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RESEARCH

Using population viability analysis and fossil records to inform the conservation of pāteke (*Anas chlorotis*)

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Abstract: Population decline and extinction are often driven by multiple stressors. Since AD 1500, the predicted global extinction rates for birds is estimated to be at least 80-times higher than the long-term background average. Pāteke/brown teal (*Anas chlorotis*) is a threatened waterfowl endemic to Aotearoa New Zealand, with a current population of c. 2500, spread across two remnant populations and a handful of reintroduction sites. The decline of pāteke since the arrival of humans results from habitat loss and fragmentation, predation, and other anthropogenic interactions. One of the two remnant populations is located on Aotea Great Barrier Island and has been declining since the 1980s. We used a combination of population viability analyses and species distribution modelling to better understand (1) the drivers of the decline on Aotea, (2) the management interventions that are most likely to reduce extinction risk and, (3) the pre-historic distribution of pāteke across Aotearoa. Our models were informed by a combination of seven years of intensive monitoring data from Aotea, and nationally distributed fossil records. Population viability analysis results suggest that over the next 100 years the pāteke population on Aotea has a 46% chance of extinction and a 99% chance of falling below an abundance of 50 individuals. Management should focus primarily on the adult life-stage, as protecting this stage resulted in the most significant increases in population growth rates. Species distribution modelling results suggest that historically, pāteke were present across much of coastal Aotearoa. Just as population declines are frequently the result of multiple stressors, multiple interventions are often required to halt extinctions. For pāteke, this will mean controlling multiple mammalian predator species, improving habitat quality, and re-establishing populations across their former range.

Keywords: brown teal, extinction, multiple stressors, population dynamics, predation, New Zealand, species distribution modelling

Introduction

Population trajectories are determined by multiple processes and stressors. Where populations are declining it is important to identify the key stressors and those which can be effectively managed. Globally, predicted extinction rates for birds since AD 1500 are estimated to be at least 80-times higher than the long-term background average (c. 100 vs 1 extinctions per million species years; Pimm et al. 2006; Cooke et al. 2023). Globally, the primary threats to bird species are predation by invasive species, climate change and land-cover and land-use changes, resulting in habitat fragmentation and degradation (Lees et al. 2022). In most cases, it is difficult to attribute a species' extinction to a single cause; instead, multiple stressors interact (whether additively, synergistically, or antagonistically) to erode population resilience (Côté et al. 2016).

Prior to human arrival in Aotearoa New Zealand (hereafter Aotearoa) in the mid-13th century (Wilmshurst et al. 2008),

pāteke/brown teal (*Anas chlorotis*) were probably among the most common waterfowl species present (Hayes & Williams 1982), although Worthy and Holdaway (2002) observed Finsch's Duck (*Chenonetta finschii*) to be the most abundance waterfowl in the fossil record. Historical reports suggest that pāteke remained widespread into the late 19th century (Buller 1882; Hayes & Williams 1982). However, pāteke are now classified as Threatened - Nationally Increasing (Robertson et al. 2021), with an estimated total population size of between 2000 and 2500 as of 2022 (The Department of Conservation 2022). Significant remnant wild populations (over 400 individuals each) persist in Northland and on Aotea Great Barrier Island (hereafter Aotea), with smaller populations re-established in a handful of locations across Aotearoa (Fig. 1). While numbers of individuals for the species appear to be increasing overall, this is not the case on Aotea. The major causes for the decline of pāteke across their range include predation by introduced species (O'Donnell
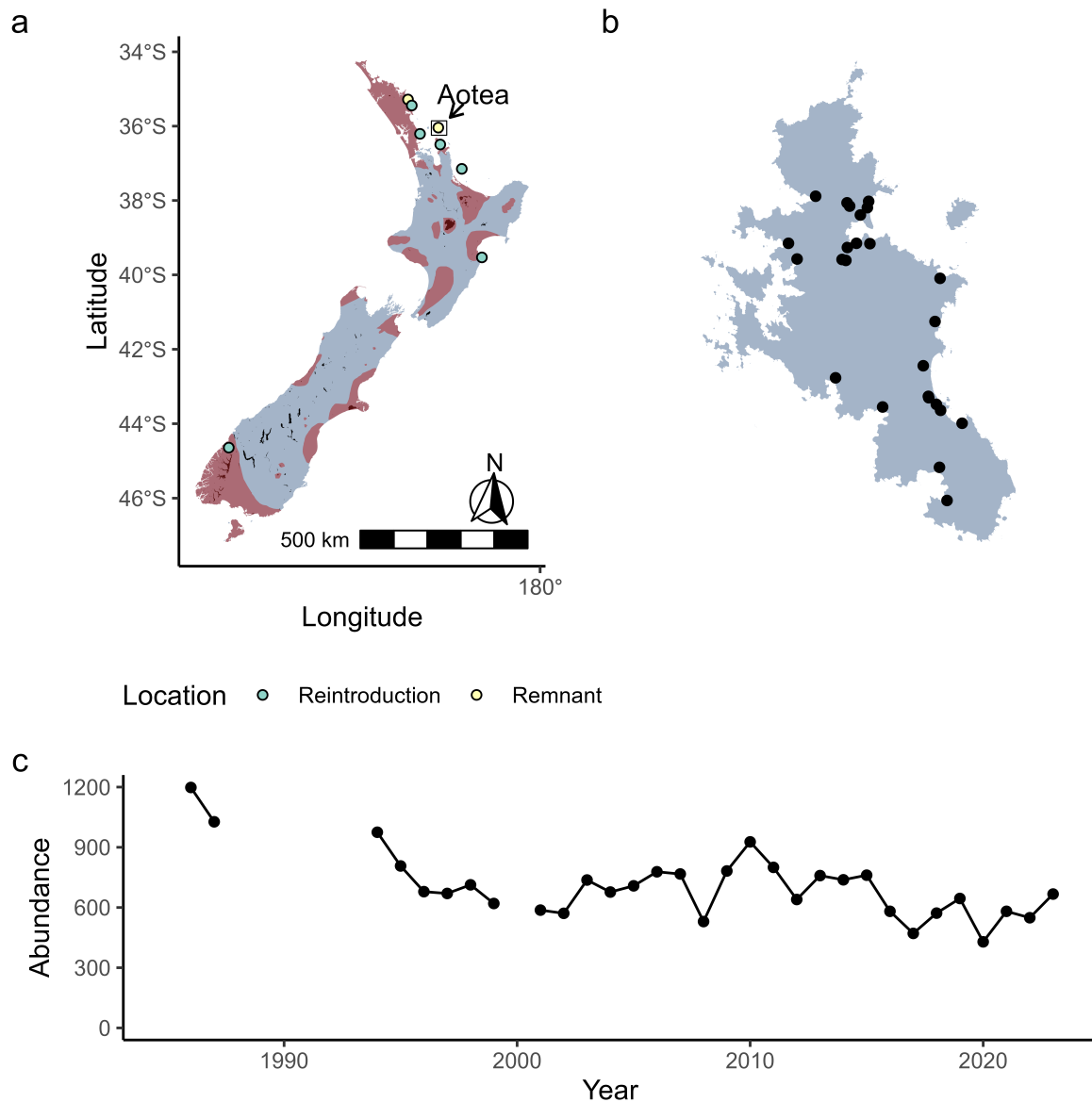
Figure 1. (a) Estimated distribution of pāteke (maroon shaded area) in the mid to late 20th century across Aotearoa, and the current significant populations of pāteke (points). Captive populations for breeding not shown. Figure recreated from Hayes and Williams (1982) and Bowker-Wright (2008). (b) Location of monitoring sites across Aotea used in this study. (c) Trend in pāteke population abundance across Aotea from 1985–2021. Data were not available for the period 1988–1993 and the year 2000.

