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RESEARCH

The conservation long game: *Leiopelma* species climate envelopes in New Zealand under a changing climate

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Abstract: Amphibians are considered susceptible to a range of potential effects generated by climate change. We applied species distribution model (SDM) techniques to predict future areas of climatic suitability for Archey's and Hochstetter's frogs under two different climate change scenarios using climate variables derived from their existing geographic extent. For Hamilton's frog their current range was too restricted to model future range, so we used past climate data from current strongholds to establish that these sites may not be suitable for this species in the long-term. Model projections for Archey's frog showed the climatically suitable area expanded and extended south as greenhouse gas concentrations increased. Under the mid-range gas concentration scenario, suitable areas were similar in 2040 and 2090, and both had an 88% overlap with the current distribution. Under the high-end gas concentration scenario suitable areas for occupancy were similar to the mid-range concentrations by 2040 (84.6% overlap), but by 2090, while their currently occupied areas remain suitable for occupancy (85.5% overlap), the suitable area stretched south resulting in a large range expansion. For Hochstetter's frog, the predicted climatically suitable area also moved south, but the proportion of their current range able to be occupied lessened as greenhouse gas concentrations increased. With the mid-range concentrations, less than half of their current areas were still suitable to occupy by 2040 and 2090 (46.1% and 35.7% respectively). The high-end greenhouse gas pathway produced a similar outcome by 2040 with only 47.3% of the current occupied area remaining suitable. Under this pathway, by 2090, suitable areas were much further south, and the northern North Island was no longer suitable for Hochstetter's frog. We conclude that a shift from traditional conservation methods will be required to allow *Leiopelma* species to persist under a changing climate.

Keywords: assisted migration, conservation, climate change, *Leiopelma*, translocation

Introduction

Amphibians are facing a global extinction crisis and currently, over one-third of all amphibian species are threatened with extinction (Stuart et al. 2004; Wake & Vredenburg 2008). Thomas et al. (2004) predicted that 12–47% of endemic frog species worldwide will go extinct by 2050 due to climate change. Climate change, both directly and indirectly, is exacerbating existing causes of decline such as habitat destruction, disease, pollution, and predation by invasive animals (Bell et al. 2004a; Stuart et al. 2004; Wake & Vredenburg 2008; Foden et al. 2013). Amphibians have a permeable skin, and their heavy reliance on water for activity and reproduction means that rainfall patterns are an important constraint for many species (Duellman & Trueb 1994). Also, as ectotherms, the rate of activity and energy use in amphibians is linked to temperature, that is at low temperatures some amphibians are unable to function, and if temperatures become atypically warm body condition can degrade (Moldowan et al. 2022).

Already, climate change is known to have shifted amphibian breeding phenology, and has negatively impacted amphibian survival, distribution, and abundance (Beebee 1995; Gibbs & Breisch 2001; Sheridan et al. 2018). Declines also appear to be occurring faster for amphibians than for other taxonomic groups such as birds and mammals due to their relatively low mobility and their sensitivity to changes in their environment (Stuart et al. 2004; Beebee & Griffiths 2005). Their sensitivity to environmental change has led prominent herpetologists to refer to amphibians as "canaries in the coal mine" (Pechmann & Wilbur 1994). Moreover, climatic changes such as decreased rainfall, increased extent of dry periods, extreme precipitation events, and increased temperatures could all act synergistically to have a detrimental effect on amphibians (Bell et al. 2004a).

Of the nine endemic *Leiopelma* species once present in New Zealand, six are extinct and the remaining three have restricted and fragmented distributions (Easton et al. 2021). The three surviving species, Hochstetter's frog (*Leiopelma hochsetteri*), Archey's frog (*L. archeyi*), and Hamilton's frog

(*L. hamiltoni*), along with the genus *Ascaphus*, represent some of the most archaic anuran lineages worldwide and all possess numerous unique traits. All three *Leiopelma* species are threatened with extinction according to the New Zealand Threat Classification System (Burns et al. 2018), with predation by invasive mammalian pests, habitat loss, and disease currently listed as their primary threats (Bishop et al. 2013). Current distributions are restricted by these pressures and key populations are at risk of local extinction, for example, an 88% decline in numbers was recorded in the stronghold Archey's frog population in the late 1990s, which has been attributed to disease and drought acting synergistically (Bell et al. 2004a). Archey's and Hochstetter's frogs are restricted to scattered refugia in the upper North Island, while Hamilton's frog is only known from four small predator free islands in the Marlborough Sounds and a single small (translocated) mainland population (Bell et al. 2010; Bishop et al. 2013). Late Holocene subfossil remains suggest the range of Hochstetter's and Hamilton's frogs were much larger prior to last glacial maximum with records across the North Island and extending south to the northwest South Island with the range of extinct species stretching to the southern part of the South Island (Worthy 1987; Fouquet et al. 2010). Extant *Leiopelma* refugia are now generally associated with unmodified habitats (Bell et al. 2004a).

The parts of New Zealand which encompass the current ranges of the endemic frog species are projected to get hotter and drier with climate change (Ministry for the Environment 2018). It is not certain how climate change will affect *Leiopelma* distribution. This uncertainty relates to both their exposure to climate change under variable projections, and to the paucity of biological information that could predict the ability of *Leiopelma* species to adapt to climate change. In terms of climate change projections, projected rainfall amounts and periodicity for New Zealand have greater variability than temperature, so the exact effects are less certain (Ministry for the Environment 2018). Climate change has been shown to exacerbate the existing pressure of invasive predators on some amphibians (Shoo et al. 2011), and uncertainty is increased by the potential for these predators to be advantaged by climate change in new and complex ways (Christie et al. 2017; Walker et al. 2019).

