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RESEARCH ARTICLE

UN decade on ecosystem restoration

Habitat provision is a major driver of native bird communities in restored urban forests

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Abstract

1. Urbanization, and the drastic loss of habitat it entails, poses a major threat to global avian biodiversity. Ecological restoration of urban forests is therefore increasingly vital for native bird conservation, but control of invasive predators may also be needed to sustain native bird populations in cities where species invasions have been particularly severe.
2. We evaluated restoration success by investigating changes in native bird communities along a restoration chronosequence of 25 restored urban forests representing 72 years of forest development, which we compared to two target reference systems and a control system. We hypothesized that total species richness and relative abundance of native forest birds would increase with the age of restoration planting. We further hypothesized that relative abundance of rats, possums and cats would negatively impact native birds, while amount of native forest in the surrounding landscape would have a positive effect.
3. We used structural equation modelling (SEM) to investigate the relative influence of forest structure (complexity index, tree height, canopy openness, basal area, species richness and density), landscape attributes (patch area, perimeter length, landscape composition within three buffer zones, distance to the nearest road and water source) and invasive mammalian predator indices of relative abundance on total species richness and relative abundance of native forest birds.
4. Species richness increased with age of restoration planting, with community composition progressing towards that found in target reference systems. SEM revealed that years restored was a direct driver of bird species richness but an indirect driver of abundance, which was directly driven by canopy openness. Contrary to our predictions, invasive mammals had no significant effect on native bird species richness or abundance.

5. Our results demonstrate that provision and improvement of habitat quantity and quality through restoration is the vital first step to re-establishing native forest bird communities in cities.

KEYWORDS
community composition, ecological restoration, invasive species, native forest birds, structural equation modelling, urban ecology

1 | INTRODUCTION

Urbanization is a major cause of biodiversity loss, as it drastically, and often irreversibly, alters original habitat and the ecological footprint of a city extends far beyond the built environment itself (Aronson et al., 2014; Grimm et al., 2008; McKinney, 2006; Seto et al., 2012; Soanes et al., 2019). Urban areas are expanding rapidly and are expected to triple by 2030 (Seto et al., 2012). Urbanization further facilitates biological invasions, which pose another major threat to biodiversity, particularly on islands (Courchamp et al., 2003; Klotz & Kühn, 2010). Despite the conservation challenges presented by urban environments, there is growing recognition of the need to protect and enhance native biodiversity in cities for the benefit of both native species and people (Ives et al., 2016; Keniger et al., 2013; Rosenzweig, 2003; Schwartz et al., 2002; Shanahan et al., 2015). Populations of native species in cities rely primarily on urban green spaces (Lepczyk et al., 2017). By providing habitat for birds, urban green spaces may also allow city residents daily contact with charismatic species, resulting in an emotional connection with nature that could be harnessed to promote public support for conservation and restoration (Miller, 2006). Urban forests, however, tend to be small and isolated, with higher levels of invasive species and decreased vegetation complexity compared to non-urban forests (Marzluff & Ewing, 2001; McKinney, 2002). Ecological restoration is a potentially powerful tool for mitigating the detrimental effects of urbanization, as it could increase the quantity and quality of habitat available to native birds in cities (Shanahan et al., 2011).

While the response of birds to restoration can be highly species specific, studies in non-urban areas have demonstrated that restoration can increase species richness and abundance, improve nesting success and result in recolonization of locally extirpated bird species (Munro et al., 2007; Ortega-Álvarez & Lindig-Cisneros, 2012). In turn, birds benefit restoration through seed dispersal, pollination, nitrogen input and insect control (Anderson et al., 2011; Ortega-Álvarez & Lindig-Cisneros, 2012). The ability of native birds to utilize forest restoration plantings will be influenced by a complex interplay of vegetation structure, landscape attributes and predation by invasive species (Belder et al., 2018). We need a mechanistic understanding of native bird community responses to urban forest restoration in order to develop management strategies to preserve and enhance native biodiversity in cities.

New Zealand's long history of isolation, which gave rise to a unique avifauna, also left the endemic birds particularly vulnerable to predation and habitat loss. Mammalian predators, particularly ship rats *Rattus rattus*, brushtail possums *Trichosurus vulpecula* and stoats *Mustela erminea*, are generally believed to pose the greatest threat to New Zealand's native forest birds in rural landscapes with large forest remnants (Innes et al., 2010; Ruffell & Didham, 2017). Little is known, however, about the impact of invasive mammals on native birds in cities (Russell & Stanley, 2018). While predation by invasive mammals is considered the primary limiting factor for forest birds in New Zealand, one study found that when forest cover in the landscape dropped below 5%, native bird species richness declined rapidly, suggesting that under certain conditions habitat loss becomes the primary limiting factor (Ruffell & Didham, 2017).

By exploring factors influencing native forest bird communities in restored urban forests, this study investigates whether urban forest restoration can benefit native birds. We investigated how total species richness, relative abundance and community composition of native forest birds varied along a restoration chronosequence, representing 72 years of forest development. We compared restored areas with two target reference systems—lowland, temperate native forest remnants within the city and beyond the city limits, as well as with a control system—unrestored urban forest. In order to determine whether and how urban forest restoration can increase native bird biodiversity in cities, and whether these restoration efforts interact with landscape features and invasive mammals, we posed two major research questions: (a) Do native forest bird species richness and relative abundance increase over time since initial restoration planting, resulting in a community structure similar to urban or rural remnants? (b) What is the relative importance of direct and indirect effects of vegetation structure, landscape composition and invasive mammal relative abundance on total species richness and relative abundance of native forest birds?

We hypothesized that total species richness and relative abundance of native forest birds would increase with the age of restoration planting, as the canopy closes and the vegetation becomes more structurally complex. We further expected that high relative abundance of rats, possums and cats *Felis catus* would negatively impact native birds, while the amount of native forest in the surrounding landscape would have a positive effect (Figure 1; see Appendix A for the detailed a priori structural equation modelling with supporting literature).

We also hypothesized that the native bird community would change with the age of restored forest and that young restoration plantings would be dominated by small insectivores or omnivores.

