National changes in occupancy of New Zealand-breeding Charadriiformes, 1969–1979 to 1999–2004

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Abstract: We analysed standardised estimates of local occupancy probability of 13 species of native wading birds, terns and gulls (order Charadriiformes) derived from the New Zealand Ornithological Society's national *Atlas of Bird Distribution* collated in 1969–1979 and 1999–2004. We show systematic patterns in changes with taxonomic level of endemism, breeding habitat (coastal or inland), and location (distance from the coast, road density, and degree of land development for agriculture and forestry). The main changes were decreases in endemic inland breeding species within their inland South Island breeding ranges, and increases in most coastal-breeding species and some inland-breeding species around much of the coast, especially near urban centres in the North Island. Our results are consistent with both intensive land use and predation contributing to widespread declines of inland-breeding species across inland South Island. Potential causes of occupancy changes around the coast are less clear, and we offer some suggestions.

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INTRODUCTION

Birds in the order Charadriiformes that breed in New Zealand are important and highly visible components of the New Zealand avifauna. A number of species are listed as threatened or at risk (Robertson *et al.* 2017; Table 1). The group includes terns and gulls (family Laridae) and waders (or 'shorebirds'; suborder Charadrii).

Some species breed mainly or only on the coast, including the endemic New Zealand dotterel (*Charadrius obscurus*) and variable oystercatcher (*Haematopus unicolor*), and the non-endemic native species New Zealand fairy tern (*Sternula nereis*), Caspian tern (*Hydroprogne caspia*), white-fronted tern (*Sterna striata*), red-billed gull (*Larus novaehollandiae*), and southern black-backed gull (*L. dominicanus*).

Table 1. New Zealand breeding Charadriiforme taxa, showing highest taxonomic level of endemism (denoted G = genus level, S = species level), family, common name, main breeding location (coastal or inland), threat status in 2016, estimated population (Popn.) size and trend from the New Zealand Threat Classification System (NZTCS) (Robertson *et al.* 2017). Asterisks denote three species that were too rare in one or both atlases of bird distribution to fit occupancy models for, and they were therefore not included in our analyses.

Species name	Family	Common name	Breeding	Status 2016	Popn. size	Popn. trend
Anarhynchus frontalis (G)	Charadriidae	Wrybill ngutu-pare	Inland	Nationally Vulnerable	1,000–5,000	STABLE +/-10%
Charadrius bicinctus bicinctus (S)	Charadriidae	Banded dotterel tūturiwhatu	Inland	Nationally Vulnerable	5,000–20,000	DEC 30–70%
Charadrius obscurus aquilonius (S)	Charadriidae	Northern New Zealand dotterel	Coastal	Recovering	1,000–5,000	INC >10%
Charadrius obscurus obscurus (S)	Charadriidae	Southern NZ dotterel tūturiwhatu	Coastal	Nationally Critical	<250	DEC >70%
*Elseyornis melanops	Charadriidae	Black-fronted dotterel	Coastal	Naturally Uncommon	1,000–5,000	INC >10%
*Thinornis novaeseelandiae (S)	Charadriidae	New Zealand shore plover tuturuatu,	Coastal	Nationally Critical	<250	STABLE +/-10%
Haematopus finschi (S)	Haematopodidae	South Island pied oystercatcher tōrea	Inland	Declining	20,000–100,000	DEC 10–50%
Haematopus unicolor (S)	Haematopodidae	Variable oystercatcher tōrea pango	Coastal	Recovering	1,000–5,000	INC >10%
Larus bulleri (S)	Laridae	Black-billed gull tarapuka	Inland	Nationally Critical	20,000–100,000	DEC >70%
Larus dominicanus dominicanus	Laridae	Southern black-backed gull karoro	Coastal	Not Threatened	>100,000	STABLE +/-10%
Larus novaehollandiae scopulinus	Laridae	Red-billed gull	Coastal	Declining	20,000–100,000	DEC 10–50%
Himantopus himantopus leucocephalus	Recurvirostridae	Australasian pied stilt poaka	Inland	Not Threatened	20,000–100,000	STABLE +/-10%
Himantopus novaezelandiae (S)	Recurvirostridae	Black stilt kakī	Inland	Nationally Critical	<250	STABLE +/-10%
Chlidonias albostriatus (S)	Sternidae	Black-fronted tern tarapirohe	Inland	Nationally Endangered	1,000–5,000	DEC 50–70%
Hydroprogne caspia	Sternidae	Caspian tern taranui	Coastal	Nationally Vulnerable	1,000–5,000	DEC 10–50%
Sterna striata	Sternidae	White-fronted tern tara	Coastal	Declining	20,000–100,000	DEC 10–50%
*Sternula nereis davisae	Sternidae	New Zealand fairy tern tara iti	Coastal	Nationally Critical	<250	STABLE +/-10%

Other species breed mainly in the inland South Island, and of these only the pied stilt (*Himantopus himantopus*) is non-endemic. Wrybill (*Anarhynchus frontalis*, endemic at the genus level) and five species-level endemics (kakī/black stilt *Himantopus novaezelandiae*, black-billed gull *Larus bulleri*, black-fronted tern *Chlidonias albostriatus*, banded dotterel *Charadrius bicinctus*, and South Island pied oystercatcher *Haematopus finschi*) breed mainly on sparsely vegetated inland braided riverbeds and outwash terraces, which formed in the Pleistocene. Some populations of a few inland breeding species remain and overwinter inland (Sagar & Geddes 1999; Sagar *et al.* 1999), but others migrate to feed in coastal habitats around New Zealand, and, in the case of some banded dotterel, on the coast of south eastern Australia (Pierce 1999).

There is considerable variation in the information available on trends in New Zealand's Charadriiformes. Waders have long been of particular interest to ornithologists, and there are long-term data from biannual counts at estuaries (Sagar *et al.* 1999). Some rarer taxa, such as northern and southern New Zealand dotterel (Dowding & Davis 2007); New Zealand fairy tern (Hansen 2006); and kakī/black stilt (Maloney & Murray 2001), are comparatively well studied and have had formal population recovery plans developed. In addition, there are estimates of long-term population changes for black-fronted tern (O'Donnell & Hoare 2011) and black-billed gull (McClellan 2009; Mischler 2018) on braided rivers, and for red-billed gull (Frost & Taylor 2018) on New Zealand coasts. These, and long-term counts of waders, terns and gulls on braided rivers (Spurr & Ledgard 2016; DOC, *unpubl. data*), have been used to inform revisions of the New Zealand Threat Classification System (NZTCS) rankings. However, spatial information that can assist in identifying national distribution and population changes in most species is scarce.

Two atlases of bird distribution compiled by the Ornithological Society of New Zealand (Bull *et al.* 1985; Robertson *et al.* 2007) are the only data sets that have recorded the spatial distributions of bird species across the whole nation. Field surveys for the atlases were undertaken from September 1969 to December 1979, and from December 1999 to November 2004, so these data potentially provide a spatially explicit, nationally comprehensive, multi-species, multi-decade (25-year) view of status and trends. However, two aspects of the data have complicated comparisons between the measurement periods: the different spatial systems and locations of the sampling units in the atlases (imperial versus metric grid squares), and differences in the level of detection effort applied across the nation between and within the two different surveys. We have recently addressed these complications and created a standardised set of data for native species from the two atlases that allows robust comparisons of their probabilities of occupancy in 2,155 10 × 10 km grid squares across New Zealand over the 25-year interval (Walker & Monks 2017, 2018).