While biological information is scarce, on the face of it, *Leiopelma* species have biological and physiological traits that make them vulnerable to climate change. For example, remnant, highly fragmented *Leiopelma* populations have limited dispersal potential (e.g. non-migratory, home ranges of a few metres squared), meaning they will be unable to move to avoid a changing climate. This low dispersal trait is coupled with high rates of cutaneous water loss for all *Leiopelma* species (Cree 1985). In Archey's frog, for example, emergence and the choice of an egg-laying site is strongly correlated with moisture related factors such as humidity, rainfall, and the wetness of vegetation (Bell 1985; Cree 1989). Maintaining water balance is a crucial component of amphibian biology, key activities such as feeding and reproduction are limited to locations and times when the risk of dehydration is minimised (Duellman & Trueb 1994). Moreover, behavioural plasticity shown in other anurans (Beebee 1995; Sheridan et al. 2018) may also be shown in *Leiopelma* species too, and if so, such flexibility could allow them to survive changes in climate, but to what extent is unknown in the absence of species-specific research in New Zealand.

With a changing climate, currently favoured conservation management techniques could fail to ensure long-term population survival of all *Leiopelma* species. Conservation management has relied on traditional techniques such as invasive predator control and translocation to predator free offshore islands, and more recently, to mainland sites (Karst et al. 2023). Predator control for mainland populations and predator surveillance for island populations are essential management tools (Bishop et al. 2013). Translocations are also proven to create 'insurance' populations for small and isolated *Leiopelma* populations (Bell et al. 2004b; Tocher & Pledger 2005; Tocher et al. 2006; Bell et al. 2010; Wren et al. 2023). The current Native Frog Recovery Plan (the guiding document for *Leiopelma* conservation) has an objective to identify suitable, safe translocation sites (Bishop et al. 2013), but the supporting criteria do not account for future climatic suitability and some sites currently prioritised for translocations may not be climatically suitable for frogs in the long term. Furthermore, some existing relict populations are located at sites which may not be suitable in the future, and these require immediate attention.

Conservation managers responsible for *Leiopelma* species face new climate-change related challenges, the so-called long game, without having fully addressed existing threats (Bishop et al. 2013). Overseas, it has been suggested that for some amphibian species, conservation managers may need to consider new *in situ* adaptive management solutions such as refuges, restoration and enhancement of breeding habitat, and the manipulation of water levels to assist in the survival and breeding of some populations where they currently exist (Shoo et al. 2011). These ideas along with *ex situ* management solutions such as assisted migration (the intentional translocation of an organism outside its indigenous range to avoid extirpation of populations or extinction of the focal species) to sites outside the current known range may also be needed to future-proof some of the most vulnerable populations (Hoegh-Guldberg et al. 2008; IUCN/SSC 2013). These ideas are novel to New Zealand frog conservation, but new tools and thinking will be necessary to complement existing, more traditional methodologies under a changing climate, at least for some *Leiopelma* species.

In this study we build species distribution models (SDMs) with climate predictors (also known as climate envelope or ecological niche models) to inform current and future conservation management decisions for two *Leiopelma* species (Archey's and Hochstetter's frogs). Such models, combined with climate change projections have been widely used to assess risk or support conservation management decisions for herpetofauna both in New Zealand (Fouquet et al. 2010; Jarvie et al. 2021) and elsewhere (Fouquet et al. 2010; Guisan et al. 2013; Jarvie & Svenning 2018; Jarvie et al. 2021). For a third species, Hamilton's frog, their current range was too restricted to model future range so instead we investigated historic trends in climate from their current population strongholds, to determine if these sites will remain suitable for occupancy in the long-term. We discuss predicted changes in climatic suitability in relation to *Leiopelma* species biology and current distribution, and outline the implications for prioritising conservation actions, survey, and selection of translocation sites.

Methods

Frog occurrence data

Leiopelma species occurrence data were sourced from the Atlas of the Amphibians and Reptiles of New Zealand, the

most comprehensive and live database containing all known *Leiopelma* records. Data for Hochstetter's, Archey's, and Hamilton's frog were included in analyses. Records in the atlas were classified as live, dead, bone (subfossil), and fossil (rock). From the total 3064 records we extracted 2982 live and dead records for which location (latitude and longitude) and species were known with certainty. Records considered by species were Hochstetter's ($n = 2432$), Archey's ($n = 519$), and Hamilton's ($n = 31$).

Climate data

Climate model data from three time periods were used for these analyses: a baseline climate period of 1986–2005, and two future climate projection periods presented as a 20-year average from 2031–2050 (termed '2040') and 2081–2100 (termed '2090'). For the future projections, six global climate models were downscaled to a 5 km resolution and then averaged together over the New Zealand landmass (Ministry for the Environment 2018). Projection data for small islands off the coast of the New Zealand mainland were not available. Low-resolution cells in the global climate models that overlap land and sea were removed in the downscaling process so only the land cells remained. This is because interpolating over mixed sea and land points can create artificial biases. The downscaled projections were available for different atmospheric greenhouse gas concentration scenarios, called representative concentration pathways (RCPs), described by the Intergovernmental Panel on Climate Change (IPCC 2013). Results are a 5 km raster of baseline and future projected climate variables over the New Zealand landmass (Ministry for the Environment 2018). Two RCPs were used in this analysis: RCP4.5 (flattening of global greenhouse gas concentrations around 2060, termed 'mid-range') and RCP8.5 (continued growth of global greenhouse gas concentrations, termed 'high-end') (Schwalm et al. 2020). Thirteen annual climate variables were considered for the SDM (Table 1). The values within each climate raster were attributed to a point and extracted for each point using the extraction tool in ArcGis (version 10.3.1) Spatial Analyst Tools (ESRI).

