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Abundance of *Leiopelma archeyi* on the Coromandel Peninsula in relation to habitat characteristics and land-use

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Published online: 31 August 2023

Abstract: Habitat disturbance is a significant factor contributing to biodiversity decline worldwide. Amphibians are particularly vulnerable because of their specific microclimatic and microhabitat requirements. In Aotearoa New Zealand, Archey's frogs (*Leiopelma archeyi*) have shown some degree of resilience to severe habitat disturbance historically. However, it is unknown how much *L. archeyi* populations are currently being impacted by historical and ongoing mining activities and development within their range. To address this issue, we conducted paired-sample abundance estimation of *L. archeyi* in two areas of the Coromandel Peninsula, Te Ika-a-Māui. Sixteen pairs of 100-m² sites (i.e. sites < 100 m from one another) were surveyed, each comprising of an area which had been disturbed (at least 50% of vegetation removed) by mining exploration or urbanisation during the past 40 years and an area that remained undisturbed over the same period of time. Disturbed sites were subdivided into three categories (1980s, 1990s, and 2020–2016) based on the time elapsed since disturbance. At each site, we performed capture-recapture of frogs over three nights, using their natural markings to identify individuals. We then used a purpose-built closed mark-recapture model to estimate frog abundance. Frog abundances varied among sites but were unrelated to the history of habitat disturbance. Rather, abundance was correlated with higher elevation and with plant species typically associated with mature forest, which was present in both disturbed and undisturbed sites. Ordination techniques used to assess vegetation composition revealed variation among sites that possibly reflects forest succession and replanting in disturbed areas. From our observations, if habitat disturbance does occur we recommend allowing sites to naturally regenerate or to plant species that contribute to leaf litter depth, microhabitat complexity, and increased moisture to promote recolonisation of sites by *L. archeyi*.

Keywords: abundance, capture-recapture, conservation, habitat disturbance, *Leiopelma archeyi*, ordination, paired-sample estimation

Introduction

Anthropogenic-induced ecosystem and habitat modification are some of the greatest threats to biodiversity worldwide (McNeely et al. 1990; UNEP-WCMC et al. 2018). Habitat is defined here as “the resources and conditions present in an area that produce occupancy by individuals of a given species and allows those individuals to survive and reproduce” (Hall et al. 1997). An understanding of a species' habitat requirements can therefore be used to explain distribution and abundance (Hall et al. 1997). When observing the impact of habitat disturbance on species, it is important to recognise that habitat, as well as a species' adaption to habitat, can vary and change over time and space (Southwood 1977; Stadtmann & Seddon 2020).

Habitat disturbance events are likely to become more common with the combined impacts of increasing human population demands and the effects of the climate crisis (Díaz et al. 2019). Amphibians are particularly vulnerable to habitat

changes because of their sensitivity to microclimate, such as the risk of desiccation or temperature-related stresses (Findlay & Houlihan 1997; Krishnamurthy 2003). Amphibians may also require multiple habitats to meet their needs across life stages within a full life cycle (Wilbur & Collins 1973; Morrison & Mathewson 2015). In the tropics, habitat fragmentation has severely impacted amphibian populations (Brook et al. 2003; Cruz-Elizalde 2016). For example, forest fragmentation to create coffee (*Coffea* spp.) plantations and pasture has led to a decrease in amphibian species number and turnover, with only generalist species able to exploit the modified environments (Cruz-Elizalde 2016). In Aotearoa New Zealand, the burning and clearing of indigenous forest by early Polynesian settlers reduced forest cover from 78% to 53% (King 1984). Forest clearance continued throughout European colonisation until only 26% of forests remained (Ministry for the Environment & Stats NZ 2018). This loss of vegetation, along with the introduction of mammalian predators, caused widespread

declines and extinctions of Aotearoa fauna including amphibians, all in the endemic genus *Leiopelma* (see Burns et al. 2018).

Habitat loss and disturbance remain ongoing threats to *Leiopelma* species (Bishop et al. 2013; Burns et al. 2018). *Leiopelma* are particularly vulnerable to habitat loss and disturbance because they occupy discrete home ranges and depend on specific microclimates to carry out their life cycles (Stephenson & Stephenson 1957; Bell 1978; Thurley & Bell 1994). They are also relatively immobile species and therefore cannot easily relocate when their home ranges are adversely affected (Essner et al. 2010; Reilly et al. 2015; Ramirez 2017).

Only *Leiopelma archeyi* and *Leiopelma hochstetteri* still occur on mainland Aotearoa, with both found on Te Ika-a-Māui/North Island. These species have suffered major range retractions and genetic bottlenecks coinciding with human arrival (Worthy 1987; Easton 2018; Seersholm et al. 2018). Habitat loss has contributed to the fragmentation of populations of *L. hochstetteri* with isolation shown to cause smaller, cytogenetically distinct populations that are at risk of potential inbreeding (Green 1994; Easton 2018). Two relict, genetically distant populations of *L. archeyi* occur on the Coromandel Peninsula and in Whareorino Conservation Area (Thurley & Bell 1994; Easton 2018). Under the Conservation Act 1987, Whareorino is categorised as stewardship land due to its “poor value” for economic use and has the weakest legal protection of all categories of conservation land. On the Coromandel, *L. archeyi* is present on private land and within the Coromandel Forest Park, protected for its recreational and biodiversity values.

Described by Archey (1922) as “living on the crest of the range, moss-covered, and damp from the elevation”, these specific resources and conditions reflect the needs of a specialist species. Terrestrial amphibians require habitat with high levels of moisture for respiratory and osmoregulatory functions, and this is thought to often limit their habitat to higher elevations with adequate humidity and rainfall (Spotila et al. 1992; Duellman & Trueb 1994; Hillyard 1999). *Leiopelma archeyi* show high rates of evaporative water loss and emergence from retreat sites is strongly correlated with humidity (< 85%), rainfall and wetness of vegetation (Bell 1985; Cree 1989; Ramirez 2017). Cree (1989) found individuals could rehydrate rapidly from wet foliage, such as *Freycinetia banksii*, and similar numbers of frogs emerged on wet nights during both summer and winter. Emerged frogs have been observed climbing tree trunks and stems of shrubs over 2 m and sitting on foliage and leaf litter (Stephenson & Stephenson 1957; Bell 1978; Cree 1989; Ramirez 2017). During the day, individuals retreat under logs, rocks and leaf litter/ fronds or in other refuges (e.g. hollow tree ferns, vegetation) (Bell 1978; Ramirez 2017; Cisternas et al. 2023).

