



Using ecological niche modelling to infer past, present and future environmental suitability for *Leiopelma hochstetteri*, an endangered New Zealand native frog

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ABSTRACT

Leiopelma hochstetteri is an endangered New Zealand frog now confined to isolated populations scattered across the North Island. A better understanding of its past, current and predicted future environmental suitability will contribute to its conservation which is in jeopardy due to human activities, feral predators, disease and climate change. Here we use ecological niche modelling with all known occurrence data ($N = 1708$) and six determinant environmental variables to elucidate current, pre-human and future environmental suitability of this species. Comparison among independent runs, subfossil records and a clamping method allow validation of models. Many areas identified as currently suitable do not host any known populations. This apparent discrepancy could be explained by several non exclusive hypotheses: the areas have not been adequately surveyed and undiscovered populations still remain, the model is over simplistic; the species' sensitivity to fragmentation and small population size; biotic interactions; historical events. An additional outcome is that apparently suitable, but frog-less areas could be targeted for future translocations. Surprisingly, pre-human conditions do not differ markedly highlighting the possibility that the range of the species was broadly fragmented before human arrival. Nevertheless, some populations, particularly on the west of the North Island may have disappeared as a result of human mediated habitat modification. Future conditions are marked with higher temperatures, which are predicted to be favourable to the species. However, such virtual gain in suitable range will probably not benefit the species given the highly fragmented nature of existing habitat and the low dispersal ability of this species.

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1. Introduction

Rates of biodiversity loss are accelerating (Pimm et al., 1995) with the increasing human dominance of Earth's natural systems (Vitousek et al., 1997; Didham et al., 2007). Amphibians are particularly threatened by this crisis (Blaustein and Dobson, 2006; Houlihan et al., 2000; Mendelson et al., 2006; Pechmann and Wilbur, 1994; Stuart et al., 2004), expected by many to become the 6th mass extinction episode (Avisé et al., 2008). The main reason for this major decline in amphibian biodiversity is their sensitivity to a wide variety of environmental perturbations which has led them

to be considered as “bio-indicators” of ecosystem health (Pounds et al., 1999, 2006; Roy, 2002; Wake and Vredenburg, 2008) and often cited as the ecological “canaries in the coal mine” (Pechmann and Wilbur, 1994). More than 1856 amphibian species are threatened with extinction and many have already disappeared (Young et al., 2004; Stuart et al., 2008). Since the early, 1990s, declining amphibian populations have attracted special attention because of multiple distinctive features: (1) recent increases in reports of population declines and species' extinctions; (2) declines seem to occur simultaneously and over great distances; with (3) even some amphibian populations in protected, supposedly undisturbed natural areas declining. The latter was alarming because it meant that habitat protection, perhaps the best way to ensure a species' survival, could fail. This has been the case for New Zealand native frogs (*Leiopelma*) with serious declines due to a climate driven epidemic of chytridiomycosis (Bell et al., 2004a; Pounds et al., 2006) in

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relatively undisturbed areas. This has also been the case in other regions, probably also because of climate change (Lips et al., 2008; Pounds et al., 1999, 2006; Stuart et al., 2004).

Amphibians' peculiar physiological constraints are extensively documented and suggest particular sensitivity to water and temperature (Feder and Burggren, 1992; Buckley and Jetz, 2007). Water is a crucial constraint and resource for amphibians due to their highly water-permeable skin and mode of reproduction (Feder and Burggren, 1992). In ectotherms, environmental temperatures influence rates of energy use and assimilation as well as performance in gathering resources and interacting with other organisms (Bennett, 1990). Temperature is thus probably a strong constraint on mobility and energy acquisition in amphibians (Bennett, 1990). Water and temperature act together in determining net primary productivity, which may restrict the number of species that can coexist (Wright, 1983; Jetz and Rahbek, 2002; Hawkins et al., 2003). Despite a relatively small land surface, New Zealand displays very sharp environmental gradients and native frogs have very restricted and fragmented ranges in the northern part of the country where mean minimum annual temperatures are the highest.

Ecological Niche Modelling (ENM) links known occurrences of species to data describing landscape and abiotic parameters, known to be important for the species' ecological requirements, to develop models of inferred environmental requirements. These models can be used to predict potential distributional patterns for the species. ENM can be projected onto paleoclimate reconstructions to identify potential past (reviewed by Nogués-Bravo (2009)) as well as future environmental suitability (Ficetola et al., 2010; Araújo et al., 2006; Thomas et al., 2004) and thus the potential past and future distribution of the species assuming niche stability over time (e.g. Heikkinen et al., 2006; Jeschke and Strayer, 2008).

Both hindcasting ecological niche to conditions experienced before human colonization, and forecasting the likely response to future climate change, can have important implication for species conservation. Human activities modify the distribution of habitats, and shape species ranges by interacting with climatic features; ENM showed that suitable areas can be quickly shifted by human modifications of landscape (Ficetola et al., 2010). Evaluating the potential distribution before human impact can allow to reconstruct the species historical range and to relate modifications of the range to human impact (Nogués-Bravo, 2009). On the other hand, evaluating changes in suitable habitat expected under scenarios of climate change can help to define future conservation strategies (Araújo et al., 2006).