To look at changing climate suitability for Hamilton's frog, monthly climate records for 1972 to 2020 were downloaded for two virtual climate stations nearest to the two original Hamilton's frog populations (Stephens Island/Takapourewa and Maud Island/Te Pākeka), as there are no long-term observations available for these locations. The virtual climate station network (VCSN) is interpolated climate data from real climate station records, and virtual stations occur on a 5 km² grid scale resolution across New Zealand (Tait et al. 2006). The data downloaded for this analysis were from the Stephens Island/Takapourewa and Miro Bay VCSN locations. Miro Bay is approximately 5 km from Maud Island/Te Pākeka. Two monthly climate variables selected as relevant to species biology, mean temperature and soil moisture deficit, were averaged for a three-month time window (January–March) within the austral summer period, and the trend over time analysed using simple linear regressions.

Statistical analysis

Boosted regression trees (BRT) were used to model areas of climatic suitability for two of the *Leiopelma* species because of the method's suitability for dealing with presence/(pseudo-) absence data, undertaking exploratory analyses with no strong *a priori* predictions, and to allow for interactions and nonlinear relationships (Elith et al. 2008; Duncan et al. 2009). Boosted regression trees have as good, or better predictive accuracy, than other methods commonly used to construct SDMs/climatic envelopes (Elith et al. 2006). Hochstetter's and Archey's frogs were modelled but Hamilton's frog could not be modelled because of its limited range. Only recent records (i.e. not fossils or subfossils) were used as confirmed presences to ensure records came from the same period as the baseline climate.

The dataset lacked true absences so, to characterise the background environmental domain, a set of "pseudo absences" (Cerasoli et al. 2017; Hijmans & Elith 2021) were generated from a master sample (van Dam-Bates et al. 2018) using balanced absence sampling (Robertson et al. 2013). Balanced absence sampling is an ordered but completely random balanced sample. An initial pool of 30 000 records across both the North and South Islands were generated from the master sample, and a different subset of these were selected for each frog species. Both islands were used because Leiopelmid fossil and sub-

Table 1. Description of climate predictor variables used (- = not used, x = used) in native frog models for Hochstetter's frog (*Leiopelma hochstetteri*), and Archey's frog (*L. archeyi*).

Predictor	Description	Used in model	
		Hochstetter's	Archey's
Mean temp	Mean annual temperature (T_{mean})	-	-
Mean max temp	Mean maximum temperature (T_{max})	-	-
Temp range	Diurnal temperature range ($T_{max} - T_{min}$)	x	x
Hot days	Number of hot days ($T_{max} > 25\ °C$)	x	x
Growing days	Number of growing degree days (base 10 °C)	x	x
Cold days	Number of cold days ($T_{max} < 5\ °C$)	x	x
Cold nights	Number of cold nights ($T_{min} < 5\ °C$)	-	-
Frost days	Number of frost nights ($T_{min} < 0\ °C$)	x	x
Dry days	Number of dry days (rainfall < 1 mm)	x	x
Wet days	Number of wet days (rainfall > 1 mm)	-	-
Heavy rain days	Number of heavy rain days (rainfall > 25 mm)	x	x
Rainfall	Annual precipitation (mm year^{-1})	x	x
PED	Potential evapotranspiration deficit (mm)	x	x

fossil records have been found across both (Worthy 1987). An equivalent number of pseudo absences were selected as there were presences for the species (Barbet-Massin et al. 2012).

All analyses were run using R version 3.6.1 (R Core Team 2021). BRT models were built using the package gbm version 2.1.1 (Ridgeway 2013). The initial models were built using the function *gbm.step* (Elith & Leathwick 2009) which is also more recently available in the dismo package (Hijmans et al. 2017). This function divides the data into 10 subsets, with stratification by prevalence, and uses cross-validation to estimate the optimal number of trees. We allowed for up to three-way interactions and specified a learning rate of 0.05 for Hochstetter's frog and 0.005 for Archey's frog. Learning rates are estimated to optimise the number of trees needed to account for differences in observations and the associated predicted error (Elith et al. 2008). Archey's frog had fewer observations so required a lower learning rate to achieve the optimum number of trees. Correlations between climate variables were explored using a graph function *pairs*, some variables were highly correlated (e.g. wet days vs dry days). An initial BRT was run to determine which were the lowest contributing of these highly correlated pairs allowing them to be removed from the candidate set to reduce multicollinearity. A second BRT was then run using nine remaining variables. From this model, backward elimination (*gbm.simplify*) was performed. This function takes the initial cross-validated model and assesses the potential to remove predictors using 10-fold cross validation, thereby determining the final suite of variables to use in a simplified BRT model from which predictions could be run. The predictive accuracy of the final BRT model was assessed by calculating the area under the receiver operating curve (AUC). This is an accepted method for BRT models using unbiased pseudo-absences and favours realised distribution models like used in this study (Duncan et al. 2009). The species climate envelopes were produced using the final simplified BRT model objects, using future climate variables to predict areas with suitable climate for the frogs (likelihood-of-finding in each pixel) under each RCP projection for each time-period. These predictions were modelled across the whole country, and for display purposes were post-hoc restricted to native forested areas (using LCDB v5.0 (Landcare Research New Zealand Ltd 2020), 'broadleaved indigenous hardwoods' and 'indigenous forest' classes), as *Leiopelma* are rarely found outside of native forest cover.

