



## Life history traits explain vulnerability of endemic forest birds and predict recovery after predator suppression

Susan Walker<sup>1\*</sup> , Adrian Monks<sup>1</sup>  and John G. Innes<sup>2</sup> 

<sup>1</sup> Manaaki Whenua – Landcare Research, Private Bag 1930, Dunedin 9054, New Zealand

<sup>2</sup> Manaaki Whenua – Landcare Research, Private Bag 3127, Hamilton 3240, New Zealand

\*Author for correspondence (Email: [walkers@landcareresearch.co.nz](mailto:walkers@landcareresearch.co.nz))

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**Abstract:** New Zealand's native forest bird species with high taxonomic levels of endemism (deep endemics) are more vulnerable to decline than species that arrived and speciated more recently. Here we use national-scale local occupancy data to show that three endemism-linked life-history traits account for greater vulnerability of deep-endemic species in the extant forest avifauna, but also that other, more subtle traits and mechanisms favour rather than hinder endemic persistence. We suggest that these traits together provide a basis for predicting changes in local occupancy following suppression of introduced mammalian predators in different landscapes. Our analyses disentangle the limiting effects of forest area, predation, and food availability for different species. They support understanding that predation by introduced mammals is the primary cause of forest bird declines and limitation today, but suggest that large tracts of native forest are essential for future restoration of endemic forest avifauna, even following suppression of introduced mammalian predators. We predict that with fewer predators (1) deep-endemic species would most successfully and rapidly recover in large tracts of warm forest, (2) scarcity of forest or food would limit recovery in larger-bodied, less mobile species and in mobile cavity-nesters, and (3) interspecific competition would become influential and produce community reassortment.

**Keywords:** cavity-nesting, endemism, food limitation, forest bird occupancy, forest scarcity, mobility, predation, traits

### Introduction

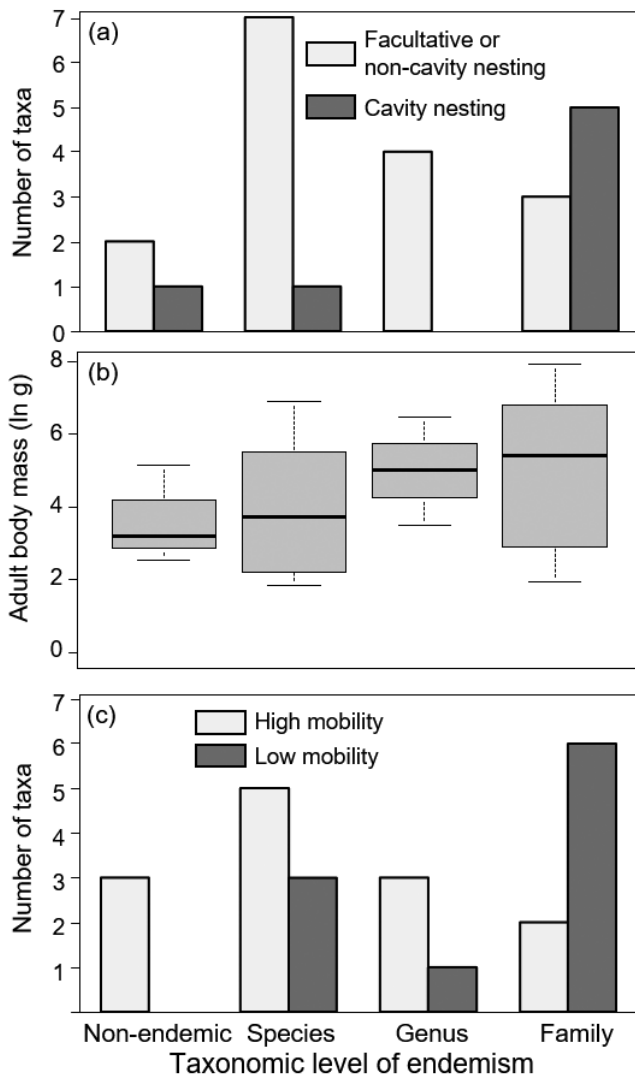
New Zealand's record of avian extinctions since human settlement is unequalled (Worthy & Holdaway 2002), and a higher proportion of vertebrate species are currently threatened than in any other country (Bradshaw et al. 2010). Native forest birds in New Zealand contribute significantly to global avian biodiversity because many taxa are endemic at the level of order, family, genus, or species. Not all forest bird species are threatened or declining; however, species that are endemic at higher taxonomic levels are more likely to have become extinct in the past and endangered since human settlement (McDowall 1969; Duncan & Blackburn 2004). As McDowall (1969) noted, the persistent relationship between avian endemism and vulnerability to decline in New Zealand “suggests some peculiarity in the evolutionary process ... which in a time related manner affects the present viability of the species”.

Numerous field studies support the conclusion of Innes et al. (2010) that introduced mammalian predators are the principal driver of modern declines in New Zealand forest bird species. Traits associated with weak predator escape responses (e.g. flightlessness, ground nesting, or cavity nesting) have been identified as the strongest life-history predictors of past extinctions, contemporary threat status, and historical range declines (Duncan & Blackburn 2004; Bronham et al. 2012;

Parlato et al. 2015). Recently, Walker et al. (2019a) showed that New Zealand native forest bird species that are obligate cavity nesters, large-bodied, or disperse poorly over land underwent more rapid declines in local occupancy between the 1970s and early 2000s where mean annual temperatures are higher. This trend is consistent with higher and more constant predation in warmer forested sites being the principal mechanism of recent forest bird declines. They predicted that a warming climate would exacerbate local extinctions of predator-vulnerable forest bird species by reducing the extent of cool thermal refugia from continuously high predation pressure below the upper limit of forests.

Walker et al. (2019a) selected their three avian life-history traits (large body size, obligate cavity-nesting, and limited mobility) to represent mechanisms that they hypothesised regulate species' local persistence or extinction. This forum article extends their analysis and discussion of forest bird occupancy patterns with two aims:

(1) We observe that each of the three life-history traits is more common in forest bird species that are endemic at higher taxonomic levels (Fig. 1). We therefore ask whether those three traits are the key peculiarities of extant endemic birds that affect their present viability, and thus provide a coherent mechanistic explanation for the modern endemism–vulnerability relationship (McDowall 1969).



**Figure 1.** Distribution of attributes: (a) cavity-nesting, (b) minimum, median (horizontal lines), interquartile range (boxes) and maximum (whiskers) adult body mass, (c) mobility of 23 extant native forest bird taxa (Table 2) across four taxonomic levels of endemism. Non-endemic native species occur elsewhere globally, but the species, genus or family of species-level, genus-level and family-level endemics occur naturally only in New Zealand.

(2) We observe that the adverse effects of large body size and limited mobility on local occupancy (Walker et al. 2019a) suggest that endemic forest bird distributions are also limited by mechanisms other than predation by introduced mammals. Limits on forest bird occupancy and recovery imposed by these additional mechanisms may become more apparent if mammalian predators are made less abundant across more extensive areas of New Zealand in future (Parkes et al. 2017).

We use hypothesised associations between life-history traits, geographical gradients, and mechanisms of limitation to disentangle the limiting effects of forest and food resource scarcity on the local occupancy of forest birds from those of predation. We then apply our mechanistic insights to predict how future outcomes of predator suppression may differ across forest bird taxa and across landscapes with different amounts of indigenous forest cover and food resources. We

compare these predictions with two recent meta-analyses of the outcomes of predator management for forest birds (Binny et al. 2020; Fea et al. 2020).