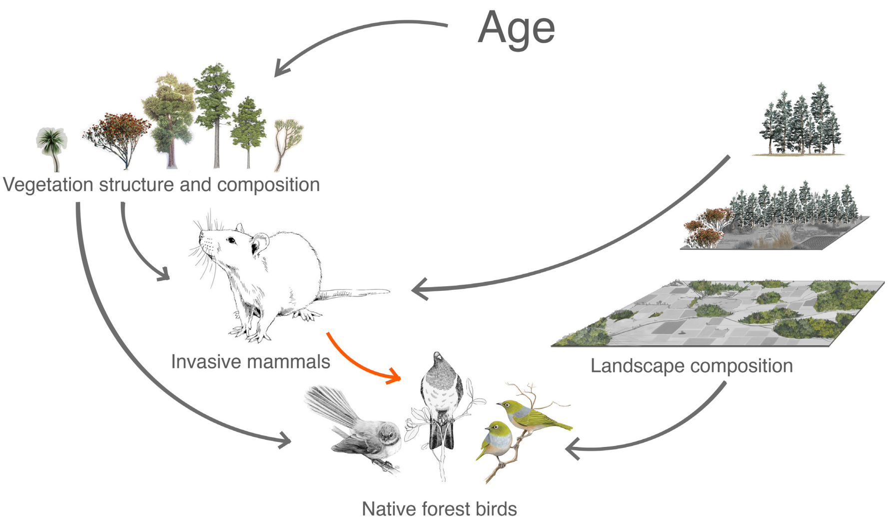

FIGURE 1 The hypothesized relationships among forest restoration and landscape composition, invasive mammals and native forest birds. Black arrows denote positive relationships, and red arrows denote negative ones

As restoration plantings age and become more similar to older urban remnants in their vegetation structure and complexity, we hypothesized that the numbers of omnivores would decrease, while the numbers of frugivores and insectivores would increase (Figure 1). Insectivores were defined as birds that only eat insects; omnivores as those that eat insects, fruit and nectar; and frugivores as those that primarily eat fruit.

2 | MATERIALS AND METHODS

2.1 | Study sites

We conducted our research in two urban landscapes centred around two cities in New Zealand's North Island, and in the two native forest remnants closest to each city. Hamilton (37°46′59.99″S, 175°16′59.99″E) has an estimated population size of 165,400 (Statistics New Zealand, 2017). The climate is temperate oceanic, with a mean annual temperature of 13.7°C and mean annual rainfall of 1,190 mm (NIWA, 2016). Hamilton is bisected by the Waikato River and spans a network of steep-sided gullies totalling approximately 770 ha or 8% of the city (Cornes et al., 2012). This gully system makes up a large proportion of Hamilton's green space (Fitzgerald et al., 2017). Despite the gully network, <2% of the city is covered by native forest (Clarkson et al., 2007). New Plymouth (39°4′0.01″S, 174°4′59.99″E) has an estimated population size of 58,300 (Statistics New Zealand, 2017). The climate is temperate oceanic with a mean annual temperature of 13.7°C and mean annual rainfall of 1,432 mm (NIWA, 2016). New Plymouth retains approximately 8.5% of its native forest cover (Clarkson et al., 2007).

The nearest rural forest remnant to Hamilton is the Hakarimata Range (37°39′45.2″S 175°07′28.1″E), which lies about 10 km northwest of Hamilton. The range forms the western boundary of the Waikato Basin with its highest point, Hakarimata, at 374 m. The range encompasses 1,850 ha of native lowland forest dominated by broadleaved podocarp species (Department of Conservation, n.d.). The nearest rural forest remnant to New Plymouth is the Kaitake Range (39°10′0″S, 173°58′1″E), encompassing about 2,400 ha of forest, which lies approximately 15 km south-west of the city. The highest point is Patuha at 684 m. The range is covered in lowland and semi-coastal forest (Clarkson, 1985).

We conducted our research in 43 forest sites comprising four types of forest across the two urban landscapes (Hamilton and New Plymouth). Due to the time-related logistic challenges of longitudinal studies that can capture larger temporal scales of habitat restoration, we used the widely implemented space-for-time chronosequence approach, which allows investigation of change over time by using multiple sites at different stages of succession as a proxy for temporal replication (Walker et al., 2010). Forest types and definitions follow those given by Wallace et al. (2017), as we used many of the same sites in our study. *Restored urban forests* ($n = 25$) are green areas within the urban matrix, dominated by native vegetation that has been intentionally planted. Restored forests were chosen to represent an age gradient from 1 to 72 years since initial planting. For the restored urban forests, a 'site' was the entire contiguous area planted with native vegetation in the same year. The sample size in each urban landscape was limited by the availability of forest restoration plantings that could fit a 20 × 60 m belt (see Bird Surveys below).

Restored urban forests were compared to three types of reference forest. *Unrestored urban forest* ($n = 6$) was defined as a forested area affected by severe anthropogenic disturbance, such as clear-felling or sand mining, that was never subsequently restored, but was left to regenerate naturally. These forests tended to be dominated by non-native vegetation. A 'site' was the patch of contiguous forest area affected by anthropogenic disturbance in the same year.

Remnant urban forest ($n = 6$) was defined as a patch of native, mature forest within the urban matrix that had never been clear-felled or mined. *Rural forest remnants* ($n = 6$) were large (>1,000 ha) areas of native lowland forest closest to the two cities. A 'site' in the rural remnants is defined as a grid of three parallel 200-m transects, with each transect a minimum of 100 m apart. Sites were a minimum of 100 m apart and were only set up below 300 m above sea level, as the goal was to sample lower altitude lowland forest. The names, years since planting, forest category and size (ha) are shown in Appendix B.

Ethical approval was not required for this study. Permission for fieldwork on public conservation land was granted by the Department of Conservation, Authorisation Number 51961-RES.

2.2 | Bird surveys

Transect lines (60–200 m length depending on the size of the site) were laid out at least 100 m apart in each of the urban sites. All terrestrial birds within a 20-m belt along each transect were counted by the same observer across all sites, thereby controlling for observer bias, during the breeding season (November–January) and during the winter (May–July), over a period of 2 years (spring 2016–winter 2018). Birds were categorized as native or introduced and, in this paper, we only include native birds in our analyses (for an analysis of the entire dataset, see Elliot Noe, 2021). Each transect was surveyed twice per study season. We changed the order in which sites were surveyed for the second visit (e.g. if a site was surveyed in the morning on the first visit, it was surveyed in the afternoon on the second) to account for diurnal patterns of bird behaviour. Only the breeding season (spring) data are used in the analyses and discussion, as they were closely matched by trends in the winter data (presented in appendices). Birds were recorded by sight and sound and were assigned to one of the two distance belts—within 10 m either side of the transect and beyond 10 m but still within the research site. Given the difficulty of accurately estimating distances from birds to the observer, especially in densely forested areas, distance sampling to correct for detectability was not used (Van Vianen et al., 2018). Therefore, our abundance estimates do not account for detectability.

Individual birds were knowingly recorded only once (e.g. if a fantail *Rhipidura fuliginosa*, followed the observer, that same individual bird was recorded as one observation) and birds flying above the canopy were not included in the analyses. Bird counts were conducted from an hour after sunrise to an hour before sunset. Counts did not take place in strong winds or heavy rain to minimize possible bias caused by weather.