Results

Frog climate envelope models

The BRT models for Hochstetter's and Archey's frogs had good to excellent predictive performance, with AUC values of 0.994 (SE = 0.002) and 0.996 (SE = 0.002) respectively. AUC values closer to 1 than 0.5 show that the models had good discriminating ability. Annual number of cold days was the most important predictor of Hochstetter's frog distribution with number of heavy rain days the next important predictor (Fig. 1). Potential evapotranspiration deficit, growing degree days above 10 °C and diurnal temperature range also contributed to the final BRT model for Hochstetter's frog. For Archey's frog, growing degree days above 10 °C was the most important predictor of distribution (Fig. 1). Rainfall was the second most important predictor, with diurnal temperature range and number of frost nights contributing, but to a lesser amount, to the final model.

Current and future climate suitability

Hochstetter's frog currently occupies areas of the northern North Island including some offshore islands (Fig. 2a; however, islands are not included in the analysis as mentioned above). The projected amount of climatically suitable area for Hochstetter's frog moved further south, and the proportion of their current range with suitable climate lessened, as greenhouse gas concentrations increased. Given the mid-range greenhouse gas concentration pathway of RCP4.5, suitable areas for Hochstetter's frogs moved to the northwest coast of the South Island (Fig. 2a), with half of their current area still suitable to occupy in 2040 and 2090, with 46.1% and 35.7% overlap
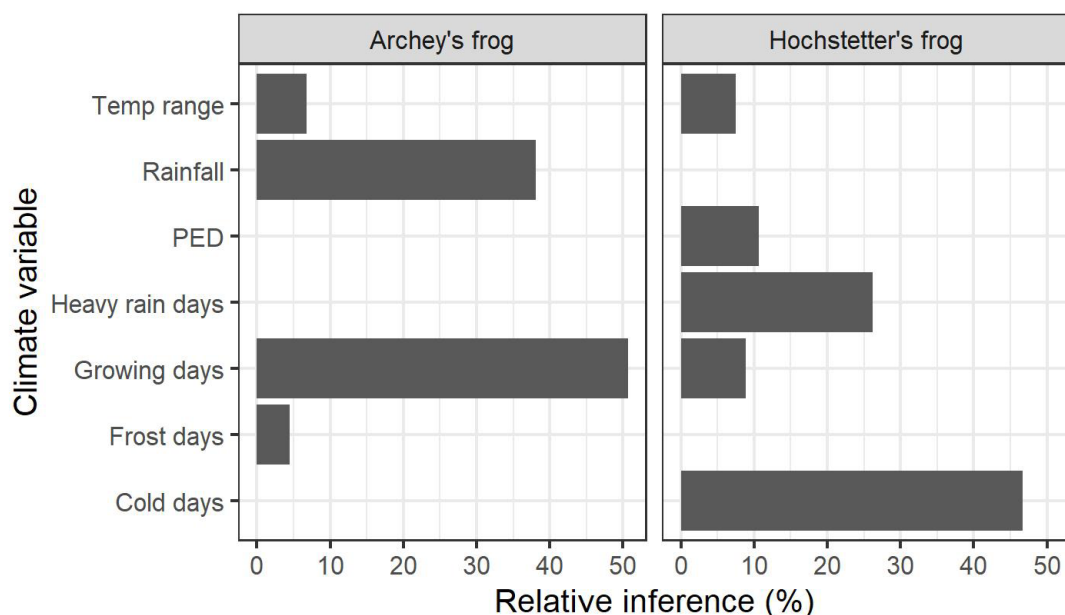

Figure 1. Relative influence of the climate predictors of Hochstetter's and Archey's frog distribution. Bars depict significant climate effects compared to the null distribution of relative influence (see Table 1 for predictors).
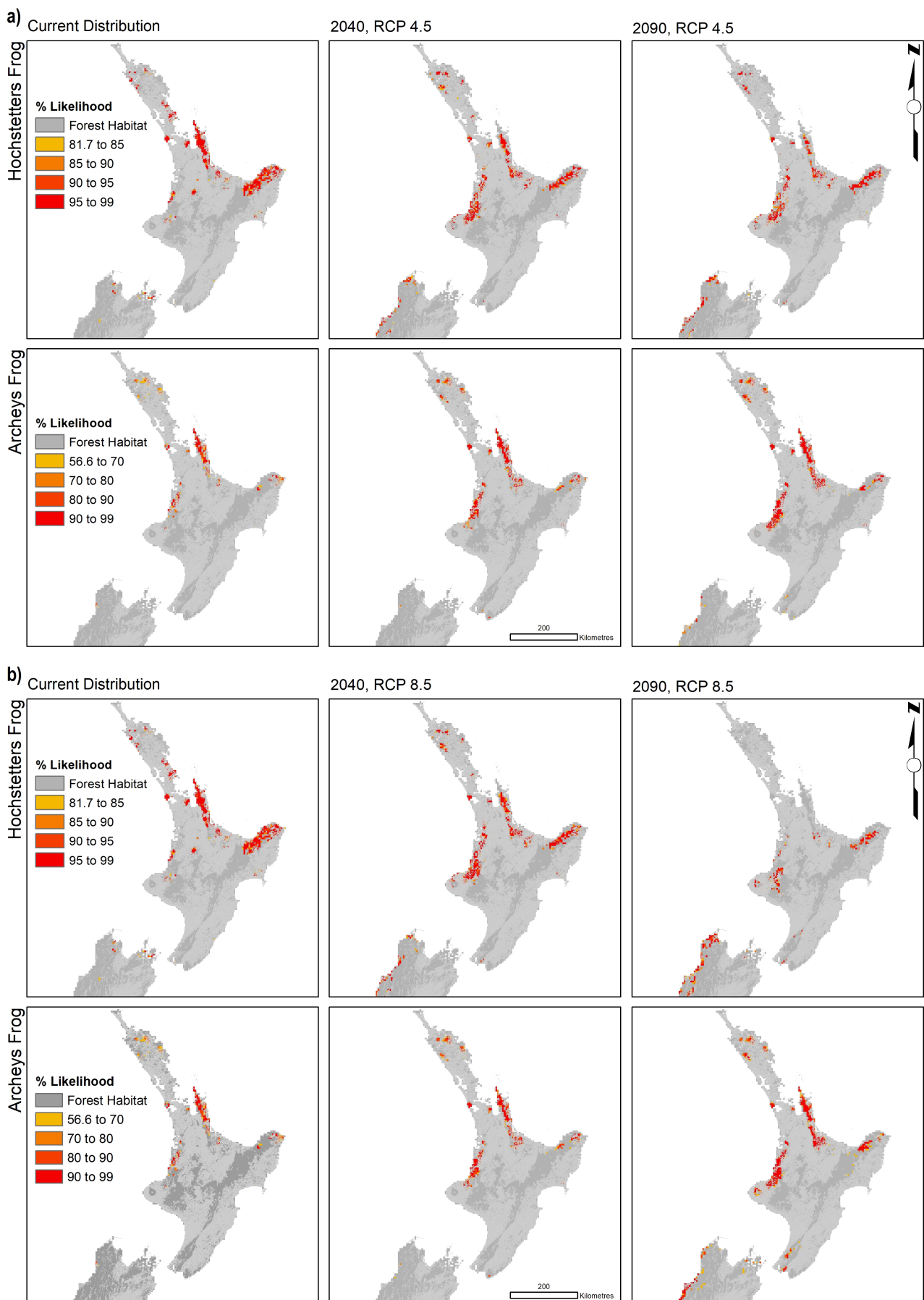
Figure 2. Change in modelled areas of frog climatic suitability predicted for 2040 and 2090 for Hochstetter's frog (*Leiopelma hochstetteri*), and Archey's frog (*L. archeyi*) for greenhouse gas concentration pathways: (a) RCP4.5, and (b) RCP8.5.

