



# Does landscape composition influence the diets of feral cats in agroecosystems?

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**Abstract** Habitat fragmentation can influence the diet of mammalian predators, potentially increasing their impact on prey species. Agroecosystems are fragmented landscapes that often have high densities of invasive mammalian predators. Feral cats are generalist predators that have successfully adapted to living in agricultural landscapes. Feral cats are known to eat rabbits, rodents, and birds, but it is unclear how landscape characteristics affect prey consumption. Here, we tested whether feral cat diet in New Zealand agroecosystems was affected by landscape composition and spatial configuration. We

examined the contents of 112 feral cat gastrointestinal tracts collected from agroecosystems in different New Zealand regions over a 3-year period. We related prey richness and composition to the landscape composition and spatial configuration in a 500-ha area within which each cat was caught. Dietary analysis showed that feral cats were consuming invertebrates, birds, rodents, and rabbits, and that there were some regional and seasonal effects. No significant differences in prey richness or composition of the diet were associated with variation in landscape composition or spatial configuration. This study confirms feral cats as generalist predators that feed on a wide range of prey types in New Zealand agroecosystems, including some native species. Our study highlights the importance of further research for understanding how current conservation interventions in New Zealand, which include revegetation and rodent control, interact with feral cat populations and behaviours to impact on future biodiversity outcomes.

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## Introduction

Feral cats occur globally in a broad range of habitats and have been implicated in the extinction of 63 species (Langham and Porter 1991; Harper 2007; Moseby et al. 2009; Doherty et al. 2016). They are opportunistic and generalist predators with a

diverse diet (Doherty et al. 2015a), predominately preying on rabbits and rodents, but also birds, reptiles, and invertebrates (Langham 1990; Alterio and Moller 1997; Strang 2018). Their diet is highly flexible, with declines in the availability of their primary prey resulting in shifts to a secondary prey species (McGregor et al. 2020; Parsons et al. 2020) or exploitation of locally abundant, easily targeted prey, such as nesting seabirds (e.g., streaked shearwater *Calonectris leucomelas*), instead of a primarily targeted prey, such as rodents (Azumi et al. 2021). Cat diet can also vary seasonally as prey abundances change, as evidenced by switching from rodents and/or lagomorphs to birds and reptiles in spring when vulnerable juveniles are present (Hervías et al. 2014; Ozella et al. 2016; Parsons et al. 2020; Rendall et al. 2022). In New Zealand agricultural landscapes, feral cats have been observed to primarily eat rodents in addition to lagomorphs (*Oryctolagus cuniculus*, *Lepus europaeus*), Australian brushtail possums (*Trichosurus vulpecula*), sheep (*Ovis aries*), and birds (Langham 1990; Strang 2018). However, to date, studies have not considered how landscape composition and spatial configuration impact feral cat diet.

Prey distribution and abundance in the landscape can affect feral cat movement and habitat use (McGregor et al. 2014; Recio et al. 2014) and, therefore, diet composition. For example, McGregor et al. (2014) observed that feral cats preferentially hunted in patches that had recently been burned, and therefore had reduced vegetation cover, thus increasing prey accessibility. While habitat selection studies have shown feral cats prefer areas with woody vegetation (Doherty et al. 2015b; Nottingham 2023), the effect of size, configuration and connectivity of habitat patches on feral cat diet has not been investigated. In New Zealand, where feral cats are a major predator of native birds, current revegetation initiatives in agroecosystems will increase connectivity between habitat patches, which may alter the feral cat predation risk profile for birds and other native species in these landscapes.

This research characterizes the feral cat diet in New Zealand agroecosystems and investigates whether cat dietary variation correlates with the composition of the landscape and configuration of woody vegetation. Specifically, we investigated whether there was any relationship between feral cat prey richness or composition and the surrounding landscape composition

and spatial configuration, including vegetation patch size, edge density and connectivity (see Supplemental Table S1 for full definitions and rationales). We predicted that higher levels of woody vegetation connectivity would be associated with higher prey richness due to the diversity of prey types that use woody vegetation as their primary habitat. Conversely, we predicted that greater connectivity of woody vegetation would be associated with fewer rabbits and other pasture-associated prey types. Understanding whether feral cat diet is affected by the vegetation landscape composition and spatial configuration will determine if targeted predator control is required alongside revegetation projects in agricultural settings.

