Patterns of niche contraction identify vital refuge areas for declining mammals

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Abstract

Aim: Investigation of realized niche contraction in declining species can help us understand how and where threats are being either mediated or tolerated across landscapes. It also provides insights into species’ sensitivity to environmental change that are unable to be identified through analysis of declines in range size or abundance alone. Here, we apply the recently proposed “niche reduction hypothesis” to investigate relationships between trends in niche breadth and geographic distribution of declining species.

Location: Northern Australia.

Methods: We compare and contrast contemporary and historical data sets to examine the relationship between extent of occurrence (EOO) and realized niche hypervolume, and investigate changes in species’ utilization of environmental space through time via generalized linear modelling and bootstrapping of historical values. We also use the “Maxent” algorithm to create and stack contemporary and historical ecological niche models (ENMs) and identify regions where resilience to threatening processes is maximized.

Results: We found larger mean reductions in niche hypervolume (39%) than EOO (30.5%), with little correlation ($r = 0.07$) between the two measures, suggesting that contraction of realized niche breadth can be largely independent of reduction in EOO. We also identified a general set of environmental conditions towards which species’ realized niches contracted. Comparison of stacked ENMs allowed us to identify regions of natural refuge where environmental conditions are associated with increased species resilience to threats, and conversely, regions where habitat suitability has declined.

Main conclusions: Examining species declines from an ecological niche perspective provides a powerful tool for understanding how environmental conditions, biotic interactions and species traits shape responses to local and global environmental changes. Quantifying reductions in niche breadth is crucial as contraction to a narrower subset of environmental space can reduce a species’ ability to tolerate other...
1 | INTRODUCTION

As the Earth enters its sixth mass extinction event (Ceballos et al., 2015; Diaz et al., 2019), disturbance to native ecosystems via habitat degradation, invasive species, land clearing and harvesting are causing declines of vertebrate species worldwide (Cardillo et al., 2008; Schipper et al., 2008). Research into species declines has typically focused on the impact that threatening processes have on the geographic distribution or abundance of a species (Channell & Lomolino, 2000b; Sagarin, Gaines, & Gaylord, 2006). Likewise, assessments of the conservation status of species typically rely on criteria relating to population size and geographic range size (IUCN, 2012). Building on these approaches, Scheele, Foster, Banks, and Lindenmayer (2017) outlined how a deeper understanding of the process of species decline can be obtained by investigating changes in the realized niche breadth of declining species through time. The niche reduction hypothesis suggests that contemporary threatening processes typically reduce the historically occupied portion of a species’ fundamental niche (the “realized niche”) to a subset of environmental conditions (the “contemporary niche”) under which threats are reduced or absent, or a species’ capacity to tolerate threat impacts is increased (Scheele et al., 2017).

Through investigating changes in niche breadth, we can begin to understand the mechanisms by which species respond to threats across their distribution, rather than focussing on the outcome of declines, a development that is crucial for informing conservation and understanding how species distributions and niches are shaped through time (Sexton, McIntyre, Angert, & Rice, 2009; Sexton, Montiel, Shay, Stephens, & Slater, 2017). A range of new analytical methods have been applied to investigate species niche dynamics; however, these methods have primarily been focused on understanding the niche in relation to invasive species (Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014; Kearney et al., 2008), climate change responses (Sax, Early, & Bellemare, 2013) and historical structuring of biodiversity (Sexton et al., 2017). As a result, changes in niche dynamics of declining species have been neglected. Further, while the ultimate and proximate causes of species declines can be difficult to determine with certainty (Frank et al., 2014; Leahy et al., 2016; Woinariski, Legge, et al., 2011), a niche lens can inform practical conservation management by quantifying the environmental conditions that contribute to species’ persistence. For example, we can identify whether refuges occur simply due to the absence of the threatening process, or due to environmental conditions that increase the capacity of the species to persist despite a threatening process. This may help prioritize the distribution of conservation resources towards species or locations that are likely to provide maximum benefit. In particular, improving management within and around refuge habitats could assist the recolonization of the surrounding landscape, increasing the geographic extent of the contemporary niche (Banks et al., 2011; Keppel et al., 2012; Scheele et al., 2017).