respectively. The high-end greenhouse gas concentration pathway of RCP8.5 produced a similar outcome by 2040 with 47.3% overlap with the current occupied area. By 2090 under RCP8.5, however, suitable areas were much further south, and the northern North Island was no longer suitable for Hochstetter's frog with only 12.0% of the current occupied area being climatically suitable (Fig. 2b). The total suitable area with climate change is a substantial range reduction for Hochstetter's frog compared to their current range (Fig. 3).

Archey's frog currently occupies the Coromandel Peninsula, and northwest Taranaki (Fig. 2a) and the projected amount of climatically suitable area expanded, extending further south, as greenhouse gas concentrations increased. Under the mid-range pathway RCP4.5, areas suitable for occupancy were similar in 2040 and 2090 (Fig. 2a), with both having an 88% overlap with their current extent. Under the high-end pathway of RCP8.5, suitable area for occupancy remained similar to the RCP4.5 in 2040 (Fig. 2b) with 84.6% overlap. By 2090 most (85.5%) of the currently occupied areas remain suitable for occupancy, and the potential areas suitable for occupancy by Archey's frog stretched much further south, down the northern half of the west coast of the South Island (Fig. 2b), resulting in a large range expansion (Fig. 3).

Hamilton's frog - historic climate

Virtual climate station data from 1972–2020, nearest to the Hamilton's frog population strongholds of Stephens Island/Takapourewa and Maud Island/Te Pākeka, showed a trend towards hotter and drier conditions over the summer months (Fig. 4). There was a significant trend of increasing mean summer temperatures for Stephens ($y = -23.32 + 0.02x$, $r^2 = 0.14$, $P = 0.01$) and Maud Island/Miro Bay ($y = -21.78 + 0.02x$, $r^2 = 0.13$, $P = 0.01$) (Fig. 4). There was also some evidence for increasing soil moisture deficit (i.e. soil moisture reductions) for both Stephens/Takapourewa ($y = 456.66 - 0.28x$, $r^2 = 0.03$, $P = 0.24$) and Maud Island/ Te Pākeka/Miro Bay ($y = 794.50 - 0.44x$, $r^2 = 0.05$, $P = 0.14$), although this trend was not significant (Fig. 4).

Discussion

We applied SDMs to predict future areas of climate suitability for Archey's and Hochstetter's frogs under two different projected climate change scenarios. For Hamilton's frog we used past climate data from current strongholds to establish that these sites may no longer be suitable for this species in the long-term. The SDMs for both Archey's frog and Hochstetter's frog predicted that the area of climatic suitability also moved south, and the proportion of their current range able to be occupied lessened as greenhouse gas concentrations increased. This effect was more pronounced for Hochstetter's frog.

The SDMs show that the current distributions of both Hochstetter's and Archey's frogs are related to temperature and rainfall variables. This finding is consistent with the results of ecological niche modelling for Hochstetter's frog (Fouquet et al. 2010) and earlier observations that *Leiopelma* species require cool, damp microclimates to survive (Cree 1989). Based on future predictions, and changes that have already occurred over the last thirty years, climate change will most likely pose a significant threat to *Leiopelma* frogs. Projections of climatically suitable areas for *Leiopelma* species shifted south, into New Zealand's South Island, as

greenhouse gas concentrations increased. This southward movement was more significant for Hochstetter's frog than Archey's frog, and represented a range shift for Hochstetter's frog, but a range expansion for Archey's. Under a high-end trajectory of greenhouse gas concentrations, only 12% of Hochstetter's future range in 2090 overlaps with their current range, compared to 85% overlap for Archey's. Although we could not specifically model climate suitability for Hamilton's frog, because they are confined to five small sites (four islands in the Marlborough Sounds and one mainland sanctuary in Wellington), a trend of rising temperatures and increasing soil moisture deficit over the past 50 years, suggests their current island refugia are becoming hotter and drier. Climate change projections indicate that this trend is likely to continue for the Marlborough Sounds, so that these islands may soon have decreased suitability for Hamilton's frog.