We calculated species richness as the total number of unique species detected at a site over the two visits. We then calculated the average species richness from the 2 years of spring bird counts. We pooled the 2 years of data and undertook counts on two different days per year to compensate for variation in weather conditions which affect bird behaviour and detectability (Hartley, 2012; Simons et al., 2007). When calculating species richness, we took into account birds detected both within the 20 m belt and beyond, but still within the site. Native forest bird relative abundance was calculated using only the birds detected within the 20 m belt, standardized as the mean number of individuals counted per 0.4 ha (i.e. a 20 × 200 m belt) across all surveys at a site. The bird count methods are a modified version of those used by Manaaki Whenua – Landcare Research in their Hamilton City biennial bird counts (e.g. Fitzgerald & Innes, 2014). These use a 20 × 500 m belt which gives numbers of birds counted per hectare. The small size of our study sites limited the maximum transect length to 200 m.

To assess the adequacy of our sampling effort in the six forest types to detect total species richness, we used sample size-based rarefaction and extrapolation sampling curves for species richness using the iNEXT package in R (Hsieh et al., 2016). We then quantified sample completeness to determine the estimated proportion of species detected from the predicted species pool by plotting sample coverage with respect to the number of sampling units (bird count transects) using the iNEXT package in R.

2.3 | Vegetation measurement

Vegetation structure and composition will determine whether a site can provide adequate nesting material, protection from predators and foraging resources for a given bird species. Vegetation variables found to increase native bird species richness or abundance include the amount of native vegetation (Chace & Walsh, 2006; Day, 1995; Marzluff & Ewing, 2001; Threlfall et al., 2016; van Heezik, Smyth, & Mathieu, 2008), vegetation complexity (Belaire et al., 2014; Marzluff & Ewing, 2001; Stagoll et al., 2010; Threlfall et al., 2016), tree height (Jokimäki, 1999; Vale & Vale, 1976) and canopy cover (Belder et al., 2018; Vesk et al., 2008).

To quantify potential foraging, roosting and nesting resources, we measured vegetation structure and composition within three randomly located 10 × 10 m^2 subplots within each site. These subplots were set up by Wallace et al. (2017) at all sites, apart from the rural forest remnants, one urban remnant and one young restored forest. Subplots were a minimum of 1 m away from each other and from the forest edge. Subplots were a maximum of 10 m from the bird transects.

Vegetation structural complexity was measured by dividing the vegetative cover into six vertical strata: <0.3, 0.3–2, 2–5, 5–12, 12–25 and >25 m above the ground. Per cent vegetation cover in each stratum was visually estimated and coded as: 1 (<1%), 2 (1%–5%), 3 (6%–25%), 4 (26%–50%), 5 (51%–75%) and 6 (76%–100%). The values for the three subplots were averaged for each stratum and the average values for each site summed up to give a single complexity index value for each replicate site, ranging from 0 to 36 (Hurst & Allen, 2007). Tree heights were measured using an inclinometer—the seven tallest canopy trees were measured per subplot, for a total of 21 trees per site and the average tree height per site was calculated. Canopy openness was measured by taking hemispherical photos of the canopy from 1 m above the ground in each subplot. Images were analysed using Gap Light Analyzer v. 2.0 (Institute of Ecosystem Studies, Millbrook, New York, USA), and the values from the three subplots were averaged to give one value for each site. All live trees ≥2.5 cm diameter at breast height (DBH = 1.4 m) rooted within the three subplots were identified to species and the DBH of each stem was recorded. DBH data were used to compute total basal area per hectare for each site. Sapling counts were conducted to provide data on the regeneration of tree and shrub species. Saplings are defined as woody plants <2.5 cm DBH and were tallied by species in one randomly chosen quarter of each subplot.

Data on canopy openness, basal area per hectare and sapling species richness and density were collected by Wallace et al. from 2015 to 2016. The same methods were used to collect data in 2017 for the sites added in this study. Data on tree height and structural complexity for all sites were collected in 2017.

2.4 | Invasive mammal monitoring

Indices of relative abundance of invasive mammals within each site were collected using chew cards for rats and possums and camera traps for cats. Chew cards are an increasingly widely used monitoring device for mammals in New Zealand, as they are cheap, easy to use and highly sensitive to possums and rodents (Forsyth et al., 2018; Sweetapple & Nugent, 2011). Chew card indices are correlated with other indices of possum and rodent abundance, which have been shown to relate to nesting success for several native bird species (Armstrong et al., 2006; Forsyth et al., 2018; Innes et al., 1999; Innes et al., 2004; Ruffell et al., 2015; Sweetapple & Nugent, 2011).

The chew cards were 10 × 20 cm sheets of corrugated plastic with the edges filled with peanut butter and aniseed. Ten chew cards were nailed to the nearest tree approximately 30 cm off the ground at 20-m intervals along the transects used for bird counts and were deployed for two nights over the same time period as the bird counts (Sweetapple & Nugent, 2011). A two-night deployment period was recommended by Ruffell et al. (2015), as it provides an appropriate balance between detection and saturation probabilities across a wide range of rat and possum relative abundances. In younger sites where the trees were too small, chew cards were mounted on metal rods. A relative index of rat and possum abundance was calculated as the proportion of chew cards bitten by rats and possums respectively.

Rats and possums were controlled by councils or community groups at most (37 of 43) study sites. Control methods varied widely among sites, but we were unable to assign a reliable index of predator control effort to each study site due to insufficient information on the timing of control and spacing of devices. Vegetation, landscape and predation will interact with predator control effort to determine mammalian presence and abundance at a site.

While there is currently no standardized survey method for cats in New Zealand, camera traps are an increasingly popular tool for monitoring feral and domestic cats (Glen et al., 2014; Nichols et al., 2019; Woolley & Hartley, 2019). Three baited camera traps at small sites (<5 ha) and five at larger ones (≥5 ha) were set up around the periphery of each site a minimum of 1 m from the edge and a maximum of 20 m from the transects, at roughly even intervals, facing inwards, to maximize the likelihood of animals entering or leaving the site detecting and investigating the camera trap lures (Lincoln, 2016). Camera traps were left out over a period of two nights. We used 2016 Browning Strike Force Elite cameras, which have a picture trigger and recovery speed of 0.65 and 1.3 s, respectively, and a detection range of 15 m. The lure consisted of cotton wool soaked in fish oil, placed in a perforated plastic vial and pegged to the ground 1.5 m in front of the cameras (Glen et al., 2014). Cameras were mounted on trees with the lens 10 cm above the ground. Cameras were programmed to take five still photographs when motion triggered. Photographs of the same species <1 min apart were counted as a single detection. A relative index of cat abundance was calculated as the number of individually distinguishable cats detected over the 48-hr period.