New Zealand's endemic frogs of the genus *Leiopelma* diverged about 200 million years ago (Ma) with the genus *Ascaphus*, its closest relative, and 250 Ma with all other living frogs according to molecular dating analyses (Roelants et al., 2007). This genus constitutes, consequently, a unique evolutionary legacy of particular importance in terms of biodiversity conservation. Since the arrival of humans and, with them, mammalian predators such as rats, several species of New Zealand's native frogs have become extinct and the others have seen their ranges shrink (Towns and Daugherty, 1994; Bell, 1994; Holyoake et al., 2001). The remaining species continue to be threatened by habitat destruction and degradation (Nájera-Hillman et al., 2009b), exotic predators (but see Nájera-Hillman et al., 2009b), population fragmentation, pathogens (Bell et al., 2004a) and the consequences of small population size (Daugherty et al., 1994; Waldman and Tocher, 1998). Today their conservation status ranges from vulnerable to critically endangered (Daugherty et al., 1994; Hitchmough et al., 2007). New Zealand Department of Conservation (DOC) has developed a long term "recovery plan" which aims to secure *Leiopelma* species from extinction and to improve their conservation status (Bishop et al.,

2009). Although the most abundant of the remaining New Zealand endemic frogs, Hochstetter's frog is categorised as "vulnerable" by the IUCN (International Union for the Conservation of Nature, Bell et al., 2004b), and "human induced loss of range" under the new Department of Conservation threatened species ranking system (Hitchmough et al., 2007).

Leiopelma hochstetteri currently occupies a highly fragmented native forest habitat north of 38°5S (Fig. 1). Late Holocene subfossil remains (Fig. 1) identified as *L. hochstetteri* appear throughout the North Island and even on the north-west of the South Island, suggesting its range was once wider (Worthy, 1987). Recently, a new population of *L. hochstetteri* was discovered at Maungatautari in the Waikato region (Baber et al., 2006). Our ignorance concerning something as simple as the distribution of extant populations reiterates the need for more research on this species. *L. hochstetteri*'s microhabitat has been characterized by Nájera-Hillman et al. (2009a) in Waitakere populations. Within its range this species prefers >160 m altitude shaded streams with cool temperatures. Occurrence was also positively associated with first order, erosive streams with volcanic acidic geology, probably because they tend to be steep and covered by coarse substrates and because they are less susceptible to flooding than larger stream and catchments.

Phylogeographical analyses demonstrated that the different patches of *L. hochstetteri* populations are genetically highly differentiated, a structure that originated in early Pleistocene, thus, much before human arrival (Fouquet et al., 2009). This result suggests that the range of the species has been fragmented by unfavourable conditions during Pleistocene climate oscillations. The climatic conditions of the Last Glacial Maximum has been estimated to be 2.5–4 °C colder than today in the North Island and also much drier (Drost et al., 2007). Such conditions would have restricted the native forest north of 38°S, a distribution that seems highly concordant to the current distribution of *L. hochstetteri*. The genetic structure among populations is so strong that conservation should target 13 major lineages (that can be considered as Evolutionary Significant Units; ESUs) from the 15 areas in which the species currently occurs to maintain the full gamut of genetic diversity and evolutionary potential of the species (Fouquet et al., 2009).

L. hochstetteri's range has probably been shaped by past climatic oscillations and landscape modifications (Fouquet et al., 2009). The current isolated populations are jeopardized by diseases and landscape modifications (Bishop et al., 2009; Nájera-Hillman et al., 2009a) and by upcoming climatic changes despite in situ management (McGlone, 2001). Moreover, these small, scattered populations each have independent evolutionary history, legacies and probably trajectories. Consequently, it is timely and important considering *L. hochstetteri*'s past, current and future distribution if we are to ensure the most efficient and effective conservation of the remaining populations of this ancient and globally significant amphibian species.

This study uses a large, comprehensive data set describing the present-day distribution of *L. hochstetteri* to model the species' ecological niche. We have then used this niche model together with historic climatic data to project backwards through time in order to estimate the potential distribution of this species in pre-human New Zealand (~1300 AD Wilmschurst et al., 2008). We then project our models into the future (2080) to evaluate how the current populations may fare under scenarios of future climate change.

There are several benefits that derive from this approach. First, niche modelling in the contemporary framework can help to identify areas where *L. hochstetteri* might still be present but is as yet undetected or to identify which additional variable is determinant for the species. Second, evaluating suitability under pre-human conditions (~1300 AD) will give insights into the potential range of *L. hochstetteri* before human activities modified New Zealand

