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RESEARCH

Do fragmented forests host sufficient birds for forest restoration on Banks Peninsula, New Zealand?

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Abstract: Agricultural areas set aside for native forest restoration are often in highly fragmented landscapes. This fragmentation can reduce local abundance of native avifauna that carry out bird-plant mutualisms for forest regeneration. Te Whenua Ora | High Bare Peak (HBP) is a fragmented forest landscape on Banks Peninsula transitioning back into continuous forest. Five-minute bird counts (5MBCs) in forest were used to compare the diversity and abundance of bird species at HBP with that of Hinewai Reserve, a nearby ecological restoration project that has naturally regenerated back into forest over more than 35 years. High Bare Peak had more introduced bird species than Hinewai, likely due to the forest patches being smaller and in close proximity to pasture, but the two sites had similar counts of pollinating and seed-dispersing native bird species. The mean number of korimako | bellbirds (*Anthornis melanura)* was the same at HBP and Hinewai (0.8 per 5MBC), and there were more tauhou | silvereyes (*Zosterops lateralis*) at HBP than at Hinewai (0.99 vs. 0.56, respectively). Kererū (*Hemiphaga novaeseelandiae*) counts were low at both Hinewai and HPB (0.2 and 0.06, respectively), but kererū are often under-represented in 5MBCs. These results indicate that bird diversity and abundance should be sufficient for bird-plant mutualisms to develop in forest patches at HBP at least to a level similar to that in Hinewai. This study suggests that small forest patches can play an important role in the restoration of native forests through maintaining populations of key pollinating and seed-dispersing bird species.

Keywords: pollination, seed dispersal

Introduction

Fragmentation of forests is usually a result of habitat loss, which reduces the quality and size of remaining habitat for species reliant on forests. Many New Zealand forest bird species are endangered, threatened, or declining, in part due to reduction in habitat and loss of connectivity with native forests (Innes et al. 2010). Native birds are the most important vertebrate pollinators and dispersers of seeds, although there are contributions from native bats and lizards (Craig et al. 2000). Today, approximately 30% of New Zealand's trees have bird-visited flowers and 59% of tree species produce fleshy fruit that is eaten by birds (Kelly et al. 2010). Prior to human arrival in New Zealand, avian seed dispersers and pollinators would have included at least four extinct species: piopio (*Turnagra capensis*), at least two moa species (*Euryapteryx* spp.), and huia (*Heteralocha acutirostris*) (Anderson et al. 2006). Many surviving seed-dispersing birds are greatly reduced in range, with only four native species being widespread on the mainland and continuing to play a large-scale functional role in seed dispersal: kererū (*Hemiphaga novaeseelandiae*), tūī (*Prosthemadera novaeseelandiae*), korimako | bellbird (*Anthornis melanura*), and the recently arrived tauhou | silvereye (*Zosterops lateralis*) (Kelly et al. 2010). The introduction of blackbirds (*Turdus merula*), song thrushes (*Turdus philomelos*), and starlings (*Sturnus vulgaris*) from Europe has filled some of the lost seed dispersing roles, although these species also play a disproportionate role in dispersing non-native weed species into native forests (MacFarlane et al. 2016).

Native forest restoration sites are usually chosen in areas with pre-existing and naturally regenerating forests (Norton et al. 2018). Many of these areas are marginal pasture lands on hill country prone to erosion and with low economic return (Trotter et al. 2005). Banks Peninsula is a good example of restoration on marginal hill country, with regeneration usually occurring through natural succession following retirement of land from farming. The largest and best-studied example is Hinewai Reserve, a 1500 ha ecological restoration area which started in 1987 as pasture with a 109 ha block of remnant forest and gorse (*Ulex europaeus*) (Fig. 1; Wilson 1988). After more than 35 years of a minimal interference management approach, where the forest was left to recover naturally (assisted by the removal of herbivorous animals and invasive weeds), Hinewai is now largely covered by continuous second-growth forest; it also includes a few fragments of old growth podocarp and red beech (*Nothofagus fusca*) (Wilson 1994; Wilson 2003). Importantly, an emerging canopy of bird-pollinated and bird-dispersed trees demonstrates that the species and densities of birds present at Hinewai have been sufficient to restore this functional relationship (Wilson 1994; Wilson et al. 2017).