### Why do endemism-linked traits matter?

Table 1 presents a set of hypotheses about how endemism-linked traits could influence geographical patterns of local occupancy through their interactions with extrinsic factors, and lead to lower local occupancy in species that have higher taxonomic levels of endemism.

We hypothesise that the key extrinsic factors are predation pressure and the abundance (or, conversely, the scarcity) of forest and food resources (Table 1). All else being equal, we expected larger areas of forest would sustain larger and therefore more viable avian populations. We also hypothesised that warmer forests would potentially support larger bird populations than cooler forests, because of their higher biological net primary production per unit area (Baisden 2006) and hence less-limiting food resources. However, we also expected that for the same reasons, warmer, more productive forests would support higher densities of introduced mammal omnivores (ship rat *Rattus rattus*, possum *Trichosurus vulpecula*), predators (e.g. stoat *Mustela nivalis*), and herbivores (e.g. ungulates), leading to higher or more continuous predation pressure and/or greater interception of the food resources that would otherwise sustain bird populations.

*Obligate cavity nesting* increases risks to forest birds from predation in New Zealand (although not always elsewhere; Brawn et al. 2011) and has been identified as the strongest predictor of modern range declines (Parlato et al. 2015). Most of the obligate cavity-nesting species in the extant forest avifauna are endemic at the taxonomic level of family (Fig. 1a).

The literature suggests that adult birds that are incubating in confined cavities are less able to escape or defend themselves against nest predators (Elliott 1996; O'Donnell 1996), and nestlings in cavities may be more frequently predated (Massaro et al. 2013). We therefore expected greater negative effects of cavity nesting on local occupancy where mammal predation pressure is higher, especially in New Zealand's warmer forests, where possum capture and ship rat tracking rates are consistently higher (Forsyth et al. 2018; Walker et al. 2019b).

*Large body size* is a characteristic of many birds on islands (Clegg & Owens 2002; Lomolino 2005) and was identified as a predictor of prehistoric (post-Māori, pre-European) extinctions of New Zealand birds by Duncan and Blackburn (2004) and Bronham et al. (2012). Many larger-bodied species have already been selectively extinction-filtered from the New Zealand avifauna, but species endemic at the level of genus and family are nevertheless still larger, on average, than non-endemics and species-level endemics in the extant avifauna that arrived and speciated more recently (Fig. 1b).

The main explanation advanced for the role of body size in prehistoric extinctions has been the vulnerability of individuals or species of certain sizes and behaviours to being physically subdued by the predators (including humans) present at the time (e.g. Duncan & Blackburn 2004; Bronham et al. 2012). However, size can matter for other reasons. Larger-bodied species typically have longer generation times (Peters 1983) and lower intrinsic rates of population increase (Sinclair et al. 2006) and are, therefore, driven to extinction more rapidly by any sustained increase in annual mortality rate, such as imposed by novel mammal predation (Brook & Bowman 2005).

**Table 1.** Mechanisms that may limit local occupancy of forest bird species with different intrinsic life history traits, and under the influence of different extrinsic factors.

Limiting characteristic or factor	Hypothesised mechanism
<b>Intrinsic (life-history) trait</b>	
Cavity nesting	Susceptibility to predation on the nest is greater, and hence vulnerability to population extirpation through predation is higher.
Large body size	Longer generation time means the impact of an increased annual mortality rate is greater for larger animals than smaller animals over the same number of years. Populations are at lower densities (number of individuals per unit area) and therefore more vulnerable to stochastic extinction. Higher per-individual energetic requirements mean that more extensive habitat and/or more abundant food resources per unit area are required to sustain a viable population. Longer generation time means slower population recovery from decline. Lower intrinsic rate of increase.
Limited mobility	Limited mobility constrains the ability to recolonise habitat following local extirpation. Limited mobility prevents the acquisition of food and other resources from distant sites, and therefore constrains successful breeding in resource-poor habitats that support lower densities of mammalian predators more of the time.
<b>Extrinsic factor</b>	
Scarcity of primary natural habitat	Smaller areas of natural habitat can sustain smaller avian populations, which are more susceptible to local extinction.
Pressure from introduced mammalian predators	Higher and/or more continuous predation pressure (e.g. due to higher density of mammalian predators) leads to more rapid extirpation of populations.
Limited food resources	Sites offering fewer food resources support smaller bird populations, which are more susceptible to local extinction due to predation or stochastic events. Sites offering more food resources support larger populations of omnivores (ship rat, possums) and herbivores (e.g. ungulates) which intercept the food resource.

**Table 2.** Native forest bird taxa (referred to as species in the text) that remain most widespread in New Zealand's three main islands. Nomenclature and Endemism level (the highest taxonomic level of endemism) follow Gill (2010) and trait assignments follow Walker et al. (2019a). Species treated as a single taxon when estimating local occupancy are indicated by asterisks. Both = the same taxon occurs in both the North Island and the South Island (including Stewart Island/Rakiura); NI, SI = different species, subspecies or recognised forms occur in the North and South islands; NI = the taxon occurs in the North Island only; SI = the taxon occurs in the South Island (including Stewart Island/Rakiura) only.

Common name	Name	Order	Family	Island	Endemism level	Maximum adult body mass (g)	Mobility	Obligate cavity nester
Whio/blue duck	<i>Hymenolaimus malacorhynchos</i>	Anseriformes	Anatidae	Both	Genus	900	less mobile	no
Kiwi*	<i>Apteryx</i> species	Apterygiformes	Apterygidae	NI, SI	Order	2800	less mobile	yes
Kererū/NZ pigeon	<i>Hemiphaga novaeseelandiae</i>	Columbiformes	Columbidae	Both	Genus	650	mobile	no
Long-tailed cuckoo	<i>Eudynamis taitensis</i>	Cuculiformes	Cuculidae	Both	Species	125	mobile	no
Shining cuckoo	<i>Chrysococcyx lucidus</i>	Cuculiformes	Cuculidae	Both	none	25	mobile	no
Kāreaarea / New Zealand falcon	<i>Falco novaeseelandiae</i>	Falconiformes	Falconidae	Both	Species	500	mobile	no
Weka	<i>Gallirallus australis</i>	Gruiformes	Rallidae	NI, SI	Species	1000	less mobile	no
Titipounamu/Rifleman	<i>Acanthisitta chloris</i>	Passeriformes	Acanthisittidae	NI, SI	Family	7	less mobile	yes
Grey warbler	<i>Gerygone igata</i>	Passeriformes	Acanthisittidae	Both	Species	6.5	mobile	no
North Island kōkako	<i>Callaeas wilsoni</i>	Passeriformes	Callaeidae	NI	Family	230	less mobile	no
Bellbird	<i>Anthornis melanura</i>	Passeriformes	Meliphagidae	Both	Genus	34	mobile	no
Tūī	<i>Prothemadera novaeseelandiae</i>	Passeriformes	Meliphagidae	Both	Genus	150	mobile	no
Brown creeper	<i>Mohoua novaeseelandiae</i>	Passeriformes	Pachycephalidae	SI	Family	13.5	less mobile	no
Whitehead	<i>Mohoua albicilla</i>	Passeriformes	Pachycephalidae	NI	Family	18.5	less mobile	no
Mohua / yellowhead	<i>Mohoua ochrocephala</i>	Passeriformes	Pachycephalidae	SI	Family	30	less mobile	yes
NZ robin*	<i>Petroica longipes</i> / <i>P. australis</i>	Passeriformes	Petroicidae	NI, SI	Species	35	less mobile	no
NZ tomtit	<i>Petroica macrocephala</i>	Passeriformes	Petroicidae	NI, SI	Species	11	less mobile	no
NZ fantail	<i>Rhipidura fuliginosa</i>	Passeriformes	Rhipiduridae	NI, SI	Species	8	mobile	no
Silvereye	<i>Zosterops lateralis</i>	Passeriformes	Zosteropidae	NI, SI	none	13	mobile	no
Kākā	<i>Nestor meridionalis</i>	Psittaciformes	Nestoridae	NI, SI	Family	575	mobile	yes
Kea	<i>Nestor notabilis</i>	Psittaciformes	Nestoridae	SI	Family	1000	mobile	yes
Kākāriki/parakeet species*	<i>Cyanoramphus auriceps</i> / <i>C. malherbi</i> / <i>C. novaeseelandiae</i>	Psittaciformes	Psittacidae	Both	Species	50	mobile	yes
Ruru/morepork	<i>Ninox novaeseelandiae</i>	Strigiformes	Strigidae	Both	none	175	mobile	yes