et al. 2015), habitat loss, negative interactions with humans (e.g. roadkill; Alley et al. 2007; Giblin 2021) and possibly starvation during droughts. Hybridisation between brown teals and mallards was described by Cole and Wood (2017) and may also be a concern through genetic swamping or decreased hybrid fitness. Ongoing efforts have been made to arrest the species decline, particularly via predator control and translocations to predator-free sanctuaries and offshore islands (Watts et al. 2016). While the species is classified as Threatened - Nationally Increasing (Robertson et al. 2021), there is considerable concern about recent population declines on Aotea, with numbers decreasing from c. 1200 in the 1980s to approximately 667 in 2023 (van der Wel 2023), see study population section in the methods for a description of population dynamics on Aotea. However, it is unknown which pressure or combination of pressures is having the most detrimental

effect on the Aotea pāteke population (Giblin 2021). To date, management has focused on predator control of cats (which predate on ducklings, fledglings, and adults) and pūkeko (a native rail which predates on eggs and ducklings of pāteke) and habitat restoration (increasing foraging, breeding, and roosting sites). While a sharp population decline from 1985–2000 was halted (possibly due to conservation interventions), with the population steady from 2000–2010, since 2010 the population has declined across Aotea. Management of the Aotea population is effectively split into two components, the individuals located at Okiwi station have received intensive habitat restoration and predator control, while conservation efforts across the rest of the island have been less intensive.

Using a stage-based matrix model based on data collected in 1999, Ferreira and Taylor (2003) estimated that pāteke populations on Aotea were declining by 17% per year, with

a predicted population halving time of just 4.1 years. Their model suggested that the critical demographic predictor of the population trajectory was the survival of breeding females. Given the renewed decline in pāteke abundance on Aotea, despite intensive and ongoing management interventions, we revisit the population viability analysis (PVA) of Ferreira and Taylor (2003) with updated data and additional analysis to infer extinction risk and inform future management opportunities. Additionally, given the goal of re-establishing self-sufficient populations of pāteke across Aotearoa, we were interested in better understanding the prehuman distribution of the species to provide a geographic context for future reintroductions.

Population viability analyses provide a way to estimate the relative effect of different stressors on populations and in particular, extinction risk. They typically rely on vital rates, estimated from demographic data combined with statistical or simulation modelling to extrapolate population trends through time (Boyce 1992; Chaudhary & Oli 2020). Using PVAs, sensitivity to changes in demographic parameters can be examined, as can the effectiveness of various management interventions. Population viability analyses have been used to study the population trajectories of a wide variety of flora and fauna, but with a bias towards charismatic and highly threatened species (Simpkins et al. 2018). Species distribution models (SDMs) are another tool that can be used to better understand changes in population distributions, such as range contractions. Species distribution models are correlative and link species observations to environmental conditions to predict where a species may potentially occur (Elith & Leathwick 2009). Such models can also be used to explore species distributions under past, present and future environmental change (e.g. as Jarvie et al. 2021 did for tuatara) and to inform decision making (e.g. identifying potential sites for interventions such as translocations as Lentini et al. (2018) did for kākāpō).

To understand the reasons for the ongoing decline of pāteke on Aotea and assess their former distribution, we used a combination of SDMs (informed by fossil records) and PVAs (informed by seven years of detailed monitoring data). In particular, we sought to, (1) use a PVA grounded in extensive empirical data from Aotea to update the model implemented by Ferreira and Taylor (2003) and forecast population dynamics under current conditions, (2) explore scenarios focusing on the effects of predator reduction and habitat improvement, to identify potential management interventions that would increase the long-term resilience of pāteke populations on Aotea, and (3) quantify the pre-human distribution of pāteke across Aotearoa based on Holocene fossil records.

Methods

Study species

Pāteke are a small (650 g) teal (Anatidae) endemic to Aotearoa. Fossil deposits suggest that before human arrival in Aotearoa c. 750 years ago (Wilmshurst et al. 2008), the species was widespread across the country, including Chatham and Stewart Islands (Worthy 2002). Since human arrival, the population has steadily declined, and the last remaining significant wild populations are in Northland and on Aotea. Pāteke disappeared from the Chatham Islands in the 1920s and Rakiura/Stewart Island in the 1970s; by 2007, the entire population count for the species was believed to be as low as just 1000 birds (Watts et al. 2016).

In Northland and on Aotea, populations of pāteke have been in decline since at least the 1980s (Ferreira & Taylor 2003). Parrish and Williams (2001, p. 135) describe range contraction across local populations in Northland over the period 1988–1999 (mean annual decline of 11%) and consider it to be "the last phase in the extirpation of this species in Northland and on the North Island". At a local level, they describe a process of slow decline followed by an abrupt crash to extinction. In some cases, population decline or collapse was rapid, and there has been no documented re-establishment of populations once lost, other than a small population on Rakino Island, in the Hauraki Gulf. Parrish and Williams (2001) speculated that droughts may be associated with population declines and wetter (e.g. La Niña) years with population increases, suggesting potential abiotic controls on breeding success. A recent decline has also occurred on Aotea, which is alarming given it has been seen as a pāteke stronghold. Around the year 2000, the decline in pāteke seemed to slow, possibly due to intensive predator control (primarily cat trapping; Watts et al. 2016); however, the longer-term decline has continued. In 2021, the population of pāteke on the island was estimated to be at its nadir at 447 individuals, representing a nearly threefold decline from 1200 in 1986; since 2021 there has been an increase in the population, and as of the 2023 survey the population is estimated to be 667 individuals.

Population viability analysis of pāteke on Aotea

Study population

As one of the final remaining strongholds for pāteke, there has been long-term monitoring of the local pāteke populations on Aotea. Annual population surveys have occurred since 1985, and from 2002 to 2008 nest surveys and tagging of individuals occurred for a subset of the population (Giblin 2021). Most of the monitoring has been centered on the largest population at Okiwi Station, with further monitoring of smaller populations across the island (Fig. 1b–c). We estimated clutch size and egg-to-duckling survival from nest survey data, duckling-to-fledgling survival rates were estimated from flock surveys, and fledgling-to-adult and adult year-on-year survival were estimated from tracking banded individuals through time (Table 1).

Table 1. Pāteke vital rates and demographic data used in the population viability analyses. Vital rates were estimated from monitoring data at Okiwi Station on Aotea, Aotearoa, 2002 – 2008.