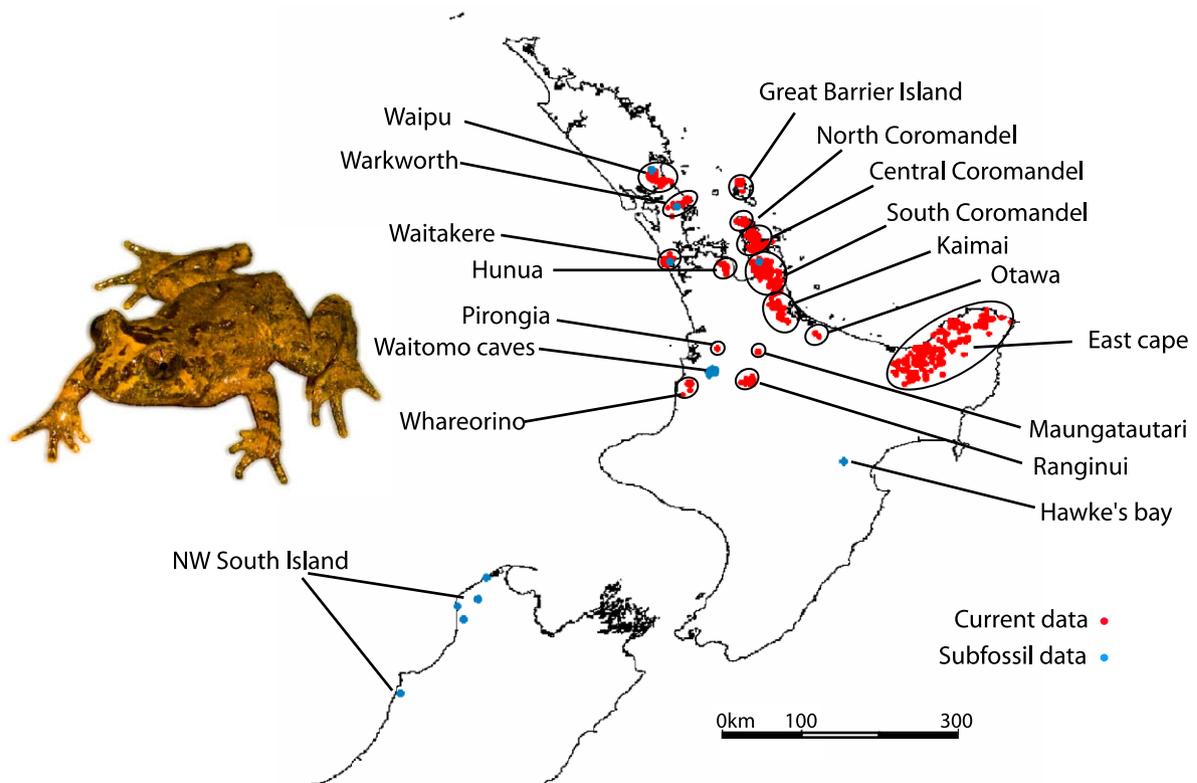


Fig. 1. Occurrence data. Red dots represent the current occurrence and blue dots the subfossil records. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

landscapes (Cook et al., 2006; McGlone, 1988), enabling estimates of the range contraction for this species following human settlement to be derived. At this time, climate was not markedly different than today (Cook et al., 2006) and forest was probably forming an almost continuous cover over New Zealand below the alpine tree line (McGlone, 1988). Such past distribution can be related to the observed genetic structure; furthermore, the availability of subfossil remains allows us to evaluate the robustness of projections of distribution into different periods (Nogués-Bravo, 2009). Finally, the identification of the species localities that can have sub-optimal conditions in the future enable us to identify populations that require special conservation efforts, potentially including direct interventions, such as active translocations.

2. Methods

2.1. Input datasets

Occurrence data for *L. hochstetteri* (Fig. 1) were drawn from the NZ Atlas of Amphibian's and Reptile Distribution (New Zealand Department of Conservation, 2009). This database represents 1708 current observation records representing all known populations recorded so far (since 1923; all these records correspond to areas where the species still occurs and/or where the habitat has not been dramatically modified) as well as 18 subfossils records from late Holocene (last 2000 years) (Worthy, 1987). The database comprises records of anecdotal observations, planned surveys and population monitoring programmes but not all potential *Leiopelma* habitat has been surveyed. Current data records are situated between latitude 38.53°S; 35.93°S and longitude 174.31°W; 178.49°W, but subfossils have been discovered as far south as 41.98°S; 171°45 W on the west coast of South Island (Worthy, 1987). Thus, we considered a mask extending from latitude 33°S

to 43°S and longitude 170°W to 179°W (Fig. 1). This spatial coverage was deliberately made larger than the actual range occupied by *L. hochstetteri* to ensure we encompassed the full extent of the predicted range.

We downloaded current climate data as well as scenarios of climate change projections (IPCC 3rd assessment data) from the WorldClim database (Hijmans et al., 2005). These data were used at a 2.5' spatial resolution and cropped to the coverage mentioned above. Two climate-change scenarios derived from HadCM3 (Hadley Centre for Climate Prediction and Research's General Circulation Model) and CCCMA (Canadian Centre for Climate Modelling and Analysis) for the period of 2080–2100 (referred to as the 2080 scenario) were used to obtain estimates of likely climatic conditions in the future. These include scenarios A2a, which envisions population growth to 15 billion by the year 2100 and rather slow economic and technological development, and B2a, which envisions slower population growth (10.4 billion by 2100) with a more rapidly evolving economy, more emphasis on environmental protection, lower emissions and therefore a less pronounced future warming. This range of scenarios gives some idea of the range of greenhouse gas emission pathways that might be taken during the next decades and the likely consequences of these on climate.

We extracted from WorldClim four climatic layers, likely representing physiological of the species (thermal limits, availability of energy and water; Rödder et al., 2009): (1) T_{max} of January (warmest month); (2) T_{min} of July (coldest month); (3) cumulated precipitation of December, January, February (driest season); (4) cumulated precipitations of June, July and August (wettest season). Furthermore, we considered two environmental layers representing topography and forest availability. As the species is associated with rocky streams, which are rarely found in lowlands, we also used average altitude in each 2.5' grid cell (obtained from <http://biogeog.berkeley.edu>). Finally, this species is exclusively associated with forest so we calculated percentage forest cover in

each 2.5' grid cell, on basis of GLC2000 land cover (<http://bio-geo.berkeley.edu>, 30 s resolution) (Fig. 2). Correlations among these six parameters were reasonably limited ($r < 0.8$ in all pairwise correlations) (Table 1).

We considered a limited number of environmental variables to increase model robustness and to reduce the risk of overfitting (Nogués-Bravo, 2009). We did not include variables representing annual climatic conditions such as average annual temperature or annual precipitation because they were strongly related to linear combinations of variables included into the analyses.

2.2. Prior expectations on niche stability and species climate equilibrium

When projected in the past or in the future such models assume niche stability, which have been tested extensively in different taxa (Holt, 1996; Peterson et al., 1999; Wiens and Graham, 2005; Martínez-Meyer and Peterson, 2006 but see Pearman et al., 2008). In the case of *Leiopelma* ssp. phylogenetic niche conserva-

Table 1

Correlations coefficients among the six environmental parameters.

