.77
Australasian crested grebe					0.01 [0.00, 0.09]	0.02 [0.00, 0.12]	0.01 [−0.05, 0.10]	0.53

	North Island				South Island			
Common name	**1969–1979**	**1999–2004**	**Change**	**LROR**	**1969–1979**	**1999–2004**	**Change**	**LROR**
Freshwater wetland cont…								
Pūkeko	0.47 [0.17, 0.68]	0.68 [0.37, 0.92]	0.22 [−0.08, 0.55]	0.39	0.17 [0.02, 0.46]	0.20 [0.01, 0.57]	0.03 [−0.16, 0.31]	0.17
Grey teal	0.01 [0.00, 0.06]	0.06 [0.00, 0.22]	0.06 [0.00, 0.19]	1.95	0.01 [0.00, 0.09]	0.08 [0.00, 0.38]	0.07 [−0.02, 0.36]	1.73
White-faced heron	0.35 [0.22, 0.51]	0.51 [0.27, 0.79]	0.16 [−0.03, 0.39]	0.38	0.24 [0.12, 0.38]	0.28 [0.09, 0.55]	0.04 [−0.10, 0.27]	0.17
Australian coot	0.00 [0.00, 0.02]	0.02 [0.00, 0.11]	0.01 [−0.01, 0.10]	1.34	0.00 [0.00, 0.04]	0.01 [0.00, 0.07]	0.01 [−0.01, 0.05]	0.77
Other open habitats								
Rock wren					0.01 [0.00, 0.07]	0.01 [0.00, 0.05]	0.00 [−0.06, 0.03]	−0.32
Paradise shelduck	0.19 [0.07, 0.79]	0.79 [0.53, 0.93]	0.60 [0.37, 0.77]	1.41	0.44 [0.11, 0.75]	0.69 [0.52, 0.82]	0.25 [−0.06, 0.62]	0.48
NZ falcon*	0.03 [0.00, 0.03]	0.03 [0.00, 0.14]	0.01 [−0.11, 0.10]	0.25	0.05 [0.02, 0.10]	0.10 [0.03, 0.22]	0.05 [−0.02, 0.16]	0.73
NZ pipit	0.27 [0.15, 0.29]	0.29 [0.07, 0.63]	0.02 [−0.17, 0.27]	0.08	0.34 [0.24, 0.47]	0.26 [0.14, 0.43]	−0.09 [−0.22, 0.06]	−0.29
Australasian harrier	0.67 [0.47, 0.89]	0.89 [0.71, 0.95]	0.22 [0.11, 0.37]	0.29	0.55 [0.32, 0.7]	0.69 [0.36, 0.89]	0.14 [−0.06, 0.31]	0.23
Spurwing plover	0.00 [0.00, 0.85]	0.85 [0.61, 0.95]	0.85 [0.61, 0.95]	5.13	0.32 [0.12, 0.55]	0.61 [0.25, 0.89]	0.29 [0.02, 0.62]	0.67
Welcome swallow	0.31 [0.06, 0.92]	0.92 [0.84, 0.96]	0.61 [0.13, 0.86]	1.06	0.04 [0.00, 0.17]	0.44 [0.14, 0.79]	0.40 [0.12, 0.73]	2.26