In this paper we use these standardised data to summarise, analyse and interpret spatial changes in the local (square-wise) probabilities of occupancy ('local occupancy') of the 13 species of New Zealand-breeding waders, terns and gulls for which we were able to derive national estimates. We use a mixed-effects modelling approach to look for systematic patterns in their changes over time in relation to taxonomic level of endemism, breeding habitat (coastal and inland), location (island and distance from the coast), and degree of human influence (road density, agricultural and forestry conversion, and urbanisation), while accounting for taxonomic relatedness among species and repeated observations at the same location.

Taxonomic level of endemism is a strong indicator of long evolutionary history in New Zealand, and of avian extinction and endangerment (McDowall 1969; Duncan & Blackburn 2004). Endemic species often have behaviours that make them susceptible to novel predators, and they may have lost traits that enable adaptation to the environments and changes associated with human settlement through their insular evolutionary history. Therefore, our first expectation was that endemic species would be less likely than non-endemic species to show a positive trend between measurement periods (a negative interaction between measurement period and level of endemism).

New Zealand's coastline provides roost and nest sites that may be less accessible (e.g. offshore and on cliffs) to bird predators than the open riverbed and outwash plain breeding habitats of the inland South Island. We therefore predicted that changes in local occupancy between 1969–1979 and 1999–2004 would differ between species that breed on the coast and those breeding inland (a positive interaction between measurement period and coastal-breeding), and between the inland and coastal habitats of species (a negative interaction between measurement period, endemism, and distance from the coast, given that we expect greater susceptibility to predation in species with higher levels of endemism and in more accessible breeding habitats).

Modification and development of habitats such as estuaries, beaches and inland outwash plains, and greater disturbance of breeding, feeding and roosting habitats, could have negative effects on some species (e.g. some waders and braided river birds; Sagar *et al.* 1999). However, human habitation may have had positive effects on other species. For example, non-endemic species such

as southern black-backed gull are associated with features such as wharves and rubbish tips (Heather & Robertson 1996), and Sagar *et al.* (1999) reported a 'remarkable' increase in the number of South Island pied oystercatchers counted in winter around the highly developed Manukau Harbour and the Firth of Thames between 1983 and 1994. Breeding success near human habitation may in some cases be assisted by predator control or eradication (e.g. New Zealand dotterel; Neate *et al.* 2011; Ogden & Dowding 2013). If human persecution has reduced in recent decades, the recovery of persecuted species (e.g. variable oystercatcher; Baker 1973) may also be associated with areas of human settlement. Overall, we expected that the effects of human settlement on species populations could be either positive or negative, depending on the characteristics and history of the species.

We hypothesised that intensive land development has had an adverse effect on the local occupancy of species that breed mainly inland in the South Island. Populations of inland-breeding species are threatened by a very wide suite of mammalian and avian predators on their breeding grounds; however, their breeding habitats have also undergone considerable loss and modification in recent decades through intensive agricultural development, afforestation, modification of flow regimes for irrigation and electricity generation, and the spread of woody weeds (Weeks *et al.* 2013; Cruz et al. 2013; Grove et al. 2015; O'Donnell et al. 2016; Peat et al. 2016). These changes may be important drivers of declines. For example, Miskelly *et al.* (2008) commented that for South Island pied oystercatcher, Australasian pied stilt, banded dotterel, and black-billed gull, '[t]he main causes for deterioration in conservation status were thought to be changes in land-use, particularly conversion of sheep farming to dairy farming'. If land development has adverse effects, we would expect decreases in occupancy to have been greater in places with more intensive agricultural development.

We use two sets of models to test these expectations. We first fitted models of the local occupancy of the thirteen most common bird species together. We used an index of road density to represent human transformation of the landscape generally, and determined how its effects interacted with time (between measurement periods), endemism level, breeding group (mainly coastal- or mainly inland-breeding), and geographic location (distance from the coast). We then analysed the local occupancy of the seven species that breed mainly inland in the South Island, examining the influence of two different and independent human transformation effects (agricultural or forestry development, and urbanisation).

METHODS

Data

Occupancy estimates for taxa

We derived standardised estimates of local probabilities of occupancy ('local occupancy') across New Zealand for extant native Charadriiform taxa that were present at human settlement and still occur and breed on New Zealand's three main islands (Table 1). Estimates were made for each of 2,155 10 × 10 km grid squares, in two measurement periods (1969–1979 and 1999–2004), from data in two national atlases of bird distribution compiled by the Ornithological Society of New Zealand (Bull *et al.* 1985; Robertson *et al.* 2007). The methods for estimating local occupancy allowed probability of detection to vary seasonally by including season (spring, summer, autumn, or winter) as a covariate, and are fully described by Walker and Monks (2019).

We were unable to derive local occupancy estimates for three taxa of interest because of their extreme rarity. These taxa were non-endemic New Zealand fairy tern, the endemic reintroduced shore plover (*Thinornis novaeseelandiae*), and the recently self-introduced black-fronted dotterel (*Elseyornis melanops*). We did not consider the recently self-introduced spur-winged plover (*Vanellus miles*, a lapwing in the subfamily Vanellinae, first recorded breeding in 1932; Heather & Robertson 1996) in this study because it occupies general open-country habitats and has a life history distinct from other native species. We recognised three taxonomic levels of endemism (non-endemic native, species-level endemic, and genus-level endemic) and used these as a proxy for the length of time that a species has been isolated in New Zealand. Taxa were classified as mainly coastal-breeding or mainly inland-breeding based on distributions in early spring (Table 1).

Geographic coverage and predictor variables

Our national grid (Fig. 1) omits all 10 × 10 km grid squares not sampled in one or both atlases, and excludes all squares covering more than 75% water (coasts and large inland lakes). Each square was assigned to either 'North Island' or 'South Island'. Near-shore 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. The islands differ in their taxa, environments and settlement histories, and are analysed separately.
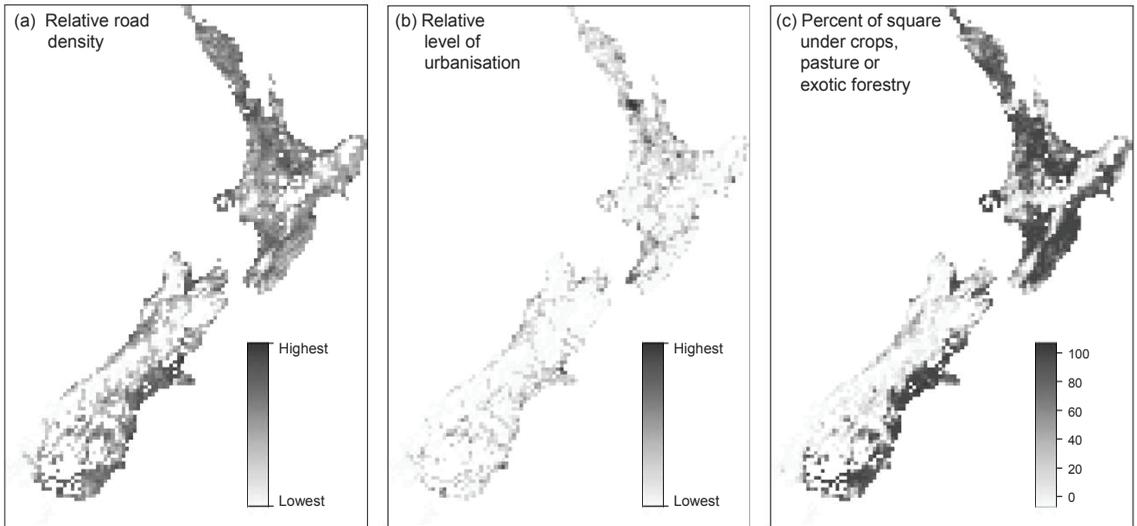
Figure 1. Distribution across New Zealand of (a) relative road density, (b) relative level of urbanisation, and (c) percent of square under crops, pasture or exotic forestry.