	T_{max} 1	T_{min} 7	Prec wet 6–8	Prec dry 12–2	Altitude
T_{max} 1					
T_{min} 7	0.78				
Prec wet 6–8	0.09	0.06			
Prec dry 12–2	0.22	0.17	0.76		
Altitude	0.72	0.79	0.13	0.17	
Forest cover	0.08	0.08	0.24	0.24	0.08

tism is expected because all are forest species occurring in the warmest part of the country (*L. archeyi* distribution is nested within *L. hochstetteri*'s one and *L. hamiltoni* in the Marlborough Sounds which is the warmest part of the south Island). Another reason for such assumption is that this group of frogs is very plesiomorphic. Their morphology appears very similar to Jurassic-era frog fossils, suggesting that they have not changed much from their ancestral form (Estes and Reig, 1973) and even *Ascaphus* (its closest relative with which *Leiopelma* diverged ~200 Ma) occupies similar type of habitat and climate.

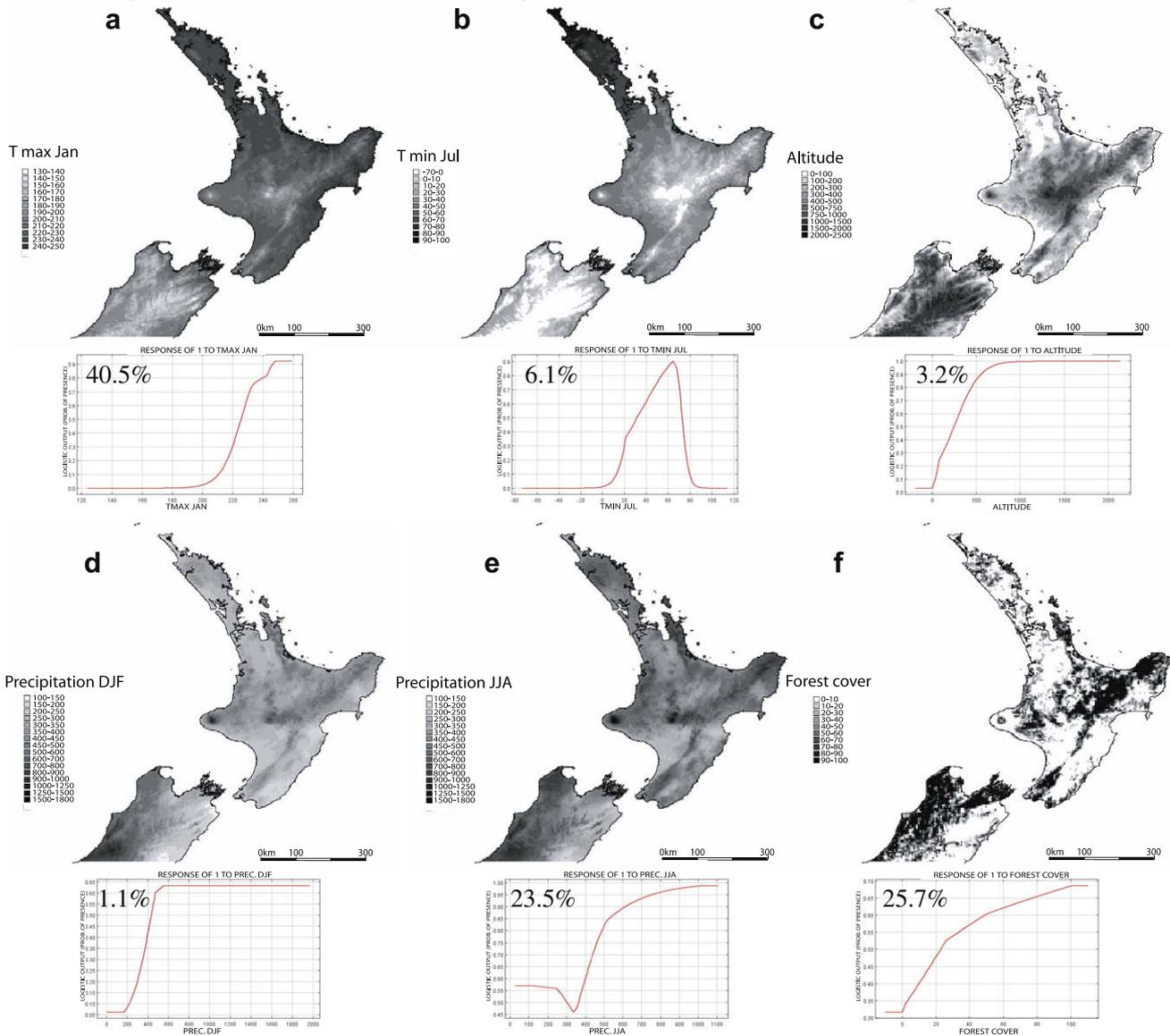


Fig. 2. Environmental layers. (a) T_{max} of January; (b) T_{min} of July; (c) altitude; (d) precipitation in December, January and February; (e) precipitations in June, July and August; (f) current forests cover and associated MAXENT response curves.

Species are said to be at equilibrium with climate if they occur in all climatically suitable areas whilst being absent from all unsuitable ones (sensu Araújo and Pearson, 2005). For example in a species with low vagility the time since last climate shift may not be sufficient to extend its range to the edges of its niche. Using such current occurrences to model the niche may lead us to underestimate the breadth of suitable environments. Due to its poor dispersal ability (Tessier et al., 1991) and past range reduction (Fouquet et al., 2009) it is possible that *L. hochstetteri* is in some form of niche disequilibrium.

Nonetheless, the dispersal ability of the species may not be as low as we could expect (T. Beauchamp, pers. comm.) and in the absence of any other information, a model, even if perhaps representing a subset of the full breadth of this species' niche, remains of significant utility.

