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MANAAKI WENUA

**Status and change in native forest birds on
New Zealand's mainland, 1969–1979 to 1999–2004**



Status and change in native forest birds on New Zealand's mainland, 1969–1979 to 1999–2004

Susan Walker, Adrian Monks, John Innes

Landcare Research

Prepared for:

Parliamentary Commissioner for the Environment

PO Box 10-241
Wellington 6143
New Zealand

May 2017

*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:

Andrew Gormley
Researcher
Landcare Research

Gary Houlston
Portfolio Leader – Enhancing Biodiversity
Landcare Research

Landcare Research Contract Report:

LC2786

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Summary

Project and client

In this report we describe patterns of status and change in 22 taxa of New Zealand's native forest birds in two measurement periods (1969–1979 and 1999–2004) for the Parliamentary Commissioner for the Environment.

This work extends a report on 64 taxa of native land birds (Walker & Monks 2017), which describes the development of a standardised national data set of bird occupancy probabilities from two national atlases of bird distribution, and summarises status and change across the native avifauna. Walker and Monks (2017) concluded that two (of six) groups of birds were in greatest need of conservation effort: endemic forest and alpine birds, and endemic wading birds, terns or gulls that breed in the inland eastern South Island. This report focuses on the 22 taxa of native forest birds found on the New Zealand mainland.

Objectives

- To investigate how scarcity of indigenous forest cover has affected native forest birds.
- To ask whether colder forests have provided native forest birds thermal refuge from predation.
- To determine how the effects of indigenous forest cover loss and temperature vary across levels of endemism and among native forest bird species.

Methods

We used standardised estimates of probabilities of occupancy for 22 native forest bird taxa in each of 2,155 10 × 10 km grid squares in two measurement periods (1969–1979 and 1999–2004). We analysed patterns of local richness and occupancy in relation to birds' taxonomic levels of endemism, and the percentage of land under indigenous forest and mean annual temperature within grid squares.

Results

Data from the two national atlases show major declines in the ranges occupied by many native forest birds across the New Zealand mainland generally, and in indigenous forests, between the 1970s and the early 2000s. These changes show clear and systematic patterns that are related to endemism level, forest cover and temperature.

Endemic bird taxa underwent the greatest relative range declines, especially (but not only) 'deep endemics' (i.e. taxa that are endemic at the level of subfamily, family or order). The largest range declines were in the remaining large indigenous forest tracts, to which many endemic taxa were largely confined by the 1970s.

Across the grid squares covered by our data the median percentage of forest range occupied by deep endemic bird taxa decreased from 15.5 to 5.3% between measurement periods in the North Island, and from 22.7 to 15.7% in the South Island. Whitehead (the North Island endemic *Mohoua albicilla*) was the only deep endemic species to show a convincing range increase.

The largest relative range declines between measurement periods were in blue duck, weka, rifleman, kākā and long-tailed cuckoo on both islands, and in North Island brown kiwi, North Island kōkako and North Island robin. There were also notable range declines in parakeet species in the North Island, and in kiwi, kererū, tūī, tomtit and morepork in the South Island.

There were net increases in range in most forest bird taxa that have arrived more recently in New Zealand (grey warbler, fantail, shining cuckoo and silvereye).

Low indigenous forest cover reduced occupancy probabilities of most native forest birds. Its negative effects were greater on deep endemic taxa.

Probabilities of occupancy in native forest birds, especially deep endemics, were significantly lower in forests that experience higher mean annual temperatures. New Zealand's colder forests, many of which are dominated by species of beech or rimu, are now its most important reservoirs of endemic forest bird populations.

Warmer-forested squares on both islands, but especially the North Island, supported few deep endemic forest birds by 1969–1979. Decreases in range occupancy between measurement periods were greater in warmer forests, where there were still remnant bird populations left to lose. These effects do not appear to be driven by higher levels of human disturbance and deforestation or fragmentation in warmer forests.

Although endemic forest bird taxa became increasingly confined to colder forests between measurement periods, their local probabilities of occupancy also decreased in colder forests over the same period.

Conclusions

Between 1969–1979 and 1999–2004 there was widespread and systematic loss of endemic forest birds from New Zealand's forests. This trend is likely to have continued since 2004.

Our results are consistent with predation by introduced mammals being the primary cause of recent decline and limitation in New Zealand's native forest birds. There may be other contributing and interacting causes, but evidence for them is weak.

Forest scarcity may have more important negative consequences for endemic forest bird conservation than has been recognised. A number of taxa appear intolerant of deforestation as well as predation, especially those that are endemic at higher taxonomic levels. Our results caution against expectations that they would be able to sustain viable populations in deforested and partially forested landscapes if mammal predators were absent.

Assuming that mammalian predators can be reduced to and sustained at the required threshold minima, restoration of viable endemic forest bird populations through predator management is more likely to be successful in large, continuous tracts of forest.

Loss of endemic forest birds from New Zealand's forests before 1969–1979 and between measurement periods varied with mean annual temperature. Cold forests (those with mean annual temperatures less than about 10°C) have become the most important strongholds of a number of endemic forest birds that have declined faster in warmer forests. The cause is likely to be higher and/or more continuous predation pressure where temperatures are warmer. However, the refuge that cold forests have provided for endemic forest bird species has also diminished, also (probably) as a consequence of ongoing predation.

Many of New Zealand's colder forests are in the South Island and are dominated by beech or rimu trees, which periodically exhibit synchronised heavy seeding. Our results explain why mast seeding events and consequent predator irruptions in these remaining cold-forest strongholds have become such critical threats to the persistence of forest bird species.

Loss of endemic forest birds is likely to be exacerbated by climate warming, by reducing the extent of cold forests where predation pressure is relatively low in most years, and by favouring cold-limited predators generally across forests. It may also increase the frequency of mast seeding events.

The opportunity to retain large viable populations of predator-vulnerable forest birds on the mainland is retreating. Large-scale predator control by aerial 1080 on public land is currently the only practical and cost-effective way to retain these populations.

1 Introduction

Throughout most of the evolutionary history of New Zealand's birds, forest has been the predominant land cover (Lee et al. 2016). As a consequence, most terrestrial native bird species that are classified within orders, families, genera and species that occur nowhere else in the world are birds that breed and feed primarily in forest habitats. Forest birds collectively represent New Zealand's largest contribution to global avian biodiversity.

Many native forest bird species became extinct following human settlement of New Zealand (Worthy & Holdaway 2002; Robertson et al. 2013), and most extant species are either in decline or threatened with extinction (Innes et al. 2010; Robertson et al. 2013). A number of taxa survive today only where predators are intensively managed at very low levels, such as on offshore or nearshore islands or in mainland sanctuaries (Towns 2011; Burns et al. 2012; Innes et al. 2012, Innes, Burns et al. 2015).

Predation by introduced mammals is understood to be the primary cause of recent declines in native forest birds (Innes et al. 2010), and protecting forest birds from predation has been a major focus of New Zealand's conservation efforts. Since the 1970s populations of several threatened forest birds and other species have been secured from extinction on offshore islands by a combination of predator eradication and translocation (Towns & Ballantine 1993; Towns & Broom 2003; Bellingham et al. 2010; Towns 2011; Miskelly & Powlesland 2013)¹. However, the principal challenge for forest bird conservation today remains to secure vulnerable species from decline in their natural habitats on the New Zealand mainland².

¹ Forest birds translocated to islands include North Island brown kiwi (*Apteryx mantelli*), little spotted kiwi (*A. owenii*), North Island weka (*Gallirallus australis greyi*), kākāpō (*Strigops habroptilus*), red-crowned and yellow-crowned parakeet/kākāriki (*Cyanoramphus novaezelandiae* and *C. auriceps*), whitehead (*Mohoua albicilla*), mōhua (*M. ochrocephala*), North Island robin (*Petroica longipes*), South Island robin (*P. australis*), hihi (*Notiomystis cincta*, North Island and South Island saddleback (*Philesturnus carunculatus rufusater* and *P. c. carunculatus*), and North Island kōkako (*Callaeas wilsoni*).

² There are several reasons for this. The supply of offshore islands suitable for pest eradication and restoration is being exhausted: few islands now remain that are nature reserves large enough to be worthwhile and distant enough from the mainland that predator reinvasion is unlikely, and that have not already been subject to pest mammal eradication (Innes et al. 2012). Some threatened species (e.g. whio/blue duck) cannot be translocated to and maintained on islands, which offer a different suite of environments from those on the mainland. Limitations to dispersal to and from offshore islands, and small founder populations, mean that island populations may require careful intervention to maintain genetic diversity (Jamieson 2015). As a result, maintaining large *in situ* populations of indigenous bird species on the mainland is the best way to achieve persistence and continued evolution, and this outcome coincides with New Zealanders' desire to see and experience native biota in their natural habitats (DOC & MfE 2000; DOC 2016).

Management and research over the last three decades have considerably advanced New Zealand's capability to sustain forest birds through predator control (Brown et al. 2015)³. They have enabled, for example, large-scale, temporally targeted aerial 1080 operations to protect mainland bird (and other) species populations from the consequences of beech-mast events in recent years ('Battle for our Birds'; Elliott & Kemp 2016); associated research could further improve the effectiveness, cost-effectiveness and hence potential scale of this management (Brown et al. 2015; Elliott & Kemp 2016). In addition, over the last two decades experience from island conservation combined with predator-proof fencing technology has allowed conservation of native forest species in community-initiated fenced mainland sanctuaries in both partly and mostly deforested landscapes (Burns et al. 2012; Innes et al. 2012).

Despite growing conservation capability and expertise, it has been clear that many of New Zealand's vulnerable native forest bird species have continued to decline on the mainland in recent decades (Innes et al. 2010; Robertson et al. 2013). In an associated report (Walker & Monks 2017), we quantified changes in forest bird occupancy between 1969–1979 and 1999–2004 using standardised, spatially explicit, national-scale data derived from the Ornithological Society of New Zealand's (OSNZ's) two national atlases of bird distribution.

Our results in a companion report (Walker & Monks 2017) showed that in addition to predation, factors associated with dense human occupation had negative effects on native forest bird species, especially deep endemics (i.e. taxa endemic to New Zealand at the levels of order, family or genus). In this report we ask how, and how much, scarcity of indigenous forest habitat affects the occupancy distributions of forest birds.

New Zealand's indigenous forest cover has been greatly reduced, from over 80% of the land area of North, South and Stewart Islands at the time of first human settlement, to approximately 24% cover by the 1970s (Newsome 1987) and 23.8% today (LCRIT 2015). The effects of indigenous forest loss on native forest bird species and communities have been little studied compared to the effects of predation (but see Diamond 1984; Stevens 2006; Barnagaud et al. 2014; Ruffell & Didham 2017).

Innes et al. (2010) suggested that scarcity of indigenous forest cover was the primary limiting factor for most forest birds in New Zealand's deforested landscapes. Recently, Ruffell and Didham (2017) showed positive effects of indigenous forest and shrubland cover⁴ on the abundances of some common forest birds near Auckland, which suggested

³ Key initiatives in mainland multi-species predator control include those undertaken for North Island kōkako (from 1989; Innes et al. 1999), mainland islands (from 1995; Saunders & Norton 2001; Gillies et al. 2003), kiwi sanctuaries (from 2000; Robertson & de Monchy 2012), Operation Ark (from 2004; Elliott & Suggate 2007); and long-term predator control programmes in sites such as the Eglinton, Hawdon and Landsborough valleys and the Catlins (O'Donnell & Phillipson 1996; O'Donnell & Hoare 2012; Hoare et al. 2013; GE Elliott, Department of Conservation, unpublished data), and large management experiments in the Tararua Range, the Marlborough Sounds and South Westland (from 2010; GE Elliott, Department of Conservation, unpublished data).

⁴ 'Indigenous forest', 'broadleaf indigenous hardwoods', and 'mānuka and kānuka'.

that abundance declined rapidly below 5–10% forest cover for grey warbler and tūī. Both studies noted that growing interest in native forest bird conservation in deforested landscapes demands a better understanding of minimum forest habitat and area requirements. We investigate here how local richness and occupancy probabilities of forest birds vary with available forest habitat and with birds' taxonomic level of endemism at a national scale, and consider the implications for forest bird conservation.

We then investigate how forest bird occupancies are affected by mean annual temperature – an environmental factor that is likely to be closely associated with the abundance of some of their key predators. Ship rat (*Rattus rattus*) and Australian brushtail possum (*Trichosurus vulpecula*) are important forest-bird predators that are generally more abundant at lower elevations, where mean annual temperatures are generally higher (Studholme 2000; Christie et al. 2009, 2017; Kemp & Elliott, unpublished data; Fraser et al. 2004; Porphyre et al. 2013). If birds in warmer forests are under higher and more continuous pressure from predation, bird species that are more susceptible to predation are likely to have been lost earlier from warmer forests. Therefore we predicted that colder forests would be the principal refuges ('thermal refuges') for populations of predator-vulnerable forest birds.

Evidence that vulnerable forest birds are becoming progressively confined to New Zealand's colder forests would have implications for forest bird conservation. Because most of New Zealand's colder forests are dominated by beech or rimu trees, this would explain and reinforce the importance of predator control in response to beech and rimu mast seeding events to protect predator-vulnerable forest birds (Elliott & Kemp 2016), whether or not mast events increase in frequency in the future (Kelly et al. 2013; Monks et al. 2016). It would also suggest that climate warming will exacerbate predation on forest birds in New Zealand forests by raising the elevation at which cold temperature limits bird predators (thus reducing the extent of the 'cold forests' zone below the treeline) and by favouring populations of cold-limited bird predators generally.

2 Background

In an associated report (Walker & Monks 2017) we describe our development of a standardised set of data for New Zealand's land birds from OSNZ's two national atlases of bird distribution. The data set allows robust comparisons of the median probabilities of occupancy (i.e. use of or presence at a site) of 64 native bird taxa across New Zealand between 1969–1979 and 1999–2004.

Using those data, we concluded that mainland range decreases between measurement periods were greatest (i) in wading birds, terns or gulls that breed mainly in the inland eastern South Island, and (ii) in forest and alpine birds, especially those endemic at high taxonomic levels (deep endemics). We concluded that predation was likely to be the primary cause of recent declines in forest and alpine birds, because there was little habitat change in remote natural areas where the declines were greatest. However, we found that factors associated with dense human occupation had additional negative effects on native forest bird species.

In this report we use the same data set as developed in Walker & Monks (2017) to further investigate spatial patterns of forest bird occupancy and identify potential drivers of change and limitations on recovery.

3 Objectives

- To investigate how scarcity of indigenous forest cover has affected native forest birds.
- To ask whether colder forests have provided native forest birds thermal refuge from predation.
- To determine how the effects of indigenous forest cover loss and temperature vary across levels of endemism and among native forest bird species.

4 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.

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 value 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. For example, in this report the taxon ‘kiwi’ in the North Island refers to all recognised forms of *Apteryx mantellii* (‘North Island kiwi taxa’) and in 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’.

5 Data

5.1 Standardised forest bird occupancy data set

Our occupancy estimates for native forest bird taxa are derived from data in two national atlases of bird distribution compiled by the OSNZ (Bull et al. 1985; Robertson et al. 2007). Field surveys for the atlases were undertaken from September 1969 to December 1979 (1969–1979) and from December 1999 to November 2004 (1999–2004). We refer to these survey periods as the first and second ‘measurement periods’.

We produced a standardised data set of median probabilities of occupancy for each of 22 indigenous forest bird taxa, at the centre of each of 2,155, 10 × 10 km grid squares, in each

measurement period. The occupancy modelling process used is described in detail in an associated report (Walker & Monks 2017). The variability in the probabilities used to calculate the medians was not 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 to fit models taking into account spatial autocorrelation – the fact that squares adjacent to each other are less independent than those further apart – which has the 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 square-wise estimates of occupancy is not represented in our analyses. Incorporating this uncertainty into our models could alter estimates of the confidence intervals on the parameters of our models and therefore the inferred ‘significance’ or otherwise of effects.

The common grid of 2,155 squares excludes all locations not sampled in one or both atlases, and excludes all squares covering more than 75% water (coasts and large inland lakes). Each grid square was assigned 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 are included in our definition of ‘South Island’. There are 1,083 North Island squares and 1,072 South Island squares, which cover 88% (99,510 km²) of the land in the North Island and 66% (99,630 km²) of the land in the South Island and Stewart Island combined.

5.2 Native forest bird taxa

We follow Innes et al. (2010) in defining native forest birds as those that breed and feed primarily in forest habitats. We differ from Innes et al. (2010) by including kea (*Nestor notabilis*) as a forest bird⁵. The 22 forest bird taxa (Appendix 1) include all extant native forest bird species that we were able to fit occupancy models for. Some of New Zealand’s extant indigenous forest bird species were recorded too rarely in the atlases for their occupancy to be estimated successfully. We omitted the following extant species or subspecies from our study: little-spotted kiwi (*Apteryx oweni*, in the order Apterygiformes), kākāpō (*Strigops habroptilus*, in the family Strigopidae), hihi/stitchbird (*Notiomystis cincta*, in the endemic family Notiomystidae; Driskell et al. 2007); and North Island and South Island saddleback (tīeke, *Philesturnus carunculatus rufusater* and *P. carunculatus carunculatus*, both in the endemic family Callaeidae). We also excluded the North and South island bush wrens (*Xenicus longipes stokesii* and *X. longipes longipes*, in the family Acanthisittidae; Ericson et al. 2002) that inhabited forest and were recorded in the first atlas (Bull et al. 1985), but are now considered to be globally extinct (Robertson et al. 2013). We excluded

⁵ O’Donnell et al. (2017) say it is a ‘popular misconception’ that kea use only alpine habitat. Kea feed and breed in forest (although not exclusively; Jackson 1963; O’Donnell & Dilks 1986; Heather & Robertson 1996) and are ‘sequential foraging specialists, commonly found in coastal and montane forests and moving among numerous seasonally available food sources’ (O’Donnell et al. 2017; Kemp et al. in prep.).

South Island kōkako (*Callaeas cinerea*), 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.

We had to combine the records of three species of parakeets/kākāriki (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, Eppink 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 occupancy models for North Island kōkako and whitehead were fitted from and interpolated to squares only on the North Island. Our models for brown creeper, kea and mohua were fitted from and interpolated only to 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 robins *Petroica longipes* and *P. australis*), subspecies, forms or varieties.

We grouped the 22 bird taxa according to their taxonomic level of endemism (Appendix 1), and applied these as a proxy for the length of time that a lineage has been isolated in New Zealand (Table 1). We refer to taxa endemic at levels 5, 6 and 7 (subfamily level and higher) collectively as 'deep endemics'.

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 forest bird taxa that are assigned to each category

Endemism level	Endemic or non-endemic	Number of forest bird taxa
1. Recently self-introduced native	Non-endemic	1 (silveryeye)
2. Non-endemic native	Non-endemic	2
3. Endemic at the species level	Endemic	9
4. Endemic at the genus level	Endemic	3
5. Endemic at the subfamily level	Endemic	1 (blue duck/whio)
6. Endemic at the family level	Endemic	7
7. Endemic at the order level	Endemic	1 (kiwi species)

5.3 Environmental characteristics of the grid squares

We calculated the percentage indigenous forest cover, median mean annual temperature, and road density across the land in each grid square from publicly available GIS surfaces (Figure 1). *Percentage indigenous forest cover* is the percentage of land in the square that is

classified as indigenous forest in the Land Cover Database (LCDB2, which is based on satellite imagery acquired during the summer 2001/02 measurement period; LCRIT 2015).

We use the estimate of percentage indigenous forest cover in summer 2001/02 in all of our analyses, for two reasons. First, overall change in the area of indigenous forest cover across New Zealand since the 1970s has not been great. Comparisons of estimates from the early 1980s (Newsome 1987) with the LCDB (LCRIT 2015) suggest a decrease from about 25.0% of New Zealand's land cover to 24.9% in 2002. A change of 0.1% may be within the margin of measurement error, and does not provide strong evidence that there has been an overall decrease in forest cover. Second, although it is likely that indigenous forest cover has decreased markedly in some squares since the data were collected for the first atlas, there is only one GIS layer available that describes the national distribution of indigenous forest cover in the early 1980s (Newsome 1987). This layer is not sufficiently accurate, in our opinion, to allow robust estimates of indigenous forest cover (and therefore change between the early 1980s and 2001/02) at the level of individual grid squares.

Mean annual temperature was calculated as the median of mean annual temperature estimated in the centre of each 100 m pixel of land in the square. It is derived from the mean annual temperature data layer underlying the LENZ data set of Leathwick et al. (2003), which is derived from temperature records between 1950 and 1980.

Road density was calculated as the length of all roads contained in the LINZ 25 m road centrelines data set (in km), divided by land area in the square (in km²).

