NEW ZEALAND JOURNAL OF ECOLOGY

RESEARCH

Species turnover in forest bird communities on Fiordland islands following predator eradications

Colin M. Miskelly[1]*, Terry C. Greene[2] iD, Pete G. McMurtrie[3], Kim Morrison[4,5], Graeme A. Taylor[6], Alan J.D. Tennyson[1] iD and Bruce W. Thomas[7,8]

[1]Museum of New Zealand Te Papa Tongarewa, PO Box 467, Wellington 6140, New Zealand
[2]Biodiversity, Department of Conservation, Private Bag 4715, Christchurch 8011, New Zealand
[3]Department of Conservation, PO Box 29, Te Anau 9600, New Zealand
[4]Fiordland National Park, Te Anau, New Zealand
[5]Present address: Strathnaver, The Terrace, Reay, by Thurso, Caithness KW14 7RQ, United Kingdom
[6]Aquatic Unit, Department of Conservation, PO Box 10420, Wellington 6143, New Zealand
[7]Ecology Division, Department of Scientific and Industrial Research, New Zealand
[8]Present address: 190 Collingwood St, Nelson 7010, New Zealand
*Author for correspondence (Email: colin.miskelly@tepapa.govt.nz)

Abstract: Recent advances in the control of mammalian predators have begun to reveal interspecific competition as a key driver in the structure of New Zealand forest bird communities once predation pressure is reduced. We present evidence that, when at high densities, South Island robins (*Petroica australis*) may be responsible for declines in a suite of smaller native and introduced songbird species. Bird surveys undertaken on 47 islands in Breaksea Sound and Dusky Sound, Fiordland, during 1974 to 1986, were repeated on the same islands in 2016 or 2019. During the first block of surveys, Norway rats (*Rattus norvegicus*) were present on two islands, and stoats (*Mustela erminea*) were known or presumed to regularly reach 43 of the remaining islands. The rats were eradicated in 1986 and 1988, and stoats have been controlled to zero density since 2001 on all 28 of the islands surveyed in Dusky Sound, and since 2008 on 12 of 19 islands surveyed in Breaksea Sound. Bird species that apparently benefited from pest mammal eradications included South Island robin (*Petroica australis*) and kākā (*Nestor meridionalis*), both of which are endemic. Species recorded less often after the eradications included tomtit (*Petroica macrocephala*), grey warbler (*Gerygone igata*), silvereye (*Zosterops lateralis*), dunnock (*Prunella modularis*), and chaffinch (*Fringilla coelebs*) – a mixture of endemic, native, and introduced species. We hypothesise that these five species have been outcompeted or displaced by the now widespread and abundant South Island robin, probably through aggressive interactions.

Keywords: bird; competition; conservation management; island restoration; New Zealand; predator eradication; species turnover

Introduction

Perceptions of the relative roles of interspecific competition and predation in determining the structure of New Zealand forest bird communities have changed greatly over time (Darwin 1859; Buller 1895; Innes et al. 2010; Miskelly 2018). The decline of endemic birds following European colonisation of New Zealand was partly attributed to endemic species being out-competed by introduced bird species (Darwin 1859; Buller 1895; Guthrie-Smith 1926; Oliver 1930). "We all know that the existing avifauna is being stamped out and destroyed by a variety of artificial causes, not the least among them being the naturalization of foreign birds by way of acclimatization" (Buller 1895). "Much has been written about the inability of New Zealand birds to withstand the competition of the newcomers; their disappearance has been predicated on account of defective morphology" (Guthrie-Smith 1926, p.204).

However, by the 1920s, predation by introduced mammals was increasingly recognised as the main factor influencing New Zealand forest bird community structure (Thomson 1922; Guthrie-Smith 1926; Oliver 1930).

Predation by ship rats (*Rattus rattus*), stoats (*Mustela erminea*), and brushtail possums (*Trichosurus vulpecula*), in particular, continued to be considered the primary driver of bird community composition in New Zealand forests for the best part of a century (Holdaway 1989; Innes & Hay 1991; Atkinson 1996; King & Murphy 2005; Elliott et al. 2010a; Innes et al. 2010; Brown et al. 2015). The greater vulnerability of deep endemic birds (i.e. those endemic at the genus or family level) to predation resulted in forest bird communities at mainland sites being dominated by shallow endemics (sensu Fea et al. 2020), recent colonists and introduced species (Duncan & Blackburn 2004; Walker et al. 2017; Miskelly 2018; Binny et al. 2020; Fea et al. 2020).

Mammalian predator control and eradication programmes throughout New Zealand have revealed that not all bird species respond positively to the removal or reduction of predation pressure, with many bird species declining after mammals are removed or suppressed (Wilson 1988; O'Donnell & Hoare 2012; Graham et al. 2013; Miskelly 2018; Fea et al. 2020). Species that benefit from pest mammal eradication are predominantly deep endemics, with many shallow endemics, recent colonists, and introduced species declining (Graham et al. 2013; Miskelly 2018; Binny et al. 2020; Fea et al. 2020). This compensatory response (with some species increasing while others decline) points to interspecific competition having a major role in the structure of forest bird communities once predation pressure is removed (Miskelly 2018; Binny et al. 2020; Fea et al. 2020).

We explore the effect of removal of introduced mammalian predators on New Zealand forest bird communities using a unique dataset from 38 small Fiordland islands where either Norway rats (*Rattus norvegicus*) or stoats were eradicated, and forest bird communities left to recover with little further management. Responses to management on these islands are compared with forest bird communities on seven nearby islands where ship rats and stoats remain present or are able to recolonise readily from the nearby South Island mainland. The low number of deep endemic bird species that were resident on or able to recolonise the managed islands provide insights into those species that have disproportionate impacts on other bird species, as many of the deep endemic species present at other New Zealand restoration sites were not present on the small islands that we surveyed.

Methods

Boat-based surveys of islands in Breaksea Sound/Te Puaitaha, and around Anchor Island/Pukenui in nearby Dusky Sound/Tamatea, Fiordland National Park, south-west New Zealand (Fig. 1) were undertaken over two time periods separated by 30 years. During the initial surveys (1974 to 1986), the objective was to undertake inventories of bird, lizard, and pest mammal presence, plus to complete baseline surveys on two islands during preparations for eradicating Norway rats (Taylor & Thomas 1989, 1993; KM, unpubl. data). Most of the bird data available from 1974 to 1986 is presence/absence data or birds per hour encounter rates contained in seven unpublished reports authored by either KM or BWT (all reports available on request from CMM, with relevant data summarised in Supplementary Material).

The second series of surveys (2016 and 2019) was primarily focused on locating and estimating the size of colonies of burrow-nesting petrels (Miskelly et al. 2017b, 2020). However, all other bird species identified during the surveys were recorded, and the number of individuals detected was estimated (e.g. Miskelly et al. 2017a, plus raw data entered in eBird).

Surveys were undertaken in December 1974 (Breaksea Sound: Breaksea Island/Te Au Moana, Hāwea Island, Wairaki Island, Gilbert Islands), October 1981 (Breaksea Sound: Breaksea Island, Hāwea Island, Wairaki Island, Gilbert Islands, John Islands; Dusky Sound: Petrel Islands), February 1983 (Breaksea Sound: Hāwea Island, Wairaki Island, Gilbert Islands, Entry Island, Harbour Islands, John Islands; Dusky Sound: Seal Islands), February 1984 (Breaksea Island; Dusky Sound: Petrel Islands, Seal Islands, western Many Islands), September 1985 (Breaksea Sound: Harbour Islands; Dusky

Sound: numerous islands around Anchor Island), October and November 1985, and March 1986 (Hāwea Island), April 1986 (Breaksea Sound: Breaksea Island, Hāwea Island, Wairaki Island, westernmost Gilbert Island), August 1986 (Breaksea Sound: large Harbour Island; Dusky Sound: Parrot Island, Passage Islands), November 1986 (Dusky Sound: islands north-east of Anchor Island), December 1986 (Dusky Sound: Petrel Islands, Seal Islands, eastern Many Islands, Passage Islands), November 2016 (Dusky Sound: Petrel Islands, islands north-east of Anchor Island, Seal Islands, western Many Islands), and December 2019 (all Breaksea Sound islands; Dusky Sound: Passage Islands, Prove Island, Thrum Cap, eastern Many Islands). The length of time ashore was not recorded for all 1974 to 1986 surveys; however, 99 single-day surveys averaged 54 min per island (range 8–525 min). In addition, there were also multi-day visits of 6–13 days on Breaksea and Hāwea Islands. Island landings in 2016 and 2019 averaged 68 min ($n = 65$, range 5–310 min), with no multi-day visits. The time spent ashore on each island during both survey periods was proportional to island size and exceeded 30 min for the 16 islands > 1 ha, and 70 min for the five islands > 10 ha.