It is likely that data showing the current distribution for *Leiopelma* frogs are not complete. New populations have been discovered over the last three decades (Thurley & Bell 1994; Bell et al. 1998; Baber et al. 2006), and more *Leiopelma* populations may remain undiscovered. In addition, SDMs trained with only current distribution data might not reflect a complete description of a species niche, limiting the reliability of the model projections. This can be problematic when modelling relict populations such as *Leiopelma* which only occupy a fraction of their former range, or that occupy marginal sites which may not be able to sustain viable populations (Elith et al. 2010). New Zealand's mainland *Leiopelma* populations occupy relict distributions that are mostly associated with forest in the upper North Island (Thurley & Bell 1994; Fouquet et al. 2010; Easton et al. 2016). There is a risk, therefore, that our climate envelope matches forest distribution in the upper North Island rather than areas with suitable climate for *Leiopelma* persistence, and following on from this, that the *Leiopelma* species modelled may actually occupy a much greater range in the future than our models predict. Incorporating fossil records into our SDMs would have been one way to address this issue but, there were very few records compared to the number of live records, these were biased toward limestone cave systems, and they also represent a different climatological period and habitat types to current conditions (Worthy 1987).

The projected range movement poleward for *Leiopelma* is consistent with global observations for other terrestrial species in response to a warming climate (Parmesan 2006; Chen et al. 2011). However, responses will likely vary by species, some species may be able to shift their distributional ranges and/or adapt their behaviour to make up for climate changes, while others cannot. A species' vulnerability to climate change is influenced by three key factors, namely their sensitivity, exposure, and adaptive capacity (Foden et al. 2013), those that cannot adapt, move, or thrive within the new normal are at greater risk of extinction. *Leiopelma* species have many qualities that could make them susceptible to the impacts of climate change. They have specialised microhabitat requirements and environmental thresholds especially for precipitation and temperature (Cree 1985, 1989; Easton 2015) and are unlikely to cross uninhabitable barriers. Though they have been recorded moving distances of up to 100 m and can recolonise emptied or restored habitat, overall, these species have poor dispersal ability both naturally, but also due to habitat fragmentation and population on islands (Tocher & Brown 2004; Germano et al. 2023). Additionally, their resilience and ability to adapt is hindered by the fact that these are K-selected species with long-generation times and
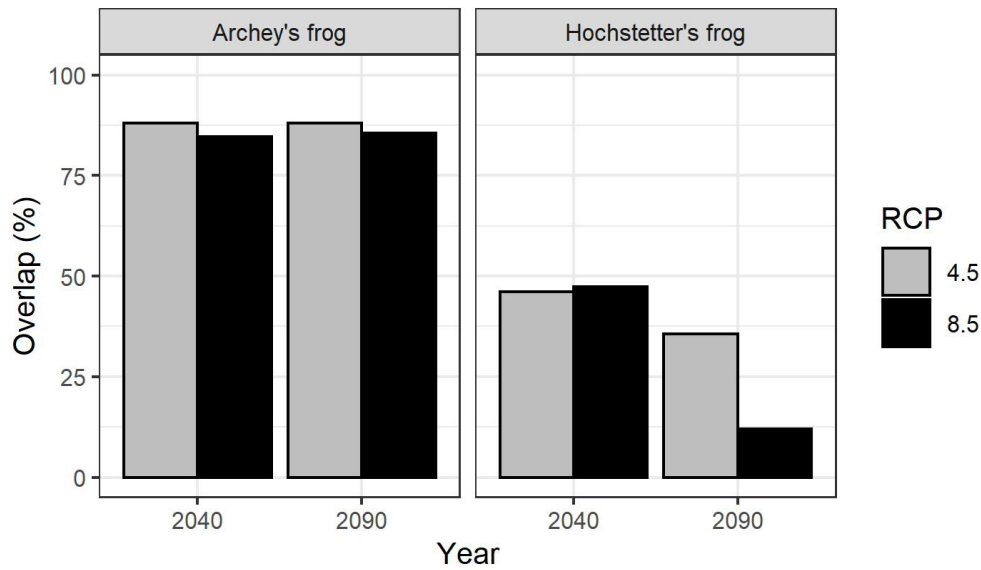
Figure 3. Overlap of projected distribution for RCP4.5 and RCP8.5 greenhouse gas concentration pathways over two time periods with current distribution for: Hochstetter's frog (*Leiopelma hochstetteri*), and Archey's frog (*L. archeyi*).
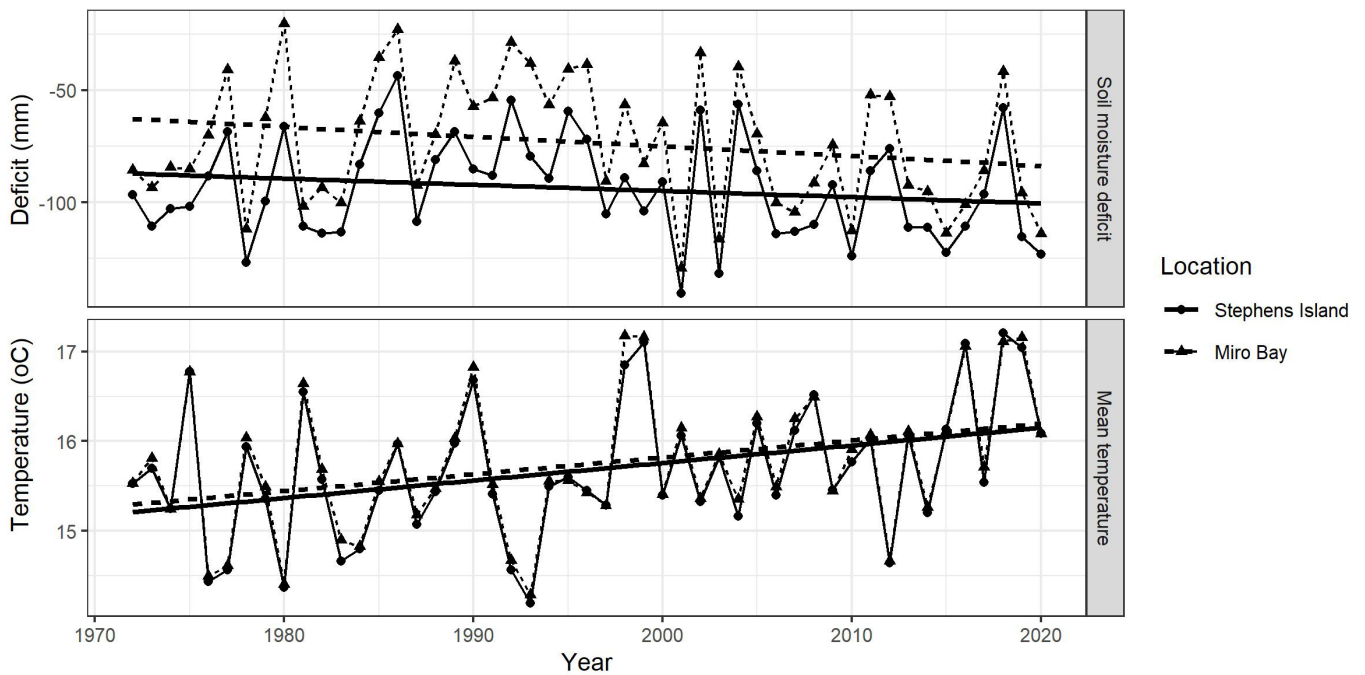