2.5 | Landscape measures

Landscape characteristics that have been shown to influence bird use of a site include the shape, size and isolation of an area. Patch size has consistently been found to positively affect species richness (Beninde et al., 2015; Donnelly & Marzluff, 2004; Drinnan, 2005; Palmer et al., 2008). A study of native bird populations on Banks Peninsula concluded that native forest within 200–400 m had a strong positive effect on birds observed within a fragment (Deconchat et al., 2009).

For each site we measured patch area, perimeter length, landscape composition within three buffer zones and distance to the nearest road and water source. Because different bird species operate on different spatial scales, landscape composition was considered according to three scales—within 200 m, 400 m and 3 km radii buffer zones around the periphery of each site. Patches of native vegetation within this range were found by Deconchat et al. (2009) to have the strongest positive effect on bird populations on Banks Peninsula, New Zealand. Initial data analysis revealed that the 200-m buffer zone was most strongly correlated with response variables (Appendix C). Therefore, further analyses only used the 200-m buffer zone. Landscape composition within the 200-m buffer zone was classified on the basis of the New Zealand Land Cover Database v. 4.1 (LCDB), which is a regularly updated national map of land cover produced from satellite imagery collected in the southern hemisphere summers of 1996/1997, 2001/2002, 2008/2009 and 2012/2013. The LCDB uses a 1-ha minimum mapping unit (MMU) and the data are referenced to the New Zealand Transverse Mercator 2000 projection (NZTM2000) which uses the NZ Geodetic Datum 2000 (NZGD2000). The LCDB categories were combined into nine land cover categories: native forest, built environment, exotic crop/grassland, exotic forest, water, native scrub, exotic scrub, gravel and native wetland. The area of each land cover type within the 200-m buffer zone was calculated using ArcGIS.

2.6 | Statistical analysis

2.6.1 | Change in bird communities with age of restored forest

We fitted GLMs with a Poisson error distribution to first determine whether any general relationships exist between time since initial restoration planting and native forest bird species richness and total abundance, as well as the abundance of the four most frequently detected native birds—fantail, tūī *Prosthemadera novaeseelandiae*, grey warbler *Gerygone igata* and silvereye *Zosterops lateralis*. We tested for differences in native bird species richness, total abundance and the abundances of the four bird species among the three reference categories (urban remnant, rural remnant and unrestored) using one-way ANOVA. We first confirmed the equality of variances across groups with the Levene's test for homoscedasticity, which is robust to departures from normality (Levene, 1960).

For a visual representation of the bird community composition (relative abundance of all native forest bird species detected) in each forest type, we used a non-metric multidimensional scaling (NMDS) ordination in the VEGAN package in R with the Bray–Curtis dissimilarity index (Oksanen, 2011). Species abundance data were square-root transformed and standardized using a Wisconsin double relativization (Oksanen, 2011). The mean number of individuals for the two springs was used in the first ordination and the mean number of individuals for the two winters was used in the second. The data matrix consists of 10 species and 43 samples.

To test for differences in bird community composition among forest types, we performed permutational multivariate analysis of variance (PERMANOVA) using the VEGAN package in the R (Anderson, 2001). Analyses were based on Bray–Curtis dissimilarity with 999 permutations. We evaluated which forest types differed significantly from each other using the pairwise 'adonis' function in the R (Martinez Arbizu, 2019).

2.6.2 | Drivers of native forest bird species richness and abundance

We first tested for spatial autocorrelation of native bird species richness and total abundance among restored forests by calculating Moran's *I* using the SPDEP package in the R. We found no evidence of spatial autocorrelation for either species richness ($I = 0.09$, $p = 0.16$) or total abundance ($I = -0.27$, $p = 0.95$). Using SEM with the PIECEWISESEM package in the R (Lefcheck, 2016), we evaluated direct and indirect effects and the relative importance of age, forest structure, landscape attributes and indices of invasive mammal abundance on native bird species richness and total abundance.

We used theory, previous studies and expert knowledge to develop an a priori model of hypothesized direct and indirect relationships among our measured variables (Appendix A). Where necessary, variables were log (base e) or square-root transformed to meet assumptions of normality, and then scaled to unit variance. We used GLMs for possum and rat indices of relative abundance which were binomially distributed (due to the binary response variable of whether a chew card detected a possum or rat over the 48-hr period), as well as for native canopy species richness, native bird species richness and total abundance which were Poisson distributed. We used the same a priori model to predict native bird species richness and total abundance. Model fit was evaluated using Shipley's test of directed separation (Fisher's *C*) where $p > 0.05$ indicates that the data do not differ significantly from the specified model. Thus, models with $p > 0.05$ represent the data well. After constructing the linear model and GLM that made up our SEM, we specified correlated errors, that is, pairs of variables that we predicted may appear to be correlated but which we did not believe to have a causal relationship (Lefcheck, 2018). We then examined the 'tests of directed separation' output to identify any significant ($p \leq 0.05$) causal pathways among our variables that we may have overlooked. Once these were added to the model, we removed non-significant ($p > 0.05$) pathways and variables that were not significantly related to the response variables one by one and examined the effect of their removal on the Akaike information criterion (AIC). We present the model with the lowest AIC score. We report the standardized coefficients for each path where possible and unstandardized coefficients for Poisson distributed data. All statistical analyses were performed in R version 3.5.2 (R Core Team, 2018).

3 | RESULTS

We observed 1,343 individuals comprising 10 species of native forest birds over the course of the study (Appendix D). Species richness at sites ranged from 0 to 8. Three endemic birds were only detected in rural remnants; one was only detected in urban and rural remnants. We detected only five native species in restored forests in both seasons. Although there were some differences in species detection rates in younger versus older restored forests, overall detection rates were high, and it is likely that only one to three species went undetected in the sites with lowest sample coverage (Figure 2). We calculated a sample coverage estimate of 100% for all six forest types (Appendix E), indicating that while we may have missed an occasional rare species, our detection rate was still extremely high.

3.1 | Change in bird communities over time

Native bird species richness increased with time since restoration (spring: Figure 3a, Table 1; winter: Appendix F). The youngest restored forests (<5 years since initial planting) lacked native forest birds. After approximately 5 years, restoration plantings were capable of supporting some native species, such as fantails and silvereyes, with further colonizations of rarer species, such as grey warblers, after 8 years. Tūī were first detected in restoration plantings after 10 years (Appendix G). Unrestored forests supported significantly fewer native bird species compared to remnants (spring: Figure 3a, Table 1, winter: Appendix F).