Data reported here was gathered from 71 islands, of which 47 were surveyed during both time periods, 7 were surveyed during 1974–1986 only, and 17 were surveyed during 2016–2019 only. The earlier island surveys were undertaken at dates spread throughout the year, while 2016–2019 surveys were all undertaken in November or December. Data for all islands and all months are presented in maps. Density estimates were not available from either time period, and so the maps and analyses presented here are based on bird species presence or absence from a large number of islands. As bird presence and conspicuousness can vary throughout the year, we undertook statistical analyses (before vs after pest mammal eradication or control) for a subset of 32 islands that were surveyed during October–December in both time periods. Of these 32 islands, Wairaki Island never had rats or stoats present, Breaksea and Hāwea Islands had Norway rats eradicated, 23 islands have had stoats controlled to zero density (stoats absent but may recolonise occasionally before being trapped), and six islands remain unmanaged (details for each island are provided in Supplementary Materials).

Statistical significance of the effect of pest eradication was judged at a per-species level, where the outcome was the number of islands that changed from bird species absence to presence, compared to the number of islands that changed from bird species presence to absence (Wan & Zhong 2002). This was tested using the binom.test function in R version 3.5.2 (R Core Team 2020).

Habitat

All sites surveyed had essentially unmodified vegetation communities, with no evidence of vegetation clearance or fire, and few if any adventive plant species noted. The Harbour Islands, John Islands, and Gilbert Islands (Breaksea Sound) are likely to be occasionally visited by red deer (*Cervus elephus*); however, no recent evidence of their presence was noted in 2019. Deer were eradicated from Anchor Island (and the small islands surrounding it) by 2007 (Crouchley et al. 2011). Brushtail possums have never been present on any of the islands in Breaksea and Dusky Sounds (Department of Conservation 2017).

Most of the islands in Breaksea and Dusky Sounds are covered from shoreline to summit in tall forest dominated by podocarps (mainly rimu *Dacrydium cupressinum* and

miro *Pectinopitys ferruginea*), southern rātā (*Metrosideros umbellata*), mountain beech (*Fucospora cliffortioides*), and kāmahi (*Weinmannia racemosa*), with a diverse subcanopy of hardwood shrubs. Small islands closer to the sea have a lower canopy mainly of inaka (*Dracophyllum longifolium*) surrounded by a coastal fringe of kokomuka (*Veronica elliptica*) and tētēaweka (*Olearia oporina*). All the islands included in this survey have at least some forest or shrub cover, but some of the outermost, exposed islands have extensive areas of *Poa astonii* tussock, the herb *Anisotome lyallii*, flax (*Phormium* spp.), and bare rock.

Rat and stoat presence, eradication, and control

Norway rats were abundant throughout southern Fiordland in the 1880s (Reischek 1888) but disappeared from most sites (including Resolution Island/Mauikatau and Anchor Island/ Pukenui) following colonisation by stoats from 1900 (Taylor 1978; Hill & Hill 1987). Stoats are very effective predators of Norway rats (Thomson 1921; Taylor 1978), and the fact that Norway rats persisted on Breaksea Island (170 ha) and Hāwea Island (9 ha), when they disappeared from all other nearby islands, indicates that stoats never reached these two outermost islands and the adjacent rat-free Wairaki Island (Taylor 1978; Taylor & Tilley 1984).

The spread of ship rats in the South Island was contemporaneous with the spread of stoats (Atkinson 1973), but ship rats failed to establish on most islands included in this study, apart from the Harbour Islands and John Islands in inner Breaksea Sound, where they remain (PM, unpubl. data). It is unclear whether ship rats out-competed Norway rats in the South Island forests, or whether the smaller, more arboreal ship rats were filling a niche vacated when Norway rats were extirpated by stoats (Atkinson 1973; Taylor 1978). Norway rats were eradicated from Hāwea Island in 1986, and from Breaksea Island in 1988 (Taylor & Thomas 1989, 1993).

Stoats were eradicated from Anchor Island and surrounding islands in 2001 and have been controlled to low density by trapping on Resolution Island since 2008 (Elliott et al. 2010b; Clayton et al. 2011; Edge et al. 2011; Wildland Consultants & DOC 2016). As stoat traps are maintained on most of the islands off the north coast of Resolution Island (from Breaksea Island to Entry Island; Department of Conservation 2017), all these islands have effectively been free of introduced mammal predators since 2008 (Miskelly et al. 2020a). The effectiveness of this trap network is evident from the dispersal and establishment of South Island robins (*Petroica australis*) reported herein. However, traps are not maintained on the Harbour Islands and John Islands, east of the northern entrance to Acheron Passage (Fig. 1), all seven of which were surveyed during both time periods. Stoats, along with ship rats, remain present on (or regularly visit) the Harbour Islands and John Islands (Department of Conservation 2017; PM, unpubl. data).

There are currently 4971 'DOC 150' stoat traps set in Breaksea and Dusky Sounds (3571 on Resolution Island), which are checked three times per annum.

Translocations of volant endemic birds to islands in Breaksea and Dusky Sounds

Few of the islands included in this study have had translocated birds released on them in the last 100 years (Hill & Hill 1987).
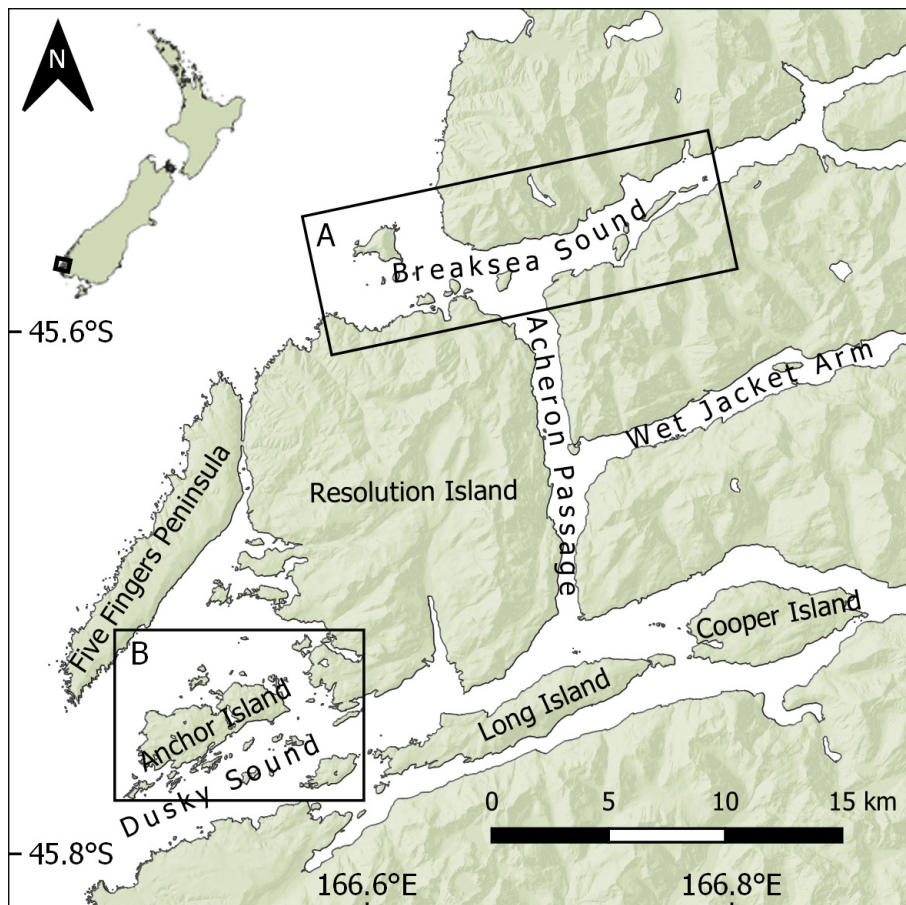
Figure 1. Locality map showing the two study areas in Breaksea Sound and Dusky Sound, Fiordland, New Zealand.

The one clear exception is Breaksea Island, where South Island saddlebacks (*Philesturnus carunculatus* = saddleback) were released in 1993, and mohua/yellowhead (*Mohoua ochrocephala*) in 1995 (Rasch & McClelland 1993; Wildland Consultants & DOC 2016). South Island robins (= robin) were translocated from Breaksea Island to Hāwea Island in 1987; however, birds have been recorded flying in both directions between the two islands (Peat & Patrick 1996; BT & GT, unpubl. data), and the 560 m water gap is well within their flying ability (Miskelly et al. 2017a, 2018), suggesting that robins would have colonised Hāwea Island naturally within a few years of rat eradication. Robins were translocated from Breaksea Island to nearby Entry Island in 1989, but the translocation failed in the absence of stoat control (Miskelly & Powlesland 2013). The robins now present on Entry Island have colonised naturally since stoat control was initiated there in 2008.

Anchor Island (1137 ha) was not included in this study, but saddlebacks, mohua, and robins were all released there between 2002–2004 (Department of Conservation 2017; Miskelly et al. 2017a). These three species have subsequently colonised a few islands (saddleback and mohua) or most islands (robin) surrounding Anchor Island, plus robins have colonised most of the islands off the north coast of Resolution Island (Miskelly et al. 2017a, and results reported herein). Mohua have also been released on Pigeon Island (3.7 km north of Anchor Island), and robins on both Pigeon Island and Indian Island (the latter is 2.7 km south-east of Anchor Island) (Miskelly et al. 2017a).