The Australian continent has experienced the highest rate of historical mammal extinctions worldwide, with 34 species becoming extinct since European colonization in 1788 (Woinarski et al., 2019). While the majority of these extinctions occurred prior to the mid-20th century (Woinarski, Burbidge, & Harrison, 2015), primarily in arid and semi-arid regions, there is growing recognition that a contemporary wave of mammal declines is underway in northern Australia (Davies et al., 2018; Fisher et al., 2014; Woinarski, Legge, et al., 2011). Susceptibility to decline and extinction in northern Australian mammals is at least partly associated with body mass, with species in a “critical weight range” (35–5,500 g) identified as most at-risk (Burbidge & McKenzie, 1989; Fisher et al., 2014; Murphy & Davies, 2014). Mammal declines in northern Australia appear to be driven by many of the same threats affecting species elsewhere around the globe, including (a) habitat degradation due to feral herbivores and pastoralism (Legge, Kennedy, Lloyd, Murphy, & Fisher, 2011; Woinarski & Ash, 2002), (b) direct or indirect effects of introduced species (Braithwaite & Griffiths, 1994; Radford et al., 2020), including increased predation due to exotic predators (Fisher et al., 2014; Frank et al., 2014), (c) inappropriate fire regimes (Lawes et al., 2015; Woinarski, Legge, et al., 2011) and (d) a changing climate (Kutt, Felderhof, Vanderwal, Stone, & Perkins, 2009; Traill et al., 2011; Williams, Bolitho, & Fox, 2003). It is important to note that there remains a high level of uncertainty about the relative importance of each of the above-mentioned threats to northern Australian mammals (Ziembicki et al., 2014).

Here, we examine the relationship between reductions in the geographic range size and environmental niche breadth of nine species, focusing on species in the critical weight range that broadly represent the Australian tropical savanna mammal assemblage. By investigating multiple species, each with different biological and ecological attributes, range size and niche breadth, we also examine broad macroecological patterns regarding the relationship between niche and range contraction (Botts, Erasmus, & Alexander, 2013; Slater, Hirst, & Sexton, 2013). We also utilize a niche lens to identify environmental conditions under which the target mammal species are persisting in the landscape, and use ecological niche modelling.
to identify regions of conservation importance. Specifically, we address the following questions:

1. Does the extent of geographic range decline correlate with the extent of contraction of the realized niche?
2. Which environmental variables (if any) are associated with niche contraction?
3. Can we predict refuge areas where environmental conditions are suitable for the persistence of individual or multiple mammal species?

To answer these questions, we use historical and contemporary records of species occurrences to quantify changing spatial patterns and niche characteristics through time, following an approach similar to that used by Moore et al. (2019). Consistent with the niche reduction hypothesis (Scheele et al., 2017), we predict that the availability of refuge habitats, where threats are reduced or absent, can be readily identified in some or all species of interest. For our study region, we predict that species persistence is likely to be promoted by low fire frequency, high vegetation cover and high rainfall, with differences in species’ responses to threats likely to result in a high level of variation in the degree to which niche declines correlate with range contractions. By investigating these processes in a suite of declining species, we identify important refuge areas for conservation and provide unique insights into the relationship between range size, niche breadth and decline severity, and changes in niche dynamics as species decline.

