

Functional group-dependent responses of forest bird communities to invasive predator control and habitat fragmentation

Shaun Morgan¹ | Nigel A. Binks^{1,2} | Raphael K. Didham^{3,4} | Andrew D. Barnes¹ 

¹Te Aka Mātuatua – School of Science, University of Waikato, Hamilton, New Zealand

²Department of Conservation, Hamilton, New Zealand

³School of Biological Sciences, University of Western Australia, Crawley, Western Australia, Australia

⁴Centre for Environment and Life Sciences, CSIRO Health & Biosecurity, Floreat, Western Australia, Australia

Correspondence

Andrew D. Barnes, Te Aka Mātuatua – School of Science, University of Waikato, Hamilton, New Zealand.

Email: andrew.barnes@waikato.ac.nz

Funding information

University of Waikato Strategic Research Fund

Editor: Eva Knop

Abstract

Aim: Mounting global pressure on bird populations from invasive predators and habitat loss has driven a rapid growth in restoration and conservation action around the world, yet the efficacy of such actions is still not well understood. We investigated the relative and interactive effects of invasive predator control and habitat fragmentation on the abundance of native birds and invasive mammalian predators in native forest fragments.

Location: Waikato region, New Zealand.

Methods: We sampled invasive mammalian predator and native bird abundances using camera traps and bird counts at 26 sites in 15 forest fragments across New Zealand's Waikato region. Fragment area, shape complexity and surrounding land cover of exotic and native forest were determined in ArcMap. We further created two composite gradients reflecting predator control intensity and temporal distribution of control based on seven quantitative variables recorded in each of the 5 years preceding data collection. Finally, we estimated the relative influence of these drivers on invasive mammals and functional groups of native birds using model averaging.

Results: Both the intensity and temporal distribution of invasive predator control significantly affected invasive predator abundance. Landscape and fragment structure were often equally important drivers of invasive predator abundances, but responses varied among invasive mammal species. Both invasive predator control intensity and fragment structure were similarly important drivers of native bird abundance, though bird community responses varied markedly between functional groups.

Main conclusions: Our findings suggest that spatial extent of invasive predator control and fragment area constrain invasive predator numbers and enhance bird abundance, especially for small insectivorous species, whilst other aspects of habitat fragmentation are less important for invasive mammals but at least as important for native bird communities. Consequently, both drivers should be given strong consideration when undertaking landscape-scale conservation and restoration of bird communities in human-altered landscapes threatened by invasive predators.

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KEYWORDS

bird functional traits, forest fragments, invasive mammalian predators, landscape structure, model averaging, pest control

1 | INTRODUCTION

At present, 14% of bird species are threatened with extinction and 40% are in decline due to habitat loss, predation by invasive species, overexploitation and climate change (BirdLife International, 2018; IUCN, 2019). Although habitat loss is regarded as the greatest threat to bird biodiversity (BirdLife International, 2018), invasive mammalian predators ("invasive predators" hereafter) are considered the greatest driver of recent extinctions, globally impacting an estimated 39% of threatened bird species (BirdLife International, 2018; Butchart, 2008).

Growing recognition of the threats posed by invasive predators to birds has driven a global expansion of conservation operations aimed at controlling or eradicating invasive predator populations on both islands and mainland regions (Jones et al., 2016). Already, studies have shown increased native bird fecundity, species richness, nesting success, survival and abundance in areas subject to invasive predator control operations, thereby demonstrating the efficacy of these methods for the conservation of native birds (Innes et al., 2010; Smith et al., 2010).

However, recent studies suggest that effective predator control may depend on the surrounding landscape context of habitat structure (Armstrong et al., 2014; García-Díaz et al., 2019; King et al., 2011). Understanding this interaction is essential for determining the regularity and intensity of predator control operations as structural landscape factors such as fragmentation and habitat connectivity influence the reinvasion potential of invasive predators. For example, in New Zealand, ship rats (*Rattus rattus*) and brushtail possums (*Trichosurus vulpecula*) can invade control-targeted areas from the surrounding landscape and recover to pre-control densities within just 2 years (Griffiths & Barron, 2016; Ji et al., 2004; King et al., 2011).

Habitat structure of fragments and landscapes such as patch area, patch shape, patch isolation and land cover can alter bird abundance and community structure (Graham & Blake, 2001; Martínez-Morales, 2005). Indeed, studies have found reduced bird abundance in smaller fragments and increased nest predation across less forested landscapes (Deconchat et al., 2009; Graham & Blake, 2001). For example, Ruffell and Didham (2017) found that benefits to native forest birds from invasive mammal control and the management of landscape forest coverage were context-dependent. Additionally, an agent-based modelling study investigating the impacts of different spatiotemporal management strategies on brushtail possum populations found that both control effort and spatial control distribution were the key drivers of invasive predator population decline (Lustig et al., 2019). However, either these studies did not assess the abundances of invasive mammalian predators or they did not assess effects on bird abundance. As previous studies have typically examined these effects in isolation (Courchamp et al., 2003), an integrative approach is required to understand the relative effects of invasive predator control and landscape structure on both invasive

predators and native birds, which is crucial for informing effective conservation management strategies (Ruffell & Didham, 2017).

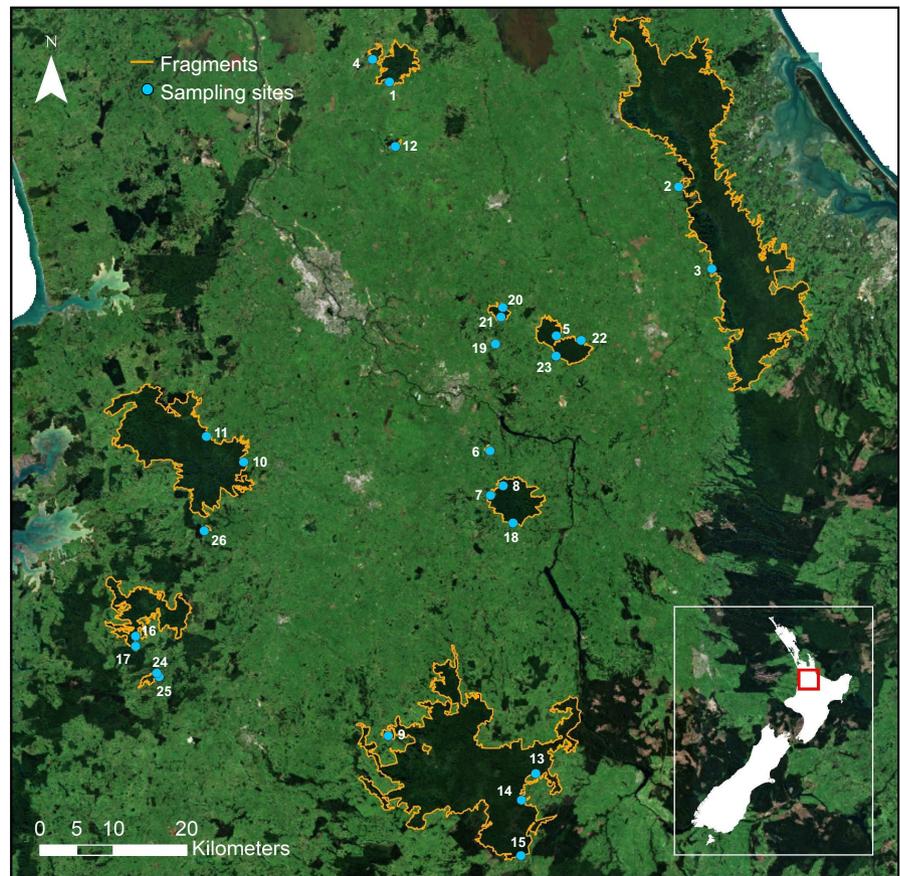
In this study, we measured the effects of the spatiotemporal intensity of invasive predator control and the structure of both fragments and the surrounding land cover, hereafter "landscape structure," on the abundance of native birds and invasive mammalian predators in native forest fragments. To do so, the abundances of invasive mammalian predators and native birds were sampled across 26 sites in 15 native forest fragments in New Zealand's Waikato region. Additionally, we quantified variation in the intensity and temporal distribution (i.e. recency) of invasive predator control for each fragment over the 5 years preceding predator abundance sampling. With these data, we first tested whether invasive predator abundance decreased as the intensity and recency of predator control increased. Using a suite of functional traits collected for each sampled bird species, we quantitatively assigned species to two major functional groups and tested whether the recency and intensity of invasive predator control increased bird abundances overall or within specific functional groups. Furthermore, we tested the relative importance of predator control versus aspects of fragment and landscape structure (e.g. area, shape, surrounding land cover) as drivers of the abundance of invasive predators and native birds.