Using publicly available GIS surfaces, we calculated for each grid square: i) road density (the square root of the length of road centrelines[1] per unit land area in km/km[2]); ii) distance from the coast (the shortest distance from the square centre to the coastline[2]); iii) degree of conversion to crop, pasture, or exotic forestry plantation (CPEF; the percentage of land in Land Cover Database [LCDB] classes 'Short-rotation Cropland', 'Orchard Vineyard & Other Perennial Crops', 'High Producing Exotic Grassland', 'Exotic Forest' or 'Forest – Harvested' in summer 2001/02; LCRIT 2015); iv) urbanisation (the percentage of land covered by LCDB classes 'Urban parkland / open space' and 'Built-up area [settlement]') (Fig. 1). Continuous variables were transformed so that they spanned similar scales and centred on zero. Coefficients of correlation showed that road density and CPEF were correlated (r = 0.69 and 0.84 on the North and South Islands, respectively), so these were not used together as model predictors. Correlations between road density, distance from the coast, and urbanisation were relatively weak ($r < 0.4$).

[1] https://data.linz.govt.nz/layer/50329-nz-road-centrelines-topo-150k/ Accessed: 1 June 2016

[2] https://data.linz.govt.nz/layer/258-nz-coastlines-topo-150k/ Accessed: 1 June 2016

Analyses

Descriptive statistics

Range contraction is an important signal of likely population decline (Caughley & Gunn 1996). Average local occupancy across squares provides an estimate of the proportion of the available geographical range occupied by bird species, and differences in those averages between measurement periods are estimates of net geographical range changes. We calculated the average and 95% confidence limits of occupancy of each species across its coastal and inland ranges on each island by drawing 1,000 samples from the posterior distributions of our estimates of local occupancy in each time period. For this purpose, coastal and inland squares were defined simply as those with centre distances less than and greater than the mean distance to the coast across all squares (*c.* 33 km), respectively. We also mapped average local occupancy across the six mainly coastal-breeding and seven mainly inland-breeding species of Charadriiformes for which we had estimates on each island.

Mixed-effects models

Local occupancy of 13 native wading bird, tern or gull species (Table 1) were analysed in *all-species models* fitted for each island. Logit-transformed occupancy probability was fitted as a linear function of the interaction between measurement period, endemism (as a two-level factor: non-endemic native or endemic), breeding habitat (predominantly coastal or inland breeding), road

Table 2. Average and upper and lower 95% confidence limits of local occupancy estimates (expressed as percentages) for the 13 native taxa in our analyses (listed by common names, with italics indicating mainly inland-breeding taxa). The table shows data for (a) all 2,155 10 × 10 km grid squares; (b) coastal squares (all those with centre distance from the coast less than the mean of 33 km); and (c) inland squares (with centre distance from the coast greater than the mean) on each island (North, South) and in each measurement period (Atlas 1 1969–1979, Atlas 2 1999–2004).