2 | MATERIALS AND METHODS

2.1 | Study species and region

We studied mammal declines in the savannas of Australia’s Northern Territory, as bounded by latitudes −11° to −16° and longitudes 129° to 138°. While some of our study species have distributions that extend beyond this area, it provides a large landscape (>300,000 km²) on which to focus our analyses while also avoiding the assumptions and biases that can be associated with ecological niche modelling across multiple regions (Crosby et al., 2019). Previous research in the region has shown that the contemporary wave of mammal declines includes Antechinus bellus (fawn antechinus), Conilurus penicillus (brush-tailed rabbit-rat), Dasyurus hallucatus (northern quoll), Mesembriomys gouldii (black-footed tree-rat), Rattus tunneyi (pale field-rat), Pseudomys nanus (western chestnut mouse), Isoodon macrurus (northern brown bandicoot), Trichosurus vulpecula (common brushtail possum) and Petaurus breviceps (sugar glider) (Braithwaite & Muller, 1997; Davies et al., 2017; Stobo-Wilson, Murphy, Cremona, & Carthew, 2019; Woinarski et al., 2010; Woinarski, Milne, & Wanganee, 2001). Importantly, despite noted declines, five of these species are still listed as Least Concern under the International Union for Conservation of Nature (IUCN) criteria, while three are Vulnerable, and one is Endangered (Table S1). All fall within the critical weight range (35–5500 g). While these species are strongly representative of the savanna mammal assemblage in this region, a number of additional species were excluded due to limited data availability, including Phascogale pirata (northern brush-tailed phascogale), Mesembriomys macrurus (golden-backed tree-rat, likely to be locally extinct) and Isoodon auratus (golden bandicoot).

2.2 | Occurrence data

We extracted all occurrences of each target species from the Atlas of Living Australia (ALA, https://www.ala.org.au/) and NR Maps (https://nrmaps.nt.gov.au/nrmaps.html) databases, using the year 1900 as a standard baseline. Occurrence data were extracted from the ALA using the “ALA4R” package (Newman, Raymond, VanDerWal, & Belbin, 2019) in the statistical analysis software R (R Core Team, 2019). Occurrences were then filtered by removing records with no date provided or where location uncertainty was thought to be greater than 500 m (Table S2). To prevent clusters of records resulting from localized survey effort having undue effects on the analysis, only one record was retained in each 1 km × 1 km pixel. A historical data set, containing occurrences from 1900 to 2019, and a contemporary data set, containing occurrences from 2000 to 2019, were created using the presence data for each species (Figure 1). All recent occurrences were thus included in the historical data set, as (a) recent occurrences typically represent populations that were historically present, and (b) this method has been shown to improve reliability of analyses of niche change through time (Martínez-Freiría, Tarroso, Rebelo, & Brito, 2016; Moore et al., 2019). Separating occurrences into two time periods, rather than three or four, split at the year 2000, allowed us to maximize the information content of available data without reducing the number of occurrences to suboptimal levels for modelling. After filtering out spatially or temporally uncertain records, we obtained between 192 and 1,015 historical presence points and between 95 and 684 contemporary presence points per species (Table S3).

While the ultimate and proximate drivers of decline in many Australian savanna mammal species are being debated, recent declines of D. hallucatus are well understood and predominantly due to the spread of invasive cane toads (Rhinella marina) (Braithwaite & Griffiths, 1994; Burnett, 1997; Shine, 2010), which are highly toxic when ingested. As contemporary island populations of D. hallucatus have not been exposed to the threat from cane toads, we removed all island records of D. hallucatus from the analyses. While there is some speculation that cane toads may be implicated in the decline of other mammal species (Radford et al., 2020; Woinarski, Ward, et al., 2011), clear evidence for this is lacking.

2.3 | Study area and background sampling

To avoid the twin problems of (a) overfitting models to bias in occurrence points and (b) under-representing the range of environmental
parameters available in the landscape (Anderson & Raza, 2010), a spatially appropriate study area for each species was first identified. Utilizing a very small study area can under-represent the range of environmental conditions available in the landscape, lead to overly restrictive estimates of species distributions and increase the impact that noise has on model fit (Anderson & Raza, 2010; Barve et al., 2011). Conversely, using the entire region as a study area may result in models being fitted to bias between the occurrence and background points, potentially overfitting to the environmental conditions present in regions where the species is known to occur (Anderson & Raza, 2010; Cooper & Soberón, 2018). As the landscapes of northern Australia are topographically very uniform with few obvious barriers to long-term patterns of dispersal, and savanna ecosystems are broadly contiguous over vast distances, we were unable to create “accessible area” polygons (sensu Barve et al., 2011; Cooper & Soberón, 2018), and so instead we used the historical extent of occurrence (EOO) for each species as a study area (as per Moore et al., 2019). We calculated the EOO using $\alpha$-hulls, a standard IUCN measure for delineating the boundaries of the geographic distribution of a species (IUCN, 2006). This method circumscribes a set of presence points in order to define the EOO of a species. To create the $\alpha$-hull for each species, we used the ashape function of the “alphahull” package in R (Pateiro-Lopez & Rodriguez-Casal, 2019) using an $\alpha$ value of two, as recommended by the IUCN (IUCN, 2006). All predictor layers were then cropped and masked to the outer limit of the EOO.