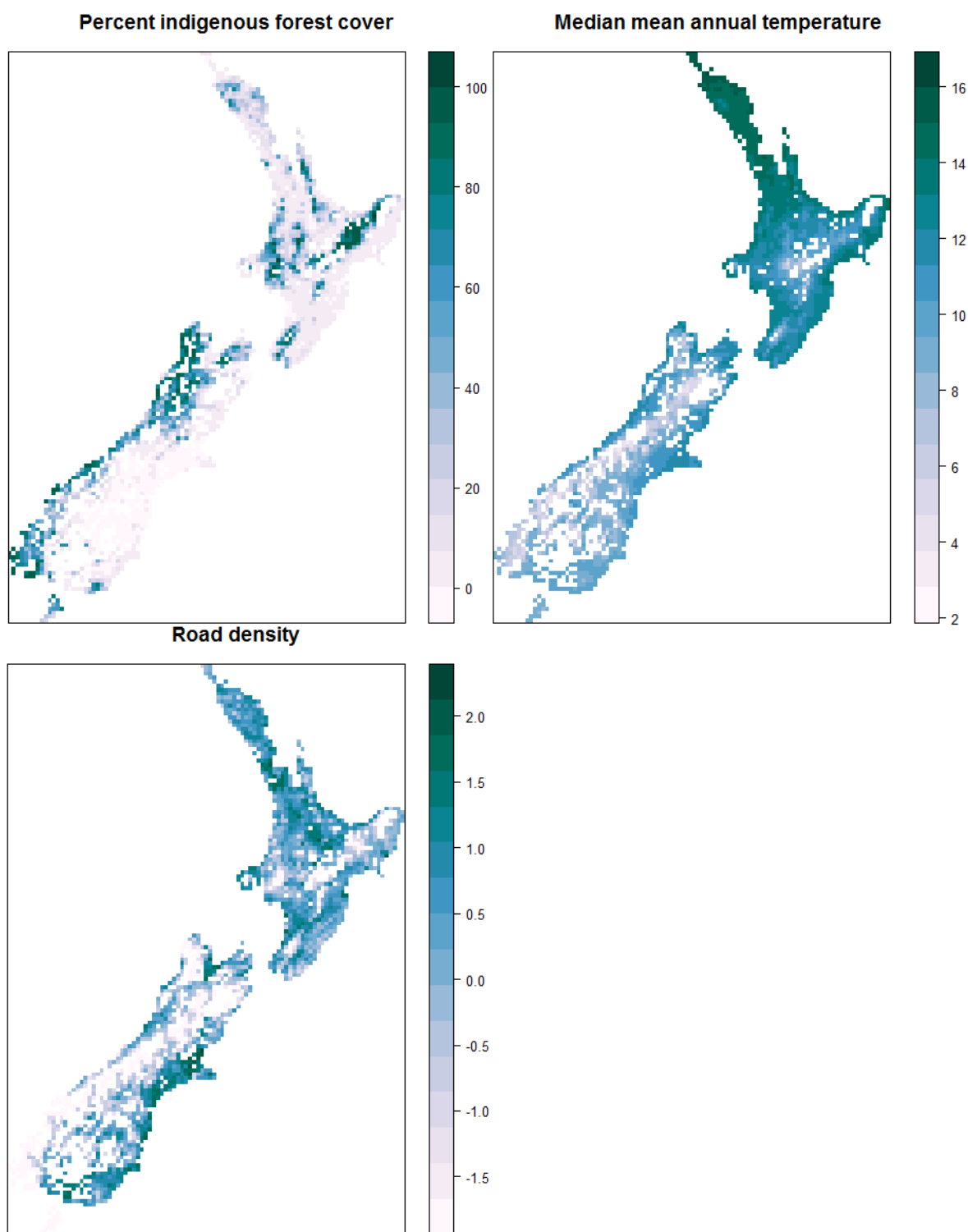


Figure 1 Environmental characteristics of the grid squares used in this report.

For the analysis we transformed these variables so that they spanned similar scales and centred them on zero. We subtracted 50% from indigenous forest cover and scaled by dividing by 100. Mean annual temperature was centred and scaled by dividing by the

standard deviation. The distribution of road density was highly non-linear. We transformed it by first taking the square root, and then centring and scaling by dividing by the standard deviation.

Temperature (represented by mean annual temperature) was expected to have an important positive effect on the abundance of key predators of native birds (especially ship rats and possums) in areas such as remaining forests that are less transformed by humans. We note that alternative temperature parameters, such as minimum annual temperature or winter temperature, may be more limiting to these predators than low mean annual temperature. However, these alternatives are generally correlated with mean annual temperature. We used road density as a proxy for the degree of human transformation of the landscape by human occupation.

We plotted paired scatter plots and coefficients of correlation to examine relationships between the square-level characteristics on each island. These show that RD (road density) and MAT (mean annual temperature) are strongly positively correlated on both islands (warmer areas are more densely settled, especially in the South Island, $r = 0.68$) (Figure 2).

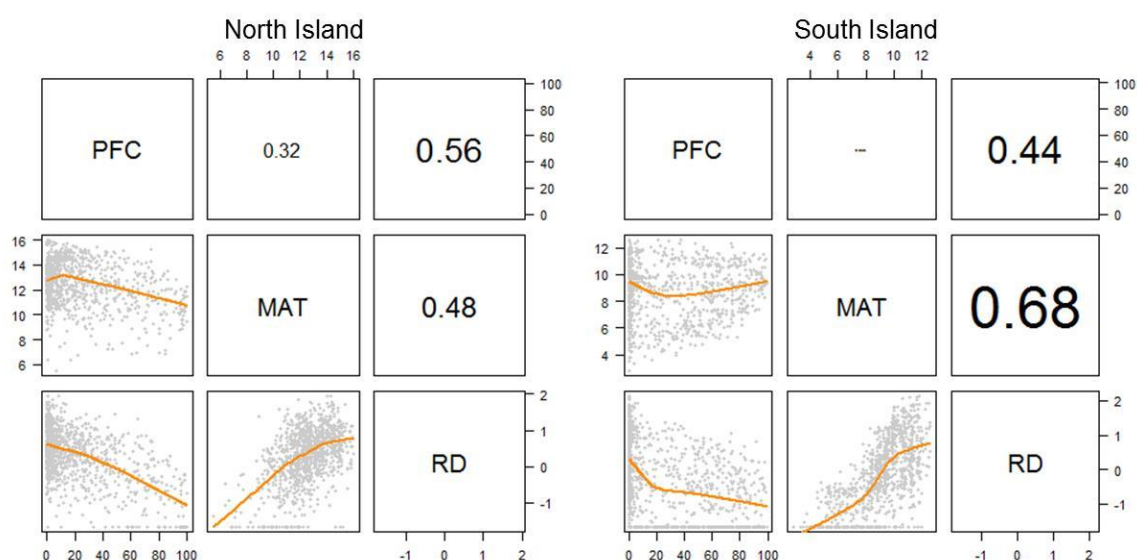


Figure 2 Relationships between characteristics of the 2,155 grid squares in the North and South Islands. The characteristics compared are labelled on the diagonal: PFC is percentage indigenous forest cover, shown on the original scale; MAT is median mean annual temperature in degrees Celsius; and RD is the scaled and centred square root of road density. In each set, plots below the diagonal show grid squares as points on scatter plots and their relationships, depicted using local regression curves, as orange lines. Upper plots show the associated coefficients of correlation (r) between pairs of characteristics, and larger text indicates stronger correlation.

Warmer and more densely settled areas also had less forest (negative correlations between PFC and both RD and MAT). This means that the effects of temperature, indigenous forest cover and road density are somewhat confounded, and we need to take care to address this in our interpretation.

6 Analyses

6.1 Summaries of status and change in occupancy

We summarise *status* in the 1999–2004 measurement period by plotting the average, interquartile range (i.e. the middle 50% of estimates) and 95% limits of median probabilities of occupancy for each bird taxon across the squares on each island. The average of median local occupancy probabilities across squares is an estimate of the proportion of the geographic range occupied by an individual bird taxon⁶.

We summarise *changes* in range occupancy between measurement periods using log range occupancy ratios (LRORs – equivalent to log response ratios; Hedges et al. 1999). 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 range contractions relative to 1969–1979, and large positive LRORs indicate large relative range increases. Range contraction is an important signal of likely population decline (Caughley & Gunn 1996).

6.2 Percentage of indigenous forest range occupied

To estimate the percentage of indigenous forest range occupied by each forest bird taxon we:

- multiplied its median probability of occupancy in each square by the area of indigenous forest in that square
- summed these estimates across squares on each island, and then
- divided the sum by the total area of forest in squares on that island.

As explained in section 5.3, we assume – due to lack of dependable indigenous forest cover data for 1969–1979 – that the same area of indigenous forest remained in both measurement periods (i.e. we assume there was no forest cover change in any grid square between measurement periods). The total area of indigenous forest covered by the 2,155 squares in 2001/02 is approximately 73% of the total mapped area of indigenous forest in New Zealand at that time.

⁶ 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.

6.3 Effects of indigenous forest cover

6.3.1 Trends in local forest bird richness with indigenous cover

We estimated the number of forest bird taxa most likely to occupy each grid square in each measurement period (local forest bird richness) by summing local median occupancy probabilities across the relevant taxa. We plotted these estimates of local forest bird richness (in total, and at different levels of endemism) against percentage indigenous forest cover (a proxy for the proportion of land available to birds as forest habitat; section 5.3), and used local regression to depict the mean trends. These trends were compared visually only, and not by fitting models.

Summing occupancy probabilities (each between 0.0 and 1.0) across taxa results in non-integer estimates of the most likely number of forest bird taxa per square. However, only a whole number of species can possibly occupy a square in reality. We fitted our local regression curves to the raw (non-integer) estimates, but follow our convention in Walker & Monks 2017 and plot local richness estimates for squares after rounding to the nearest integer, showing the most likely 'real' outcome.

6.3.2 Trends in probabilities of occupancy with indigenous cover

We fitted and plotted locally weighted regression curves of the median occupancy probability of individual taxa on percentage indigenous forest cover for each taxon, island and measurement period. As with local richness trends (section 6.3.1), these are presented for visual comparison only.

We then supplemented these purely descriptive approaches (sections 6.3.1 and 6.3.2) with models that test whether percentage indigenous forest cover, time (measurement period) and endemism level 'significantly' affected median occupancy probabilities of native forest birds, and how they interact. These models were fitted as linear mixed effects (lme) models using the R package lme4⁷.

Median occupancy probability was modelled as the logit (natural log of $x/(1-x)$) of the probability(x). 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 family. Measurement period was a two-level factor predictor variable, and we treated

⁷ 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 linear mixed effects (lme) models in Appendix 7.

levels of endemism as a centred continuous predictor variable with equally spaced⁸ integer values of –3 (recently self-introduced) to 3 (endemic at the taxonomic level of order). Responses of occupancy probability to these predictors were fitted as linear terms.

Our models of 64 native land birds in Walker & Monks (2017) showed (1) that deep endemic birds had lower median occupancy probabilities than non-endemic taxa, and showed bigger decreases in occupancy probabilities between measurement periods; and (2) that factors associated with human occupation (represented by an index of road density) have inhibiting effects on forest birds, with greater effects on deep endemics. For our subset of native 22 forest bird taxa, we expected that the main predictors of occupancy and occupancy change would be endemism level and loss of indigenous forest cover (associated with human transformation of the landscape).

We fitted a model (Model F1) for each island with a full three-way interaction of measurement period, endemism level and percentage indigenous forest cover as predictors, and plotted their effects. We expected that:

- median probabilities of occupancy would increase with percentage indigenous forest cover (which represents available primary habitat)
- if forest loss is more harmful to birds from lineages that have evolved longer on a New Zealand land mass with few non-forest environments until the Pleistocene (Lee et al. 2016), the effects of indigenous forest cover and endemism level on occupancy would interact
- recent (i.e. 1969–1979 to 1999–2004) decreases in forest bird occupancy probabilities would have been greater in squares with more indigenous forest cover, because occupancy probabilities were low in deforested squares by 1969–1979 (i.e. there were fewer left to lose)
- the greater decreases in occupancy probabilities in deep endemics (compared to non-endemic taxa) would occur mainly in places with more indigenous forest cover, because we expected that by 1969–1979 deep endemics would have been more thoroughly extirpated from deforested places than non-endemic taxa.

6.4 Effects of temperature on occupancy probabilities

Ship rats and possums are important predators of native forest birds and are known to be more abundant in warmer environments. If forest bird populations are under greater and/or more continuous pressure from predation in warmer environments, predation-susceptible species will have been lost more rapidly, and earlier, from warmer squares than colder

⁸ We use endemism level as a proxy for the length of time that a taxon's lineage has evolved in New Zealand. Equal spacing of endemism levels seems appropriate because there is an approximately linear relationship between equally spaced levels and estimated dates of phylogenetic divergence of these taxa from their nearest non-native relatives (S Walker, A Monks, BJM Potter and J Innes, unpublished data).

squares. If forest habitat is also important for forest birds, we would expect cold forested squares to be the principal refuges ('thermal refuges') of populations of predator-vulnerable forest birds.

To test these expectations, we fitted lme models of native forest bird median occupancy probabilities for each island, with a full four-way interaction of measurement period, endemism level, indigenous forest cover and temperature (Model F2). Each model also included a term for road density, and the interaction between endemism and road density, because we anticipated (based on results in Walker & Monks 2017) that squares with more roads at any given indigenous forest cover and temperature could have lower occupancy probabilities of deep endemic birds and higher occupancy probabilities of non-endemics.

We plotted the effects of these variables, with the following expectations.

- Native forest birds would have lower median occupancy probabilities in warmer squares than in colder squares (where we expect greater and more continuous pressure from predation).
- The adverse effects of warmer temperature would be greater on deep endemics, which evolved longer on a New Zealand land mass without predatory mammals.
- Negative effects of temperature would be more evident at higher levels of forest cover, because warmer temperatures can only adversely affect native forest birds that depend on forest habitat where they survive.
- Negative effects of temperature in squares with high forest cover would be greater on deep endemic birds, which are likely to be more sensitive to predation than non-endemic taxa.

We did not expect that local occupancy probabilities of forest birds would necessarily have declined more between measurement periods in warmer squares. This was because we anticipated that warmer squares might have already lost most of their vulnerable birds prior to 1969–1979, leaving few left to lose.

6.5 Effects of temperature in 'deep forests'

Warmer sites in New Zealand are generally more densely inhabited and disturbed by humans (see Figure 2). As far as possible we wanted to isolate the effects of temperature from those of human disturbance, which could potentially also affect occupancy.

We therefore next analysed data only from those squares with $\geq 50\%$ indigenous forest cover, which we call 'deep forests'. The samples are relatively small: 162 North Island squares (15% of the 1,082 in our full data set) and 277 South Island squares (26% of 1,073). Nevertheless, because these squares are the least disturbed by humans, evidence for temperature effects here would give us greater confidence that factors other than greater human disturbance are responsible.

We fitted models of native forest bird occupancy in deep forests with a three-way interaction of measurement period, endemism level and temperature. We included road

density and indigenous forest cover as fixed effects because even these deep forest squares experience certain amounts of human disturbance, and we expected levels of both human disturbance and indigenous forest cover to have additional effects on native forest bird occupancy. Species and family were again random effects in these models.

Lastly, we show how median probabilities of occupancy in individual native forest bird taxa varied across the temperature gradients in remaining deep forests. We did this by fitting and plotting local regression curves of occupancy probabilities on median mean annual temperature in deep forests on both islands, in each measurement period.

6.6 Cold forests: thermal refuges from predation?

Although we expected that predation pressures in cold forests would be lower than in warm forests much of the time, colder forests are not free from predators. In addition, many colder forests are beech or rimu-dominated and periodically experience large predator irruptions associated with mast seeding events (Ruscoe et al. 2004; Harper 2005; Brown et al. 2015; Elliott & Kemp 2016). We used fitted effects from our deep forest models (Model F3) to assess whether the thermal refuge provided for native forest bird populations by cold forests had diminished over time.

We defined a thermal refuge effect as the difference in occupancy probability between a cold site and a warm site, all else (i.e. endemism level and indigenous forest cover) being equal. We used our deep forest models (fitted as described in section 6.5) to predict occupancy probabilities in warm sites and cold sites on each island for birds at each level of endemism in each measurement period. We then subtracted estimates of occupancy probabilities in warm sites from estimates in cold sites and compared these differences (i.e. thermal refuge effects) between 1969–1979 and 1999–2004.

We needed to calculate thermal refuge effects over realistic intervals of temperature on each island. On each island we use a 4.5°C interval of mean annual temperature (MAT): 9.1 to 13.6°C in the North Island and 6.6 to 11.3°C in the South Island. These ranges approximately encompass the central 90% of median MAT values in deep forest squares on each island.

7 Results

7.1 Status and change in occupancy

We fitted occupancy models for 22 native forest bird taxa (Walker & Monks 2017), of which 19 occur in the North Island and 20 in the South Island. These taxa are listed in Appendix 1, along with their scientific names and highest taxonomic levels of endemism. Figure 3 summarises their status in 1999–2004, and changes in range occupancy between measurement periods (as log ratios of range occupancy, LRORs) on each island. In each plot we arrange taxa in order of decreasing level of endemism, and in order of increasing range

occupancy within endemism levels. Appendix 2 summarises the occupancy status of taxa in each measurement period and tabulates their LRORs.

Figure 3a and Appendix 2 show that the most range restricted of native forest bird taxa on both islands in 1999–2004 were endemic at the order, family and subfamily levels, or at the species level (weka, blue duck, kiwi species, kākā and long-tailed cuckoo on both islands, North Island kōkako, parakeet species and rifleman in the North Island, and mohua in the South Island). Two species-level endemics (grey warbler and fantail) and the self-introduced silvereve occupied the largest geographic ranges on both islands.

Range occupancies differed greatly between the North and South Island in some taxa: for example rifleman, bellbird and tomtit occupied considerably larger ranges in the South Island than the North Island, while kererū, tūi, grey warbler, fantail, morepork, shining cuckoo and silvereve occupied larger ranges in the North Island (Figure 3a, Appendix 2).

The log ratio of range occupancy (LROR) is a relative rather than absolute measure of change in a species range. The most negative log range occupancy ratios show that the largest relative range declines between measurement periods occurred in blue duck, weka, rifleman, kākā and long-tailed cuckoo on both islands, and in North Island brown kiwi, North Island kōkako and North Island robin in the North Island (Figure 3b, Appendix 2). LRORs also show notable range declines in parakeet species in the North Island, and in kererū, morepork, tūi, tomtit and kiwi taxa in the South Island.

LRORs were positive for parakeet/kākāriki species in the South Island, for whitehead, kererū and tūi in the North Island, and for bellbird, grey warbler, fantail, shining cuckoo and silvereve on both islands.

When interpreting LRORs it is important to note that we do not display confidence limits, which may be considerable in some taxa. Furthermore, although LRORs give us better resolution of relative changes in taxa that are comparatively rare, estimates for rarer taxa should be regarded with particular caution. This is because they will be more strongly influenced by chance variations in the location of sampling effort between the two atlases, and by records in one or two grid cells, than more widespread taxa.

For example, although the LROR for mohua in the South Island was positive (Figure 3b, Appendix 2), the net increase in range and the positive LROR largely reflect records, in the late 1990s, of a newly discovered population on Mt Stokes in Marlborough. This population subsequently became extinct (Gaze 2003). The LROR is faithful to data in the atlases, but the large relative increase that it shows in mohua range is unlikely to have actually occurred.

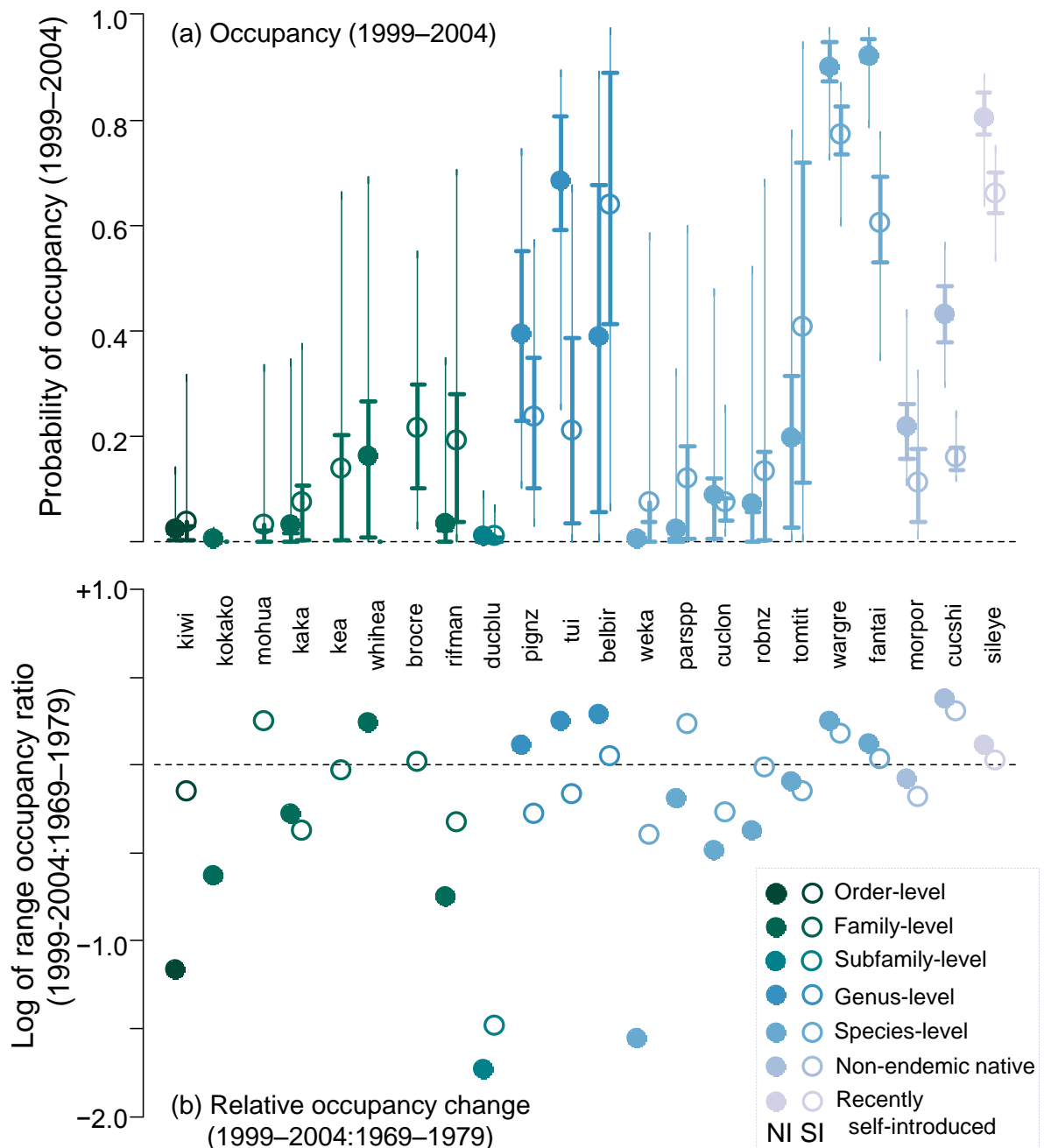


Figure 3 (a) Occupancy probabilities of native forest birds in 1999–2004, showing the mean (equivalent to range occupancy) and upper and lower (50% and 95%) bounds of estimated probabilities of occupancy in 1999–2004 for each native forest bird across squares in the North and South Islands (filled and hollow symbols, respectively); and (b) magnitude of relative change in range occupancy 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 = mohua/yellowhead; kaka = kākā; kea = kea; whihea = whitehead; brocre = brown creeper; rifman = rifleman/tītipounamu; 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/ruru; cucshi = shining cuckoo; sileye = silvereye.