2 | METHOD

2.1 | Study area

This study was conducted across a 1.14 million hectare area of the central Waikato region of New Zealand's North Island (Figure 1). The Waikato region's temperate climate and productive soils have led to agriculture dominating regional land-use, with dairy farmland alone covering 28.7% of the region (Stats, 2018). Prior to human settlement, native podocarp-broadleaved forests covered an estimated 94% of the region (Ewers et al., 2006), and the country was devoid of native terrestrial mammals with the exception of three species of small bat (Atkinson, 2006). Since the settlement of the Waikato region, first by Polynesians and later by Europeans, regional native forest coverage has fallen to 21% (Landcare Research, 2015; MacLeod & Moller, 2006), and a range of invasive mammalian predators including ship rat, brushtail possum and stoat (*Mustela erminea*) have been introduced (Atkinson, 2006). Because of the lack of natural mammalian predators, native forest birds are particularly at risk from these invasive mammalian predators, with much evidence pointing towards mammalian predation as a major cause of species decline (Innes et al., 2010). Consequently, a range of invasive predator control operations have been established throughout the Waikato. The coverage and intensity of these operations vary greatly, and whilst reserves such as Sanctuary

FIGURE 1 Distribution of sampled native forest fragments and individual sampling sites across the Waikato region, located in the North Island of New Zealand (see map inset). The 15 forest fragments are outlined in orange and the 26 sampling sites are represented by blue points (labelled by site number according to the sequence in Appendix S1). Image of New Zealand 10 m Satellite Imagery (2017) sourced from the LINZ Data Service and licensed for reuse under the Creative Commons 4.0 New Zealand Licence



Mountain Maungatautari receive extremely intensive ground-control, many forests like the Kaimai-Mamaku Conservation Park are effectively uncontrolled (Appendix S1).

2.2 | Site selection and experimental design

The 26 study sites were selected within 15 mixed podocarp-broadleaf forest remnant fragments with areas ranging from 14 hectares to over 41,000 hectares (Appendix S2; Figure 1). Study sites were selected to include a wide diversity of historical control types within the past 5 years, ranging from fragments that had no active control through to continuous and complete coverage of control across all five preceding years. Fragments were selected to be as similar as possible in three main criteria: (1) all fragments have had livestock exclusion fencing at the forest edge for at least 10 years, (2) no major tree felling occurred within the past 30 years and (3) each fragment was at least 10 ha to ensure that fragments were not over-represented by edge habitat, and with a minimum width from edge to edge of 200 m. This minimum width yielded a threshold under which adjoining habitat patches would be considered separate fragments (i.e. forest <200 m was considered a corridor).

The delineation of the native mixed podocarp-broadleaf fragments and the distance/area measurements were performed using ArcMap 10.6.1 based primarily on Waikato 0.5 m Rural Aerial Photos (2012–2013) and Bay of Plenty 0.4 m Rural Aerial Photos (2010–2012) in

conjunction with the New Zealand Land Cover Database (v4.1). Aerial photos were obtained from the LINZ data service and licensed for reuse under the Creative Commons 4.0 International Licence. Defining the fragment edges of several forested regions proved difficult as large, forested areas were often tenuously connected by narrow corridors and bisected by roads. Consequently, a distinction was made between core and edge habitat to account for the potential influence of edges on habitat use by native birds and invasive mammalian predators (i.e. edge effects). Specifically, as many studies have found significantly increased nest predation along temperate forest edges (Batáry & Báldi, 2004; Vetter et al., 2013), areas of native forest fragments that narrowed to <200 m were considered habitat edge that lacked core habitat and were therefore treated as matrix habitat. Similarly, studies have found that narrow linear clearings created by roads can have negative impacts on the movements of understory forest birds and some small mammals (Goosem, 2001; Lees & Peres, 2009). Consequently, public roads with a lack of continuous tree canopy were treated as fragment edges.

2.3 | Invasive predator monitoring

The 26 sampling sites in which native birds and invasive predators were monitored were selected to be flat (<15° slope) and at a consistent distance of 40 m from the nearest forest edge, to spatially control for edge effects. Sampling occurred over a 7-month period from December 2018 to July 2019 in an effort to avoid invasive

predator control operations which are typically conducted between July and November when seasonal predator population irruptions typically occur (Elliott & Kemp, 2016).

The abundance of invasive mammalian predators was estimated using motion-sensing infra-red trail cameras (Browning Elite HD model BTC-5HDE) intermittently distributed across all 26 forest sites. A single camera was deployed at each of the 40-m sampling sites at a height of 0.2 m above the ground, mounted on a wooden stake. To minimize false triggering and allow for unobstructed photographs, dense vegetation was removed where necessary to give cameras a clear line of site of at least 2 m. Each site was repeatedly sampled over three to five periods of up to 28 days duration for each period, though various technical issues with the cameras meant that individual sampling periods varied from 1 to 28 days, yielding total sampling periods that varied from 38 to 117 days across the sites. Cameras were set to take five consecutive 10 megapixel photos over a period of 6 s, with a 10-s time delay between trigger events to avoid excessive numbers of events capturing the same individual that might remain at a site for an extended period. Each set of five consecutive photos was considered a single photographic event for the purposes of recording invasive predator presence/absence.

A commonly used detection threshold of 30 min was adopted to separate notionally “independent” detection events, as past studies using this interval have typically focused on small mammals similar to the rodent and mustelid species common to New Zealand forests (Gerber et al., 2010; Nichols et al., 2017). Species counts were recorded, and statistical analyses were performed on taxon groupings selected based on their high abundance and ubiquity across sites: brushtail possums, ship rats and total mammalian predators.