Larger animals also typically have lower population densities (Peters 1983; Stephens et al. 2019), and populations with lower numbers of individuals are at greater risk of extinction through stochastic events (Fischer & Lindenmayer 2007).

Per-individual energetic needs also increase with body size (Peters 1983; Jetz et al. 2004), so that viable populations of larger birds need larger areas of forest or forests that produce more food per hectare, to meet their energetic requirements. Conversely, we expect smaller-bodied species (with their intrinsically higher population densities, shorter generation times, and higher rates of population increase) to be more robust to extinction by stochastic events, the resource limitations imposed by small habitat patches and cooler, less productive forests, and the elevated annual mortality caused by higher predation pressure in warmer forests.

The third endemism-linked trait is *limited mobility*, which we define here as a weak ability to colonise or forage in distant forested sites across land over a period of years to decades. Flightlessness is a strong indicator of limited mobility and is common among endemic birds of islands (Diamond 1981), but past extinctions and declines have left only two flightless forest birds among the 23 species in our data set (Table 2). Endemics in our extinction-filtered set of extant birds are, nevertheless, likely to be less mobile than comparatively recent arrivals (Fig. 1c).

Limited mobility was identified as an influential predictor of bird occupancy by Spurr (1979) and Diamond (1984). Diamond's focus was on water-crossing ability and occupancy of "virtual" (i.e. forest patches) and real islands, whereas we, and Spurr (1979), mainly consider capability to move across land. Nevertheless, the principal mechanism we invoke is the same: limited mobility constrains reinvasion and recolonisation after population reduction or extirpation, and renders populations less able to recover from reductions and more susceptible to local population extinction (Spurr 1979; Diamond 1984). We also hypothesise that limited mobility exacerbates the adverse effects of local scarcity of food resources by preventing individuals from foraging widely (e.g. beyond safe nesting or roosting locations in less productive forests where there are few predators, or beyond small forest patches) (Table 1). Therefore we predicted that limited mobility would exacerbate the disadvantages of large body size in endemic species where forest or food resource are scarce and that higher mobility would mitigate those disadvantages.

We tested our hypotheses in two stages. First, we asked whether local occupancy decreased with endemism level, consistent with McDowall (1969). Then we tested whether the three life-history traits are the evolved peculiarities that can explain mechanistically why occupancy is lower, and continues to decrease faster, in forest birds from lineages that have evolved longer in New Zealand.

## Endemism level explains occupancy patterns

Using R software (R Core Team 2020), we fitted linear mixed-effects models (in package lmer; Bates et al. 2015) of logit-transformed standardised estimates of local occupancy probabilities for 23 extant native forest bird taxa (hereafter 'species') in 2155 grid squares of 10 × 10 km. The estimates of local occupancy (the probability that a species was actually present in a particular grid square) were derived by Walker and Monks (2018) from the Ornithological Society of New Zealand's two national atlases of bird distribution, collated

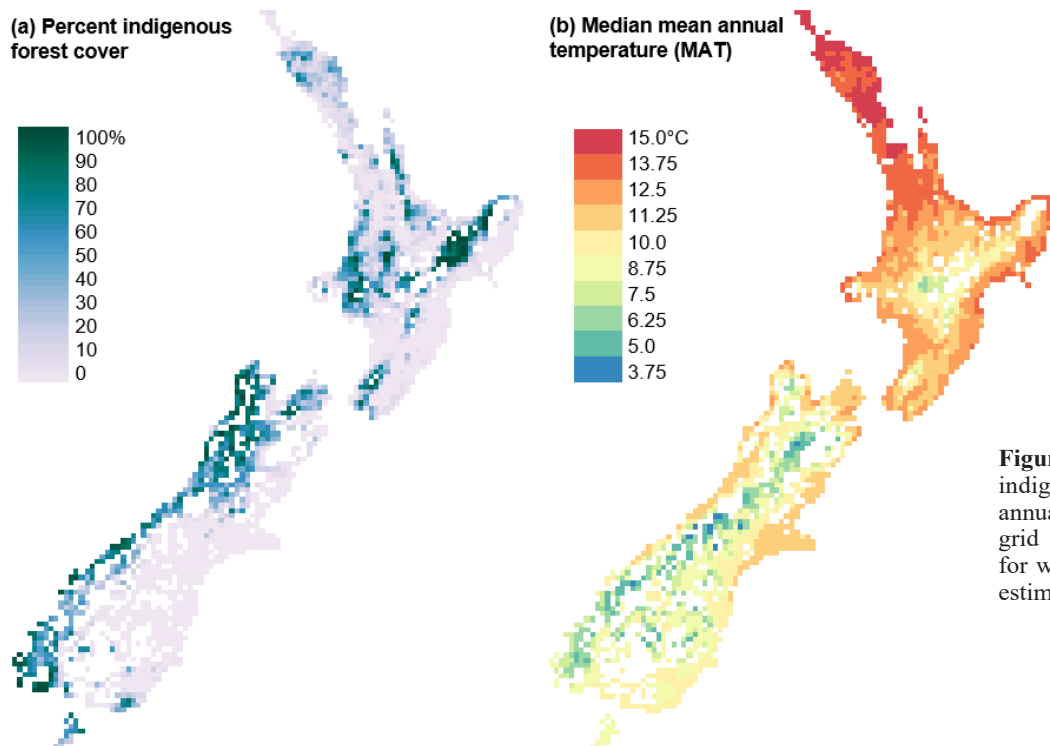
in two measurement periods (1969–1979, Bull et al. 1985; 1999–2004, Robertson et al. 2007) using a consistent survey protocol. Walker and Monks (2018) estimated probability of occupancy for each atlas grid square using a Bayesian mixture model for each species that combined probabilities of detection and occupancy to allow for unbiased estimates of occupancy (MacKenzie et al. 2002; Bailey et al. 2014). The process used observations from only complete sheets, because incomplete lists and casual observations in the Atlas sampled unknown proportions of each grid square and its fauna, and thus bias the probability of detection in a grid square downwards by unknown quantities.