7.2 Percentage of indigenous forest range occupied

Table 2 shows the estimated percentage of the potential forest range on each island that was occupied by each forest bird taxon in each measurement period across the grid squares covered in our data set. Appendix 3 shows these statistics graphically. Appendix 4 tabulates the hectares of land we estimate to be occupied by each taxon within the forest range covered by the data set on each island.

Table 2 Percentage of potential forest range that was occupied by birds of forest habitats in the North and South Islands in 1969–1979 and 1999–2004, based on median occupancy estimates across those grid squares sampled in both measurement periods. Hyphens indicate that the species does not occur on the island. We include New Zealand falcon/kārearea in this list for completeness, because the forest form ('bush falcon') can occur in forest. EL denotes endemism level (O = order, F = family, SF = subfamily, G = genus, S = species, N = non-endemic native, RSI = recently self-introduced). Note that we assumed that the area of forest covered by a grid square in 1969–1979 was the same as in 1999–2004 (for explanation see section 5.3)

EL	North Island (2,111,170 ha forest in 1,082 squares)		South Island (2,528,255 ha forest in 1,073 squares)		
	1969–1979	1999–2004	1969–1979	1999–2004	
O	Kiwi species	16.6	3.5	8.7	7.1
F	North island kōkako	2.5	1.1	-	-
F	Mohua/yellowhead	-	-	4.8	6.0
F	Kākā	13.1	7.1	22.7	15.7
F	Kea	-	-	26.5	24.8
F	Whitehead/pōpokatea	23.9	29.4	-	-
F	Brown creeper	-	-	28.7	29.1
F	Rifleman/tītipounamu	20.8	7.7	39.3	30.6
SF	Blue duck/whio	14.3	3.0	8.9	1.6
G	Kererū	52.7	51.6	51.3	32.7
G	Tūī	70.6	76.6	47.0	37.8
G	Bellbird	45.8	57.6	89.4	85.6
S	New Zealand falcon/kārearea	4.6	4.7	5.5	11.0
S	Parakeet/kākāriki species	9.6	6.5	16.6	23.6
S	Weka species	1.5	1.0	24.2	15.5
S	Long-tailed cuckoo/koekoeā	31.3	17.4	13.8	10.7
S	New Zealand robin/toutouwai	28.5	16.2	30.6	28.1
S	New Zealand tomtit	44.9	40.3	77.2	69.9
S	Grey warbler/riroriro	72.6	91.0	69.9	78.9
S	New Zealand fantail/pīwakawaka	83.4	93.0	70.5	66.6
N	Morepork/ruru	30.9	25.5	21.0	18.8
N	Shining cuckoo/pīpīwharau	33.1	46.2	13.6	17.0
RSI	Silvereye	72.0	81.0	69.6	67.5

When interpreting these estimates it is again important to note that they are based on median estimates of occupancy for each grid square, and that confidence intervals are absent because we did not incorporate uncertainty in square-wise (local) estimates of occupancy probability into the calculations (see our discussion in section 4.2.3). In some taxa these confidence intervals may be large.

Based on these estimates, four (North Island kōkako, kārearea, parakeet species and weka) of 20 forest bird taxa occupied less than 10% of the North Island forests in our 1,082 squares in 1969–1979. By 1999–2004 North Island brown kiwi, kākā, rifleman and blue duck also occupied less than 10% of these forests, and the median percentage of forest range occupied by a deep endemic bird had decreased from 15.5 to 5.3%.

The forest ranges of kererū, long-tailed cuckoo, North Island robin, New Zealand tomtit and morepork also decreased in the North Island, while those of whitehead, tūī, bellbird, grey warbler, fantail, shining cuckoo and silvereye increased.

The median percentage of South Island forests occupied by the seven remaining deep endemic taxa had decreased from 22.7 to 15.7% between measurement periods across our 1,073 squares. Decreases in forest range occupied by kiwi (9 to 7%), kākā (23 to 16%), kea (27 to 25%), rifleman (39 to 31%) and blue duck (9 to 2%) all contributed to this change.

The South Island forest ranges of kererū, tūī, bellbird, weka, long-tailed cuckoo, South Island robin, tomtit, fantail and morepork also decreased between measurement periods, while those of New Zealand falcon, parakeet species, grey warbler and shining cuckoo increased.

7.3 Effects of indigenous forest cover

7.3.1 Trends in local forest bird richness with indigenous cover

Local richness of native forest birds generally increased with indigenous forest cover (Figure 4). Relatively few forest bird taxa inhabit completely deforested squares on either island, and squares with more forest support more taxa. In Appendix 5 we map status and change in local richness alongside percentage indigenous forest cover: visual comparison of these maps shows the association between indigenous forest cover and local forest bird richness.

In the South Island, trends of local richness on percentage indigenous forest cover resemble classical species area curves (Rosenzweig 1995). They approximate power curves (because richness is more sensitive to changes in forest cover where forest cover is low) and do not completely level off at high forest cover.

In the North Island, trends in local richness on indigenous forest cover were approximately linear, with no hint of levelling off. Thus forest bird richness is sensitive to changes in forest cover even in more heavily forested landscapes.

There was little evidence of sharp indigenous forest-cover thresholds on either island. Generally, the more indigenous forest cover in a square, the greater the number of forest bird taxa likely to be present.

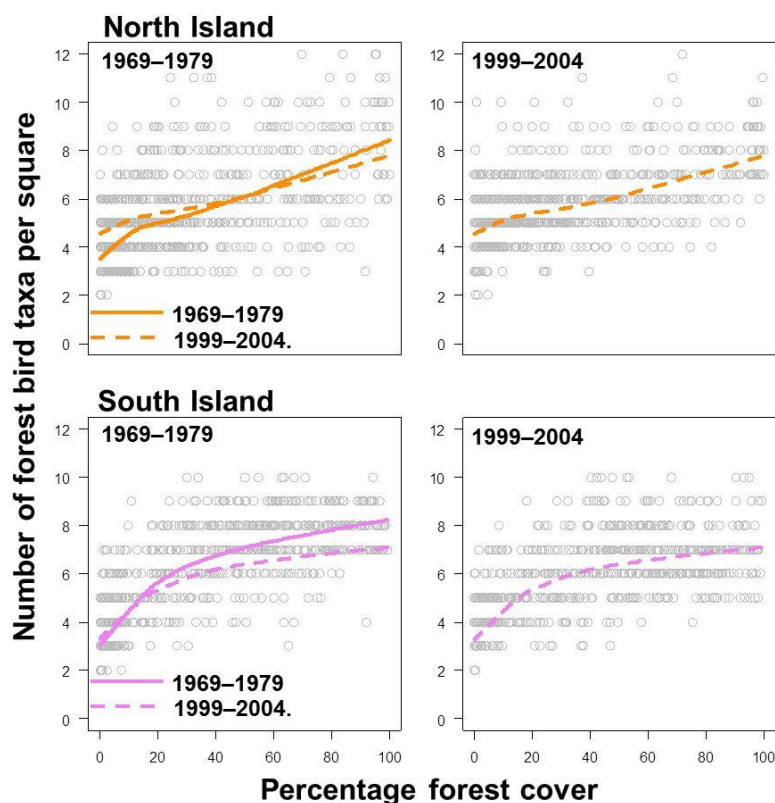


Figure 4 Plots of rounded estimates of local richness of all 22 forest bird taxa on indigenous forest cover, showing status in 1969–1979 (left pair of plots in each quadrant) and 1999–2004 (right pair of plots) for the North (upper pair of plots, with orange lines) and South (lower pair, with magenta lines) Islands. Local regression curves (fitted using raw, unrounded richness estimates) are shown as bold lines (solid for 1969–1979 and dashed for 1999–2004). The 1999–2004 local regression curve (dashed) is superimposed on the 1969–1979 plot to aid comparison between measurement periods.

The positive effect of indigenous forest cover appears to have diminished between measurement periods. In the North Island this was because local forest bird richness increased, on average, in the most deforested squares between measurement periods, and decreased in squares with the most forest cover (upper plots in Figure 4). In the South Island, the smaller positive effect of forest cover was simply because average local richness of forest birds decreased across squares with more than about 20% forest cover (lower plots in Figure 4).

On both islands the largest net decreases in local richness between measurement periods were in the most completely forested squares, which had previously supported the largest numbers of forest bird species. As noted in section 5.3, indigenous forest cover is unlikely to have changed greatly between measurement periods in the majority of squares, pointing to causes other than deforestation.

On both islands the effects of forest cover on local richness appear to be stronger on endemic forest birds, while numbers of non-endemic forest birds per square varied little with forest cover (Figure 5a–d). In the South Island the average local richness of forest birds appears to have decreased between measurement periods in taxa endemic at all levels and especially in forested squares (Figure 5a–c), while average local richness of non-endemic taxa showed little change anywhere (Figure 5d).

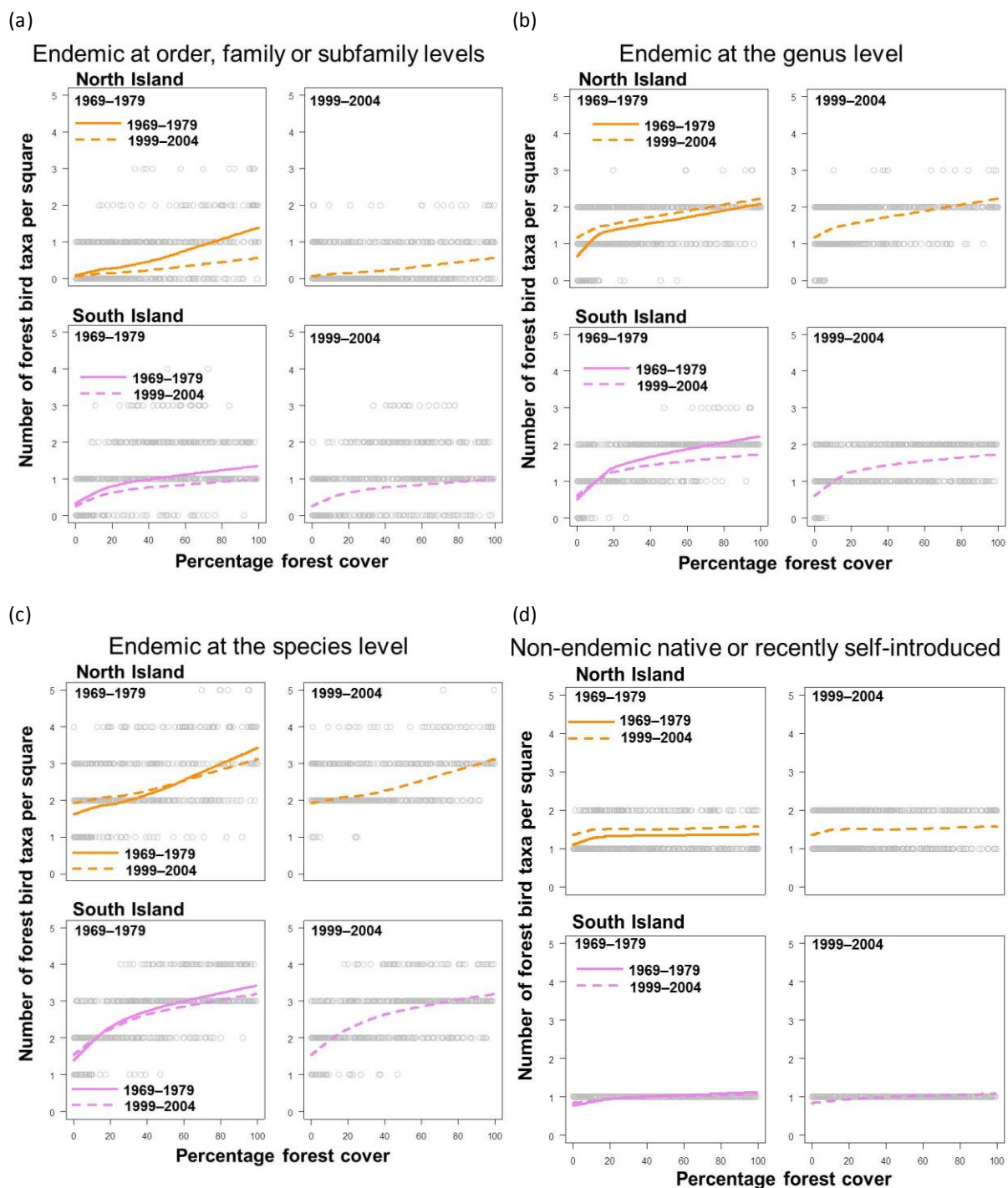


Figure 5 Plots of rounded estimates local richness of forest bird taxa (number of forest bird taxa per square) on indigenous forest cover, showing taxa grouped into those endemic at levels of (a) order, family or subfamily, (b) genus, and (c) species, and (d) non-endemic native or recently self-introduced species. Note that although the y axis scales are the same for (a) to (d), the size of the pool of taxa (n) differs. Each quadrant of plots shows status in 1969–1979 (left pair of plots in each quadrant) and 1999–2004 (right pair of plots) for the North Island (upper pair of plots, with orange lines) and South Island (lower pair, with magenta lines). Local regression curves (fitted using raw, unrounded richness estimates) are shown as bold lines (solid for 1969–1979 and dashed for 1999–2004). The 1999–2004 local regression curve (dashed) is superimposed on the 1969–1970 plot to aid comparison.

In the North Island:

- local richness of deep endemic forest birds decreased, on average, between measurement periods (Figure 5a): the greatest average decreases were in squares with the most forest, and there was less change in deforested squares where deep endemics were already absent in 1969–1979
- local richness of genus-level-endemic (Figure 5b) and non-endemic forest birds (Figure 5d) increased, on average, across all levels of forest cover
- local richness of species-level-endemic forest birds increased in less-forested squares but decreased in more forested squares (Figure 5c).

7.3.2 Trends in probabilities of occupancy with indigenous cover

Relationships between median occupancy probabilities of individual forest bird taxa and indigenous forest cover are shown as fitted local regression curves in Figure 6. As with the local richness trends (section 7.3.1), they are presented for visual comparison only.

Positive associations between occupancy probabilities and indigenous forest cover can be seen in all but the two rarest endemic birds (North Island kōkako and mohua). However, it is also evident that the shapes of relationships varied greatly among taxa, and within the same taxon on different islands.

Occupancy probabilities of fantail, grey warbler, shining cuckoo and silvereye – all taxa in lineages that arrived relatively recently in New Zealand – were the least clearly related to forest cover.

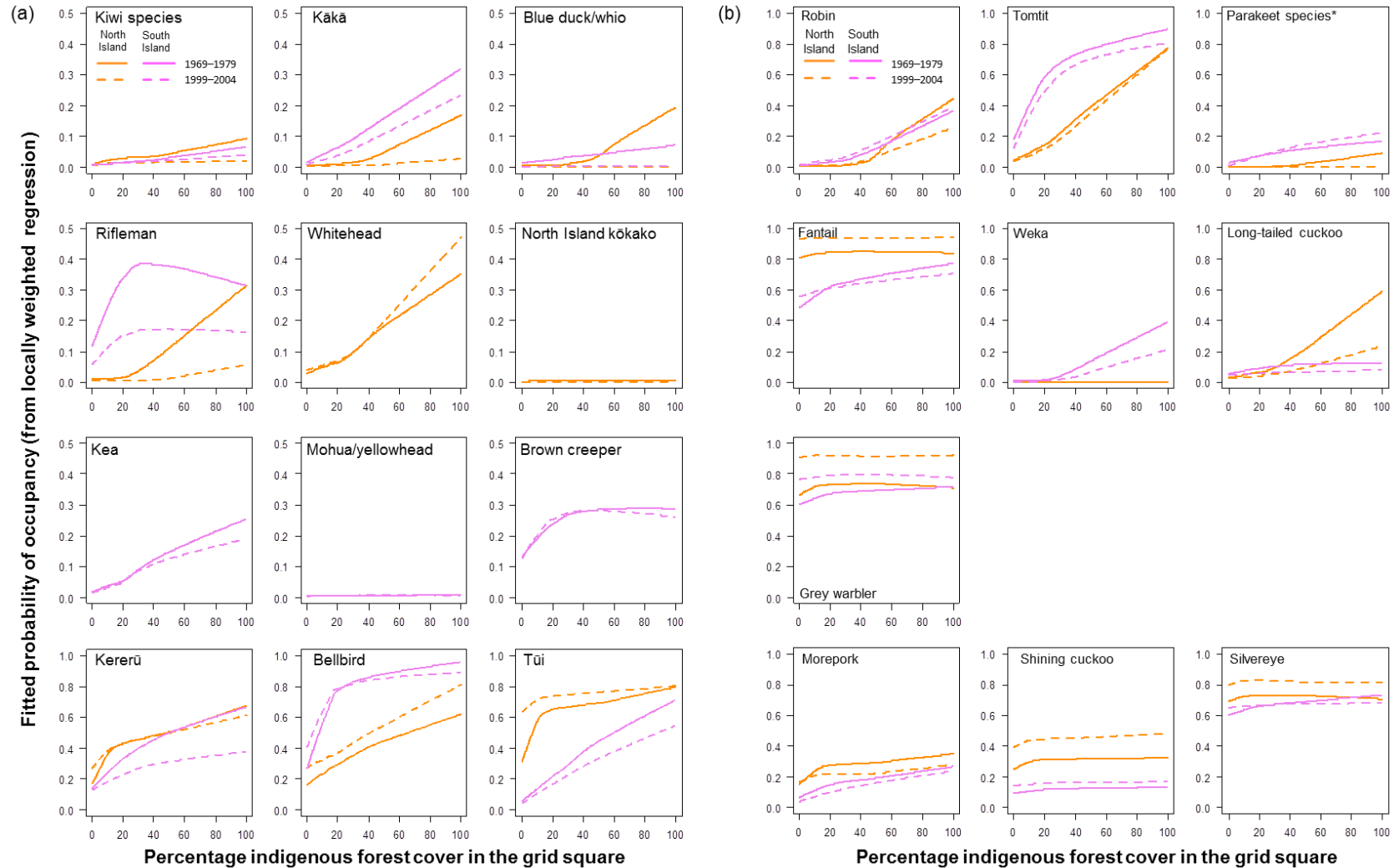


Figure 6 Fitted local regression curves of occupancy probabilities of individual native forest bird taxa on **percentage indigenous forest cover** in grid squares in the North and South islands in two measurement periods (1969–1979 shown as solid lines, 1999–2004 in dashed lines). Plots in (a) show only taxa endemic at the level of genus or higher, and plots in (b) show taxa that are species-level endemics, non-endemic native, or recently self-introduced. Note that the y-axis scale maximum is 0.5 in the first nine plots in (a), and 1.0 in all others.

The results of our models of median occupancy probability in relation to measurement period, endemism level and indigenous forest cover (Model F1) are plotted in Figure 7 and the associated parameter estimates and confidence intervals are tabulated in Table A6.1 (in Appendix 6). We consider that there is strong support for an effect (i.e. it is statistically 'significant') when 95% confidence intervals of parameter estimates exclude zero.

The models show that percentage indigenous forest cover had profound effects on the median occupancy probabilities of native forest birds on both islands. Fitted probabilities of occupancy at '100% indigenous forest cover' (Figure 7b,d) are much higher than in deforested squares (Figure 7a,c) and positive parameter estimates for *indigenous forest cover* in Table A6.1 are large.