Appendix 6 Local richness of endemic and non-endemic taxa

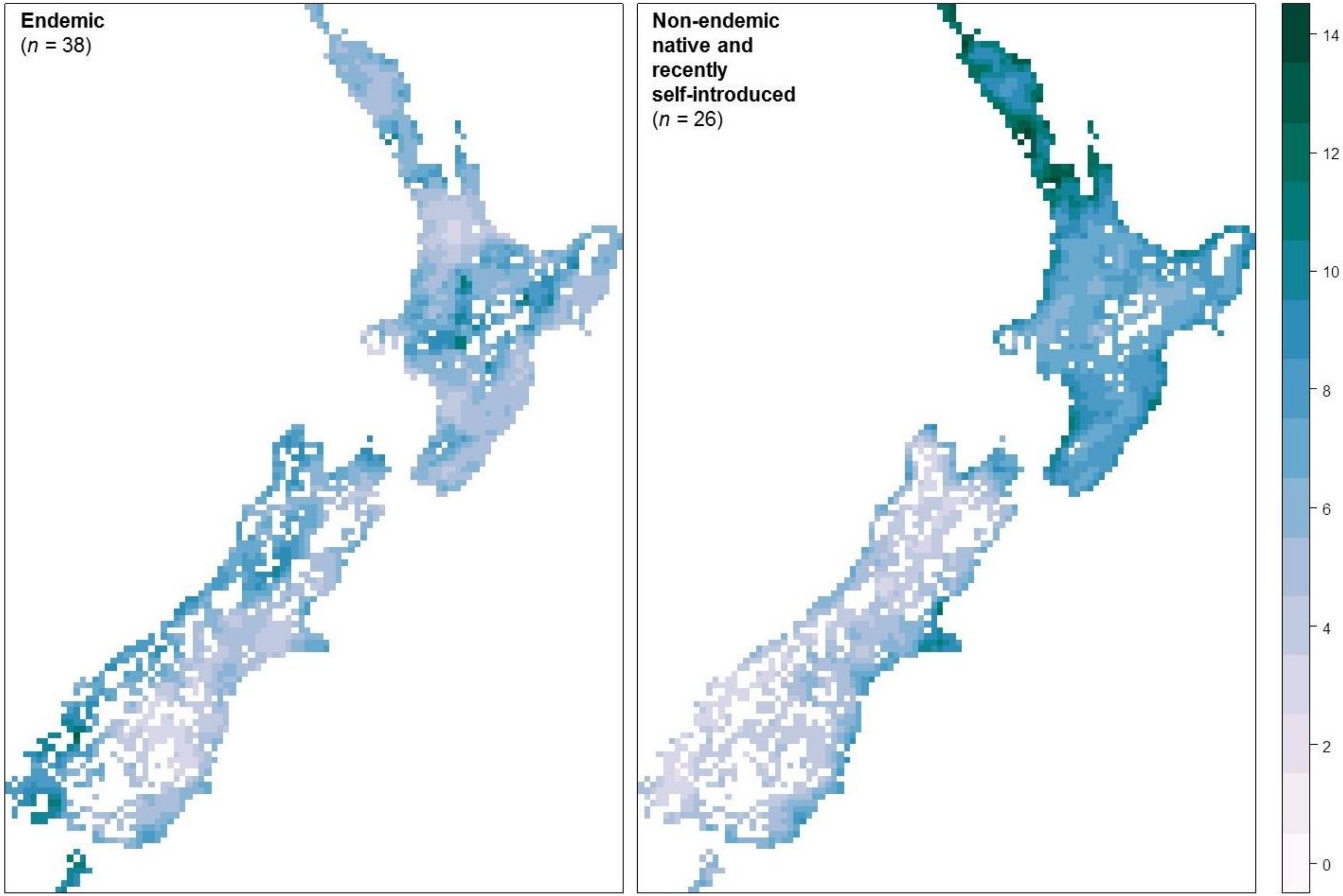

Figure A6a Local richness of endemic and non-endemic taxa across the 2,155 grid squares in 1999−2004, rounded to the nearest integer.