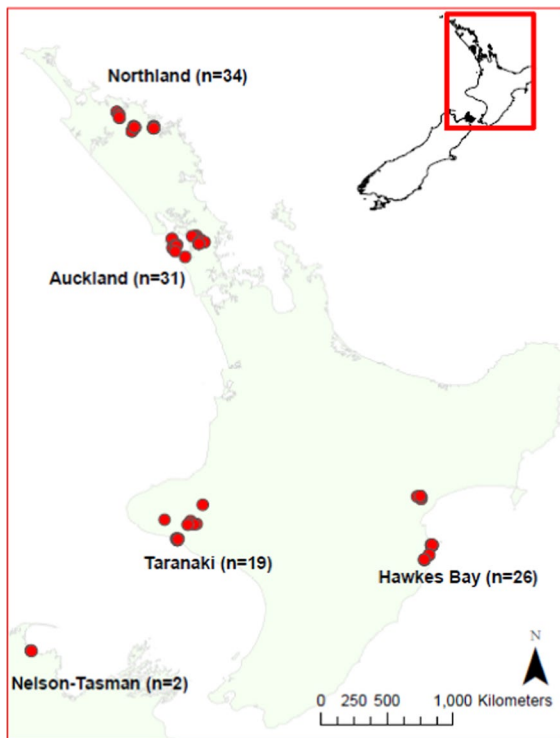
## Methods

### Feral cat collection

We obtained 103 feral cats that had been killed (both live and kill trapped or shot) on farms as part of pest control programs. The feral cats came from five different regions: Northland, Auckland, Taranaki, Hawke's Bay and Nelson-Tasman (Fig. 1, supplemental Table S2). Cats were shipped to the laboratory for dietary analysis, along with their geolocation. Nine additional carcasses of cats previously used in a GPS-tracking study in the Auckland region (Nottingham 2023) were also included in this dataset. We sexed and weighed each cat and measured the length from the nose to the base of the tail. Due to transportation logistics, seven of the cats had their legs or head removed by pest controllers prior to delivery so an accurate weight or measurement was not possible for these individuals.

### Feral cat dietary analysis

Stomachs and intestines were removed from each cat and weighed before and after the contents were removed. The contents were then washed with water through a fine-mesh sieve and were separated initially into hair, bone, feather, invertebrate, and other contents so that they could be divided into six broad food categories: rabbit, rodent (rats and mice), bird, invertebrate, reptiles and 'other', which included possum, sheep, eel and frog. Hair samples were examined under a microscope and compared to hair



**Fig. 1** Sample regions and number of captured feral cats included in the dietary analysis (total  $n=112$ )

identification factsheets (Lowe and Wehi 2017a, b, c, d, e, f) and/or reference samples if available. An attempt was made to identify bird remains to species morphologically (e.g., feathers, bone morphometrics) with the assistance of ornithological experts. Any rabbit that was observed in cats caught in traps baited with rabbit was recorded as bait rather than food; 37 cats were not recorded as eating rabbit for this reason. These cats were spread evenly across regions. The percentage frequency of occurrence of each category was calculated by dividing the total number of samples in each category by the total number of samples and multiplying this by 100.

#### Landscape structure and configuration

We used the ArcGIS (10.7.1; ESRI Inc., Redlands, California, USA) Geographic Information Systems (GIS) software to create a buffer around each cat's capture geocoordinates (as supplied by pest control teams). The geocoordinates were assumed to be the midpoint of their home range and a buffer of radius

500 ha was generated in ArcGIS around this point, based on the mean home range sizes of feral cats in New Zealand (supplemental Table S3). Every buffer area was given a unique cluster identification number (Cluster ID); where two or more buffer areas overlapped spatially, these were each given the same cluster identification number (supplemental Figure S1). Land use categories from New Zealand's Land Cover Database (LCDB, version 5.0; Landcare Research New Zealand Ltd 2020) were reclassified to simplify the land use types into five categories: forest, shrub, infrastructure, water, and other (which included mines and dumps, sand and gravel, gravel and rock, herbaceous freshwater or saline and mangroves) (supplemental Table S4). These were then reclassified into six new derived categories: exotic forest, exotic grassland, indigenous forest, mixed exotic shrubland (including gorse, broom, kānuka (*Kunzea* spp.), mānuka (*Leptospermum scoparium*) or fernland), infrastructure, and other. We then calculated the proportions of the different land uses within each buffer area.

A specific set of landscape metrics were computed to describe variation in the relative spatial configuration and connectivity of the study landscapes (Supplemental Table S1); to do this, ArcGIS was used to convert the reclassified land use categories to a raster with a resolution of 5 m, which was then exported to use within the FRAGSTATS (4.2.1) landscape metric analysis software (McGarigal and Ene 2013). For the land use that had been classified as forest (exotic and native), shrubland and manuka/fernland, FRAGSTATS was used to calculate the area-weighted mean woody patch area (the sum of all woody patches within the buffer area multiplied by the total of woody patches divided by the total area), the edge density, which provided a measure of patch shape (the sum of the lengths of all the habitat patches divided by the total landscape area in hectares), and the clumpiness index, which measures the degree of fragmentation of the landscape (based on the proportional deviation of the proportion of the same class type that would be expected if patch type were randomly distributed spatially) (McGarigal and Ene 2013). The clumpiness index produces values between 1 and  $-1$ ; highly fragmented landscapes are assigned high values (as high as 1), and landscapes with large blocks of homogeneous vegetation are assigned low values (as low as  $-1$ ) (McGarigal and Ene 2013). Landscapes with

randomly distributed woody patches were assigned a value of zero. Further information on these metrics and other metrics that were considered can be found in supplemental Table S1.