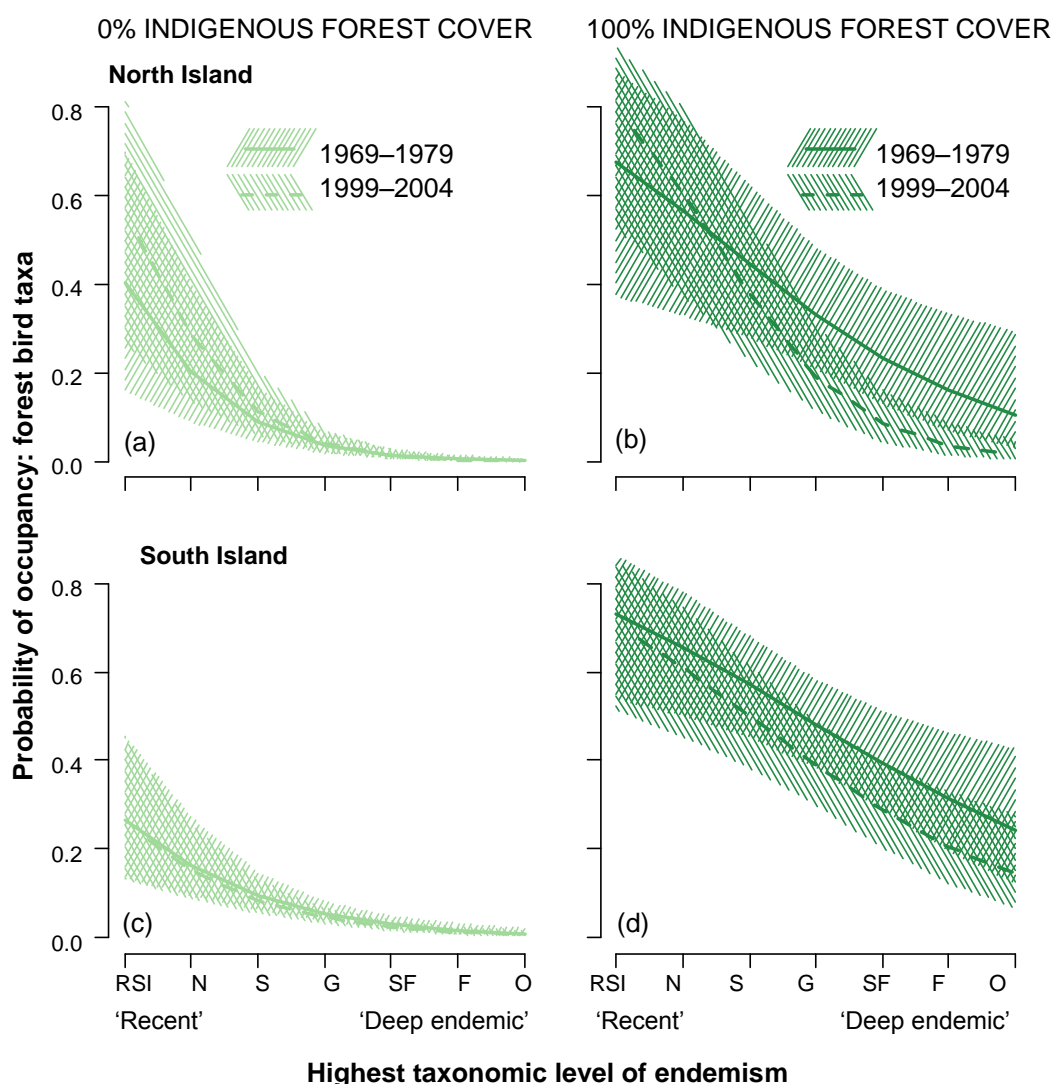


Figure 7 Fitted effects (and hatched standard errors of effects) on fitted probabilities of occupancy in the 22 native forest bird taxa in the North and South Islands (upper and lower row of plots, respectively) (Model F1). Endemism level is shown on horizontal axes (RSI = recently self-introduced, N = non-endemic native, S = species level, G = genus level, SF = subfamily level, F = family level, O = order level). Measurement periods are distinguished by solid and dashed lines and different angles of hatching of standard error intervals. Levels of indigenous forest cover are distinguished by colour: effects in squares with no indigenous forest cover (a, b) are coloured in light green and those in squares with 100% indigenous forest cover (b, d) are coloured in dark green.

The models also show the following:

- Bird taxa that are endemic at higher taxonomic levels were more dependent on forest cover (i.e. parameter estimates for the *endemism level:indigenous forest cover* interactions are positive in Table A6.1). By 1969–1979 fitted occupancy probabilities for deep endemic birds were near zero in deforested squares (Figure 7a,c), but remained above zero in squares with 100% indigenous forest (Figure 7b,d)
- Occupancy probabilities decreased more between measurement periods in squares with more indigenous forest (parameter estimates for *measurement period:indigenous forest cover* interactions are negative in Table A6.1). Figure 7 clearly shows these greater decreases in occupancy probabilities in squares with '100% indigenous forest' (Figure 7b,d) than in deforested squares (Figure 7a,c), where there was little left to lose by 1969–1979.
- The higher recent rates of decrease in squares with high indigenous forest cover were more severe for deep endemics (negative parameter estimates for three-way *measurement period:endemism level:indigenous forest cover* interactions in Table A6.1). This can be seen in Figure 7b and 7d, where, at '100% indigenous forest cover', greater decreases in occupancy probabilities between measurement periods are evident at the deep endemic ends of the horizontal axes. The effect is clearer in the North Island, where occupancy probabilities also increased between measurement periods in 'Recent' taxa (Figure 7b) than in the South Island, where 95% confidence intervals of parameter estimates in our lme models did not quite exclude zero (Table A6.1).

The following patterns in forest birds were consistent with those identified across a larger set of 64 land bird taxa (section 7.4 in Walker & Monks 2017).

- Deep endemic forest bird taxa had lower occupancy probabilities than non-endemic taxa (parameter estimates for *endemism level* in Table A6.1 and slopes on endemism level in Figure 7 are negative).
- Deeper endemics showed greater decreases in occupancy probabilities between measurement periods (parameter estimates for the *measurement period:endemism level* interaction in Table A6.1 are negative). In the North Island, occupancy probabilities increased in non-endemic taxa; this can be seen as dashed lines positioned above solid lines at the left of Figure 7a and 7b.

7.4 Effects of temperature on occupancy probabilities

The fits of our models of native forest bird median occupancy probabilities were greatly improved by including mean annual temperature⁹ (*temperature*) as a term in a four-way interaction with *measurement period*, *endemism level* and *indigenous forest cover*, and also by including a term for *road density* and the interaction between *endemism level* and *road density* (Model F2). These results are tabulated in Table A6.2 (in Appendix 6) and shown graphically in Figures 8 and 9.

The models revealed that:

- native forest bird occupancy probabilities were lower in warmer squares than in colder squares at average levels of endemism and indigenous forest cover (negative parameter estimates for *temperature* on both islands; Table A6.2)
- at average levels of indigenous forest cover, high temperatures had greater negative effects on the occupancy probabilities of birds that are endemic at higher taxonomic levels (negative parameter estimates for *endemism level:temperature* interactions in Table A6.2); this effect can be seen in Figure 8 by comparing fitted effects for deep endemics between subplots for cooler temperatures (Figure 8a,d) and those for warmer temperatures (Figure 8b, c, e).

Negative *measurement period:temperature* parameter estimates (Table A6.2 in Appendix 6) show that at the average level of endemism (i.e. genus level), decreases in forest bird occupancy probabilities between measurement periods were larger in warmer squares on both islands, despite lower initial (1969–1979) probabilities of occupancy there.

⁹ The range of mean annual temperatures covered by completely forested squares is larger in the North Island than in the South Island (Figure 2). Accordingly, we limit estimated effects from our South Island model to that narrower realistic temperature range (9.6–12.3°C vs 8.3–13.6°C in the North Island).

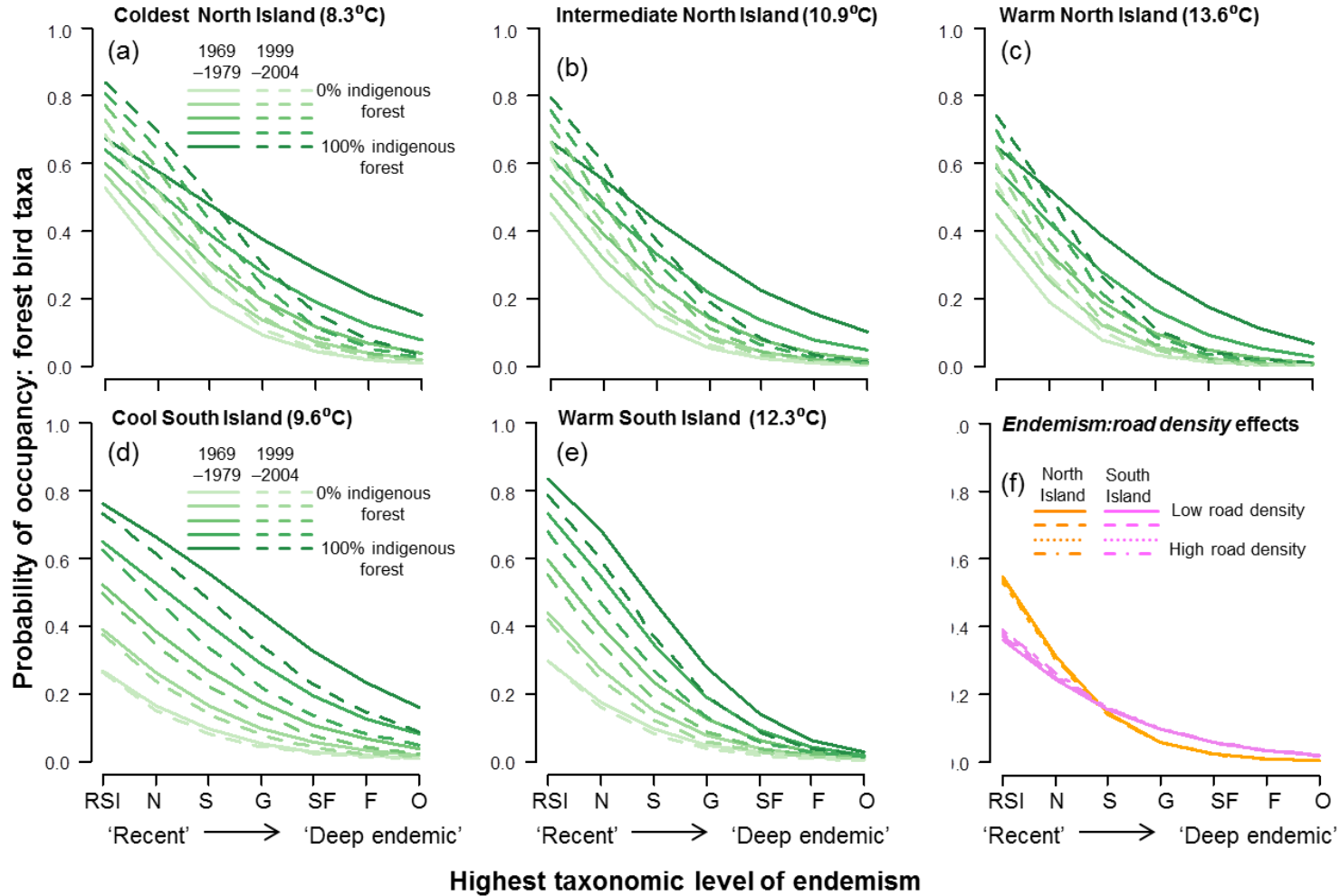


Figure 8 Fitted effects of temperature, endemism level (horizontal axes), measurement period (distinguished by solid lines for 1969–1979 and dashed lines for 1999–2004), and indigenous forest cover (darker green lines for higher indigenous forest cover) on fitted probabilities of occupancy in the 22 native forest bird taxa in the North and South Islands (upper and lower row of plots, respectively) (Model F2). Effects are shown across realistic temperature ranges for 100% forest cover on each island (Figure 2): (a) 8.3°C, (b) 10.9°C and (c) 13.6°C median mean annual temperature (MAT) in the North Island, and (d) 9.6°C and (e) 12.3°C MAT in the South Island. RSI = recently self-introduced, N = non-endemic native, S = species level, G = genus level, SF = subfamily level, F = family level, O = order level.

However, *measurement period:temperature* interactions varied with both the level of forest cover and the endemism level of the taxa. This variation is shown separately in Figure 9, in which we plot temperature along the horizontal axis.

- In the North Island the larger recent decreases in occupancy in warmer places were more pronounced where there was more indigenous forest cover. This is indicated by a significant negative three-way interaction effect (*measurement period:indigenous forest cover:temperature*) in the North Island model (Table A6.2). This effect can be seen most clearly by comparing Figure 9b and 9c with Figure 9k and 9l, which show greater losses in warm forested squares (Figure 9k and 9l) where probabilities of occupancy were higher in 1969–1979), and that there was little was left to lose in warm deforested squares by 1969–1979 (Figure 9b, c).
- In the South Island there was instead a negative three-way interaction between *endemism level, indigenous forest cover* and *temperature* (Table A6.2). By 1969–1979 deep endemics were absent, regardless of temperature, where forest cover had been lost (Figure 9c; see also Figure 8d, e) and were already much rarer in warmer forests than in cooler forests (Figure 9l; see also Figure 8d, e). The median occupancy probabilities of non-endemic taxa in the South Island were also affected by forest scarcity, although not to the same extreme extent as deep endemics, but they appeared relatively impervious to temperature gradients.
- Probably because there was so little left to lose in warmer South Island forests by the 1970s, occupancy probabilities of deep endemics actually decreased more between measurement periods in cooler forests (Figure 9l), whereas non-endemics decreased more in warmer forests (Figure 9j). These effects contributed towards a negative (albeit not quite significant) parameter estimate for the four-way interaction between *measurement period, endemism level, indigenous forest cover* and *temperature* in the South Island (Table A6.2).

We also found a negative effect of *road density* and a negative interaction between *endemism:road density* in the South Island (Table A6.2). These effects are plotted in Figure 8f (above). Although including these road density terms improved the fits of both models, their effects in the North Island were weak (95% confidence limits of parameter estimates did not exclude zero) and opposite in direction to those in the South Island (Table A6.2). The somewhat stronger effects in the South Island suggest that non-endemic forest species (e.g. morepork, shining cuckoo and silvereye) were more likely to be present in squares with higher road densities.

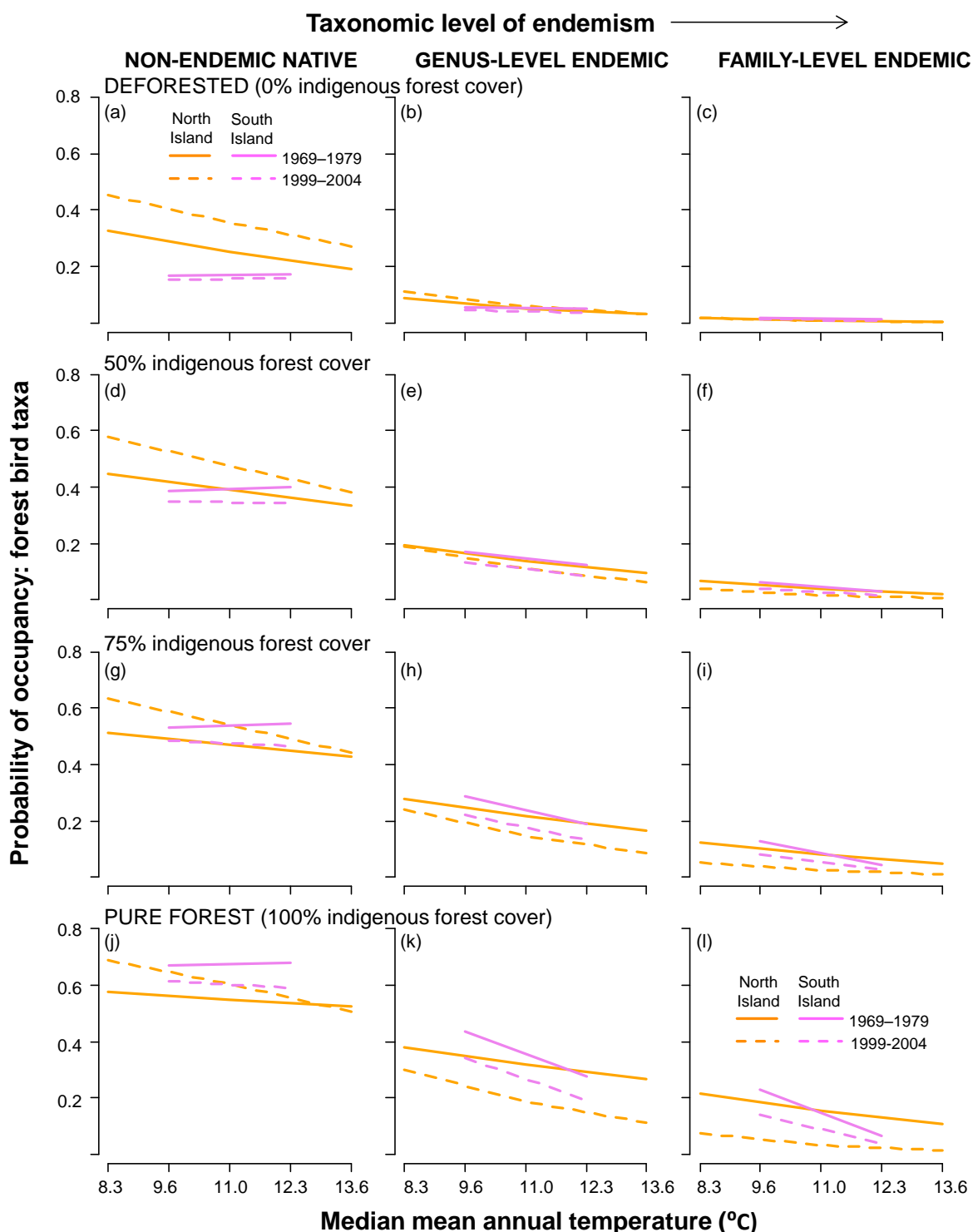


Figure 9 Fitted effects of temperature on probabilities of occupancy for native forest bird taxa at three levels of endemicism (non-endemic native, genus-level endemic and family-level endemic) and four levels of indigenous forest cover (four rows of subplots) in models for the North Island (orange lines) and South Island (magenta lines) (Model F2). Solid and dashed lines indicate effects in 1969–1979 and 1999–2004, respectively. Effects are shown across realistic temperature ranges for 100% forest cover on each island (Figure 2): 8.3°C to 13.6°C median mean annual temperature (MAT) in the North Island, and 9.6°C to 12.3°C MAT in the South Island.

7.5 Effects of temperature in deep forests

Even in ‘deep forest’ squares (with $\geq 50\%$ indigenous forest cover) higher road densities indicate that there has been a greater degree of human occupation and disturbance in squares that are warmer, especially in the South Island ($r = 0.64$; Figure 10). This means, unfortunately, that we cannot completely isolate the effects of temperature from other factors associated with the presence of humans: road density will only represent the effects of human occupation insofar as it is not correlated with temperature. However, the deep forest models (Model F3) are able to demonstrate that temperature affects native bird occupancy probabilities where the influences of human occupation are least.

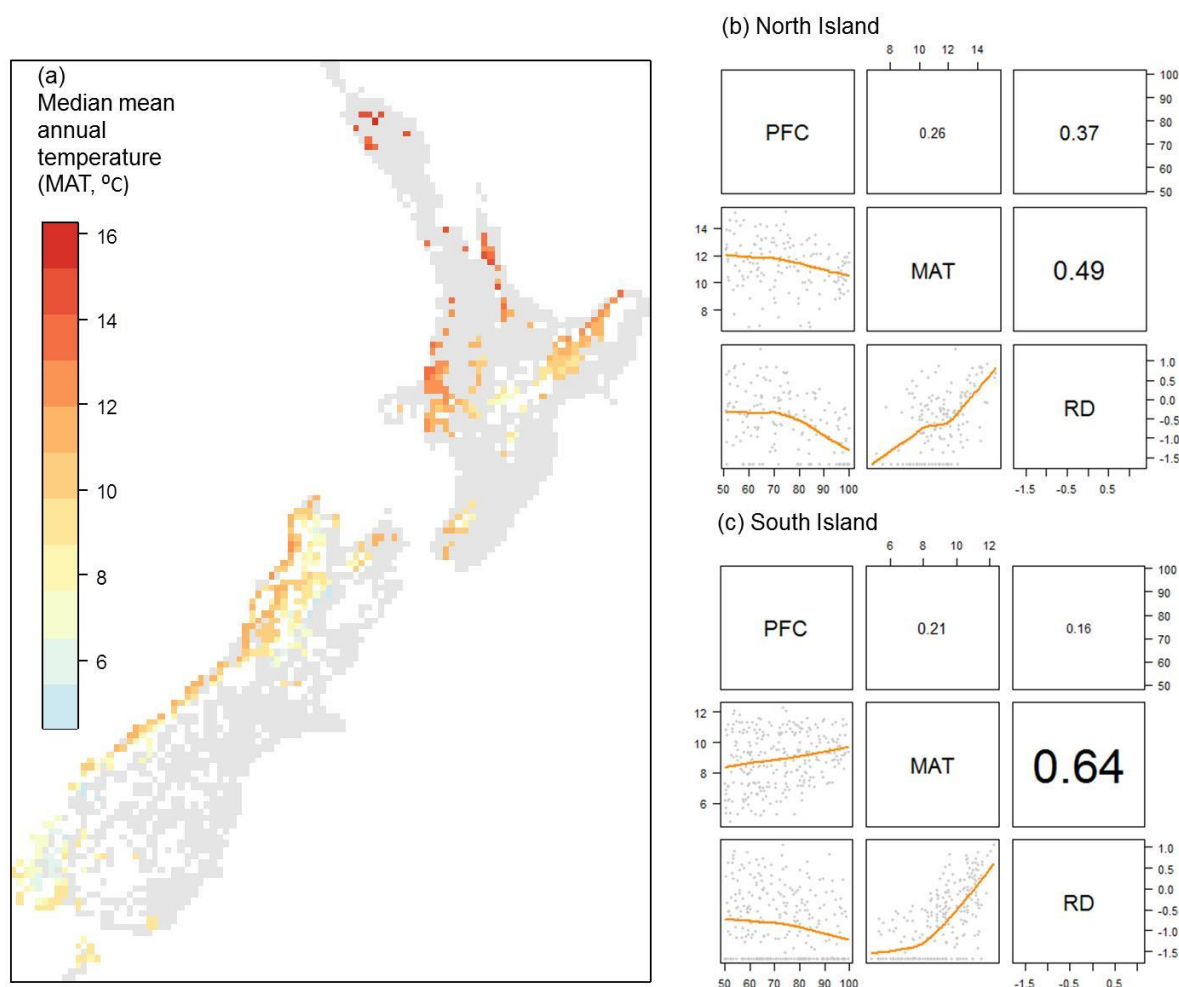


Figure 10 (a) Map showing the median mean annual temperature (MAT, in °C) in 162 grid squares in the North Island and in 277 squares in the South Island that have $\geq 50\%$ indigenous forest cover; and (b and c) the relationships between the environmental characteristics in those squares. The characteristics compared are labelled on the diagonal (PFC = percentage indigenous forest cover, MAT = median mean annual temperature, RD = scaled and centred square root of road density). In each set, subplots below the diagonal show grid squares as points on scatter plots and their relationships (depicted using a local regression curves, as orange lines). Upper plots show the associated coefficients of correlation between pairs of characteristics, with larger text indicating stronger correlation.