Parameter	Symbol	Mean	SD	N
Number of eggs per clutch	N_{egg}	4.86	1.50	50
Probability of egg hatching	s_{egg}	0.43	0.38	31
Probability duckling survives to fledgling	s_{duck}	0.48	0.47	26
Probability fledgling survives to adult	s_{fledge}	0.20	0.15	78
Probability adult survival	s_{ad}	0.86	0.06	157
Proportion females in the population	P_f	0.5		
Proportion adults breeding	P_b	0.75		
Extrinsic conditions	E_c	1		
Environmental variability	E_v	0.05		

Model overview
Following Ferreira and Taylor (2003), we used a stage-structured matrix model to represent pāteke population dynamics. Our model considered both males and females and assumed a 1:1 sex ratio with 75% of adults reproducing each year (Barker & Williams 2002). We modelled three population stages, (1) ducklings, (2) fledglings, and (3) adults, with each differing in their mortality rates. Ducklings were defined as individuals within their first two months of hatching (mean age of fledging is 55 days). Fledglings were individuals two to six months old. Adults were reproductive individuals over six months old. We assumed that one complete cycle of the model was equivalent to one year in time, which was broken down as ducklings (0–2 months), fledglings (2–6 months), adults (6–12 months).

Fecundity, mortality rates and stage transitions
Each year some fraction (including sex ratio and proportion of individuals breeding) of the adult population produce ducklings with the number being the product of fecundity (clutch size) and survival rate of eggs to ducklings. This structure follows the pre-breeding census representation described in Kendall et al. (2019). Environmental conditions (E_{con}) were assumed to affect all life stages and were a function of two parameters – extrinsic conditions (E_c) and environmental variability (E_v) – where environmental conditions were drawn from a Gaussian distribution $N[\mu = E_c, \sigma = E_v]$. Clutch size ($N_{egg}$) was drawn from a Poisson distribution ($\lambda = N[\mu = N_{egg\_mean}, \sigma = N_{egg\_sd}]$), number of ducklings ($N_{duck}$) was drawn from a binomial distribution and was a function of N_{egg} and egg survival (s_{egg}):

$$B\left(n = N_{egg}, p = N[\mu = s_{egg_{mean}}, \sigma = s_{egg\_sd}]\right) \cdot E_{con} \qquad (1)$$

We did not differentiate causes of mortality in the model as this information was not available; rather all causes are represented in a single stage-specific mortality rate (Table 1). The number of fledglings (N_{fledge}) produced was drawn from a binomial distribution and was a function of N_{duck} and duckling survival (s_{duck}):

$$B\left(n = N_{duck}, p = N[\mu = s_{duck\_mean}, \sigma = s_{duck\_sd}]\right) \cdot E_{con} \quad (2)$$

The number of adults (N_{ad}) produced was a function of new adults transitioning from fledglings to adults and the number of existing adults that survived the year. New adults were drawn from a binomial distribution and were a function of N_{fledge} and fledgling survival (s_{fledge}):

$$B\left(n = N_{fledge}, p = N[\mu = s_{fledge\_mean}, \sigma = s_{fledge\_sd}]\right) \cdot E_{con} \quad (3)$$

Adult year-on-year survival was drawn from a binomial distribution and was a function of the number of existing adults (N_{ad}) and adult survival (s_{ad}):

$$B\left(n = N_{ad}, p = N[\mu = s_{ad\_mean}, \sigma = s_{ad\_sd}]\right) \cdot E_{con} \qquad (4)$$

In the absence of any data or evidence for their presence, we did not consider Allee or density effects.

Model execution
We initiated the model with $n = 667$ adults (2023 population size), ran the model for 100 years, and ran 10 000 replicate simulations. We used the model to determine probability of extinction in 100 years, median time to extinction, and the intrinsic rate of increase (r). We also evaluated the risk of quasi-extinction – that is the risk of decline below some population abundance threshold (here, $n < 50$) at which the risk of total extinction becomes much higher (Morris & Doak 2002). We identified the demographic parameters most likely to influence extinction risk via a global sensitivity analysis (SA) and we evaluated a series of management interventions designed to increase pāteke abundance and hence reduce extinction risk.

Sensitivity analysis
To evaluate the model's response to variation in parameter values, we conducted a global SA in which we measured model output (time to extinction) while simultaneously varying all input parameters (Drechsler 1998). Global SA is robust in the presence of nonlinear responses and interactions among parameters (Prowse et al., 2016). The global SA was conducted using Latin hypercube sampling (Stein 1987) and analysed using boosted regression trees (BRTs; Elith et al. 2008). Latin hypercube sampling subdivides the parameter space evenly into k partitions and then samples randomly within each to ensure even coverage of the parameter space (Prowse et al. 2016). We sampled 3×10^4 combinations of 13 parameters (Appendix S1 in Supplementary Material), for each parameter combination we ran a single simulation for 100 generations (following Nield et al. 2020). We then used a gradient boosting algorithm (XGBoost) to determine which model parameters were most important for predicting time to extinction using the caret v 6.0-90 package (Kuhn 2021) in R v 4.1.1 (R Core Team 2021). Each model's hyper-parameters were tuned using five-fold cross-validation and a grid-based sampling of plausible hyper-parameter values. The best-fitting set of hyper-parameters was chosen based on the lowest root mean square error (RMSE). Following this, partial dependence curves were produced to show the effect of parameters on the response variable time to extinction (Elith et al. 2008).

Management-focused analysis of model parameters
We examined the effect of potential management interventions on the mean intrinsic growth rate ($\bar{r}$) for pāteke on Aotea. We were interested in interventions that could affect demographic parameters in the model, such as stage-specific mortality rates and the proportion of birds nesting each year. Predation of pāteke by rats, cats, kāhu (swamp harrier), and pūkeko have been observed, and each of these threats has been (inconsistently) controlled to some level in the past (Giblin 2021). Additionally, starvation, roadkill, and lack of suitable habitat have been associated with pāteke mortality on Aotea (Watts et al. 2016; Giblin 2021). However, there are no data linking each threat to specific changes in demographic rates. Therefore, rather than trying to estimate the effects of each of these threats individually, we focused on the effect on $\bar{r}$ of increasing demographic parameters and discuss which threats are most likely to be associated with each demographic parameter. We assumed that management interventions would reduce mortality for either egg, duckling, fledgling or adult pāteke mortality, or increase the proportion of pāteke nesting each year. For each management intervention we tested a low, medium, and high-effort scenario, where the low, medium, and high-effort scenarios resulted in a 5, 10 and 15% increase in the given demographic rate, respectively. We ran the model for 100 years (i.e. 100 generations) with 1000 replicate model runs and all other model parameters set to default values (Table 1).