2.4 | Native bird monitoring

Forest bird abundance was monitored using stationary 5-min bird counts at each of the 26 sampling sites. This study utilized a variation of the 5-min bird count method developed by the New Zealand Department of Scientific and Industrial Research in 1975 (Hartley, 2012). Over the 5-min period, the number and species of birds seen or heard were recorded within a 20 m radius. During the first 3 min, all birds were identified and counted, whereas in the last 2 min, only individuals that could clearly be identified as different to those detected in the first 3 min were recorded. Point counts were conducted three times at each site over a span of 3 months from April to July of 2019, and only on dry days to standardize visibility and bird behaviour among sites. Only native species were retained for further analysis, and birds that could not be identified or only appeared once during the study were omitted (Appendix S1).

2.5 | Surrounding landscape and habitat fragment structure data

The aerial imagery used to delineate study site fragments was used in conjunction with the New Zealand Land Cover Database (v4.1)

in ArcMap to classify land cover within a 5 km radius outside of the edge of each fragment. The “manuka and/or kanuka,” “broadleaved indigenous hardwood” and “indigenous forest” classes were grouped to create a “native forest” class, whilst the “exotic forest” class was recorded separately. Waikato 0.5 m Rural Aerial Photos (2012–2013) and Bay of Plenty 0.4 m Rural Aerial Photos (2010–2012) were again used to ground truth the Land Cover Database classification and, where necessary, polygons were reclassified.

The proportional coverage of native forest and exotic forest within 1 km and 1–5 km buffer zones around the perimeter of each fragment (i.e. fragment-adjacent) were then determined in ArcMap (Appendix S2) to quantify landscape-level features. Fragment area, fragment edge length and fractal dimension index (FDI) variables were also calculated for each of the study fragments (Appendix S2) as there is strong evidence of their influence on species abundance and dispersal success (Calabrese & Fagan, 2004; Ewers & Didham, 2007; Graham & Blake, 2001). Fragment perimeters and areas were calculated in ArcMap and used to determine the FDI as two times the natural logarithm of fragment perimeter (m) divided by the natural logarithm of fragment area (m²) using the formula $(FDI = 2(\ln(Fp/Fa)))$, where Fp is the fragment perimeter and Fa is fragment area. FDI typically varies between 1 and 2, with higher values indicating fragment shapes with more complex perimeters (McGarigal & Marks, 1995).

2.6 | Invasive predator control data

Invasive predator control records for each study fragment and the surrounding 5 km from the edge of each fragment were obtained for a 5-year period prior to the final camera monitoring day at each site. Data were collected from records obtained from landowners, land managers and groups and organizations involved with invasive predator control operations across our study locations.

Our aim was to record a broad set of fragment-level “input” variables that characterize invasive predator control efforts, from which an orthogonal set of composite variables could be created using PCA to deal with expected inter-correlation among input variables. The seven classes of input variables comprised: (1) the minimum distance from each study fragment to the nearest invasive predator-controlled area (including controlled areas within study fragments), along with six variables describing the proportion of each study fragment that received, (2) general invasive predator control, (3) poison-based predator control, (4) trapping-based predator control, (5) rat control, (6) possum control and (7) both rat and possum control. Values were calculated for the 15 study fragments for each of the 5 years preceding bird monitoring, yielding a total of 35 input variables (Appendix S3).

2.7 | Constructing invasive predator control indices using principal component analysis

All data analyses were performed in R version 4.0.0 (R Core Team, 2020). Unlike previous studies that have focussed on categorical

predator control indices such as poison/trapping density (Ruffell & Didham, 2017), we developed continuous variables using PCA (with unit variance scaling) on a range of invasive predator control input variables (Appendix S3) using the R package “FactoMineR” (Lê et al., 2008). Based on the PCA biplot (Figure 2), the first component was interpreted as “invasive predator control intensity” due to the strong positive correlation of variables relating to the spatial coverage of predator control along the principal axis. Thus, increasing values of this first component equate to increasing intensity of spatial coverage in invasive predator control measures. This component explained 50.3% of the variance in the data (Figure S4). For the second component, positive vectors were generally associated with more recent predator control years (1–2), whilst negative vectors were generally associated with earlier predator control years (4–5). Consequently, the second component was interpreted as the “temporal distribution of invasive predator control,” which equates to a continuous index describing the recency of control over 5 years. This component explained 17.6% of the variance (Figure S4).

2.8 | Quantifying bird community functional groups

To examine responses in native bird communities to invasive predator control and landscape structure, bird species were first grouped by their shared functional traits (Bregman et al., 2016; Watson et al., 2004) to detect trait-dependent differences in species sensitivity. These functional groups were generated using the “dbFD” function in the FD package (Laliberté & Legendre, 2010; Laliberté et al., 2014). To construct these groups, specific functional traits (Appendix S5) and abundances (Appendix S6) were used to create a Gower dissimilarity matrix, from which a dendrogram was created using Ward’s clustering method that revealed a distinct separation between

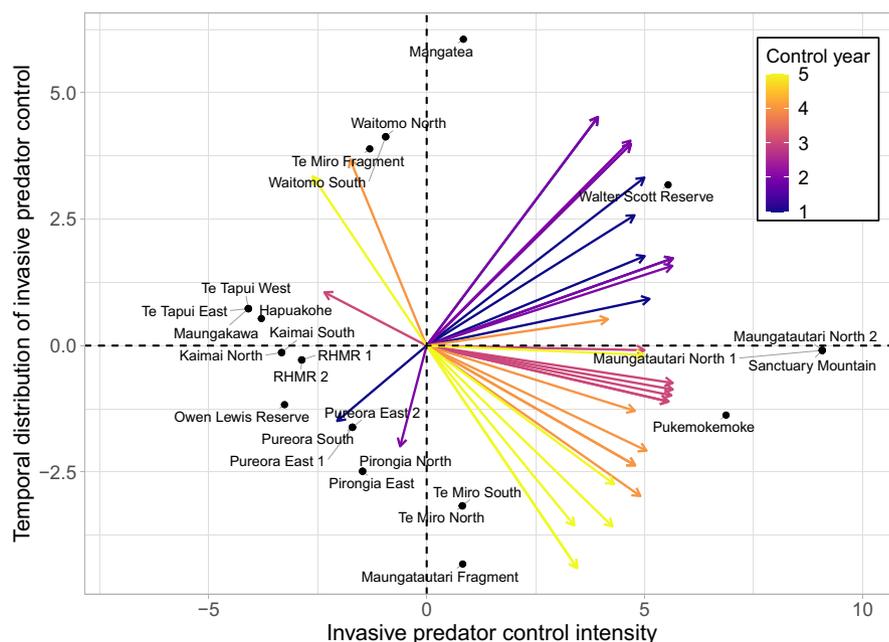
insectivores and nectarivores (Appendix S7). The abundance of birds within these functional groups was quantified to determine the effects of invasive predator control and landscape structure on the abundances of different functional groups. Analyses were then conducted on functional groups that had sufficient numbers to detect differences across samples. Specifically, these groups included functional group 1 (hereafter, “nectarivores”), functional group 2 (hereafter “insectivores”) and the overall bird community (including all native species across the four identified functional groups; Appendix S5).