2.3. Data analysis

We used Maxent 3.2.1 (Phillips et al., 2006; Phillips and Dudík, 2008) to model environmental suitability. Maxent is a machine learning method estimating species distribution by finding the probability distribution of maximum entropy (i.e. that is closest to uniform) subject to constraints representing our incomplete information about distribution. The constraints are that the expected value of environmental variables should match its average over sampling locations (Phillips et al., 2006). The model evaluates the suitability of each grid cell as a function of environmental variables at that cell. We used a logistic output of Maxent, with suitability values ranging from 0 (fully unsuitable habitat) to 1 (optimal habitat) (Phillips and Dudík, 2008). In the last few years, Maxent has become a standard tool for ENM because it has been shown to outperform some of the more traditional software solutions for such analyses (Elith et al., 2006). Comparative analyses showed that Maxent is among the best performing ENM methods, as it has performance similar to techniques using presence–absence data (Elith and Graham, 2009) and shows good performance using both small and large datasets (Wisz et al., 2008). The effectiveness Maxent has been proven by its ability to correctly predict changes in species distribution following environmental modifications (Ficetola et al., 2009, 2010) and new localities for poorly known species (Pearson et al., 2007). We used linear, quadratic and hinge features with default convergence threshold (10^{-5}) and maximum number of iterations (500). We considered only one presence record per grid cell. Following Pearson et al. (2007), we used the 10th percentile training presence as a suitability threshold, i.e. we assumed that a cell is suitable if its suitability score is greater than the 10th percentile of training presence points.

We used the area under the receiver operating characteristic curve (AUC; Manel et al., 2001) as a threshold independent method for model validation (but see Lobo et al., 2008). We used cross-validation to evaluate the robustness of Maxent models. We divided the presence points in five groups; we then run the model five times, each time using a different group of cases, representing 20% of presences, as test points and the 80% remaining subsets as training cases (Nogués-Braxo, 2009). We then evaluated the performance of models, by comparing AUCs and correct classification rates. Furthermore, we calculated correlation among suitability maps obtained using the five groups and using the complete dataset, as a measure of similarity among predictions obtained using different datasets.

After evaluating the present-day suitability for *L. hochstetteri*, we used the Maxent model to project suitability back to (1), pre-human conditions (~1300 AD, Wilmshurst et al., 2008) using the same climatic (Cook et al., 2006) and elevation conditions but assuming a homogenous, 100% forest cover at altitude <1500 m

(McGlone, 1988). We used two approaches to evaluate the models ability to correctly predict the distribution of subfossils. First, we used a χ^2 test (1 df) comparing observed frequencies of correct and incorrect predictions, to evaluate if our models predict distribution in the past significantly better than expected under random expectations (Roura-Pascual et al., 2004). Furthermore, we calculated the AUC of models predicting subfossil distribution. We repeated this analysis using all subfossils together and considering separately subfossils from the north and south island. We then used the Maxent model to forward projected future conditions (assuming no change in forest distribution from the present situation) according to (2) HadCM3 scenarios A2 and B2 and (3) according to CCCMA scenarios A2a and B2a.

Extrapolating models to future conditions can be particularly problematic when models are projected outside the range of environmental conditions used for calibration (Fitzpatrick and Hargrove, 2009). We therefore used two approaches to evaluate the robustness of our projections. First, we used Maxent to calculate “clamping”, which shows where environmental variables are outside their calibration range, which might affect predicted suitability (Phillips et al., 2006). We also used the approach of Fitzpatrick and Hargrove (2009) to evaluate the occurrence of non-analogous conditions caused by multivariate combinations of variables. The results of this analysis (supplementary material) did not provide areas with non-analogous conditions different from those identified by clamping; therefore we report the results of clamping only.

3. Results

3.1. Suitability model

Occurrence data led to 281 grid cells with current presence records. The most important variables explaining the presence of *L. hochstetteri* were maximum temperature in January (40.5% contribution to Maxent model), forest cover (25.7%) and winter precipitations (23.5%) (Fig. 2). The three other variables had a minor contribution: 6.1% for minimum temperature in July, 3.2% for altitude and 1.1% for summer precipitations. *L. hochstetteri* was strongly associated to areas with high forest cover. Furthermore, it was positively related to summer temperature, with favourable temperature above 20 °C and associated to areas with winter precipitation above, 200 mm; suitability was limited in lowlands (Fig. 2). The AUC of the model was very high (0.945), which indicates a good fit of the model. The 10th percentile training presence logistic threshold was 0.242. We consequently used this value as suitability threshold (Pearson et al., 2007). According to this threshold, 13.8% of the land considered was suitable for the species.

Cross-validation suggests that the Maxent model is quite robust. In all the cross-validated models, the AUC calculated for the test data was high and similar to the one of training data (range: 0.907–0.949). Furthermore, using the 10th percentile training presence threshold, all the cross-validated models correctly predicted suitability in the majority of test cases (range: 78–91% of cases; average prediction rate expected under randomness: 14%). Predicted suitability was very similar across all the replicated models ($r \geq 0.97$ in all pairwise correlations) and was very similar between the replicated models and the model considering all the presence points ($r \geq 0.97$ in all pairwise correlations). For this reason, in subsequent analyses we considered the model built using all the presence points.

3.2. Current suitability

The most suitable areas (suitability >0.85, highest class on Fig. 3a chosen arbitrarily for illustrative purpose) are situated in

the northern Coromandel peninsula, on Great Barrier Island and in the Northland. Areas with suitability between 0.7 and 0.85 correspond to the rest of the Coromandel Peninsula, Great Barrier Island, East Cape, Northland, Little Barrier Island and a few cells in the Bay of Plenty (Kaimai, Otawa and Lake Rotama). Among those highly suitable areas, those in Little Barrier Island and near Lake Rotama, and some in the Northland, are not known to harbour any populations of *L. hochstetteri* (Fig. 3a). The most distinctive areas are in the Northland (#1), between the Bay of Plenty and Gisborne (#8) and south of Ruatoria (#7).

