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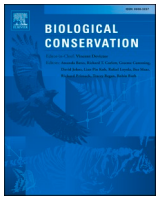

Declines in greater bilby (*Macrotis lagotis*) geographic range and realised niche are best explained by the invasive red fox (*Vulpes vulpes*)

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[2] Jigalong Rangers, Punmu Rangers, Parnngurr Rangers, and Kunawarritji Rangers.

[3] Nyul Nyul Rangers and Paruku Rangers.

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ABSTRACT

Understanding the factors driving species' range and niche contractions can help us identify how and where threats to those species are being mediated or tolerated. Here, we used the 'niche reduction hypothesis' to investigate changes in the geographic range and realised niche of the greater bilby (*Macrotis lagotis*). We compiled bilby occurrence records to estimate changes in the geographic range (extent of occurrence, EOO) and realised niche for two time periods: historical (1900–2022) and contemporary (2000−2022). We used one-class support vector machine models to measure realised niche size, comparing decline in realised niche to decline in EOO through time. Ecological niche models (ENM) were then used to quantify environmental factors influencing the historical and contemporary realised niche, and to determine the extent to which environmental conditions may mediate threats (particularly introduced predators). Bilby EOO declined by 70% through time, while realised niche size declined by 46%. Fire frequency was an important predictor in both the historical and contemporary ENMs, while red fox (*Vulpes vulpes*) density became important only in the contemporary ENM, suggesting that foxes are contributing to contemporary bilby declines. Bilbies contracted to areas with lower fox densities, lower average normalised difference vegetation index values, higher fire frequency, and higher average temperatures. Environmental conditions likely limit fox distribution (leading to contraction of bilbies to fox-free areas) and/or mediate fox impacts (leading to greater population resilience to fox predation). Future research should enhance understanding of how environmental factors facilitate predator impacts and how these vary across environmental space. Such knowledge will likely improve understanding of how to manage threats facing bilbies across their distribution.

1. Introduction

A central challenge in ecology is understanding the factors that shape the geographic ranges and niches of species. Range and niche reductions – precursors of extinction – are increasingly common across the world and are driven primarily by widespread human activity and associated environmental degradation (Ceballos et al., 2017; Johnson et al., 2017). Consequently, there is an urgency and increasing focus on quantifying species' responses to changes in the physical environment (Carscadden et al., 2020; Jimenez et al., 2021). One approach widely used for this purpose is ecological niche modelling (also known as species distribution modelling). Ecological niche models (ENM) relate the presence of one or more species to environmental data and are typically used for ecological inference or to predict areas of potentially suitable habitat (Guisan et al., 2013). The use of ENMs has increased over recent decades, leading to the development of many methods to deal with different data inputs (e.g., occurrence, presence/absence, and abundance data, Elith et al., 2011).

Ecological niche modelling is underpinned by two key concepts: (1) the 'fundamental niche', defined as the suite of environments or resources that a species can inhabit or use (typically defined by physiological limits or thresholds) and (2) the 'realised niche', defined as the portion of the fundamental niche that is occupied by the species, as constrained by biotic interactions and evolutionary mechanisms (e.g., dispersal ability) (Hutchinson, 1957). The 'niche reduction hypothesis' proposed by Scheele et al. (2017) suggests that heterogeneity in threat impacts across environmental space can lead to reductions in the realised niche breadth of declining species. Conventional research often assumes that the severity or abundance of threats are the primary drivers of species' decline (Tulloch et al., 2015). However, an increasing body of evidence shows that environmental conditions, biotic interactions, and disturbances can either mitigate or amplify the effects of threats on various aspects of species' ecology or on the ability of a species to persist in the presence of those impacts (i.e., their 'threat tolerance') (Brook et al., 2008; Doherty et al., 2015). This heterogeneity in the impacts and tolerance of threats across environmental space can drive changes in species' realised niche breadth. For example, non-random habitat loss (e.g., timber harvesting) can eliminate species from areas of their niche where the disturbance is concentrated (Simmonds et al., 2017), while exotic predators can exclude species from parts of their niche where low habitat complexity enables predators to hunt more effectively (Doherty et al., 2015). Consequently, the 'contemporary realised niche' of many threatened species may be significantly more restricted than the 'historical realised niche' (i.e., prior to the emergence of novel threats).

While it is widely accepted that both abiotic and biotic factors influence the geographic ranges and realised niches of species, the role of biotic factors in contributing to changes in range and niche size has received less attention (Wisz et al., 2013; Carscadden et al., 2020; Scheele et al., 2023). Biotic interactions affect species' spatial distributions via several mechanisms, including predation, competition, mutualism, and parasitism (Bascompte, 2009). These interactions vary through space and time and in strength for different compositions of species, and they are often linked to other processes associated with environmental change (Gilman et al., 2010; Anderson, 2017). For example, some species may be more likely to persist in the presence of a specific pollinator, while others may be negatively affected by predators, consumers, or parasites (Linder et al., 2012; Anderson, 2017).

An example of a strong biotic interaction is between invasive mammalian predators and their prey. Invasive mammalian predators are one of the leading causes of biodiversity loss globally and have been associated with the decline and extinction of numerous species worldwide (Doherty et al., 2016). In Australia, the feral cat (*Felis catus*) and the European red fox (*Vulpes vulpes*) have been implicated in almost all mammal extinctions that have occurred since European settlement (Woinarski et al., 2015). These extinctions have been most pronounced in the arid and semi-arid regions of Australia (McKenzie et al., 2007). Although the link between invasive predators and mammal extinctions is well documented, there is little understanding of how abiotic and biotic factors combine to drive the ongoing range contractions of some of these mammals.

Here, we use the niche reduction hypothesis as a framework to quantify changes in the realised niche of an Australian arid-zone marsupial threatened by invasive mammalian predators: the greater bilby (*Macrotis lagotis*), hereafter referred to as the bilby. The bilby is an iconic digging mammal of great ecological and cultural importance (DCCEEW, 2023). It is a habitat generalist, having previously occupied a vast area across most of arid and semi-arid Australia (Southgate, 1990) (Fig. 1). However, since European colonisation, the bilby has contracted from the southern and eastern parts of its range, most likely in response to the spread of cats and foxes in combination with detrimental fire and grazing regimes (DCCEEW, 2023). While it is widely accepted that cats and foxes are major contributors to bilby decline (Moseby et al., 2011; Cramer et al., 2017; DCCEEW, 2023), this has not yet been quantified on a range-wide scale. Furthermore, it is unclear whether these predators have contributed to a reduction in realised niche or if environmental conditions may be mediating their impacts on bilbies in some locations.

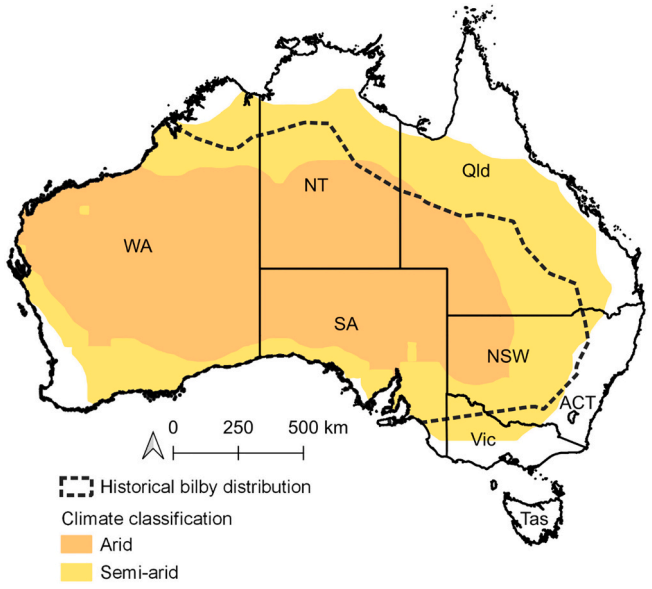

Fig. 1. Map of Australia showing the states and territories, the extent of arid and semi-arid regions, and the extent of the historical distribution of the greater bilby (*Macrotis lagotis*). Arid and semi-arid regions were identified using the Köppen-Geiger climate classification system (Beck et al., 2018). WA: Western Australia, NT: Northern Territory, Qld: Queensland, SA: South Australia, NSW: New South Wales, ACT: Australian Capital Territory, Vic: Victoria, Tas: Tasmania.