Results

Species with a wider distribution following pest mammal eradications

Few forest bird species responded positively at a landscape scale to eradication of predatory mammals on Fiordland islands. South Island saddleback and mohua could only be reintroduced after rats or stoats were eradicated, but their limited dispersal ability (Miskelly et al. 2017a) meant that we encountered them on only four (saddleback) and three (mohua) islands other than release sites. Colonisation of these additional islands required water crossings of no more than 100 m (saddleback) and 65 m (mohua) from the release sites, leaving much suitable habitat inaccessible to them. Distribution maps for all forest birds recorded in the two surveys (including saddleback and mohua) are presented in Supplementary Materials.

Two stronger-flying species with the potential to reach all study islands showed a significant response to pest mammal eradication (Table 1, Figs 2, 3). Robins were confined to Breaksea Island during 1974–1986 and increased dramatically there after rat eradication (authors, pers. obs.). During the 2016–2019 surveys, robins were found on an additional 47 islands where they had previously been absent, including 30 that had been visited during 1974–1986 (Table 1, Fig. 2). In addition to being widely distributed, robins were the most frequently encountered birds during the second block of surveys (Table 2). However, robins had not colonised the unmanaged

Table 1. The number of islands where 21 forest bird species were encountered before (T1) and after (T2) eradication of rats or stoats, based on a sample of 26 managed and six unmanaged Fiordland islands. Species are ranked in order of how much their distributions changed between the two surveys, with those showing the greatest increase in distribution at the top. Blue highlighting shows the two species that increased significantly in range on managed islands between the two surveys, and orange highlighting shows six species that decreased significantly in range. There were no significant changes in distribution on unmanaged islands. Scientific names are provided in the footnote.

Species	Managed (n = 26)				Unmanaged (n = 6)			
	T1	T2	Change	P	T1	T2	Change	P
South Island robin	1	18	0.730	<0.001	0	0	0	NA
Kākā	3	10	0.270	0.006	3	2	-0.167	1
New Zealand falcon	0	3	0.135	0.062	0	0	0	NA
Yellow-crowned parakeet	3	6	0.135	0.125	1	2	0.167	1
South Island saddleback	0	3	0.081	0.25	0	0	0	NA
Mohua	0	3	0.081	0.25	0	0	0	NA
Rifleman	0	1	0.027	1	0	0	0	NA
Bellbird	19	20	0.027	1	3	4	0	1
Kea	0	0	0	NA	0	1	0.167	1
Tūī	1	0	-0.027	1	0	2	0.333	0.5
Blackbird	9	7	-0.027	1	2	0	-0.333	0.5
Long-tailed cuckoo	3	1	-0.054	0.5	0	1	0.167	1
Brown creeper	4	1	-0.054	0.5	1	1	0	NA
New Zealand fantail	6	4	-0.108	0.219	2	2	0	NA
Weka	3	0	-0.135	0.062	0	1	0.167	1
Kererū	7	3	-0.243	0.012	1	0	-0.167	1
Chaffinch	5	0	-0.243	0.004	1	4	0.5	0.25
Grey warbler	11	3	-0.270	0.013	3	4	0	1
Dunnock	8	0	-0.297	0.001	0	0	0	NA
Silvereye	10	1	-0.378	<0.001	0	3	0.5	0.25
Tomtit	12	3	-0.486	<0.001	2	6	0.5	0.25

South Island robin *Petroica australis*; Kākā *Nestor meridionalis*; New Zealand falcon *Falco novaeseelandiae*; Yellow-crowned parakeet/kākāriki/ *Cyanoramphus auriceps*; South Island saddleback *Philesturnus carunculatus*; Mohua/yellowhead *Mohoua ochrocephala*; Rifleman *Acanthisitta chloris*; Bellbird *Anthornis melanura*; Kea *Nestor notabilis*; Tūī *Prosthemadera novaeseelandiae*; Blackbird *Turdus merula*; Long-tailed cuckoo *Eudynamys taitensis*; Brown creeper/pīpipi *Mohoua novaeseelandiae*; New Zealand fantail *Rhipidura fuliginosa*; Weka *Gallirallus australis*; Kererū/New Zealand pigeon *Hemiphaga novaeseelandiae*; Chaffinch *Fringilla coelebs*; Grey warbler *Gerygone igata*; Dunnock *Prunella modularis*; Silvereye *Zosterops lateralis*; Tomtit *Petroica macrocephala*.
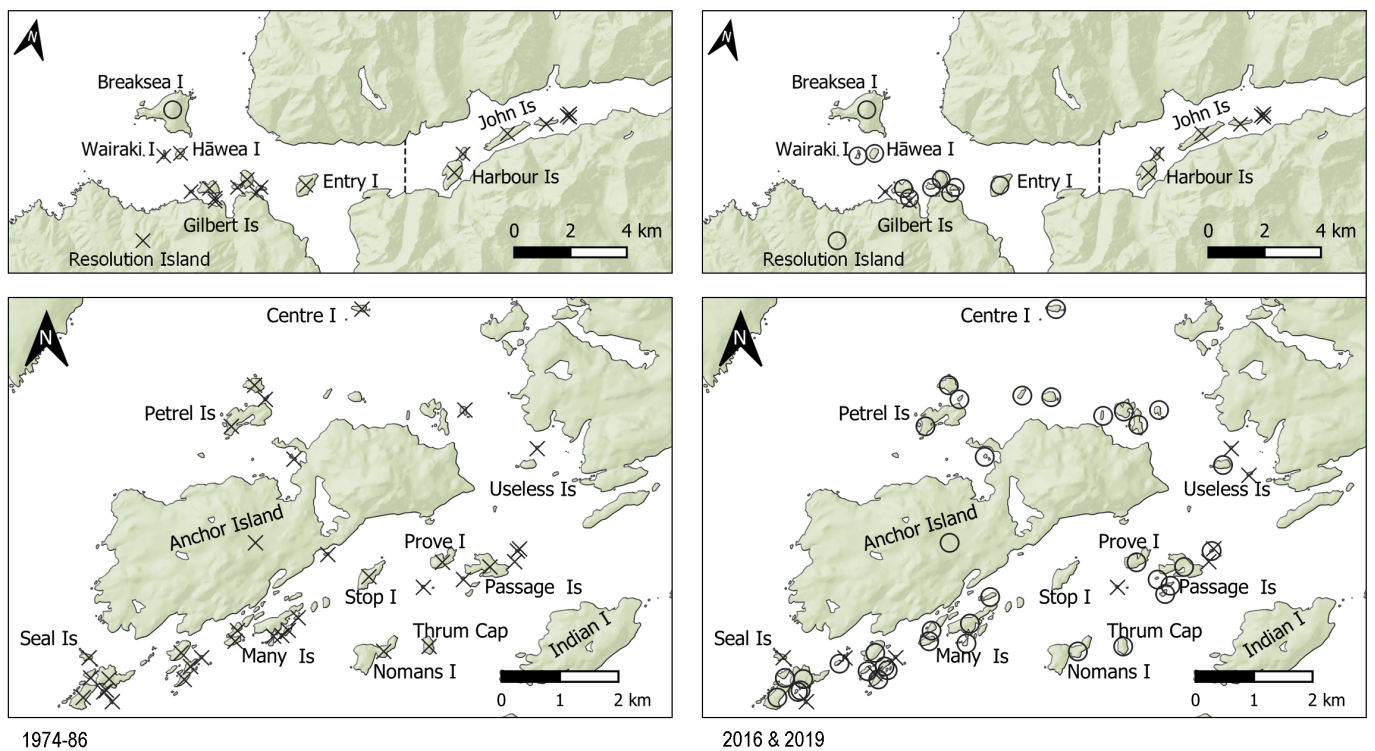
Figure 2. Distribution of South Island robin (*Petroica australis*) on 71 Fiordland islands over two time periods (○ = one or more robin seen or heard; X = island visited but no robins recorded). Islands east of the dashed line received no management intervention.
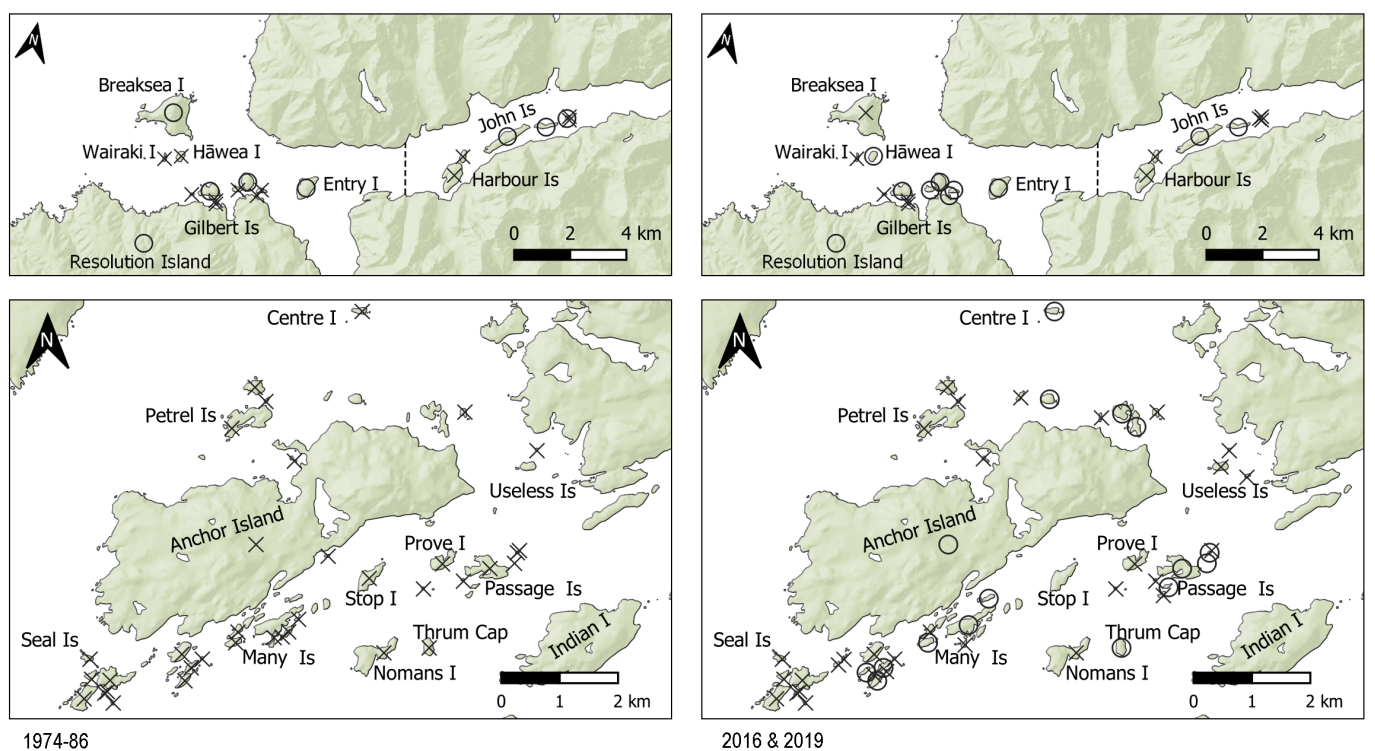
Figure 3. Distribution of kākā (*Nestor meridionalis*) on 71 Fiordland islands over two time periods (○ = one or more kākā seen or heard; X = island visited but no kākā recorded). Islands east of the dashed line received no management intervention.