Over 1996–2001, the Coromandel *L. archeyi* population suffered a major reduction and remains at suppressed yet stable numbers (Bell et al. 2004; Burns et al. 2018). Disease was suggested to be the most likely cause of this decline (Bell et al. 2004). To reduce the risk of further decline a new wild population was established (Smale & Wallace 2006; Cisternas et al. 2021). Environmental criteria used to select the site for the new population was formed at a macrohabitat scale. These features were not informative for the microhabitat conditions frogs would experience at the new site (Pukeokahu forest, Pureora), and evidently habitat quality did not match that of the donor site (Whareorino) (Cisternas et al. 2021). As an emergency translocation, it was not feasible to conduct multi-

scale site assessments on the microhabitat use of *L. archeyi* prior to translocation. It is apparent, however, that this level of investigation into the resources and environmental conditions that *L. archeyi* select, such as in our study, is critical knowledge for the improved management of this species.

Recovery actions for *L. archeyi* and *L. hochstetteri*, both classified as At Risk – Declining, include increasing our understanding of microhabitat requirements and how land-use activities may impact on these requirements (Bishop et al. 2013). Under the Crowns Mineral Act 1991, mining is a permitted activity on conservation land and has been highlighted as an activity that could impact *L. archeyi* populations in southern Coromandel (Bishop et al. 2013; Burns et al. 2018). Aotearoa native frogs and their habitats are protected by the Wildlife Act (1953) and Resource Management Act (1991). Consequently, disturbance or destruction of frog habitat needs to be accompanied by management actions to address these effects. Such actions may include restoration of habitat, and as such, it is important to understand habitat requirements.

The aims of this study were to estimate the effects of historical (<50 years) small-scale (100 m²) vegetation clearance on the abundance of *L. archeyi* on the Coromandel Peninsula. We simultaneously estimated effects of vegetation composition and other habitat characteristics (including elevation, dominant vegetation, and percentage of canopy cover) on abundance, partly because these factors may explain the underlying mechanism of disturbance effects but also to understand other factors driving frog presence. Understanding the spatial and temporal habitat requirements for *L. archeyi* will allow us to better select areas to protect from disturbance, identify potential translocation sites, and potentially restore habitats disturbed and degraded as a result of human activities, thus expanding the species’ potential range.

Methods

Sampling design

Field sampling was carried out in two forested areas on the Coromandel Peninsula (Te Ika-a-Māui Aotearoa/North Island, New Zealand). We refer to these locations as ‘WKP’ and ‘MFE’ to avoid revealing site information that could lead to poaching. WKP has a history of mining exploration since the early 20th century whereas MFE was subdivided into 24 private properties in the 1990s. We selected 16 pairs of 100-m² (10 × 10 m) survey sites, with each pair consisting of a disturbed site and an adjacent undisturbed site (Fig. 1), separated by only 20–100 m to ensure that physiography and orientation were comparable. WKP had 12 pairs of sites distributed over an area of 32 ha and MFE had 4 pairs distributed over 11 ha (totalling 32 sites), with these numbers reflecting the relative extent of habitat disturbance within these two areas.

Locations of past exploration sites at WKP were obtained from OceanaGold (NZ) Ltd, and locations of disturbed sites at MFE were provided by a local resident with knowledge of the area. Historical aerial photographs show large amounts of vegetation loss throughout WKP and MFE prior to 1980 due to farming or logging practises. Sites were therefore classed as disturbed if > 50% of vegetation had been cleared after 1980, and the disturbed sites were further sub-divided into three categories depending on the year of disturbance (1980s, 1990s, 2010–2016) (Fig. 1). No frog surveys had been performed at these locations prior to this study.

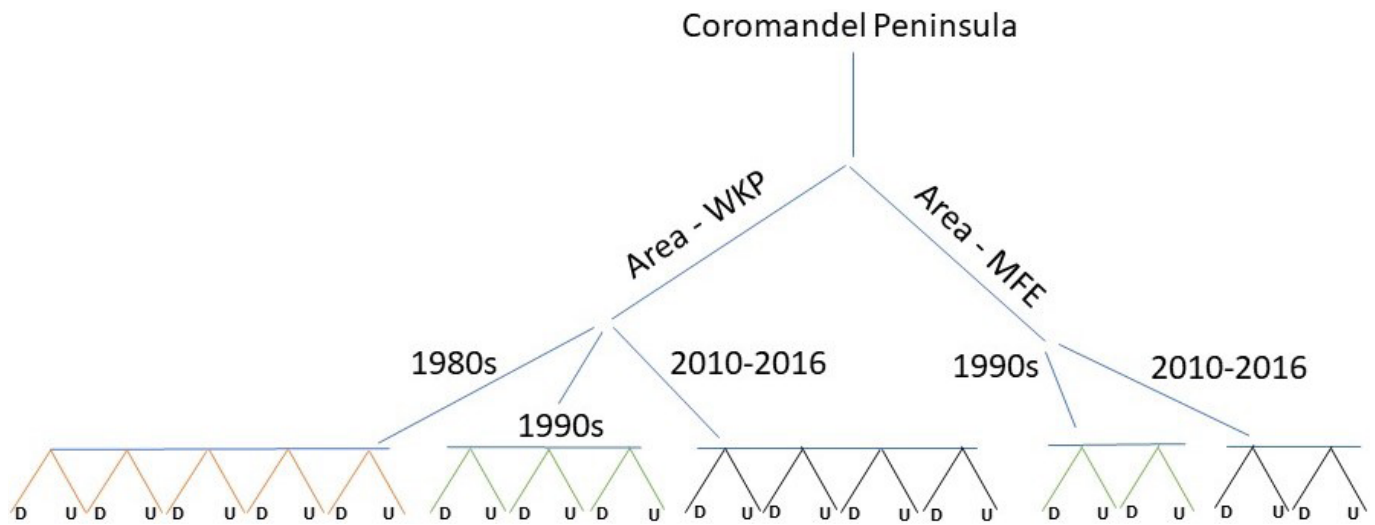


Figure 1. Sampling design to assess the effect of disturbance on abundance of *Leiopelma archeyi*. Sixteen pairs of 100-m² (10 × 10 m) survey sites, with each pair comprising a disturbed site (D) and an adjacent undisturbed site (U), were selected within two study areas (WKP (associated with exploration mining) and MFE (associated with housing and roading development)) on the Coromandel Peninsula. Sites were disturbed by exploration mining or roading/ housing development in these two areas during the 1980s (orange on figure), 1990s (green) and 2010–2016 (black).