Prehistoric distribution of pāteke inferred from fossils

We used a Maximum Entropy (MaxEnt; Phillips et al. 2017) SDM to determine the potential pre-human (c. 3000 yr BP) distribution of pāteke across Aotearoa. The MaxEnt algorithm estimates the probability of occurrence for a given species at a given site by comparing environmental conditions at known occupied sites to the available environmental conditions in the study region and is designed for presence only data (Merow et al. 2013). We used known pre-human fossil locations to describe pre-human pāteke presence (Appendix S2; Worthy 2002). Although pāteke are described as widespread into the late 19th century (Buller 1882; Hayes & Williams 1982) this information is not spatial and so could not be included in the model. Likewise, we did not include current remnant populations as it is unclear how they relate to pre-historic distributions and have also been subjected to management interventions – our focus is on the potential pre-historic distribution of the species. An initial dataset of 76 fossil records was spatially thinned so that fossils were at least one kilometre apart; this resulted in a final dataset of 68 fossil records. Many of the deposits were not well-dated, so we only used those classified as Holocene age. While climate has changed during the Holocene, in the absence of dated fossils or high-resolution climate data (e.g. the PaleoView data is at $2.5 \times 2.5°$ Fordham et al. 2017) we assume that the current climate is broadly representative of the environments these fossilised individuals experienced. Over the last 3000 years, Aotearoa's climate has not changed sufficiently to be detected against climate reconstructed from fossil pollen records (Wilmshurst et al. 2007). We randomly sampled 10 000 background points from across all of Aotearoa, weighted by a bias layer, to account for taphonomic differences (i.e., preservation biases) across the landscape. The taphonomic bias layer was created by using all known locations of Holocene age fossils across Aotearoa (9064 fossils; Worthy 2002; Worthy & Scofield unpubl. data), thinning these observations to a 1 km range, and modelling their distribution using a MaxEnt algorithm following the methods outlined above for pāteke fossil modelling; this is similar to one of the scenarios evaluated by Lentini et al. (2018). Probability of occurrence was predicted using fivefold cross-validation, with all hyper-parameters set to default values. The SDM's predictive accuracy was evaluated using the Area Under the receiver operator Curve (AUC) for each replicate (Fielding & Bell 1997). The AUC provides a measure of a model's discriminatory ability and is on a scale of 0–1, with a value of 0.5 indicating discrimination no better than chance alone. We assessed the contribution of each predictor based on how much its removal from the model diluted the model's performance. Predictions of habitat suitability were expressed on a complementary log-log scale.

Environmental data

We selected nine environmental covariates as predictors of probable pāteke distribution (Appendix S3). Elevation, soil induration (hardness), precipitation during the driest month, minimum winter (July) temperature, topographic wetness index, annual water deficit, and distance to coast were obtained from the New Zealand Environmental Data Stack (NZEnvDS version 1.1; McCarthy et al. 2021). Distance to waterbody was calculated as the minimum distance of a presence observation (i.e. a pāteke fossil) to a river (McCarthy et al. 2021) or lake (https://data.linz.govt.nz/layer/50293-nz-lake-polygons-topo-150k, sourced from the Land Information New Zealand Data

Service and licensed for reuse under the CC BY 4.0 licence.) in QGIS v 3.18.3 (QGIS Development Team 2021). This parameter is calculated based on; the current waterbody position we acknowledge that this may have changed over time (e.g. through the loss of wetlands); however, given that pāteke are waterfowl, the availability of water is likely a key determinant of their distribution. Finally, a layer of Aotearoa's prehistoric (c. 3000 years BP) vegetation cover (https://lris.scinfo.org.nz/layer/48289-potential-vegetation-of-new-zealand from the Land Resource Information Systems Portal created by Landcare Research New Zealand Limited), with 24 vegetation classes, was simplified to six vegetation classes (Appendix S4) following the vegetation classifications of Wiser and de Caceres (2013). We used prehistoric vegetation cover as there has been widespread forest loss since human arrival in Aotearoa c. 750 years ago (Ewers et al. 2006; Perry et al. 2012). We simplified the vegetation typology as we had relatively few occurrence points relative to the number of vegetation classes, and we were interested in broad patterns rather than association with very specific vegetation assemblages. Multicollinearity between predictors was investigated using Pearson correlation coefficients (PCC). When variables were strongly correlated ($PCC > |0.7|$) one of the covariates was removed to maintain model interpretability (Dormann et al. 2007). The final set of predictors consisted of eight layers; elevation was strongly correlated with minimum winter temperature ($PCC = 0.76$), so we removed it (Appendix S5). We removed elevation rather than minimum winter temperature as elevation *per se* is unlikely to affect pāteke directly, rather it is a catch-all variable that is correlated with many climatic predictors. Before analysis, all environmental layers were standardised to the New Zealand Transverse Mercator 2000 projection at a 100 m × 100 m resolution.

Software

All analyses were conducted in R 4.1.1 (R Core Team 2021); we used the tidyverse meta package v 1.3.1 (Wickham et al. 2019) for data wrangling and visualization, while geospatial data were handled with the terra package v 1.5.17 (Hijmans 2024). Predictor correlations were checked using the ENMTools package v 1.0.5 (Warren & Dinnage 2021; Warren et al. 2021), MaxEnt models were constructed using the dismo v 1.3.3 package (Hijmans et al. 2017), pdp v 0.7.0 (Greenwell 2017) was used to fit partial dependence plots, and maps of the probability of pāteke occurrence were produced using rasterVis v 0.50.2 (Perpinan-Lamigueiro & Hijmans 2021).