Taxonomic level of endemism (sourced from Gill 2010) was represented in our models by a ordinal variable of four integers: 1 = non-endemic, 2 = species-level endemic, 3 = genus-level endemic, and 4 = deep endemic (endemic at subfamily, family or order level). We assume that these taxonomic levels represent increasing lengths of time that lineages have evolved on New Zealand; this assumption is supported by phylogenetic data showing that New Zealand forest bird species with higher taxonomic levels of endemism diverged earlier from their closest relatives outside New Zealand (BCM Potter, unpublished data derived from the global phylogeny of Jetz et al. 2012).

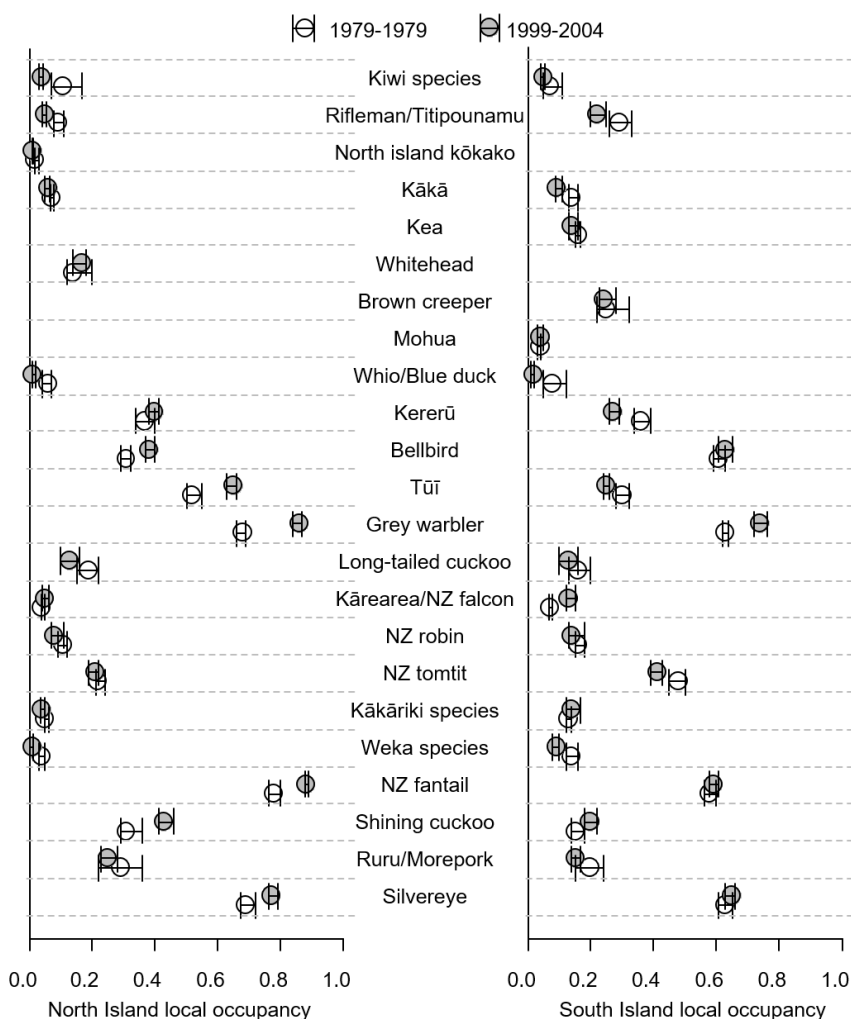
Other fixed-effect predictors in the models were time (first or second atlas measurement period), percentage of land in the square under the indigenous forest land cover class (referred to as forest cover) in 2001, and the median mean annual temperature (MAT) across land in the square (Fig. 2; Walker et al. 2019b; the same forest cover and MAT values were used in each time period, as data indicate no significant overall change). We assumed that the percentage of a square covered by forest best represented the amount of primary (unlogged) forest available to birds, and hence best represents availability of the associated food and other resources, such as nesting sites and shelter; and that squares with higher mean annual temperatures produced more food resources per unit area and also supported more predators and omnivores. Each model included random effects for bird species and bird family, and for grid square identity. Exploratory conditional autoregressive (CAR) models showed that indigenous forest cover is correlated with spatial terms, so that forest cover parameters were unable to be estimated. However, the concordance of other parameter estimates in equivalent CAR and lme models suggested that those in the lme models were robust despite not accounting for spatial autocorrelation.

Walker & Monks (2018) preserved the variability in their estimates of local occupancy within grid squares so that this could be incorporated into future analyses. In this analysis, we fitted 1000 replicates of each mixed model, with each replicate using a different draw from those preserved posterior estimates of local occupancy as the response (Walker & Monks 2018; Fig. 3).

Fixed effect predictors of local occupancy in Model 1 were a full three-way interaction between time (measurement period), endemism level, and forest availability. We fitted these interactions because we expected endemic species (which evolved in almost wholly forested landscapes before human arrival) to be rarer where forest was scarce, and to have substantially completed declines in deforested landscapes by our first measurement period. In Model 2, we substituted a basis function (a generalised additive model with a 3 df regression spline smooth of forest cover) for the linear term to allow non-linear responses of local occupancy to forest



**Figure 2.** (a) Percentage of land under indigenous forest cover, (b) mean annual temperature across the 2155 grid squares of 10 × 10 kilometre for which we have local occupancy estimates for 23 forest bird taxa.



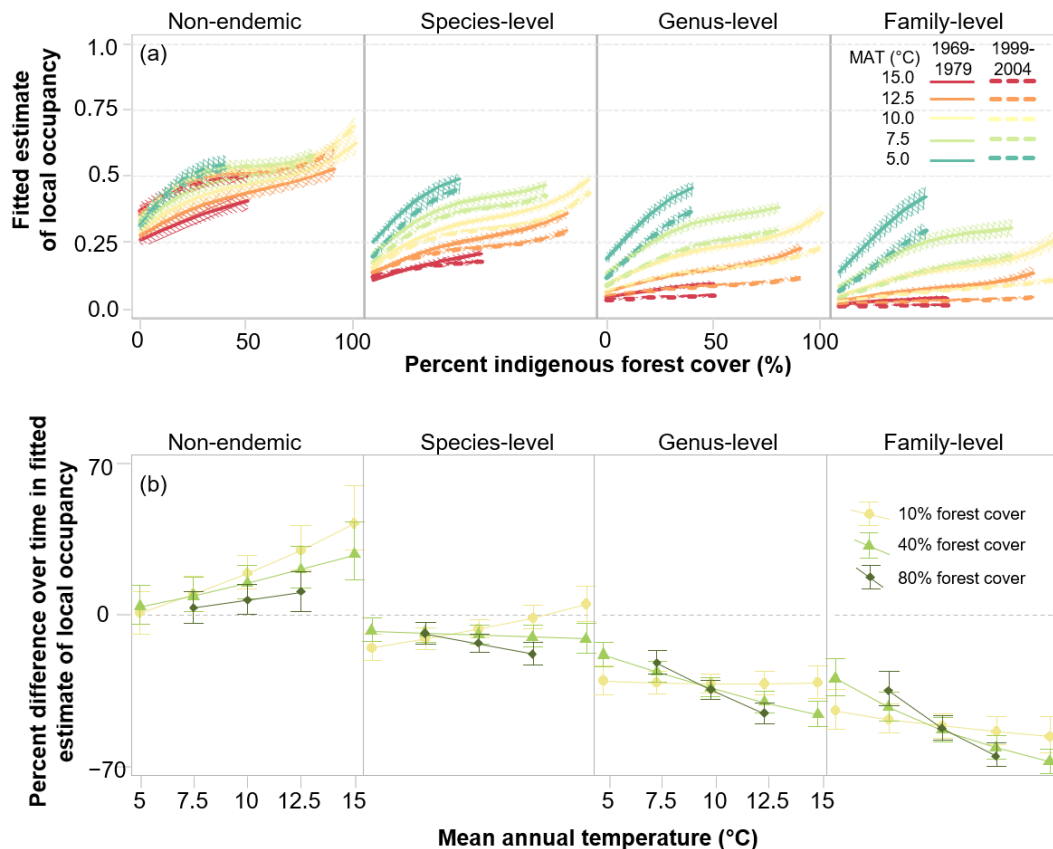
**Figure 3.** Medians and 95% intervals of estimates of the average probability of local occupancy ('range occupancy') across 10 × 10-km grid squares on New Zealand's North and South islands in two measurement periods (1969–1979 and 1999–2004) for the 23 forest bird taxa listed in Table 2. The estimates were made by Walker and Monks (2018) for 1083 North Island squares and 1072 South Island squares, covering similar areas of land on each island (99 510 and 99 630 km<sup>2</sup>, respectively).