Native bird total abundance did not increase significantly with time since restoration (spring: Figure 3b, winter: Appendix F). Remnants supported significantly higher total abundances of native birds compared to unrestored forests (Figure 3b, Table 1). When focusing on individual bird species, regression models revealed that

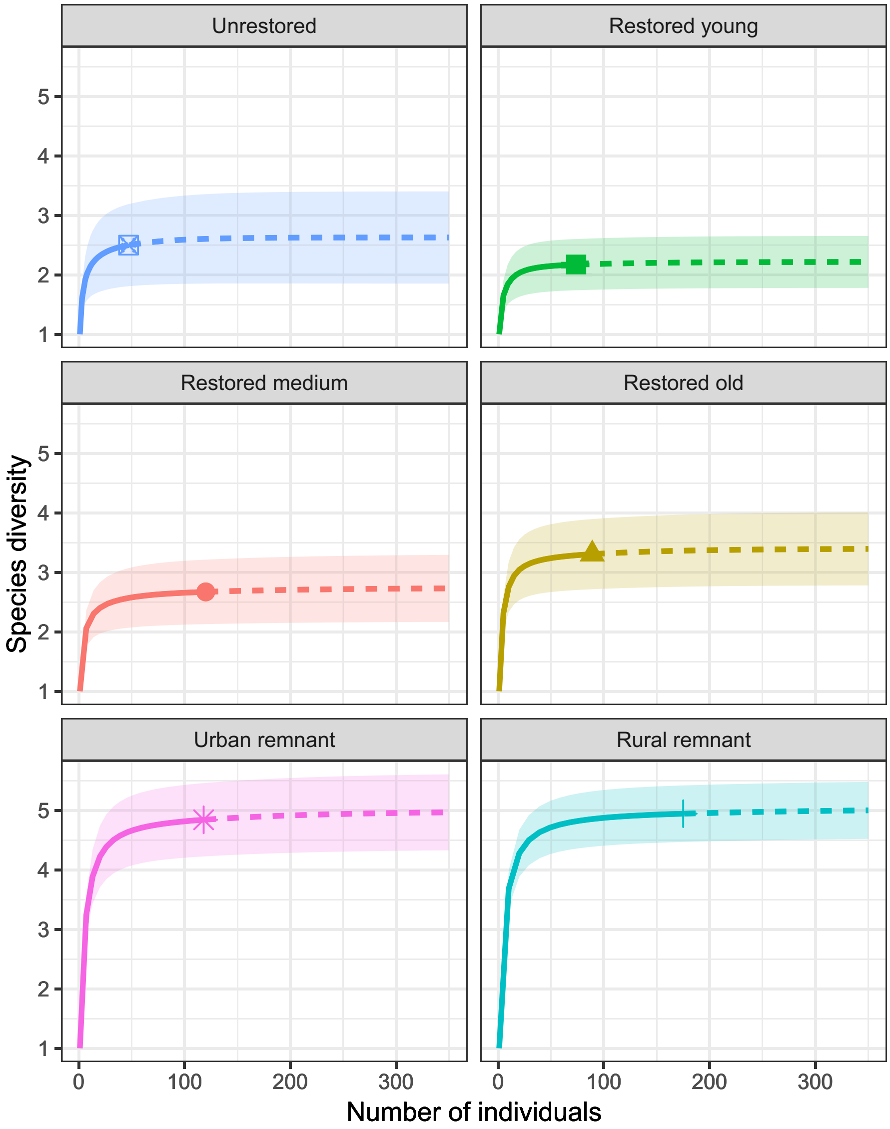

FIGURE 2 Sample size-based rarefaction (solid line segment) and extrapolation (dotted line segments) sampling curves for species richness ($q = 0$) with 95% confidence intervals (shaded areas) for the spring bird count data at six forest types. Forest types are represented by different symbols and colours. Restored sites were divided into young (1–10, $n = 8$), medium (13–27, $n = 10$) and old (34–72, $n = 7$)

fantail and tūī abundance increased with time since restoration (Appendix G). Compared to unrestored sites, both urban and rural remnants supported significantly higher abundances of fantails, while rural remnants supported more grey warblers. The effect of age of restored forest on grey warbler and silvereye abundance was not significant (Appendix G).

In addition to changes in species richness, the NMDS ordination revealed shifts in native bird community composition across site age and forest type (spring: Figure 3c, winter: Appendix F). In particular, we found a distinct gradient of bird community dissimilarity, that is, a shift in the polygons from the bottom right corner (young restored forests) through to the top left corner (urban and rural remnant forests). PERMANOVA revealed significant differences in the structure of the native bird community, that is, in the relative abundances of bird species that make up the species assemblages in these forests, among forest types for the spring ($F_{5,37} = 3.31$, $p = 0.001$) and winter ($F_{5,37} = 2.93$, $p = 0.001$). We found that for the spring data, rural remnants differed significantly from four other forest types—unrestored, young, medium and old restored.

3.2 | Drivers of native forest bird species richness and abundance

Native bird species richness and total abundance decreased significantly with increasing canopy openness and increased with basal area, tree height, native sapling species richness and native canopy species richness (Appendix H). Species richness further increased with vegetation complexity. Of the landscape attributes, site area had a significant, positive effect on native bird species richness and total abundance (Appendix I). Species richness also increased with perimeter length (Appendix I) and amount of native forest cover in a 200-m buffer (Appendix B). No significant effect was found for built environment, exotic grass cover, exotic forest cover or amount of water in the surrounding 200-m buffer (Appendix B). Contrary to our predictions, rat, possum and cat relative abundance had no significant effect on native bird species richness or total abundance (Appendix J).

The final native bird species richness SEM fit the data well (Figure 4a), explaining 59% of the variation in native bird species