To investigate this, we quantified environmental conditions within the historical and contemporary geographic ranges of the bilby, compared the magnitude of range reductions to niche reductions (i.e., declines in niche breadth), and investigated changes in the ability of different environmental variables to influence historical and contemporary bilby niche models. Specifically, we were interested in investigating whether cats and foxes are driving reductions in bilby range and realised niche, and determining the extent to which other biophysical conditions (e.g., fire frequency, vegetation cover) may alleviate or amplify their impacts.

Table 1
Sources and descriptions of data included in greater bilby (*Macrotis lagotis*) ecological niche models.

Source	Data description
The *Action Plan for Australian Mammals 2012* (Woinarski et al., 2014)	Occurrence records compiled from multiple sources, with obvious erroneous records deleted. Includes all native Australian mammals.
Arid Zone Monitoring Project (Legge et al., 2024)	Occurrence records collated across the arid and semi-arid zones of Australia from multiple data providers (government, Indigenous organisations, non-government organisations, natural resource management agencies, and universities). Records with no dates or where species were detected inside a predator exclosure were omitted.
Historical records from Queensland and New South Wales (Silcock et al., 2023)	Occurrence records prior to 1900 and with no date were excluded, as were records categorised as having low spatial precision or low confidence.
Contemporary records from Queensland (Queensland DESI, unpublished data; Save the Bilby Fund, unpublished data)	Unpublished contemporary occurrence records from Queensland. Only fresh/active records were included.
Contemporary records from the Northern Territory (TNRM unpublished data)	Unpublished data collected during broad-scale surveys undertaken in the Northern Territory from 2020 to 2022. Two types of surveys were conducted: (1) ground-based sign searches (standardised by time and area) and (2) standardised aerial surveys with ground-truthing to confirm species ID and age of sign. Only fresh/active records were included.
Contemporary records from Western Australia (DBCA, unpublished data)	Unpublished occurrence records from Western Australia that were not included in the AZM database (i.e., those collected from 2020 to 2022). Obtained from the DBCA 'NatureMap' repository.

AZM: Arid Zone Monitoring, DBCA: Department of Biodiversity, Conservation and Attractions (Western Australia), DESI: Department of Environment, Science and Innovation (Queensland), TNRM: Territory Natural Resource Management.

2. Methods

2.1. Occurrence data

We compiled records of bilby occurrences from multiple data sources. These included (1) data collated for the *Action Plan for Australian Mammals 2012* (APAM) (Woinarski et al., 2014), (2) a national dataset of track plot records obtained from various data providers as part of the Arid Zone Monitoring (AZM) project (Legge et al., 2024), encompassing records from numerous ranger groups actively protecting bilbies on Indigenous lands, (3) historical and contemporary records from the eastern parts of the bilby's range (Silcock et al., 2023; Queensland Department of Environment, Science and Innovation, unpublished data; Save the Bilby Fund, unpublished data), and (4) recent unpublished records from broad-scale surveys conducted from 2020 to 2022 by Territory Natural Resource Management (TNRM) and the Western Australian Department of Biodiversity, Conservation and Attractions (DBCA) (see Table 1 for details). While some datasets contained non-detections (locations where the bilby was searched for but not detected, e.g., the AZM and TNRM databases), most records were presence-only. To integrate the datasets, we reduced all data to presence-only. Data were collated and checked for obvious errors or duplicate records. Where data had been collated from broader sources (e.g., APAM and AZM databases), they were screened by experts to omit erroneous records considered well outside the bilby's known range. This was done conservatively, so records were omitted only if there was a high level of confidence that they were spurious. Records with no dates or low spatial precision, or where bilbies were detected inside a predator exclosure, were also omitted, although we included records from reintroduced wild populations within the historical range that may be subjected to varying levels of predator management (e.g., Matuwa, Western Australia).

We separated the data into two datasets: (1) a 'historical' dataset, including occurrence records from 1900 to 2022 and (2) a 'contemporary' dataset, including occurrence records from 2000 to 2022. We chose the year 2000 as the separation point for historical and contemporary datasets, as it allowed us to have a large number of presences both before and after this point, enabling the development of separate niche models for the two time periods based on similar data inputs (see Appendix Table S1). We were interested in comparing historical and contemporary realised niches, so we included all recent occurrence records in the historical dataset. This was justified because there was no evidence to suggest that bilbies have expanded into new areas over the timeframe of our study. Furthermore, the inclusion of new survey methodologies in recent decades (Southgate et al., 2005) has enabled the surveying of remote and previously inaccessible areas. This approach – including all records in the historical dataset – has also been shown to improve the reliability of analyses of niche change (Martínez-Freiría et al., 2016). To minimise the possibility that localised survey efforts would bias the analysis (e.g., where sampling was undertaken regularly at the same site or nearby sites), we only included records

spaced ≥4 km apart. This spacing was chosen based on published bilby home ranges (e.g., Moseby and O'Donnell, 2003) and aimed to ensure that individual bilbies were unlikely to be detected more than once in a single survey period (i.e., this spacing was greater than the largest male home range (3.16 km^2) recorded in Moseby and O'Donnell, 2003). This approach of including only independent records is commonly used to minimise issues associated with clustered sampling and spatial bias (Boria et al., 2014; Aiello-Lammens et al., 2015; Low et al., 2021). Records were selected at random for inclusion in each respective dataset using the 'thin' function of the 'spThin' package (version 0.2.0, Aiello-Lammens et al., 2015) in R (version 4.2.1, R Core Team, 2022).

2.2. Environmental data

We included several predictor variables in our models. These included spatially derived variables from satellite data and from other sources that were available for the entire historical range of the bilby (Table 2). Predictor variables were selected based on prior knowledge of bilby ecology and factors driving mammal species distributions more generally (obtained from the peer-reviewed literature). For example, fire, climate (Southgate et al., 2007a), and vegetation cover and/or productivity (McDonald et al., 2015) have been shown to influence the distribution of bilbies and many other mammals globally (Hortal et al., 2008; Beale et al., 2018; McDonald et al., 2018; Senior et al., 2021).

We created surfaces of the average annual rainfall, minimum temperature of the coolest month, and maximum temperature of the warmest month using gridded data (5-km resolution) from the Queensland Government SILO (Scientific Information for Land Owners) database (Jeffrey et al., 2001) for the entire historical range. SILO provides daily meteorological datasets for a range of climate variables in ready-to-use formats suitable for ecological modelling, research, and climate applications. We chose to use SILO data over global interpolated climate surfaces (e.g., WorldClim, CHELSA) because SILO data are likely more accurate and appropriate for Australia and provide a better representation of the temporal scale of our observations. Climatic surfaces derived from global databases have been shown to be highly correlated with the equivalent surfaces derived from the Australian-based SILO database (e.g., see von Takach et al., 2020), confirming that they are likely to provide robust representations of mean climatic conditions across the study area.

Given the broad temporal range of occurrence records, we acknowledge there may have been shifts in environmental conditions (e.g., an increase in the severity of impacts associated with drought or aridification). In an attempt to address this, we created a series of predictor variables (primarily representing different categorisations of rainfall) representing anomalies (i.e., the difference from the long-term average) and shorter-term averages (i.e., the averages in the 9-month period or 12-month period prior to each observation record). We found that these predictors were highly correlated, so opted to retain long-term averages for ease of interpretation.