scarcity. In Model 3 we introduced a fourth, fully interacting MAT term, expecting more deeply endemic species to be rarer where forest was scarce and to have decreased most rapidly between measurement periods in warmer forests where predation rates are higher (Table 3). We used the second-order Akaike Information Criterion (AICc corrected for small sample size or AICc; Burnham & Anderson 2002) across the 1000 replicates to select the best model, and fixed effects r-squared to assess model fit.

Model 3 was the best of these three models (there was no overlap with the AICcs for the next-best model), although its fixed-effects r-squared was low (0.19; Table 3). Parameter estimates (Appendix S1 in Supplementary Materials) and fitted effects (Fig. 4; Fox & Hong 2009) show interacting and compounding negative effects of endemism level, indigenous forest scarcity, temperature and measurement period on local occupancy. Forest bird species that are endemic at higher taxonomic levels have lower probabilities of occupancy in

**Table 3.** Comparisons of fitted models of median local occupancy from most complex to simplest. All models included random intercept effects for family, species and grid square. *k* = number of parameters; AICc = the median second order Akaike’s Information Criterion (Burnham & Anderson 2002); ΔAICc = the difference in median AICc from that of the best model; βtime = effect of measurement period; βend = effect of endemism level; βcav, βbodsze, and βmob = effects of the species attributes cavity nesting, body size (maximum adult mass), and mobility; βfor and βtemp = effects of grid-square level percentage forest cover and median mean annual temperature, respectively; (bs) = a basis function, which is a generalised additive model with a 3 df regression spline smooth of forest cover. \* indicates interacting effects.

Name	Model	<i>k</i>	AICc	ΔAICc	Fixed effects r-squared
Model 6	~ α + βtime * βcav * βbodsze * βmob * β(bs)for * βtemp + βtime * βend * β(bs) for * βtemp	148	338147.6	0	0.553
Model 5	~ α + βtime * βcav * βbodsze * βmob * β(bs)for * βtemp + βend	133	339029.5	882.0	0.536
Model 4	~ α + βtime * βcav * βbodsze * βmob * β(bs)for * βtemp	132	339028.3	880.7	0.557
Model 3	~ α + βtime * βend * β(bs)for * βtemp	36	348039.7	9892.6	0.190
Model 2	~ α + βtime * βend * β(bs)for	20	350828.7	12681.6	0.165
Model 1	~ α + βtime * βend * βfor	12	351109.5	12962.4	0.160



**Figure 4.** Medians and 95% intervals of effects on probability of local occupancy in 23 forest bird taxa across New Zealand fitted by our Model 3, showing: (a) fitted effects of measurement period (solid 1969–1979 in upper row vs 1999–2004 dashed lines in lower row), environment (with indigenous forest cover on the horizontal axis and temperature in different colours), and endemism level (subplots), and (b) percentage difference over time between measurement periods (1969–1979 and 1999–2004) in fitted effects of environment (with temperature on the horizontal axis and indigenous forest cover in different colours) and endemism level.

sites that are warmer and/or have low proportions of forest cover, and higher probabilities of occupancy in squares that are colder and are well forested (Fig. 4a). The local occupancy of species endemic at higher taxonomic levels decreased significantly between measurement periods, and the largest proportional decreases in local occupancy were in family-level endemic species in warmer, well-forested squares (Fig. 4b). Local occupancy of non-endemic species increased in warmer squares, and their largest proportional increases were in warm squares with little remaining indigenous forest.

These results support McDowall's (1969) observation that more deeply endemic species are more vulnerable to loss, and our expectations that they would be more vulnerable to forest scarcity as well as predation by introduced mammals.

### Endemism-linked life-history traits explain occupancy patterns better

We fitted a further series of models to determine whether endemism-linked life-history traits (and our associated hypothetical mechanisms) were sufficient to explain the effect of endemism level on vulnerability to loss. We used the values for body size and the assignments for obligate cavity nesting and high or low mobility adopted and explained by Walker et al. (2019b). The binary index of mobility represents species' ability to colonise across land or to forage in distant forested sites within years to decades. Mobile species are flighted and range widely across New Zealand's main islands. Less mobile species are flightless or have typical dispersal distances of individuals within tens of kilometres (although juveniles may occasionally cross non-forested land, water barriers, and large distances).

In Model 4, we substituted fixed-effect terms for obligate cavity-nesting, body size, and mobility for endemism level in Model 3 (Table 3). This model, with six interacting fixed-effect terms (measurement period, the three life-history traits, a non-linear basis function of percentage forest cover, and MAT) was the model selected and described by Walker et al. 2019b, with lower AICc and higher r-squared (0.557) than Model 3. We fitted two further models to assess whether endemism and its interactions were able to explain more than traits alone: (1) in Model 5, we added endemism level as a non-interactive fixed-effect term to Model 4, and (2) in Model 6, we added the four-way interaction between time, endemism, temperature and forest cover (i.e. Model 3) to Model 4. AICc values indicated that Model 6 was the best supported of the set, given the data (its model weight was 1, and there was no overlap with AICcs for the next-best model in 1000 replicates). Model 6 had a slightly lower fixed-effects r-squared (0.553) than Model 4 (0.557). The full model r-squared for Model 6 was 0.713 and the same as for Model 4.

We adopted Model 6 as our best model and Figs. 5a and b show the fitted effects of the traits and endemism-level components, respectively. Subplots in Fig. 5a represent the range of combinations of life-history traits in the 23 extant forest bird species, and show that many high-order (5-way and 6-way) interactions are significant (i.e. 95% confidence limits do not overlap zero; Appendix S2), supporting the presentation of such a complex model. Interacting effects of time, forest cover, temperature, and traits fitted by Model 6 were extremely similar to those in Model 4, which excludes endemism and was the best model of Walker et al. (2019b). However, the residual effects of endemism level in Model 6

(i.e. endemism effects after accounting for life-history traits; Appendix S2; Fig. 5b) differed substantially from those fitted in our Model 3 (Fig. 4), which did not include traits.