Figure 4. Changes in summer weather (Jan–Mar) over a 48-year period (1972 to 2020) for VCSN data points near Miro Bay (dashed line) and Stephens Island (solid line) near Maud Island in the Marlborough Sounds. Climate variables displayed are mean monthly temperature and soil moisture deficit. Trend lines represent a simple linear regression.

low reproductive outputs (Bell 2010). The fact that they have already faced recent genetic bottlenecks, as well as reduced diversity and numbers is also not in their favour (Easton 2018).

Although extinctions have been predicted for many amphibian species (Thomas et al. 2004), it has been suggested that some temperate zone frogs may find increased areas of climate suitability as the climate warms (Fouquet et al. 2010). There is little experimental research to test the temperature related physiological limits of *Leiopelma* species (Easton 2015), though some field observations of climatic influences on behaviour exist (Newman 1977; Bell 1978; Newman et al. 1978; Cree 1989). One laboratory study showed that Hochstetter's frogs selected temperatures between 15.3 and 20.9 °C, though it is possible that higher average and upper limits would have been possible, however warmer conditions were not available in the study (Easton 2015). Activity and emergence patterns of native frogs are highly correlated with moisture related factors, but observational studies found only weak or no correlation with temperature and wind (Newman 1977; Bell 1978; Newman et al. 1978; Cree 1989). Further physiological studies are needed to determine the most accurate environmental bounds for successful survival of *Leiopelma*

and increase understanding of how they will respond to future climate change.

Leiopelma are already under threat from multiple pressures, and the results of this study suggest it is likely that climate change will compound these pressures and management will need to be applied in new ways. Introduced mammalian predators, disease, the genetic impacts of small, isolated populations and habitat destruction are already severely impacting *Leiopelma* (Bell et al. 2004a; Bishop et al. 2013). The stronghold Archey's frog populations in Coromandel have yet to recover from a crash of 88% over 20 years ago (Bell et al. 2004a; Bell & Pledger 2015). Hamilton's frog on Takapourewa, the most genetically diverse population of that species, is likely at carrying capacity at around 300 individuals (JMG, pers. obs.). Furthermore, some *Leiopelma* species, such as Hamilton's frog, are in locations which are drought-prone and have little natural water. A range of management tools are already in use or recommended. Improving predator control methodologies and establishing predator-free populations are priorities in the Recovery Plan (Bishop et al. 2013). Landscape-scale rat control has been tested for Hochstetter's frogs with mixed results showing both positive and no improvement for frog populations depending on the study (Musset 2005; Nájera–Hillman et al. 2009; Longson et al. 2017; Crossland et al. 2023). For Archey's frogs, rat control has been shown to improve adult survival, but reduce juvenile and subadult survival (Germano et al. 2023). Translocations to create new populations have already occurred for some *Leiopelma* species (Bell et al. 2004b; Tocher & Pledger 2005; Bell et al. 2010). These translocations have largely been within similar climatic and ecological regions as existing populations (Wren et al. 2023). Hamilton's frog has been successfully translocated to two additional islands in the Marlborough Sounds near to their stronghold Maud Island and Stephens Island locations (Tocher & Pledger 2005; Bell et al. 2010). Archey's frog, however, has no predator-free populations (Bishop et al. 2013). It is likely that new management options and the identification of management pathways will need to occur to ensure *Leiopelma* resilience in a changing climate.