From this study area, a set of 10,000 background (pseudo-absence) points were then sampled. To compensate for spatial sampling bias in the occurrence data for each species, we modified our sampling of background points by incorporating a probability function that corresponded to the bias in sampling effort. Sampling effort across the study area was estimated by producing a two-dimensional Gaussian kernel density grid of records of small- and medium-sized (<5,500 g) non-flying native mammals. The kernel density grid was created using the kde2d function of the “MASS” package (Venables & Ripley, 2002), with the default normal reference bandwidth calculation. The number of occurrences used to estimate sampling bias for each species of interest varied between approximately 1,000 and 15,000, depending on the size of the study area and the number of islands incorporated into the analysis. This method thus allows for

**FIGURE 1** Location of all historical (orange) and contemporary (red) occurrence points used to investigate patterns of geographic and niche decline in nine species from the savanna mammal assemblage of northern Australia. The regional capital, Darwin, is represented by a green star in each map.
sampling proportionally more background points from geographic areas that have been subjected to a greater survey effort, and fewer background points from less well surveyed regions. This method of target group sampling is commonly used to account for spatial bias in sampling effort (Molloy, Davis, Dunlop, & van Etten, 2017; Phillips et al., 2009; Syfert, Smith, & Coomes, 2013).

2.4 | Environmental covariates

We obtained environmental predictors for use in ecological niche models from a variety of sources (Table 1). Covariates were only included if they had either previously been identified as important determinants of mammal species distributions or we considered them to be relevant to our study area and species. For example, topographic ruggedness, elevation, vegetation cover, and climatic gradients have previously been shown to determine species occurrence in various locations around the world (Badgley et al., 2017; Hortal, Rodríguez, Nieto-Díaz, & Lobo, 2008; McDonald, Stewart, & Dickman, 2018; Molloy et al., 2017; Moore et al., 2019). Similarly, the frequency and intensity of wildfire can play an important role in predicting species distributions and occupancy (Beale et al., 2018; Corey et al., 2019; Einoder et al., 2018). Region-wide satellite-derived records only extend back to the year 2000, and so we make the assumption that fire frequency and vegetation cover metrics recorded from 2000 to 2018 are indicative of longer-term spatial patterns of these variables. As most ready-to-use climate databases, such as CHELSA (Karger et al., 2017), WORLDCLIM (Fick & Hijmans, 2017) and AWAP (Jones, Wang, & Fawcett, 2009), do not cover the full temporal span of our occurrence points, we used custom R scripts to produce mean climate surfaces for annual rainfall, maximum temperature of the warmest month and minimum temperature of the coldest month, from 1900 to 2019, using gridded data in the SILO database (Jeffrey, Carter, Moodie, & Beswick, 2001). This government database provides daily spatial interpolations for the whole of Australia at 5 km resolution. These climate surfaces were highly correlated (correlation coefficient > 0.97 for the three covariates) with equivalent surfaces from the widely used WORLDCLIM data set, suggesting that they are robust representations of mean climatic conditions across the landscape for the entire period being investigated. The SILO data set also more accurately portrays the drivers of rainfall patterns in the region, that is large-scale atmospheric features such as the Madden–Julian Oscillation (which modulates monsoonal and tropical cyclone activity), than does the CHELSA database, which shows a greater topographic influence on rainfall than we would expect for the region.

All covariate layers were imported into R and unified to produce rasters with the same resolution (approximately 1 km × 1 km), extent and projection (Figure S1). We then extracted values for each covariate from each raster at all coordinates of species occurrences.