2.9 | Statistical analyses

Prior to model construction, we performed mean-centring and standard deviation-based scaling on predictor variables to enable direct comparisons of effect sizes among models. We then tested the effects of both invasive predator control indices (predator control intensity and temporal distribution of invasive predator control) and fragmentation (fragment-level and landscape-level predictors) on invasive predator counts (brushtail possum, ship rat and total mammalian predators) and native bird abundance using generalized linear mixed effects models (GLMM) in the “lme4” package (Bates et al., 2015). Each model contained a random effect term specifying fragment identity, and a model offset for the (log-transformed) number of monitoring days completed at each site to account for variation in sampling effort across sites. Variance inflation factors (VIF) were determined for each full model before the inclusion of the interaction terms, and all variables were deemed independent based on a commonly used maximum threshold of 10 (O’Brien, 2007).

To determine whether the PCA axes used to describe the intensity and temporal distribution of invasive predator control were able to explain variation in invasive mammal abundance quantified

FIGURE 2 PCA biplot displaying the component scores and variable loadings obtained from the PCA of 35 variables describing invasive predator control. Labelled points represent the first (invasive predator control intensity) and second (temporal distribution of invasive predator control) PC scores for each sampling site. The direction of the vector arrows indicates the correlation of each variable with the PCs, whilst vector length indicates the strength of the contribution of each variable to the PCs. Vector colour corresponds to the number of years prior to monitoring that each invasive predator control variable is describing



from our camera trap sampling, we tested for the effects of invasive predator control on predator counts using generalized linear regression with a negative binomial error distribution to account for overdispersion. A Likelihood Ratio Test (LRT) was undertaken to test the statistical support for more complex models containing both invasive predator control predictor variables over more simplified models based on AIC values (see below for more details on model selection) using the "anova" function in the "stats" package (R Core Team, 2020).

To test for the relative effects of invasive predator control and landscape structure on invasive mammal and native bird abundance, the GLMM for each bird and invasive predator response variable included the full set of two invasive predator control and six landscape predictor variables. The models also included interaction terms between each invasive predator control variable and representative fragment-scale and landscape-scale variables. To select these representative variables, separate PCAs (with unit variance scaling) were performed on landscape-scale and fragment-scale predictors to identify a single variable within each set that was most highly correlated with the first component in each PCA (Appendix S8) (Lê et al., 2008). "Fragment area" and "native forest cover (<1 km)" were subsequently selected as appropriate representative predictors, with first components explaining 77.2% of fragment-scale and 53.4% of landscape-scale variance, respectively (Figure S9). Bird response variables were modelled with a Poisson error distribution, and predator responses were modelled with a negative binomial error distribution to account for overdispersion.

For each full model, the automated model selection function ("dredge") in the "MuMIn" package was used to compute all models for every potential predictor variable combination and rank them by AICc (Bartón, 2020). Models with a maximum $\Delta AICc$ of 2 compared to the model with the lowest AICc were extracted for model averaging. This cut-off balanced the number of models to limit the model-averaged coefficient uncertainty associated with increasing the number of models, whilst including enough models to be certain that the "best model" was not excluded (Grueber et al., 2011). The model averaging function ("model.avg") in the "MuMIn" package was used to create the reduced model set and perform the maximum likelihood model averaging. Following the zero method (full average) of model averaging, zero value estimates were assigned to parameters that were absent from subset models before the overall averaged parameters were calculated (Burnham & Anderson, 2002). This approach decreases the effect sizes (and errors) of predictors restricted to low weighted models and is recommended when aiming to determine which factors have the strongest effect on the response variable (Nakagawa & Freckleton, 2011). The model averaging function also returned the sums of model Akaike weights for each term over all models containing that term. As in Jochum et al. (2017), these values can be interpreted as indicators of variable importance. Akaike weighted likelihood-ratio based pseudo- R^2 values were then calculated for each of the subset models within each averaged model set (Cox & Snell, 1989). These values were averaged to determine an R^2 value for each of the averaged models as an

indicator of model fit, and confidence intervals (95%) were determined for model parameters.

3 | RESULTS

3.1 | Effects of predator control on invasive predators

Approximately 1,840 days of camera-trap footage were recorded across 26 sites located in 15 separate native forest fragments across New Zealand's Waikato region. From this footage, 957 sightings of invasive mammalian predators were recorded from seven different species, with brushtail possums and ship rats accounting for 90.1% of these observations. Model selection retained the control intensity variable in total invasive predator and brushtail possum models, but not in the ship rat model, for which the null model was selected. The temporal distribution of control variable was removed from all models.

Invasive predator control had a consistently negative effect on the observed abundance of all invasive predator classes (Figure 3a). There was a significant negative effect of control intensity on both total invasive predator abundance ($\beta = -.935$, $z = -4.545$, $df = 22$, $p < .001$) and brushtail possum abundance ($\beta = -1.013$, $z = -3.021$, $df = 22$, $p = .003$) in single predictor models. In contrast, ship rat abundance responded less to invasive predator control (Figure 3a; $\beta = -.672$, $z = -1.927$, $df = 22$, $p = .054$).

The temporal distribution of invasive predator control had only a very weak, positive effect on the total abundance of invasive predators (Figure 3b), supporting its removal from the total invasive predator abundance model. The temporal distribution of control had weak negative effects on ship rat abundance and weak positive effects on brushtail possum abundance (Figure 3b), and it did not have a statistically significant effect on either possum abundance ($\beta = .302$, $z = 0.991$, $df = 22$, $p = .322$) or ship rat abundance ($\beta = -.337$, $z = -1.157$, $df = 22$, $p = .247$). See Appendix S10 for all model statistics.

3.2 | Relative effects of invasive predator control and landscape structure

Model averaging selected between 1 and 9 top models for each native bird and invasive predator response variable from the full set of predictor variables describing invasive predator control and landscape structure (see Table 1 for all standardized coefficients, variable importance factors and model inclusion counts from averaged models). Only the control intensity predictor appeared at least once in every model set. R-squared values for averaged models ranged from 0.32 to 0.96.