Table 2. Encounter rates (individuals per hour) for the five most widely encountered bird species on small islands in Breaksea and Dusky Sounds before (1974–1986) and after (2016–2019) pest animal management.

Period	1974–86	2016–19
Hours	**46.2**	**68.0**
Bellbird	4.2	3.9
South Island robin	0	4.4
Tomtit	1.5	0.3
Blackbird	0.3	0.5
Grey warbler	0.5	0.2

Harbour Islands and John Islands, despite them being within robin flight range from Entry Island via the adjacent South Island mainland (Miskelly et al. 2017a).

Kākā (*Nestor meridionalis*) were present on several of the islands in Breaksea Sound throughout the study; however, they were not recorded on or around Anchor Island during 1974–1986 (Fig. 3). They are now abundant on Anchor Island, and we recorded them on 15 nearby islands (Fig. 3).

Species apparently unaffected by pest mammal eradications

The endemic bellbird (*Anthornis melanura*) and the introduced blackbird (*Turdus merula*) were both widespread before and after pest mammal eradications (Table 1; Figs 4, 5). There was no apparent change in bellbird or blackbird encounter rates following pest mammal suppression (Table 2).

Species with reduced distributions following pest mammal eradications

Six species were encountered on significantly fewer islands after pest mammal eradications (Appendix S1 in Supplementary Materials). Kererū (*Hemiphaga novaeseelandiae*) were observed on few islands in 2016 and 2019, and two of these (islets north-east of Anchor Island) were sites that were not surveyed during 1974–1986 and so were excluded from analysis (Appendix S4). Kererū regularly fly tens of kilometres in search of seasonal food sources (Clout et al. 1986, 1991; Powlesland et al. 2011). Further surveys at other times of the year are required to determine whether kererū distribution in coastal Fiordland has been influenced by stoat and rat eradication.

The five remaining species that were recorded on significantly fewer islands in 2016 and 2019 were all small passerines: the shallow endemics tomtit (*Petroica macrocephala*) and grey warbler (*Gerygone igata*), the recent coloniser silvereye (*Zosterops lateralis*), and the introduced dunnock (*Prunella modularis*) and chaffinch (*Fringilla coelebs*) (Appendix S1).

Following stoat eradication, tomtits disappeared from all the small islands around Anchor Island (Fig. 6). Norway rat eradication also apparently led to local extinction of tomtits on Breaksea and Hāwea Islands; however, they were still present on several islands in Breaksea Sound, including the unmanaged Harbour and John Islands (Fig. 6).

Silvereyes were encountered on fewer islands than tomtits during 1974–1986, and all but disappeared from managed islands following stoat and rat eradication (Fig. 7). They remain present on the unmanaged Harbour and John Islands (Fig. 7).

Dunnocks were detected on 16 islands during 1974–1986; however, they were not recorded on the Harbour and John Islands (Fig. 8). Dunnocks were not detected at any site following the eradication of stoats and rats (Fig. 8). Chaffinches disappeared from all but one managed site; however, they were recorded on four of the five (unmanaged) John Islands in 2019 (Fig. 9).

Bird communities on non-treatment islands over time

There were no significant changes in bird communities on the Harbour and John Islands (combined) in Breaksea Sound between 1974–1986 and 2019 (Appendix S1). These seven islands have received no pest mammal control effort.

Discussion

**Forest bird species that benefitted from predator release**

The two species that benefitted most from pest mammal eradications on Fiordland islands (robin and kākā) are large or medium-sized endemic species that typically nest in tree-holes or cavities. These characters fit the pattern for species that benefitted from pest mammal control based on a meta-analysis of 24 New Zealand restoration projects (Fea et al. 2020).

Outcome monitoring data for entire bird communities, with adequate baselines or controls, have been published for only a few New Zealand restoration sites (Dilks et al. 2003; Graham et al. 2013; Miskelly 2018; Bombaci et al. 2018; Fea et al. 2020; Ralph et al. 2020), with robins and kākā consistently among the species that benefitted from pest mammal eradications. However, O'Donnell & Hoare (2012) did not detect any increase in kākā in response to pest mammal control in the Landsborough Valley, South Westland.

South Island saddleback and mohua were successfully translocated to several Fiordland islands following pest mammal eradications (Miskelly & Powlesland 2013; Department of Conservation 2017; Miskelly et al. 2017a). However, their limited dispersal ability has meant that they have been unable to disperse to many of the islands that we surveyed (Miskelly et al. 2017a, 2018). Poor dispersal ability may also have contributed to rifleman and brown creeper/pīpipi (*Mohoua novaeseelandiae*) (both of which are also deep endemics) failing to respond to pest mammal eradications on islands in Breaksea and Dusky Sounds (Table 1).