	NORTH ISLAND		SOUTH ISLAND	
	Atlas 1	**Atlas 2**	**Atlas 1**	**Atlas 2**
(a) ALL SQUARES				
Caspian tern	13.6 [12.1, 15.2]	17.1 [16.3, 17.9]	5.8 [5, 6.6]	8.5 [7.8, 9.2]
New Zealand dotterel (S)	4.1 [3.2, 5.8]	3.9 [3.5, 4.3]	0.3 [0.2, 0.5]	0.5 [0.3, 0.6]
Variable oystercatcher (S)	9.0 [8.1, 9.9]	15.1 [14.4, 15.7]	9.1 [8.2, 9.9]	12.0 [11.3, 12.7]
White-fronted tern	13.3 [12, 14.7]	15.0 [14.1, 16.0]	11.2 [10, 12.5]	12.2 [11.3, 13.1]
Red-billed gull	21.0 [19.9, 22.2]	23.6 [22.8, 24.4]	12.3 [11.4, 13.2]	14.9 [14.1, 15.7]
Southern black-backed gull	41.8 [40.7, 42.9]	46.5 [45.6, 47.5]	60.0 [58.8, 61.2]	60.2 [58.9, 61.4]
Black-billed gull (S)	2.6 [2.3, 2.9]	4.6 [4.2, 5.1]	21.9 [21.0, 22.9]	17.0 [15.9, 18.4]
Black stilt (S)	0.1 [0.1, 0.2]	0.2 [0.1, 0.3]	1.2 [0.9, 1.7]	1.3 [1.1, 1.5]
Black-fronted tern (S)	0.3 [0.2, 0.5]	0.3 [0.2, 0.5]	15.2 [14.2, 16.5]	16.8 [15.1, 18.7]
Wrybill (G)	1.5 [1.2, 1.7]	1.6 [1.4, 1.9]	1.8 [1.5, 2.1]	1.7 [1.4, 2.1]
Banded dotterel (S)	5.9 [5.4, 6.5]	6.4 [5.8, 7.1]	16.4 [15.5, 17.3]	12.8 [11.7, 13.9]
SI pied oystercatcher (S)	4.0 [3.5, 4.5]	9.5 [9.0, 9.9]	35.3 [33.1, 38.6]	32.9 [31.6, 34.1]
Australasian pied stilt	25.0 [24.1, 26]	27.6 [26.7, 28.5]	18.7 [17.9, 19.6]	17.4 [16.6, 18.3]
(b) COASTAL SQUARES				
Caspian tern	17.2 [15.3, 19.2]	23.0 [22.1, 24.0]	7.4 [6.4, 8.4]	10.9 [10.1, 11.7]
New Zealand dotterel (S)	5.3 [4.1, 7.6]	5.1 [4.7, 5.5]	0.5 [0.3, 0.7]	0.5 [0.3, 0.7]
Variable oystercatcher (S)	11.9 [10.9, 13.0]	21.7 [20.8, 22.6]	13.7 [12.4, 14.9]	19.6 [18.6, 20.6]
White-fronted tern	17.0 [15.3, 18.6]	20.5 [19.3, 21.8]	16.4 [14.8, 18.0]	18.7 [17.5, 20.0]
Red-billed gull	28.5 [27.1, 30.1]	33.8 [32.9, 34.8]	18.6 [17.5, 19.8]	23.7 [22.7, 24.7]
Southern black-backed gull	48.0 [46.9, 49.1]	54.4 [53.5, 55.5]	60.8 [59.5, 62.1]	64.5 [63.2, 65.8]
Black-billed gull (S)	2.7 [2.4, 3.1]	5.5 [5.0, 6.0]	20.5 [19.4, 21.6]	17.7 [16.5, 19.1]
Black stilt (S)	0.2 [0.1, 0.3]	0.2 [0.1, 0.3]	0.6 [0.4, 0.8]	0.7 [0.5, 1.0]
Black-fronted tern (S)	0.4 [0.3, 0.5]	0.4 [0.3, 0.5]	9.7 [8.8, 10.7]	14.0 [12.6, 15.6]
Wrybill (G)	1.8 [1.5, 2.1]	2.1 [1.8, 2.3]	1.2 [1.0, 1.5]	1.7 [1.4, 2.0]
Banded dotterel (S)	6.7 [6.2, 7.3]	8.0 [7.3, 8.8]	13.7 [12.7, 14.7]	12.4 [11.3, 13.5]
SI pied oystercatcher (S)	5.0 [4.5, 5.7]	13.0 [12.5, 13.6]	30.8 [28.7, 33.6]	33.1 [31.7, 34.5]
Australasian pied stilt	27.8 [26.8, 28.9]	32.7 [31.8, 33.7]	18.0 [17.2, 19.0]	19.5 [18.6, 20.5]
(c) INLAND SQUARES				
Caspian tern	7.2 [6.0, 8.6]	6.7 [5.8, 7.8]	3.9 [3.2, 4.8]	5.7 [4.8, 6.5]
New Zealand dotterel (S)	2.0 [1.3, 3.1]	1.8 [1.2, 2.4]	0.2 [0.1, 0.4]	0.4 [0.2, 0.6]
Variable oystercatcher (S)	3.9 [3.0, 4.8]	3.6 [2.7, 4.5]	3.8 [3.0, 4.7]	3.5 [2.8, 4.4]
White-fronted tern	7.0 [5.6, 8.4]	5.6 [4.4, 6.8]	5.4 [4.4, 6.5]	4.8 [3.7, 5.9]
Red-billed gull	8.2 [7.0, 9.5]	5.9 [4.9, 7.0]	5.1 [4.2, 6.1]	5.0 [4.1, 6.0]
Southern black-backed gull	31.2 [29.6, 32.9]	32.9 [31.4, 34.6]	59.0 [57.6, 60.5]	55.4 [53.7, 57.2]
Black-billed gull (S)	2.3 [1.9, 2.7]	3.1 [2.6, 3.7]	23.7 [22.4, 25]	16.2 [14.9, 17.7]
Black stilt (S)	0.1 [0.0, 0.2]	0.2 [0.1, 0.3]	1.9 [1.5, 2.7]	1.9 [1.6, 2.3]
Black-fronted tern (S)	0.3 [0.1, 0.4]	0.3 [0.1, 0.4]	21.4 [19.9, 23.2]	19.9 [17.5, 22.6]
Wrybill (G)	0.9 [0.7, 1.3]	0.9 [0.6, 1.3]	2.3 [1.9, 2.8]	1.7 [1.3, 2.2]
Banded dotterel (S)	4.4 [3.8, 5.1]	3.6 [3.0, 4.4]	19.5 [18.3, 20.8]	13.2 [11.8, 14.7]
SI pied oystercatcher (S)	2.2 [1.6, 2.7]	3.4 [2.6, 4.1]	40.5 [38.0, 44.1]	32.6 [30.9, 34.1]
Australasian pied stilt	20.1 [18.8, 21.5]	18.6 [17.3, 19.8]	19.5 [18.4, 20.5]	15.1 [13.9, 16.3]

density, and distance from the coast (fixed effects). Each model included taxon and unique grid square as random effects to address the non-independence of repeated measures on the same taxon and in the same location, respectively.

Our second model set (*inland-breeding species models)* was fitted to test our prediction that local occupancy of mainly inland breeding species had been adversely affected by intensive land development (rather than by density of human occupation more generally, as indicated by road density). We analysed patterns in (logit-transformed) local occupancy of the seven species of inland-breeding native wading bird, tern and gull species only, on each island. Fixed effects were measurement period, endemism level (three levels: non-endemic native, species-level endemic, genus-level endemic), percentage of land developed for agriculture and forestry, and distance from the coast, and their interactions. A fixed effect term for the two-way interaction between measurement period and urbanisation was also included, to determine whether observed increases in counts of inland breeding species in harbours near major centres of urbanisation (Sagar *et al.* 1999) were corroborated by local occupancy data.

We used maximum-likelihood estimation with function lmer in the lme4 library (Bates *et al.* 2015) for R (R Development Core Team 2017) to fit our models, and the effects library for R (Fox & Hong 2009) to estimate fixed effects. Each model for each island was fitted 1,000 times, with each repetition using a different sample from the posterior distribution of logit-transformed local occupancy probability for each species. The median and confidence limits of parameter estimates, and fitted fixed effects were estimated across the 1,000 models. We considered that there is support for an effect (i.e. it is statistically 'significant') when the 95% confidence intervals of parameter estimates exclude zero. Fitted effects were back-transformed to proportions and plotted.

We also fitted exploratory models, which included a conditional spatial autoregression (CAR) term as a random effect to account for correlation between neighbouring squares. Many of these models failed to converge (an indication that the data do not fit the CAR model well). In those that did converge, the spatial term did not materially alter parameter estimates for fixed effects compared to models fitted without the CAR term. Our approach therefore ignores spatial autocorrelation.

RESULTS

Descriptive statistics

Most coastal-breeding taxa occupied higher proportions of squares in the North Island than in the South Island, especially in squares nearer the coast (i.e. centres <33 km from the nearest coastline; Table 2a, b). The exception in this group was southern black-backed gull, which was more common in the South Island. The ranges occupied by Caspian tern, variable oystercatcher, white-fronted tern, red-billed gull, and southern black-backed gull increased significantly (i.e. estimate confidence limits do not overlap) between measurement periods near the coast (Table 2b). Variable oystercatcher showed the largest coastal increase among coastal breeders (9.8% in the North Island, 5.9% in the South), followed by southern black-backed gull (6.4%, 3.7%), Caspian tern (5.8%, 3.5%), and red-billed gull (5.3%, 5.1%).

Five of the seven mainly inland-breeding species occupied larger ranges in the South Island than in the North Island and were most commonly recorded in 'inland' South Island (i.e. square centres >33 km from the coast; Table 2a, c). The two exceptions were wrybill, which occurred in about 2% of coastal squares in the North Island (over-wintering range) and inland South Island (breeding range) squares in both measurement periods, and Australasian pied stilt, which occurred most commonly on the coast of the North Island. Local occupancy of five inland-breeding species (black-billed gull, black-fronted tern, banded dotterel, South Island pied oystercatcher and Australasian pied stilt) decreased significantly across the inland squares in the South Island that are their principal breeding habitat (Table 2c). The local occupancy of black-billed gull also decreased significantly on the South Island's coast (Table 2b).