3.3. Pre-human suitability

The projection of the suitability using a homogenous forest cover supposedly corresponding to conditions before human arrival reveals a different picture (Fig. 3b). The strongest differences are on the western part of the North Island, where conditions were suitable for *L. hochstetteri*, while the quasi absence of forest today limit the species to very small patches. However, we note that these populations (Whareorino, Maungatautari, Ranginui, Pirongia [unconfirmed] as well as Waitakere) have lower climatic suitability according to our model (0.24–0.4) even assuming continuous forest cover. Surprisingly, the projected past range appears fragmented and a major break oriented North–South (via Thames–Cambridge–Te Kuiti) delimit two mostly continuous blocks of suitable habitat.

The model projected into the past predicted presence in the localities with subfossils significantly better than random expectations ($\chi^2_1 = 8.7$, $P = 0.003$), but the AUC of the model was low (AUC = 0.693). When we only use the South Island subfossils as the sole test data, AUC dropped to 0.32, and subfossils were predicted worst than under random expectations (although not significantly so; ($\chi^2_1 = 0.7$, $P = 0.4$)). However, the model performed very well when considering only the North Island subfossils as test data (AUC = 0.837) and predicted presence in the localities with subfossils significantly better than random expectations ($\chi^2_1 = 16.1$, $P < 0.001$). Those southern remains are clearly out of any suitable areas predicted for current and pre-human times (Figs. 2 and 3). The Hawke's Bay subfossils do however abut a zone of high suitability.

3.4. Future suitability

The analysis of clamping showed that, under scenarios of climate change, non-analogous climatic conditions potentially affecting the results of our analysis can occur particularly on the Bay of Plenty and the east coast of the North Island (sup. mat.). The CCCMA-A2 scenario was the one with the largest areas with high clamping; clamping was considerably lower under the B2 scenarios and under the HadCM3-A2 scenario. Nevertheless, clamping suggests that the results remain robust for the majority of the study area. Even under the CCCMA-A2 scenario, clamping was low (<0.2) for 77% of the study area.

Simulated climate change might be favourable to *L. hochstetteri* (Fig. 3c–f). The increase in temperature and precipitation is predicted to increase the extent of suitable areas. This is true for both scenarios and both models. The few differences observed occur mostly between the two different B2a scenarios, simulating a less rapid increase in temperature and precipitation.

In contrast, suitability is predicted to become low (<0.242) in Northland, where the most northern populations live, as well as in the Waitakere mountains and Great Barrier Island. Suitability is also expected to decrease at the tip of the Coromandel Peninsula. Among the areas that appear highly suitable and could be targeted for translocation Tuhua/Mayor Island (#6 on fig. 3a) and the forested protected areas east of Taupo can be flagged.

4. Discussion

4.1. Current conditions

The modelled current environmental suitability is markedly different from the known distribution of *L. hochstetteri*. This can be explained by several non exclusive hypotheses: (1) the areas have not been adequately surveyed and undiscovered populations still remain; (2) areas appear suitable due to an over simplistic model; (3) species/climate disequilibrium; (4) the species' sensitivity to fragmentation and small population size has resulted in many local extinctions; (5) biotic interactions like the distribution of predators has led to local extinction of populations; (6) historical events like Taupo's eruption destroyed some populations.

4.1.1. Undiscovered populations still remain

Recently, a new population of *L. hochstetteri* has been discovered in Mount Maungatautari (Baber et al., 2006) and Otawa and Kaimai range populations have also only recently been documented (Gemmell et al., 2003). This highlights that other populations of this secretive species may also be undocumented. Modelling is a rapid and cost effective tool to focus the search for still undocumented populations. The most suitable grids harbouring patches of native forests and rocky streams should be targeted. They are flagged from 1 to 8 in Fig. 2a. This possibility could be easily tested with a search for the species in those areas identified as suitable but "frog-less" and may lead to the discovery of new population(s) or may allow the identifications of determinant variable(s) that we omitted which may explain the absence of the species from these areas (see hereafter). As a matter of fact, some of these areas have been already surveyed without lead to new records (T. Beauchamp, pers. comm.).

4.1.2. The model is overly simplistic

This second possibility could be explained by variables that we did not take into account and lead to consider those suitable areas as potentially false positive. First, some suitable patches of forest in fact correspond to recent growth or plantations that are not optimal habitat for *L. hochstetteri*. Occurrences in non old growth native forest are probably recent colonization from adjacent preserved forest. Nevertheless, in order to be conservative we included all types of forest given *L. hochstetteri* can even inhabit pine plantations (T. Thurley, pers. comm.). Moreover, many of the suitable, but "frog-less" patches we have identified do harbour native forest and other parameters have to be invoked to explain the absence of frogs from these locals.

Our models are based on large-scale variables, but factors occurring at local scale and microhabitat features can be extremely important for species distribution but have not been directly taken into account. Nájera-Hillman et al. (2009a) has demonstrated that some microhabitat parameters are important to explain the distribution and abundance of the species, such as water temperature, shading and geological features of streams. Unfortunately, microhabitat variables are rarely available in large scale datasets and are very difficult to integrate in models; nevertheless, it might be possible to integrate large scale models on bioclimatic suitability with more local scale data to refine the performance of models and to perform analyses in localities of interest (Brambilla et al., 2009). Moreover, stochasticity of the habitat may be an important component with streams being often subject to slips that destroy habitat and populations (T. Beauchamp, pers. comm.).