New Zealand conservationists have long been aware that our deep-endemic birds are more vulnerable to mammalian predators than are introduced species and those that have recently colonised New Zealand from Australia (Holdaway 1989, 1999; Innes & Hay 1991; Duncan & Blackburn 2004; Innes et al. 2010; Fea et al. 2020). The relationship between "degree of endemism" and the length of time each lineage has been in New Zealand was first proposed by Fleming (1962). Deep endemic birds exhibit a suite of behaviours and life history traits that make them especially vulnerable to mammalian predators (including reduced flying ability, naïvety to predators, delayed maturity, and low fecundity), and it is assumed that these traits evolved in response to reduced predation pressure compared to their nearest relatives (typically in continental Australia) that co-evolved with numerous predatory mammals and reptiles (McNab 1994; Holdaway 1999; Starling-Windhof et al. 2011, Bromham et al. 2012, Parlato et al. 2015). While it is intuitively apparent that these deep endemic birds would respond positively to the removal of predation pressure, it is counterintuitive that other more fecund bird species (including
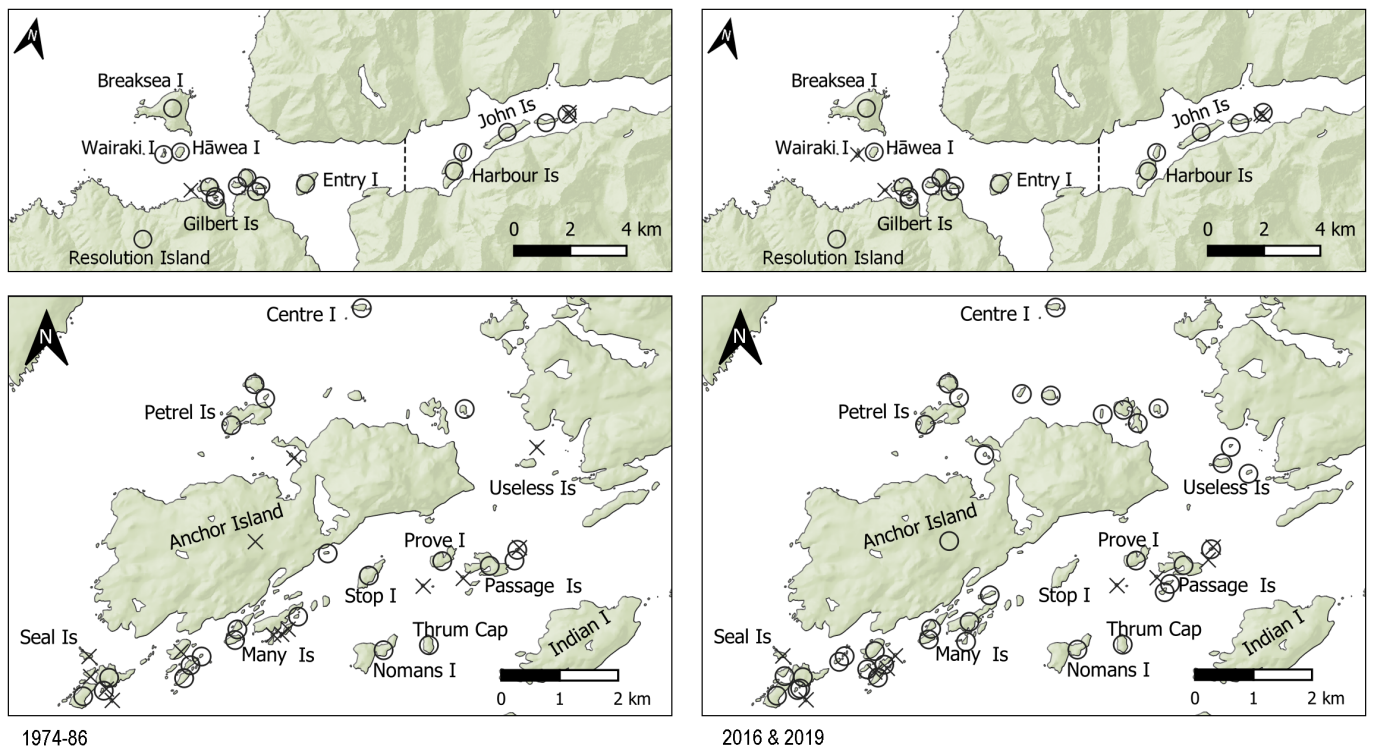
Figure 4. Distribution of bellbird/korimako (*Anthornis melanura*) on 71 Fiordland islands over two time periods (○ = one or more bellbird seen or heard; X = island visited but no bellbirds recorded). Islands east of the dashed line received no management intervention.
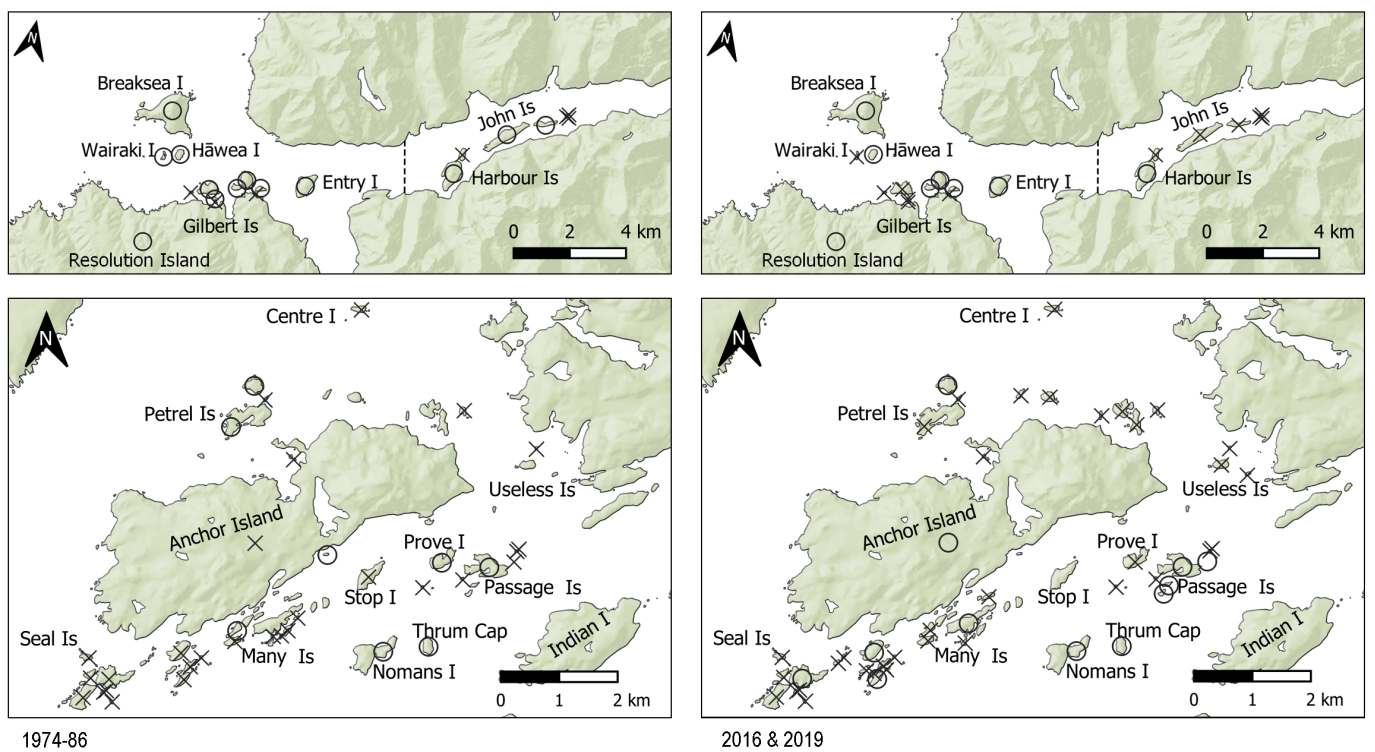