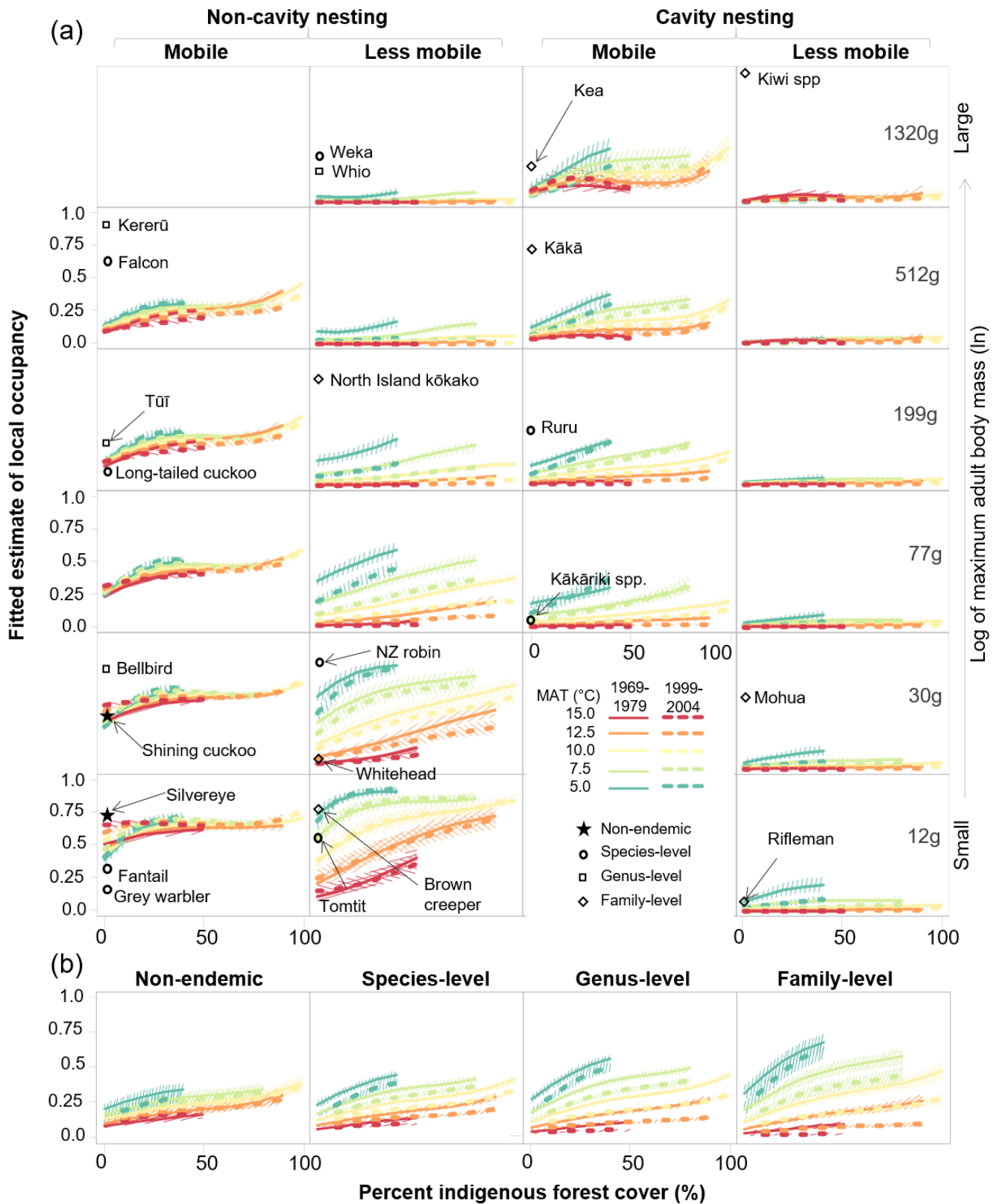
Together, our results suggest that cavity nesting, large body size and limited mobility explain most – but not quite all – of the effects of endemism on modern local occupancy patterns. Notably, the residual effects of endemism level imply that our mechanistic framework may fail to capture subtle endemism-linked life-history attributes and mechanisms that favour, rather than hinder, the persistence of deep endemics, especially in cooler and well-forested environments (Fig. 5b).

### Life-history traits that limit endemic birds, mechanisms, and outcomes

The interactions among traits and environment in our best model (Model 6) show that warmer temperatures and cavity nesting (indicating pressure from and susceptibility to predation, respectively) have strong negative effects on local occupancy. Negative effects of warm temperatures on the local occupancy of endemic forest bird species extended into well-forested environments (Figs. 4, 5). This pattern, and more rapid recent declines in cavity-nesting species in warm forests than in cold forests (third and fourth columns of Fig. 5a), led Walker et al. (2019b) to conclude that greater occupancy declines in endemic forest birds in warmer indigenous forests were caused by higher rates of mammal predation. However, the model also suggests that predation is an insufficient explanation for contemporary patterns of local occupancy in the forest avifauna. Interactions between species' body size and mobility and gradients of temperature and indigenous forest cover (Fig. 5a) indicate that forest and food scarcity could limit some groups of forest bird species more than others even after removing predators. We discuss these indications next.

Here we suggest that if warmth is a reasonable proxy for median predation pressure, species that remain common in colder squares (which have lower average net primary productivity) with little forest (where predators are usually few), but not in warmer squares, will also be robust to forest and food scarcity when mammal predation pressure is low. Model 6 shows that small, less-mobile, facultative and non-cavity-nesting species (tomtit *Petroica macrocephala*, robin *Petroica* spp., whitehead *Mohoua albicilla*, and brown creeper *Mohoua novaeseelandiae*) have persisted better in cool squares than in warm squares, and remain comparatively common in cool places with little forest (lower second column of Fig. 5a). This outcome supports our prediction that small body size will allow relatively large populations with inherently low vulnerability to stochastic local extinctions to persist in small forest patches and other food resource-limited environments. It also suggests that their (assumed) limited dispersal ability (Table 2) has not prevented these species from repopulating or maintaining genetic viability in small or isolated patches of cool indigenous forest where predation pressure is relatively low much of the time. We conclude that tomtit, robin, whitehead, and brown creeper would become common even in landscapes with little forest remaining if predation by introduced mammals were reduced.

Three other groups of species have persisted better in cold forests than in warm forests. However, these groups show distinct decreases in local occupancy as forest cover decreases in cooler squares, indicating a level of dependence on forest cover regardless of predation.



**Figure 5.** Medians and 95% intervals of fitted effects of measurement period (solid 1969–1979 vs 1999–2004 dashed lines), environment, and (a) life history traits, and (b) taxonomic level of endemism on the probability of local occupancy in 23 forest bird taxa (species) in New Zealand’s North and South (including Stewart) Islands, from our best model (Model 6). Percentage indigenous forest cover spans 0 – 100% on the horizontal axes of subplots and median mean annual temperature (MAT) is shown as jade to red coloured lines. In (a), fitted estimates for six levels of adult body mass (on the natural log scale) are shown in different rows of subplots; non-cavity-nesting and cavity-nesting species are shown in the left and right pairs of columns, respectively, and levels of mobility are shown as alternate columns; labelled symbols at the left of each subplot show the taxonomic level of endemism of the contributing forest bird species. The vertical position of each species indicates its maximum adult body mass, and the horizontal column indicates its assignment to mobility and cavity nesting categories. In (b), the four columns show fitted effects on all species within each of the four taxonomic levels of endemism.