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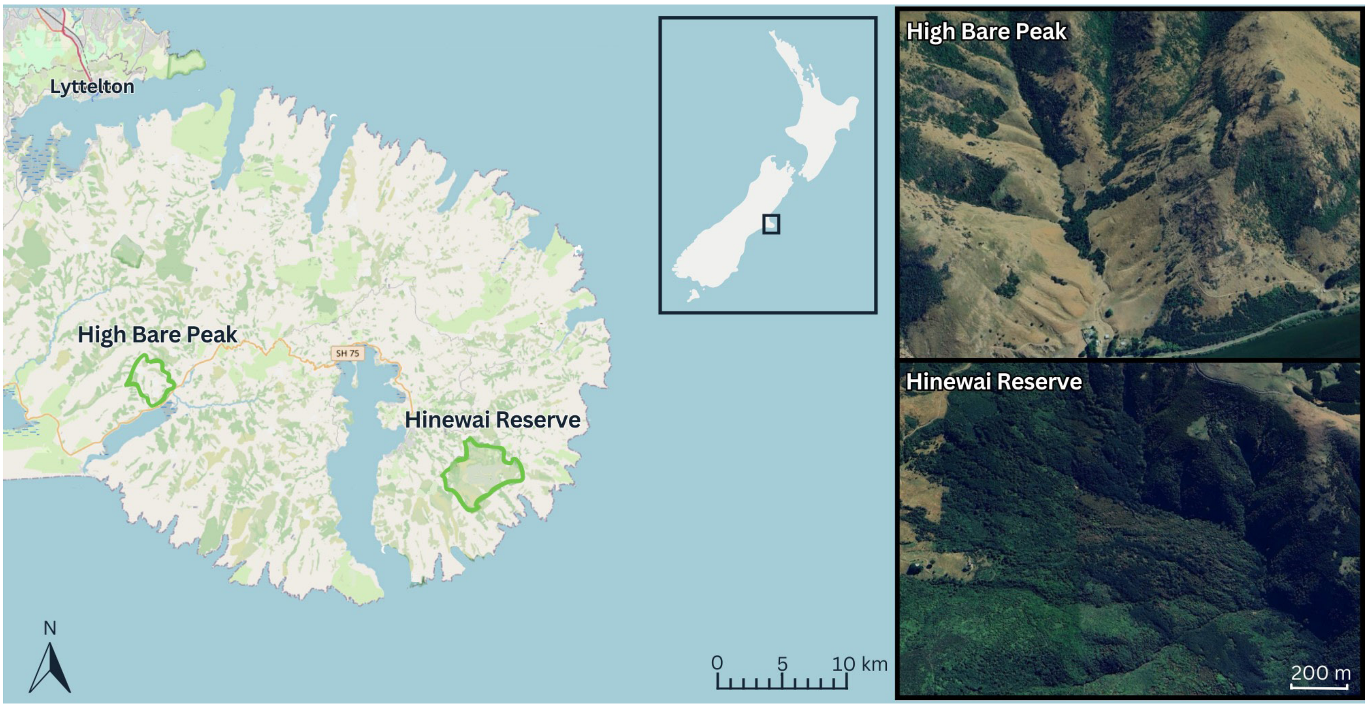

Figure 1. Location of Te Whenua Ora | High Bare Peak and Hinewai Reserve on Banks Peninsula. Green patches represent vegetation features. Images to the right show the greater extent of native forest cover clearly evidenced at Hinewai. Images modified from NZ Topo Map and Google Earth.