Some inland-breeding species increased in range across squares near the coast. Black-billed gull, banded dotterel, South Island pied oystercatcher and Australasian pied stilt increased significantly around the North Island coast, and black fronted tern was more likely to occupy South Island coastal squares in the second measurement period (Table 2b).

Maps of average square-wise local occupancy of coastal-breeding species in the two measurement periods show net increases in squares around most of New Zealand's coastline between 1969–1979 and 1999–2004 (Fig. 2a). These increases were generally larger in the North Island, and were not evident on the west coast of the South Island. Average local occupancy across inland-breeding species also increased on some parts of the coast (Fig. 2b), but decreased across much of the inland southern South Island (i.e. the Canterbury Plains, Central Otago and Southland). Areas of moderately high average local occupancy of inland-breeding species were widespread across the southern interior South Island in 1969–1979 (Fig. 2b). By 1999–2004, such areas had become more geographically confined and more centred on the upper Waitaki (Mackenzie) basin, as a consequence of the inland range declines of multiple species (Table 2c).

(a) COASTAL-BREEDING (*n* = 6)

1969–1979   1999–2004
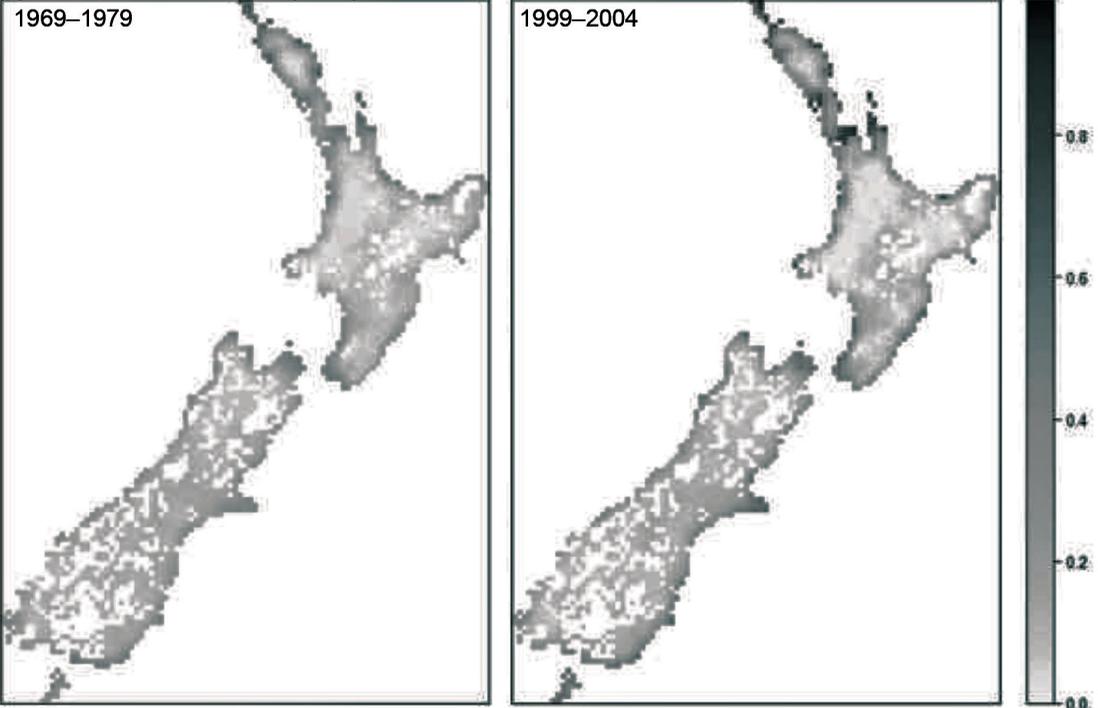
(b) INLAND-BREEDING (*n* = 7)

1969–1979   1999–2004
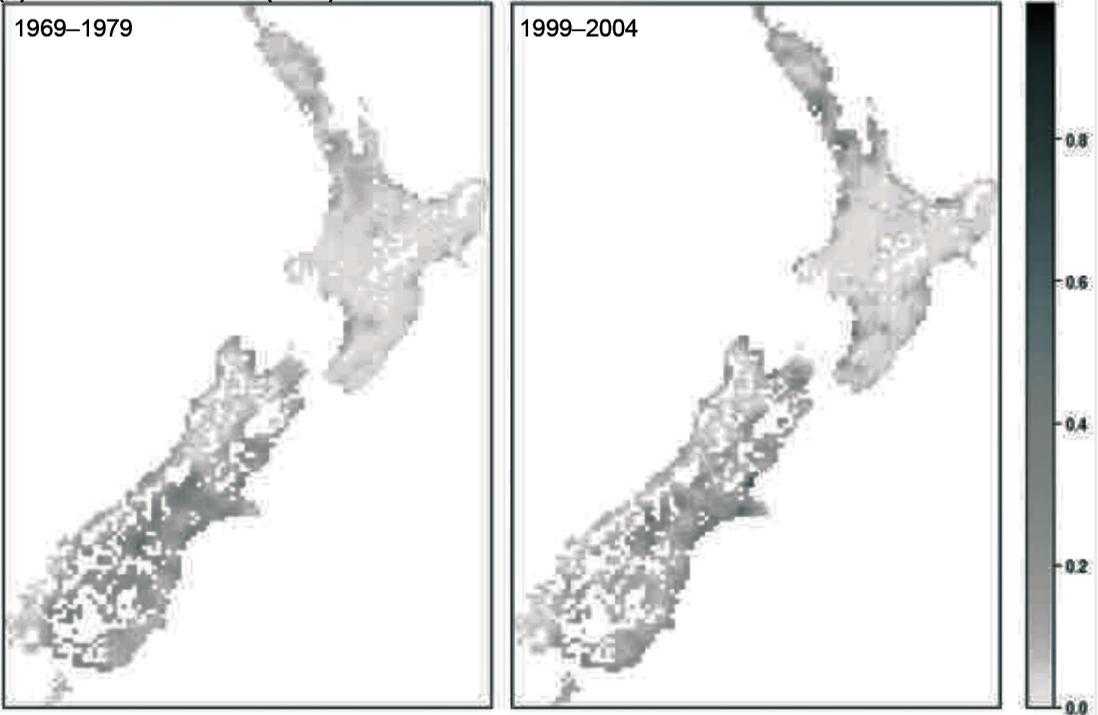
Figure 2. Average local occupancy (shades of grey) of (a) six mainly coastal-breeding and (b) seven mainly inland-breeding species of Charadriiformes.

Mixed-effects models

Parameter estimates from our all-species models are provided in Table 3, and we plot fitted effects from the model along a horizontal axis of distance from the coast (range 0 to 110 km) in Fig. 3.