To characterize the landscapes, a principal component analysis (PCA) was used to reduce the dimensionality of the explanatory variables: the proportions of each land use type, the area-weighted mean patch area, edge density and clumpiness index. The proportions of infrastructure, exotic shrub and crop proportions were excluded because these sub-categories comprised a low proportion of the areas analyzed (infrastructure mean=0.004%; exotic shrub mean=0.001%; crop mean=0.0004%). We included the first three principal components in subsequent modelling because they each accounted for greater than 10% of variation and together accounted for 69% of the variation.

#### *Are there seasonal or regional differences in feral cat diet?*

Differences in prey frequencies among the regions and among the seasons were tested using Chi-squared comparisons. The number of each of the dominant prey types in the feral cat diet (invertebrates, birds, rodents, rabbits) were compared with the number of all prey types not of that type (Medina and Garcia 2007).

#### *How do landscape composition and spatial configuration affect the prey richness of feral cat diet?*

The relationship between the prey richness (dependent variable), and the first three principal components for spatial landscape metrics, region and season (independent variables), was tested using a mixed effects generalized linear model with a Poisson error distribution. Cluster ID was included as a random effect to control for the lack of spatial independence in the data. We used an information-theoretic approach (Burnham and Anderson 2003) to model selection, where we used AICc values to compare an intercept-only model to models including each of the variables individually, as well as a model with all the variables. We used the 'DHARMA' package (Hartig 2022) to examine the distribution and the dispersion

of the residuals to determine if the models met model assumptions.

#### *How do landscape composition and spatial configuration affect the composition of feral cat diet?*

We used a mixed effects permutational analysis of variance (PERMANOVA) to test for a relationship between prey composition and the independent variables (the first three PCs, region, and season). The analysis was applied to the Jaccard dissimilarity matrix of prey occurrence in the individual cat samples, with cluster ID as the grouping variable. The PERMANOVA was implemented using the vegan package in R (Oksanen et al. 2018). The data were also split into males and females and PERMANOVA was used to analyze the same relationships (i.e., prey composition vs. independent variables).

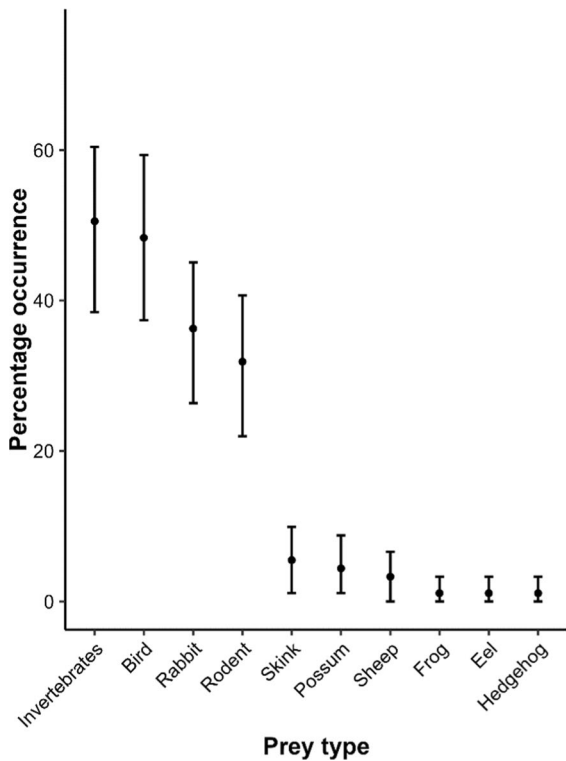
## Results

The guts of 112 feral cats from the central and northern parts of New Zealand (Fig. 1, supplemental Table S5) were examined; 93 cat samples contained prey items and 19 were empty. The cats ranged in weight from 538 to 5500 g; 71 were males, 34 were females and 7 were unknown (supplemental Table S5). Most of the cats were caught in Northland and Auckland; only two cats were caught in Nelson-Tasman (Fig. 1, Table 1). Most of the cats were collected in winter (39) followed by decreasing numbers in spring (25), summer (22) and autumn (16) (Table 1).

Feral cats in this study had predominantly eaten invertebrates including wētā, birds, rabbits, and rodents (Fig. 2, supplemental Tables S6 and S7). Fewer cats had consumed rabbits. There were significant regional differences in the frequency of rabbits found in feral cat guts ( $\chi^2=11.43$ ,  $P=0.02$ ) but no significant seasonal differences ( $\chi^2=6.23$ ,  $P=0.18$ ). Rabbit was eaten most commonly in Taranaki (63% of guts) while rabbits were seen less frequently in Hawke's Bay (19% of guts; Table 1, Fig. 3). Birds were one of the most common prey types in guts (present in 48% of guts); more than half of the guts from Auckland and Taranaki contained bird remains (Table 1). However, there were no significant regional ( $\chi^2=6.39$ ,  $P=0.17$ ) or seasonal differences