Results

Population viability analysis

Model dynamics

Using estimates of demographic parameters from the 2002–2008 Aotea survey data, the pāteke population went extinct ($n = 0$) within 100 years in 46% of model runs ($n = 1000$) and went quasi-extinct ($n < 50$) in 99% of runs (Fig. 2). Median time to extinction and quasi-extinction were 103 years (10th and 90th percentiles: 76–140 years) and 45 years (10th and 90th percentiles: 31–65), respectively. The deterministic model (all standard deviations set to 0) had a finite rate of increase (λ) of 0.95 (halving time of 12.8 years) and the elasticity of adult survival was 0.77, indicating this stage contributes the most to population growth. Our stochastic model consistently had $\bar{r}$ values below 0, ranging from −0.17 to −0.03 (Fig. 3).
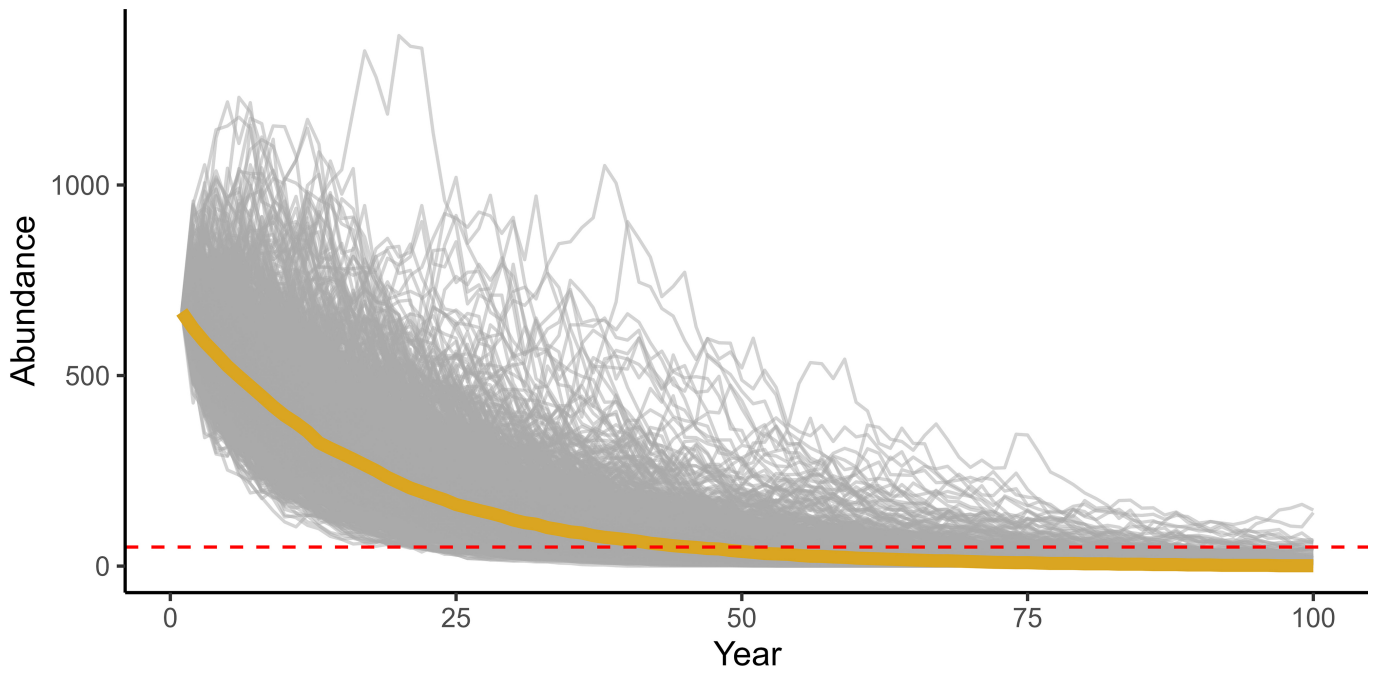
Figure 2. Pāteke abundance from the stage-structured population model, starting with an adult population size of 667 individuals (estimated 2023 population size). Grey lines are 1000 replicate model runs, the solid yellow line is median abundance, and the dashed red line is the quasi-extinction threshold of $n = 50$ individuals.
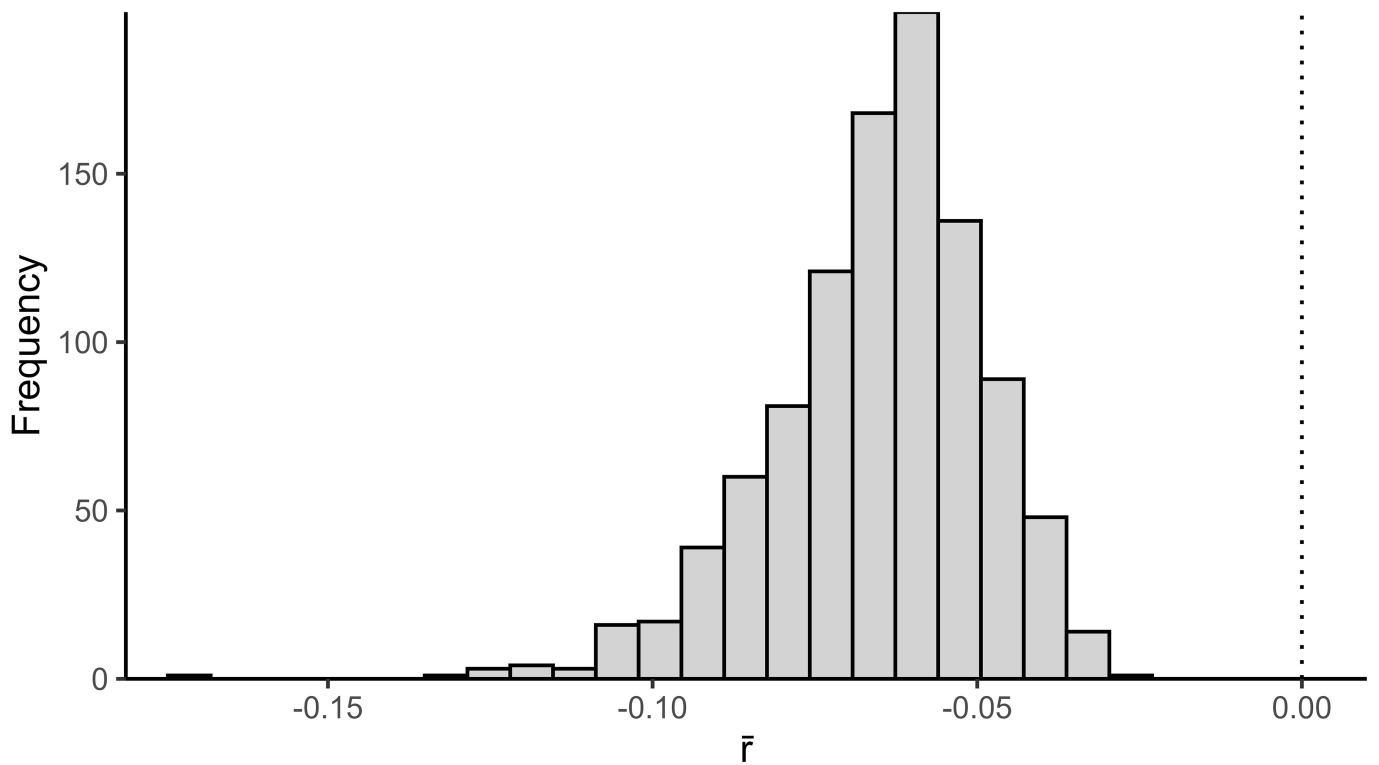

Figure 3. Distribution of mean intrinsic rate of increase ($\bar{r}$) values for the pāteke population on Aotea, estimated from 1000 replicate model runs. The dashed vertical line (0.0) indicates stable growth.

Sensitivity analysis

Global sensitivity analysis showed that the PVA response variable time to extinction was most sensitive to changes in adult survival (mean). Changes to other parameters had negligible effect on time to extinction (Fig. 4). Additionally, we found that temporally varying extrinsic conditions and environmental variability both decreased time to extinction (Appendix S6).