Field methods

Frog surveys

We surveyed sites over 33 nights between 14 November 2018 and 20 March 2019, which encompassed most of the breeding and parental-care period (October–February) for *L. archeyi* (Bell 1978; Cisternas et al. 2022). One to two pairs of sites were surveyed each night over three consecutive nights (from 2000 to 0700 hrs) to enable abundance estimation using capture-recapture methods (see below). Surveying a site involved dividing the area of each site into lanes 3 m wide and 10 m in length among a team of two to three people. This allowed each person to search a path of 1–1.5 m at a time, while slowly walking the length of the site (10 m). These search paths changed each night to reduce the impacts of searcher disturbance on frog detection. The order in which sites in a pair were searched was also alternated. Surveying mostly involved searching for emerged frogs. However, dead fern fronds were carefully lifted if present because they are known to be preferred refuges and substrates for *L. archeyi* and are easily replaced with minimal risk to undetected frogs. Surveys were mostly conducted on nights with air temperature > 9°C and humidity > 80% to avoid nights likely to have low frog emergence (Bell 1978; Cree 1989; Ramirez 2017). Three sites had one survey night < 9°C. We recorded the temperature and humidity before and after each survey using a Kestrel 3000 and a Kestrel 5000 pocket weather meter.

Each frog found was initially photographed on the substrate where it was encountered, and its location marked using a Garmin GPSMAP 64st global positioning system (GPS) (5 m margin of error). Using powder-free nitrile gloves, we then placed the frog into its own pre-numbered clean ziplock bag and measured its snout-vent length (SVL) in mm using digital callipers. Frogs were grouped into three size categories: < 18 mm SVL (juveniles), 18–24 mm SVL (sub-adults), and > 24 mm SVL (adults). Natural markings can be used to assign individual *L. archeyi*, so close-up photographs were taken to record unique markings and any peculiarities (Bradfield

2004). The captured frog was left inside the bag and pegged off the ground in the site until the site was surveyed for that one night to avoid recapture or trampling. No frog was left inside a bag > 2 h and all frogs were returned to where they were captured.

Habitat characteristics

To investigate habitat characteristics that potentially influence *L. archeyi* abundance, we performed reconnaissance plot vegetation descriptions (RECCEs) (Allen & McLennan 1983; Allen 1992) from January–March 2019 after the completion of each frog surveys at each site (i.e. after three consecutive nights). We estimated vegetative cover of all the species or taxa within each site at six standard height tiers (0.3 m, 0.3–2 m, 2–4 m, 5–12 m, 12–25 m, > 25 m) and one epiphytic class (Allen & McLennan 1983). Vegetative cover was taken to be the species' foliage shadow at solar zenith in each tier (Redpath & Rapson 2015) and assigned to one of six cover-abundance classes (<1%, 1–5%, 6–25%, 26–50%, 51–76%, 76–100%) for each tier height (Allen & McLennan 1983). We also recorded the approximate average canopy height of the dominant vegetation (to the nearest m), the canopy cover above 1.35 m (from proportion of sky blocked out by vegetation; Allen & McLennan 1983), and elevation. Vegetation species which had been replanted by OceanaGold (NZ) Ltd after exploration in two of the 1980s sites and four of the 2010–2016 sites were noted.

Data analysis

Vegetation analysis

We characterised vegetation composition across sites using ordination techniques to assess how vegetation was affected by disturbance and whether this was a useful predictor of frog abundance. For each plant species (or taxon), the maximum cover category across all tiers from the REECE data were linearised in respect to the midpoint of each cover class by square-root transformation. Sample sites were arranged along a gradient of similarity with respect to vegetation composition

using principal components analysis (PCA) in CANOCO, Version 4.55 (Ter Braak & Smilauer 2002). The variance explained by axis 1 and axis 2 was then used in the frog abundance estimate model (See section below with PCA1 and PCA2).

The pattern of the vegetation composition was further explored by categorising the species and taxa into functional groups (see Appendix S1 in Supplementary Material), as we thought this might give a meaningful indication of habitat quality for frogs given that their phytotaxonomic skills are unknown. The ordination was otherwise similar to that when plants were divided by species or taxon.

Frog abundance estimates

We used closed-population mark-recapture models to estimate abundance of frogs at each site. Under these models, it was assumed that no birth, death, immigration, and emigration would occur within a 100 m² site over three consecutive survey nights. This assumption seemed reasonable given that previous studies on *L. archeyi* have shown that individuals typically move 1.5–3 m throughout the night and go back to the same refuge, or near that refuge, each dawn (Cree 1989; Ramirez 2017). We developed purpose-built code (Appendix S2) in OpenBUGS version 3.2.3. which fits models to data using Markov chain Monte Carlo (MCMC) methods (Spiegelhalter et al. 2014; McCarthy 2007). The flexibility of MCMC fitting allowed us to simultaneously model multiple sites with few nights per site, which would not have been possible with standard models.

Under these models, the probability of a frog being captured (p) or recaptured (c) at site i on night j was given by:

$$\text{logit}(c[i,j]) \leftarrow a.p + b.T * T[i,j] + b.H * H[i,j] + re.t.p[\text{night}[i,j]] \quad (1)$$

$$\text{logit}(p[i,j]) \leftarrow \text{logit}(c[i,j]) + b.B \quad (2)$$

where $a.p$ is the intercept, T and H are the temperature and humidity, $b.T$ and $b.H$ are the effect of these variables on detection probability, $b.B$ is the effect of capture on subsequent recapture probability, and $re.t.p$ is a nightly random to allow for changes in detection probability not explained by temperature and humidity. Sites were otherwise assumed to have equal detection probabilities.