The single top model that was selected for total invasive predator abundance contained both of the predator control predictors, in addition to fragment area and its interactions with the predator

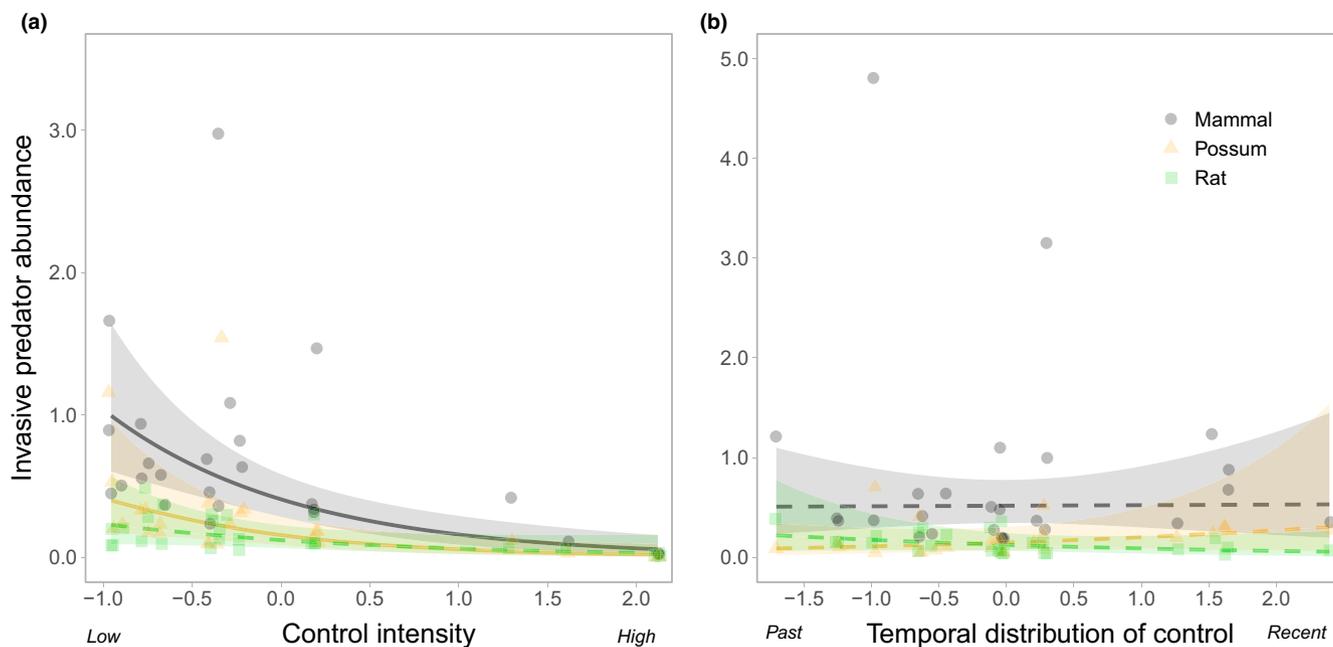


FIGURE 3 Responses of invasive predator abundances to (a) the intensity of invasive predator control, and (b) the temporal distribution of invasive predator control. Plots show partial effects and partial residuals for invasive predator abundance whilst holding other predictors at their means. Points, fitted lines and 95% confidence intervals are grouped by abundance of all invasive predators, possums only and rats only. Solid and dashed lines indicate significant ($p < .05$) and non-significant ($p > .05$) relationships, respectively

control predictors. Each predictor had a negative effect on the total abundance of invasive predators, with stronger effects associated with area ($\beta = -4.333$), control intensity ($\beta = -4.975$) and their interaction, whereby the negative effect of control intensity on invasive predators was stronger in larger versus smaller fragments ($\beta = -5.317$). The effects of the temporal distribution of control ($\beta = -2.994$) and its negative interaction with area ($\beta = -3.097$) were slightly weaker in comparison. The same predictors were also the most important predictors of brushtail possum abundance, with similar relative effects sizes to the total abundance model, and with each variable included in at least seven of the nine top models. The remaining landscape structure predictors, aside from exotic forest cover (<1 km), were also included in the top model set, though their effects were considerably weaker (Table 1).

In contrast, the temporal distribution of control and fragment area were not included in the top rat response model set, and control intensity had a relatively weak negative effect on ship rat abundance ($\beta = -0.077$), whilst three landscape structure variables had similarly dominant effects. Both fractal dimension index and surrounding native forest cover (<1 km) had positive effects on ship rat abundance ($\beta = 1.002$; 0.955), whilst a negative effect was associated with native forest cover (1–5 km) ($\beta = -0.921$). No interaction terms were included in the top model set.

As expected, the effects of invasive predator control intensity on the total abundance of native birds ($\beta = 0.216$) outweighed the effects of all other variables aside from fragment area which had a similarly strong positive effect ($\beta = 0.170$). The three next most important landscape effects were included in five of the nine top

models and had a combined negative effect size of similar magnitude to fragment area, albeit negative ($\beta = -0.180$; Figure 4, Appendix S11). Insectivorous birds responded similarly strongly to fragment area ($\beta = 0.159$) and control intensity ($\beta = 0.232$), both of which appeared in every top model. Exotic forest cover (<1 km) also had a relatively strong negative effect on insectivore abundance ($\beta = -0.163$; Figure 4, Appendix S11).

A broader range of variables emerged as similarly important predictors of nectarivore abundance. The temporal distribution of control, surrounding native forest cover (<1 km), and their associated interaction term each had negative effects and were included in all nine top models ($\beta = -0.303$; -0.114 ; -0.705). Furthermore, control intensity had a strong positive effect on nectarivores ($\beta = 0.552$; Figure 4, Appendix S11) and had a similarly strong interaction with surrounding native forest cover (0.489 ; Figure 4, Appendix S11), whereby the positive effects of control intensity were stronger in fragments with higher surrounding native forest cover. Control intensity and its interaction with surrounding native forest cover (<1 km) were included in eight of the nine top models of nectarivores abundance.

4 | DISCUSSION

We found that increased intensity of invasive predator control generally had negative effects on the abundance of invasive predators and positive effects on the abundance of native birds. Control intensity, fragment area and the temporal distribution of control were generally more important drivers of invasive predator abundance

TABLE 1 Model averaging results for invasive predator and native bird abundances

Averaged model	Standardized estimate	Variable importance	Model inclusions	Total number of models	Averaged model R^2
Total invasive predator abundance					
Area	-4.3331	—	1	1	.935
Control intensity	-4.9753	—	1		
Temporal distribution of control	-2.9943	—	1		
Area: Control intensity	-5.3170	—	1		
Area: Temporal distribution of control	-3.0965	—	1		
Brush-tail possum abundance					
Area	-11.6411	1.000	5	5	.960
Control intensity	-10.0074	1.000	5		
Temporal distribution of control	-4.6324	1.000	5		
Area: Control intensity	-14.4148	1.000	5		
Area: Temporal distribution of control	-7.7281	1.000	5		
Native forest cover (<1 km)	-0.3109	0.685	3		
Exotic forest cover (1–5 km)	0.4759	0.470	3		
Fractal dimension index	-0.0995	0.183	1		
Native forest cover (1–5 km)	-0.0557	0.132	1		
Ship rat abundance					
Fractal dimension index	1.0022	1.000	5	5	.878
Native forest cover (<1 km)	0.9547	0.866	4		
Native forest cover (1–5 km)	-0.9206	0.866	4		
Exotic forest cover (1–5 km)	-0.1032	0.238	1		
Exotic forest cover (<1 km)	-0.0648	0.166	1		
Control intensity	-0.0772	0.156	1		
Total native bird abundance					
Control intensity	0.2163	1.000	9	9	.381
Area	0.1700	1.000	9		
Fractal dimension index	-0.0844	0.586	5		
Exotic forest cover (<1 km)	-0.0604	0.548	5		
Native forest cover (<1 km)	-0.0351	0.448	5		
Native forest cover (1–5 km)	-0.0065	0.088	1		
Temporal distribution of control	0.0024	0.070	1		
Temporal distribution of control: Native forest cover (<1 km)	-0.0088	0.070	1		
Nectarivore abundance					
Temporal distribution of control	-0.3029	1.000	9	9	.370
Native forest cover (<1 km)	-0.1135	1.000	9		
Temporal distribution of control: Native forest cover (<1 km)	-0.7045	1.000	9		
Control intensity	0.5519	0.908	8		
Control intensity: Native forest cover (<1 km)	0.4894	0.908	8		
Fractal dimension index	-0.2813	0.762	7		
Native forest cover (1–5 km)	0.2039	0.418	4		
Exotic forest cover (<1 km)	0.0622	0.254	3		
Area	0.0514	0.228	2		