The first of the three groups is mobile cavity-nesting forest birds of all body sizes (kea *Nestor notabilis*, kākā *Nestor meridionalis*, ruru *Ninox novaeseelandiae* and kākārīki *Cyanoramphus* spp.; third column of Fig. 5a). Their continued (albeit declining) occupation of colder, forested landscapes where we assume local food resources may be limited is consistent with an ability to forage widely, or to readily re-establish populations following local extirpations. Lower levels of predation would probably lead to increased local occupancy of mobile cavity-nesting species in warm forests, where they are presently scarce or absent, as well as in cool forests. Local occupancy in this group decreased sharply with decreasing indigenous forest cover even in cooler environments. The mechanism leading to a requirement for forest is unknown, and may involve the need for mature forest trees to provide food or nest sites for breeding. Regardless, mobile cavity-nesters may not readily reoccupy landscapes with little remaining forest, except perhaps as seasonally-foraging non-residents (e.g. kea and kākā visiting urban centres in the winter).

Large-bodied, mobile, non-cavity nesting species (represented by kererū *Hemiphaga novaeseelandiae* and kārearea *Falco novaeseelandiae*; upper first column of Fig. 5a) are the second group more likely to occupy cold forests than warm forests. However, compared to large, mobile, cavity-nesting species (represented by kea and kākā), they occupied warm forests more often; occupied cool, well-forested squares less often; and decreased in local occupancy more gradually with decreasing forest cover. This pattern is consistent with food being more limiting, and predation and forest cover less limiting for kererū and kārearea than for the large, mobile, cavity-nesting parrots. We conclude that lower predation levels would probably lead to increases in local occupancy of large, mobile, non-cavity-nesting species in warm forests and in warmer landscapes with moderate forest cover. However, we would expect increases to be more modest in cooler forests and other situations where food resources are more limited.

The third group (small, less-mobile, cavity-nesting species titipounamu/rifleman *Acanthisitta chloris* and mohua *Mohoua ochrocephala*) was effectively absent from warm forests and deforested squares in recent decades and became more strongly confined to the coldest forested squares between our measurement periods (lower fourth column of Fig. 5a). Lower levels of predation could allow populations of these species to gradually expand downslope from present cold-forest thermal refuges to reoccupy adjacent warmer forests. Our model is not informative about whether small, less-mobile cavity nesters can survive in small, isolated forest patches, because their occupancy probabilities were very low even in the coldest sites with little forest. However, small body size is predicted to favour the maintenance of viable populations in small forest patches, some translocated cohorts have survived and increased on small, predator-free islands (rifleman Leech et al. 2007; mohua Miskelly et al. 2017; both species Miskelly & Powlesland 2013), and rifleman has persisted in some very small mainland forested sites (Withers 2013). Under low predation pressure, limited ability to cross non-forest gaps would limit their ability to establish new populations, and to re-establish populations following stochastic local extinctions. Therefore small, less-mobile cavity-nesting species may not reoccupy isolated forest patches without assistance, and could need ongoing intervention to maintain populations in smaller fragments.

Large, less-mobile species (kiwi *Apteryx* spp., whio *Hymenolaimus malacorhynchos*, weka *Gallirallus australis*,

and North Island kōkako *Callaeas wilsoni*) seldom occupied even cool, well-forested squares in 1969–1979 or 1999–2004 (upper second and fourth columns of Fig. 5a). Therefore, neither lower predation rates in cooler sites, nor reduced need to cross non-forest gaps (because of larger and more continuous forest areas), appear to have offset the combined disadvantage of large size and limited mobility. The extreme rarity of large, less-mobile species across all New Zealand environments is consistent with four hypothesised mechanisms of decline and extirpation:

- (1) In larger-bodied species, population densities are inherently lower and more constrained by limited food resources in the cooler, less productive forests, where predator densities are presently lower.
- (2) Limited mobility hinders recolonisation of sites following local extirpation.
- (3) Warmer landscapes with little forest are currently inimical because high predation rates combine with elevated risk of extinction by deterministic and stochastic factors, because small forest fragments support few large-bodied individuals (Brook & Bowman 2005; Fischer & Lindenmayer 2007).
- (4) Warmer, well-forested landscapes are also unoccupied because higher predation rates (and possibly pre-emptive capture of the food resource by omnivorous ship rats and possums, and by introduced herbivores; Innes et al. 2010) prevent persistence of the larger populations that large areas of productive forest could potentially support.

Reduced predation would not mitigate the first and second mechanisms. However, it would moderate extinction risk in warm landscapes with little forest, and alleviate the primary constraint on forest bird populations in large areas of warm forest. Therefore, large, less-mobile species might successfully reoccupy large, warm, predator-free forest tracts, but their increases in cooler forests would be slower. Large, less-mobile species may not maintain viable populations in small forest patches, nor recolonise isolated patches following local extinctions, so translocation and ongoing population management would be needed. However, weka (which has the greatest dispersal capability of this group; Coleman et al. 1983; Riddell & Riddell 2012) may need limited assistance once re-established.

Small, mobile, and facultative or non-cavity-nesting forest bird species have been resistant to forest scarcity and predation. Non-endemic silvereye *Zosterops lateralis* and shining cuckoo *Chrysococcyx lucidus*, species-level endemic grey warbler *Gerygone igata* and fantail *Rhipidura fuliginosa*, and genus-level endemic bellbird *Anthornis melanura* were the species most likely to occupy New Zealand's warm and now largely deforested landscapes, as well as warmer forests, in 1999–2004 (lower left subplots of Fig. 5a). This was the only group of species to increase in local occupancy in warmer, largely deforested and forested environments between 1969–1979 and 1999–2004, and to occupy warmer environments more consistently than the cooler environments where we expect fewer predators.

Lower temperatures had a modest impact on the local occupancy of smaller mobile non-cavity-nesters, consistent with our prediction that small-bodied species would not be especially sensitive to scarcity of food. And, rather than a result of food scarcity itself, the negative effect of cold may be an outcome of competition (for food or other resources) with the less-mobile, small, non-cavity-nesting species that are more likely to be present in cooler sites (Fig. 5). If so, we would predict the outcome we are starting to see in practice (Miskelly

2018; Fea et al. 2020) of reduced predation pressure leading to lower indices of abundance in species such as silvereye, grey warbler and fantail, concurrent with increases in less-mobile tomtit, robin, whitehead or brown creeper.

## Residual effects of endemism level, and possible mechanisms

The significant interacting effects of endemism level, forest cover, and temperature in our best model indicate that, all else being equal, deep endemic species (right hand subplot of Fig. 5b) have an advantage over less deeply endemic species (subplots to the left of Fig. 5b) in cooler environments. The fitted effects show that deep endemics are more likely to occupy cooler forests, and are less sensitive to scarcity of forest cover where temperatures are lower. Our hypotheses did not anticipate these effects, and we suggest two non-exclusive causes without (as yet) mechanistic explanations:

(1) More deeply endemic species are better adapted to cold and to dense forests, and are therefore superior competitors for resources in cool, densely forested environments. Consequently, less deeply endemic species are unlikely to penetrate colder environments and deep forests in the absence (or with a low abundance) of predatory mammals.