The deep forest models (Model F3) show that native forest birds were less likely to occupy forested squares with more roads (parameter estimates for *road density* were negative; Table A6.3 in Appendix 6). This effect of road density was more pronounced in the South Island than in the North Island.

Parameter estimates for indigenous forest cover were positive on both islands, although clearer in the North Island than in the South Island (where 95% confidence intervals did not quite exclude zero; Table A6.3). This means that even across squares with >50% land under indigenous forest cover, native forest birds had higher probabilities of occupancy in squares with more indigenous forest.

After accounting for variation in forest cover and road density, our models showed clear effects of temperature in deep forests. This is consistent with colder forests retaining deep-endemic forest birds longer.

Figure 11 illustrates the effects of temperature and endemism level on occupancy probabilities in deep forests.

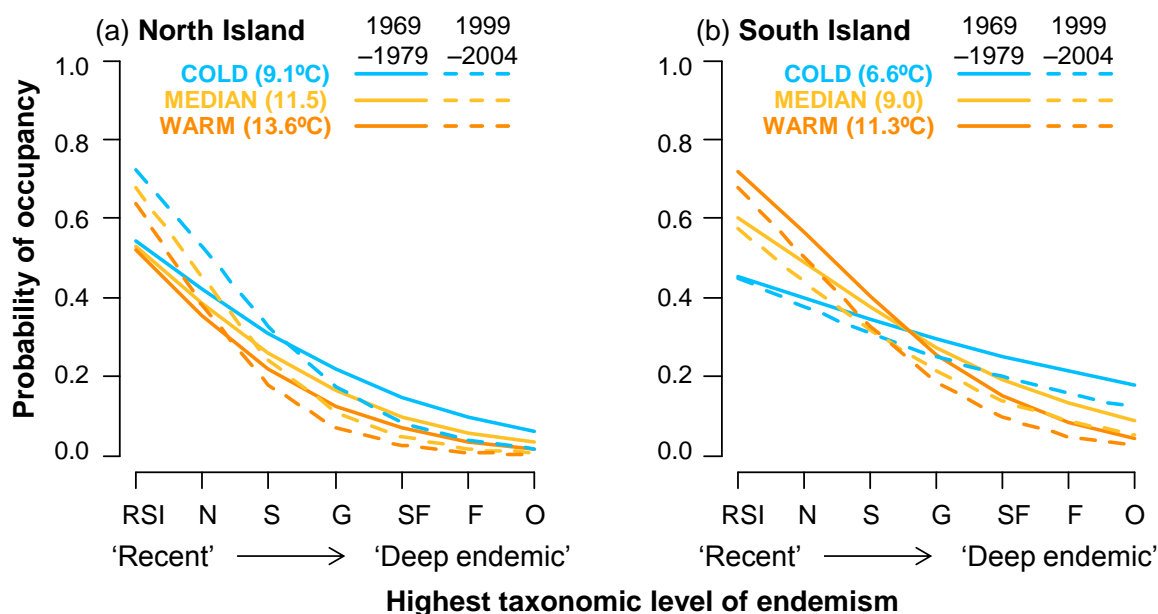


Figure 11 Effects of endemism level on native forest birds' probabilities of occupancy in deep forest squares with different mean annual temperatures in two measurement periods, in deep forest models for the North Island (a, left) and South Island (b, right) (Model F3). Levels of endemism are indicated as RSI = recently self-introduced, N = non-endemic native, S = species level, G = genus level, SF = subfamily level, F = family level, and O = order level. The COLD, MEDIAN and WARM mean annual temperatures shown are the 10th, 50th and 90th percentiles, respectively, across deep forest squares on each island.

Figure 11 shows that:

- forest bird occupancy probabilities were lower in warmer deep forest squares (*temperature* parameter estimates in Table A6.3 are negative), as can be seen by comparing occupancy estimates in the WARM squares in Figure 11 with those in the MEDIAN and COLD squares
- temperature had greater negative effects on deep endemics (*endemism level:temperature* parameter estimates in Table A6.3 are negative), as can be seen by comparing the steeper slopes in the WARM squares in Figure 11 with the less-steep slopes in the COLD squares.

The net outcome was that between measurement periods endemic forest bird taxa became increasingly confined to colder forests (they were even less likely to occur in warm forests in 1999–2004 than in 1969–1979), while over the same period their local probabilities of occupancy decreased in those cold-forest refuges (Figure 11).

Occupancy probabilities of native forest birds decreased more in warmer forests than in colder forests between atlases (negative *measurement period: temperature* effects in Table A6.3) at the average (i.e. genus) level of endemism, despite lower initial (i.e. 1969–1979) probabilities of occupancy there. However, as shown in Figure 12, the *measurement period: temperature* effect differed according to the endemism level of the forest birds.

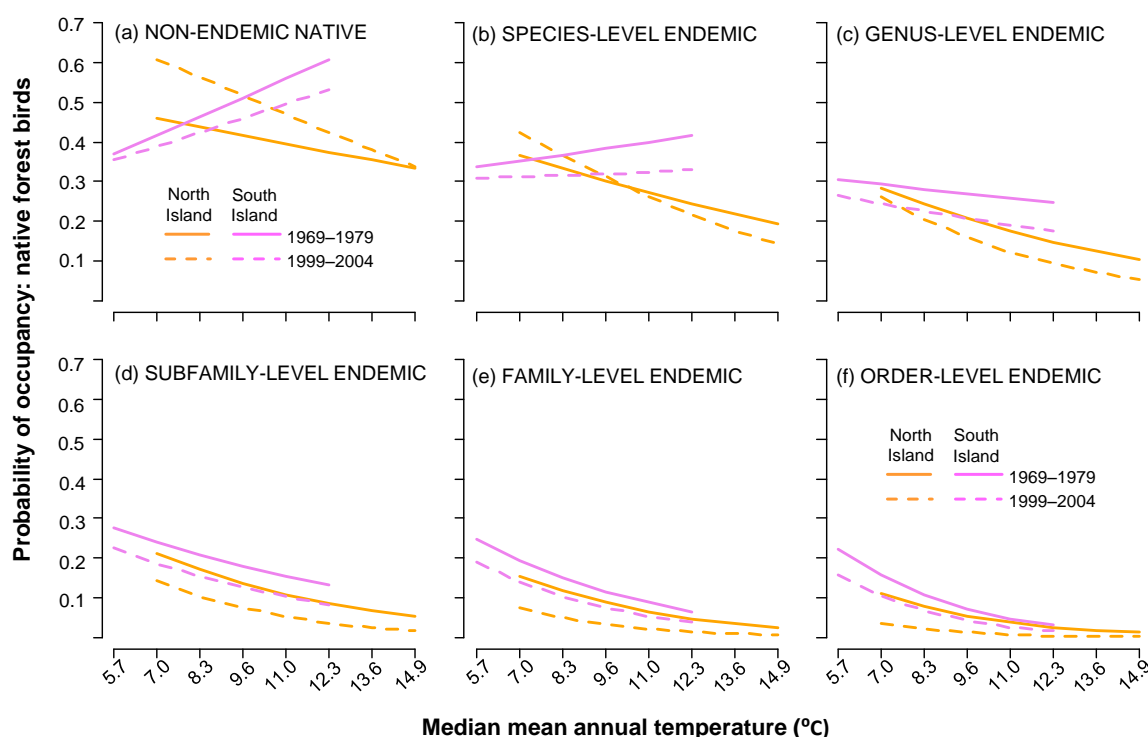


Figure 12 Effects of temperature on native forest birds' probabilities of occupancy in deep forest squares in two measurement periods (1969–1979, shown as solid lines, and 1999–2004, shown as dashed lines) in the North Island (orange lines) and South Island (magenta lines) deep forest models. The six subplots (a to f) show fitted effects at six of our seven levels of endemism (in ascending order from native non-endemic to order-level endemic taxa).

Figure 12 shows differences between fitted probabilities of occupancy in 1969–1979 and 1999–2004 along a horizontal axis of median mean annual temperature at six of our seven levels of endemism, from non-endemic native (Figure 12a) to order-level endemics (Figure 12f).

The results show that decreases in occupancy probabilities in warmer forests between measurement periods were not consistently greater in birds with higher levels of endemism (Figure 12a–f), which is why parameter estimates for three-way interactions (*measurement period:endemism level:temperature*) were not significantly different from zero on either island (Table A6.3). Instead, the greatest occupancy decreases in warmer forests were in birds at intermediate levels of endemism (especially species and genus levels; i.e. Figure 12b,c). The explanation is likely to be that deep endemics (Figure 12d–f) were unable to decrease more in warm forests because there was comparatively little left to lose by 1969–1979.

Figures 13 and 14 show how average occupancy probabilities of individual native forest bird taxa varied with mean annual temperature in deep forests, on both islands and in each measurement period. It is important to note that in fitting these local regression curves we did not account for the effects of forest cover or road density (as we did in our deep forest models shown in Figures 11 and 12 above).

Negative slopes (downward-sloping lines) in Figures 13 and 14 show that occupancy probabilities were lower in warmer forests in a number of taxa: whitehead, kererū and bellbird in the North Island; kiwi, kea, mohua and brown creeper in the South Island; and kākā, blue duck, rifleman, robin, tomtit, parakeet species, long-tailed cuckoo (which is a nest parasite of whitehead), mohua and brown creeper on both islands.

These negative trends due to temperature were especially linear and striking for some smaller forest birds (most notably rifleman, whitehead, mohua, robin, tomtit, parakeet species) but not exclusively. For example, in the South Island, kiwi, kea, kākā and blue duck occupancy probabilities also decreased with mean annual temperature. In the North Island, occupancy probabilities of kererū, bellbird and long-tailed cuckoo showed dramatic declines in forests with mean annual temperatures above about 12°C.

Figures 13 and 14 show that kākā and blue duck on both islands, rifleman, North Island robin, parakeet species, long-tailed cuckoo in the North Island, and kiwi and mohua in the South Island, were already largely confined to colder forests by the 1970s. Their occupancy probabilities decreased further between measurement periods, but especially in the colder forests, where there was more left to lose.

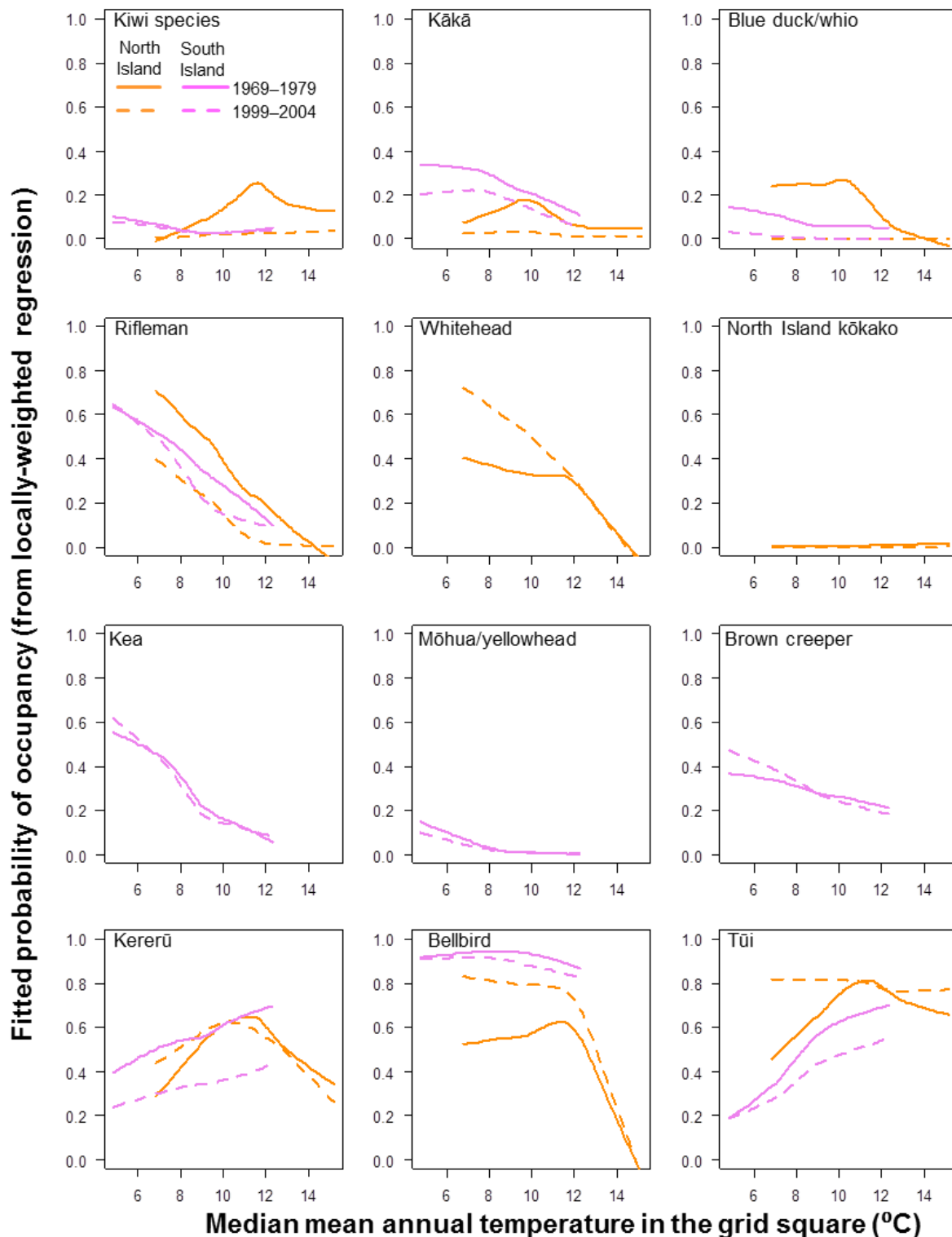


Figure 13 Fitted local regression curves of occupancy probabilities of individual native forest bird taxa on **median mean annual temperature** (°C) in grid squares in deep forests (i.e. squares with ≥50% indigenous forest cover) in the North and South Islands in two measurement periods (1969–1979, shown as solid lines, and 1999–2004, in dashed lines). The figure shows only those taxa that are endemic at the level of genus or higher.

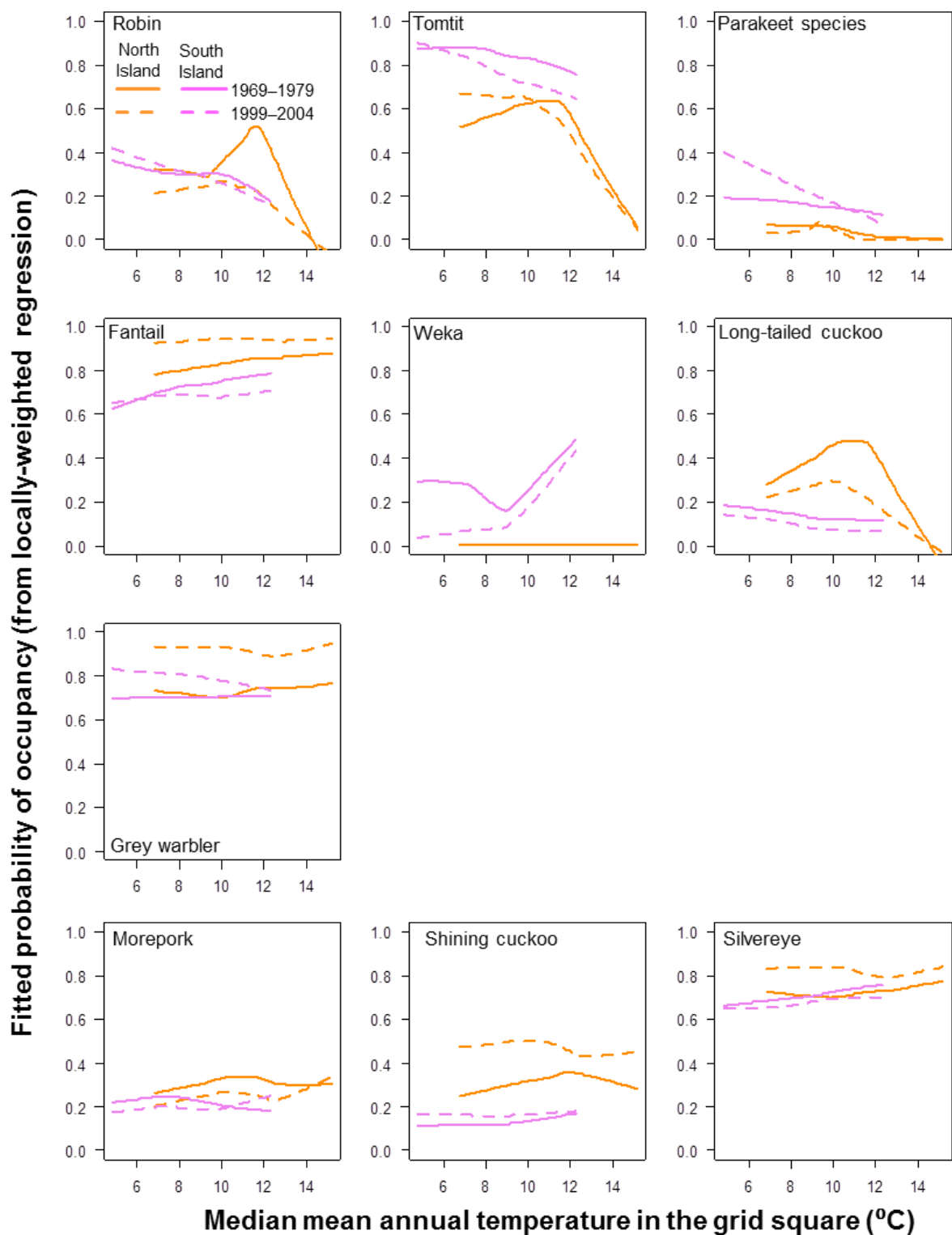


Figure 14 Fitted local regression curves of occupancy probabilities of individual native forest bird taxa on **median mean annual temperature** (°C) in grid squares in deep forests (i.e. squares with $\geq 50\%$ indigenous forest cover) in the North and South Islands in two measurement periods (1969–1979, shown as solid lines, and 1999–2004, in dashed lines). The figure shows the seven forest bird taxa that are endemic at the species level, and the three non-endemic taxa.

Three other types of change also contributed to endemic native forest bird taxa becoming more confined to colder forests between measurement periods.

- The probabilities of occupancy decreased more in the warmer parts of the forest range (North Island brown kiwi, North Island kōkako and kererū in the North Island, and rifleman, kererū, bellbird, tūi, fantail and long-tailed cuckoo in the South Island).
- The probabilities of occupancy increased in the colder parts of the range between measurement periods, but showed little change in warmer forests where there was less left to lose in 1969–1979 (whitehead and bellbird in the North Island).
- The occupancy probabilities decreased in the warmer parts of the forest range and increased in colder squares (tomtit on both islands, kererū in the North Island, kea, brown creeper, robin and parakeet species in the South Island).

Occupancy probabilities in the grey warbler, its non-endemic nest-parasite the shining cuckoo, and the non-endemic morepork did not appear to vary greatly with temperature in deep forests. Patterns of change with temperature appear quite anomalous in two taxa.

- Weka was the only taxon that decreased more in the colder portion of its forest range (in the South Island), and its occupancy probabilities were higher in warmer forests in both measurement periods.
- Tūi increased in both the warmer and colder portions of its forest range in the North Island, in clear contrast to a marked general decrease in its occupancy probabilities (which were greater in warmer forests) in the South Island.

7.6 Cold forests: thermal refuges from predation?

The above results (sections 7.4 and 7.5) are consistent with our prediction that cold forests would be thermal refuges from predation for endemic forest birds. We define a thermal refuge effect as the difference in occupancy probability between a colder site and a warmer site, all else being equal.

Figure 15 illustrates how we estimate and plot mean thermal refuge effects for forest birds at different levels of endemism, using North Island deep forest squares in 1969–1979 as an example. The raw data for these estimates are mean fitted probabilities of occupancy from our deep forests models (Model F3, section 7.5), estimated at forest sites that experience two different mean annual temperatures (COLD and WARM) on each island.

The example shows that mean occupancy probabilities of endemic forest birds were higher in cold forests than in warm forests (Figure 15a). This leads to a positive thermal refuge effect (Figure 15b), which is what we would expect if predation pressure was higher in warmer forests. The positive difference in mean occupancy between cold and warm sites was greatest for species- and genus-level endemics (the highest point of the curve in Figure 15b). This is because as occupancy probabilities approach zero in warm forests towards the deep endemic end of the horizontal axis, the curve of occupancy for endemism in warm forests flattens out more than in cold forests.