Te Whenua Ora | High Bare Peak (HBP) in Little River is a typical example of the present landscape of Banks Peninsula, with the land used for pastoral farming for over 100 years and patches of regenerating forest surviving in areas less accessible to livestock. Kānuka (*Kunzea ericoides*) is an early successional and wind-dispersed forest species that is common at both HBP and Hinewai. The 540 ha property at HBP was recently purchased for the purpose of conservation, primarily through natural regeneration of native forest. Given the highly modified landscape and fragmentation of the forest at HBP, the landowners were concerned that native bird diversity and abundance would be low, which might then constrain regeneration. In this study we compared the bird fauna of HBP with that of Hinewai Reserve. By comparing these two sites we determined whether the avifauna differs between a newly established reserve with only fragmented forest patches and an older reserve which is nearly continuous forest. We aimed to determine whether the current avifauna at HBP includes the most important bird species for pollination and seed dispersal of native plants. Specifically, we addressed the following questions: (1) what is the species composition of avifauna at HBP and Hinewai?; (2) are the abundances of pollinating and seed-dispersing birds at HBP likely to be sufficient to facilitate forest regeneration?

Methods

To compare bird species richness and relative abundance we used five-minute bird counts (5MBC) at both HBP (43°46'S, 172°45'E) and Hinewai (43°49'S, 173°01'E) (Dawson & Bull 1975). We chose 5MBCs for this study as they are comparable to other studies using 5MBCs, with over 200 000 counts undertaken in New Zealand since the method was developed (Hartley 2012). Five-minute bird counts give a good indication of the species present and an index of their relative abundance (Hartley 2012).

Count stations at both locations were restricted to areas of native forest, as our study focused on forest recovery through seed dispersal and pollination by forest birds. At HBP the forest is dominated by kānuka, an early successional species, and a variety of second-growth forest species (Wilson 1992). The forest at Hinewai is similarly dominated by kānuka, and mixed second-growth forest, but has a higher abundance of species susceptible to animal browsing, such as fivefinger (*Pseudopanax arboreus*) and sevenfinger (*Schefflera digitata*). The main difference is the large presence of gorse and remnant red beech forest at Hinewai (Wilson et al. 2017) and areas of open pasture and pine forests at HBP. Both properties were subject to light levels of predator control during the study period, which mostly targeted possums (*Trichosurus vulpecula*).

Ten bird count stations were set up at each site, and each station was spaced at least 100 m apart (most > 200 m) to avoid double counting (Dawson 1981). The bird counts were run in September–October 2023, as birds are most conspicuous in spring. In total, 180 5MBCs were completed over ten days, with 90 counts at each of the two sites. Two trained observers counted birds at one location on the same day, starting at opposite ends of the site. The next day the same process was repeated at the other location. The only exception was 5–6 October, when only a single observer recorded birds. At each location the species and number of birds seen or heard was recorded. If a bird was seen first and later heard, or vice versa, only the first instance was recorded.

Some studies using 5MBCs set a distance boundary of 50 m, but we instead recorded all birds seen and heard regardless of distance. In practice, all visual sightings were within c. 25 m due to the dense nature of the forest. Likewise, the dense vegetation also made it difficult to ascertain if a call or song from a bird was within or beyond a 50 m boundary. To avoid making such arbitrary decisions, we included all birds heard, although in practice it was judged that most of these were within 50 m of the observer. Any birds seen between sites were also noted, but not included in the counts. Bird counts took place between 07:30 and 13:00 hrs NZDT to avoid the morning chorus and the heat of the afternoon. The start time was recorded for each count. Counting took place only on days with no to light wind (leaves rustling, but branches not in constant motion) and no precipitation.

The avian community composition of the two sites was compared using permutational multivariate analysis of variance; this was implemented using *adonis2* with a Bray Curtis distance matrix from the "vegan" package (Oksanen et al. 2013) in R version 4.2.1 (R Core Team 2022). Differences in relative abundances between HBP and Hinewai for each bird species were analysed using a Generalised Linear Mixed Model (GLMM) from the "glmmTMB" package (Brooks et al. 2023). We also used a GLMM to test whether combined total counts of the five main pollinating and seed dispersing species (kererū, bellbird, silvereye, song thrush, and blackbird; Kelly et al. 2006) were similar between the two locations. Both GLMMs had a Poisson error distribution, location as the fixed effect, random terms for station number and date to account for repeated counts, and row ID to allow for overdispersion. The package "car" was used to generate analysis of deviance (Fox et al. 2012).