When estimating abundance, we first obtained unconstrained estimates of the numbers of frogs at each site, i.e. without explanatory variables used to explain the variation among sites. This allowed us to check that subsequent models gave reasonable fit to these data. We then fitted two additional models to assess whether abundance was affected by disturbance and habitat characteristics. In both cases the number of frogs at a site, $N[i]$, was taken to be sampled from a Poisson distribution with expected value $mu[i]$. Under the first model the expected abundance was given by:

$$a.mu + b.dist * dist[i] + b.dist90 * dist90[i] + b.dist10 * dist10[i] + b.area * area[i] + re.pair[pair[i]] \quad (3)$$

where $b.dist$ is the overall effect of disturbance and accounts for sites disturbed during the 1980s, $b.dist90$ and $b.dist10$ allow for potential differences due to the age of the disturbance (1990 and 2010–2016), $b.area$ is the effect of the area (WKP vs MFE, with WKP as reference), and $re.pair$ is a random effect accounting for residual variation among pairs

of sites. Under the second model the expected abundance was:

$$a.mu + b.pca1 * pca1[i] + b.pca2 * pca2[i] + b.ele * ele[i] + b.canper * std.canper[i] + b.domveg * domveg[i] + re.pair[pair[i]] \quad (4)$$

where $b.pca1$ and $b.pca2$ is the effect of vegetation composition (see vegetation analysis for an explanation of these parameters), $b.ele$ is the effect of elevation, $b.canper$ is the effect of canopy cover above 1.35 m, and $b.domveg$ is the effect of the average height of dominant vegetation. The explanatory variables were standardised prior to analysis to allow for easier interpretation of effect sizes.

The model had uninformative priors (normal distributions with mean 0 and precision 0.1 for main parameters, uniform distributions ranging from 0–1 for hyperparameters) and were run in two chains for 41 000 samples with the first 500 samples discarded as burn-in.

Results

Frog surveys and habitat characteristics

A total of 176 individual *L. archeyi* were found during 96 surveys within the 32 sites, comprising 150 at WKP and 26 at MFE (see Appendix S3 for individual site information). Between 1–9 frogs were found at WKP sites disturbed during 1980s, whereas 0–15 frogs were found at adjacent undisturbed sites (Appendix S3). Sites disturbed during the 1990s at WKP had 3–10 frogs found and 0–13 frogs were found at adjacent undisturbed sites. Between 2–12 frogs were found at WKP sites disturbed during 2010–2016, whereas 4–18 frogs were found in adjacent undisturbed sites. One frog was found in a site disturbed during the 1990s at MFE, whereas no frogs were found in adjacent undisturbed sites. Between 3–14 frogs were found in sites disturbed during 2010–2016 at MFE, whereas 1–7 frogs were found in adjacent undisturbed sites (Appendix S3). There were 29 recaptured individuals overall. Of the 176 individuals, 92 were adults (> 24 mm SVL), 54 were subadults (18–24 mm) and 38 were juveniles (< 18 mm), with all metamorphosed life-stages found within disturbed and undisturbed sites (Fig. 2).

Mean temperature and relative humidity during surveys ranged between 9.0–18.5°C and 83–99%, respectively. Sixteen surveys were conducted in rain (17%), 33 when vegetation was wet (34 %) and 47 surveys when vegetation was dry (49 %).

Elevation ranged between 149–448 m among sites, and some sites at both extremes of this range had relatively high numbers of frogs (> 7 captured) (Appendix S3). The height of the dominant vegetation and the canopy cover above 1.35 m also varied among sites (Appendix S1). On average, disturbed sites had lower dominant vegetation heights (9.7 m) than undisturbed sites (13.9 m) as well as a lower percentage of canopy cover above 1.35 m (51 %) than undisturbed sites (81%). A total of 95 plant taxa were identified within the 24 sites at WKP, and 60 plant taxa identified within the 8 sites at MFE (Appendix S1).

Vegetation analysis

The PCA on vegetative cover scores of individual plant species and taxa (Fig. 3) indicated that axes 1 and 2 explained 33% and 16% of the variance among sites respectively. Axis 1 was positively associated with forest species such as *Cyathea*

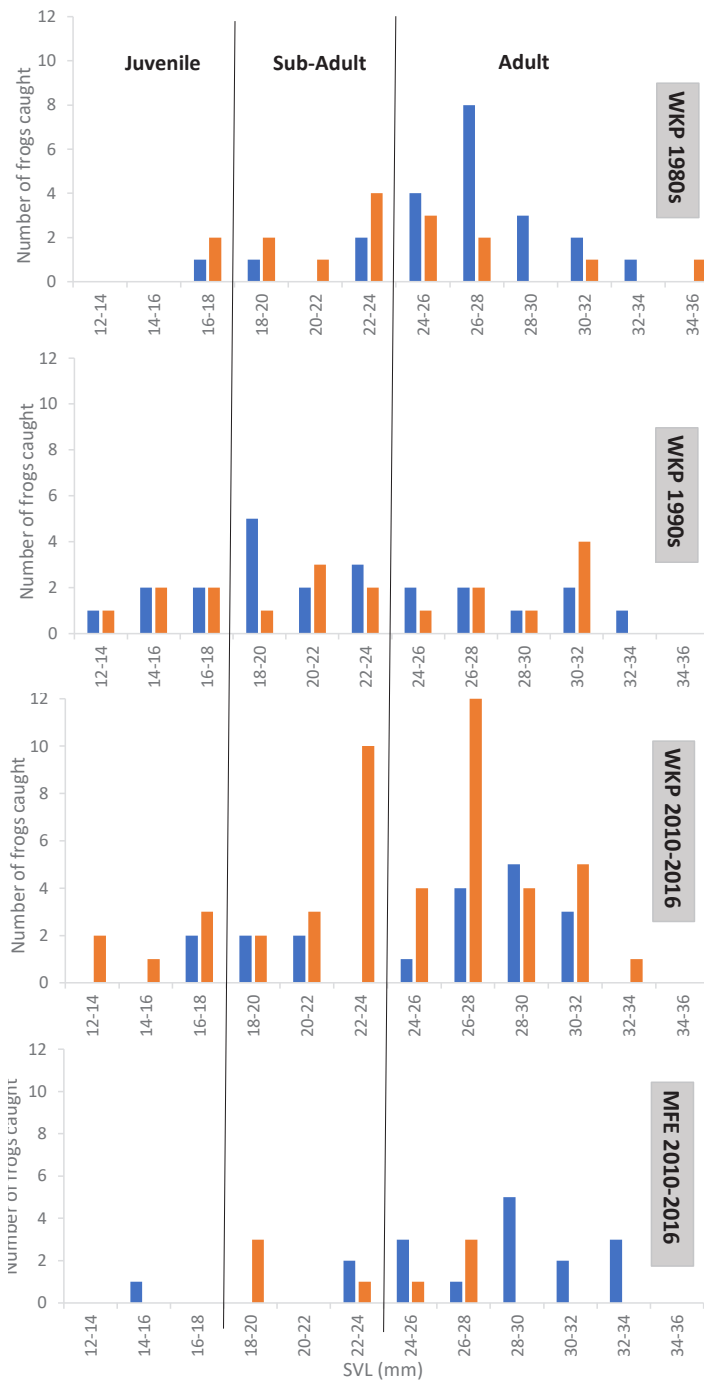


Figure 2. Number of *Leiolopma archeyi* in different size classes found in two areas, WKP and MFE on the Coromandel Peninsula. Size classes are based on snout-to-vent length (SVL), with juveniles < 18 mm, sub-adults 18–24 mm and adults > 24 mm). Within areas, survey sites with different disturbance histories (1980s, 1990s or from 2010–2016) were selected. Disturbed sites (blue) are paired with neighbouring undisturbed sites (orange). MFE 1990s sites are not included in the figure because only one adult frog was in these sites.