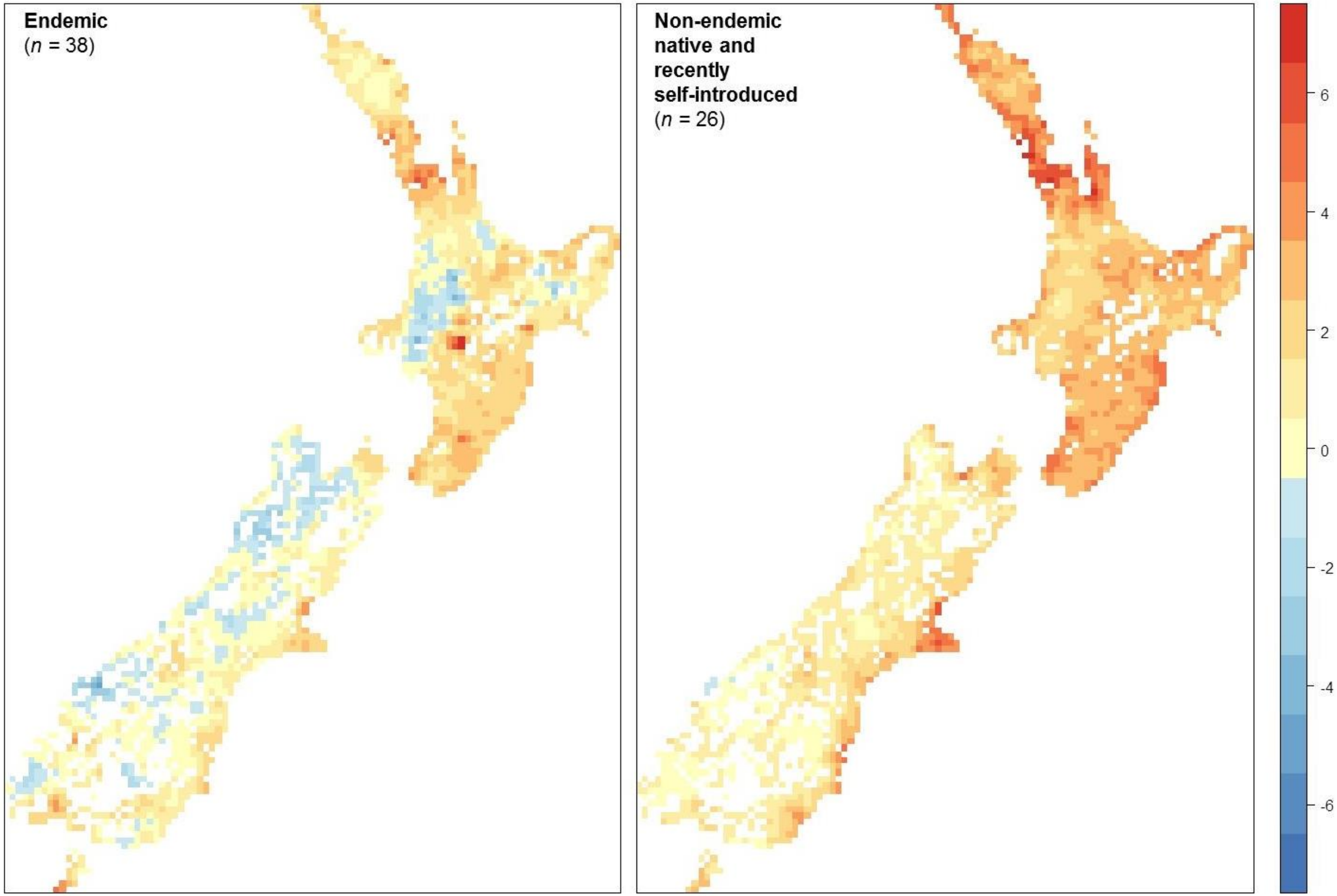

Figure A6b Change in local richness of endemic and non-endemic taxa across the 2,155 grid squares, derived by subtracting local richness in the 1969−1979 measurement period from that in the 1999−2004 measurement period and rounding to the nearest integer.

Appendix 7 Parameter estimates from linear mixed effects models

Table A7.1 Parameter estimates from the simple linear mixed effects (lme) model of probabilities of occupancy in the 64 native land-bird taxa in the North and South Islands (a, b). Estimates are parameter estimates, and are shown on the logit scale of the response variable. Lower and upper 95% confidence limits (CL) are bounds of 95% higher posterior density intervals (HPDI) of parameter estimates. We consider there is strong support for an effect (i.e. it is statistically significant) when the 95% confidence intervals of parameter estimates in the table exclude zero. The t-value is the parameter estimate divided by the standard error

(a) North Island Model	**Estimate**	**Lower 95% CL**	**Upper 95% CL**	**t-value**
Intercept	−3.42	−4.28	−2.60	−7.78
Measurement period	−0.08	−0.11	−0.06	−6.08
Endemism level	−0.36	−0.81	0.11	−1.55
Road density	−0.37	−0.40	−0.34	−22.98
Measurement period:Endemism level	−0.48	−0.49	−0.47	−65.59
Measurement period:Road density	0.19	0.16	0.22	11.48
Endemism level:Road density	−0.23	−0.24	−0.22	−35.06
Measurement period:Endemism level:Road density	0.04	0.03	0.06	4.77
(b) South Island Model	**Estimate**	**Lower 95% CL**	**Upper 95% CL**	**t-value**
Intercept	−3.26	−3.91	−2.60	−9.41
Measurement period	−0.08	−0.10	−0.06	−7.82
Endemism level	−0.11	−0.47	0.25	−0.58
Road density	−0.31	−0.34	−0.29	−26.11
Measurement period:Endemism level	−0.24	−0.26	−0.23	−41.86
Measurement period:Road density	0.03	0.01	0.05	3.17
Endemism level:Road density	−0.19	−0.20	−0.18	−49.13
Measurement period:Endemism level:Road density	−0.04	−0.05	−0.02	−6.61