Results

At HBP a total of 23 bird species were observed (11 native and 12 introduced), while at Hinewai 17 species were observed (9 native and 8 introduced; Table 1). One bird species was recorded at Hinewai but not HBP (rifleman), while seven mainly open-country species were recorded at HBP but not Hinewai (Australasian harrier, kingfisher, welcome swallow, California quail, goldfinch, redpoll, and starling; scientific names in Table 1). The multivariate analysis of variance comparing the bird community composition of HBP and Hinewai found a significant difference between the two sites ($F_{(1–18)} = 14.32$, $P < 0.001$).

The second set of analyses tested whether each bird species was more prevalent at HBP or Hinewai (Table 2). HBP had more introduced granivorous birds, with significantly more chaffinches, greenfinches, and yellowhammers compared to Hinewai (Table 1). The only native birds which were

Table 1. Mean number of birds heard or seen per 5MBC within Hinewai and HBP. The statistical significance of differences between the two sites is shown by the P value generated by the GLMM; bold values indicate significance and the site with the higher mean.

Scientific name	Common names	Hinewai	HBP	P
Native/endemic birds				
Acanthisitta chloris	tītitipounamu, rifleman	0.111	0	0.993
Anthornis melanura	korimako, bellbird	0.844	0.756	0.655
Chrysococcyx lucidus	pīpīwharauroa, shining cuckoo	0.044	0.089	0.370
Circus approximans	kāhu, Australasian harrier	0	0.044	0.999
Gerygone igata	riroriro, grey warbler	0.933	**1.500**	**< 0.001**
Halcyon sancta	kōtare, kingfisher	0	0.022	0.999
Hemiphaga novaeseelandiae	kererū	**0.222**	0.056	**0.034**
Hirundo neoxena	warou, welcome swallow	0	0.078	0.999
Mohoua novaeseelandiae	pīpipi, brown creeper	**1.489**	0.344	**< 0.001**
Rhipidura fuliginosa	pīwakawaka, fantail	0.533	**0.800**	**0.039**
Petroica macrocephala	miromiro, tomtit	**1.133**	0.167	**< 0.001**
Zosterops lateralis	tauhou, silvereye	0.556	**0.989**	**0.022**
Introduced birds				
Acanthis flammea	redpoll	0	0.022	0.999
Alauda arvensis	skylark	0.022	0.022	0.999
Callipepla californica	California quail	0	0.222	0.999
Carduelis carduelis	goldfinch	0	0.033	0.999
Carduelis chloris	greenfinch	0.033	**0.444**	**< 0.001**
Emberiza citrinella	yellowhammer	0.011	**0.333**	**< 0.001**
Fringilla coelebs	chaffinch	0.422	**1.700**	**< 0.001**
Gymnorhina tibicen	Australian magpie	0.011	**0.267**	**0.003**
Prunella modularis	dunnock	0.067	0.078	0.767
Sturnus vulgaris	starling	0	0.011	0.999
Turdus merula	blackbird	0.356	0.400	0.744
Turdus philomelos	song thrush	0.378	0.200	0.088
Important seed dispersers and pollinators	Combined total of bellbird, silvereye, kererū, blackbird and song thrush	2.356	2.401	0.951

Table 2. An example of the GLMM model used for each bird species (in this case, bellbird) to test for significant differences between locations with analysis of deviance and summary data generated by the model formula: glmmTMB(Bellbird ~ Location + (1|Station.number) + (1|Date) + (1|RowID), family=poisson). Significant effects ($p < 0.05$) are shown in bold.

Response: bellbird	**X^2**	**Df**	**Pr(> chisq)**	
Location	0.199	1	0.655	
Random effects	**Variance**	**Std. Dev.**		
Station.number	> 0.001	0.378		
Date	> 0.001	0.044		
RowID	> 0.001	> 0.001		
	Estimate	**Std. Error**	**Z value**	**P value**
(Intercept)	−0.357	0.179	−1.989	**0.047**
LocationHinewai	0.108	0.243	0.446	0.655

significantly more common at HBP than Hinewai were grey warblers, fantails, and silvereyes (Table 1). Grey warblers and chaffinches occurred in 93% of 5MBC at HBP, with both species averaging > 1 per count. In contrast, Hinewai had significantly higher counts of brown creepers and tomtits than HBP (Table 1), with > 1 individual of each species recorded per 5MBC at Hinewai. Bellbirds, shining cuckoos, blackbirds, song thrushes, dunnocks, and skylarks were observed in similar numbers at both locations (Table 1).