dealbata, *Kunzea robusta*, *Pterophylla silvicola*, and *Knightia excelsa* and negatively associated with early-succession species such as such as ground ferns and tufted herbs. There was a clear distinction between the two areas sampled. WKP sites had a stronger association with tree species commonly seen in mature forests, such as *P. silvicola* and *Phyllocladus trichomanoides*, as well as *Schoenus tendo* which is associated with regenerating *Agathis australis* or *K. robusta*. Sites within MFE had a higher cover of *Beilschmiedia tawa* and *Rhopalostylis sapida* as well as tree ferns and understory species, including *Geniostoma ligustrifolium*. There were no clear distinctions between sites in different disturbance classes (Fig. 3).

The PCA using functional groups gave similar results, but with less distinction between WKP and MFE, and more broadly overlapping error bars in general (Appendix S4). In addition,

PCA loadings were poorly associated with forest maturity. We therefore used the PCA axes from the first analysis (with individual taxa) as potential predictors of frog abundance.

Frog abundance estimates

The average probability of capturing a previously undetected frog was estimated to be 0.32 (obtained by back-transforming parameter *a.p*; Tables 1, 2). This means that, on average, about 32% of frogs at a site on the first night were detected and 68% by the end of the third night. There was a significant negative effect of capture on subsequent detection of individual frogs (parameter *b.B*; Table 1), with recapture probability dropping to 10%. Temperature and humidity did not have a significant effect on detection probability in the model, with 95% credible intervals overlapping zero (Tables 1, 2).

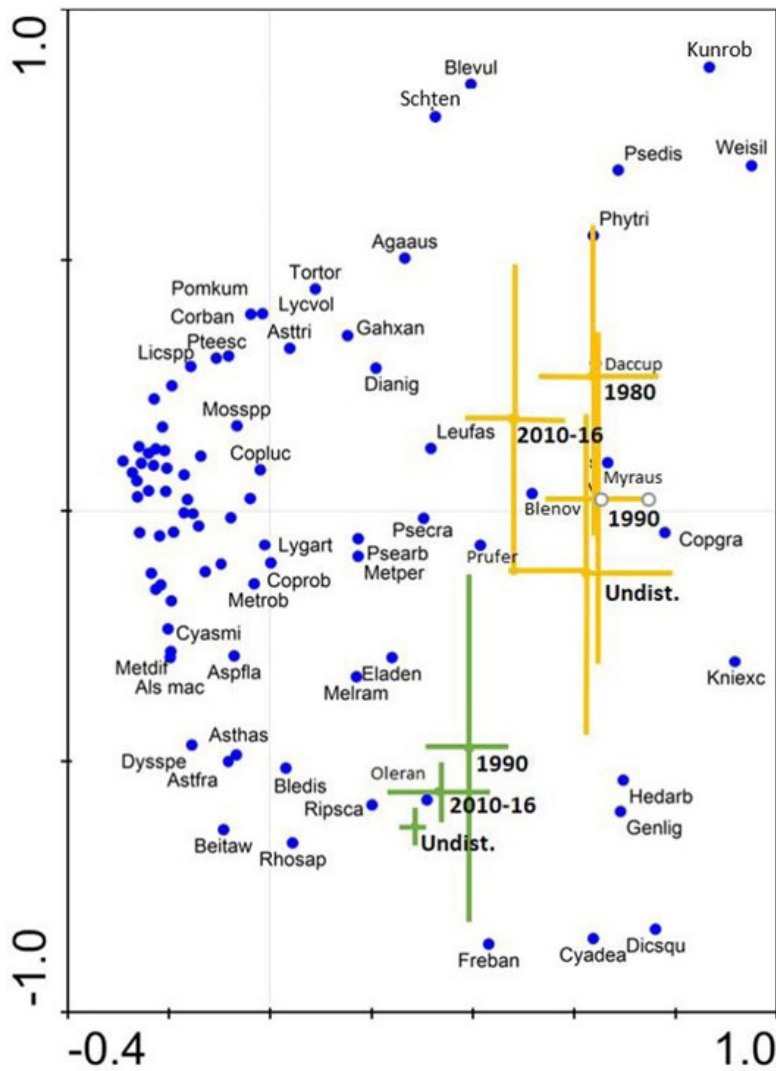


Figure 3. Unscaled PCA biplot of the maximum vegetative cover values from the RECCE tier data at each of the sampled sites. Crosses represent means and standard deviations for undisturbed sites and sites in the three disturbance periods at WKP (yellow) and MFE (green). Labels indicate 6-letter species codes for all the named plant species, and as groups for other taxa; see Appendix S1. Labels were removed for the clustered species on the mid left of the figure due to an inability to distinguish overlapping codes. See vegetation analysis section of main text for loading results.

Table 1. Means and 95% credible limits (CL) for the parameters used to model effects of area (WKP vs MFE) and disturbance on *L. archeyi* abundance (N) at the 32 sites, and effects of temperature and humidity on initial capture probability (c) and recapture probability (p). Temperature and humidity were standardised, and WKP is the reference group for the area comparison.