In the North Island (Fig. 3 upper row) the model showed that non-endemic species increased overall between measurement periods while local occupancy of endemic species decreased overall (a negative measurement period: endemic interaction in Table 3). Occupancy changes were also positive overall on the coast, whereas they decreased inland (negative measurement period: distance from coast interaction). Increases in non-endemic species were significantly greater where road densities were higher (positive measurement period: endemic: road density interaction), and the greatest increases were in coastal-breeding species in areas of high road density (positive measurement period: road density: coastal-breeding interaction). Fitted estimates from the model indicate that the average occupancy of non-endemic coastal-breeding species increased from 38.7 [36.0, 41.5]% in 1969–1979 to 51.9 [49.1, 54.6]% in 1999–2004 on the densely settled coasts (i.e. with high road density; Fig. 3), while change in these species was negligible on remote coasts with no roads (24.3 [21.6, 27.3]% to 25.3 [22.5, 28.2]%).
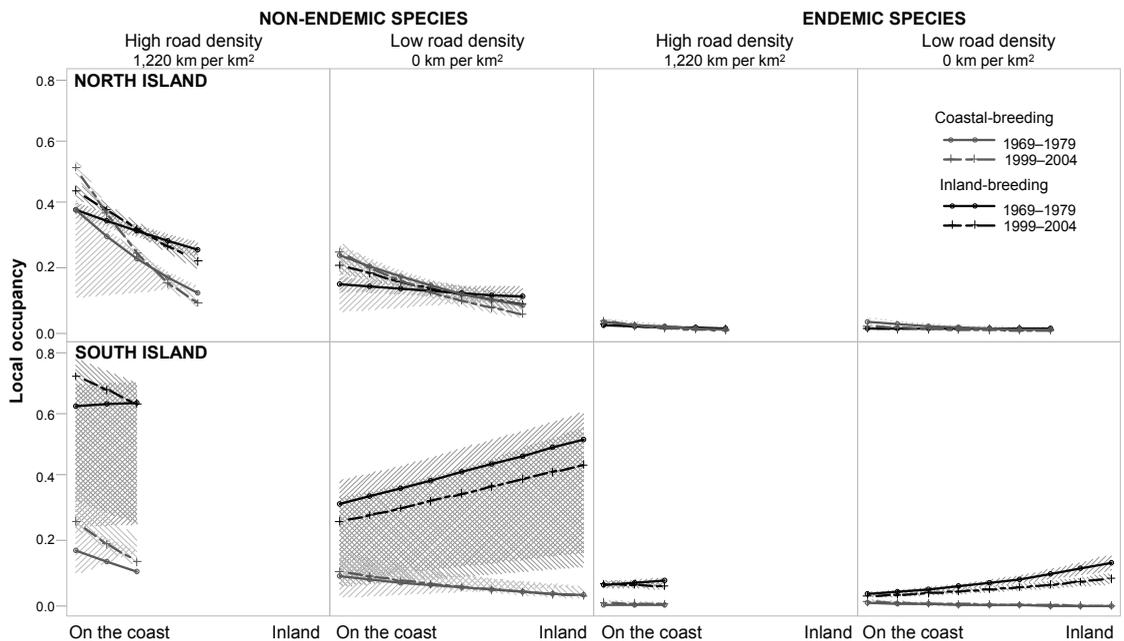
Figure 3. Fitted effects on local occupancy in six non-endemic and seven endemic species of New Zealand-breeding Charadriiformes from models for the North and South Islands (upper and lower rows), showing the interacting effects of endemism (left vs right quadrants of subplots), measurement period (open circles joined by solid lines for 1969–1979 and crosses joined by dashed lines for 1999–2004), coastal- or inland breeding habit (grey or black symbols and lines), and realistic combinations of centre distance inland from the coast (0 to 110 km, horizontal axes) and road density (high on the left vs low on the right). Hatched polygons show the 95% intervals of effects fitted in 1,000 models.

In the South Island, increases in non-endemic coastal- and inland-breeding species in areas of denser settlement contrasted with net decreases in the local occupancy of endemic inland breeding species in less settled squares between 1969–1979 and 1999–2004 (Fig. 3, lower row). This was reflected in a positive four-way interaction between measurement period, endemism, road density, and coastal breeding (Table 3). Decreases in local occupancy across all species were greater in inland squares (negative measurement period: distance from coast interaction), and a net increase in the local occupancy of coastal-breeding species contrasted with a net decrease in inland-breeding species (positive measurement period: coastal-breeding interaction).

Effects fitted in our *inland breeding species models* are plotted on gradients of agriculture and exotic forestry development (Fig. 4a) and urbanisation (Fig. 4b), and model parameter estimates are provided in Table 4.

Table 3. Median parameter estimates from North and South Island models of the local occupancy of the 13 native coastal and inland breeding species in our analyses. Lower and upper 95% confidence limits (CL) represent the 95% intervals of estimates from 1,000 models, each fitted to a different sample from the posterior distribution of logit-transformed occupancy probability for each species. Parameters are considered statistically significant when the 95% limits exclude zero, and these are shown in bold.

Term	Median estimate	Lower 95% CL	Upper 95% CL	Median estimate	Lower 95% CL	Upper 95% CL
Intercept	**−1.09**	**−1.18**	**−1.01**	−0.09	−1.71	0.19
Measurement period (Atlas 2 1999–2004 vs Atlas 1 1969–1979)	**0.33**	**0.22**	**0.45**	0.07	−0.08	0.22
Endemic	**−2.96**	**−3.12**	**−2.81**	**−2.81**	**−3.16**	**−1.34**
Distance from coast	**−0.20**	**−0.27**	**−0.15**	**0.13**	**0.08**	**0.18**
Road density	**0.36**	**0.29**	**0.43**	**0.36**	**0.30**	**0.43**
Coastal-breeding	**0.30**	**0.17**	**0.45**	−1.80	−2.15	0.31
Measurement period: endemic	**−0.32**	**−0.54**	**−0.09**	−0.13	−0.33	0.11
Measurement period: distance from coast	**−0.23**	**−0.31**	**−0.14**	**−0.22**	**−0.31**	**−0.14**
Endemic: distance from coast	0.01	−0.07	0.10	**0.15**	**0.09**	**0.21**
Measurement period: road density	−0.05	−0.14	0.05	**0.20**	**0.09**	**0.31**
Endemic: road density	**−0.22**	**−0.33**	**−0.13**	**−0.19**	**−0.27**	**−0.11**
Distance from coast: road density	−0.05	−0.10	0.00	**−0.05**	**−0.09**	**−0.01**
Measurement period: coastal-breeding	−0.04	−0.20	0.11	**0.26**	**0.08**	**0.43**
Endemic: coastal-breeding	**0.35**	**0.06**	**0.66**	−0.10	−1.81	0.34
Distance from coast: coastal-breeding	**−0.38**	**−0.47**	**−0.30**	**−0.53**	**−0.61**	**−0.46**
Road density: coastal-breeding	**−0.17**	**−0.25**	**−0.08**	**−0.16**	**−0.25**	**−0.08**
Measurement period: endemic: distance from coast	0.10	−0.03	0.22	0.02	−0.08	0.12
Measurement period: endemic: road density	**0.15**	**0.01**	**0.28**	**−0.14**	**−0.26**	**−0.01**
Measurement period: distance from coast: road density	0.00	−0.07	0.07	**−0.12**	**−0.19**	**−0.05**
Endemic: distance from coast: road density	−0.02	−0.09	0.05	0.00	−0.05	0.05
Measurement period: endemic: coastal-breeding	−0.23	−0.58	0.14	0.27	−0.18	0.74
Measurement period: distance from coast: coastal-breeding	−0.07	−0.19	0.05	0.06	−0.06	0.17
Endemic: distance from coast: coastal-breeding	0.02	−0.15	0.20	−0.09	−0.23	0.03
Measurement period: road density: coastal-breeding	**0.19**	**0.07**	**0.30**	−0.08	−0.22	0.05
Endemic: road density: coastal-breeding	0.03	−0.15	0.20	**−0.22**	**−0.35**	**−0.09**
Distance from coast: road density: coastal-breeding	−0.04	−0.11	0.02	−0.03	−0.08	0.02
Measurement period: endemic: distance from coast: road density	−0.05	−0.16	0.05	0.06	−0.02	0.14
Measurement period: endemic: distance from coast: coastal-breeding	0.01	−0.21	0.25	0.02	−0.16	0.21
Measurement period: endemic: road density: coastal-breeding	−0.09	−0.33	0.15	**0.19**	**0.01**	**0.38**
Measurement period: distance from coast: road density: coastal-breeding	−0.09	−0.18	0.01	0.06	−0.03	0.15
Endemic: distance from coast: road density: coastal-breeding	0.08	−0.06	0.22	**0.17**	**0.09**	**0.26**
Measurement period: endemic: distance from coast: road density: coastal-breeding	0.02	−0.16	0.20	−0.09	−0.22	0.03