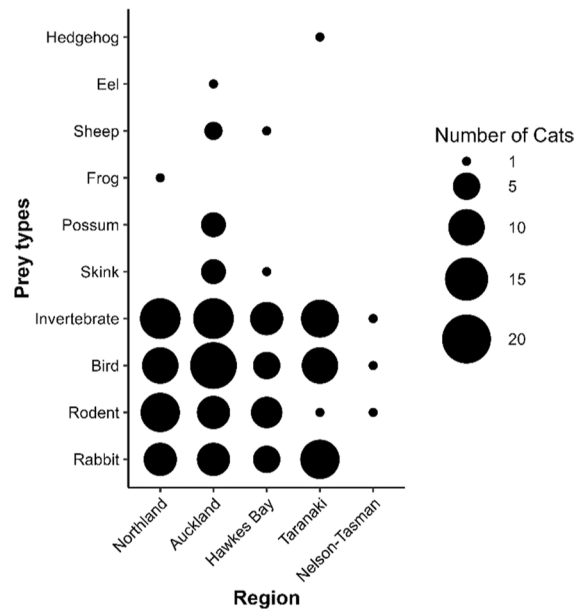
**Table 1** Number of feral cat gut contents grouped by region or season, with the proportion containing rabbit (not including where rabbit was present, but had been used as bait in traps), rodents, bird or invertebrate remains

	Number of cats	Proportion of cat samples containing				Empty guts
		Rabbit	Rodent	Bird	Invertebrate	
<i>Region</i>						
Northland	34	0.24	0.35	0.29	0.38	0.21
Auckland	31	0.26	0.26	0.58	0.42	0.03
Hawkes Bay	26	0.19	0.27	0.19	0.31	0.35
Taranaki	19	0.63	0.05	0.53	0.58	0.11
Nelson-Tasman	2	0.00	0.50	0.50	0.50	0.00
<i>Season</i>						
Summer	22	0.36	0.14	0.41	0.45	0.23
Autumn	16	0.19	0.38	0.44	0.63	0.13
Winter	39	0.31	0.33	0.33	0.21	0.28
Spring	25	0.36	0.00	0.44	0.44	0.04



**Fig. 2** Percentage of cat gut contents ( $n=91$  cats) containing each prey type (% frequency of occurrence) with bootstrapped 95% confidence intervals. Rabbit was not counted as present when used as bait in traps

( $\chi^2=0.74$ ,  $P=0.94$ ) in the frequency of guts containing birds. Weak regional differences in consumption of rodents were observed ( $\chi^2=9.00$ ,  $P=0.06$ ); Northland had higher percent frequency of rodents



**Fig. 3** The relative numbers of cats that had each of the prey types for each region: Northland ( $n=34$ ), Auckland ( $n=31$ ), Hawkes Bay ( $n=26$ ), Taranaki ( $n=19$ ), and Nelson-Tasman ( $n=2$ ). The prey types included rabbit (*Oryctolagus cuniculus*), rodents (*Rattus* spp. or *Mus musculus*), birds, invertebrates, skinks, possum (*Trichosurus vulpecula*), frog (*Litoria aurea*), sheep (*Ovis aries*), eel (*Anguilla* sp.), and hedgehog (*Erinaceus europaeus*)

than Auckland, Hawke’s Bay and Taranaki, and Taranaki had a much lower frequency of occurrence of rodents (Table 1, Fig. 3). There were seasonal differences observed in the numbers of rodents seen in the guts ( $\chi^2=22.23$ ,  $P=0.0001$ ); no rodents were

observed in any guts that were collected in spring (Table 1). Invertebrates were found in the guts at a higher frequency in autumn (0.63) (Table 1) and a lower frequency during winter (0.21) ( $\chi^2=10.35$ ,  $P=0.03$ ), with no regional differences observed ( $\chi^2=1.83$ ,  $P=0.76$ ).

#### Landscape composition and spatial configuration of the feral cats' capture locations

The mean woody patch area ranged from  $0.88 \pm 0.58$  to  $483 \pm 0$  ha with a mean of  $66 \pm 132$  ha and differed between the regions. Auckland, Hawke's Bay and Taranaki had smaller woody patches on average, while Northland (had, on average, larger woody patches (supplemental Figure S2). Taranaki appeared to have two distinct groups of sites, with one grouping having a smaller area-weighted mean woody patch area and the other having much larger woody patches. Edge density values were similar among the four main regions, ranging from  $0.84 \text{ m ha}^{-1}$  (in Northland) to  $48.5 \text{ m ha}^{-1}$  (in Auckland) (supplemental Figure S2). The clumpiness index ranged from 0.84 (in Auckland) to almost one in Hawke's Bay and Northland (supplemental Figure S2).