Parameter	Meaning	Mean	2.5% CL	97.5% CL
<i>a.mu</i>	Intercept: $\log(N)$ at average undisturbed site at WKP	1.88	1.04	2.66
<i>b.dist</i>	Overall effect of disturbance on $\log(N)$	0.20	-0.40	0.80
<i>b.90</i>	Effect of disturbance during 1990s on $\log(N)$	0.02	-0.78	0.83
<i>b.10</i>	Effect of disturbance during 2010–16 on $\log(N)$	-0.56	-1.30	0.17
<i>b.area</i>	Effect of the area (MFE vs WKP) on $\log(N)$	-1.02	-2.55	0.43
<i>s.pair</i>	Residual standard deviation in $\log(N)$ among pairs of sites	1.15	0.68	1.91
<i>a.p</i>	Intercept: $\text{logit}(c)$ on an average night	-0.77	-1.56	-0.10
<i>b.B</i>	$\text{logit}(p) - \text{logit}(c)$, i.e. effect of capture on subsequent recapture probability	-1.47	-2.36	-0.51
<i>b.H</i>	Effect of humidity on $\text{logit}(p)$ and $\text{logit}(c)$	0.20	-0.13	0.50
<i>b.T</i>	Effect of temperature on $\text{logit}(p)$ and $\text{logit}(c)$	-0.06	-0.32	0.23
<i>s.t.p</i>	Residual standard deviation in $\text{logit}(p)$ and $\text{logit}(c)$ among nights	0.38	0.07	0.77

The estimated abundances at the 32 100-m² sites ranged from 0 to 25 frogs (Fig. 4). Based on abundance parameters shown in Table 1, there were on average 6.5 frogs within undisturbed sites in WKP, 7.9 frogs at sites disturbed during the 1980s, 8.1 frogs for sites disturbed during the 1990s, and 4.6 frogs for sites disturbed between 2010–2016, with a

similar pattern at MFE but with abundances 37% that of WKP. However, these differences are not significant, as the 95% credible intervals for the relevant effects (*b.dist*, *b.90*, *b.10*, *b.area*) all overlap zero (Table 1). Ignoring the disturbance classes, the numbers of frogs at an average site was estimated to be 6.4 (95% credible interval 3.1–12.6) for WKP and 2.8

Table 2. Means and 95% credible limits (CL) for the parameters used to model the effects of habitat variables on frog abundance (N) within 32 sites at WKP and MFE. All explanatory variables were standardised. The estimates for the detection parameters ($a.p$, $b.B$, $b.H$, $b.T$) were very similar to those shown in Table 1.

Parameter	Meaning	Mean	2.5% CL	97.5% CL
$a.mu$	Intercept: $\log(N)$ at average undisturbed site at WKP or MFE	1.42	0.80	2.02
$b.pca1$	Effect of $pca1$ on $\log(N)$	1.25	0.50	2.11
$b.pca2$	Effect of $pca2$ on $\log(N)$	-0.17	-0.48	0.12
$b.ele$	Effect of elevation on $\log(N)$	0.70	0.03	1.44
$b.canper$	Effect of canopy cover above 1.35 m on $\log(N)$	-0.31	-0.91	0.25
$b.domveg$	Effect of height of dominant vegetation on $\log(N)$ estimates	-0.13	-0.72	0.42
$s.pair$	Residual standard deviation in $\log(N)$ among pairs of sites	1.13	0.71	1.76

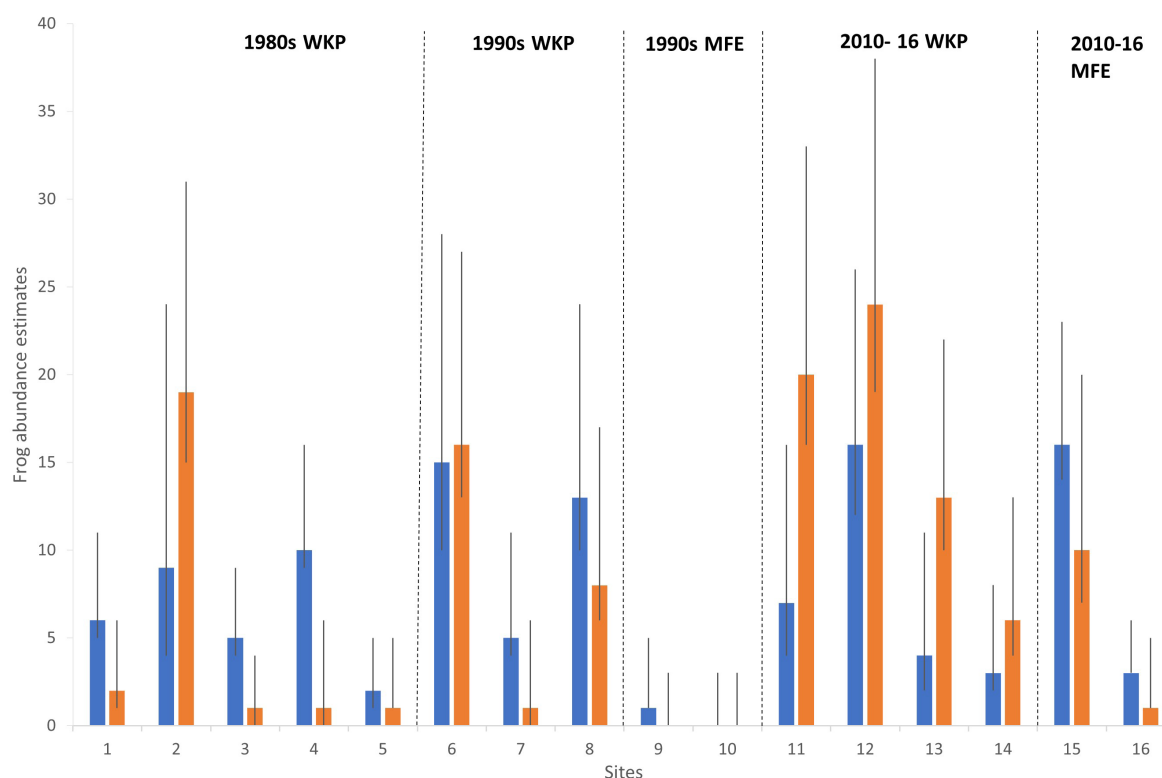


Figure 4. Estimates and 95% credible intervals for frog abundance within paired sites ($n = 16$) at WKP and MFE when modelled in relation to the effects of area (WKP vs. MFE) and disturbance history (1980s, 1990s and 2010–2016). Blue bars indicate disturbed sites and orange bars indicate undisturbed sites. The estimated abundances at the 32 sites ranged from 0 to 25 frogs. The effects of area and disturbance on abundance were not significant.

for MFE (0.7–6.9). This would give densities of 644 ha^{-1} and 276 ha^{-1} if extrapolated to that scale. However, abundance was highly variable among sites at both WKP and MFE (Fig. 4) and the total area sampled was only 0.32 ha.