Figure 5. Distribution of Eurasian blackbird (*Turdus merula*) on 71 Fiordland islands over two time periods (○ = one or more blackbird seen or heard; X = island visited but no blackbirds recorded). Islands east of the dashed line received no management intervention.
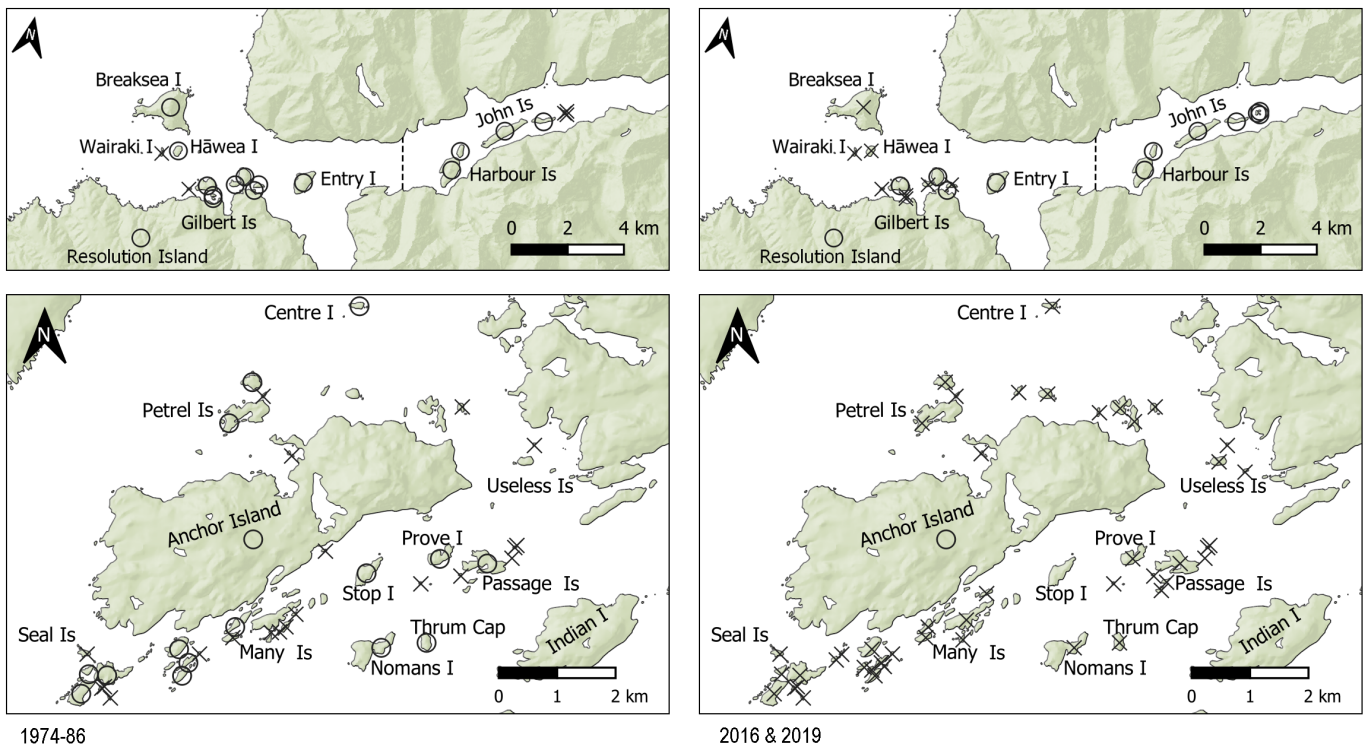
Figure 6. Distribution of South Island tomtit/ngirungiru (*Petroica macrocephala*) on 71 Fiordland islands over two time periods (○ = one or more tomtit seen or heard; X = island visited but no tomtits recorded). Islands east of the dashed line received no management intervention.
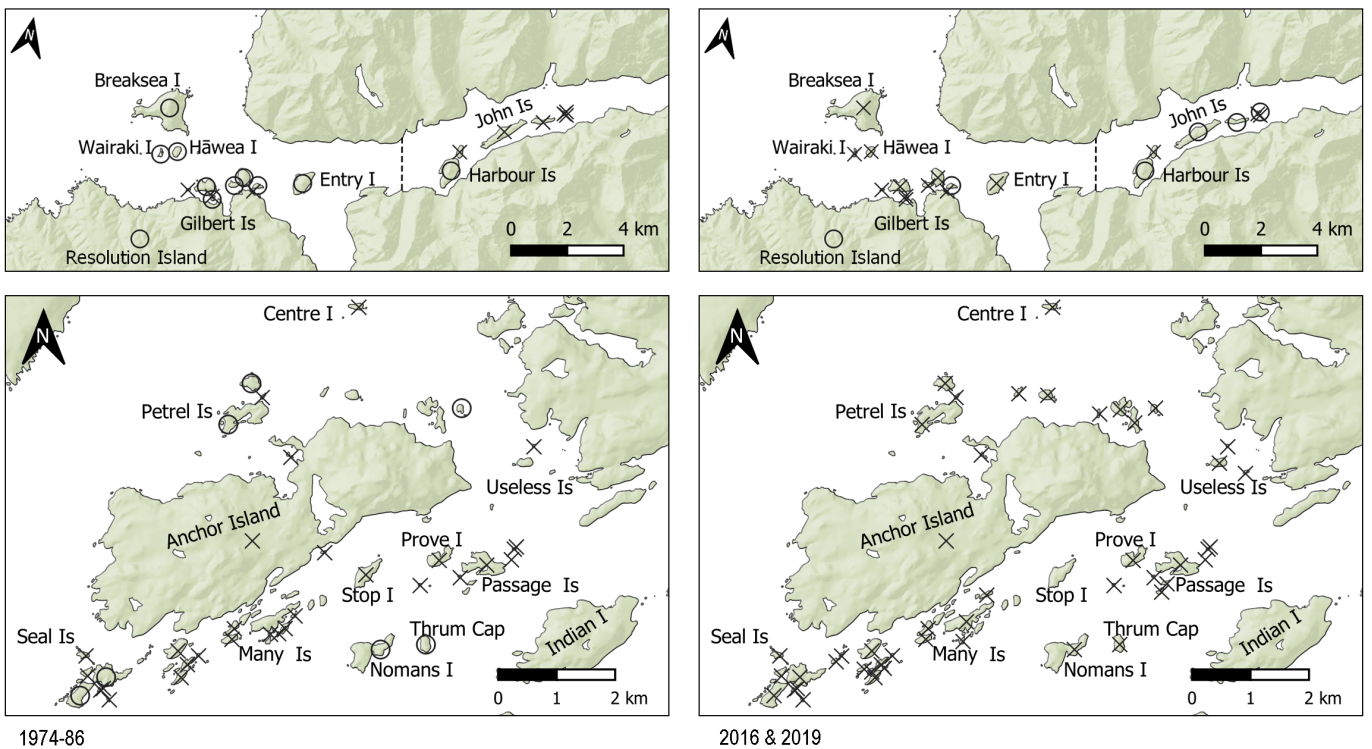
Figure 7. Distribution of silvereye/tauhou (*Zosterops lateralis*) on 71 Fiordland islands over two time periods (○ = one or more silvereye seen or heard; X = island visited but no silvereyes recorded). Islands east of the dashed line received no management intervention.
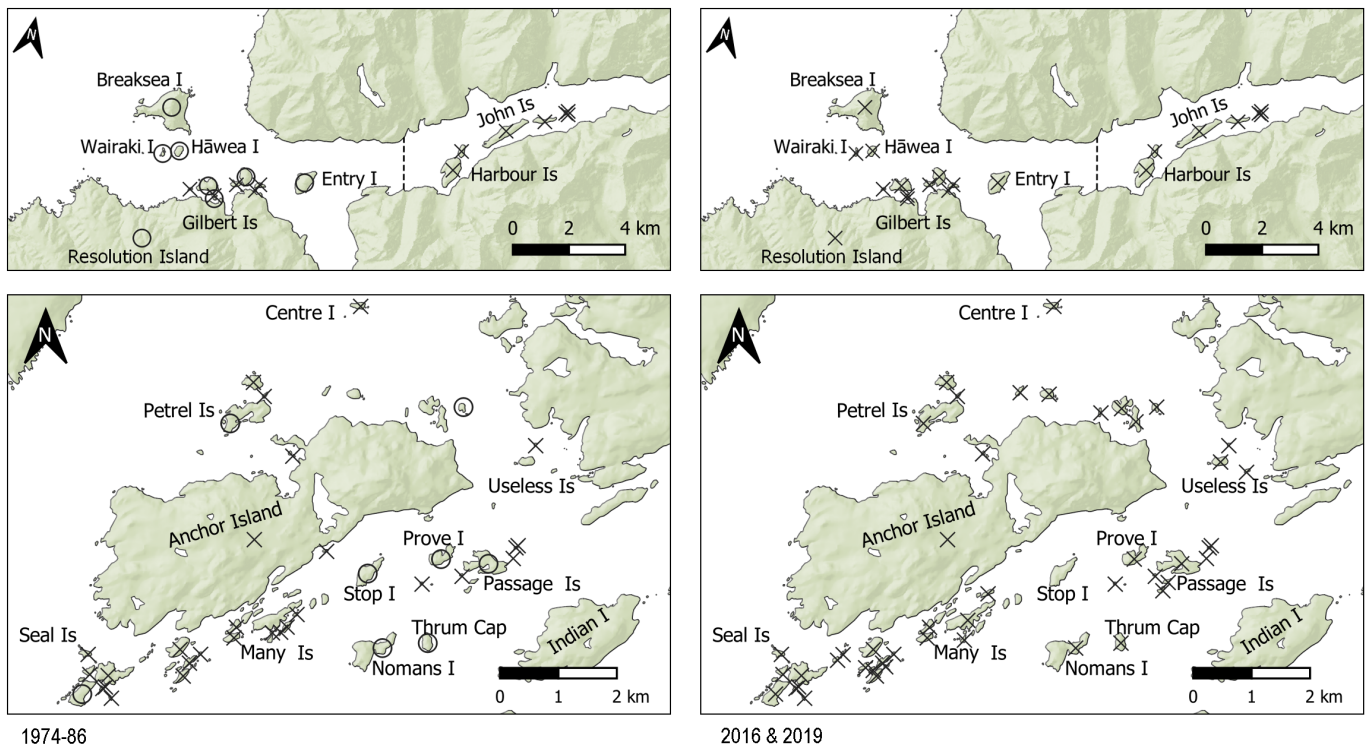
Figure 8. Distribution of dunnock (*Prunella modularis*) on 71 Fiordland islands over two time periods (○ = one or more dunnock seen or heard; X = island visited but no dunnocks recorded). Islands east of the dashed line received no management intervention.
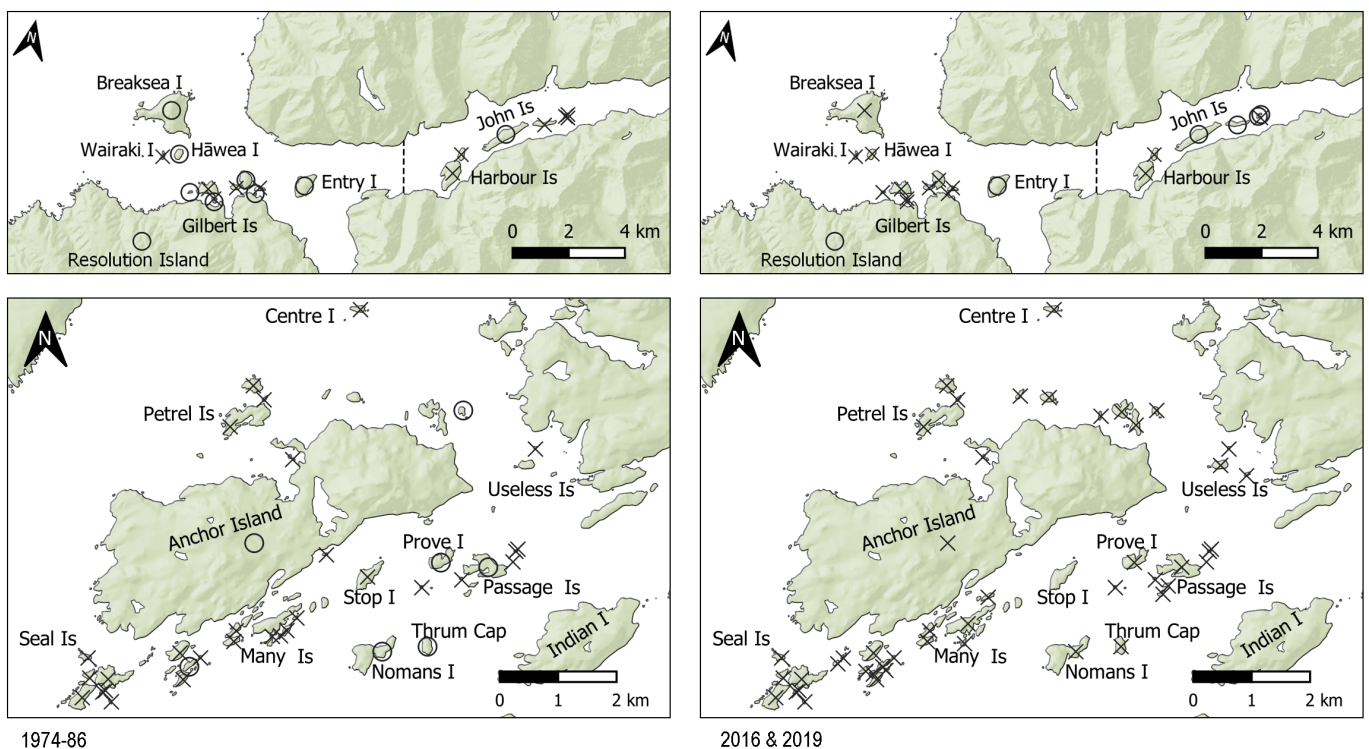
Figure 9. Distribution of chaffinch (*Fringilla coelebs*) on 71 Fiordland islands over two time periods (○ = one or more chaffinch seen or heard; X = island visited but no chaffinches recorded). Islands east of the dashed line received no management intervention.