Exotic grassland covered the greatest proportion of area within the 500-m buffers in which each cat was caught, ranging from 14% in Northland to 97% in Auckland (supplemental Figure S3). Many of the cats from Northland were captured in areas with a substantial proportion of exotic forest (maximum of 70%) and either mānuka, kānuka shrublands or fernland (maximum of Northland) (supplemental Figure S3). However, most of the buffers surrounding the cat capture locations from Hawke's Bay and Auckland, and around half from Taranaki, did not have any of this land cover. Indigenous forest was the dominant

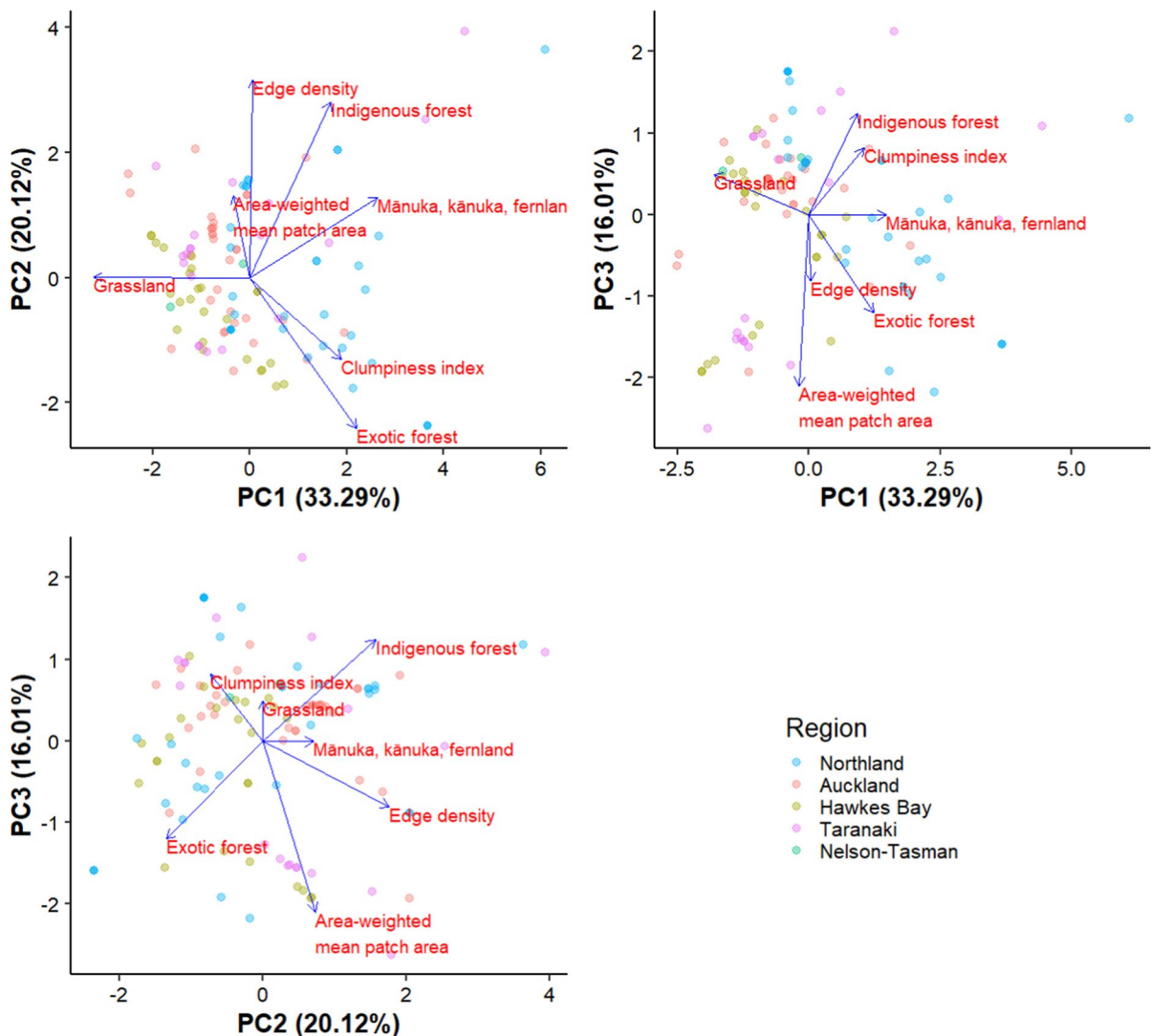
land cover (along with exotic grassland) inside the buffers for Taranaki, with a maximum of 58% indigenous forest cover in Taranaki. Few cats were captured in areas containing exotic shrub, which included gorse and broom, infrastructure or crops (supplemental Figure S4).

The first principal component, which explained 33% of the variation, described a gradient of ratios of the proportion of exotic grassland to the proportions of each of the woody vegetation types, as well as increases in the clumpiness index (Table 2, Fig. 4, supplemental Table S8). The second principal component explained a further 20% of the variation (supplemental Table S8). Low values of this component indicate a higher proportion of exotic forest and a higher clumpiness index. Higher values corresponded to a higher edge density, area-weighted mean patch area and higher proportions of indigenous vegetation. The third principal component explained a further 16% of the variation (Table 2, Fig. 4, supplemental Table S8). Lower values equated to higher edge density, higher area-weighted mean patch area and a higher proportion of exotic forest (Table 2, Fig. 4). Higher values indicated larger median patch area, a higher proportion of indigenous forest and a greater clumping of patches.