TABLE 1 (Continued)

Averaged model	Standardized estimate	Variable importance	Model inclusions	Total number of models	Averaged model R^2
Insectivore abundance					
Area	0.1588	1.000	3	3	.317
Control intensity	0.2319	1.000	3		
Exotic forest cover (<1 km)	-0.1626	1.000	3		
Area: Control intensity	-0.1220	0.375	1		
Fractal dimension index	-0.0108	0.174	1		

Note: The table is split into models headed by each model's response variable (bold). Predictor variables included in the top model set (i.e. models within $\Delta AICc$ 2 from the model with the lowest $AICc$) are listed beneath each response heading. Model estimates are averages of regression coefficients from the top model set, whilst variable importance gives the Akaike weight sums over all models in which the explanatory variable appears. "Model inclusions" indicates the number of times each variable appears in the top model set. The total number of models in each set and the AIC-weighted average R^2 value for each averaged model are also given.

than adjacent forest cover, though the effects of each variable were conditional as the associated interaction terms were also important. Conversely, ship rats responded much more strongly to both fragment structure and adjacent forest cover. Total native bird abundance was largely driven by control intensity and fragment area, as was insectivore abundance, which also responded strongly to exotic forest cover (<1 km). The two predator control predictors and surrounding native forest cover <1 km (including interactions with both predator control variables) were the key drivers of nectarivore abundance. The presence and interactions of both predator control and landscape structure predictors in each top model set does, however, suggest that each are valuable for predicting invasive predator and native bird abundances. Overall, our findings suggest that bird conservation action in fragmented and invaded landscapes should focus simultaneously on increasing the spatial coverage of predator control whilst maximizing both the size of forest fragments and cover of native forest in the surrounding landscape. Therefore, by demonstrating the benefits of implementing a landscape perspective for restoring native bird communities, we highlight the importance of integrating spatial ecology into the restoration and management of native biodiversity.

4.1 | Effects of invasive predator control on invasive predators and native birds

The dominant negative effect of invasive predator control intensity on the total abundance of invasive mammalian predators was unsurprising as many studies have demonstrated the efficacy of mammalian predator control operations (Courchamp et al., 2003; Elliott & Kemp, 2016; Van Vianen et al., 2018). However, where other studies have typically classified control intensity categorically as a function of trap/poison density and the number of active trap/poison days (Lustig et al., 2019; Ruffell et al., 2015), the continuous index used in this study was based on the proportion of fragment habitat controlled over 5 years. Although such scale-based indices have not been widely used, similar negative trends are still to be expected as numerous studies have suggested that increasing the size of a

controlled area prolongs the effects of periodic treatment on invasive predators by reducing immigration-driven reinvasion (Brown et al., 2015; Griffiths & Barron, 2016; Lustig et al., 2019).

The abundance of brushtail possums was strongly reduced by the intensity of invasive predator control, whilst the abundances of all native bird classes were enhanced. The temporal distribution of predator control also appeared to have some importance for possum abundance based on model averaging, though its effect was not statistically significant, suggesting a relatively weak influence of temporal distribution of control efforts on invasive predators in comparison to the spatial intensity of control measures.

Conversely, ship rats were not strongly affected by predator control at all. One explanation for this could be that ship rats can breed rapidly and disperse quickly across hundreds of metres of pastoral habitat to repopulate post-control fragments within months (King et al., 2011). Consequently, the use of predominantly periodic control operations across the study sites may not have been frequent enough to significantly suppress populations across the monitoring period. Indeed, Ruffell et al. (2015) found that only high-intensity ongoing poison baiting could significantly reduce the abundances of rats and possums. It is also possible that the efficacy of invasive predator suppression could reflect more intensive targeting of possums compared to rats, though there did not appear to be obvious discrepancies in the control measures enacted that would target either species more strongly across the sites (Appendix S3). Additionally, our models did not account for possible competitive release of ship rat populations, which has often been observed in fragments with reduced brushtail possum abundances (Griffiths & Barron, 2016).

The strong positive effect of invasive predator control intensity on the total abundance of native birds was also expected due to the resulting reductions in predation pressure and competition for food (Innes et al., 2010). Interestingly, of the different bird functional groups, only the abundance of insectivores was significantly affected by both the intensity of invasive predator control and the total invasive predator abundance. The superior gap-crossing ability of the nectarivores (Appendix S5) could explain their lack of response to changes in predator abundance as it may enable improved