4.1.3. Species/climate disequilibrium and historical events

As mentioned previously *L. hochstetteri* has supposedly low dispersal ability and may have not colonized all suitable areas. This

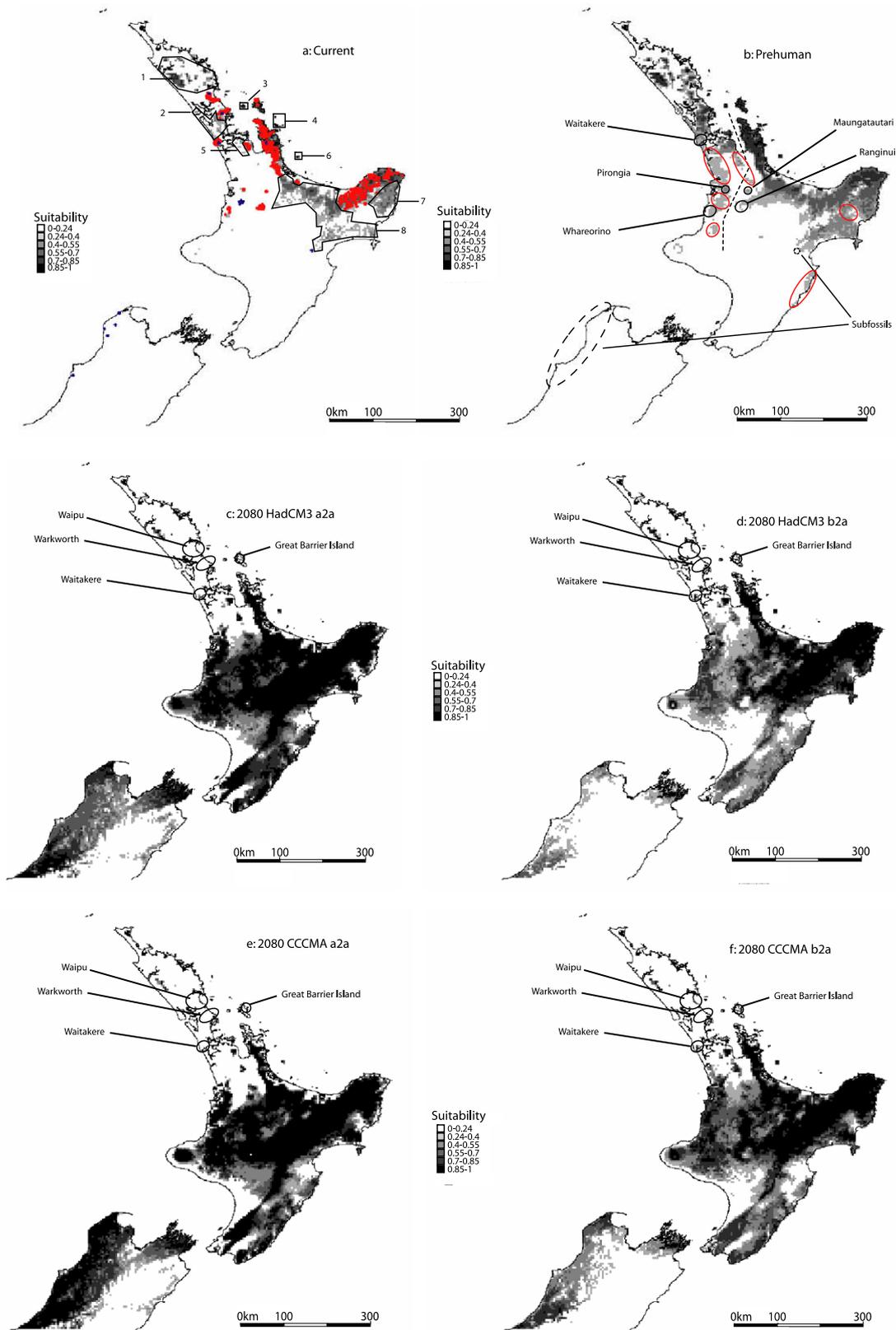


Fig. 3. Modelled environmental suitability. (a) Modelled current distribution of the environmental suitability. We indicated eight zones where the species is supposedly absent but the conditions optimal. (1) Northland; (2) North of Auckland; (3) Little Barrier Island; (4) North Coromandel Islands; (5) South of Auckland; (6) Mayor Island; (7) South East Cape; (8) Bay of Plenty to Hawkes Bay. (b) Modelled pre-human distribution of the environmental suitability. We indicated location of current populations and subfossils that are not in a climatic optimum. We also indicate a major east-west "break" in this distribution (dashed line) and past suitable areas (red circles). (c) Modelled future (2080) distribution of the environmental suitability according to two scenarios and two different models. We indicated the locations of the populations for which climatic condition could become unsuitable. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

species is consequently susceptible to be at disequilibrium. Another possibility is that volcanism may have had dramatic impacts on native frog populations, as well as other species in the central zone of North Island (Gemmell et al., 2004). Lake Taupo is known to have had particularly destructive eruptions c. 3300 years BP and c. 1850 years BP (Sparks et al., 1995). The later event is known to have completely destroyed forest in an 80 km radius and undoubtedly had much wider effects. It is tempting to speculate that the significant gap between western and eastern populations of Hochstetter's frog through the central zone of North Island, and the absence of any native frog species between the upper North Island and upper South Island (Holyoake et al., 2001), is a consequence of that eruption. Nevertheless, such an event cannot alone explain the absence of the species in the other suitable areas.

4.1.4. Local extinctions and biotic interactions

The deleterious effect of fragmentation and small deme size could also interact with environmental suitability. Small fragments often host small populations, which are threatened by the joint effects of demographic and genetic stochasticity (Cushman, 2006). Nevertheless, some localities (Whareorino, Maungatautari and Ranginui) harbour small and isolated populations suggesting that under some circumstances the species can persist in such conditions.

Biotic interactions are a further parameter not included in our models that can influence species distribution. In New Zealand, several predatory mammals have been introduced and while these have had negative effects on much of New Zealand's terrestrial fauna (Didham et al., 2007), there is little direct evidence, thus far that introduced mammals have had a widespread effect on amphibian populations. For example, Wells (2007) and Nájera-Hillman et al. (2009b) found no support for a significant impact of feral mammals' density on *L. hochstetteri* abundance.

