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Using fossil records to inform reintroduction of the kakapo as a refugee species

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ABSTRACT

Many threatened species persist only as relict populations occupying a fraction of their former distribution, in habitats which may not be optimal for supporting viable populations. Following population growth of one such species, the kakapo (*Strigops habroptilus*), conservation managers are faced with the challenge of identifying suitable locations for reintroduction. Areas which support habitat conditions typical of those occupied by kakapo in the past have the greatest potential to support future populations. We collated occurrences of kakapo from recent fossil records, then used MaxEnt to model the past distribution of kakapo across New Zealand, and contemporary areas suitable for reintroductions based on extant habitat and present-day climate. We validated our models against three independent data sets of the most recent relict populations. Our models suggest that kakapo once occurred in mountain beech and Hall's totara or broadleaf forests with moderate to high precipitation and milder winters. Areas predicted to be environmentally suitable for kakapo in contemporary New Zealand include the west coast of the South Island, the west and north-east of the North Island and the southern side of Lake Taupo. Assuming that known threats of introduced predators can be managed, our study suggests that suitable kakapo habitat persists in New Zealand, and here we offer insight into locations for future population establishment. Given the finite carrying capacity of offshore islands, this is an important first step which will enable kakapo managers to prioritise focal areas and also highlights the benefits and potential pitfalls of using these modelling approaches for refugee species.

1. Introduction

Species declines and extinctions resulting from anthropogenic changes have accelerated in recent decades (Dirzo et al., 2014). In response, the field of conservation biology has expanded dramatically, and intensive and expensive management interventions such as translocations (Schwartz and Martin, 2013) and captive breeding (Balmford et al., 1996) are being increasingly recommended and implemented. These approaches aim to avoid extinction and promote species recovery (e.g. Griffiths and Pavajeau, 2008; Miskelly and Powlesland, 2013; Ostrowski et al., 1998), and are often focussed on the protection and restoration of habitat that can sustain viable populations of threatened species (e.g. Armstrong and Ewen, 2002; Webb and Shine, 2000). However, many species persist in only a fraction of their former distribution (e.g. Fanshawe et al., 1991; McLennan et al., 1996).

For conservation managers, establishing new insurance populations when the former extent of a species' distribution is unknown is fraught with uncertainty (Caughley, 1994; Norris, 2004). This is because in the case of 'refugee' species, the areas where they persist are suboptimal, marginal habitats (Cromsigt et al., 2012; Kerley et al., 2012a) with their distributions being a legacy of spatial heterogeneity in threatening processes (Kerley et al., 2012b). For instance, relict populations of the Lord Howe Island Woodhen (*Gallirallus sylvestris*) were isolated on mountaintops inaccessible to predators. When released from predation pressure by an eradication program, the species reoccupied lower altitudes and their populations recovered to densities not achieved even in the predator-free mountaintop habitat (Brook et al., 1997; Caughley, 1994). Consideration of the legacy of these threatening processes is important for conservation managers because scarce resources may be wasted attempting to re-establish populations in unsuitable habitat. Conversely, opportunities to protect and enhance areas of suitable habitat may be missed if they remain unidentified.

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Data on the former range of species that declined prior to the establishment of contemporary monitoring programs are rarely available. However fossil records are recognised as a potentially valuable source of information that can provide unique insights for conservation. For example, the endangered black-footed ferret (*Mustela nigripes*) has conventionally been thought to form part of an obligate predator-prey relationship with prairie dogs (*Cynomys*), and consideration of potential reintroduction sites for the species was limited to areas where *Cynomys* occur. However fossil evidence indicates that black-footed ferrets historically persisted in areas without these prey, which may be equally suitable (Owen et al., 2000). Likewise, Mallorca's midwife toad (*Alytes muletensis*) was known only from the island's fossil record until extant populations were rediscovered in the mid-1980s. Subsequent captive breeding and reintroduction programs guided by these records have resulted in the successful establishment of populations in its former range (Bloxam and Tonge, 1995). While cases such as these exemplify how reintroduction decisions can draw on fossil records, these data are typically difficult to collate, or are biased and of unreliable provenance.

Recent advances in species distribution modelling that use presence-only and presence-background data sets (Guisan and Thuiller, 2005) now present us with an opportunity to incorporate potentially biased past data into conservation decision-making in a systematic way. One candidate species for this is the kakapo (*Strigops habroptilus*), an iconic, endangered, flightless nocturnal parrot. Kakapo are known to have been widespread across New Zealand (Williams, 1956), but due to habitat loss and predation by introduced mammals they have declined dramatically since human settlement (Butler, 1989) with the entire population currently consisting of less than 200 individuals. Few, if any, kakapo now remain within their former range (Lloyd and Powlesland, 1994). Emergency management intervention led to the removal of all known surviving individuals from Stewart Island and the Fiordland region on the South Island to predator-free offshore islands outside of their past distribution from 1972 to 1992 (Lloyd and Powlesland, 1994). Decades of intensive management of these island populations has resulted in substantial population growth (Elliott et al., 2001), but the limited carrying capacity of offshore islands (Neill, 2008) is looming as a major challenge for the continued recovery of this species.