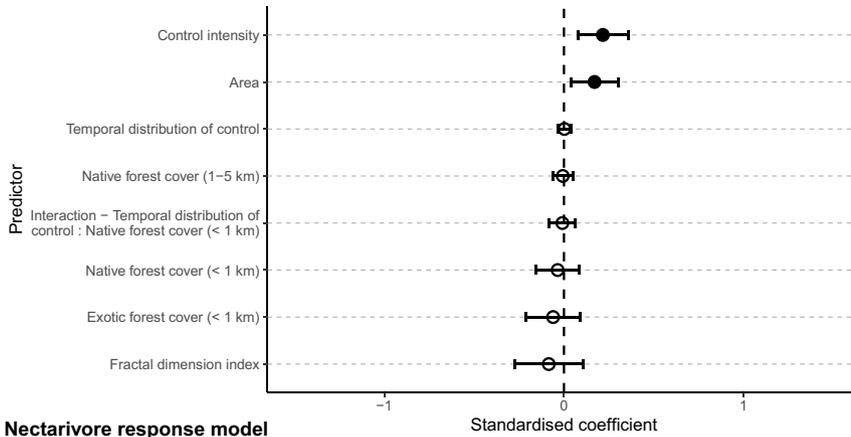
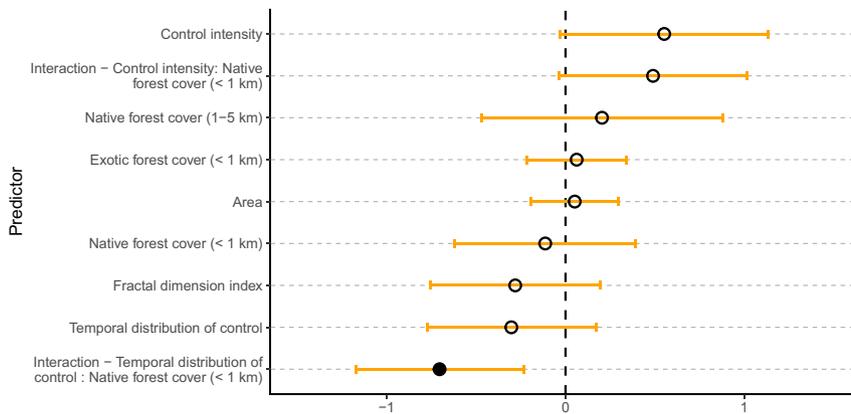
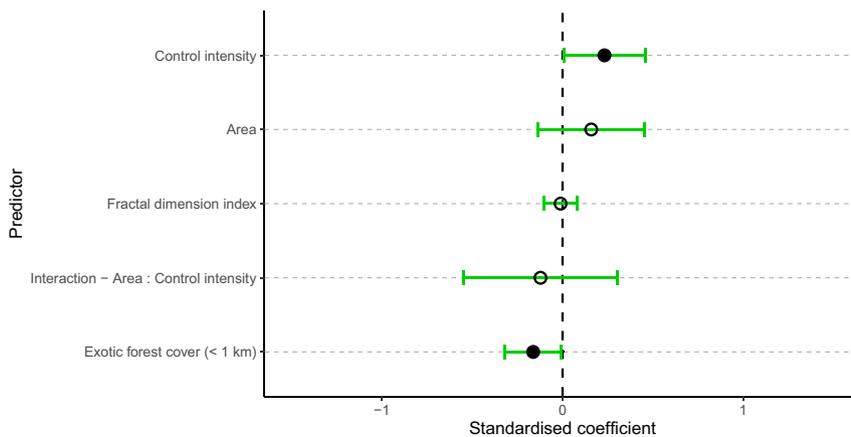
(a) Native bird response model**(b) Nectarivore response model****(c) Insectivore response model**

FIGURE 4 Forest plots showing relationships between native bird abundance classes and the landscape structure and predator control predictor variables included in associated averaged models. Plots display the standardized estimates and confidence intervals (95%) for model-averaged predictors of response variables (a) native birds, (b) nectarivores and (c) insectivores. Open circles indicate that the confidence interval includes zero (no effect), whilst solid circles indicate that zero is not included within the confidence interval

predator avoidance and greater rates of patch recolonization where predation is higher (Hanski, 1998; Lees & Peres, 2009). That said, it is also possible that the nectarivore functional group did not respond strongly to invasive predator control measures due to the underrepresentation of nectarivore species that have already gone extinct, or are highly threatened (Fea et al., 2021). Nevertheless, the species included in our study are broadly representative of typical native bird communities in the studied landscape, and therefore provide a realistic assessment of invasive predator control and habitat fragmentation effects on remnant native bird communities.

Our results appear to somewhat contradict previous findings that similar assemblages of insectivorous bird species were no more abundant in predator controlled sites than in uncontrolled sites,

whilst nectarivorous species were significantly more abundant (Innes et al., 2004; Ruffell & Didham, 2017). Ruffell and Didham (2017) proposed that the general absence of insectivore responses may have been due to ineffectual predator control or weak predation pressure. Our results did not support this assertion as invasive predator control intensity significantly reduced invasive predator abundance, and higher numbers of native birds, particularly insectivores, were found where invasive predator numbers were suppressed, illustrating both the strength of predation pressure and efficacy of invasive predator control.

These contradictory findings are more likely due to differences in how predator control intensity was defined. Whilst studies such as Ruffell and Didham (2017) have classified predator control intensity

in a categorical manner based primarily on poison/trapping density and application frequency (sub-annual and annual), this study utilized a continuous index based on the spatial coverage of predator control within isolated fragments. In fact, the former is more closely related to our index of the temporal distribution of control which was similarly found to have very little effect on the abundance of birds and invasive predators in our study. Taken together, our results suggest that increasing the spatial coverage of invasive predator control may be considerably more important for reducing invasive mammal numbers and enhancing native bird abundance than the timing of control operations, particularly with respect to insectivores.

The lack of significant effects of the timing of invasive predator control on any response variable was unexpected as post-control population recovery of mammalian predators and native birds is generally observable within a 0–5 years window (Armstrong, 2017; Griffiths & Barron, 2016; Le Corre et al., 2015; Van Vianen et al., 2018). This suggests that either the temporal interval was too large to capture the effects of sub-annual control on predator species capable of more rapid population recovery (e.g. ship rats), or that the effects of predator control may last more than 5 years (i.e. the time span of the study was too short) (Van Vianen et al., 2018). In other words, following an initial post-control population decline, predator populations may increase to pre-control levels within 1 year, or they may remain at relatively low levels for more than 5 years with native bird populations already recovered. With the data collected in our study, however, we are unable to identify which of these scenarios are likely at play, but this will be critical for further deciphering the temporal dynamics of invasive predator control impacts on native bird communities.

4.2 | Invasive predator control and fragment area affects predators more than surrounding land cover

As we expected based on the strong effects of invasive predator control detected in the initial linear models, the intensity of invasive predator control was a more dominant driver of total invasive predator abundance and possum abundance than most landscape structure variables, with the exception of fragment area which was similarly dominant.

The negative temporal effect suggests that possum numbers are lower in fragments under more recent control, aligning with population recovery lag-time theory, which suggests a delay in the recovery of a species following suppression (e.g. Ji et al., 2004).

Interestingly, the main effect of fragment area was negative, as were both of the associated interaction terms. This suggests that for larger fragments, increases in the recency and intensity of predator control result in sharper declines in the total abundance of invasive predators and possums. Conversely, it suggests that increases in the recency and intensity of predator control in smaller fragments have little or no effect on the total abundance of invasive predators and possums. Though we can only speculate, this negative effect of fragment area on possum abundance could be due to the longer time

required for possums to recolonize larger fragments to a density that is detectable by camera trapping.

In contrast, ship rats were far more responsive to landscape variables than either predator control variable, which is in keeping with past studies that demonstrate sensitivity of rodents and other small mammals to structural landscape features (Crooks, 2002; Presley et al., 2019). Interestingly, the proportion of native forest within both 1 km and 1–5 km ranges from the study fragments were highly important, yet the two variables had opposing effects (positive vs negative, respectively) on ship rat abundance. This suggests that the effect of native forest cover is scale-dependent; a phenomenon that has been demonstrated across a range of scales for a variety of species and landscapes (Deconchat et al., 2009; Smith et al., 2011). For example, as ship rats are typically most abundant in New Zealand's lowland podocarp forests (King et al., 1996), increasing native forest cover would likely strengthen the persistence of local populations against predator control and other disturbances by providing a larger, more connected source of recruitment (Crouzeilles et al., 2014). This effect would potentially be stronger over smaller spatial scales (e.g. 1 km) as ship rats typically move only short distances (i.e. <200 m) and have non-exclusive home ranges of <1 ha (King et al., 1996), suggesting that only close-range forest habitat would influence their within-fragment abundance. Whilst our results imply that surrounding native habitat may be somewhat important for recolonizing fragments, the negative effects of native forest cover at 1–5 km indicate that there are complex landscape dynamics that require further targeted investigations.