Management-focused analysis of model parameters

Only the management intervention that focused on the demographic parameter mean adult year-on-year (YoY) survival guaranteed positive growth rates across 100 model replicates, across the medium and high treatment scenarios (Fig. 5). The most effective management scenarios were those that focused on mean adult YoY survival, followed by those that increased all demographic parameters equally or increased the proportion of breeding individuals (habitat).
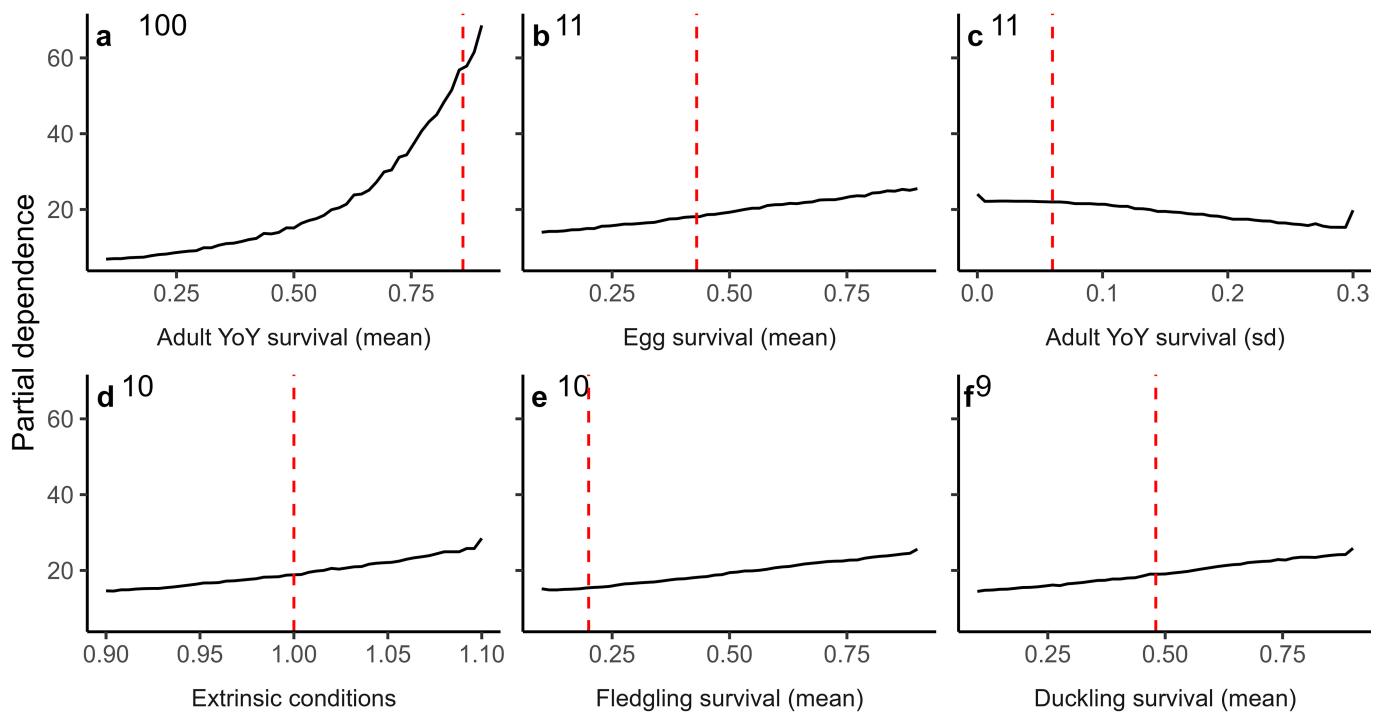
Figure 4. Partial dependence of "time to extinction" on each of the six most important model parameters. Inset values are variable importance scores. Vertical red dashed-lines are the default values used in the PVA models. Adult YoY survival is adult year-on-year survival.
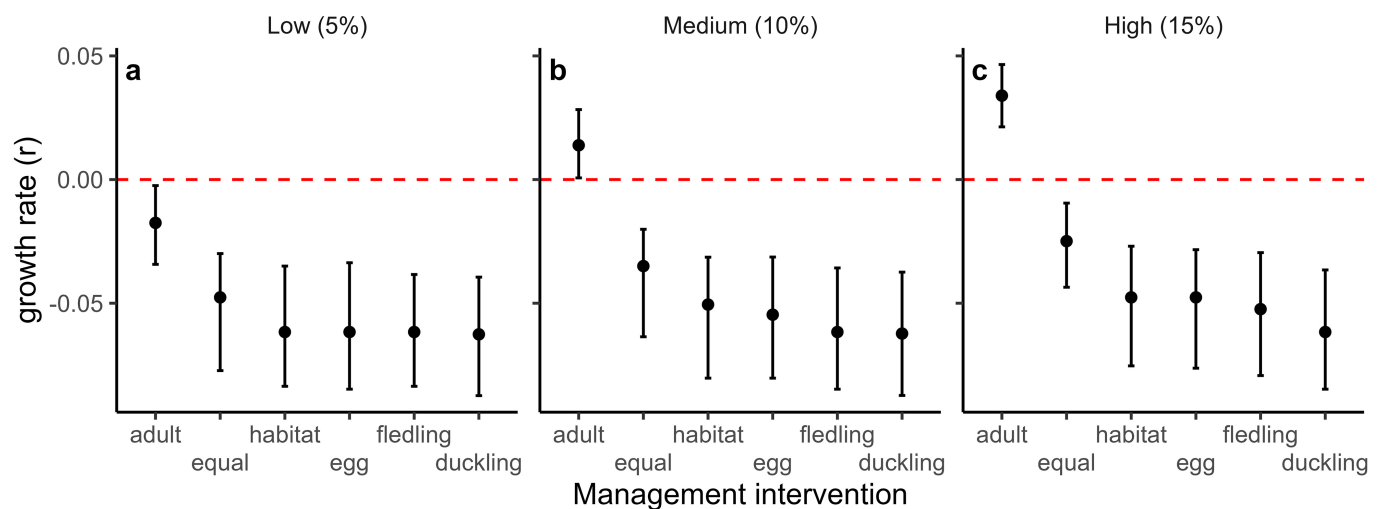
Figure 5. The effect of management interventions aimed at individual demographic parameters on pāteke population growth rate ($\bar{r}$). Interventions "egg", "duckling", "fledgling", and "adult" increased mean survival of the given parameter in Table 1 by 5, 10, or 15% ("Low", "Medium", and "High" respectively), "habitat" increased the proportion of birds nesting and "equal" increased all parameters by a 1, 2, or 3% simultaneously ("Low", "Medium" and "High" respectively). Points are medians and error bars 10th and 90th percentiles. Dashed horizontal lines indicate a growth rate of zero (a stable population). Columns "Low", "Medium" and "High" represent management scenarios where survival and the proportion of individuals breeding are increased by 5%, 10% or 15%, respectively.

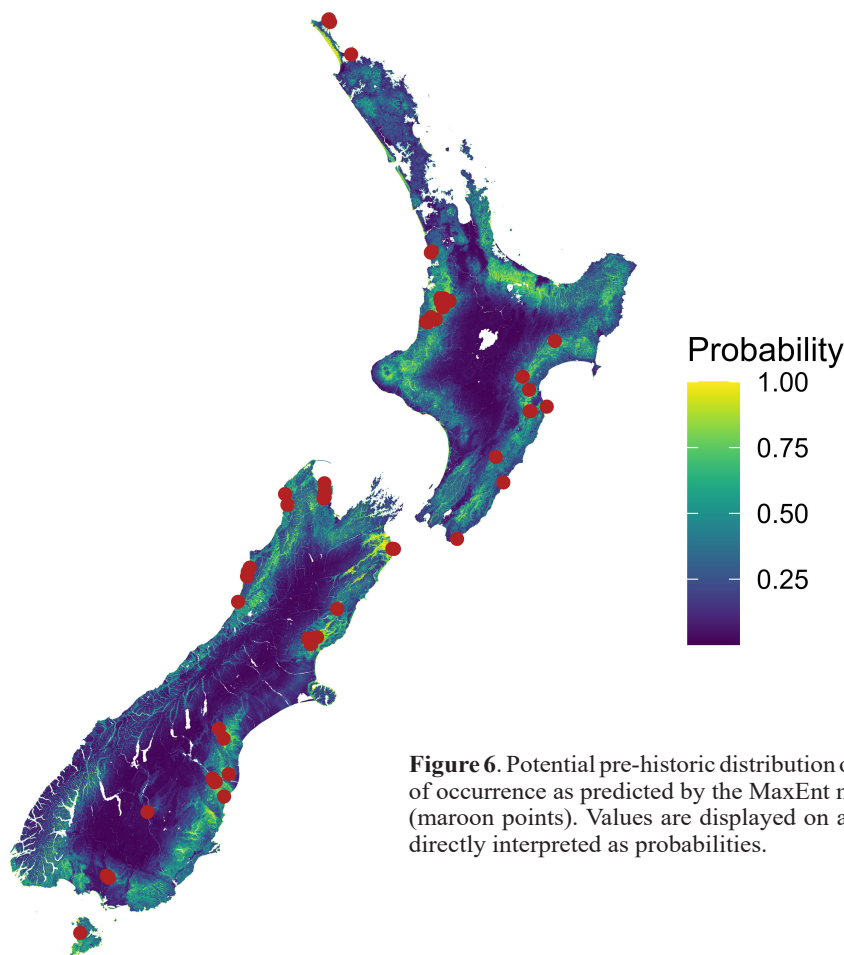**Inferred potential pre-historic distribution of pāteke**