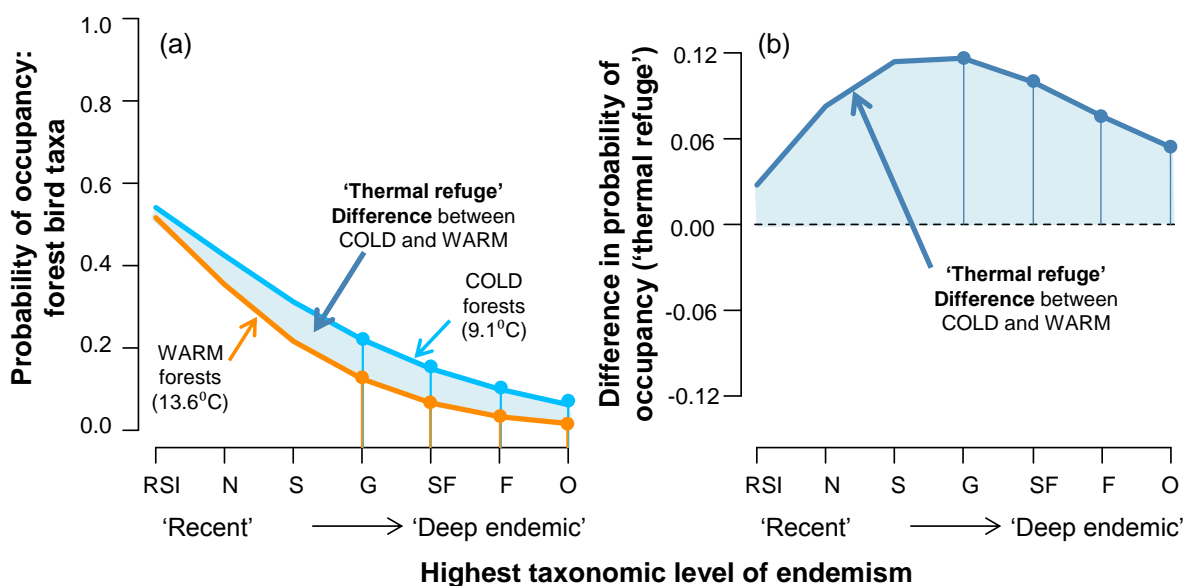


Figure 15 Estimating mean thermal refuge in North Island deep forests in 1969–1979. Thermal refuge is the difference in probability of occupancy between sites with cold and warm temperatures. Levels of endemism are indicated as RSI = recently self-introduced, N = non-endemic native, S = species level, G = genus level, SF = subfamily level, F = family level, and O = order level. The plot on the left (a) shows the mean occupancy probabilities in WARM deep forests (13.6°C mean annual temperature, or MAT) and COLD deep forests (9.1°C mean annual temperature or MAT). The vertical axis of plot (b) is the thermal refuge, which is the difference between mean fitted occupancy probabilities in COLD and WARM forests.

Figure 16 shows mean thermal refuge effects on both islands in each of the two measurement periods. Figure 16a and c show the raw data for these estimates, which are the mean fitted probabilities of occupancy from our deep forests models at forest sites at cold and warm mean annual temperatures on each island. Figure 16b and d simply rearrange the mean occupancy probabilities in Figure 16a and c to show the *differences* in the means between colder and warmer sites on the vertical axis.

In the North Island (Figure 16a, b), native forest birds at all levels of endemism were more likely to occupy colder forests than warmer forests in both measurement periods. Occupancy probabilities were invariably higher in colder forests, so differences in occupancy probability were positive (i.e. above zero in Figure 16b) at all endemism levels.

In contrast, in the South Island (Figure 16c, d) non-endemic birds were less likely to occupy colder forests. The negative thermal refuge effect in the South Island (left-hand side of Figure 16d) largely reflects the more rapid and complete invasion of warmer South Island forests by recently self-introduced silvereye (Figure 14). The effect diminished between 1969–1979 and 1999–2004 as silvereye – and therefore occupancy probabilities for non-endemic birds – decreased somewhat in warmer (but not colder) forests.

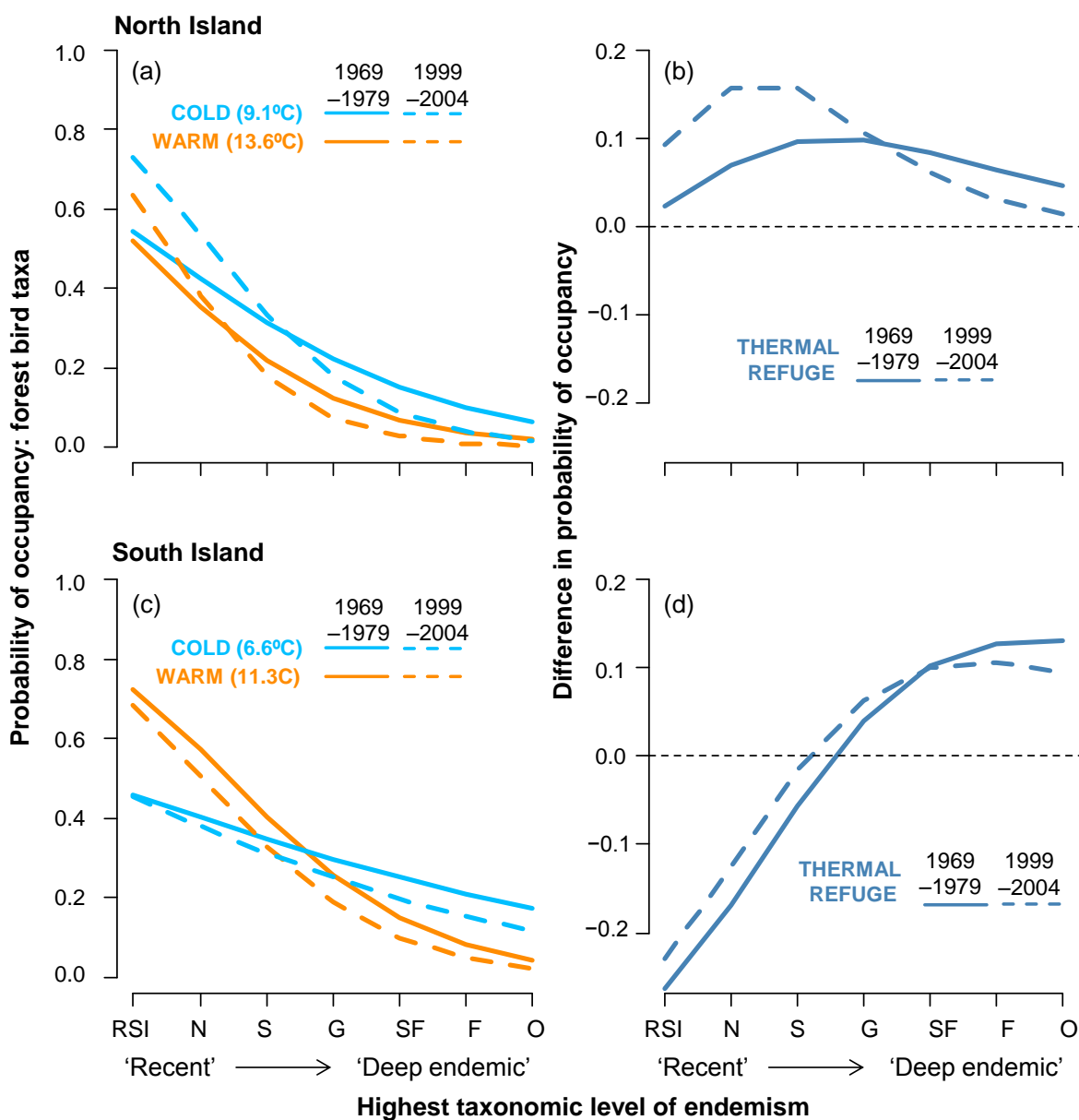


Figure 16 Thermal refuge effects for bird taxa at different levels of endemism (horizontal axes) in two measurement periods in North Island and South Island squares (upper and lower rows of plots, respectively). We define a thermal refuge effect as the difference in occupancy probability between a cold site and a warm site, all else being equal. The left column of plots shows probabilities of occupancy in COLD (blue) and WARM (orange) sites in forests at the two measurement periods (solid and dashed lines), and the right column of plots shows the average thermal refuge at different levels of endemism in 1969–1979 (solid lines) and 1999–2004 (dashed lines).

These results suggest that the thermal refuge provided by cold forests for birds that are endemic at high taxonomic levels decreased between measurement periods on both islands (Figure 16b, d). This was because loss of deep endemics between measurement periods was slower in warm forests, where there was relatively little left to lose by 1969–1979. In contrast, loss was able to continue in colder forests where there was, initially, more left to lose.

More generally, our results also indicate that:

- there is a pattern of advancing loss of endemic forest birds in forests between and within the two islands, which is apparently related to mean annual temperature (loss occurs earlier in warmer forests) as well as endemism level (deeper endemics are lost earlier)
- the amount of thermal refuge provided by colder forests – where loss rates are typically slower – has changed over time
- these changes depend on how advanced the loss of occupancy has become in both warm and cold forests, because loss rates necessarily slow once there is little left to lose.

Loss of deeper endemic birds occurred earliest and most completely in New Zealand's warmest forests (Figure 16a). Deep endemic birds were almost completely extirpated from warm North Island forests by 1969–1979, but loss lagged behind in colder North Island forests, which provided some thermal refuge (Figure 16b). Between measurement periods, continued loss in colder North Island forests largely removed that thermal refuge for deep endemic forest birds. However, some endemic forest bird taxa which remained relatively widespread (especially species- and genus-level endemics) continued to be lost faster from warm forests than from cold forests. Therefore, at the same time as refuge for deep endemics was decreasing, cold North Island forests became more important thermal refuges for other endemic forest bird taxa – mainly those that are endemic at lower taxonomic levels.

In 1969–1979, loss of endemic forest birds was least advanced in the coldest forests in the South Island, which are New Zealand's coldest forests overall (Figure 16c). Prior rates of loss had been slower than in warmer South Island forests, and considerably slower than in most North Island forests (Figure 16a), so these cold South Island forests provided New Zealand's principal thermal refuge for deep endemic forest birds at that time (Figure 16d). Between 1969–1979 and 1999–2004 this refuge was diminished because loss of deep endemic birds continued in the cold South Island forests that they still occupied.

Just as in the North Island, species- and genus-level endemics continued to be lost faster from warm forests in the South Island than from its cold forests between measurement periods (Figure 16c). Cold South Island forests therefore became more important thermal refuges for some endemic forest bird taxa that remain relatively widespread, at the same time as they were losing rarer, deep endemic taxa.

8 Discussion

8.1 Continuation of forest bird declines

The general conclusion of our study – that many native forest bird species declined in New Zealand in the last three decades of the 20th century – supports the high level of conservation concern that many taxa are accorded by the New Zealand Threat Classification System (Robertson et al. 2013) and suggests others may be in more serious trouble than previously appreciated (e.g. tomtit, South Island rifleman).

We were able to create and analyse a standardised set of occupancy data from the two atlases of bird distribution using modern computational methods. This allowed national-scale comparisons between 1969–1979 and 1999–2004, which supplement the ‘summary of observed changes in distribution’ in the second atlas of bird distribution in New Zealand (Appendix K of Robertson et al. 2007). Our results also support accounts of declines in other studies of individual taxa and long-term changes in forest bird populations; for example, in Northland (Pierce et al. 1993), the central North Island (Smith & Westbrooke 2004) and Nelson Lakes National Park (Elliott et al. 2010).

The pattern of loss between measurement periods continued earlier trends in relation to endemism level, deforestation and environment. Before the 1970s, native forest bird species that are endemic at higher taxonomic levels (especially those in an endemic order, family or subfamily – deep endemics) were lost earlier and more completely from deforested landscapes and from warmer forests.

This pattern of loss persisted between 1969–1979 and 1999–2004, although loss rates were slower where there was little left to lose. The generally lower rates of loss in colder forests have resulted in cold forests becoming important reservoirs of endemic forest bird populations and diversity, especially for deep endemics. However, because cold forests are not immune from loss, the thermal refuge they provide is temporary.

This persistent pattern of forest bird declines suggests that without meaningful management intervention, a number of endemic forest bird species will continue to decline to extreme scarcity or extinction across mainland forests, and that the greatest losses will now occur in cold South Island forests.

8.2 Primary cause of native forest bird declines

Our results are consistent with others’ conclusions that predation by introduced mammals is probably the primary cause of declines and limitations of native forest birds in remaining large native forest tracts (Innes et al. 2010). Between 1969–1979 and 1999–2004 the

greatest range declines in native forest birds occurred in New Zealand's remote natural areas of forest habitat, where the extent of indigenous forest cover changed little.

We cannot rule out changes in habitat quality, food supply and/or disease, and even minor amounts of forest loss,¹⁰ as factors that possibly contributed to these declines (Innes et al. 2010). However, those factors would not explain why observed range declines were greatest in deep endemics, whose lineages have evolved longer on New Zealand without mammalian predators (including deep endemic North Island kōkako, mainland kiwi taxa, rifleman, kākā and blue duck on both islands, and the genus-level endemics tūi and kererū in the South Island). Endemic taxa may have more specialised diets, or be more vulnerable to disease, but the diets, morphologies and behaviours of declining endemics are very diverse, and predation alone is probably an adequate explanation (Innes et al. 2010).

8.3 Modern effects of past deforestation

The reason that the greatest modern losses of forest birds have occurred in remaining forests is that many predator-vulnerable species were already essentially absent from deforested landscapes by the 1970s. Our results suggest that in addition to predation, scarcity of indigenous forest cover could be an important – and possibly underestimated – limitation to the occupancy of forest bird species¹¹.

Our models showed clear negative effects of forest scarcity on the occupancy probabilities of most forest bird taxa. Moreover, these effects appear to extend well beyond New Zealand's most deforested landscapes, where forest scarcity is recognised as a primary limitation (Innes et al. 2010)¹². We could identify no thresholds of indigenous forest cover above which most forest birds could occupy landscapes. Rather, local richness, and occupancy probabilities for several individual forest bird taxa were sensitive to differences in levels of indigenous forest cover even where forest was relatively abundant. In other

¹⁰ As noted in section 5.3, nationally the reduction in forest area between 1969–1979 and 1999–2004 was small compared with historical losses. Comparison areas mapped as forest in Newsome 1987 and LCDB (LCRIT 2015) suggest non-negligible amounts of forest clearance did occur in a few grid squares. We did not attempt to determine whether differences between these data sets represent real forest clearance (or regeneration) or differences in mapping resolution and accuracy. We therefore cannot determine whether, or how much, forest clearance between 1969–1979 and 1999–2004 affected bird occupancy probabilities.

¹¹ Lower amounts of indigenous forest cover in New Zealand landscapes are associated with many other factors, including environment (e.g. warmer temperatures), different suites and abundances of bird predators and competitors, higher densities of human settlement (e.g. as indicated by our road density index), and different and more intense anthropogenic modification and disturbance (e.g. by fire, agriculture and/or plantation forestry). We cannot fully separate the effects of indigenous forest habitat provision from these factors, because they are confounded. When we refer to the scarcity of indigenous forest cover we are mindful that many factors associated with deforestation could contribute to limitations to occupancy of forest bird species, in addition to forest habitat availability.

¹² For example, Innes et al. (2010) concluded that 'Forest loss is clearly primarily responsible for forest bird decline or extinction in some regions or localities where no or little forest is left, and habitat restoration is a necessary precursor to forest bird re-establishment there'.

studies, relatively low forest-cover thresholds have been identified for widespread and common New Zealand forest birds (e.g. 5 to 10% for grey warbler and tūi around Auckland; Ruffell & Didham 2017; Stevens 2006). Our results may differ because the widespread and common species that are still amenable to study are less sensitive to habitat as well as to predation, and because we were able to consider a greater number of forest bird species.

We found strong interactions between the effects of endemism level and indigenous forest cover. These indicate that indigenous forest scarcity has been more detrimental to forest bird taxa that are endemic at the level of species and higher, compared to non-endemic taxa. It has been particularly unfavourable to birds in lineages which have evolved longer in New Zealand. Just as endemic forest birds are more vulnerable to predation than native non-endemics and recently self-introduced taxa, they appear also to be more vulnerable to loss or scarcity of indigenous forest cover (and/or associated factors).

Our study does not identify life-history traits that explain why deep endemic forest birds depend more on large forest tracts. Relevant traits could be similar to or different from recognised correlates of extinction, range restriction or decline in New Zealand, such as long fledgling and incubation times, small clutch size, habitat specialisation, poor flying ability, and ground or cavity nesting (Cassey 2001; Duncan & Blackburn 2004; Parlato et al. 2015). Demographic traits may play a part, because the influence of stochastic (random) forces on populations increases as habitat dwindles (Fischer & Lindenmayer 2007). For example, forest fragment size limits population size, and smaller populations are more vulnerable to extinction through demographic stochasticity (high variance in population growth rates), especially if the species has low ability to recover quickly from low numbers and if maximum population size is small (Lande 1993; Caughley & Gunn 1996). Fragments also provide limited microhabitat diversity to buffer populations against environmental fluctuations, from which recovery may be needed (Fischer & Lindenmayer 2007).

Ecological factors that contribute to species' dependence on large forest areas generally are reasonably well known (e.g. Newton 1998). For example, deforested landscapes can fail to accommodate natal dispersal and genetic exchange in a metapopulation. Therefore, translocations are now required to avoid genetic impoverishment in isolated populations of a number of endemic New Zealand birds (e.g. Jamieson 2015; Taylor et al. 2017). There may also be inadequate resources for feeding and breeding, and numerous associated factors (see footnote 9, above) can lower fecundity and/or raise mortality rates. Many such limitations to population persistence can interact with predation, and perhaps normally do (Newton 1998; Innes et al. 2010). In that case, removing predation might alleviate some of the relative disadvantage faced by predation-vulnerable endemic species in deforested landscapes. However, data remain insufficient to assume this will be the case.

We recognise that some highly predator-sensitive endemic forest bird species can persist, at least in the short term, in very small predator-free sites (e.g. stitchbird/hihi, saddleback/tieke and little spotted kiwi; Hooson & Jamieson 2003; Burns et al. 2012), and there have been many apparently successful reintroductions to islands and very small forested fenced sanctuaries. However, population growth does not necessarily indicate that small isolated populations of long-lived New Zealand birds are viable in the longer term (e.g. Taylor et al. 2017).

Overall, our results suggest that a number of predator-vulnerable endemic forest birds cannot tolerate deforestation, and caution against expectations that they would be able to sustain viable populations in deforested and partially forested landscapes if mammal predators were absent.

8.4 Cold forests: shrinking thermal refuge

Because of the negative effects of forest scarcity discussed above, restoration of viable forest bird populations through predator management is likely to be more successful in the remaining large continuous tracts of forest. These forest tracts are also the remaining strongholds of a number of endemic bird species on the mainland.

Not all forests acted as strongholds: by 1999–2004, populations of native birds had been eliminated from many warmer forests. This strong effect of forest temperature probably reflects higher predation pressure in warmer forests, which makes cold forests relative 'thermal refuges' from decline (Elliott et al. 2010; Christie et al. 2009, 2017). This is indicated by two patterns. First, deep endemic species, which have evolved longer on New Zealand without mammalian predators, had disappeared more rapidly and completely from warmer forests, while non-endemic taxa were less sensitive to forest temperature variation¹³. Second, temperature effects were clear even in the most heavily forested squares where there is the lowest likelihood that other temperature-correlated human disturbances contributed to bird loss.

Endemic birds became increasingly confined to colder forests between the two atlas measurement periods in our study, but at the same time populations in the thermal refuges provided by colder forests were themselves depleted (i.e. occupancy probabilities decreased in cold forests, as well as in warm forests). This pattern suggests that colder forests have been providing only a temporary refuge for endemic forest bird populations because average rates of loss have been lower, but not negligible.

Many of New Zealand's remaining colder forests are in the South Island and are either beech forests or rimu forests, which periodically 'mast', triggering rodent and stoat irruptions that can severely reduce or eliminate remaining populations of endemic forest birds (e.g. King 1983; Elliott & O'Donnell 1988; Elliott 1996; O'Donnell 1996; Gaze 2003). By showing how endemic bird population strongholds have become increasingly confined to cold forests, our results explain how mast seeding events and consequent predator

¹³ We cannot rule out disease as a contributing cause. However, as noted by Innes et al. (2010) '[d]ocumented accounts of the effects of avian diseases in New Zealand are rarer than speculation about them, and data on free-living birds rarer than on captives'. Avian malaria has caused native bird declines in warmer sites on Hawaii (van Riper et al. 1986), and is also more prevalent in exotic birds at lower elevations in New Zealand (Niebuhr et al. 2016). Evidence of the effects of avian malaria on populations of native bird populations in the wild in New Zealand remains absent (Tompkins 2007; Niebuhr et al. 2016), although it occurs in translocated populations (Howe et al. 2012). To explain the patterns in our results, endemic bird taxa would need to be more susceptible to disease, as well as to predation.

irruptions have become such critical threats to the persistence of forest bird species in New Zealand (Elliott & Kemp 2016). They also explain the high importance of responsive predator-control programmes such as 'Battle for our Birds' (Elliott & Kemp 2016).

Ship rats (*Rattus rattus*) contribute to the decline and extinction of native forest birds, and are known to be sensitive to temperature (Innes 2005; Studholme 2000; J. Kemp & G. Elliott, Department of Conservation, unpublished data). Brown et al. (2015) suggested that New Zealand forests could be classified on the basis of the abundance and dynamics of ship rats, and that different forest classes required different predator management regimes to restore native forest birds. Our results are consistent with this idea, and add to it. We show major temperature-related variation in predator-vulnerable forest bird populations across New Zealand forests, and conclude that different predation levels are probably the cause. Especially striking decreases in occupancy probability with forest temperature in smaller species (rifleman, robin and tomtit on both islands, brown creeper, mohua and parakeets in the South Island, whitehead and bellbird in the North Island) that are preyed on by ship rats (e.g. Moors 1983; Brown 1997; Brown et al. 1998; Dilks et al. 2003) suggest that ship rats play a key role.