Fractal dimension index also had an important positive effect on ship rat abundance, suggesting that fragments with complex edges and high edge-to-area ratios support greater ship rat populations. Generally, fragments with complex edges tend to have greater population turnover and reduced population stability due to an increase in the likelihood of an individual encountering an edge (Ewers & Didham, 2006). However, fragments with greater proportions of edge habitat are also more strongly influenced by edge effects which can lead to increases in the abundance of habitat generalist species (Ewers & Didham, 2006), such as ship rats, thereby providing a potential explanation for this positive effect in our study. Our findings demonstrate the considerable variability in how invasive predator species can respond to control measures and landscape structure.

4.3 | Invasive predator control and landscape structure jointly influence native bird abundance

Both invasive predator control intensity and fragment area were consistently the most important predictors of total native bird abundance and insectivore abundance, whereas temporal distribution of control and surrounding native forest cover (<1 km) were more important predictors of nectarivore abundance. Indeed, mammalian predator invasion and landscape structure have both previously been shown to impact a variety of avian species (Bregman et al., 2014; Innes et al., 2010; Jones et al., 2016).

The negative effects of fractal dimension index and surrounding native forest cover (<1 km) on total bird abundance contrasts with their positive effects on ship rat abundance, suggesting that the negative response of native birds to fragments with greater proportions of edge habitat and higher proportions of fragment-adjacent native forest may be due to increased nest predation by ship rats. Such effects are, however, typically contextually dependent on a broader range of landscape factors and species-specific relationships (Lahti, 2001; Vetter et al., 2013), such as varying generation times and recovery rates of different birds. This appeared to be the case in our study as fractal dimension index exhibited a stronger relative effect on the abundance of nectarivores than insectivores.

However, the most important effects on nectarivores were from the invasive predator control variables and native forest cover (<1 km). The negative effect of the temporal distribution of control points to advantages in less recent control efforts, potentially due to lag-time in nectarivore population recovery. Additionally, we found an interaction between predator control variables and native forest cover (<1 km), indicating that the importance of control intensity and how recently invasive predators have been controlled depends on native forest cover in the surrounding landscape. Specifically, in fragments with greater surrounding native forest cover, higher intensity of invasive predator control resulted in larger increases in nectarivore abundance, whereas increased recency of invasive predator control resulted in larger reductions of nectarivores in this landscape context. This suggests that the efficacy of predator control for enhancing native bird populations is largely dependent on the surrounding cover of native forest in the wider landscape. Therefore, efforts to restore native bird communities in fragmented landscapes should simultaneously focus on enhancing surrounding native forest cover as well as maintaining high intensity of invasive predator control to maximize biodiversity benefits. The relatively low value of the averaged model's AIC-weighted R^2 value ($R^2 = .370$) does, however, suggest that other important (unmeasured) variables likely contribute to variation in the abundance of nectarivorous birds.

The vulnerability of insectivores to predation and habitat loss is highlighted by the equally dominant positive effects of control intensity and fragment area on insectivore abundance. Whilst increasing habitat area typically has a positive effect on bird communities, the minimum area required to sustain forest bird populations is highly species-dependent (Innes et al., 2010; Watson et al., 2004). Terrestrial insectivore populations tend to be particularly area-sensitive, likely due to their typically limited inter-patch dispersal abilities (Martensen et al., 2008). The invertebrate food resources of ground-foraging insectivores have also been found to decline significantly with decreasing fragment size (Zanette et al., 2000). Consequently, insectivores in smaller fragments are likely to suffer greater bottom-up control due to a more limited food supply (Karr et al., 1992). Interestingly, the surrounding exotic forest cover (<1 km) also had a relatively important negative effect on the abundance of insectivores. This effect is somewhat expected as lower native bird abundances have generally been recorded in New Zealand's exotic pine forests than in native forests due to reduced provisions

of food and nesting habitat (Clout & Gaze, 1984; Deconchat et al., 2009). Overall, the intensity of invasive predator control and landscape structure jointly influences native bird abundance, though the relative importance of specific aspects of landscape structure is context-dependent.

5 | CONCLUSIONS

We demonstrate the importance of both predator control and landscape structure for the conservation of native birds in native forest fragments. In particular, our results suggest that the annual spatial coverage of invasive predator control operations is more important for native bird conservation than the temporal distribution of said operations across the preceding 5 years. At the same time, we show that conservation efforts should also focus on preventing further reduction in the size of habitat fragments and expansion of habitat edges, whilst also restoring native forest cover in the surrounding landscape. That said, we show significant variation in species-specific responses of invasive predators and functional group-specific responses of native birds to predator control and landscape structure. Our results indicate that, whilst currently employed control measures can effectively suppress invasive predator populations, the structure of habitat fragments and overall landscape cover also play an important role in invasive predator numbers. Similarly, varying effects of these factors were evident across the bird functional groups, with insectivores responding more strongly to fragment area and control intensity, and nectarivores responding more strongly to the temporal and spatial aspects of predator control in different ways depending on surrounding native forest cover at the landscape scale. Consequently, strategies for conserving and restoring native bird communities in predator-invaded fragmented landscapes need to account for taxon-dependent and functional group-dependent responses of invasive predators and native birds to invasive species control measures and landscape structure.

ACKNOWLEDGEMENTS

For providing us with historical records of invasive predator control, our thanks goes to Andrew McConnell and the Biosecurity team at Waikato Regional Council, Raymond Tana and Julia Loepelt from the Department of Conservation, Melissa Sinton from the QEII National Trust, Daniel Howie from the Maungatautari Ecological Island Trust, Steve McClunie and Dianne June from the Mount Pirongia Restoration Society, David Peters and Emma Cronin from the Aongatete Forest Restoration Trust, Colleen Grayling from the Howick Tramping Club, Phillip Dawson from OSPRI New Zealand and Neil Fitzgerald from Forest & Bird. This project was supported by the University of Waikato Strategic Research Fund. We also thank the two anonymous reviewers for their highly valuable suggestions.

CONFLICT OF INTEREST

The authors declare that they have no competing interests.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ddi.13539>.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

ORCID

Andrew D. Barnes  <https://orcid.org/0000-0002-6499-381X>

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BIOSKETCH

Shaun Morgan is an MSc graduate at the University of Waikato with an interest in forest bird conservation. In particular, he is concerned with the large-scale applications of invasive predator control methods and the effects of landscape structure on birds and their mammalian predators.

Author contributions: SM and ADB conceptualized the research, with NAB and RKD contributing to its development. NAB and SM collected and processed the data. SM and ADB performed the analysis and SM drafted the manuscript. All authors contributed to the final draft and approved the final manuscript.

SUPPORTING INFORMATION

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How to cite this article: Morgan, S., Binks, N. A., Didham, R. K., & Barnes, A. D. (2022). Functional group-dependent responses of forest bird communities to invasive predator control and habitat fragmentation. *Diversity and Distributions*, 00, 1–15. <https://doi.org/10.1111/ddi.13539>