Region-wide satellite-derived records of fire and vegetation cover were only available from the year 2000 onwards. We used the 500-m resolution monthly burnt area products from the Moderate Resolution Imaging Spectroradiometer (MODIS) satellite sensor (MCD64A1, version 6) from the United States National Aeronautics and Space Administration (NASA) to calculate average fire frequency from late 2000 to 2022 (Giglio et al., 2015). We used the normalised difference vegetation index (NDVI) as a proxy for vegetation productivity, which potentially influences bilby distribution through the provisioning of food and shelter. NDVI measures the difference between near-infrared light, which is reflected by vegetation, and red light, which is absorbed by vegetation, to derive an indicator of vegetation 'greenness' (i.e., density and health) (Cramer et al., 1999). We downloaded pre-processed 16-day NDVI gridded data at 500-m resolution from the MODIS satellite sensor (MOD13A1, version 6) (Didan, 2005) and calculated the average NDVI from late 2000 to 2022. We acknowledge that these layers are unlikely to be indicative of longer-term spatial patterns in fire frequency and NDVI. However, we argue that including them is a better solution than omitting them from the analysis entirely, given their likely importance in shaping bilby distribution and realised niche. We chose to use MODIS over other satellites because it offers appropriate spatial resolution, consistency over time, has undergone extensive validation, and is likely more suitable for use in Australia (Schroeder et al., 2021). We used recently developed models of cat (Legge et al., 2017) and fox (Stobo-Wilson et al., 2022) density to investigate whether these species were contributing to declines in the bilby's geographic range and realised niche. The density layers were created by extrapolating local estimates of density (n = 91 for cats and n = 44 for foxes) with several environmental and geographic variables.

All predictor variables were imported into R (version 4.2.1; R Core Team, 2022) using the 'terra' package (version 1.7.39; Hijmans, 2022), re-projected to the Geocentric Datum of Australia 2020 Australian

Table 2
A description of the environmental variables considered to be important drivers of bilby (*Macrotis lagotis*) niche tolerance, including sources of data.

Variable	Description	Source(s)
Average annual rainfall	The average annual rainfall (mm) over the entire sampling period (1900–2022).	Created from monthly spatial interpolations of climate data at 5-km resolution. Sourced from the SILO database: https://www.longpaddock.qld.gov.au/silo (accessed April 2023).
Minimum temperature of the coolest month	The minimum temperature of the coolest month (on average, in degrees Celsius) between 1957 and 2022.	Created from monthly spatial interpolations of climate data at 5-km resolution. Sourced from the SILO database: https://www.longpaddock.qld.gov.au/silo (accessed April 2023).
Maximum temperature of the warmest month	The maximum temperature of the warmest month (on average, in degrees Celsius) between 1957 and 2022.	Created from monthly spatial interpolations of climate data at 5-km resolution. Sourced from the SILO database: https://www.longpaddock.qld.gov.au/silo (accessed April 2023).
Fire frequency	The number of times each site burnt over the period where data were available (2000–2022).	Derived from MODIS satellite imagery at 500-m resolution (monthly Terra imagery, MCD64A1, version 6). Sourced from NASA: https://www.earthdata.nasa.gov (accessed December 2022).
Average NDVI	Calculated using the near-infrared (reflected by vegetation) and red light (absorbed by vegetation) wavelength, averaged over the period for which data were available (2000–2022).	Derived from MODIS satellite imagery at 500-m resolution (16-day Terra imagery, MOD13A1 Version 6). Sourced from NASA: https://www.earthdata.nasa.gov (accessed December 2022).
Cat density	Modelled density of cats derived from extrapolation of 91 published and unpublished estimates of cat density across Australia.	Legge et al. (2017).
Fox density	Modelled density of foxes derived from extrapolation of 44 spatially distinct published and unpublished estimates of fox density across Australia.	Stobo-Wilson et al. (2022).

MODIS: Moderate Resolution Imaging Spectroradiometer, NASA: National Aeronautics and Space Administration (United States), NDVI: Normalised Difference Vegetation Index. SILO: Scientific Information for Land Owners

Albers coordinate reference system, and resampled using bilinear interpolation to the resolution of the MODIS-derived layers (approximately 500 m). We chose the 500-m resolution because fire and vegetation cover can be patchy at finer scales. We then extracted the data from each predictor variable at all occurrence locations in our dataset.

Following the recommendations of Merow et al. (2013), we tested for collinearity among predictor variables, removing predictors that contributed high variance inflation factor (VIF) scores. While high collinearity among predictor variables is widely recognised as being of less concern for machine-learning methods such as MaxEnt (compared to other types of models) (Elith et al., 2011), this only holds true when predictive accuracy is the primary goal of the analysis. Because we were also interested in investigating the environmental drivers of bilby distribution, we considered this approach likely to produce more interpretable models (Merow et al., 2013). We compared VIF scores among predictors and removed variables based on a pre-selected threshold of five, as per Zuur et al. (2010). In cases where two predictors contributed high VIF scores, we selected the predictor with greater ecological relevance for inclusion. Given data limitations associated with constructing separate historical and contemporary environmental predictors (particularly for NDVI and fire frequency), we opted to incorporate one set of environmental predictors for models of historical and contemporary distributions of niche (as per McDonald et al., 2018; Moore et al., 2019; von Takach et al., 2020).

Other recognised threats to bilbies are grazing by large herbivores and European rabbits (*Oryctolagus cuniculus*) and possibly predation by dingoes (*Canis dingo*) (McDonald et al., 2015; DCCEEW, 2023). Impacts associated with livestock are typically most severe on pastoral stations with high stocking rates (DCCEEW, 2023); however, stocking rate information is not readily available nor are there any wide-scale data available on large herbivore occurrence or density. We tested the influence of land use as a proxy for grazing impacts (i.e., 'pastoral' vs. 'non-pastoral') but found that it did not improve model performance, possibly because impacts vary at finer spatial scales (i.e., increasing severity with proximity to permanent water points; Landsberg et al., 1997). NDVI is often positively associated with the occurrence of herbivores due to the provision of food resources (Young et al., 2022), so inclusion of this variable in our models is likely to account for some changes in grazing intensity due to changes in plant productivity.

Wide-scale estimates of rabbit density (e.g., Brown et al., 2020) were not suitable for our purposes, as there was little coverage across the contemporary bilby range. Dingoes are known to take bilbies as prey but have not been substantially linked to the decline of the species (Southgate et al., 2007b), although wild canids have been identified as a potential threat in Queensland (Augusteyn et al., 2021). Dingoes may also have a positive influence on bilbies through suppression or displacement of cats and foxes (Letnic et al., 2009; Kennedy et al., 2012). There are, however, currently no wide-scale data available on dingo densities. Creating new datasets suitable for incorporation in our models was beyond the scope of this study, so we were not able to consider impacts associated with grazing by large herbivores and or possible impacts associated with dingoes in further analyses.

Given that bilbies are burrowers, another important predictor influencing their distribution may be soil type. However, we were unable to locate any suitable soil layers for use in our models at the scale of our study beyond those that were coded categorically. Given the computational requirements of running hypervolume models, it was not feasible to include any categorical predictors in our analysis. We tested the influence of elevation as a proxy for soil type but, like land use, found that it did not improve model performance.

2.3. Range and niche change

In order to examine changes in the bilby's geographic range, we calculated the extent of occurrence (EOO, i.e., the area contained within the shortest continuous boundary that can be drawn to encompass all known occurrence records) using the historical and contemporary datasets. To do this, we constructed alpha hulls around the occurrence records for the two time periods using the 'ashape' function of the 'alphahull' package in R (Pateiro-Lopez and Rodriguez-Casal, 2009). Alpha hulls are generalisations of convex polygons that can account for discontinuities in species distributions and are a standard measure recommended by the International Union for Conservation of Nature (IUCN) for evaluating declines in a species' EOO across two time periods (IUCN, 2022). As per IUCN recommendations, we used a value of $a = 2$ (IUCN, 2024).