### Table 1 | Summary of predictor variables collated for use in ecological niche modelling of declining mammal species in northern Australian savannas

| Short name  | Full name                                           | Description and source                                                                                                                                 |
|-------------|-----------------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------------------------------|
| Rainfall    | Mean annual rainfall (mm)                           | Created from daily spatial interpolations of climate data at 5 km resolution provided by the SILO database (https://www.longpaddock.qld.gov.au/silo/) |
| MaxTemp     | Maximum temperature of warmest month (°C)           | Created from daily spatial interpolations of climate data at 5 km resolution provided by the SILO database (https://www.longpaddock.qld.gov.au/silo/) |
| MinTemp     | Minimum temperature of coldest month (°C)           | Created from daily spatial interpolations of climate data at 5 km resolution provided by the SILO database (https://www.longpaddock.qld.gov.au/silo/) |
| Elevation   | Elevation (m above mean sea level)                  | Three arcsecond digital elevation model (DEM), obtained from Geoscience Australia (http://www.ga.gov.au/)                                               |
| TWI         | Topographic wetness (index)                         | Estimates the relative wetness within a catchment. Calculated as log e (specific catchment area/ slope). Obtained from the CSIRO data collection (Gallant & Austin, 2012: Gallant, Dowling, & Austin, 2012) |
| TRI         | Topographic ruggedness (index)                      | A measure of topographic heterogeneity based on elevation differences between adjacent pixels. Created in R using the terrain function of the ‘raster’ package (Hijmans, 2017) and the DEM |
| VegCover    | Mean vegetation fractional cover (%)                | The percentage of photosynthetic vegetation, calculated by averaging the vegetation fractional cover identified by MODIS imagery from 2000 to 2018 using the month of September (after annual grass has died off), was obtained from TERN Auscover (http://www.auscover.org.au/) (Guerschman et al., 2009) |
| FireFreq    | Mean fire frequency (count)                         | A 250 m resolution fire frequency layer (number of times burnt in the 19-year period 2000–2018) derived from MODIS satellite imagery. Obtained from the North Australian Fire Information website (https://www.firenorth.org.au/) |
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(Figure S2) as well as all background points, and any points with missing data were removed. To visualize relationships between predictor variables, we created pairwise scatterplots with correlation coefficients for all combinations of predictor variables using 1,000 randomly sampled points from the data set (Figure S3). While Maxent is quite robust to correlations between variables (Elith et al., 2011), we minimized potential bias due to collinearity through the use of variance inflation factors (VIFs). We used the \textit{vif} function of the package “usdm” (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014) to calculate VIFs based on the square of the multiple correlation coefficient resulting from regressing a predictor variable against all other predictor variables. We then excluded one of any pair that had a VIF ≥ 10, retaining the variable we considered most biologically relevant.

2.5 | Range reduction and niche contraction

Having already created an $\alpha$-hull for the historical EOO of each species, we also created a contemporary $\alpha$-hull using only the contemporary presence points. We then calculated the difference in the area of the historical and contemporary $\alpha$-hulls to determine the change in EOO of each species through time. To estimate the size of the ecological niche in both time periods for each species, we calculated niche hypervolumes using a one-class support vector machine (SVM) method, via the \textit{hypervolume}_{svm} function (with default $\gamma$ value of 0.5) of the “hypervolume” package (Blonder & Harris, 2018). Niche hypervolumes measure the multidimensional space (volume) defined within the bounds of scaled and centred environmental predictor variables (Blonder et al., 2018; Tingley, Vallinoto, Sequeira, & Kearney, 2014). The SVM method was used because hypervolumes with different numbers of data points have the same overall sampling effort, and it allows for outlier inclusion while generating a smooth boundary around the data, facilitating comparisons between time periods. We then calculated the difference between the historical and contemporary hypervolumes to measure change in the ecological niche for each species. To visualize the relationship between reduction in the EOO and reduction in the ecological niche, we plotted the difference (as a percentage) between time periods for each parameter against one another for each species.

2.6 | Quantifying change in the utilization of environmental space

We used two approaches to quantify the change in utilization of environmental space for each mammal species. First, we extracted the values for all eight environmental predictors at 10,000 random points within the contemporary and historical $\alpha$-hulls for each species and created generalized linear models (GLMs) for each environmental predictor variable to determine whether time period was significantly associated with a change in that variable. Coefficients and 95% confidence intervals were extracted from the GLMs and plotted. A significant difference between time periods was identified for each variable based on the $p$-value of a Wald test of significance, with the base \textit{summary} function used to obtain $p$-values for each covariate which were then tabulated.