The analysis of abundance with respect to habitat characteristics indicated a significant positive association between abundance and PCA1 (axis 1) (Table 2), meaning there tended to be more frogs with more mature vegetation. There was a weak negative correlation with PCA2 (axis 2), also suggesting slightly greater abundance at sites associated with mature vegetation species. There was no indication that frog abundance was associated with canopy cover or height of the dominant vegetation (Table 2). However, frog abundance was positively associated with elevation (Table 2).

Discussion

In this study, we explored the abundance of *L. archeyi* within sites on the Coromandel Peninsula and their association with habitat disturbance, vegetation composition and elevation. In relation to habitat disturbance, our results indicated similar abundances of *L. archeyi* between disturbed (road, housing and mining exploration that occurred during the past 40 years) and undisturbed sites. Instead, *L. archeyi* abundance was correlated with higher elevation and vegetation composition, including species that are representative of mature forests. Temperature and humidity did not influence detection during our surveys as they were conducted during optimal climatic conditions. Lastly, at sites where frogs were present, frogs representing all metamorphosed life-stages were detected regardless of the history of habitat disturbance.

Habitat disturbance impacts on *Leiopelma archeyi*

Although there was no indication that present day frog abundance was affected by historical habitat disturbance at our study sites, we emphasise that our study results do not suggest that frogs are not vulnerable to such habitat loss. *Leiopelma archeyi* populations are presumed to be vulnerable to wide-scale fragmentation owing to the spatial and temporal dynamic nature of amphibians (Gibbs 1998). The resulting open canopy and lack of understory immediately following disturbance, whether natural or human-induced, causes a reduction in habitat structural complexity and can lead to changes in microclimatic conditions such as temperature, some of which can be unfavourable for a species that is at risk of desiccation (Decena et al. 2020).

Limitations

It is difficult to determine specific disturbance impacts (exploration mining at WKP or roading and housing-related activities at MFE) on *L. archeyi* abundance given that there were fewer sites surveyed at MFE leading to low statistical power. In addition, because of this low sample size at MFE, an interaction term to assess any differences in effects of disturbance between the areas was not appropriate. However, the unconstrained estimates did not give any indication that the two disturbance types reflected a different pattern. The small scale (10×10 m) of vegetation clearance and the location of sites in a continuous forest block is likely to have led to quick reestablishment of vegetation species that provided adequate microhabitat for *L. archeyi* at both WKP and MFE.

Our study was specifically designed to assess impacts of disturbance, so does not necessarily reflect typical *L. archeyi* densities in WKP and MFE or other forested areas over the Coromandel Peninsula. Frog abundances in our sites were lower than those observed on four 100-m² grids in Whareorino (Herangi Range, Te Ika-a-Māui/North Island), where monitoring has been conducted for four nights annually since 2005/06 (Haigh et al. 2007; Germano et al. 2023). It is possible that frog abundance is lower at our study sites due to factors such as historical disturbance (pre-1980), densities of mammalian predators, habitat structure (e.g. availability of crevices providing protection from predators), habitat quality, or disease (Bell & Bishop 2018). However, the sampling at Whareorino was designed to assess the effectiveness of rodent control for increasing the *L. archeyi* population and targeted sites with high frog densities to enable mark-recapture modelling. The reported abundance estimates (Germano et al. 2023) are therefore unlikely to be representative of the whole Whareorino population which is distributed over about 600 ha. One thing that is clear from our study is that frog density can be highly variable among 100-m² sites, even in close proximity, so this variation needs to be accounted for in future sampling designs and analyses.

Vegetation differences

The pattern shown in the vegetation characteristics from disturbance caused historically at MFE and WKP indicated tentative differences between all three age categories and the paired undisturbed sites. As expected, plant species tended to be less mature in the disturbed sites, especially those disturbed more recently. Sites at MFE, as well as undisturbed sites, sites modified during the 1990s, and sites that remained unplanted since habitat clearance during the 1980s at WKP all comprised a greater abundance of plant species that produced deep leaf

litter and dense ground cover. The structural complexity of these disturbed sites with secondary forest, and hence microhabitat variability, had similar abundance of *L. archeyi* to undisturbed sites possibly due to the accumulation of these resources. The increase in the number of microhabitats available for species as forest succession progresses has been seen in other studies on amphibians (Ash 1997; Hernandez-Ordóñez et al. 2015). For example, terrestrial plethodontid salamanders in North Carolina recolonised sites 4–6 years after timber harvesting once litter had reformed and it was estimated that after 20–24 years salamander abundance at these sites would recover to pre-disturbance levels as plant species matured (Ash 1997). Based on our results, it appears that resources can become adequate for frogs within a decade since initial disturbance, although the quality of this habitat is unknown.

The replanting of sites at WKP with tree species *Kunzea robusta* and *Agathis australis* is also likely to have contributed to the tentative differences between sites. Replanting with saplings will modify the environment for early successional species by increased shading. As a result, sites replanted with *K. robusta* and *A. australis* will have a different successional trajectory than communities associated natural succession. This trajectory might not provide suitable resources or conditions for the recolonisation of sites by *L. archeyi*.

Frog association with habitat characteristics

Particular plant species are associated with higher *L. archeyi* abundance, likely due to their contribution to the forest-floor microhabitats or their use by *L. archeyi* during emergence. *Leiopelma archeyi* emerge in greatest numbers on wet nights when forest microhabitats are moist and relative humidity is high (> 85 %) (Cree 1989). Our PCA analysis highlighted the differences in vegetation composition among sites, and based on our models, these differences in habitat quality were shown to influence *L. archeyi* abundance. Vegetation that provided resources and conditions required by *L. archeyi*, such as moisture retention and structural complexity for refuge, were recorded within all the sites but to varying degrees. Sites disturbed during the 1980s and 1990s that were naturally recolonised by forest species, which are now in various stages of maturity, supported frog populations with estimates ranging from 1 to 15 individuals per 100-m² site. Mature forest species, such as *Knightia excelsa*, were often recorded in these sites and were associated with higher frog abundance. In particular, frogs were observed using the leaf litter of such species to shelter under. Depending on the plant species and composition, slow decomposition of foliage litter promotes accumulation and the formation of humus, which is good for moisture retention, as well as promoting invertebrate prey diversity and abundance.

Other forest species associated with higher frog abundance included tree ferns, such as *Cyathea dealbata*, which also contribute to the leaf litter and increased moisture retention. Often present in the early stages of succession, tree ferns were recognised as valuable habitat features during frog emergence. We frequently observed *L. archeyi* climbing or perching on the plants. Thurley (1996) hypothesised that the retention of moisture from deep litter in the crown of the fern was important for large frogs during dry weather and increased the distribution of the species in areas otherwise lacking moist areas to shelter. Cisternas et al. (2022) observed frogs using tree ferns as oviposition sites, and the importance of these plants during the breeding and brooding life cycle of the frog needs further investigation.