(2) Endemism level is a proxy for aspects of the evolutionary loss of defences against mammal predation not represented by the obligate cavity-nesting trait, and more deeply endemic species are superior competitors where mammal predation pressure is low. The consequence would be that reduced mammal predation will favour recovery of more deeply endemic species generally over those in lineages that arrived more recently in evolutionary time.

## Implications for conservation

The implications of our results for conservation can be presented as three predictions:

### Recovery potential in deforested landscapes is limited

Forest scarcity will limit the population recovery of some, but not all, forest birds. Our results caution that regardless of predator densities, largely deforested production and urban landscapes may not readily support populations of larger, less-mobile endemic species, or breeding populations of most mobile cavity-nesting species.

Some larger, less-mobile and highly predator-vulnerable species (kiwi, North Island kōkako, tīeke *Philesturnus* spp.) currently depend for their persistence on intensive predator and population management in small (< 2000 ha) patches of warm, mainland forest and on islands. Innes et al. (2010) point out that some populations have been sustained in small forest patches for at least some decades (e.g. little spotted kiwi *Apteryx owenii*, tīeke). Nevertheless, inherently small population sizes and limited ability to disperse mean this group of species is the most likely to need active management to top up small isolated sites and maintain genetic variation even in a predator-free landscape. Mobile cavity-nesting species are also unlikely to establish breeding populations in places with little forest (and, as discussed above, we do not yet fully understand why).

A more encouraging inference from our results is that

smaller, less-mobile endemic species may be quite capable of persisting in relatively small and isolated forest patches, if they can reach those patches initially (e.g. through translocation). Furthermore, as the contribution of predation to local population extinctions diminishes, limited ability to recolonise sites should become a less influential constraint on persistence.

### Warm forests: opportunity and challenge

Because forest scarcity is disadvantageous to most endemic forest birds regardless of predation, restoration of populations is likely to be more successful in large tracts of forest. However, all large forest tracts are not equal, either for bird species or for conservation management. Cooler forests have become the main refuges of endemic forest bird species today (Walker et al. 2019b). However, they are likely to be intrinsically suboptimal environments, especially for larger-bodied species, which require more food to maintain sizeable populations and are less capable of travelling distances to obtain it.

Warmer, more productive forests offer the best prospects for recovery of populations of most endemic bird species, but it is much more challenging to maintain low densities of bird predators at scale in warm forests than in cooler, beech-dominated forests (Brown et al. 2015; Elliott & Kemp 2016). Large remaining areas of warm forest still present substantial technical barriers to effective, landscape-scale predator management, which would need to be overcome to realise this outcome. Our results suggest that food resource productivity is important for larger avian species, and therefore potentially socially contentious control of introduced herbivores (e.g. deer, goats), as well as omnivores (e.g. pigs, possums, ship rats), may be needed to assist population recoveries (Innes et al. 2010).

### Community reassignment

Reduced predation pressure may result in avian community reassignment rather than increases in all species (Innes et al. 2010). The warmest and floristically richest forests are likely to show the greatest and most rapid increases in local forest bird richness, especially in more deeply endemic, larger, less mobile or cavity-nesting species. Cooler forests are likely to undergo similar but more subtle shifts, because they retain more endemic species now, and because lower food resource productivity will constrain population increases in less mobile, larger-bodied species. Testing this prediction will require analyses of bird outcomes of management across environmental gradients.

The rise to dominance of non-endemic and less deeply endemic small, mobile, non-cavity-nesting species (illustrated by our results) may be reversed in landscapes with less forest as small, less-mobile species that appear less dependent on high levels of forest cover (tomtit, robin, brown creeper) are released from predation pressure. Growing numbers of studies record displacement of silvereye, grey warbler and fantail by less-mobile and/or more deeply endemic species on islands and in fenced sanctuaries where predator densities have been maintained at low levels (Miskelly & Robertson 2002; Miskelly 2018; Fea et al. 2020; Binny et al. 2020). Our model shows reciprocal trends in the local occupancy of small insectivorous species along national temperature gradients, consistent with less-mobile tomtit and robin being competitively superior to more-mobile silvereye, grey warbler and fantail under conditions of low predation pressure.

The residual effects of endemism level in our model suggest, further, that deeper endemic forest birds generally (and not only small endemic non-cavity nesters) may be competitively superior to those that are evolutionarily more recent where

predators are few. If this interpretation of our model is correct, competitive interactions following suppression of mammalian predators would lead to greater dominance of endemic species. Results of two recent meta-analyses of forest bird outcomes of management are consistent with these predictions: Binny et al. (2020) showed that deeply endemic birds showed the greatest benefits from release from predation in ecosanctuaries compared with less deeply endemic or introduced species; and Fea et al. (2020) showed that deep endemic species, and (more tentatively) cavity-nesters, benefitted most from both low and high intensities of mammal control.

## Conclusions

Changes in local occupancy in New Zealand's forest avifauna between 1969–1979 and 1999–2004s were spatially and biologically predictable. More deeply endemic species continued to decline in their remaining forests, while species in lineages that arrived most recently in New Zealand expanded their ranges, especially in warmer environments with little forest. Local occupancy declines were greater in species with one or more of three endemism-linked life-history traits: obligate cavity nesting, large size and/or limited mobility. Range expansions were greatest in small, relatively mobile species that do not nest in cavities.

Our combination of intrinsic species' traits and extrinsic factors reconciles the understanding that predation by introduced mammals is the primary cause of forest bird declines and limitation (Innes et al. 2010), with Diamond's (1984) conclusion that the future of New Zealand's endemic forest birds hinges on preserving large tracts of native forest. Three life-history traits and two geographical variables (representing three extrinsic factors) together provide a coherent explanation for why more deeply endemic extant bird species are more vulnerable (McDowall 1969) to both deforestation and predation, and a mechanistic basis for predicting the future of different forest bird species with the suppression of introduced mammalian predators in different landscapes. Other traits and mechanisms associated with deep endemism are not captured by the framework, and these may favour deep endemics over evolutionarily recent arrivals under reduced pressure from mammalian predators.

Three predictions emerge about the outcomes for native forest birds of the suppression of mammalian predators:

- (1) The deep-endemic forest avifauna will be most successfully restored in large tracts of warm forest; that is, in the remaining mid to low-elevation tracts of podocarp broadleaved and mixed beech forests of the North Island and the northwestern South Island.
- (2) Local scarcity of either forest or food will limit the recovery of larger-bodied, less-mobile species and mobile cavity nesters, even where predators are successfully suppressed.
- (3) Interspecific competition will lead to a reassortment of avian forest bird communities, with deeper endemic species replacing those in more recently-arrived lineages that have become common in warm and deforested landscapes since human settlement.

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## Author contributions

SW: conceptualisation, methodology, formal analysis, data curation, writing – original draft, review and editing, visualisation. AM: methodology, formal analysis, writing – original draft, review and editing. JI: writing – original draft, review & editing.

## Data availability

All data are held in and available from the permanent data storage repository of Manaaki Whenua – Landcare Research (<https://datastore.landcareresearch.co.nz/>)

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## Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

**Appendix S1.** Median parameter estimates and 95% confidence limits from our Model 3 of probabilities of occupancy in 23 native forest bird taxa (species) in 2155 squares of 10 × 10 km across New Zealand.

**Appendix S2.** Median parameter estimates and 95% confidence limits from our Model 6 of probabilities of occupancy in 23 native forest bird taxa (species) in 2155 squares of 10 × 10 km across New Zealand.

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