Some birds that are known to occur in these locations were not recorded in the counts. New Zealand falcon (*Falco novaeseelandiae*) and morepork (*Ninox novaeseelandiae*) have been sighted at both HBP and Hinewai but were not observed in our survey. Tūī were reintroduced at Hinewai in 2009–2010 (Wilson et al. 2017), but were not observed. A California quail was observed once at Hinewai, but only outside of the count stations, and was not included in the results.

To assess how the pollinating and seed-dispersing avifauna compare between HBP and Hinewai, combined totals of the key species (bellbird, silvereye, kererū, blackbird, and song thrush) were compared between the two locations. There was no significant difference in the combined counts between HBP and Hinewai (Table 1). When we considered one species at a time, mean counts of bellbird, blackbird, and song thrush were not significantly different between locations (Fig. 2). Silvereyes were common at both locations, though significantly more so at HBP. Low numbers of kererū were recorded overall, but significantly more were counted at Hinewai.

Discussion

Our surveys found the fragmented forests at HBP hosted all the native bird species observed at Hinewai except for rifleman. Mean numbers of important pollinating and seed-dispersing birds were similar at both sites, suggesting that lack of bird mutualists is unlikely to be an obstacle to forest regeneration at HPB. In 2016, after 35 years of forest recovery at Hinewai, about half of the forest was mixed second-growth forest. This included bird-dispersed species such as tree fuchsia (*Fuchsia excorticata*) and mahoe (*Melicytus ramiflorus*), which are common at Hinewai (Wilson et al. 2017). Given the success of native forest regeneration at Hinewai, this would suggest HBP has good potential for facilitated regeneration by birds.

Effect of fragmentation on bird diversity

HBP had a greater diversity of bird species than Hinewai. This is probably the result of a higher degree of fragmentation at HBP and greater diversity of habitat types (pasture, native forest, and pine forest) leading to increased species diversity (Andrén 1994). In this instance, more introduced and open-country bird species were recorded at HBP than at Hinewai.

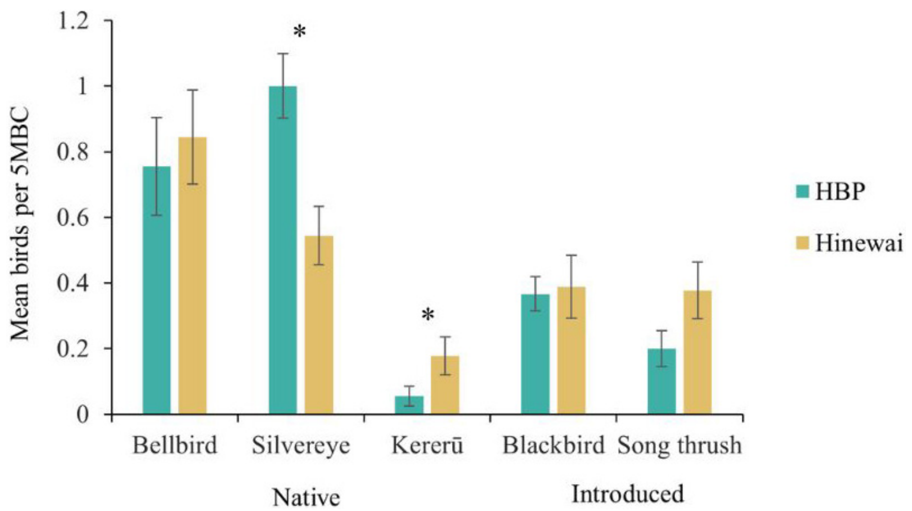

Figure 2. The mean number of important seed-disperser and pollinator avifauna seen or heard during a 5MBC at HBP and Hinewai with standard error of the mean. Asterisk* denotes species with significant difference ($p < 0.05$) between locations based on the GLMM.