Feral cat gut contents from Northland, in general, were collected from cats whose locations had relatively low area-weighted mean patch area and a high clumpiness index, with marked differences in the values of these variables between grassland and the indigenous or kānuka, mānuka and fernland vegetation (Table 2, Fig. 4). In general, gut contents from Auckland appeared to come from cats located in three different types of landscapes; one small group with relative high edge density and area-weighted mean patch area, another that had a relatively high

**Table 2** The loadings of each of the land cover variables and landscape spatial metrics for each of first three principal components (% variance explained)

Variables	PC1 (33%)	PC2 (20%)	PC3 (16%)
Edge density	0.01	0.59	-0.27
Area-weighted mean patch area	-0.06	0.24	-0.70
Clumpiness Index	0.35	-0.24	0.27
Proportion of exotic forest	0.41	-0.45	-0.40
Proportion of exotic grassland	-0.60	0.00	0.17
Proportion of indigenous forest	0.31	0.52	0.41
Proportion of mānuka or kānuka or fernland	0.49	0.24	0.00



**Fig. 4** Biplots for the first three components of a principal component analysis of the landscape composition and spatial configuration (area-weighted mean patch area, edge density, clumpiness index, proportion of exotic forest, grassland, indigenous forest and mānuka, kānuka or fernland). Feral cat

clumpiness index and high proportion of indigenous or kānuka, mānuka and fernland vegetation, and a third with similar clumpiness indices but relatively high proportions of grassland (Fig. 4). Guts collected from the Taranaki and Hawke's Bay regions were generally from sites with relatively high area-weighted mean patch areas and high edge densities, or sites with relatively low area-weighted mean patch area and edge density, and higher clumpiness indices (Fig. 4).

gut collection locations shown as circles and coloured by the region that they were located in (Auckland ( $n=31$ ), Hawkes Bay ( $n=26$ ), Taranaki ( $n=19$ ), Northland ( $n=34$ ) and Nelson-Tasman ( $n=2$ ))

How do landscape composition and spatial configuration affect the prey richness of feral cat diet?

The most parsimonious model for prey richness was the intercept only model. Thus, there was no detectable relationship observed between the landscape composition and spatial configuration variables that were tested and the prey richness in the feral cat diet (supplemental Table S9 and S10).

## How do landscape composition and spatial configuration affect the composition of feral cat diet?

For all cats, there were no significant relationships between diet and the landscape metrics summarized by PC1 ( $F=1.93$ ,  $df=1$ ,  $P=0.16$ , supplemental Table S11), PC2 ( $F=1.61$ ,  $df=1$ ,  $P=0.16$ ), and PC3 ( $F=0.72$ ,  $df=1$ ,  $P=0.39$ ). Similarly, there were no differences among regions ( $F=1.89$ ,  $df=4$ ,  $P=0.10$ ) or seasons ( $F=2.10$ ,  $df=4$ ,  $P=0.39$ ). This result was the same for the male and female subsets ( $P>0.05$ ) (supplemental Tables S12 and S13).

## Discussion

Contrary to our predictions, we found no significant relationships between feral cat prey richness or composition and the surrounding landscape composition and spatial configuration. Feral cats from the North Island and upper South Island in New Zealand agroecosystems consumed a diverse diet, dominated by invertebrates, birds, rabbits and rodents. The feral cats in this study came from landscapes with varying levels of exotic forest, indigenous forest, mānuka or kānuka shrublands and grasslands. Regions differed in these landscape compositions, which, given the high variation in number of cat samples per region and the high variation in cat diets, may have obscured any landscape-level patterns in the effects of woody vegetation area and configuration on cat diet.

### Feral cat diet

Previous research on feral cat diet in New Zealand agricultural landscapes is broadly consistent with what we observed in feral cat guts. Prior studies show that feral cats eat primarily rodents in addition to lagomorphs, possums and sheep, although the frequency of these other prey types varies among studies (Langham 1990; Strang 2018). In addition to the dominant prey types (invertebrates, birds, rabbits, and rodents), feral cats in this study were also observed to be eating native eels, skinks and wētā. As some cats were trapped rather than shot there could have been bias in the data due to digestion from trapped cats prior to death. Regional differences were observed for the frequency of rabbits and weak differences among regions were observed for rodent frequency

in the guts. Seasonal differences were observed in the frequency of rodents and invertebrates, and, as expected, invertebrates were less frequent in guts during winter. Rodents in New Zealand vary seasonally in density due to seasonal breeding and food availability, with density being lowest in spring and early summer (Vattiato et al. 2023). Seasonal differences in the frequency of occurrence of invertebrates and rodents have previously been observed in studies that have assessed feral cat diet in relation to changing prey availability (e.g. Yip et al. 2015). Potentially, with a larger sample size, stronger seasonal and regional effects may have been observed in our study. Although, accumulation curves for all the cats (supplemental Figure S5) and for each region (supplemental Figure S6) show that they are approaching an asymptote.