shallow endemics, recent colonists, and introduced species) do not increase when predatory mammals are eradicated (Miskelly 2018; Binny et al. 2020).

Species that declined following predator eradication

A striking finding of the Fiordland island surveys was the large number of bird species that were encountered less often following eradication of Norway rats and stoats, most notably a suite of small-bodied insectivores (tomtit, silvereye, dunnock, chaffinch, and grey warbler). With the exception of tomtit (which is present at few restoration sites) these species were among the six species that had negative or neutral responses to pest mammal control throughout New Zealand (Fea et al. 2020).

The two most comprehensive and well-documented bird restoration sites in New Zealand are Tiritiri Mātangi Island in the Hauraki Gulf, and the fenced Zealandia/Karori Sanctuary in Wellington, with eleven and nine successful bird translocations respectively by 2012 (Miskelly & Powlesland 2013; Parker 2013). In addition to the large latitudinal differences between Tiritiri Mātangi (36°S), Zealandia (41°S), and our Fiordland sites (46°S), the contrast between the conservation histories of these three forested sites is considerable.

The Fiordland islands that we surveyed have essentially unmodified vegetation communities (Ledgard et al. 2010; Wildland Consultants & Department of Conservation 2016), and almost all the endemic bird recovery has been through natural dispersal rather than translocations. Tiritiri Mātangi was a formerly farmed 254 ha island that has been transformed through the planting of more than 280 000 native trees and shrubs (Galbraith & Cooper 2013). The island held substantial natural populations of both tūī and bellbird, and red-crowned parakeet (*Cyanoramphus novaezelandiae*), and North Island saddleback (*Philesturnus rufusater*) had already been translocated to and established on the island before bird community monitoring was initiated (Graham et al. 2013). Zealandia is a 225 ha former farm and urban water-supply reservoir predominantly covered in young, naturally re-established forest, and situated on the urban/rural fringe (Lynch 2019). The first block of bird counts at Zealandia was completed a year before the fence was built (or any bird species translocated), and revealed a bird community with a near-absence of deep endemic species (with the exception of low numbers of tūī; Miskelly 2018). Despite these differences, the bird community responses to predator suppression, and the subsequent reintroduction or colonisation of additional deep endemic bird species, at all three sites have been remarkably similar.

With the exception of tūī (which increased markedly), few of the resident Zealandia birds showed any significant response to pest mammal eradication per se. This suggests that the other species that had survived at the site in the presence of ship rats, stoats, and possums were not limited by mammal predation (Miskelly 2018). However, nine species (including silvereye, fantail (*Rhipidura fuliginosa*), grey warbler, chaffinch, and dunnock) declined once several deep endemic bird species were successfully re-established at the site and tūī had increased further (Miskelly 2018). In addition to the resident species that declined following the re-establishment of a deep-endemic bird community, an attempted translocation of tomtits failed, apparently due to increasing aggression from an expanding North Island robin (*Petroica longipes*) population (Empson & Fastier 2013).

The only resident passerine species that increased significantly on Tiritiri Mātangi during the restoration project (including kiore eradication) were the deep endemic bellbird and tūī (Graham et al. 2013). In contrast, there were significant declines in six other passerine species, including dunnock, silvereye, fantail, and grey warbler (Graham et al. 2013). As at Zealandia, attempts to translocate tomtits to Tiritiri Mātangi were unsuccessful (Parker 2013).

While we did not record a statistically significant decline in fantails on Fiordland islands, they were always a rare component of the forest bird community there. We recorded fantails on only five out of 40 restoration islands in 2016–2019, when they had been found on ten of these islands before rats and stoats were eradicated. In contrast, their presence on the non-treatment islands was unchanged (three out of seven in both time periods).

When viewed across all three sites, silvereye, fantail, tomtit, grey warbler, dunnock, and chaffinch all appear to do better in the presence of predatory mammals than they do when exposed to a deep-endemic bird community.

Competition as a limiting factor for New Zealand forest birds

The most likely explanation for insectivorous bird species declining following the eradication of predators is that they have been out-competed by those (deep endemic) bird species that responded positively to predator release (Graham et al. 2013; Miskelly 2018; Binny et al. 2020; Fea et al. 2020). It is unclear whether declines in small insectivorous birds on Tiritiri Mātangi and at Zealandia can be attributed to one or a few strong competitors given the number of deep endemic species that are now abundant at these sites (Graham et al. 2013; Miskelly 2018). Competition from a suite of endemic species (including whitehead (*Mohoua albicilla*), robin, tūī, and saddleback) was considered the most plausible explanation for large declines in resident native insectivores (including two shallow endemic species) and introduced birds at Zealandia (Miskelly 2018). Endemic species that have been mentioned as "robust" competitors include whitehead, bellbird, North Island robin, and South Island robin (Miskelly & Robertson 2002; Empson & Fastier 2013; Graham et al. 2013; Miskelly et al. 2017a; Miskelly et al. 2020b; Elliott et al. 2020). In addition, New Zealand's two deep endemic honeyeaters (tūī and bellbird) are considered to compete with each other, with either species dominant at different sites (Craig et al. 1981; Miskelly & Robertson 2002; Miskelly 2018).

The situation is clearer on Fiordland islands, where only two species responded positively to predator suppression. The South Island robin is the only predominantly insectivorous species of the two and was encountered on nearly twice as many islands as kākā. South Island robin was suggested as the reason why tomtits had disappeared from many islands in Dusky Sound (Miskelly et al. 2017a). The more comprehensive dataset presented herein points to the spread of South Island robin to nearly all islands in Breaksea and Dusky Sounds as being the likely explanation for the decline and disappearance of a guild of small insectivorous passerines. We suggest that the closely related North Island robin played a similar role at Zealandia, and possibly on Tiritiri Mātangi.

On a few mammal-free islands elsewhere, bellbirds reach extremely high densities and have been reported to have competitive impacts on tūī, tomtit, silvereye, and dunnock (Sagar & Scofield 2006; Miskelly et al. 2020b; Elliott et al. 2020). However, we found no evidence for bellbirds increasing in range or abundance following pest mammal eradication or control on small islands in Fiordland.