The introduced greenfinch and yellowhammer use native forest edges for breeding or roosting then travel to nearby pasture for foraging (Barbaro et al. 2012). In contrast, the forest at Hinewai is largely continuous, with greater distances to forest edges from the count stations. The smaller size of the forest patches at HBP meant edge effects of pasture birds entering the forest were more pronounced (Murcia 1995). Significantly more kererū, tomtits, and brown creepers were counted at Hinewai. These native bird species tend to use the interior of forests more than the edges (Barbaro et al. 2012). Brown creepers and tomtits are insectivores, whose main food sources are typically forest edge-avoiders, which could explain their higher abundance at Hinewai (Barbaro et al. 2012). The only native birds present which prefer forest edges to the interior of forests were silvereyes, which could account for their higher abundance at HBP (Deconchat et al. 2009; Barbaro et al. 2012).

The only bird species recorded at Hinewai and not at HBP was the rifleman, which is one of the least common forest birds on Banks Peninsula (Deconchat et al. 2009; Barbaro et al. 2012). The only rifleman counted in the study were seen in the red beech forest at Hinewai, in a remnant old growth forest fragment. Red beech occurs naturally only in the south-west corner of Banks Peninsula (Wilson 1988). Rifleman are thought to be sensitive to fragmentation, as they have limited dispersal ability and nest in cavities, which are more common in areas with old trees (Deconchat et al. 2009; Khwaja et al. 2023). As the forest cover at HBP increases, habitat may become better suited for rifleman.

Seed dispersal

Dispersal of seeds by frugivores is important for the maintenance of plant communities (Carpenter et al. 2017). Hinewai and HBP had similar numbers of native seed-dispersing species (kererū, bellbird, and silvereye) and two introduced seed-dispersing species (blackbird and song thrush). However, the number of birds required for good seed dispersal is hard to define. Kelly et al. (2010) summarised studies on the dispersal of ten different New Zealand plant species, and only one of these, karo (*Pittosporum crassifolium*), showed clear evidence of dispersal failure in the absence of bird dispersers. In predator-free areas with more native bird frugivores, the number of seeds dispersed was higher than in mainland sites with predators (Bombaci et al. 2021), but this does not necessarily mean that there is dispersal failure on the mainland. Kelly et al. (2010) found little evidence of dispersal failure in the plant species they examined, as medium to high densities of birds can still remove all ripe fruit from a tree.

The mean kererū counts at HBP and Hinewai are within the range found at long-term predator-controlled fenced and unfenced sanctuaries across New Zealand, but have the potential to improve (Carpenter et al. 2021). Kererū are important seed dispersers of many native plants in New Zealand, and are known to eat the fruit of over 70 species (Clout & Hay 1989). They are the main disperser of fruit > 14 mm in diameter, which are produced by five tree species (Kelly et al. 2010). None of these large-fruited species are native to Banks Peninsula (Wilson 1988), so dispersal failure of large fruit is unlikely to be a problem in this region.

Introduced blackbirds and song thrushes were included as seed-dispersing species as they disperse native seeds, though their quantitative importance is less than that of native birds (Kelly et al. 2006). Kelly et al. (2006) found introduced birds accounted for 5% of visits to native flowers and fruit, with the blackbird responsible for 3.9% of all visits to fruit. Introduced birds also facilitate the spread of unwanted weed species, which are less likely to be spread by natives (MacFarlane et al. 2016).

Silvereyes and bellbirds are important seed dispersers as both are able to eat fruit up to 10 mm in diameter, which covers the majority of native fruiting species (Kelly et al. 2010). Other plant species with fruit diameter larger than 10 mm can be dispersed by both blackbirds and kererū, including tītoki (*Alectryon excelsus*) and supplejack (*Ripogonum scandens*) (Kelly et al. 2010) which are present at HBP. A mean of 2.0 bellbirds were counted per 5MBC on islands and protected areas (Murphy & Kelly 2001), which is higher than the average bellbird counts in this study (1.36 per 5MBC). However, the lower counts of bellbirds might be compensated for by the higher counts of silvereye at HBP than at Hinewai, which would improve the rate of seed dispersal at HBP. The total number of seed-dispersing species was similar at both sites, and given the success of tree regeneration at Hinewai, we suggest that populations of seed-dispersing species at HBP should be sufficient for native forest regeneration.