We did not find any definitive evidence of other native species in feral cat diets, such as native birds; however, this could have been because we were unable to identify most bird samples to species level (supplemental Table S6). It is likely that a proportion of these birds would be native species given the dominance of indigenous forest in some of the buffer areas, and that native species are more likely to be present in indigenous forest than pasture (MacLeod et al. 2008; van Heezik et al. 2008; Barbaro et al. 2012; Barnagaud et al. 2014; 2022), and that cats have shown a preference for forest habitat (Nottingham 2023). Bird remains were also relatively common in other feral cat studies: 24% ( $n=361$  scats; sheep and beef farm) (Langham 1990), 36% ( $n=158$  guts; scrubby farmland, tussock grasslands) (Borkin 1999), >40% ( $n=432$  scats, island with forest and farmland) (Strang 2018) and 44% of samples ( $n=9$  guts, farmland) (Bramley 1996). These studies did not quantify land cover, and the surprisingly high frequency of guts containing birds in our study compared to some previous studies could be due to differences in landscape composition. Previous research in Hawke's Bay has shown that birds have been more commonly observed in the scats of feral cats during spring and summer (Langham 1990). In contrast, there were no significant increases in frequency occurrence of birds in the cat guts during spring in our study.

Prior research consistently shows that feral cat diet reflects prey availability; the results from this study seem inconsistent with this pattern, both regionally and seasonally. For example, although



rabbits occur throughout New Zealand, some regions are likely to have a higher abundance of rabbits due to the distribution of their preferred habitat conditions. Rabbits prefer <1000 mm of rainfall annually and light soil (NPCA 2012). For example, Hawke's Bay and Nelson-Tasman are relatively dry, and high numbers of rabbits have been recorded in Hawke's Bay (de Burgh et al. 2021), while Taranaki and Northland have much wetter climates and we would have anticipated fewer rabbits. However, our results show the opposite of this, with a higher frequency of occurrence of rabbit in guts from Taranaki compared to Hawke's Bay. The relative frequency of rabbits in cat guts was likely to have been undercounted for some regions due to excluding rabbit observations from cats caught where rabbit was used as bait, which is common in predator control programs. In prior research in Hawke's Bay, rabbits were present in only 3% of cat scats (n=361), and were not abundant in the study area (Langham 1990). In contrast, where rabbits were relatively more common, it was observed that 61% (n=158 guts; Central Otago; Borkin 1999) and 56% (n=9 guts; East Cape; Bramley 1996) of the guts contained rabbits. Borkin (1999) also observed seasonal differences in central Otago with greater rabbit consumption during spring, while no seasonal differences were observed in our study.

Rodent occurrence in the cat guts showed seasonal differences and potential weak regional differences, with very few rodents seen in Taranaki. There are several projects currently occurring in Taranaki related to New Zealand's Predator Free 2050 goal, which aims to eradicate rats. This intensive control could have meant that there were fewer rodents available as prey for cats (Rotokare Scenic Reserve 2013; Tompkins 2018). This could be why very few rodents were found in cat guts from Taranaki; a higher frequency of guts contained birds and invertebrates. There were also seasonal differences observed in rodent occurrence, with no rodents detected in guts during spring, aligning with seasonal patterns in pest density reviewed by Vattiato et al (2023). Changes in the frequency of occurrence of rodents present in the gut, particularly in habitats that are likely to have fewer rodents due to planned rat eradications, is concerning if cats prey-switch to birds and invertebrates (Yip et al. 2015; Azumi et al. 2021).

How do landscape composition and spatial configuration affect the prey richness and composition of feral cat diet?

For an opportunistic predator like the feral cat, dietary composition usually depends on prey availability, which would be expected to vary between different habitats. For example, cats might be expected to consume more rodents in forest habitat (Walker et al. 2019; Burge et al. 2021), and more rabbits in exotic grassland (Norbury et al. 2021; Barnagaud et al. 2022). Surprisingly, we observed no significant effect of landscape composition and spatial configuration on species richness and composition of prey in the guts of feral cats.. These non-significant results are in contrast to prior research. For example, Kutt (2011) showed a higher frequency of occurrence of invertebrates in stomachs collected from grassland habitat and more amphibians in stomachs collected from woodland habitat in the tropical savannas of Australia.

Several factors could explain why we did not find an effect of changing landscape composition, spatial configuration and composition on the feral cat diet. The variation among landscapes observed in this study may not have offered enough variation in prey availability to result in detectable dietary differences. Alternatively, or in addition, the landcover database land-use layer could have been too low resolution to enable the demonstration of landscape differences at an appropriate scale for feral cats. For instance, the resolution of the landcover database land-use layer (1:50,000) meant that small patches of woody vegetation less than one hectare would not have been quantified by the landscape metrics used in this study. Unexpectedly, we did not observe differences in prey richness or dietary composition among cats caught in landscapes with differences in woody vegetation patch area. This was despite the expectation that larger patches are likely to support a greater abundance and richness of animals (Diamond 1975; Palmeirim et al. 2020); however, several small patches can support more animals than a single large habitat patch (Fahrig and Storch 2020). We possibly did not see any effect of patch size because some sites had many patches, whereas others had fewer, but much larger, patches.