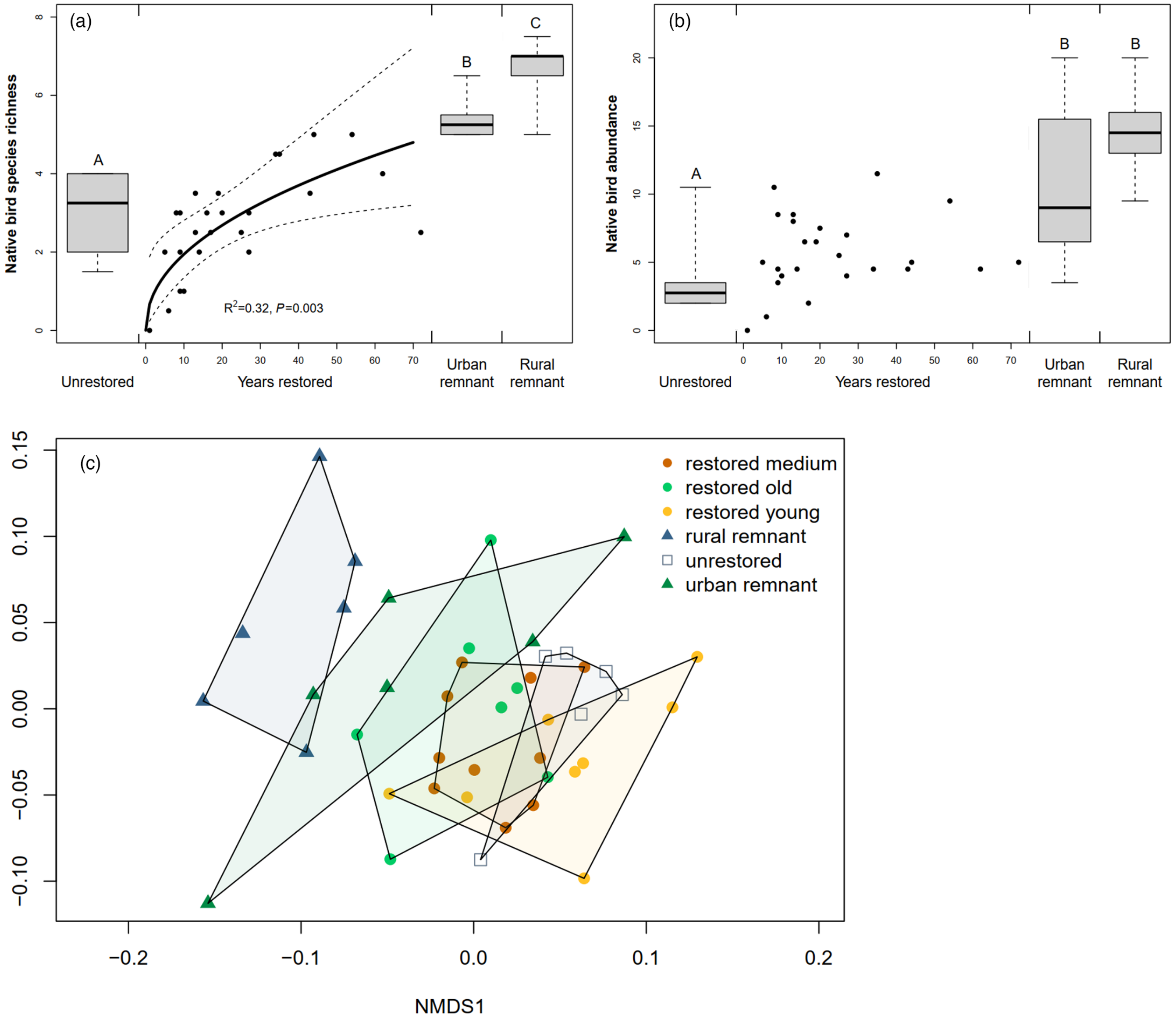

FIGURE 3 Mean native bird (a) species richness and (b) total abundance (individuals per 0.4 ha) for spring counts in restored forests over time (middle section of each bivariate plot, *n* = 25), compared with unrestored, urban and rural remnants (boxplots). Different letters above the bars indicate significant differences among sites ($p \le 0.05$). Scatterplot points represent individual restored forests. Significant relationships are shown with solid lines which represent the fitted values from a Poisson regression model. (c) Plot of the first two dimensions of the non-metric multidimensional scaling (NMDS) ordination of the 43 study sites and mean spring native bird total abundance data (stress = 0.18). The distance between points on the ordination is a relative measure of their similarity. Site types are represented by different symbols and colours (each point is a site). Restored sites were divided into young (1–10, *n* = 8), medium (13–27, *n* = 10) and old (34–72, *n* = 7)

richness (for a table summary of results from the SEM, see Appendix K). The model also explained a large proportion of variation in the relative indices of rat (93%) and possum (94%) abundance. For further analyses of the invasive mammal data, see Appendix L. The final native bird species richness model revealed a strong effect of age on native bird species richness that was not explained by the effects of age on measured vegetation variables. No other variables had significant effects on native bird species richness. Native forest cover within a 200-m buffer zone had a non-significant positive effect on native bird species richness. As predicted, basal area was greater in older restoration plantings, which in turn decreased canopy openness. Native tree species richness and vegetation complexity increased with age of restored forest. Rat abundance was higher with higher levels of vegetation complexity, canopy openness and basal area, but responded negatively to native tree species richness. Possum abundance was negatively affected by canopy openness, amount of native forest cover within a 200-m buffer zone, patch area and amount of built environment within a 200-m buffer.

The final native bird total abundance model fit the data well (Figure 4b), explaining 40% of the variation in native bird total abundance (Appendix K). The model revealed a strong, negative effect of canopy openness on native bird total abundance. Possum abundance

TABLE 1 Results of ANOVA and Tukey's post hoc test for spring native bird community data

Variables	Unrestored Mean (*SD*)	Urban remnant Mean (*SD*)	Rural remnant Mean (*SD*)	*F*	*p*
Spring					
Native bird species richness	3.00 (1.14)^{a}	5.42 (0.58)^{b}	6.67 (0.88)^{b}	25.97	<0.001*
Native bird abundance	3.92 (3.28)^{a}	10.58 (6.07)^{b}	14.58 (3.47)^{b}	8.75	0.003*
Fantail abundance	0.75 (0.52)^{a}	2.67 (1.54)^{b}	4.17 (1.03)^{b}	14.24	<0.001*
Tūī abundance	0.17 (0.26)	1.5 (1.34)	1.25 (1.44)	2.29	0.135
Grey warbler abundance	0.08 (0.20)^{a}	0.75 (0.69)^{ab}	1.58 (0.86)^{b}	8.08	0.004*
Silvereye abundance	2.75 (3.33)	4.17 (3.06)	5.25 (2.60)	1.04	0.378

Asterisks indicate significant differences among sites ($p \le 0.05$). Superscripts indicate which pairwise comparisons are statistically different.

and native forest cover within a 200-m buffer had non-significant, negative effects on native bird total abundance.

4 | DISCUSSION

The results of our study provide new insight into how native bird communities change with the age of restored urban forests and pinpoint the drivers of this change. We found clear support for the importance of restoring urban forests to improve native forest bird diversity. In response to our main research questions, we found that (a) native forest bird species richness increased with the age of restoration site, and community composition was on a trajectory towards that found in urban remnants but there was still a gap between restored forests and target reference systems. Furthermore, we found that the increase in native bird total abundance with forest age was mediated by a decrease in canopy openness. Additionally, we found that (b) forest structure and age were the only significant drivers of native forest bird communities in restored urban forests.