The pāteke fossil SDM (AUC: mean 0.80 ± 0.02 SD indicates moderate model fit) suggested that much of coastal Aotearoa was probably suitable for pāteke before human arrival (Fig. 6). Distance to the coast was the most important predictor (contribution $45.3\% \pm 5.5$ SD) of pre-human habitat suitability (Appendix S7). While Holocene pāteke fossils have been found relatively far inland (e.g. Earnscleugh cave, Central Otago; Worthy 1998), we had few fossils from inland sites, which may have contributed to the model underpredicting the potential for pāteke to occupy non-coastal locations. However, the predicted distribution does match the current coastal and low-elevation distribution of the species. The next most important group of predictors were the topographic wetness index ($16.4\% \pm 4.0$ SD), annual water deficit ($15.5\% \pm 2.7$ SD) and vegetation type ($12.8\% \pm 3.9$), with habitat suitability positively associated with intermediate topographic wetness, low annual water deficit, and dune and wetland vegetation cover classes (Fig. 7).

Discussion

The conservation of threatened species requires identifying threats and then understanding the demographic pressures that these individually and collectively impose on the focal species (Boyce 1992). Lee and Jetz (2010) showed that for most species,

a complex set of interactions (among traits, environment, and human pressures) drive species to extinction. A global analysis of threatened Anatidae suggested that the main pressures they face are habitat change, over-exploitation (hunting), and introduced species (predation and hybridisation; Green 1996). Pāteke are at risk from predation, the effects of climate change, and habitat loss, and our population projections demonstrate that under current conditions, there is a substantial risk of them suffering extinction on Aotea (46% chance of extinction within 100 years). Our estimated population halving time of 12.8 years is longer than the previous estimate of 4.1 years (Ferreira & Taylor 2003), suggesting management interventions in the subsequent two decades have reduced population declines, but not to the point where the population is safe (halving time is dependent on the assumption of underlying exponential growth/decline, rather than potential stabilisation due to density-dependent feedbacks and must be interpreted with this caveat in mind).

Our analyses consistently demonstrate that adult survival is the key to stabilising this decline (Fig. 3–5); hence, management strategies that target this life-stage will be most effective. Predation is the key threat to pāteke populations on Aotea and on mainland Aotearoa (O'Donnell et al. 2015). There is little quantitative data available on the relative threat that different predator species pose to pāteke, or the extent to which they determine mortality rates across the different life-stages. A more nuanced understanding of the effect of

Figure 6. Potential pre-historic distribution of pāteke. Warmer colors indicate a higher probability of occurrence as predicted by the MaxEnt model with the 68 fossil occurrence records overlaid (maroon points). Values are displayed on a complementary log-log scale and, as such, can be directly interpreted as probabilities.
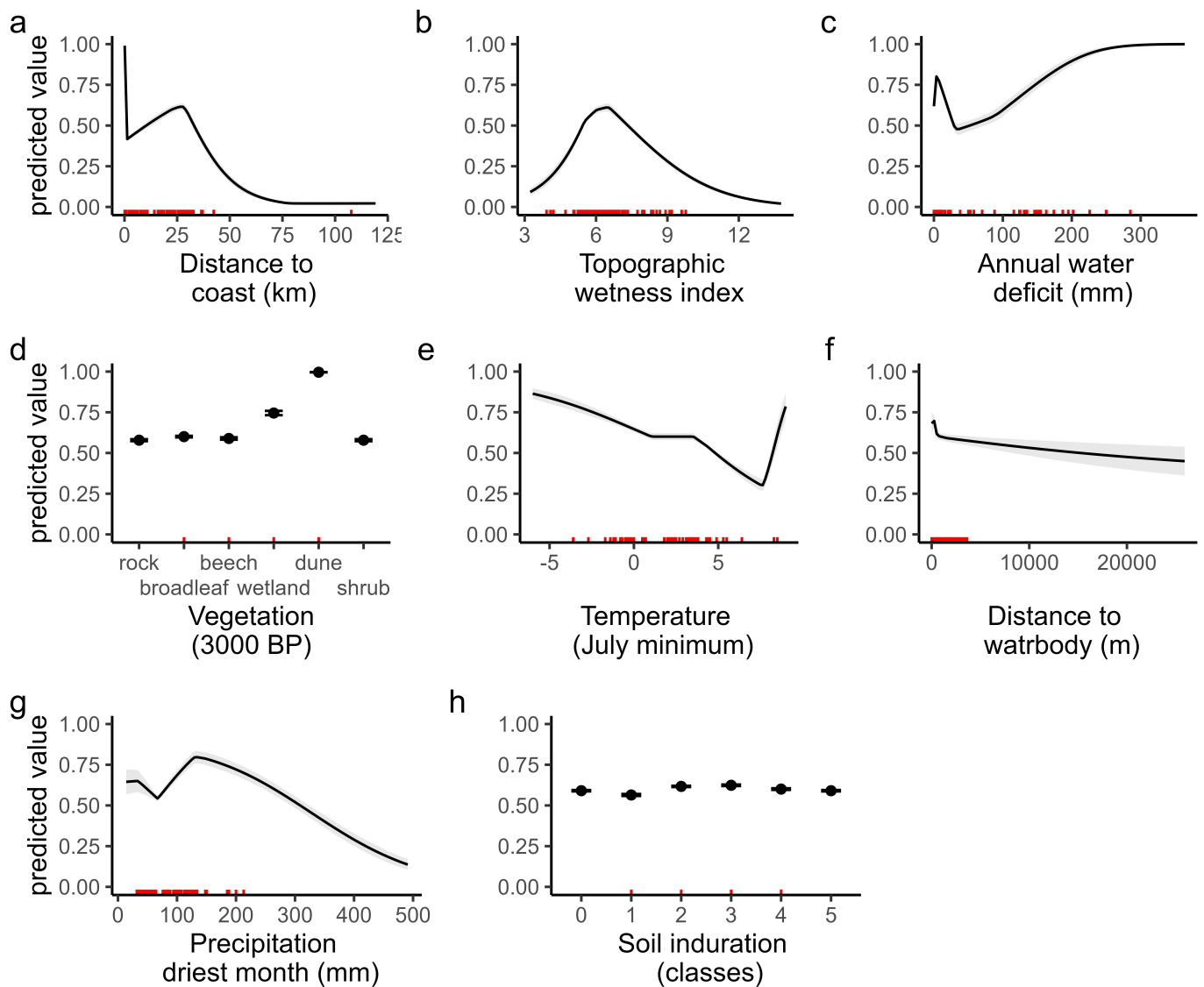
Figure 7. Marginal effects plots for the seven environmental predictors used in the MaxEnxt model of the potential distribution of pāteke. For the vegetation predictor, rock = bare rock, broadleaf = broadleaf/podocarp forest, beech = beech forest, wetland = wetlands, dune = dunes and shrub = mixed species vegetation (Appendix S4). Soil induration classes represent 1 = weakly indurated to 5 = very strongly indurated, and 0 = areas where there was no soil attribute recorded. Ribbons and error bars represent ± one standard error.

predators may be challenging to develop because it is difficult to confidently and consistently attribute mortality to specific causes, especially when dead individuals are not recovered. In addition to predation, Parrish and Williams (2001) speculate that grazing livestock can displace pāteke from breeding sites along wetter areas during droughts; such effects could be addressed by appropriate stock management. The longer-term implications of climate change (potentially reduced water flows and increased drought in northern Aotearoa) are more difficult to predict, but are unlikely to favour pāteke, especially if they are associated with increased environmental variability.