In order to express the sizes of the historical and contemporary niches (i.e., the niche breadth), we calculated niche hypervolumes using the one-class support vector machine method, with default parameters $\nu = 0.01$ and $\gamma = 0.5$, implemented via the 'hypervolume_svm' function in the 'hypervolume' package in R (Blonder and Harris, 2018). Niche hypervolumes measure the multidimensional space defined within the bounds of scaled and centred environmental predictor variables (Tingley et al., 2014). Hypervolume size is positively correlated with the number of records used in construction (Blonder and Harris, 2018), so we accounted for differences in the number of occurrence records in the historical and contemporary datasets to compare changes in hypervolume size between time periods (as per Scheele et al., 2023). This involved calculating historical hypervolumes with a random selection of occurrence records representing the same number of records that were present in the contemporary dataset. Following Scheele et al. (2023), we constructed 1000 historical hypervolumes to account for variability associated with the random subsampling of occurrence records. We also constructed 200 contemporary hypervolumes using only records from the contemporary dataset to quantify the minor variability associated with the stochastic algorithms defined in the modelling process (Scheele et al., 2023).

We defined hypervolumes by the bounds of our chosen predictors (after scaling and centring each predictor) (Table 2), excluding average rainfall, as it contributed a high VIF score due to being highly correlated with average NDVI (Appendix Table S2). We chose to use average NDVI rather than rainfall, because NDVI is potentially a better representation of available food and shelter resources, and data were available at a finer resolution.

We calculated the difference between the average historical and contemporary niche volumes to measure change in the ecological niche of the bilby through time. We then tested for a significant difference in niche volume using a Wilcoxon rank sum test.

To visualise the differences between the historical and contemporary niches, we randomly selected one historical niche hypervolume and one contemporary niche hypervolume, and used principal component analysis (PCA) to reduce the number of variables (i.e., dimensions) while retaining as much of the original variation in the data as possible. PCA was undertaken using the 'prcomp' function from base R (R Core Team, 2022). We then created three-dimensional plots using the first three principal components of each hypervolume (i.e., those containing the majority of the variance in the data) and overlaid the historical and contemporary plots on top of one another to assess overlap and changes in niche space through time. The three-dimensional plots were generated using the 'scatterplot3d' package in R (Ligges and Mächler, 2003). To quantify shifts in the bilby's realised niche through time, we calculated the centroids of the same randomly selected historical and contemporary hypervolumes using the 'get_centroid' function from the 'hypervolume' package (Blonder and Harris, 2018). To measure the shift of centroids over time, we calculated the Euclidean distance between the centroids, where a greater distance indicated a more substantial shift in the conditions that bilbies currently occupy, compared to those historically occupied.

2.4. Quantifying changes in the use of environmental space through time

In order to quantify changes in the environmental conditions

available to the bilby through time, we sampled each of the variables of interest at 404 random points within the historical and contemporary EOOs of the bilby, taking into consideration potential sampling bias (using the bias layers described in Section 2.5). This number of points was the maximum available within the contemporary range, given the resolution and the proportion of cells with no data available in the bias layer (i.e., large areas of unsurveyed potential habitat throughout the central desert regions of the Northern Territory and Western Australia). We used generalised linear models to compare the average values of the environmental predictors between the two time periods. We considered there to be a significant difference between time periods when the 95% confidence intervals of a given variable did not overlap.

2.5. Niche models and background sampling

We used maximum entropy modelling (the 'MaxEnt' algorithm; Phillips et al., 2006) to create ecological niche models using the 'dismo' package (Hijmans et al., 2022). We used MaxEnt because it has been shown to perform well, particularly when spatially variable sampling effort (common in occurrence data) is taken into consideration and when many background (or 'pseudo-absence') points are sampled from the wider landscape (Elith et al., 2011). In order to account for variation in sampling effort, we created a bias layer using a target-group background sampling approach (Phillips et al., 2009; Merow et al., 2013). Target-group sampling uses the presence locations of taxonomically related species observed using the same techniques as the focal species to estimate sampling, under the assumption that those surveys would have recorded the focal species had it occurred there (Phillips et al., 2009; Merow et al., 2013). We defined our target group as mammals readily detected by their sign (e.g., tracks, scat, diggings), given that almost all bilby records are records of their sign rather than direct captures or sightings. Bilby sign is unique and can be distinguished from the sign of other arid-zone mammals (Southgate et al., 2018), so it is likely that bilbies would be detected if present in areas where other animals were detected by their sign. We created two bias layers representing the temporal scale of each of our datasets: (1) 1900–2022 (historical dataset) and (2) 2000–2022 (contemporary dataset), using data collated for the APAM (Woinarski et al., 2014) and including occurrence records from all mammal species recorded as part of the AZM project (Appendix Table S3, Legge et al., 2019). From this subset of data, we randomly sampled a set of 10,000 background points. To quantify the environmental conditions within the realised niche, we modelled bilby occurrence as a function of our chosen predictors (Table 2), excluding average rainfall due to high collinearity with average NDVI.

Starting with the historical dataset (and including all the historical occurrence records), we tested a range of feature-class combinations – including linear only; linear and quadratic; and linear, quadratic and product – and regularisation coefficients (beta multiplier values from 0.5 to 3, in increments of 0.5). We performed *k*-fold cross-validation on each model with five replicates to reduce overfitting. This involved randomly splitting the data into $k = 5$ subsets or 'folds', using four subsets for training the model, testing the model against the one subset that was left out previously, repeating this five times (i.e., until the model was trained and tested on all subsets of data), and generating an overall prediction error by taking the average of all errors calculated (Kuhn, 2022). We then compared models using cross-validated area under the operating curve (AUC) values to assist in determining the best model (i.e., the one with the highest AUC) for further inference and prediction. We used AUC for model comparison because it is well established in the literature (e.g., see Phillips et al., 2006; Elith and Leathwick, 2009; Elith et al., 2011; Lahoz-Monfort et al., 2014; Muscatello et al., 2021). The contribution of variables to the best model was assessed using permutation importance values, calculated by alternating the predictor values between presence and background points and recording the effect this has on the model AUC (Phillips, 2011). Finally, we repeated these steps to build a model using the contemporary dataset for comparison (constructed using data from the same geographic extent as the historical models).

3. Results

After thinning, the final historical database (spanning 1900–2022) consisted of 1923 records, and the contemporary database (spanning 2000–2022) consisted of 881 records. The EOO, as estimated by alpha hulls, declined by ~70%, equating to a total reduction in area of 3,067,429 km^2 (Fig. 2). We also observed a significant (albeit smaller) reduction in realised niche breadth (measured as average hypervolumes) between the historical and contemporary datasets (45.5%, $p < 0.01$) (Fig. 3). There was, however, greater uncertainty in the hypervolume size for the historical range (1000 hypervolumes with subsampled data) than in the contemporary range (200 hypervolumes) (Fig. 2, Appendix Table S4).

There was a large amount of overlap in the randomly selected historical and contemporary hypervolumes (Fig. 4). Despite this, there was some evidence to suggest a change in the conditions currently occupied by the bilby, as quantified by a Euclidean distance of 1.418 units between the historical and contemporary niche centroids.