4.1 | Change in bird communities over time

As found in previous, non-urban studies, native forest bird species richness increased with the age of restored forest (Gould & Mackey, 2015; Munro et al., 2011). Our results reveal that native species were being added over time, as opposed to a turnover of species as detected in other studies (e.g. Gould & Mackey, 2015; Lindenmayer et al., 2016). The younger forests supported small-bodied insectivores and omnivores (fantail, silvereye and grey warbler), while older plantings additionally supported a larger frugivore (tūī). This increase in native species richness suggests that older sites provide a greater variety of resources, meeting the needs of more species over time. Contrary to our predictions, numbers of omnivores (silvereyes) did not decrease with the age of forest. However, numbers of one insectivore (fantails) and one frugivore (tūī) did increase with the age of forest.

We detected a maximum of five native forest bird species in any single restored urban forest. A study of the effects of forest fragmentation on native birds in Auckland similarly found only five native species regularly occurring year-round at study sites (Stevens, 2006). While the total New Zealand forest avifauna comprises ~50 native species (Innes et al., 2010), large forest parks typically harbour only 15 to 20 species (MacLeod et al., 2012). In New Zealand cities, it is extremely uncommon to find more than 10 native bird species in urban forests (e.g. Heggie-Gracie et al., 2020; Spurr, 2012). Therefore, the low number of native forest bird species detected in this study reflects the current realized diversity in urban ecosystems.

None of the native birds detected in urban restored forests were of conservation concern, but instead are relatively widespread and common on the New Zealand mainland. These species are either large and able to move extended distances, using many forest patches to meet their needs (e.g. tūī, male 120 g and female 90 g; kererū, 650 g), or are small omnivorous or insectivorous birds that are capable of using non-forest habitat, such as gardens and hedgerows (e.g. silvereyes, 13 g; grey warblers, 6.5 g; and fantails, 8 g; Heather & Robertson, 2015). The native birds detected in urban areas in this study are also capable of persisting despite certain levels of predation by invasive mammals (Burge et al., 2017; Innes et al., 2004).

While it appears that native bird species richness and community composition in restored areas are progressing towards levels found in urban forest remnants, there is still a gap between the oldest restored areas and urban remnants. Thus, it may take more than 72 years since initial restoration planting for a forest to provide the same quality of habitat as remnant forest in cities. Previous studies similarly concluded that bird community composition in restored sites remains significantly different from that in remnant vegetation, highlighting the long-term investment required by restoration (Brady & Noske, 2010; Gould & Mackey, 2015). It may take many decades before the benefits of restoration for native wildlife become evident (Mac Nally et al., 2010; Stagoll et al., 2010). Alternatively, restored urban forests may never reach the same level of native forest bird habitat provision as urban remnants, resulting instead in an alternative stable state (Hobbs & Norton, 1996).

Bird community composition of rural remnants differed significantly from all other forest types. Rural remnants supported higher numbers of grey warblers, fantails and kererū, and were the

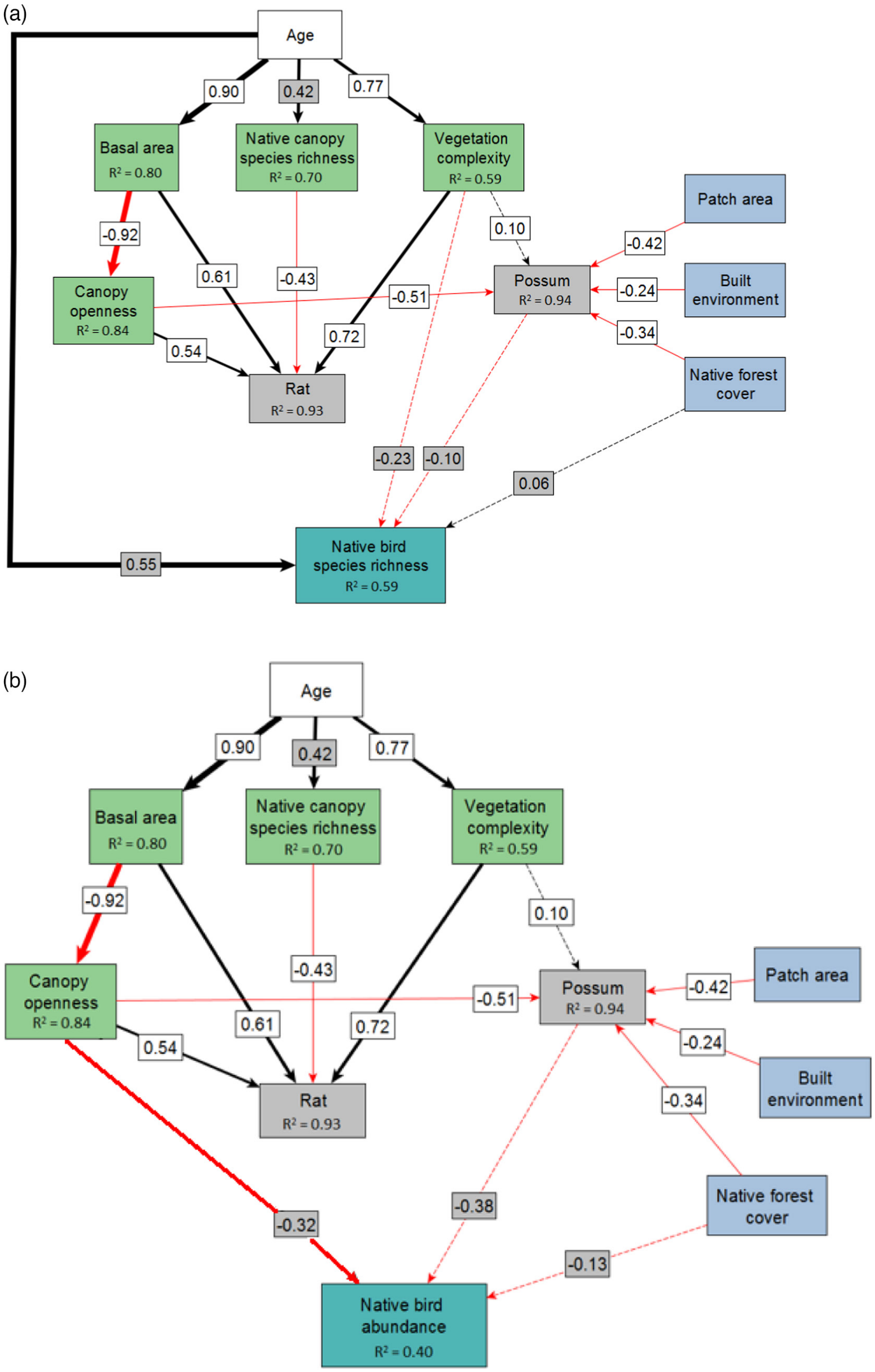

FIGURE 4 Structural equation modelling (SEM), illustrating drivers of native bird species richness (a) and abundance (b). Coefficients of determination (R^2) are shown for all response variables. Numbers in white boxes on arrows denote standardized path coefficients, whereas numbers in grey boxes denote unstandardized path coefficients. Arrow thickness is scaled to illustrate the relative strength of effects. Black arrows denote positive relationships, and red arrows denote negative ones. Dashed arrows indicate non-significant relationships ($p < 0.05$) which, however, improve overall model fit. The model for native bird species richness (AIC = 85.65, Fisher's $C = 31.65$, $p = 0.82$, $df = 40$) and abundance (AIC = 83.09, Fisher's $C = 31.09$, $p = 0.89$, $df = 42$) fits the data well