We had expected to see an effect of edge density on the richness or composition of the diet. Edge habitat is

likely to be more complex than the surrounding open habitat of exotic grassland, and can provide habitat for a variety of different species (Seaton et al. 2010; Barbaro et al. 2014), resulting in greater diversity in the diet. Increased predation in edge habitat has been attributed to higher prey density resulting in increased numbers of predators and predator activity (Chalfoun et al. 2002), as predators from the surrounding habitat move into edge habitat patches and target prey there (Andren and Angelstam 1988). For example, nests on the edge of habitat patches are more susceptible to predation (Andren and Angelstam 1988; Sedláček et al. 2014; Colombo and Segura 2021), which is often attributed to predators preferentially selecting edge habitat (Oehler and Litvaitis 1996). The lack of effect seen in our study could have been a result of not having sufficient range in edge densities. Our previous research, which tracked feral cats across Auckland farmland, showed that individual cats have strong preference for particular habitat types, most often woody patches (Nottingham 2023).

We did not observe any differences in diet composition between males ( $n=56$ ) and females ( $n=29$ ). This contrasts with the results of other studies (with much larger sample sizes). For example, Rendall et al. (2022) ( $n=692$ ) showed male cats ate more rabbits than females, and Moseby et al. (2021) ( $n=1748$ ) also found that large (predominantly male) cats ate more rabbits.

## Implications

The potential impact of feral cat predation in agroecosystems should not be underestimated based on the findings of this study. The prey species that feral cats were consuming in this study, which included rabbits, rodents, birds and invertebrates, are likely to be highly abundant in agroecosystems and thus can support abundant feral cat populations (Norbury et al. 1998; Norbury and Jones 2015). Ongoing habitat restoration is likely to result in increased native species populations in, or adjacent to, agroecosystems. There are a number of projects encouraging revegetation on sheep and beef cattle farms, with an emphasis on using indigenous vegetation (Suryaningrum et al. 2022; The Forest Bridge Trust 2022). There is also increasing predator control on farms, which includes possums, mustelids and rats, but not necessarily cats. If this control results in a reduction of mustelids

and rats, there should be an increase in bird populations (Binny et al. 2020). Our study showed that, in Taranaki, a high proportion of cat guts contained birds, which was likely related to the landscape being subjected to greater rodent control. In this region, there was a lower occurrence of rodents in the guts and also a higher frequency of guts containing birds and invertebrates. However, revegetation would also be expected to increase the abundance of birds and invertebrates, particularly native species (Moller et al. 2008). These native species would then be at risk of predation from cats. Rat control may have resulted in cats prey-switching to birds. Rabbit control could also be at risk of causing cats to prey-switch to birds, although rabbits are not being targeted by Predator Free 2050.

Determining the effect of changes in vegetation on feral cat predation will require longitudinal diet studies. Further, it will be important to determine if prey-switching is occurring in habitats where rat numbers are being reduced. Replicated before-after control-impact (BACI) studies (Underwood 1994) would be an appropriate methodology to determine the effects of changing prey population densities on feral cat diet, including both rodents and rabbits as important factors.

The opportunistic nature of the sample collection in this study has likely affected the results that landscape composition and spatial configuration were not observed to significantly affect cat diet. Ideally, future research would use a stratified random sample to collect feral cat guts from a wide range of sheep and beef farms from a representative range of New Zealand regions over a period of several years. The landscapes would need to have wide variation in area and configuration of woody vegetation with sufficient replication of conditions. Directly observing feral cat hunting behavior with cameras on collars (Hernandez et al. 2018) could provide greater information on feral cat behavior, individual differences in hunting behavior, and whether different landscapes provide different levels of hunting success. Collar cameras have been able to determine the number of kills per day, hunting success, most common prey captured and the timing of hunting (McGregor et al. 2015; Hernandez et al. 2018). Different hunting success in different habitats can also provide information about what prey is more likely to be at risk and possibly ways to modify the habitat to decrease feral cat hunting success

(McGregor et al. 2015). Having a greater understanding of prey species composition, prey type frequencies per day and whether this varies by landscape, would allow estimation of feral cat impact on particular prey and how this may be affected by changes in landscape management.

## Conclusion

The results of this study show cats in New Zealand agroecosystems consume a diverse range of prey types; however, variation among landscapes was not significantly related to variation in feral cat diet. Some seasonal differences in feral cat diet were observed that are likely to be related to seasonal variation in prey availability. A randomized, stratified sample could help elucidate if there are landscape effects on cat diet that were not observed in this study. Direct observations of predatory behavior could also provide more information on feral cat diet in agroecosystems.

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## Declarations

**Competing interests** Authors have no competing interests.

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