The performance of the MaxEnt models was moderate to high, with test AUC values of the highest ranked models averaging 0.68 (standard error (SE) = 0.002) and 0.76 (SE = 0.002) for the historical and contemporary models, respectively (Appendix Table S5). The regularisation parameter had no influence on the test AUC for either model

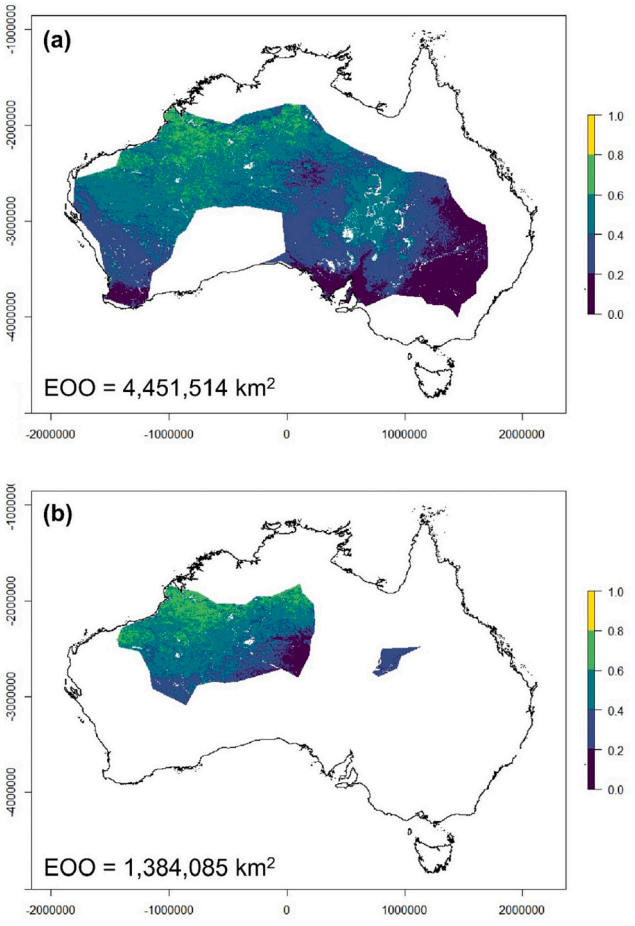

Fig. 2. Predicted niche suitability for the greater bilby (*Macrotis lagotis*), within the species' estimated (a) historical and (b) contemporary extent of occurrence (EOO). Colouring within the EOO represents niche suitability (where 0 is unsuitable and 1 is highly suitable) predicted by MaxEnt models. EOO was estimated from alpha hulls.

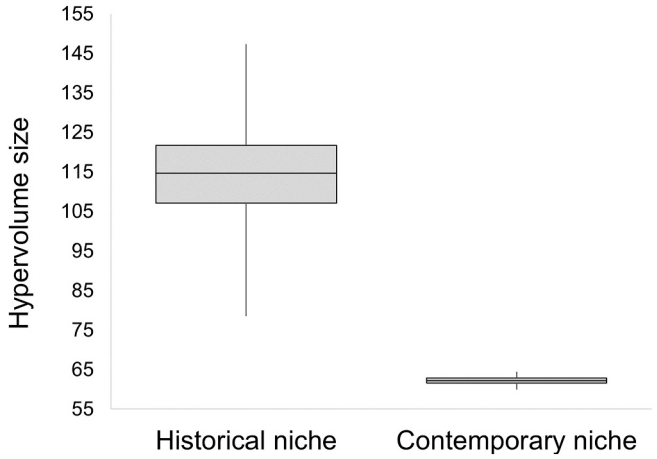

Fig. 3. Average niche hypervolume (shown separately for the historical and contemporary niches) of the bilby (*Macrotis lagotis*). Note that the historical hypervolume was calculated by sub-sampling the occurrence records present in the historical dataset 1000 times (using the same number of points as in the contemporary dataset, $n = 928$). The variability presented for the contemporary hypervolume represents variability associated with constructing hypervolumes using the stochastic algorithms defined in the modelling process. Lower and upper box boundaries are the first and third quartiles, respectively, the central box line is the median, and the lower and upper whiskers are the minimum and maximum values, respectively.

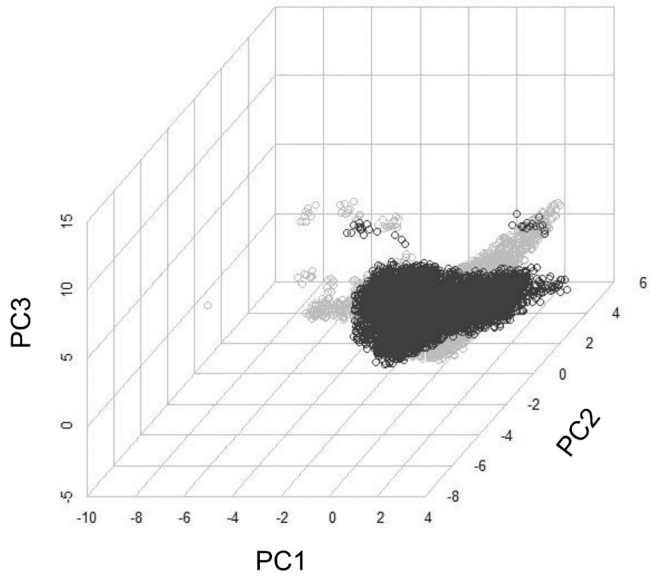

Fig. 4. A randomly selected contemporary hypervolume (dark grey) overlain on a randomly selected historical hypervolume (light grey) to allow for visualisation of shifts in bilby niche breadth. A principal component analysis was performed on the data to reduce dimensionality (from six to three) to allow for visualisation in the three-dimensional space. The first three principal components of each hypervolume were plotted to ensure the majority of the variance in the data was captured.

(Appendix Table S5). Average fire frequency contributed the highest permutation importance to the historical ENM (53.9), followed by average NDVI (21.6), average minimum temperature of the coolest month (17.7), and average maximum temperature of the warmest month (5.7). Cat and fox densities were of comparatively little importance (combined total of <2; Appendix Table S6). Fire frequency remained the most important predictor in the contemporary ENM (50.4), followed by fox density (22.5), and minimum temperature of the coolest month (20.3), which maintained similar importance when compared to the historical model. By contrast, average NDVI became less important (4.6). Relatively little change was observed in permutation importance for average maximum temperature of the warmest month (2.2) or cat density (0) (Appendix Table S6), both of which contributed little to the historical and contemporary models.

There were clear differences in the average values of environmental predictors within the historical and contemporary EOOs of the bilby (Fig. 5). Bilbies have contracted to areas with lower fox densities (Fig. 5b), lower average NDVI (Fig. 5c), higher fire frequency (Fig. 5d), higher average minimum temperature of the coolest month (Fig. 5e), and higher average maximum temperature of the warmest month (Fig. 5f). There was no significant difference in cat densities between the historical and contemporary EOOs (Fig. 5a).

4. Discussion

We used ENMs to quantify changes in the geographic range and ecological niche of a declining marsupial, the bilby – one of Australia's most iconic threatened species – across its entire distribution, confirming a reduction in both EOO and niche volume through time. We observed a ~70% reduction in range, which was smaller than range declines reported elsewhere (DCCEEW, 2023). This is likely due to differences in data sources used to discern historical EOO boundaries. For example, the historical EOO presented in the *National Bilby Recovery Plan* (DCCEEW, 2023) includes parts of south Western Australia and north-west South Australia that are not captured by our historical ENM. The probable cause for this discrepancy is that data from those regions either pre-dates our timeframe of interest (1900 onwards) or did not meet our criteria for inclusion (e.g., due to low location accuracy or no record of date of observation). Our reported decline is thus likely to underestimate the true decline in bilby EOO.