The North Island model showed two clear effects on inland-breeding species:

1. an increase between 1969–1979 and 1999–2004 in non-endemic Australasian pied stilt near the coast (Fig. 4a) but not inland (a positive three-way interaction between measurement period, endemism level, and distance from the coast; Fig. 4a)
2. an increase across all inland-breeding species in more urbanised environments (a positive measurement period: urbanisation interaction; Fig. 4b).

In the South Island model there was a positive four-way interaction between measurement period, endemism level, distance from the coast, and the degree of agriculture and forestry development. This interaction reflects that between 1969–1979 and 1999–2004 average fitted local occupancy of non-endemic species in more-developed squares inland (98% of land developed, 110 km from the coast) fell from 88.0 [82.3, 92.6]% to 62.2 [50.2, 73.6]%, and that of species-level endemics from 14.4 [11.4, 17.7]% to 4.4 [3.4, 5.7]%. Fitted effects suggest that genus-level endemic wrybill was already almost
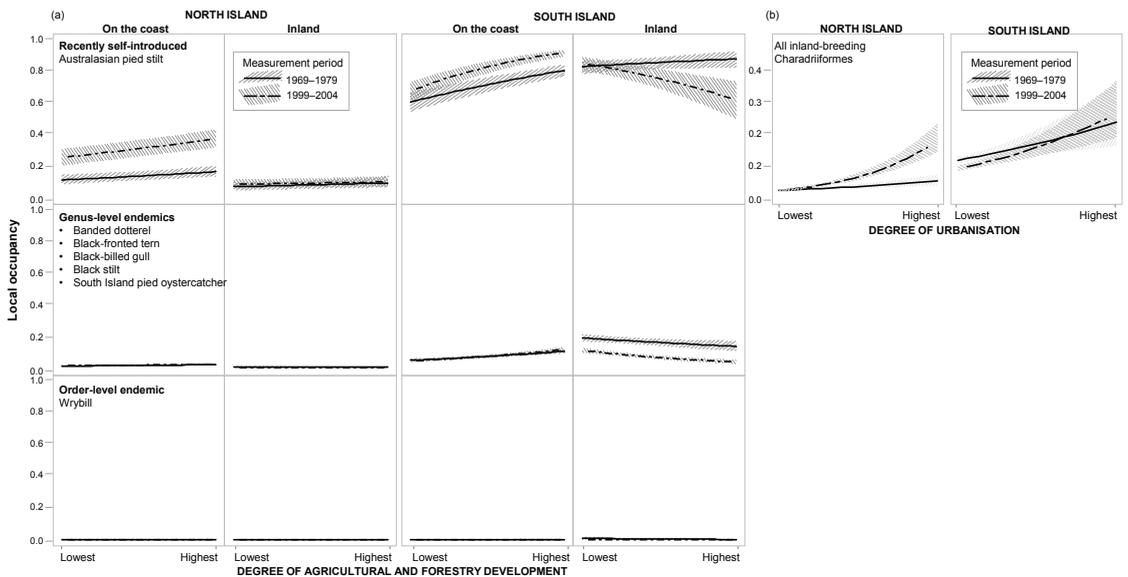
Figure 4. Fitted effects on local occupancy in seven inland-breeding Charadriiformes, from separate models fitted for the North and South Islands. Hatched polygons are 95% intervals of fitted effects in bootstrapped models. (a) shows interacting effects of time (solid lines for 1969–1979 and dashed lines for 1999–2004), endemism level (rows – the species at each level are listed), geographical position (on the coast or inland, left and right columns), and degree of agricultural and forestry development (horizontal axis); (b) shows interacting effects of time and degree of urbanisation. Hatched polygons show the 95% intervals of effects fitted in 1,000 models.

absent from much-developed inland squares in 1969–1979 but nevertheless declined even further (from 0.4 [0.2, 0.3]% to 0.1 [0.1, 0.3]%). Fitted local occupancy decreases in completely undeveloped inland squares were negligible in non-endemic species (83.2 [78.3, 86.7]% to 85.3 [80.4, 89.0]%), but significant in species-level (19.7 [17.6, 21.8]% to 11.8 [10.4, 13.3]%) and genus-level (1.2 [0.8, 1.8]% to 0.3 [0.2, 0.5]%) endemics. There was no significant association between local occupancy changes in inland-breeding species and more urbanised environments in the South Island (Table 4, Fig. 4b).

DISCUSSION

The results confirmed our hypotheses that changes in the local occupancy of Charadriiforme species between 1969–1979 and 1999–2004 varied both with characteristics of the species (endemism, breeding location) and geographical factors (distance from the coast, density of human occupation, and intensity of land use). The main changes were a decrease in the occupancy of endemic inland breeding wading birds, terns, and gulls in their inland South Island breeding ranges, and increases in the occupancy of a number of coastal- and inland-breeding species

Table 4. Median parameter estimates from North and South Island models of local occupancy of seven inland breeding Charadriiforme species. Lower and upper 95% confidence limits (CL) represent the 95% intervals of estimates from 1,000 models, each fitted to a different sample from the posterior distribution of logit-transformed occupancy probability for each species. Parameters are considered statistically significant when the 95% limits exclude zero, and these are shown in bold.