Extinction risk in small populations increases with environmental variability (Boyce et al. 2006), which makes representing such stochasticity a critical component of any PVA (Boyce 1992). Our PVA represents environmental conditions using a temporally uncorrelated Gaussian distribution, with the mean representing the long-term suitability of the conditions (with 1.0 representing current conditions) and the standard

deviation representing annual variation around that mean. Under pressures such as climate change, we might therefore expect declining mean suitability if rainfall decreases, and increased variability as droughts become more common. Our model analyses demonstrate that long-term shifts in mean (suitability) conditions strongly influence population risk (Appendix S6). Increased environment variability also increases the risk of pāteke extinction but slightly less than changes in mean conditions. Climate projections for northern Aotearoa to the end of the 21st century indicate (1) warming temperatures with heightened temperature extremes and (2) decreased precipitation with increased severity and frequency of droughts (Ministry for the Environment 2018). These projections are concerning as they suggest that conditions on Aotea will become less favourable for pāteke, and it is difficult for managers to confront such changes directly. If environmental variability becomes a critical determinant of population change, PVA models suggest there is an important

role for buffers (e.g. safer sites) that protect populations from short-term unfavourable conditions (Grimm et al. 2005). We model environmental stochasticity simplistically as an uncorrelated white noise; in reality, temporal environmental variables are autocorrelated, and this correlation may be strengthening under climate change (Di Cecco & Gouhier 2018).

Our PVA is aggregated (cohort-based) in structure and does not represent individual birds or interactions between individuals. Important individual-level interactions (such as social learning) will be influenced by, and may even influence, population dynamics (Gil et al. 2018). For example, pāteke (especially sub-adults) gather in summer at the upper tide level in creeks, ponds and drains (The Department of Conservation 2011), and these meetings allow the reassortment of mates and probably also meeting between juveniles as potential mates (Sheridan & Waldman 2020; John Ogden pers. comm.). As pāteke numbers decline, such gatherings will be poorly attended, and the collective memory of these meeting sites will be eroded, potentially inducing Allee-type effects. Understanding such dynamics will also be important in developing effective management strategies for the species. A further concern is the potential hybridisation with mallard ducks (Cole & Wood 2017); even if the fitness of hybrids is higher, such inter-breeding can result in the genetic swamping of the rarer species. However, these dynamics and those related to Allee effects and flocking behaviour are difficult to explore with an aggregated population model such as that we adopt here. The next step to explore how these pressures influence population dynamics would be to develop an individual-based model (DeAngelis & Mooij 2005) that can track the fate of individual birds.

Expanding the number and size of pāteke populations is a conservation priority. While their current distribution is too restricted to make inferences via SDMs about present-day habitat suitability on a national scale, we have a good understanding of their pre-historic distribution. Pāteke were probably one of the most widespread and possibly abundant waterfowl species in Aotearoa, based on (1) their known distribution in the late 19th century (Buller 1882; Hayes & Williams 1982), (2) fossil records (Worthy 2002), and (3) our SDM of prehistoric distribution based on fossil records (Fig. 6). The broad former distribution of pāteke suggests that where habitat degradation has not been too severe and predator numbers are suppressed, reintroductions are possible. Unfortunately, both wetlands and dunes are two of the most threatened and degraded ecosystem types in Aotearoa (Holdaway et al. 2012). It is hardly a coincidence that much of the pāteke's preferred habitat has been destroyed, with what remains home to a suite of invasive mammalian predators, and the species has collapsed to the brink of extinction. Across Aotearoa, wetlands have decreased in area by roughly 90% compared to pre-European levels, from an estimated 2 500 000 ha to less than 250 000 ha (McGlone 2009; Dymond et al. 2021). Wetlands provide essential pāteke habitat for breeding, foraging, and predator avoidance. Likewise, dunes have dramatically reduced in area across Aotearoa; since the early 1900s, the area of dune habitat has been reduced from 129 000 ha to about 39 000 ha in 2000 (Hilton 2006). Increasing the rate and scale of wetland and dune protection and restoration across Aotearoa would provide further opportunities for pāteke reintroductions, in addition to the intrinsic benefits of restoring these threatened ecosystems.

Our analysis of pāteke population dynamics has incorporated a national-level assessment of potential habitat based on sub-fossil deposits and a local population viability analysis based on data from Aotea. While Aotearoa has lost a large proportion of its pre-human vegetation cover (Ewers et al. 2006), and widespread transformation and loss of wetlands (McGlone 2009), our SDM suggests that there is still a significant amount of potential habitat available for pāteke (coastal environments, particularly dunes and wetlands), which is currently unsuitable due to the presence of invasive species. There is growing interest in integrating different forms of spatial modelling at different spatial scales to inform conservation management (Ferraz et al. 2021). While we do not couple the two models, they do provide complementary information. Species distribution models can be used to show potential habitat ranges (and, in this case, confirm the potential broad distribution of the species) and could be used to provide estimates of the population carrying capacity in spatially explicit dynamic PVAs (Franklin 2010). SDMs, alongside other spatial prioritization methods, could be used to identify suitable habitat for future translocations (Barlow et al. 2021) and to explore geographic trends in mortality and reproduction (e.g. how do such trends correlate with inferred habitat quality?). Such an approach could also be applied in the future to assess how predator numbers and habitat quality might change under climate change and the potential implications for habitat distribution. Where available, data describing anthropogenic pressures (e.g. invasive species presence or control, land-use change) could be integrated with historically informed SDMs to predict 'Anthropocene refugia' (sensu Monsarrat et al. 2019). If finer-scale SDMs could be developed for the current pāteke range, more integrated models could be developed. In short, integrated and multi-scale spatial modelling of population dynamics has the potential to provide powerful insights into the risks faced by threatened species.

Acknowledgements

Additional information and declarations

for us to share Pāteke fossil location information, however we have rounded the location coordinate to two decimal places. Contact the data owners to request full access. Summary data used in the modelling and associated code is openly available at https://zenodo.org/doi/10.5281/zenodo.7378972.

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Supplementary Material

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

Appendix S1. Latin hypercube sampling protocol of pāteke demographic parameters for the global sensitivity analysis.

Appendix S2. Global positioning system coordinates for pāteke fossil locations, rounded to two decimal places.

Appendix S3. Environmental variables used in MaxEnt species distribution models of pāteke across New Zealand.

Appendix S4. Classes in the prehistoric New Zealand vegetation land cover layer and the simplified classification.

Appendix S5. Pairwise correlations between environmental predictors selected for use in the MaxEnt species distribution model of pāteke occurrence.

Appendix S6. Analysis of varying environmental conditions through time.

Appendix S7. Percent contributions of environmental predictors to the SDM.

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