Table A7.2 Parameter estimates from the lme models of inland-breeding wading bird, tern and gull occupancy probabilities for (a) the North Island and (b) the South Island (Model 3). Estimates are parameter estimates, and are shown on the logit scale of the response variable. Lower and upper 95% confidence limits (CL) are bounds of 95% higher posterior density intervals (HPDI) of parameter estimates: we consider there is strong support for an effect when the 95% limits exclude zero. The t-value is the parameter estimate divided by the standard error

(a) North Island Model	**Estimate**	**Lower 95% CL**	**Upper 95% CL**	**t-value**
Intercept	−4.86	−5.96	−3.73	−8.19
Measurement period	0.12	0.07	0.16	4.88
Endemism level	−1.37	−1.41	−1.32	−54.66
Distance from coast	−0.27	−0.32	−0.24	−12.82
Agriculture and forestry	0.09	0.04	0.14	3.83
Urbanisation	0.10	0.07	0.14	5.74
Measurement period:Endemism level	−0.30	−0.35	−0.26	−12.65
Measurement period:Distance from coast	−0.17	−0.21	−0.12	−7.34
Endemism level:Distance from coast	−0.03	−0.06	0.00	−2.21
Measurement period:Agriculture and forestry	0.00	−0.05	0.05	−0.03
Endemism level:Agriculture and forestry	−0.05	−0.08	−0.01	−2.62
Distance from coast:Agriculture and forestry	−0.08	−0.12	−0.03	−3.39
Measurement period:Urbanisation	0.10	0.06	0.14	5.10
Measurement period:Endemism level:Distance from coast	0.10	0.06	0.15	4.71
Measurement period:Endemism level:Agriculture and forestry	−0.01	−0.05	0.04	−0.31
Measurement period:Distance from coast:Agriculture and forestry	0.01	−0.03	0.05	0.52
Endemism level:Distance from coast:Agriculture and forestry	−0.02	−0.06	0.01	−1.46
Measurement period:Endemism level:Distance from coast:Agriculture and forestry	0.02	−0.02	0.07	0.93

(b) South Island Model	**Estimate**	**Lower 95% CL**	**Upper 95% CL**	**t-value**
Intercept	−2.74	−4.39	−0.74	−3.01
Measurement period	−0.17	−0.21	−0.14	−8.66
Endemism level	−2.08	−2.49	−1.59	−9.23
Distance from coast	0.28	0.23	0.33	10.24
Agriculture and forestry	0.21	0.17	0.25	9.32
Urbanisation	0.07	−0.01	0.14	1.87
Measurement period:Endemism level	−0.07	−0.10	−0.02	−3.37
Measurement period:Distance from coast	−0.33	−0.37	−0.28	−14.60
Endemism level:Distance from coast	−0.01	−0.04	0.02	−0.65
Measurement period:Agriculture and forestry	−0.04	−0.08	0.00	−1.89
Endemism level:Agriculture and forestry	−0.10	−0.12	−0.07	−7.43
Distance from coast:Agriculture and forestry	−0.17	−0.22	−0.12	−6.62
Measurement period:Urbanisation	0.06	0.00	0.11	1.78
Measurement period:Endemism level:Distance from coast	0.06	0.02	0.10	2.73
Measurement period:Endemism level:Agriculture and forestry	−0.01	−0.05	0.02	−0.59
Measurement period:Distance from coast:Agriculture and forestry	−0.10	−0.14	−0.05	−4.52
Endemism level:Distance from coast:Agriculture and forestry	−0.04	−0.07	−0.01	−2.62
Measurement period:Endemism level:Distance from coast:Agriculture and forestry	0.10	0.06	0.14	4.36