The modelled decline in realised niche relative to the decline in EOO (45.5% and 70% reduction, respectively), was much smaller than in other studies using comparable analyses for other declining Australian mammals. For example, Moore et al. (2019) estimated proportionate declines in both EOO and niche volume for the northern quoll (*Dasyurus hallucatus*) across two of four discrete populations, while von Takach et al. (2020) found that niche declines in six species (out of nine examined) of northern Australian mammal followed steeper trajectories than EOO declines. This discrepancy may be explained by differences in spatial scale. We covered the entire contemporary EOO of the bilby (spanning over half the Australian mainland), while the other studies focused on much smaller areas. It is thus likely that the biophysical conditions over the range of the bilby are more variable than in the ranges of the species examined in the other studies. Although this may have contributed to the relatively greater niche breadth for the bilby, it is plausible that the bilby's apparent broad niche breadth is real. The bilby is a generalist omnivore with a high level of digestive flexibility, capable of switching between diverse food sources in response to food availability (Gibson, 2001; Gibson and Hume, 2004; Southgate and Carthew, 2006). It is also capable of living in a wide range of habitats, as evidenced by its historically broad distribution across three quarters of the Australian continent (Southgate, 1990; Cramer et al., 2017; Silcock et al., 2023). While it would be useful to quantify bilby range and niche reductions at a regional scale, this is not currently possible for much of the extant population due to a lack of clear understanding of population boundaries. This is primarily due to the absence of long-term monitoring at appropriate spatial scales, made more difficult by the tendency of bilbies to move around the landscape in response to resources (Southgate, 1990; Southgate et al., 2018). This is particularly true in the northern central desert region of Australia, an area thought to support a large proportion of the remaining bilby population (DCCEEW, 2023).

An important difference between our study and others that have investigated niche declines in Australian mammals is the difference in the timing of declines. Arid and semi-arid Australia has long been

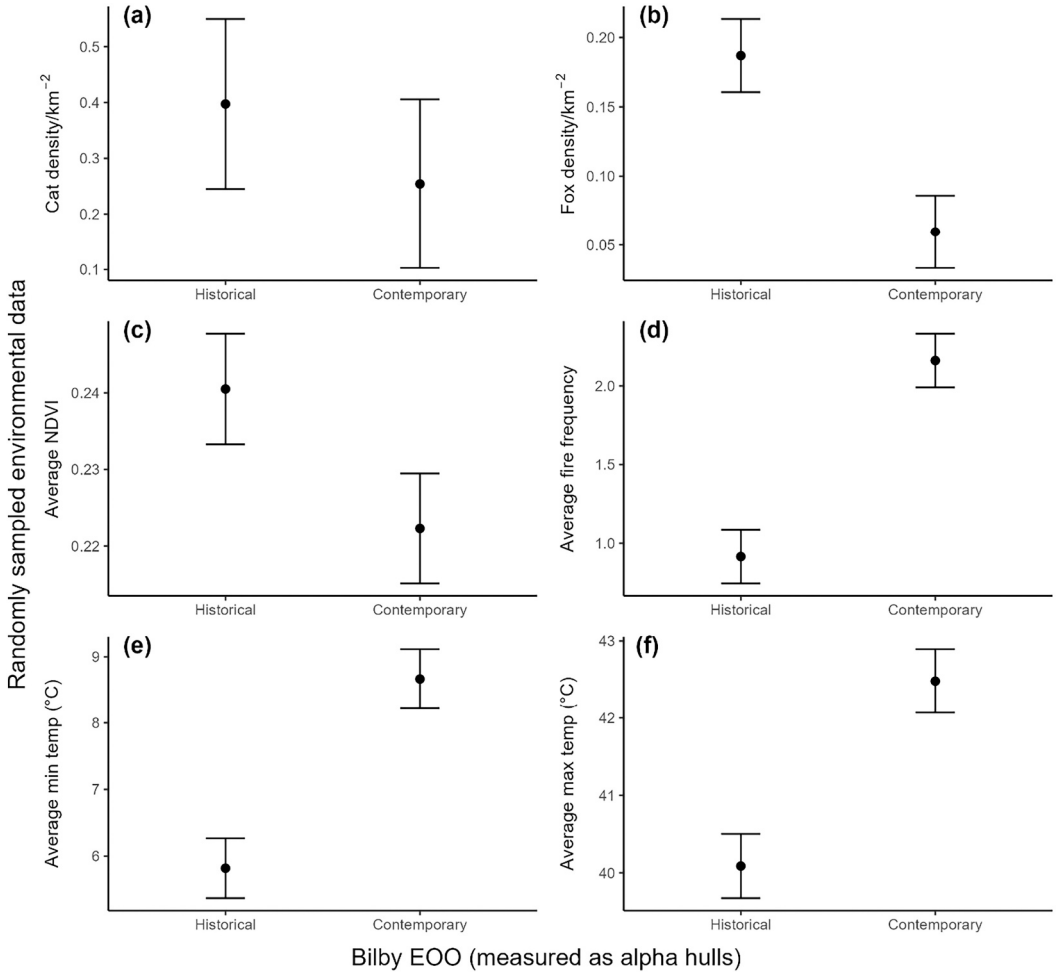

Fig. 5. Plots comparing random samples of predictor variables within the historical and contemporary extents of occurrence (EOO; measured as alpha hulls) of the greater bilby (*Macrotis lagotis*). (a) Cat (*Felis catus*) density (km^{-2}), (b) fox (*Vulpes vulpes*) density (km^{-2}), (c) average NDVI, (d) average fire frequency from 2000 to 2022, (e) average minimum temperature of the coolest month (°C), and (f) average maximum temperature of the warmest month (°C). Values were extracted for 405 sites representing the total number of cells with values within the contemporary range. Error bars represent 95% confidence intervals.

subjected to widespread mammal declines and local extinctions (Woinarski et al., 2019). By contrast, mammal declines in northern Australia – the subjects of Moore et al. (2019) and von Takach et al. (2020) – are just now being realised (Cremona et al., 2022). It is likely that the bilby's generalist ecology and historically wide-ranging distribution are part of the reason for its persistence, as species with smaller geographical ranges and narrower habitat breadths are generally more vulnerable to extinction (Chichorro et al., 2019).

Another important factor may be differences in the ecological requirements of the species studied. For example, the northern quoll and the central rock-rat (*Zyzomys pedunculatus*) have contracted to more complex, topographically rugged areas, which are likely to be less exposed to key threats (including fire and introduced predators; McDonald et al., 2018; Moore et al., 2019). Rugged landscapes are one of the few habitat types that are unsuitable for bilbies, due to their need to construct burrows. This highlights the need for species-specific studies investigating changes in niche through time.

There was evidence to suggest significant overlap between the historical and contemporary niches of the bilby. This overlap could indicate that bilbies have maintained access to similar resources and habitats across time scales. However, the presence of overlap alone does not fully capture the extent of niche contraction but rather suggests that the bilby has not completely abandoned its historical range. Our observation of a shift in niche centroids (quantified by a Euclidean distance of 1.418 units) suggests that there has been some change in the environmental conditions that the bilby occupies. In the following sections, we discuss the mechanisms that may have led to this change, the implications of reduced niche breadth for bilby persistence, and future research and management directions to enable better conservation outcomes for wild bilby populations.

4.1. Environmental correlates of the bilby's contemporary realised niche

Using MaxEnt modelling, we identified the strongest correlates of the bilby's contemporary realised niche. We found that fire frequency and fox density were the most important predictors of those tested. While fire frequency was also an important predictor of the historical realised niche, fox density did not contribute at all, providing strong evidence to suggest that foxes are contributing to current bilby declines. This is consistent with expert opinion and localised observations showing that bilbies are unable to thrive in the presence of foxes (Abbott, 2001; DCCEEW, 2023). The relationship between bilby realised niche and fire was quadratic. Bilbies are persisting in areas with moderate fire frequencies – up to nine burns in the 23-year period for which data were available, with areas subject to lower or higher fire frequencies being less likely to support bilbies. While some studies conducted at a smaller scale and with more homogeneous vegetation have also shown a positive relationship between bilby occurrence and fire frequency (e.g., in the Tanami Desert; Southgate et al., 2007a), others have shown strong association of bilby abundance with areas that are long unburnt or that

burn infrequently (DCCEEW, 2023). For example, in the northern and higher rainfall areas of their range on the Dampier Peninsula in Western Australia, bilbies prefer long-unburnt habitat, and this may reflect the generally higher fire frequencies experienced in this area (Moore et al., 2024). The largest known wild population in this region occurs in coastal sand dunes where fire is excluded or fire frequencies are extremely low (Moore et al., 2024). It is thus likely that the relationship between bilby occurrence and fire is complex, and impacts associated with fire may be exacerbated by other factors (discussed further in Section 4.2).