Pervasive trends of decreasing occupancy with increasing temperature suggests that climate warming may exacerbate predation on native forest birds in the future. It is likely to raise the elevation at which cold temperatures limit ship rat populations in most years (Christie et al. 2017), reducing the extent of forests that are cold enough to limit heavy or continuous predation. Warming is also likely to favour cold-limited predators generally, and hence increase predation pressure on forest birds over much of their remaining forest range. Finally, although it is still uncertain whether climate warming will increase the frequency of beech and rimu mast events (Kelly et al. 2013; Monks et al 2016), which trigger rodent and stoat irruptions, this is a real possibility.

8.5 Island differences

Indications of the future outcomes of warmer temperatures may already be evident when we compare the status of and trends in forest birds between the North Island and the generally cooler South Island. Overall, but perhaps most especially in smaller birds,¹⁴ range declines in endemic forest birds have been greater in forests in the North Island than in the South Island (both before the 1970s and between 1969–1979 and 1999–2004). Although the North Island forests are more fragmented and average road density is higher, our results suggest higher average temperatures have exacerbated bird declines.

Changes between our two measurement periods indicate that while loss of endemic forest birds in the South Island has lagged behind that in the North Island, it has been catching up

¹⁴ Rifleman, bellbird, robin, tomtit and parakeet, which, as we note above, may be more sensitive to rat predation. The complete extirpation of bellbirds, whiteheads, robins and New Zealand falcons from Northland in the second half of the 19th century (Robertson et al. 2007) is a striking example. Bartle and Sagar (1987) thought the cause a mystery, but others suggest that predation by ship rats was probably the cause (Lee 2005).

in recent decades. This may be partly because there were comparatively fewer populations remaining to lose in the North Island by the 1970s.

8.6 Changes in forest bird range occupancy after 2004

The data we analyse are now at least 13 years old. Are the trends that we show likely to have continued after that time? We suggest that for the most part they will have, because the extent of landscape-scale multi-species pest control has remained small relative to the area of forests¹⁵.

Aerial 1080 remains New Zealand's only practical and cost-effective large-scale multiple-predator control tool (Wright 2011; Brown et al. 2015). Until recently its use has mainly targeted possums rather than multiple bird predators, and most sites were not located to coincide with important residual populations of native birds (Parkes et al. 2017)¹⁶. Recent DOC operations have covered much larger areas, and have targeted multiple predators where and when species populations are vulnerable (Elliott & Kemp 2016)¹⁷, and preliminary monitoring data suggest they have slowed bird declines at those sites¹⁸. Nevertheless, the great majority of New Zealand forests still do not receive any predator management.

Our data set obviously does not account for changes in the distributions and abundances of threatened species that have been subject to intensive pest management since 2004. This management may have reversed declines across parts of their ranges, but examples suggest overall mainland range declines continue.

¹⁵ We note that the time period of our data largely precedes the implementation of sustained 'large-scale' (i.e. >1,000 ha) ground control operations to control mammal pests for conservation on the New Zealand mainland. However, Department of Conservation (DOC) 'mainland islands' were established between 1995 and 1997 (Saunders & Norton 2001) and other areas were subject to repeated aerial 1080 applications by DOC or by the former Animal Health Board in the time period between atlas measurement periods (Hoare et al. 2013; Brown et al. 2015). Some of these operations could conceivably have resulted in bird population changes detectable in our data set, but their effect is likely to have been insignificant at the scale of our analyses.

¹⁶ Important exceptions are sites included in DOC's Operation Ark (and its successors). For example, Tbfree annual reports document 233,890, 352,786, 302,409 and 286,393 hectares of aerial 1080 control for possums from 2009/10 to 2012/13 (mainly in forests), and much larger areas of possum ground control (although mainly in non-forest habitats). Spatial data for DOC aerial 1080 operations suggest that they treated considerably smaller areas (i.e. <50%) with aerial 1080 than Tbfree over the same time periods.

¹⁷ Elliott and Kemp (2016) report that in 'Battle for our Birds' operations, DOC applied aerial 1080 to 694,000 ha (equivalent to 11% of the area of New Zealand's remaining forests) in 2014 with the primary goal of preventing mast-driven rodent outbreaks and subsequent stoat irruptions at key sites for native species. In the 2016/17 spring and summer, DOC intends to treat 894,400 ha (equivalent to 14% of the remaining forest area) <http://www.doc.govt.nz/our-work/battle-for-our-birds/pest-control-operations-in-2016/> (accessed 23 February 2017).

¹⁸ <http://www.doc.govt.nz/our-work/battle-for-our-birds/battle-for-our-birds-monitoring-results/> (accessed 23 February 2017).

- In 1999, 330 pairs of North Island kōkako were estimated to remain in 13 relic mainland populations. There are now over 1,100 pairs occupying about 19,000 ha of forest due to intensive, mainly ground-based, pest control at mainland sites (J. Innes and others, unpublished data). All unmanaged kōkako populations are now extinct, however.
- Only small proportions of the geographic ranges of kiwi have been managed. Kiwi populations have recovered in some sites with intensive pest management (Robertson & de Monchy 2012; Tansell et al. 2016), but only about 24% of the estimated 68,000 remaining kiwi are under some management¹⁹ (Innes, Eppink et al. 2015). Consistent with the trends shown in our analysis, Innes, Eppink et al. (2015) concluded that kiwi populations with no management continued to decline.
- Some populations of blue duck/whio are now intensively managed (Glaser et al. 2010), in some parts of its range. Some managed populations are recovering, while others are not (e.g. Central North Island Blue Duck Trust 2016; A. Smart, Department of Conservation, unpublished data). Population models suggest depletion and local extinction of remaining unmanaged populations is likely to have continued (Whitehead et al. 2010).

8.7 Overall patterns and variations among places and bird taxa

We have focused here on major patterns revealed by the two atlases of bird distribution across the native forest avifauna as a whole. It is rare in ecology for such systematic and general effects to be caused by a number of different exceptional or special circumstances (Caughley & Gunn 1996). Rather, they are likely to arise from a single major driver, which we conclude is probably pervasive mammalian predation.

There was, however, considerable variation among forest bird species in their responses to both indigenous forest cover and temperature, which we have not explored here. Investigating how this variation is related to life history, history and perhaps chance could yield new insights for native bird conservation. Two especially intriguing deviations from the overall patterns of distribution and change were evident in tūī in the North Island, and in weka in both islands.

- Tūī increased its range remarkably in the lower North Island between measurement periods, especially, but not only, in deforested landscapes. In the same period tūī range declined across the South Island, especially in warmer forests. Although predator control is known to benefit tūī populations, the range increase in tūī in the North Island was too extensive to be accounted for by an increase in the area under predator control in the same period. Besides, the same geographic pattern of increase was not seen in any other predator-vulnerable forest bird taxon. Highly mobile tūī may

¹⁹ The percentage of individuals under management varies greatly between taxa: from 100% for little spotted kiwi (*Apteryx owenii*) to 2% for Rakiura tokoeka (*Apteryx australis lawryi*).

have benefitted from maturing, diverse, flowering and fruiting plants in planted gardens and parks (Spurr 2012). However, there is no obvious explanation for why this effect would have occurred so markedly in the deforested North Island but not in the deforested South Island.

- Weka was anomalous because its range declines between measurement periods were greater in colder forests than in warm forests. Spatial data show a pattern of decline that indicates wholesale loss, rather than population declines, across large contiguous areas in eastern North Island, Kahurangi and remote Fiordland. There were also noticeable areas of re-colonisation in central Westland and the Marlborough Sounds. These patterns suggest that predation – or at least the suite of predators afflicting most other endemic forest birds – may not be the primary contributor to declines and limitations in weka on the New Zealand mainland.

9 Conclusions

Between 1969–1979 and 1999–2004 there was widespread and systematic loss of endemic forest birds from New Zealand's forests. This trend is likely to have continued since 2004.

Our results are consistent with predation by introduced mammals being the primary cause of recent declines and limitation in New Zealand's native forest birds. There may be other contributing and interacting causes, but evidence for these is weak.

Forest scarcity may have more important negative consequences for endemic forest bird conservation than has been recognised. A number of taxa appear intolerant of deforestation as well as predation, especially those that are endemic at higher taxonomic levels. Our results caution against expectations that they would be able to sustain viable populations in deforested and partially forested landscapes if mammal predators were absent.

Assuming that mammalian predators can be reduced to and sustained at required threshold minima, restoration of viable endemic forest bird populations through predator management is more likely to be successful in large, continuous tracts of forest.

Loss of endemic forest birds from New Zealand's forests before 1969–1979 and between 1969–1979 and 1999–2004 varied with mean annual temperature. Cold forests (those with mean annual temperatures less than about 10°C) have become the most important strongholds of a number of endemic forest birds that have declined faster in warmer forests. The cause is likely to be higher and/or more continuous predation pressure where temperatures are warmer. However, the refuge that cold forests have provided for endemic forest bird species has also diminished, also (probably) as a consequence of ongoing predation.

Many of New Zealand's colder forests are in the South Island and are dominated by beech or rimu trees, which periodically exhibit synchronised heavy seeding. Our results explain why mast seeding events and consequent predator irruptions in these remaining cold-forest strongholds have become such critical threats to the persistence of forest bird species.

Loss of endemic forest birds is likely to be exacerbated by climate warming, by reducing the extent of cold forests where predation pressure is relatively low in most years, and by favouring cold-limited predators generally across forests. It may also increase the frequency of mast seeding events.

The opportunity to retain large viable populations of predator-vulnerable forest birds on the mainland is retreating. Large-scale predator control by aerial 1080 on public land is currently the only practical and cost-effective way to retain these populations.

10 Acknowledgements

We thank the Ornithological Society of New Zealand for allowing us to use their unique databases, and are grateful to the hundreds of observers who contributed the data on which this study is based. The Parliamentary Commissioner for the Environment commissioned and funded this report and co-funded the occupancy modelling component. Development of this work has been funded by Core Funding from the Ministry of Business, Innovation and Employment to Landcare Research over the last 2 years. We are grateful to Andrew Gormley (Landcare Research, Lincoln) for assisting our first attempts to apply occupancy modelling to the OSNZ atlas data, and for reviewing this report. Christine Harper and Ray Prebble helped us to initiate and complete this project, respectively, and we have many other colleagues to thank, especially in Landcare Research and the Department of Conservation, who have provided insightful feedback and review.

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Appendix 1 Native forest bird taxa

Table A1 The 22 native forest bird taxa included in our models and analyses, showing their common names (used, generally in shortened form, in the text of this report) and Latin (scientific) names, families and orders. Nomenclature follows Gill (2010). Endemism is the highest taxonomic level of endemism; N-E native = non-endemic native, RS-Introd. = recently self-introduced. In the 'Islands' column, NI/SI means that different species or subspecies are recognised in the North and South Islands; NI taxa occur only in the North Island; SI taxa occur only in the South Island. Asterisks indicate that a single combined national model was fitted for all species, subspecies or recognised forms because of difficulty in distinguishing them from records in the atlases. We modelled together: all mainland kiwi taxa (i.e. all North Island brown kiwi 'kinds', and South Island rowi, great spotted kiwi, and all tokoeka); orange-fronted, yellow-crowned and red-crowned parakeets; North and South Island rifleman; North and South Island tomtit; North and South Island fantail; North, South and Stewart Island robin; and all weka subspecies

Common_name	Latin (scientific) name	Family	Order	Endemism	Islands
Kiwi species*	<i>Apteryx</i> species	Apterygidae	Apterygiformes	Order	NI/SI
Rifleman/tītipounamu*	<i>Acanthisitta chloris</i> subspecies	Acanthisittidae	Passeriformes	Family	NI/SI
North Island kōkako	<i>Callaeas wilsoni</i>	Callaeidae	Passeriformes	Family	NI
Kākā*	<i>Nestor meridionalis</i>	Nestoridae	Psittaciformes	Family	NI/SI
Kea	<i>Nestor notabilis</i>	Nestoridae	Psittaciformes	Family	SI
Whitehead/pōpokatea	<i>Mohoua albicilla</i>	Pachycephalidae	Passeriformes	Family	NI
Brown creeper	<i>Mohoua novaeseelandiae</i>	Pachycephalidae	Passeriformes	Family	SI
Mohua/yellowhead	<i>Mohoua ochrocephala</i>	Pachycephalidae	Passeriformes	Family	SI
Blue duck/whio	<i>Hymenolaimus malacorhynchos</i>	Anatidae	Anseriformes	Subfamily	NI/SI
Kererū	<i>Hemiphaga novaeseelandiae</i>	Columbidae	Columbiformes	Genus	
Bellbird	<i>Anthornis melanura melanura</i>	Meliphagidae	Passeriformes	Genus	
Tūī	<i>Prothemadera novaeseelandiae novaeseelandiae</i>	Meliphagidae	Passeriformes	Genus	
Grey warbler/riroriro	<i>Gerygone igata</i>	Acanthizidae	Passeriformes	Species	
Long-tailed cuckoo/koekoeā	<i>Eudynamys taitensis</i>	Cuculidae	Cuculiformes	Species	
New Zealand robin/toutouwai*	<i>Petroica longipes</i> and <i>P. australis</i> subspecies	Petroicidae	Passeriformes	Species	NI/SI
New Zealand tomtit*	<i>Petroica macrocephala</i> subspecies	Petroicidae	Passeriformes	Species	NI/SI
Parakeet/kākāriki (mainland species)*	<i>Cyanoramphus</i> spp	Psittacidae	Psittaciformes	Species	
Weka species*	<i>Gallirallus australis</i> subspecies	Rallidae	Gruiformes	Species	
New Zealand fantail/pīwakawaka*	<i>Rhipidura fuliginosa</i> subspecies	Rhipiduridae	Passeriformes	Species	NI/SI
Shining cuckoo	<i>Chrysococcyx lucidus lucidus</i>	Cuculidae	Cuculiformes	N-E native	
Morepork/ruru	<i>Ninox novaeseelandiae novaeseelandiae</i>	Strigidae	Strigiformes	N-E native	
Silvereye	<i>Zosterops lateralis lateralis</i>	Zosteropidae	Passeriformes	RS-Introd.	

Appendix 2 Status and change in native forest bird taxa

Table A2 The 22 taxa of native forest birds, 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 fitted 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', and all robin species)

Common name	North Island (1,082 squares)				South Island (1,073 squares)			
	1969–1979	1999–2004	Change	LROR	1969–1979	1999–2004	Change	LROR
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/tīti pounamu*	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
Whitehead/pōpokatea					0.21 [0.07, 0.44]	0.22 [0.02, 0.55]	0.00 [-0.16, 0.22]	0.01
Brown creeper	0.13 [0.00, 0.16]	0.16 [0.00, 0.69]	0.03 [-0.22, 0.41]	0.24				
Mohua/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/riroriro	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/koekoeā	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
New Zealand robin/toutouwai*	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
New Zealand 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/kākāriki*	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]	-0.40
Fantail/pīwakawaka*	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/ruru	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

Appendix 3 Percentage of forest ranges occupied by native forest bird taxa

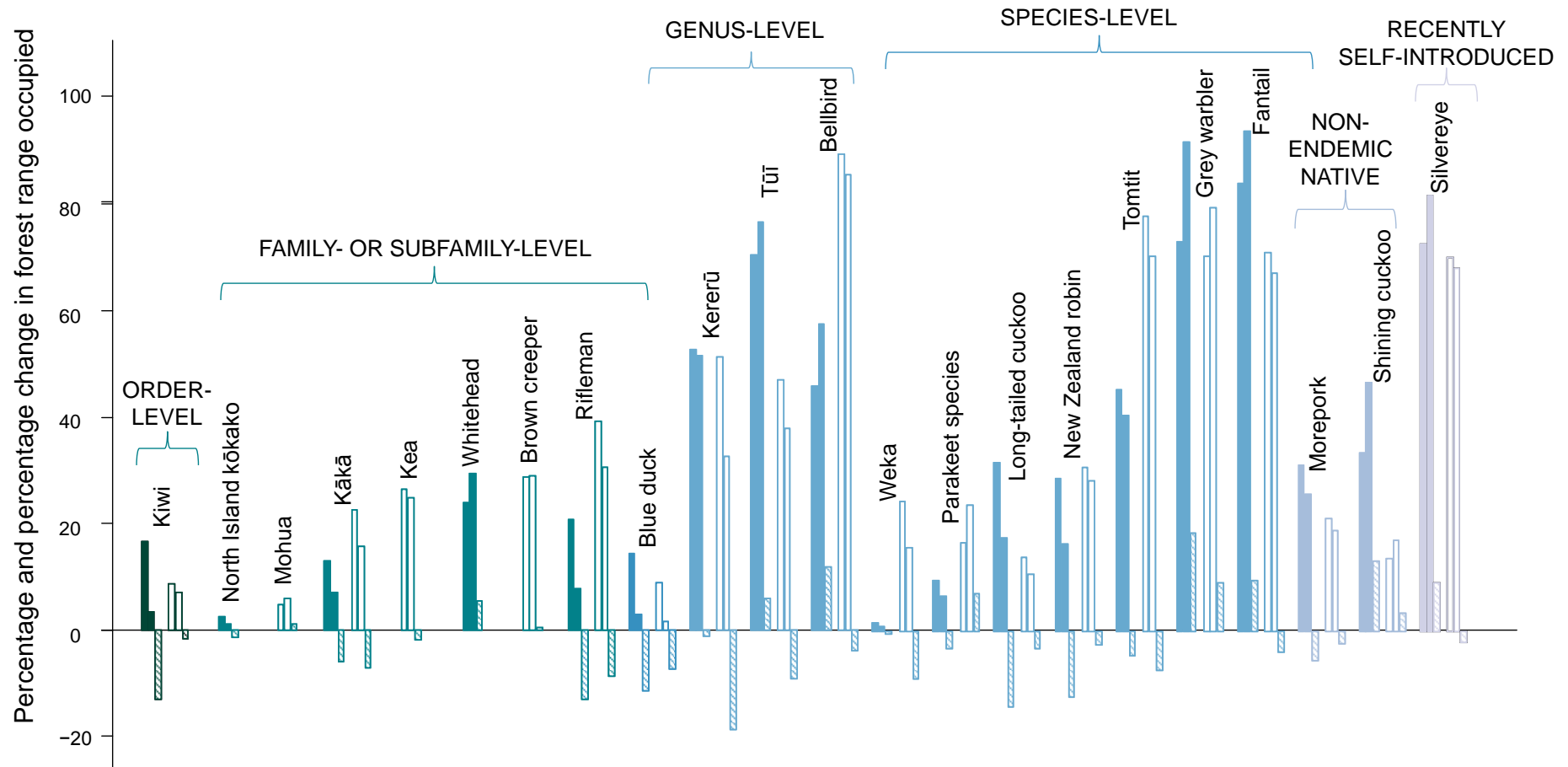


Figure A3 Bar graph showing percentage and percentage change in potential forest range occupied by native forest bird taxa, identified by common name, calculated from median occupancy probabilities. Solid bars represent percentage of North Island forest range occupied; hollow bars represent percentage of South Island forest range occupied. A trio of bars is presented for each island occupied by a taxon: in each trio, the first bar is the percentage range occupied in 1969–1979, the second bar is the percentage range occupied in 1999–2004, and the third (hatched) bar is the change in percentage of forest range occupied between 1969–1979 and 1999–2004. Hatched bars below the horizontal axis indicate a net range decrease. Highest taxonomic level of endemism is indicated by parentheses and distinguished by colour. 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.