Interspecific competition may occur through either or both exploitative competition and the more obvious interference competition (Schoener 1983). Both mechanisms have been proposed for interactions between endemic New Zealand bird species, with North Island robins observed harassing tomtits that were carrying food to nestlings (interference competition), and bellbirds able to access flowers inside small divaricating shrubs and from less robust perches than the much larger tūī (exploitative competition; Craig et al. 1981; Empson & Fastier 2013).

New Zealand robins feed mainly on the ground, with South Island robins at Kowhai Bush, Kaikoura, spending 90% of their foraging time on and within 2 metres of the ground (Powlesland 1981a). It is therefore expected that robins could compete directly for food with other species that spend much time foraging on the ground, including tomtit, dunnock, and chaffinch. It is less likely that robins would compete for food with bird species that feed almost entirely in the canopy (e.g. grey warbler and silvereye), especially given that their prey is predominantly invertebrate species that spend their entire life-cycle among canopy foliage (Higgins & Peter 2002; Higgins et al. 2006). New Zealand robins are frequently observed being aggressive to each other (Flack 1976; Powlesland 1981b, 1983; Armstrong 1995; Armstrong et al. 1995). Agonistic displays are also directed at other species (including tomtit, fantail, and silvereye), and South Island robins were reported chasing and attacking other species that entered their territories or came close to nests, as well as aggressively defending food caches against other species (Flack 1976; Powlesland 1981b). This points to direct aggression by robins being the most likely reason why smaller bird species decline on (or are excluded from) small islands when robins become abundant.

The role of interspecific competition in structuring bird communities is widely accepted in continental ecosystems (Ricklefs & Travis 1980; Wiens 1983; Lovette & Hochachka 2006; Brown 2007; Dorazio et al. 2015), yet has received little attention from New Zealand ecologists, who have focused on the role of predation (Holdaway 1989; Innes et al. 2010). When competition has been raised as a potential limiting factor for endemic New Zealand birds, this was mainly in relation to competition from introduced mammals and vespulid wasps, rather than other bird species (Leathwick et al. 1983; Clout et al. 1995; Beggs 2001; Innes et al. 2010).

It has long been recognised that introduced bird species are a minor component of bird communities at New Zealand sites with intact forest and few or no introduced mammals present (Diamond & Veitch 1981; McCallum 1982; Girardet et al. 2001; Miskelly & Robertson 2001; Innes et al. 2010; Miskelly 2018). The observed declines of introduced bird species as deep endemic bird communities recovered at restoration sites (including Tiritiri Mātangi, Zealandia, and Fiordland islands), point to most introduced bird species as being competitively inferior to deep endemic New Zealand birds in the absence of mammalian predators. This is a complete reversal of the perceptions of early New Zealand ecologists, who considered introduced European birds to be competitively superior to endemic species (Buller 1895; Guthrie-Smith 1926; Oliver 1930).

Restoration of Fiordland islands

Restoration of Fiordland islands has focussed on the largest islands, including Resolution, Secretary, Anchor, Breaksea, Chalky, and Coal Islands (Edge et al. 2011; Miskelly & Powlesland 2013; Department of Conservation 2017; Carey 2020). The majority of islands that we surveyed are mainly regarded as "stepping-stone islands", providing potential pathways for stoats and other predators to reinvade nearby larger islands (Elliott et al. 2010b; Clayton et al. 2011; Edge et al. 2011). Where traps are maintained on small islands in Dusky and Breaksea Sounds, it is in order to prevent stoats and rats reinvading Anchor, Resolution, and Breaksea Islands, rather than having a primary goal of protecting birds on the smaller islands (Elliott et al. 2010b). The small size of the islands that we surveyed (most of which are less than 10 ha in size; Miskelly et al. 2017b, 2020) also makes them too small to maintain viable populations of land bird species, unless as part of a larger metapopulation able to move between the islands and the adjacent mainland. This means that many Fiordland islands, even if free of introduced mammals, will hold only a subset of the land bird species present on adjacent restoration islands (Department of Conservation 2017).

Anchor and Resolution Islands between them have almost the full range of surviving South Island forest bird species (Department of Conservation 2017; Miskelly et al. 2017a). However, three species that were formerly present have become extinct in the last 120 years (bush wren *Xenicus longipes*, South Island kokako *Callaeas cinerea*, and South Island piopio *Turnagra capensis*), and a further species (red-crowned parakeet) is locally extinct (Hoare 1982; Hill & Hill 1987; Miskelly et al. 2017a).

In the absence of introduced mammals, red-crowned parakeets are typically the dominant parakeet species on islands near the New Zealand mainland, and they have completely displaced yellow-crowned parakeets on at least three islands (Miskelly 1999). The red-crowned parakeet was the only parakeet species reported in the Dusky Sound catchment by Johann & Georg Forster in 1773, and Richard Henry from 1894 to 1908 (Hoare 1982; Hill & Hill 1987). It is considered extinct on the South Island mainland and all its inshore islands, following the last records in the 1980s (Read & McClelland 1984; Butler 1986), but still survives north of Cook Strait and south of Foveaux Strait (Robertson et al. 2007). Yellow-crowned parakeets were identified at two mainland sites in the Dusky and Breaksea Sound catchments by 1979, in addition to five islands in these two fiords during 1974–1986 (Bull et al. 1985, and data herein). Following stoat eradication or suppression, yellow-crowned parakeets have become widespread on islands in Dusky and Breaksea Sounds, occupying habitat where the congeneric red-crowned parakeet was formerly exclusively present. The presence of yellow-crowned parakeets (and the absence of red-crowned parakeets) is a lasting signature of human impacts on these otherwise near-pristine islands. This presents a dilemma for Fiordland conservation managers, who must choose between attempting restoration (reintroduction of red-crowned parakeets from beyond the region), and maintaining an existing population of another endemic species (also of restricted distribution) that colonised the catchments naturally, and which may die-out if red-crowned parakeets are reintroduced.

Our work also has implications for managers of ecological restoration sites throughout New Zealand. While eradication or suppression of introduced predators is likely to result in increased densities of deep endemic bird species (or opportunities for their re-introduction), restoration of robins (in particular) may result in the decline, disappearance or exclusion of other native bird species, including some endemic species.

Acknowledgements

Author contributions

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Supplementary Material

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

Appendix S1. Table of data on islands surveyed and bird species recorded, including island names, locations, and areas, dates and durations of surveys, observers, and evidence of mammal presence, available in .xlsx file.

Appendix S2. Distribution of New Zealand falcon (*Falco novaeseelandiae*) on 71 Fiordland islands over two time periods.

Appendix S3. Distribution of weka (*Gallirallus australis*) on 71 Fiordland islands over two time periods.

Appendix S4. Distribution of kererū (*Hemiphaga novaeseelandiae*) on 71 Fiordland islands over two time periods.

Appendix S5. Distribution of kākā (*Nestor meridionalis*) on 71 Fiordland islands over two time periods.

Appendix S6. Distribution of kea (*Nestor notabilis*) on 71 Fiordland islands over two time periods.

Appendix S7. Distribution of yellow-crowned parakeet (*Cyanoramphus auriceps*) on 71 Fiordland islands over two time periods.

Appendix S8. Distribution of long-tailed cuckoo (*Eudynamys taitensis*) on 71 Fiordland islands over two time periods.

Appendix S9. Distribution of rifleman (*Acanthisitta chloris*) on 71 Fiordland islands over two time periods.

Appendix S10. Distribution of South Island saddleback (*Philesturnus carunculatus*) on 71 Fiordland islands over two time periods.

Appendix S11. Distribution of grey warbler (*Gerygone igata*) on 71 Fiordland islands over two time periods.

Appendix S12. Distribution of bellbird (*Anthornis melanura*) on 71 Fiordland islands over two time periods.

Appendix S13. Distribution of tūī (*Prosthemadera novaeseelandiae*) on 71 Fiordland islands over two time periods.

Appendix S14. Distribution of mohua (*Mohoua ochrocephala*) on 71 Fiordland islands over two time periods.

Appendix S15. Distribution of brown creeper (*Mohoua novaeseelandiae*) on 71 Fiordland islands over two time periods.

Appendix S16. Distribution of New Zealand fantail (*Rhipidura fuliginosa*) on 71 Fiordland islands over two time periods.

Appendix S17. Distribution of tomtit (*Petroica macrocephala*) on 71 Fiordland islands over two time periods.

Appendix S18. Distribution of South Island robin (*Petroica australis*) on 71 Fiordland islands over two time periods.

Appendix S19. Distribution of silvereye (*Zosterops lateralis*) on 71 Fiordland islands over two time periods.

Appendix S20. Distribution of blackbird (*Turdus merula*) on 71 Fiordland islands over two time periods.

Appendix S21. Distribution of dunnock (*Prunella modularis*) on 71 Fiordland islands over two time periods.

Appendix S22. Distribution of chaffinch (*Fringilla coelebs*) on 71 Fiordland islands over two time periods.

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