Another issue could also be the occurrence of previous undocumented chytridiomycosis epidemics. Despite disease surveys of most *L. hochstetteri* populations (Department of Conservation, unpublished data), investigations have failed to detect the fungus in this species. Recent research *Leiopelma* ssp. skin secretions seem to inhibit pathogenic zoospores (Melzer and Bishop, 2009).

All these possibilities are non-mutually exclusive and could have interacted to lead to the current pattern.

4.2. A tool for conservation in situ and translocation

The central and western part of the species range still harbour relict populations (Whareorino, Maungatautari, Ranginui, Pirongia as well as Waitakere) that do not seem to inhabit a highly suitable climatic environment. If the models are correct, these populations may be at some risk of future extinction due to climatic stochasticity, small population size and other factors and may be in need of special attention. Moreover, Fouquet et al. (2009) as well as Green (1994) demonstrated the unique genetic characteristics of each of these populations, each of which is worthy of consideration as an evolutionary significant unit.

One interesting point that can be drawn is that our simulations reveal that some offshore islands (3, 4, 6) appear to harbour suitable conditions for *L. hochstetteri* (but see future suitability). Such islands could be targets for future translocations. A recent analysis showed that reintroductions have been frequently successful in amphibians (Griffiths and Pavajeau, 2008). This type of action has been used frequently in New Zealand for conservation, and has even been applied successfully to another endemic frog *L. hamiltoni* (Tocher and Pledger, 2005). Saunders (1995) recorded ~400 translocations of 50 taxa. Unfortunately, many translocations have been undertaken as isolated activities, frequently under crisis conditions, and there has often been little understanding of the causes

of success or failure (Armstrong and McLean, 1995). In a review of translocation programmes for amphibians and reptiles, Dodd and Seigel (1991) found doubtful the effectiveness of translocation as a conservation strategy. One of the reasons for this may be the lack of considering environmental suitability in a modelling framework – the successful translocation of *L. hamiltoni* was from one offshore island to another only a few kilometres from the founding population (Tocher and Pledger, 2005). Given the unique genetic features of many populations (Fouquet et al., 2009) translocation may be useful in case in situ management fails, which may be the case given the upcoming impacts of climate change, chytridiomycosis, as well as potential failing of feral predator population management in the mainland.

4.3. Pre-human

Surprisingly, pre-human suitability modelling does not support a much wider range than we currently observe (Fig. 3b). Areas mainly in the west, the centre and the southern part of East Cape could have been suitable enough to harbour *L. hochstetteri* populations when the forest cover was intact; nevertheless, the modelled range appears limited to north of 39.5°S and is still fragmented. Consequently, human induced modifications of the landscape have reduced the range of the species but perhaps to a lesser extent than previously thought (Green, 1994). An environmental break between western and eastern populations is clear. Moreover, given the species association with streams, landscape features such as large rivers might break the connectivity between populations even across what is apparently a band of continuously suitable environment. Given the low vagility of the species (Tessier et al., 1991) and the fact that environmental suitability probably increased since LGM until human arrival, it is likely that this interconnectivity was even much lower until relatively recently. This could explain why the species retained such a strong genetic structure originating during early Pleistocene (Fouquet et al., 2009).

This projection also revealed that fossil remains from late Holocene discovered in the west coast of South Island are located in an area with climatic conditions extremely different from those where present day populations live. The west coast is currently colder than the present range of *L. hochstetteri*, and was certainly even colder during LGM. A natural, colonization of the South Island after the LGM is unlikely; indeed, Worthy and Holdaway (1994) estimated that no interchange of terrestrial vertebrates between North and South Islands occurred during the last 30,000 years. Consequently, it is possible that the *Leiopelma* remains found on South Island are not closely related to current *L. hochstetteri* populations. Amphibian morphology is notoriously cryptic (Cherry et al., 1978; Stuart et al., 2006) so that evolutionary entities that diverged long ago often lack any morphological differences. It would not be surprising that a plesiomorphic genus such as *Leiopelma* (Estes and Reig, 1973) also shows this pattern. Consequently, we raise the possibility that the subfossils from the west coast of South Island belonged to a different *Leiopelma* lineage.

4.4. Future conditions

The area of predicted future suitability is strikingly different from the current situation and much larger under all of the predicted future scenarios. Future predictions may be not robust in the east coast, but they seem robust in most of the study area, at least for the CCMA-A2 scenario (supplementary material). Our model suggests that most of the North Island may become suitable by 2080, because of the increase in temperature. Higher temperatures triggered pattern is reminiscent of studies on invasive species (Rödger and Weinsheimer, 2009; Ficetola et al., 2010), which respond to climate modification by shifting their range toward the

poles (Parmesan et al., 1999). However, given the currently fragmented nature of the available habitat and *L. hochstetteri*'s low dispersal ability and limited reproduction rate, the species may be unable to benefit from the widening of areas climatically suitable. Assuming unlimited dispersal, Araújo et al. (2006) observe a similar picture for several species of European amphibians. Unfortunately, an unlimited dispersal is unrealistic, especially for species with limited vagility, and in presence of habitat fragmentation. Moreover, the ability of species to cope with climate warming may be offset by projected decreases in the availability of water.

What is more, the northernmost populations (Northland, Wai-takere and Great Barrier Island) in the north of the North Island may shift to unsuitable conditions. Again, this is comparable to the loss of suitable climate space for amphibians that has been projected to occur in the south–west of Europe by Araújo et al. (2006). This is however to be taken with caution given the model is based on current occurrence, and the species is limited by the northern extent of the land, where the temperatures are currently the highest observed across the range, thus correlative models cannot realistically predict the upper temperature tolerance of this species.

Finally, projections via niche models can also help to identify areas that may become over time suitable for this species in the prospect of eventual translocations. Some of the areas identified as suitable for translocations given current climatic conditions do not stay as such by 2080; it will be important taking a longer term view to translocations, selecting regions that not only appear suitable now, but predicted to remain suitable in the future.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2010.03.012.

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