Appendix 4 Estimated area of forest range occupied by native forest bird taxa

Table A4 Estimated area of potential forest range (in hectares) that was occupied by birds of forest habitats in the North and South Islands in 1969–1979 and 1999–2004, based on median occupancy estimates across those grid squares sampled in both measurement periods. Hyphens indicate that the species does not occur on the island. We include kārearea in this list for completeness, because the forest form ('bush falcon') can occur in forest. EL denotes endemism level (O = order, F = family, SF = subfamily, G = genus, S = species, N = non-endemic native, RSI = recently self-introduced). Estimates are rounded to the nearest 100 ha. Note that we assumed that the area of forest covered by a grid square in 1969–1979 was the same as in 1999–2004 (see sections 5.1 and 5.2)

EL		North Island (total = 2,111,200 ha forest in 1,082 squares)		South Island (total = 2,528,300 ha forest in 1,073 squares)	
		1969–1979	1999–2004	1969–1979	1999–2004
O	Kiwi species	350,700	73,300	219,700	180,700
F	North island kōkako	52,600	24,200	-	-
F	Mōhua/yellowhead	-	-	120,200	150,700
F	Kākā	277,100	150,700	573,100	397,700
F	Kea	-	-	669,800	626,200
F	Whitehead/pōpokatea	504,500	620,900	-	-
F	Brown creeper	-	-	725,800	734,800
F	Rifleman/tītipounamu	439,400	162,500	992,400	773,600
SF	Blue duck/whio	302,600	62,500	225,300	39,400
G	Kererū	1,112,600	1,089,900	1,295,900	827,900
G	Tūī	1,490,100	1,617,200	1,188,400	955,500
G	Bellbird	966,700	1,216,700	2,261,200	2,164,800
S	New Zealand falcon/kārearea	98,000	98,300	139,200	278,000
S	Parakeet/kākāriki species	202,300	136,800	420,400	595,600
S	Weka species	31,300	21,100	611,700	390,900
S	Long-tailed cuckoo/koekoeā	660,400	366,700	347,800	270,900
S	New Zealand robin/toutouwai	602,000	341,900	774,700	710,600
S	New Zealand tomtit	947,400	851,000	1,952,700	1,766,200
S	Grey warbler/riroriro	1,533,500	1,921,000	1,767,800	1,994,500
S	New Zealand fantail/pīwakawaka	1,761,100	1,964,200	1,781,600	1,684,400
N	Morepork/ruru	652,600	539,000	531,500	474,800
N	Shining cuckoo/pīpīwharauoa	698,100	974,900	343,500	428,800
RSI	Silvereye	1,520,400	1,710,500	1,758,900	1,707,200

Appendix 5 Native forest bird local richness and percentage forest cover

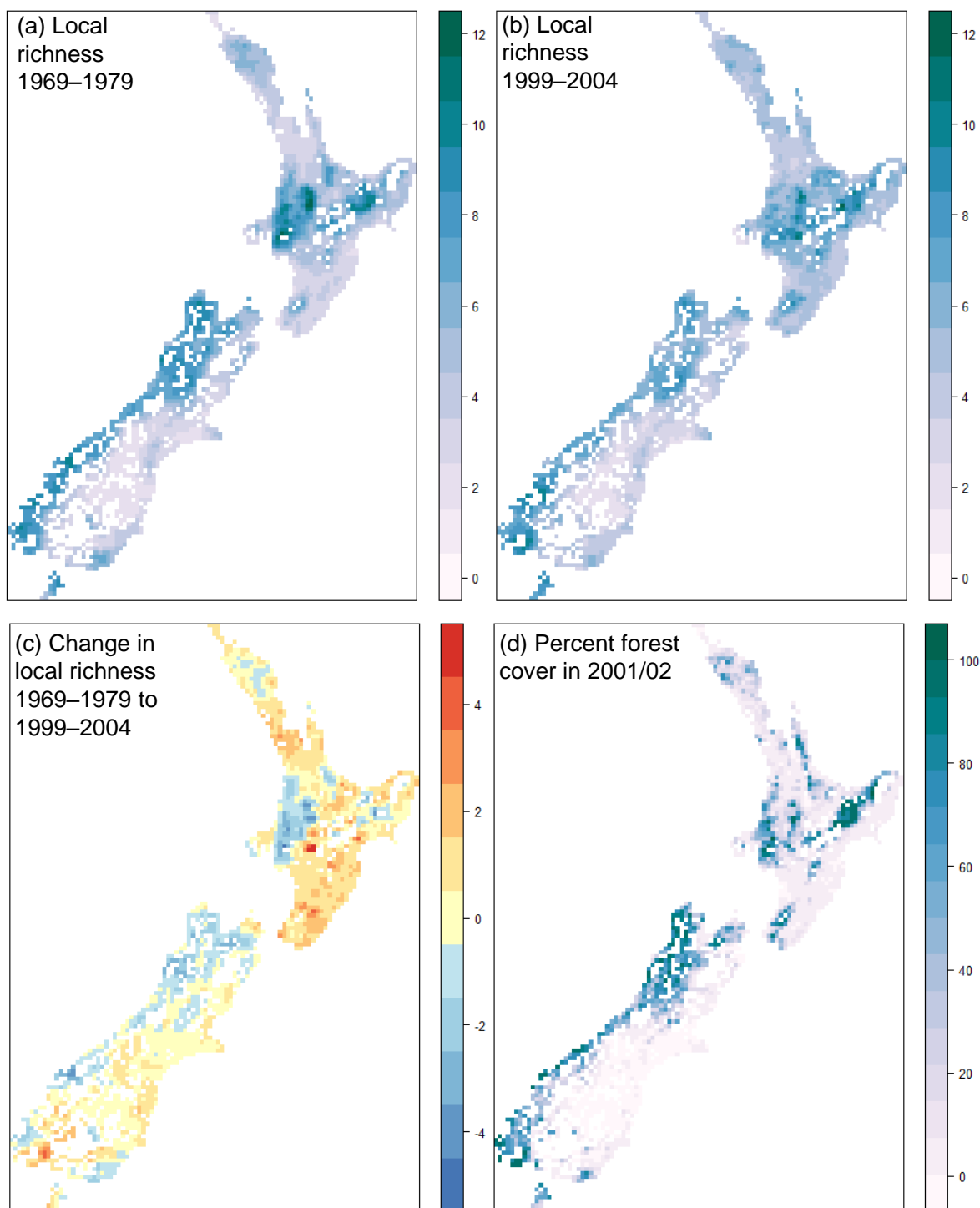


Figure A5 Maps of local richness (number of taxa per square) of all native forest bird taxa in (a) 1969–1979 and (b) 1999–2004, and (c) change in local richness between 1969–1979 and 1999–2004. Map (d) shows the percentage of land in each square under indigenous forest cover in the austral summer of 2001/02, according to the Land Cover Database (LCRIT 2015).

Appendix 6 Parameter estimates from linear mixed effects models

Table A6.1 Parameter estimates from a model of probabilities of occupancy in native forest bird taxa in the North and South Islands. Estimates are parameter estimates, and are shown on the logit scale of the data. Lower and upper bounds of 95% higher posterior density intervals (HPDI) of parameter estimates are shown. 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. The t-value is the parameter estimate divided by the standard error

NORTH ISLAND MODEL	Estimate	Lower 95% CL	Upper 95% CL	t-value
Intercept	-2.00	-3.04	-0.75	-3.21
Measurement period	-0.32	-0.37	-0.27	-13.07
Endemism level	-0.73	-1.45	-0.03	-1.99
Indigenous forest cover	2.61	2.46	2.78	31.34
Measurement period:Endemism level	-0.32	-0.35	-0.29	-21.20
Measurement period:Indigenous forest cover	-0.83	-0.97	-0.72	-13.38
Endemism level:Indigenous forest cover	0.49	0.43	0.54	18.05
Measurement period:Endemism level: Indigenous forest cover	-0.28	-0.36	-0.21	-7.36
SOUTH ISLAND MODEL	Estimate	Lower 95% CL	Upper 95% CL	t-value
Intercept	-1.45	-2.16	-0.59	-3.62
Measurement period	-0.29	-0.33	-0.26	-15.76
Endemism level	-0.48	-0.95	0.01	-1.97
Indigenous forest cover	2.76	2.63	2.90	42.73
Measurement period:Endemism level	-0.07	-0.10	-0.05	-6.60
Measurement period:Indigenous forest cover	-0.18	-0.27	-0.09	-3.86
Endemism level:Indigenous forest cover	0.25	0.21	0.29	12.60
Measurement period:Endemism level: Indigenous forest cover	-0.04	-0.10	0.01	-1.36

Table A6.2 Parameter estimates from the model of native forest bird occupancy that includes temperature. Estimates are estimated effects, and are shown on the logit scale of the data. Lower and upper 95% confidence limits (CL) of effects are shown: limits that exclude zero are considered to be statistically significant, and the t-value is the estimate divided by the standard error

NORTH ISLAND MODEL	Estimate	Lower 95% CL	Upper 95% CL	t-value
Intercept	-1.81	-3.16	-0.63	-2.91
Measurement period	-0.26	-0.31	-0.21	-10.02
Endemism level	-0.69	-1.37	0.04	-1.89
Indigenous forest cover	2.19	2.00	2.37	23.15
Temperature	-0.43	-0.52	-0.34	-9.28
Road density	0.03	-0.03	0.10	1.08
Endemism level:Road density	0.01	-0.01	0.03	1.25
Measurement period:Endemism level	-0.31	-0.34	-0.28	-19.11
Measurement period:Indigenous forest cover	-0.87	-1.01	-0.74	-12.27
Endemism level:Indigenous forest cover	0.43	0.37	0.49	12.86
Measurement period:Temperature	-0.22	-0.29	-0.15	-5.92
Endemism level:Temperature	-0.09	-0.12	-0.05	-5.23
Indigenous forest cover:Temperature	0.30	0.07	0.53	2.53
Measurement period:Endemism level: Indigenous forest cover	-0.30	-0.38	-0.21	-6.79
Measurement period:Endemism level:Temperature	-0.03	-0.07	0.01	-1.23
Measurement period:Indigenous forest cover: Temperature	-0.27	-0.48	-0.07	-2.71
Endemism level:Indigenous forest cover:Temperature	0.02	-0.06	0.11	0.56
Measurement period:Endemism level: Indigenous forest cover:Temperature	-0.01	-0.14	0.09	-0.21
SOUTH ISLAND MODEL	Estimate	Lower 95% CL	Upper 95% CL	t-value
Intercept	-1.75	-2.50	-0.91	-4.34
Measurement period	-0.34	-0.40	-0.29	-12.38
Endemism level	-0.66	-1.11	-0.16	-2.72
Indigenous forest cover	2.06	1.87	2.25	21.18
Temperature	-0.26	-0.34	-0.19	-6.25
Road density	-0.15	-0.21	-0.10	-5.79
Endemism level:Road density	-0.02	-0.03	0.00	-2.53
Measurement period:Endemism level	-0.07	-0.10	-0.04	-4.21
Measurement period:Indigenous forest cover	-0.19	-0.32	-0.07	-2.85
Endemism level:Indigenous forest cover	-0.01	-0.07	0.04	-0.36
Measurement period:Temperature	-0.07	-0.12	-0.02	-2.50
Endemism level:Temperature	-0.22	-0.25	-0.20	-17.04
Indigenous forest cover:Temperature	-0.66	-0.84	-0.47	-7.03
Measurement period:Endemism level: Indigenous forest cover	0.01	-0.08	0.09	0.18
Measurement period:Endemism level:Temperature	0.00	-0.02	0.04	0.28
Measurement period:Indigenous forest cover: Temperature	-0.01	-0.13	0.12	-0.11
Endemism level:Indigenous forest cover:Temperature	-0.31	-0.38	-0.25	-10.12
Measurement period:Endemism level: Indigenous forest cover:Temperature	0.07	-0.01	0.17	1.56

Table A6.3 Parameter estimates from the model of native forest bird occupancy probabilities in deep forests only (squares with >50% indigenous forest cover). Estimates are estimated effects, and are shown on the logit scale of the data. Lower and upper 95% higher posterior density intervals (HPDI) of effects are shown: intervals that exclude zero are considered to be statistically significant. The t-value is the estimate divided by the standard error

NORTH ISLAND MODEL	Estimate	Lower 95% CL	Upper 95% CL	t-value
Intercept	-1.96	-3.25	-0.91	-3.17
Measurement period	-0.42	-0.50	-0.33	-9.54
Endemism level	-0.56	-1.22	0.14	-1.60
Temperature	-0.41	-0.59	-0.21	-4.19
Indigenous forest cover	1.30	0.58	2.01	3.44
Road density	-0.16	-0.31	-0.01	-2.01
Measurement period:Endemism level	-0.36	-0.41	-0.31	-13.42
Measurement period:Temperature	-0.21	-0.32	-0.06	-3.14
Endemism level:Temperature	-0.12	-0.17	-0.06	-4.09
Measurement period:Endemism level:Temperature	0.00	-0.07	0.08	-0.08
SOUTH ISLAND MODEL	Estimate	Lower 95% CL	Upper 95% CL	t-value
Intercept	-1.31	-1.99	-0.50	-3.28
Measurement period	-0.40	-0.48	-0.32	-9.85
Endemism level	-0.64	-1.10	-0.17	-2.68
Temperature	-0.11	-0.21	-0.01	-2.29
Indigenous forest cover	0.27	-0.07	0.58	1.63
Road density	-0.23	-0.30	-0.16	-6.20
Measurement period:Endemism level	-0.07	-0.12	-0.02	-2.87
Measurement period:Temperature	-0.10	-0.17	-0.02	-2.43
Endemism level:Temperature	-0.25	-0.29	-0.22	-14.55
Measurement period:Endemism level:Temperature	0.00	-0.05	0.05	-0.02

Appendix 7 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 6.3 to 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.

However, fitting models to these data that do take spatial autocorrelation into account is computationally challenging because our two measurement periods provide more than one observation for the same spatial location. To be confident that our lme model results are robust, we attempted to also fit the models in this report 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). This appendix reports the results of that parallel modelling process.

Methods

We attempted to fit CAR model equivalents of each of the lme models in this report.

- CAR Model F1 fitted native forest bird occupancy probabilities for each island with a full three-way interaction of measurement period, endemism level and percentage indigenous forest cover as predictors. These models are the CAR equivalent of the lme Model F1 described in section 6.3.2 (results in section 7.3.2).
- CAR Model F2 extended CAR Model F1 by including temperature in a full four-way interaction of measurement period, endemism level, indigenous forest cover and temperature. It also included a term for road density and the interaction between endemism and road density. This model is equivalent to the lme Model F2 described in section 6.4 (and results in section 7.4).
- CAR Model F3 fitted native forest bird occupancy in deep forests (squares with $\geq 50\%$ indigenous forest cover) with a three-way interaction of measurement period, endemism level and temperature. Road density and indigenous forest cover were also fixed effects. This is the CAR equivalent of the lme Model F3 described in section 6.5 and results section 7.5.

The Bayesian CAR model approach is described in detail in Appendix 4 of our associated report (Walker & Monks 2017). CAR model convergence was assessed via visual inspection of trace plots and calculation of the \hat{r} statistic (Gelman et al. 2004).

Results

All parameters in two of the three CAR models for the North Island converged (CAR Model F1 and CAR Model F2). However, none of the CAR models for the South Island data converged, and CAR Model F3 for the North Island also failed to converge. In all models that failed to converge, it was the parameter controlling spatial dependence and the intercept that had not converged.

The comparatively 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 than in the North Island.

In the two North Island models that converged, occupancy probabilities predicted from the fixed effects in the CAR models covered much smaller ranges than those from the lme models (Table A7.1).

The parameter estimate for indigenous forest cover in CAR model F1 was much lower than that in the lme model, although credible intervals showed it was still highly significant (Table A7.2). All other parameter estimates were very similar to those in the equivalent lme model.

The parameter estimate for indigenous forest cover in CAR model F2 for the North Island was lower than that in the lme model, although the 95% credible interval again clearly excluded zero (Table A7.3). The parameter estimate for the *indigenous forest cover:temperature* interaction was also lower than in the lme, and the 95% credible interval in the CAR model included zero, whereas that for the lme did not. All other parameter estimates in CAR model F2 were very similar to those in the lme model, including all interaction terms that led to our interpretation that cold forests provide a thermal refuge for deep endemic taxa.

Table A7.1. Ranges of occupancy probabilities predicted by fixed effects in the lme models and CAR models

NORTH ISLAND MODEL	lme model range	CAR model range
Model F1	0.001–0.800	0.001–0.604
Model F2	0.001–0.879	0.001–0.699

Table A7.2 Comparison of parameter estimates from the lme Model F1 and CAR Model F1 of probabilities of occupancy in native forest bird taxa in the North and South Islands: 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

NORTH ISLAND MODEL	Lme estimate	95% lme CL	CAR estimate	95% CAR CL
Intercept	-2.00	[-3.04, -0.75]	-2.26	[-3.84, -0.74]
Measurement period	-0.32	[-0.37, -0.27]	-0.32	[-0.37, -0.27]
Endemism level	-0.73	[-1.45, -0.03]	-0.70	[-1.59, 0.14]
Indigenous forest cover	2.61	[2.46, 2.78]	1.51	[1.36, 1.64]
Measurement period:Endemism level	-0.32	[-0.35, -0.29]	-0.32	[-0.35, -0.29]
Measurement period:Indigenous forest cover	-0.83	[-0.97, -0.72]	-0.83	[-0.95, -0.71]
Endemism level:Indigenous forest cover	0.49	[0.43, 0.54]	0.49	[0.44, 0.54]
Measurement period:Endemism level: Indigenous forest cover	-0.28	[-0.36, -0.21]	-0.28	[-0.36, -0.21]

Table A7.3 Comparison of parameter estimates from the lme Model F2 and CAR Model F2 of probabilities of occupancy in native forest bird taxa that include temperature: 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

NORTH ISLAND MODEL	Lme estimate	95% lme CL	CAR estimate	95% CAR CL
Intercept	-1.81	[-3.16, -0.63]	-2.14	[-3.52, -0.81]
Measurement period	-0.26	[-0.31, -0.21]	-0.26	[-0.31, -0.21]
Endemism level	-0.69	[-1.37, 0.04]	-0.68	[-1.54, 0.17]
Indigenous forest cover	2.19	[2.00, 2.37]	1.28	[1.11, 1.45]
Temperature	-0.43	[-0.52, -0.34]	-0.43	[-0.55, -0.31]
Road density	0.03	[-0.03, 0.1]	0.03	[-0.02, 0.08]
Measurement period:Endemism level	-0.31	[-0.34, -0.28]	-0.31	[-0.34, -0.28]
Measurement period:Indigenous forest cover	-0.87	[-1.01, -0.74]	-0.87	[-1.01, -0.73]
Endemism level:Indigenous forest cover	0.43	[0.37, 0.49]	0.43	[0.36, 0.49]
Measurement period:Temperature	-0.22	[-0.29, -0.15]	-0.22	[-0.29, -0.14]
Endemism level:Temperature	-0.09	[-0.12, -0.05]	-0.09	[-0.12, -0.05]
Indigenous forest cover:Temperature	0.30	[0.07, 0.53]	0.12	[-0.08, 0.32]
Endemism level:Road density	0.01	[-0.01, 0.03]	0.01	[-0.01, 0.03]
Measurement period:Endemism level: Indigenous forest cover	-0.30	[-0.38, -0.21]	-0.30	[-0.38, -0.21]
Measurement period:Endemism level:Temperature	-0.03	[-0.07, 0.01]	-0.03	[-0.07, 0.02]
Measurement period:Indigenous forest cover: Temperature	-0.27	[-0.48, -0.07]	-0.27	[-0.47, -0.06]
Endemism level:Indigenous forest cover:Temperature	0.02	[-0.06, 0.11]	0.03	[-0.06, 0.11]
Measurement period:Endemism level: Indigenous forest cover:Temperature	-0.01	[-0.14, 0.09]	-0.01	[-0.14, 0.11]

If parameters in a model can be predicted from one another, coefficient estimates for one or both parameters may not be valid. We suspected that because forest cover is strongly spatially aggregated, our spatial term and might be correlated with it, leading to the poor predictive performance of the indigenous forest cover fixed effect in the CAR models. We therefore calculated the mean CAR effect for each grid from CAR Model F3 and plotted it against the indigenous forest cover term (Figure A7). Inspection showed strong positive correlation, which is linear on the log-log scale of the model.

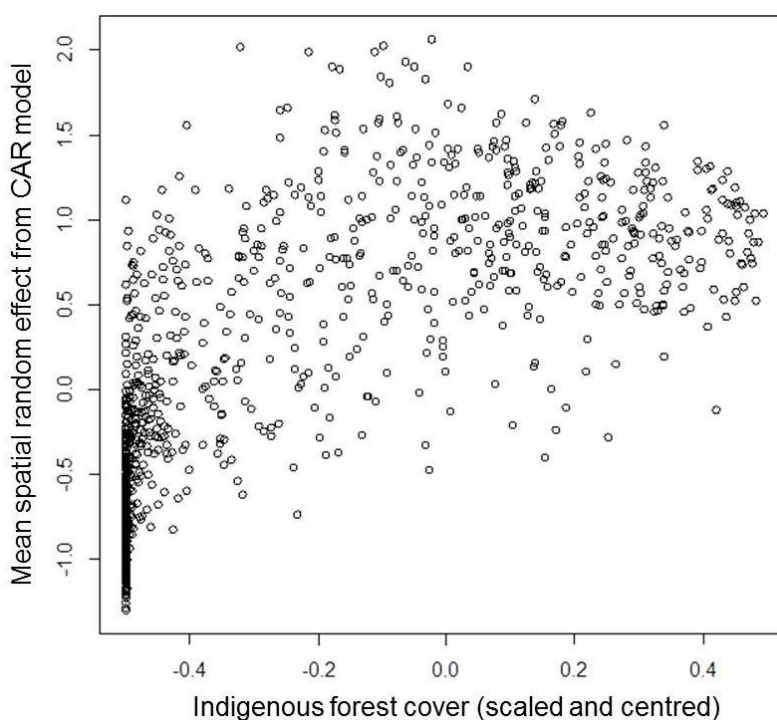


Figure 17 Plot of the mean spatial random effect term for each square from CAR Model F3 against scaled and centred indigenous forest cover.

Discussion

Close concordance of most parameter estimates in the converged CAR models with those in the equivalent lme models suggests that those effects identified by the lme models are robust.

The lower parameter estimates for indigenous forest cover in those two CAR models could be interpreted to suggest that our lme models overemphasised the positive effect of forest cover on occupancy probabilities of native forest birds. However, we are not satisfied that the lower maxima (and smaller ranges) of occupancy probabilities predicted by fixed effects in the two converged CAR models (Table A7.1) are realistic. Considering this, we prefer an alternative explanation: the CAR models were simply not able to identify the best estimates of the values of the forest cover parameters. Preliminary inspection of South Island CAR models (that had not quite converged) also showed lower estimates of the indigenous forest

cover parameter, and fixed effects predicted even more severely compressed and unrealistic ranges of occupancy values.

We think the primary reason for the poor predictive performance of the CAR models is that our spatial term and indigenous forest cover are correlated because forest cover is strongly spatially aggregated. Parameters estimates for the indigenous forest cover term in the CAR models are therefore unlikely to be valid. The solution to this problem is to include only one of the correlated parameters in the model. Therefore it may not be possible to properly account for spatial autocorrelation *and* assess the effect of indigenous forest cover on occupancy probabilities.