While the above method examined the differences between historical and contemporary $\alpha$-hulls, we considered that differences between $\alpha$-hulls may not be fully representative of the points within the $\alpha$-hulls that are being occupied by species. To address this, we used bootstrap hypothesis testing (Fisher & Hall, 1990) to determine whether the values of environmental covariates at contemporary presence points were likely to be a random subset of the historical values. The values of environmental covariates at each presence point for each species were extracted from raster layers, and the historical data were sampled 10,000 times using the same number of presence points as there was in the contemporary data set, taking the mean value of each bootstrap. A two-tailed significance test (i.e. testing whether the contemporary mean value was in either the upper 2.5% or lower 2.5% of the bootstrapped probability distribution) was then used to determine the probability that the contemporary mean value of a covariate would result from a random subset of historical values. All $p$-values were then tabulated.

2.7 | Niche model creation and evaluation

We used the “Maxent” algorithm (Phillips, Anderson, Dudik, Schapire, & Blair, 2017; Phillips, Anderson, & Schapire, 2006) to create ecological niche models and predict habitat suitability for each species across geographic space. We used Maxent because its predictions have been shown to perform well when accounting for sampling bias and by utilizing a large number of background points from the landscape (Elith et al., 2011; Syfert et al., 2013). The default output of Maxent is a habitat suitability value that has undergone a logistic post-transformation, in an attempt to obtain a value that is as close to the probability of occurrence as possible, given the environment (Calabrese, Certain, Kraan, & Dormann, 2014; Elith et al., 2011). A model selection process allowed us to determine the best Maxent model from a set of competing models, each model with different parameter combinations. We used the \textit{ENMeval} function from the “ENMeval” package (Muscarella et al., 2014) to test a range of regularization coefficients (beta multiplier values from 0.5 to 3, in increments of 0.5) and feature class combinations (linear only, linear and quadratic, and linear, quadratic and product). The most appropriate model parameters were then identified using the Akaike information criterion, standardized for small sample sizes. Using a measure of fit to determine model parameters, as opposed to using default values, is appropriate when investigating small numbers of target species (Merow, Smith, & Silander, 2013). The top model parameters were then run using the maxent function of the “dismo” package (Hijmans, Phillips, Leathwick, & Elith, 2017), using five cross-validation runs. Average values across all cross-validation runs for two metrics were extracted from the model output. These metrics included (a) the area under the curve (AUC) of a receiver operating characteristic,
which estimates overall model fit via a threshold-independent measure of predictivity, and (b) permutation importance, a measure of the relevance of each predictor variable to the response variable. To calculate permutation importance, the values of a predictor variable are first randomly permuted among the occurrence and background points, the model is re-evaluated, and the resulting drop in the AUC value is calculated and normalized to a percentage (Phillips, 2017; Searcy & Shaffer, 2016).

2.8 | Multispecies ecological suitability

We imported each ecological niche model prediction into R and unified rasters to the same resolution, extent and projection. We then overlaid the rasters for each time period and summed the habitat suitability values across all layers without any threshold (Calabrese et al., 2014), producing two maps of multispecies ecological suitability across the eight declining mammal species. While we do not necessarily consider these to be true species richness maps, the maps do allow us to (a) make inferences about the spatial pattern of richness across the landscape, and (b) identify regions in which these mammal species are likely to be more resilient to contemporary ecological threats. Probabilistic stacking of ENMs has been shown to outperform other methods of predicting the spatial distribution of species assemblages, including binary stacking or use of joint species distribution models (Zurell et al., 2020).

3 | RESULTS

3.1 | Range reduction and niche contraction

Most species showed substantial reductions in their EOO and niche hypervolumes between time periods (Figure 2). The smallest and largest proportional declines in EOO across time periods were observed for *I. macrourus* (1.8%) and *C. penicillatus* (68.8%).