The minimum temperature of the coolest month had similar importance in both the historical and contemporary models. Bilby persistence in areas with higher minimum temperatures may reflect aspects of the bilby's ecology – bilbies are nocturnal, and occupy spiralling burrows up to 2 m deep, which are able to maintain relatively constant temperatures and protect individuals from temperature extremes (Chapman, 2013). Average NDVI became less important in the contemporary realised niche. Despite this, there was some evidence that bilbies are persisting in areas with lower NDVI. In arid and semi-arid areas, NDVI is often positively associated with the occurrence of herbivores, largely due the provision of food resources (e.g., Young et al., 2022). However, this relationship is less clear for omnivorous species such as the bilby, which may be less reliant on highly productive vegetation as a food source or only rely on these resources at some times (e.g., soon after fire when shrubs that support root-dwelling larvae have been burnt, Liddle, 2016). Additionally, areas with low NDVI may have sparse vegetation or open ground which may benefit a highly mobile species such as the bilby (Southgate, 1990; Dawson et al., 2018). An alternative explanation is that bilbies have contracted to areas with lower NDVI because these areas are less likely to support large herbivores or be used for livestock grazing (Hunt et al., 2014). However, large herbivores may also contribute to reductions in NDVI through grazing and trampling (Fensham et al., 2010). This warrants further investigation.

We found limited evidence to suggest that cat density was contributing to bilby EOO and niche reductions, despite cats being widely considered as a key threat to bilby populations (Moseby and O'Donnell, 2003; Moseby et al., 2012). It is possible that cat impacts on bilby EOO and niche reduction were not detected due to the scale of our study, particularly given the widespread distribution of cats. Cats occupy >99% of Australia's land area, occur in all types of habitats across all land tenures, and are currently only absent from predator-proof fenced areas and some islands (Legge et al., 2018). While we found that bilbies had, on average, contracted to areas of slightly lower cat densities (though this was not significant), we suspect that there was too little variation in our cat density predictor across the contemporary bilby EOO to enable us to properly investigate cat impacts on bilby range and niche reduction. This is supported by the low r^2 associated with the cat model (0.049), which Legge et al. (2017) attributed to the lack of clear spatial variation and relatively unimportant environmental predictors used to construct it. By contrast, the fox density model performed relatively well (Stobo-Wilson et al., 2022), suggesting that our inferences related to fox contributions to bilby range and niche contractions are more valid. Cat densities fluctuate seasonally in arid areas (Legge et al., 2017), so it is also likely that our models missed local impacts associated with transient periods when cat numbers were high. Nonetheless, while much evidence exists showing that cats prey on bilbies (Paltridge, 2002; Moseby et al., 2011), the upper limits of cat densities at which wild bilbies can persist are unknown (although this has been experimentally tested in a fenced reserve, see Moseby et al., 2019). Furthermore, Berris et al. (2020) found similar adult survival rates in two translocated bilby populations (one free of cats, one with cats) but low recruitment rates and low numbers of subadults in the population exposed to cats, despite high female bilby fecundity. It is thus highly likely that cats have more localised impacts on bilby populations, particularly in conjunction with other threatening processes (e.g., fire). This warrants further investigation.

A caveat of our study is that we did not consider some of the key threats likely driving declines in bilby realised niche, including grazing and other forms of habitat degradation caused by introduced herbivores, as well as the severity, size/extent, and timing of fire, and other, more complex measures of fire behaviour. Our inferences are also likely affected by the simplistic nature of some of our environmental predictors, such as using NDVI over more sophisticated measures of vegetation diversity and structure, and the temporal scale over which data were available. Due to the large spatial scale of this research, appropriate environmental variables to capture these key threats and nuanced environmental characteristics are not currently available. Hence, research at regional scales where such data is available would provide complementary information to this study and assist with improving local conservation outcomes.

4.2. Likely causes of niche reductions – variation in threat intensity or mediation of threat impact?

Environmental conditions may influence a species' realised niche in two ways: (1) the species contracts to areas where a threat is absent (i.e., bilbies are persisting in locations where environmental conditions are unsuitable for foxes), or (2) a threatening process is mediated by the environmental conditions in a way that enables the species to tolerate the threat impact (Scheele et al., 2017). It is likely that both processes are at play across the bilby EOO. For example, fox density emerged as a key predictor in the contemporary realised niche, such that bilbies have contracted to areas with lower average fox densities. This association may be attributed to multiple factors. Firstly, foxes are opportunistic, omnivorous predators (Cavallini and Volpi, 1995) that consume a broad range of vertebrates, invertebrates, and plant material (Fleming et al., 2021). However, many studies have identified the importance of lagomorphs (principally European rabbits) in their diets, both in Australia and elsewhere (Soe et al., 2017; Fleming et al., 2021). Where rabbits are available, they are a significant component of foxes' diets, and the decline of rabbits due to drought and disease has had significant impacts on fox populations in some places (Saunders et al., 1995). Therefore, fox and rabbit distributions appear to be linked and, for bilbies, the risk of predation from foxes may be higher where rabbit distribution has supported fox dispersal. High rabbit densities may elevate fox densities (Saunders et al., 1995), and impacts on bilbies may be most severe following rabbit 'busts', when elevated numbers of foxes may need to switch to other prey sources (Pech and Hood, 1998). Rabbits also compete with bilbies for resources (DCCEEW, 2023), putting further pressure on populations in locations where they are abundant. Both foxes and rabbits are sensitive to changes in climate and, in Australia, their populations are more limited and restricted to fewer habitat types in the northern and more recently occupied areas of their distribution (Saunders et al., 1995; Williams et al., 1995). By contrast, bilbies have contracted to the driest and least fertile parts of their former range (with the exception of the north-west), as demonstrated here via the trend of contracting to areas with lower average NDVI, and documented elsewhere (Southgate, 1990; Southgate et al., 2007a).

Secondly, foxes may require access to free water at times, which may not be readily available in many parts of the contemporary bilby niche during drought periods. For example, in a study on field metabolic rates and water turnover in temperate New South Wales, Winstanley et al. (2003) found that foxes likely supplemented their dietary water intake by drinking from artificial water sources. Similarly, Roshier et al. (2021) found that foxes use artificial watering points in a semi-arid environment in south-western New South Wales. Brawata and Neeman (2011) found that the spatial activity of foxes was modified by the presence of dingoes around artificial watering points in desert environments in New South Wales and South Australia – in areas where dingoes were controlled, fox activity was highest near water. This strongly suggests that foxes use free water when accessible, indicating that there is a benefit in doing so. Therefore, an increase in artificial watering points to

support pastoralism (Walsh and Cowley, 2016) could be supporting the northward expansion of foxes. For example, the expansion and intensification of agriculture and irrigated cattle fodder production in the Kimberley region of Western Australia (DCCEEW, 2023) could be facilitating the movement of foxes into areas that would otherwise be inaccessible, due to an absence of natural water bodies. Unlike foxes, bilbies are physiologically well-equipped to conserve water. Gibson and Hume (2000) found that the mean water influx rate of a population of bilbies in Queensland did not differ between summer and winter, and that the water influx rate of the bilby was significantly lower than that predicted for a marsupial of its size (indicating an excellent ability to conserve water). We were not able to investigate the influence of rainfall on the bilby's realised niche due to high collinearity with other variables of interest (notably, average NDVI). However, we found that bilbies had contracted to areas of higher average minimum and maximum temperatures within their contemporary realised niche, which may be limiting fox distribution. Stobo-Wilson et al. (2022) found a significant negative relationship between fox density and mean annual temperature, which may be attributed in part to the foxes' potential need for free water to maintain metabolic balance under high temperatures. This provides further support to suggest that environmental conditions may mediate fox impacts on bilbies by limiting fox distribution and abundance in some areas.