Implications for conservation management

Managing threatened native species to ensure they continue to survive in future under a changing climate is a conservation long game with many unknowns. It raises questions around how to get the right balance of *in situ* versus *ex situ* management. There is a need to increase the numbers of *Leiopelma*, so managing existing causes of decline should remain a priority, to create larger, more stable, and better-connected populations to increase resilience. However, translocations (i.e. assisted migration) to other climatically suitable sites is another potential management option which should be considered. *Leiopelma* populations have shown that they can increase in number and recolonise nearby areas when predator pressure is controlled, and suitable habitat is readily available (Germano et al. 2023). Therefore, identifying habitat which will remain, or become, suitable under climate change is particularly important for the conservation management of relict species like *Leiopelma*. Adaptation pathway planning is a tool which has been used to identify suitable management options to increase resilience to future climate change, allowing managers to prioritise actions at different points along alternate paths, depending on changing context, such as when or if a nominated threshold is exceeded (Jacobs et al. 2019; Cradock-Henry et al. 2021). We recommend development of climate change adaptation pathways for all

Leiopelma species to ensure the correct balance and staging of *in situ* versus *ex situ* management is achieved.

Translocation planning needs to include consideration of the long-term suitability of release sites under potential future conditions, not just current climate conditions. *Leiopelma* translocations have traditionally focussed on predator free island release sites, but with climate change these may no longer be suitable and translocation onto the mainland may be the best option. For instance, while conservationists have created insurance populations of Hamilton's frog on islands in the Marlborough Sounds (Bell et al. 2010), four of the five populations (Takapourewa, Maud/Te Pakeka, Nukuwaiata, and Motuara Islands) are already experiencing climate trends that will be detrimental to the frogs' survival. Consideration should be given trying to grow the Takapourewa population now in preparation for assisted colonisation in the next 10–20 years, with the goal to extend the range of this species on to the Northwest coast of the South Island. This option, however, is tempered by the presence of mammalian predators over most of mainland New Zealand and may also be tempered by the presence of exotic frog species such as the brown tree frog, *Litoria ewingii*, a widespread species over the South Island (Van Winkel et al. 2018). All *Leiopelma* species are susceptible to predation and unless predator control methodologies become more efficacious, southward movement of *Leiopelma* species and of Hamilton's frog onto the mainland is not a viable option. More research is needed to see whether Hamilton's frogs can survive on the mainland with the predator suppression tools currently available. Long-term planning is needed to prepare predator-free sites that could be used as release sites for assisted migration of the species most at risk of extinction due to warmer and dryer conditions in their current range. Until these are secured, translocations to predator-free islands and *in situ* management, accounting for future climate suitability, remains the best tool for *Leiopelma* species.

As with amphibians overseas, there is a need to apply new tools to *in situ* management of *Leiopelma* species under a changing climate (Shoo et al. 2011). Unexplored, *in situ* management options are available, examples include extending rocky habitat and the addition of an artificial rain regime for Archey's and Hamilton's frogs (e.g. sprinklers). On Takapourewa, fencing additional habitat to exclude tuatara should also be considered to grow the very small (c. 300 individuals) but genetically diverse population so that future translocations are possible. In the face of drought, increasing shade and leaf litter density by decreasing introduced browser pressure on plant undergrowth, through fencing or hunting, is another management tool with potential for both islands and mainland New Zealand (Wardle et al. 2001). Small scale predator proof fences are another possible mainland management tool which have proven successful for *Powelliphanta* snails, a species with similar microhabitat requirements and predation threats (K Walker, DOC, pers. comm.). These *in situ* management actions should be informed by research to avoid such actions generating perverse and unintended outcomes on vulnerable *Leiopelma* populations.

Long-term monitoring and research are needed to increase our understanding of how climate change will impact on existing populations of frogs and improve the accuracy of the climate suitability models developed in this study. Improved physiological data are needed for all *Leiopelma* species, especially about the temperature and moisture tolerances. This would improve models such as the ones in this study and would also feed directly into both *ex-situ* and *in situ* management

decisions (Shoo et al. 2011). Continuing existing monitoring for Archey's and Hamilton's frogs over the coming decades is especially important, as is establishing monitoring of at-risk populations (e.g. Northland population of Hochstetter's frog), with techniques that are accurate and sensitive enough to detect change. Monitoring data will provide insights to refine management of *Leiopelma* populations under a changing climate and with the application of new tools. Finally, the climate suitability maps in this study show areas which are currently suitable for Archey's and Hochstetter's frog but without presence recorded. Survey work in these areas would help to extend knowledge of their current range and refine future modelling, although we caution against limiting surveys for *Leiopelma* species to only these areas.

Historical climate data and future projections show that climate change needs to be accounted for in the long-term strategic planning for *Leiopelma* frog conservation. Forward planning is required to effectively manage *Leiopelma* species under a changing climate. Reliance on tools like predator-free islands and translocations will not be enough to preserve all *Leiopelma* species under a changing climate. Waiting for predator control tools to become more efficacious is too risky, given this may need to include mice, for which current control tools are limited and this would potentially push the time frame out too far. Further research is needed to help inform future models and adaptive management decisions. Long-term monitoring is needed to monitor change in frog populations over coming decades. Current populations need to be grown, and genetic diversity preserved to put native frogs in the best position for future management. Translocations within the current range must consider the long-term climate suitability of sites. Consideration should also be given as to whether assisted migration over the next 20–30 years is required for the *Leiopelma* species and genetic lineages most at risk from climate change.

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Additional Information and Declarations

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