Pollination

Pollination of native trees in New Zealand appears to be more at risk from the loss and decline of native avifauna than seed dispersal (Anderson et al. 2006; Kelly et al. 2010). Bellbirds, tūī, and silvereyes are the most common avian visitors to native flowers in New Zealand (Kelly et al. 2010), although of these three, only bellbirds and silvereyes were seen at HBP and Hinewai. No tūī were seen or heard during the counts at either site. Tūī are currently recolonising the peninsula after disappearing around 1990 (Wilson et al. 2017). The New Zealand Garden Bird Survey saw tūī increase in counts by 266% between 2012 and 2022 in Canterbury (Spurr 2012; MacLeod et al. 2022). Given that tūī fly up to 30 km to search for food (Bergquist 1985), the spread of tūī into HBP (and Hinewai) could be encouraged through additional plantings of trees that produce nectar. An increase in the distribution of tūī will then in turn improve regeneration rates of other native plant species.

A previous study of tree fuchsia (*Fuchsia excorticata*) pollination at Hinewai Reserve showed that flowers were only visited by bellbirds and silvereyes, and had a pollen score below the threshold considered adequate for fruit production (Robertson et al. 2008); this suggests that pollination was limited at the time of the study. Both tree fuchsia and small-leaved kōwhai (*Sophora microphylla*), which are present at HBP and Hinewai, are typically pollen limited on the mainland (Anderson et al. 2006; Robertson et al. 2008). Silvereyes can be effective pollinators, but their beaks are too short for the larger hermaphrodite flowers of tree fuchsia (Robertson et al. 2008) and *Sophora* spp. (Kelly et al. 2006), so they act as nectar robbers on these two species. Instead, tūī and bellbird are more effective pollinators of these larger flowers. While birds such as chaffinches and house sparrows occasionally visit native flowers, their contribution to pollination is minor (Kelly et al. 2006). Even though bird-facilitated pollination could be limited for some plant species at both HBP and Hinewai, the success of regeneration at Hinewai means that fragmented forests can still have sufficient natural regeneration occurring. Increasing pest control is one method that can increase native bird populations (James & Clout 1996; Kelly et al. 2005), which can improve pollination services by bellbirds and tūī (Iles & Kelly 2014).

Forest connectivity, not the size of the forest, is a major contributor to avifauna richness and abundance in Banks

Peninsula (Barbaro et al. 2012). Small and highly fragmented forest patches can host important bird-plant mutualisms if they are well connected within the landscape (Aubert 2016). The abundance of birds observed at HBP suggests that the patches are well connected, despite the degree of fragmentation. Bellbirds, silvereyes, and kererū are all capable of crossing gaps larger than 5 km (Innes et al. 2022). This allows for connections between forest patches surrounding HBP and for the spread of seeds across pasture gaps (Innes et al. 2022).

Our findings indicate that restoration of native forest at HBP is unlikely to be hindered by a shortage of key fruit-dispersing bird species, although more work is needed to determine whether pollinator limitation is limiting fruit set. Most native bird species found in Banks Peninsula forests were observed at both HBP and Hinewai, except the rifleman, which was only observed at Hinewai. Both locations hosted similar abundances of important pollinator and fruit-eating species. Abundances were sufficient for successful plant-bird mutualisms to occur, maintaining forest regeneration (Aubert 2016). Both locations also have the potential to improve their plant-bird mutualisms, especially pollination rates, with an increase in native bird abundances through predator control (Bombaci et al. 2021). Our results suggest that small, fragmented forests can be important for the conservation of native avifauna and their contribution to biodiversity should not be overlooked. Such fragments can especially serve as starting points from which to expand and create larger and more continuous forested areas in the future.

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Additional Information and Declarations

Conflicts of interest: The authors declare no conflicts of interest.

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Author contributions: MG, JB, and DK conceived the idea and designed the study. MG carried out data collection and analysis and wrote the manuscript, with editorial contributions from JB and DK.

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