We recorded an association between frog abundance and low-growing forest species that contributed to forest-floor complexity, including *Blechnum discolor* (fern) and *Gahnia* spp. (sedge). Rushes, ferns, and restiads have densely tangled culms and fronds, in which individual *L. archeyi* were observed using during emergence or predator avoidance, given the retention of moisture and relatively small interstitial spaces. Thurley (1996) described a clear relationship between frog size and retreat site, with smaller frogs (10–27 mm SVL) tending to use vegetative sites, in particular sites with low-growing forest species such as *Carex uncinata* (hook grass) and *Microlaena avenacea* (rice grass). Sites comprising of open habitat (e.g. sparsely distributed ground plant cover) in a Department of Conservation survey at Whareorino were regarded as poorer habitat quality for juvenile frogs (Easton 2020), and this was observed during our study as juvenile frogs tended to be rarer in disturbed sites with sparse ground cover. Sites left to naturally regenerate through succession had a wider range of frog size classes suggesting that *L. archeyi* have a reasonable ability to survive this type of disturbance.

The increased abundance of *L. archeyi* at higher elevation could be attributed to increased rainfall and humidity (Duellman & Trueb 1994; Archey 1922; Bell 1978). Rainfall patterns in the Coromandel are closely related to elevation (Chappell 2013), and fog and mist often prevail on the peaks of the Coromandel Ranges even at the height of summer (Archey 1922). As a terrestrial amphibian with limited dispersal, temperature and moisture conditions must be suitable for an adequate duration to allow for rehydration and successful foraging (Cree 1989). Thurley (1996) suggested that the predominance of *L. archeyi* at higher elevations could also be attributable to the reduction of understory vegetation by grazers (deer, goats, possums and pigs) at lower elevations, causing a drier environment less suited to frogs. Historical burning of lowland forest for agriculture has also reduced the range of *L. archeyi* by removing key habitat required for persistence (Thurley 1996; Bell & Bishop 2018). Lastly, it has also been theorised that escape from predation by introduced mammalian species, such as *Rattus* spp., could account for greater frog abundance at higher elevations. *Rattus norvegicus* (Norway rats) are generally absent from higher elevations (O'Donnell et al. 2017) and trap catch data for *R. rattus* (ship rats) collected across an altitudinal gradient showed a negative effect of increasing elevation (Christie et al. 2017). Molecular assessments of rat stomach contents and the collection of *L. archeyi* remains with distinctive rat bite marks have confirmed predation events (Thurley & Bell 1994; Egeter et al. 2019). Research on the factors driving elevational gradients and the effects of predation will be beneficial for the future management of *L. archeyi* on mainland Aotearoa New Zealand.

The history of habitat disturbance from the mining sector and the conflict between conservation and economic objectives makes it essential to understand the impacts of disturbance to make informed land-use decisions. A habitat of good quality may need to be engineered (restored or created) to aid colonisation, and as such, it is important to understand habitat requirements and the ecology of the target species. While our results showed that current frog abundance was not significantly affected by historical habitat disturbance during the 1980s, 1990s and 2010–2016, there were clear site features that contributed to higher abundance and habitat preference of *L. archeyi*. In our study sites (100 m²), the abundance of *L. archeyi* was positively associated with higher elevation and was typically associated with mature forest. Firstly, we

recommend the prevention of future habitat loss to conserve mature forest and structural complexity. Second, if habitat disturbance occurs, we recommend allowing sites to naturally regenerate. If consent conditions require replanting, we suggest planting species that enable deep layers of leaf litter to accumulate, promote microhabitat complexity, and retain adequate humidity in order to maximise the likelihood of *L. archeyi* persistence in the face of further human land-use and climate change.

Acknowledgements

Tēnā koutou Mahakirau Forest Estate for allowing EH into your sanctuary and homes. A big thank you to Sara Smerdon for sharing your knowledge, kindness, and time during these surveys. Arden Haar and Daniel Papworth, EH couldn't have asked for better research assistants. Jill Rapson, ka pai to your resilience on this project and your contribution to the vegetation analysis, we are greatly indebted. We are very grateful to OceanaGold (NZ) Ltd for logistical and financial support. Thank you to Phil Bishop, Javiera Cisternas, Luke Easton, Patricia Ramirez, Amanda Haigh, Ben Bell, Rob Chappell, Lucy Bridgman, and Avi Holzapfel for sharing your expertise. Aroha nui to our wonderful families who provide us with support. EH's work was carried out for completion of a Master of Science in Conservation Biology degree at Massey University.

Additional Information and Declarations

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

Funding: Financial support for this project was provided by Massey University (Massey University Masterate Scholarship), Mohamed bin Zayed Species Conservation Fund, Boffa Miskell Ltd and OceanaGold (NZ) Ltd.

Ethics: This research was approved by the New Zealand Department of Conservation (permit number 67982-RES) and the Massey University Animal Ethics Committee.

Data availability: The data and code used in this article are available in the Supplementary Material.

Author contributions: EH conducted the 2018–2019 fieldwork and initial data analysis, and wrote the thesis that this paper was based on; EH designed the study with contribution from KM and DA, and DA designed and primarily conducted the abundance and detection analyses presented here. Both DA and KM contributed to the draft writing of the manuscript.

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Received: 9 February 2022; accepted: 7 July 2022

Editorial board member: Javeria Cisternas

Supplementary material

Additional supporting information may be found in the supplementary material file for this article:

Appendix S1. Vegetation species recorded in 16 paired 100 m² sites in WKP and MFE on the Coromandel peninsula to determine the effect of habitat features on the abundance of *Leiopelma archeyi*.

Appendix S2. Data and OpenBUGS code for the closed-population mark-recapture analysis. See article webpage on NZES website for this article to download .zip file.

Appendix S3. Number of *Leiopelma archeyi* captured, individually identified, and released during three nights of surveying in 16 paired 100 m² disturbed and undisturbed sites in two areas (WKP & MFE) on the Coromandel peninsula.

Appendix S4. Unscaled PCA biplot of the means and standard deviations from the disturbance periods and undisturbed sites at WKP (yellow) and MFE (green) plotted with the functional groups derived from the maximum cover values from the RECCE tier data.

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