Term	NORTH ISLAND			SOUTH ISLAND		
	Median estimate	Lower 95% CL	Upper 95% CL	Median estimate	Lower 95% CL	Upper 95% CL
Intercept	**−3.75**	**−3.87**	**−3.62**	**−2.44**	**−2.55**	**−2.34**
Measurement period	0.08	−0.06	0.24	0.00	−0.14	0.15
Endemism level	**−1.91**	**−2.16**	**−1.66**	**−3.36**	**−3.63**	**−3.13**
Distance from coast	**−0.20**	**−0.25**	**−0.14**	**0.22**	**0.17**	**0.26**
Agricultural/forestry conversion	**0.14**	**0.08**	**0.20**	**0.28**	**0.23**	**0.32**
Urbanisation	**0.05**	**0.04**	**0.08**	**0.05**	**0.02**	**0.09**
Measurement period: endemism level	**−0.94**	**−1.15**	**−0.72**	**−0.64**	**−0.92**	**−0.34**
Measurement period: distance from coast	**−0.14**	**−0.22**	**−0.06**	**−0.23**	**−0.29**	**−0.18**
Endemism level: distance from coast	0.00	−0.09	0.08	0.00	−0.08	0.08
Measurement period: agricultural/forestry conversion	−0.03	−0.11	0.06	**0.08**	**0.01**	**0.15**
Endemism level: agricultural/forestry conversion	−0.02	−0.11	0.08	−0.09	−0.19	0.02
Distance from coast: agricultural/forestry conversion	**−0.06**	**−0.11**	**−0.02**	**−0.10**	**−0.14**	**−0.07**
Measurement period: urbanisation	**0.09**	**0.06**	**0.12**	0.03	−0.02	0.07
Measurement period: endemism level: distance from coast	**0.15**	**0.05**	**0.26**	0.08	−0.02	0.18
Measurement period: endemism level: agricultural/forestry conversion	−0.07	−0.20	0.05	**−0.17**	**−0.30**	**−0.04**
Measurement period: distance from coast: agricultural/forestry conversion	0.01	−0.05	0.07	**−0.08**	**−0.13**	**−0.04**
Endemism level: distance from coast: agricultural/forestry conversion	−0.04	−0.11	0.02	−0.05	−0.12	0.02
Measurement period: endemism level: distance from coast: agricultural/forestry conversion	0.05	−0.04	0.14	**0.13**	**0.04**	**0.23**

around the coast, especially near urban centres in the North Island.

In the 1970s many parts of inland South Island supported breeding populations of multiple species of inland-breeding wading birds, terns, and gulls. The principal breeding habitats were braided riverbeds, outwash terraces, and moraines, which occur east of the Southern Alps, mostly from inland Canterbury to Southland. These habitats are rare internationally: most other unmodified examples of these habitats occur in the extreme high-latitude parts of Canada, Alaska, and Siberia, and braided river reaches in the Himalayas and Andes are typically highly modified (Gray & Harding 2007). It seems likely that the combination of globally unusual habitat and the absence of mammalian predators enabled the evolution of an endemic New Zealand fauna of 'internal migrants' with specialised foraging and annual migration patterns.

A number of inland breeding species underwent substantial range contractions across the inland South Island between the 1970s and early 2000s. This overall trend is consistent with results from a number of studies on inland South Island braided rivers throughout this 25-year period, which identified local declines in breeding populations of black-billed gull (McClellan 2009; but see Spurr & Ledgard 2016 and Mischler 2018), black stilt (Keedwell, Maloney *et al.* 2002; Keedwell, Sanders *et al.* 2002), black-fronted tern (O'Donnell & Hoare 2011), and banded dotterel (Pierce 1999; Rebergen *et al.* 1998; Keedwell & Sanders 2002), and across

multiple species including wrybill and Australasian pied stilt (Maloney 1999; O'Donnell 2000; Sanders & Maloney 2002; Spurr & Ledgard 2016). Declines have been attributed to several interacting threats, in particular predation by introduced mammals, modification of braided riverbed habitats by weed invasion, alterations in flow regimes (O'Donnell & Moore 1983; Hughey 1985; Caruso 2006; McClellan 2009; Cruz *et al.* 2013), and loss of habitat to development (Innes & Saunders 2012; Grove *et al.* 2015; Peat *et al*. 2016).

The rising threat status of some inland-breeding species has been specifically linked to an expansion in the cultivation and irrigation of key breeding habitats on inland braided river margins and outwash plains in recent decades (Miskelly *et al.* 2008). Our study supports this link by showing that recent occupancy declines have been significantly greater in inland squares that are more developed for agriculture, cropping and forestry than in less-developed inland squares. However, the patterns also show continued (albeit slower) attrition of local occupancy of endemic species in the less-developed areas, where predation rather than habitat loss is likely to be the main driver of declines. Therefore, our results suggest that both management of predators and protection of remaining breeding habitats from agricultural conversion and weed invasion are needed to sustain endemic inland-breeding Charadriiforme species in the interior South Island. Effective protection through predator management has proven difficult and expensive because of the large and diverse suite of predators involved and rapid predator reinvasion when not implemented at a landscape scale (Innes & Saunders 2012; O'Donnell *et al.* 2016). It can be achieved (O'Donnell & Hoare 2011; Cruz *et al.* 2013; Monks *et al.* 2013; Spurr & Ledgard 2016), but can only be successful if the breeding habitats themselves remain available and suitable.

Occupancy of a number of coastal-breeding Charadriiforme species increased between measurement periods on New Zealand's settled coastlines and harbours, especially near North Island urban centres. Most of the species that increased are non-endemic, although the largest species range increase was in endemic variable oystercatcher. Increases in the geographical range and local occupancy of red-billed gull are consistent with a trend to 'more, generally smaller, colonies' since the mid-1960s indicated by breeding-colony counts (Frost & Taylor 2018). Some species that breed only (wrybill) or mainly (South Island pied oystercatcher, banded dotterel) in inland South Island habitats but overwinter on North Island coasts showed occupancy declines in their breeding habitats but increases in non-breeding coastal sites (Table 2b,c). Changes in local occupancy of waders derived from the Atlases were generally consistent with the trends recorded in the National Wader Count scheme between 1983 and 1994 and reported by Sagar *et al.* (1999).

We are not sure what explains the striking increases in local occupancy associated with more densely populated parts of the coastline. There are a number of possibilities.

1. Increased numbers of human observers around the coast and in cities (Robertson *et al.* 2007, pp. 20–21) might account for these increases, but we think this is unlikely because our occupancy models account for observer effort.

2. Habitat changes in coastal and harbour environments may have favoured some species; for example, through eutrophication increasing the productivity of feeding environments. This would be contrary to the concerns raised by Sagar *et al.* (1999) that increasing habitat loss and degradation of estuaries caused by human settlement and encroachment, drainage for agriculture, pollution, and fishing and associated disturbance might be having negative effects.

3. Alternatively, increases in local occupancy might reflect increases in bird movement and dispersal in response to increased disturbance by growing numbers of people at shorebird overwintering sites.

4. The trends may reflect recovery of some species from earlier human persecution (e.g. variable oystercatcher was widely shot as a 'choice table bird' before 1940; Baker 1973).

5. Australasian pied stilt arrived from Australia in the early 19th century (Heather & Robertson 1996) and may still be naturally expanding its coastal range.

6. Some species may be adapting behaviourally to human disturbance of various kinds, and even to mammal predation. Non-endemic species that have arrived in New Zealand more recently in evolutionary time are more likely than endemic species to have traits that confer resilience to continental selection pressures, or to retain the capability to adapt to human settlement and highly transformed landscapes.

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