only sites where we detected whiteheads *Mohoua albicilla*, tomtits *Petroica macrocephala* and bellbirds *Anthornis melanura*. Seven decades of restoration can increase the number of native bird species able to use resources provided by an urban forest, but there is no replacing the habitat value of large tracts of native forest to native birds. Restoration was always meant to supplement conservation, and our results indicate that we cannot afford to lose the few remaining forest remnants within cities, as well as those beyond the city limits. Protection of existing forest remnants should be a priority in a broader strategy, which also seeks to create new habitat and corridors between them.

4.2 | Drivers of native forest bird species richness and abundance

Our SEM demonstrated that age was the single measured variable with a strong significant effect on native bird species richness. This effect of age was not mediated by tree basal area, native canopy species richness or vegetation complexity, or by the impact of these vegetation attributes on rats and possums. This may suggest that as time since restoration increases, more species have the opportunity to colonize or discover the area (Derhé et al., 2016; Fernandez-Juricic & Jokimäki, 2001). Alternatively, time since restoration could affect variables not directly measured in this study, such as the provision of nectar, fruit and invertebrates by these restored forests throughout the year and over time. We recommend future studies investigate the seasonal provision of fruit and nectar in restored urban areas, and how this changes over time. Invertebrates are an important food source both during the breeding season and winter, when fruit, nectar and foliage resources are scarce (Bouma et al., 2013; Gray & van Heezik, 2016). Several studies have shown that native insects prefer native plants and further research is needed to identify the indirect bottom-up effects of forest restoration on bird communities driven by important resources, such as invertebrates (Barnes et al., 2017; Bouma et al., 2013; Threlfall et al., 2016).

Our SEM demonstrated that native bird total abundance was significantly and negatively influenced by canopy openness, which in turn decreased with time since restoration. Thus, while we did not detect a direct effect of age on total abundance, our SEM revealed an indirect effect, mediated by canopy openness. Previous studies have found that the development of dense canopies is important for providing shelter and food to small birds, with an increase in canopy cover promoting bird species richness and total abundance (Belder et al., 2018; Blair, 2004; Vesk et al., 2008). Dense canopy developed in our study sites approximately 18 years after restoration planting (Wallace et al., 2017). Wallace et al. (2017) recommend that to achieve successful native tree regeneration, management activities should focus on promoting rapid canopy closure. Our results suggest that this may further maximize the number of native birds benefiting from restoration planting.

Contrary to our predictions, our SEMs found no relationship between rat and cat relative abundance and native bird species richness or total abundance. We did, however, find non-significant negative effects of possum abundance on both native bird species richness and total abundance. Further studies are needed to see if this relationship becomes significant with a larger sample size. Rats and cats do prey on native birds and, in the case of rats, on their eggs (Innes et al., 2015; Morgan et al., 2011; van Heezik, Ludwig, et al., 2008). However, studies suggest three of our widely detected native birds (grey warbler, fantail and silvereye) are capable of coping with a certain level of predation. Ruffell and Didham (2017) found that the abundance of four of the native bird species that they modelled (grey warbler, fantail, silvereye and tomtit) did not differ between landscapes with and without pest control. Similarly, Innes et al. (2004) observed that the relative abundances of these four species did not increase significantly following pest control. As proposed by Shochat et al. (2006), we suggest that the bird communities we detected in our study represent the 'ghost of predation past'—bird species that are highly vulnerable to predation by invasive predators have already disappeared from New Zealand cities. The native bird species that remain are those that can survive despite current levels of predation by invasive mammals.

Some caution should be taken with interpreting our results, given that our ability to detect effects of cats on native birds may have been constrained by the 48-hr camera trapping period we used for monitoring cat relative abundance. While two nights is the recommended deployment time for chew cards, some studies have suggested that feral cat monitoring requires a minimum of 1–2 weeks, given the ability of feral cats to travel large distances (Bengsen et al., 2012; Glen et al., 2014; Robley et al., 2010; Ruffell et al., 2015). Domestic cats, however, have smaller home ranges compared to feral cats (Horn et al., 2011; Schmidt et al., 2007) and camera trapping studies of domestic cat abundance in urban areas have used shorter sampling periods, accordingly (e.g. 72 hr, Elizondo & Loss, 2016). Therefore, we believe that the sampling effort of our camera trapping was still sufficient to detect relevant variation in domestic cat activity in our study sites.

We did not find significant responses in the mammal communities to urban forest restoration. The patterns in rat and possum abundance indices will have been influenced by varying levels of predator control. However, we did find evidence for threshold responses in rats and possums, which were never detected in the youngest restored forests. Our results suggest that rats and possums prefer a certain level of vegetation complexity, canopy cover and tree height to use a restoration planting. Once these habitat requirements are met after approximately 9 years, rats and possums are relatively widespread in restoration plantings. Thus, our results indicate that the changes in vegetation structure and complexity with age of restored forest which benefit native forest birds also provide habitat for invasive predators.

Although predation by invasive mammals in large tracts of native forest may be the main agent of decline for native forest birds in New Zealand, our results suggest that in cities, especially poorly vegetated ones, lack of habitat is the most important limiting factor for native forest bird species still remaining in urban areas. These results support findings by Walker et al. (2014) that in addition to predation, habitat loss may be an important, and at times underestimated, limitation on native forest birds. Innes et al. (2010) concluded that in areas where very little native forest remained, habitat restoration would be a necessary precursor to the re-establishment of native birds.

In urban areas characterized by extreme deforestation and habitat modification, we show that increasing the quantity and quality of native forest through restoration is necessarily the first step in re-establishing native forest bird communities, followed or accompanied by invasive mammal control. These findings highlight the considerable opportunity of forest restoration to enhance native bird diversity through local-scale urban green space management, allowing us to reconcile human development with protection and enhancement of native biodiversity in cities. As the human population continues to shift to cities, urban restoration provides a path forward in reconnecting people with their native environments.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHORS' CONTRIBUTIONS

E.E.N., J.I. and B.D.C. conceived the ideas and designed the methodology; E.E.N. collected the data; E.E.N., C.J. and A.B. analysed the data; E.E.N. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available from Figshare https://doi.org/10.6084/m9.figshare.19427015.v1 (Elliot Noe et al., 2022).

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