In the future, conservation managers aim to establish at least one "self-sustaining, unmanaged [kakapo] population as a functioning part of the ecosystem in a protected habitat" (Neill, 2008). To achieve this aim, understanding the past distribution of kakapo is a priority for identifying, preparing and managing potential locations for their release. Areas which are climatically suitable and support vegetation and geologies typical of the kakapo's past distribution are likely to have the greatest potential to support populations in to the future. However, as yet only anecdotal and qualitative accounts are available to suggest where suitable areas occur (Clout and Merton, 1998; Tipa, 1996). To support future decisions about locations for reintroductions, we synthesised data on the past distribution of kakapo using Holocene fossil records from dune, swamp and karst sites across mainland New Zealand. By using contemporary approaches to address the biases inherent in fossil data, we are able to quantify (1) the past suitability of mainland New Zealand for kakapo and (2) areas across contemporary mainland New Zealand which support climates and habitats suitable for potential kakapo reintroductions.

2. Methods

2.1. Kakapo records

The former distribution of kakapo extended across New Zealand, encompassing the North, South and Stewart Islands (Clout and Merton, 1998). Here we present and synthesise four separate datasets, made up of Holocene and recent kakapo records and midden deposits (Fig. 1). For the purpose of clarity we herein refer to the period pre-dating human occupation of New Zealand as the Holocene or 'past', and the period following occupation as 'recent', 'modern', or 'current'. The Holocene data are 216 fossil records from dune, swamp and karst sites ('fossil sites' herein) across the North and South Islands (but not Stewart Island). Locations were collated from published records (Appendix A, Table A1). The recent records consist of locations of the last remaining populations of wild kakapo in New Zealand from Fiordland in the South Island and Stewart Island between 1982 and 1997, prior to management intervention to translocate survivors (Lloyd and Powlesland, 1994). Data were sourced from detailed historical descriptions for Fiordland (Atkinson and Merton, 2006; Butler, 2006; Gray, 1977; Johnson, 1976; Powlesland et al., 1995) and mapped locations on Stewart Island (Stirnemann et al. unpublished data). The Fiordland population consisted of only male birds [n = 13]. The Stewart Island population consisted of male [n = 42] and female [n = 20] kakapo. The location of Maori (the indigenous people of New Zealand) midden deposits containing kakapo remains [n = 45] were collated from published records. Finally, the location of fossil sites [n = 603] where avian fossil deposits have been excavated, but which did not contain kakapo fossils, were also collated from published records.

2.2. Environmental predictors

Gridded estimates of four terrain variables, three paleoclimate variables, four soil variables and a pre-European vegetation layer were used (see Appendix A, Table A2 and A3) to describe each 90 × 90 m cell of New Zealand (n = 1,572,014,640). These twelve covariates were chosen to represent key habitat features or limiting factors for this species. Further, covariates were also selected if they were thought to influence fossil deposition (e.g. lithology).

2.2.1. Terrain

Elevation underpinned all of our terrain metrics. A three second (approx. 90 m) resolution Digital Elevation Model (DEM) for New Zealand was built (JA Stein, unpublished data) using the ANU DEM algorithm (Hutchinson, 2015) from digital topographic data sourced from Land Information New Zealand (LINZ) through the Land Resource Information System (LRIS) portal. These comprised 1:50,000 scale contour vector and point elevation data. From this DEM, we calculated the four terrain variables used in our analyses. Relief was the range in elevation for an area buffered around each grid cell. We used a 50 ha buffer, the approximate size of the kakapo home range (Best and Powlesland, 1985; Moorhouse and Powlesland, 1991). The northerly component of aspect was calculated as the cosine of the angle of aspect, and the easterly component of aspect as the sine of that angle. A Topographic Wetness Index (TWI) gives the relative position in the landscape, and is the ratio of the upslope area of each grid cell, derived from surface flow directions, and divided by cell width adjusted for aspect of inflow direction (specific catchment), to the local slope of the grid cell.

2.2.2. Climate

Climate is a primary determinant of the distribution of biota, with bioclimatic variables forming the basis of many spatial analyses (Booth et al., 2014). Here, we used three 'Bioclim' grids for the purposes of our analyses. For Holocene kakapo models, we used downscaled (to 30 s) predictions of annual precipitation (Bio12) and minimum temperature of the coldest month (Bio6) for the mid-Holocene, based on the Beijing Climate Centre Climate System Model (BCC-CSM1-1) and sourced from the WorldClim database (Hijmans et al., 2005). The nine GCM paleoclimate predictions were similar for these variables across New Zealand and for our point data specifically (Appendix A, Fig. A1), and the BCC-CSM1-1 layers were chosen as this model appeared to yield moderate predictions. The corresponding present-day Bio6 and Bio12 layers were used for modern kakapo potential habitat predictions and were also sourced from WorldClim, while mean annual solar radiation was