It is also likely that other environmental conditions mediate the impacts of foxes (and possibly cats) on bilbies. For example, some studies have shown that foxes and cats exploit recently burnt areas due to increased hunting efficacy (McGregor et al., 2014; Leahy et al., 2016; Hradsky et al., 2017), while others have suggested that more complex habitats can alleviate the impacts of predation on native animals (Doherty et al., 2015, 2022; Hohnen et al., 2016). Predation rates may also be influenced by grazing and pastoralism – grazing, like fire, reduces ground cover, and as discussed, predators (especially foxes) may be sustained at elevated numbers by watering points established for stock in pastoral regions (DCCEEW, 2023). While our results suggested that bilbies have contracted to more open and less productive areas (i.e., those with lower average NDVI) and areas with moderate fire frequencies, it is important to note that these variables do not provide any information about habitat complexity, including at the lower ground level, or the severity of wildfires. Ground-based experiments are needed to further investigate these relationships and to discern if they are contributing to bilby EOO and niche reductions.

Another important consideration is that modelled fox densities in the northern parts of the bilby's range (i.e., where bilbies have contracted to) correspond to areas with the least amount of data, the smallest and most dispersed human populations, and the least amount of survey activity. This may have led to underestimates of fox densities in these regions. Field data to corroborate the model do not currently exist, and although anecdotal evidence suggests that fox densities are increasing in these regions, this is a key knowledge gap that warrants further investigation. If fox prevalence is increasing in the northern parts of the bilby's range, this is likely to have severe consequences for bilby populations, and urgent management intervention may be required.

4.3. Implications associated with reduced niche breadth

A species' risk of extinction is typically assessed using knowledge of its spatial and temporal distribution (i.e., using the categories and criteria developed by the IUCN) and rarely incorporates information about environmental preferences or ecological niche (Breiner et al., 2017). This is despite extensive knowledge regarding the role of environmental preferences in shaping genetic differentiation and divergence (Lee and Mitchell-Olds, 2011) and the geographic structure of species' abundance patterns (Martínez-Meyer et al., 2013). Using simulation modelling, Breiner et al. (2017) found that changes in niche breadth often corresponded to changes in geographic range size but with considerable variation among species. They also found that changes in niche breadth could provide valuable additional information to assist with assessments of extinction risk for declining species, beyond what could be obtained from measuring changes in geographic range alone. Similarly, other studies have highlighted the importance of considering changes in realised niche as part of assessments of extinction risk, arguing that species may be at greater risk than appreciated if they are only evaluated against range metrics under IUCN criteria (von Takach et al., 2020). This perceived increase in risk is due to species inhabiting a narrower set of environmental conditions, which may make them more vulnerable to changing environments and threatening processes. For example, declining species that undergo reductions in their realised niche also have the potential to experience a decline in their fundamental niche if there is a loss of adaptive genetic diversity associated with environmental conditions that no longer occur in the realised niche (von Takach et al., 2020).

Our results demonstrate a significant reduction in the bilby's geographic range and a notable, but less severe, reduction in realised niche. This suggests that the bilby is persisting in a broader range of environmental conditions than might be expected given the extent of its geographic contraction, which may have important implications for conservation. For example, it may mean that the bilby has retained a greater portion of genetic diversity than would be predicted solely based on its reduced EOO. This could have positive implications for the species, which may be better equipped than expected to adapt to new or changing environments.

Nevertheless, the observed contraction in niche breadth could impact the bilby's resilience to future changes and threats – while some adaptive potential remains, the bilby is now restricted to a narrower set of environmental conditions, which may increase its vulnerability to emerging threats. Such questions might apply in a conservation context if land managers intend to reintroduce individuals of a species to areas where they have been previously extirpated, which has been identified as a priority for future management of bilby populations (DCCEEW, 2023).

4.4. Future research and management directions for improving conservation outcomes

Ecological niche modelling provides an understanding of the conditions under which species can persist and the geographic location of those conditions, making it a powerful tool for informing conservation outcomes. This is particularly true for a species like the bilby, which occurs across large, remote, and difficult-to-access parts of Australia. Our models identified fox density as a key predictor of bilby declines, indicating a necessity for better understanding of fox population dynamics across the bilby's range and under changing climates. Analysis of fox populations, together with niche models, may be informative in planning conservation actions. For example, such approaches could assist in identifying bilby refuge locations for protection (e.g., Selwood and Zimmer, 2020), conserving a range of different niche conditions, or implementing targeted control in areas where bilbies are likely to be at high risk of predation by foxes (e.g., in areas with suboptimal predicted niche suitability).

We emphasise that further work is needed to tease apart some of the complex relationships likely driving reductions in the bilby's realised niche. This includes gaining an increased understanding of predator population dynamics, how predators interact with various biophysical conditions (i.e., fire, vegetation complexity, pastoralism), and how such interactions might vary across environmental space. Obtaining such knowledge is likely to improve our understanding on how to manage key threats facing wild bilby populations, enabling persistence of bilbies into the future.

CRediT authorship contribution statement

Hayley M. Geyle: Writing – review & editing, Writing – original

draft, Visualization, Software, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization, Investigation. **Alys R. Young:** Writing – review & editing, Software, Methodology, Data curation, Conceptualization. **Brett P. Murphy:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Chris R. Dickman:** Writing – review & editing, Supervision, Conceptualization. **Christine Schlesinger:** Writing – review & editing, Supervision, Conceptualization. **Kelly M. Dixon:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Conceptualization. **Harry Moore:** Writing – review & editing, Software, Investigation. **Sarah Legge:** Writing – review & editing, Project administration, Data curation. **Jennifer Silcock:** Writing – review & editing, Investigation. **Naomi Indigo:** Writing – review & editing, Data curation. **Martin Dziminski:** Writing – review & editing, Investigation. **Bruce Greatwich:** Writing – review & editing, Investigation. **Thomas M. Newsome:** Writing – review & editing, Investigation. **Rachel Paltridge:** Writing – review & editing, Investigation. **Rick Southgate:** Writing – review & editing. **Cassandra Arkinstall:** Investigation. **Kevin Bradley:** Investigation. **Central Land Council Rangers:** Investigation. **Nigel Jackett:** Investigation. **Kanyirninpa Jukurrpa Rangers:** Investigation. **Karajarri Rangers:** Investigation. **Kiwirrkurra Rangers:** Investigation. **Kimberley Land Council Land and Sea Management Unit:** Investigation. **Danae Moore:** Writing – review & editing. **Ngurrara Rangers:** Investigation. **Parna Ngururrpa Aboriginal Corporation:** Investigation. **Nyangumarta Rangers:** Investigation. **Nyikina Mangala Rangers:** Investigation. **Anja Skroblin:** Writing – review & editing, Data curation. **Darren M. Southwell:** Writing – review & editing, Data curation. **Laurie Tait:** Investigation. **Kim Webeck:** Investigation. **Wiluna Martu Rangers:** Investigation. **Yawuru Country Managers:** Investigation. **Sam Banks:** Writing – review & editing, Supervision, Methodology, Conceptualization.

Declaration of competing interest

The authors declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110872.

Data availability

A large proportion of the occurrence data used in this study are owned by third-party organisations and were shared under the condition that they would not be made publicly available. Historical records from Queensland are available as Supplementary material in Silcock et al. (2023). All environmental spatial data used in the analysis are publicly available, and sources and links are listed in Table 2.

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