**FIGURE 2** Reductions in niche hypervolume and alpha (α) hull areas (i.e. extent of occurrence) between a historical and a contemporary time period for nine species of mammals in northern Australian savannas. Panel (a) shows the absolute values of parameters whereas panel (b) shows the percentage reduction in each parameter. The dashed line in panel (b) represents a 1:1 relationship.
respectively. The smallest and largest proportional declines in niche hypervolume across time periods were observed for P. nanus (24.9%) and T. vulpecula (50%), respectively. Six of the nine species showed greater reductions in niche hypervolume than in EOO (Figure 2), suggesting that they have declined to a subset of their historical niche. The mean reduction in niche hypervolume (39%) was slightly larger than the mean reduction in the EOO (30.5%), with a very weak correlation ($r = 0.07$) between the two parameters. We found a moderate level of correlation ($r = -0.34$) between the historical EOO and reduction in EOO, and a moderate correlation ($r = -0.48$) between the historical niche hypervolume and extent of niche contraction. Interestingly, while historical EOO was moderately correlated ($r = -0.57$) with the decline in niche hypervolume, the historical niche hypervolume showed no correlation ($r = 0.001$) with the decline in EOO.

Patterns of change in covariate values at real presence points were broadly similar to the results observed for the $\alpha$-hull comparisons, including a general shift towards areas of higher rainfall, lower maximum temperature and higher minimum temperature. However, some notable differences were observed. Importantly, contemporary values of fire frequency did not show significant increases from historical values for most species (Table 2). In fact, contemporary presence points of I. macrourus, T. vulpecula, P. breviceps and R. tunneyi showed significant or near-significant shifts towards areas of lower fire frequency, despite the contemporary $\alpha$-hulls for T. vulpecula, P. breviceps and R. tunneyi having significantly higher fire frequencies than historical $\alpha$-hulls. The importance of vegetation cover was also more pronounced in the bootstrapping results, with six of the nine species showing significant or near-significant shifts towards areas of higher vegetation cover.

### 3.3 | Ecological niche modelling

Ecological niche models produced using Maxent (Figures S5 and S6) showed moderate to high AUC values (Table S4), suggesting that model fits were suitable for analysis. As is typically found with ENM training and testing datasets, the AUC values for the testing data were typically close to, but slightly lower than, the values for the training data.

Permutation importance values were mostly similar across time periods, with most covariates showing absolute changes of less than five percentage points between historical and contemporary niche models (Table S6). Four species showed changes in more than 10 percentage points in at least one covariate, including A. bellus (MinTemp), P. nanus (VegCover and Elevation), R. tunneyi (Elevation and MinTemp) and T. vulpecula (Rainfall). This suggests that these species have experienced a large shift in these predictors across time periods. For example, the results for P. nanus show that its historical occurrence was largely predicted by rainfall, elevation and ruggedness, whereas its contemporary occurrence is much more related to vegetation cover.
While there was a high level of variation between species in the permutation importance values of the contemporary ecological niche models, Rainfall, Elevation and MinTemp each had importance values that were >20% for at least three species (Table 3).

### 3.4 | Multispecies ecological suitability

Summing the predicted probabilities of occurrence across species showed that there are well-defined regions that are likely to be providing contemporary refuges for multiple declining species (Figure 3). Visualizing differences in multispecies habitat suitability between time periods showed that the highest values were observed for the Cobourg Peninsula, parts of the Tiwi Islands, and islands in the north-east of the study area. These areas are broadly characterized by higher rainfall, milder climates and relatively tall open-forest vegetation communities. In contrast, declines in suitability were observed across large areas of the western half of the study region (including one of the largest reserved areas in Australia, Kakadu National Park) and the south-eastern coastline: areas typically characterized by higher maximum temperatures, lower rainfall and lower, more open woodland vegetation communities.

### 4 | DISCUSSION

We investigated patterns of niche and range reduction in nine species of declining savanna mammals and found that niche declines typically followed a different, and often steeper, trajectory to declines in range size. We found significant contractions in the occurrence of multiple species into areas of higher rainfall, higher minimum temperatures, lower maximum temperatures, lower fire frequencies and higher vegetation cover. It is likely that, under such conditions, threats are reduced and/or species have a greater capacity to tolerate those threats. With analogous threatening processes emerging across many of the world’s ecosystems (Abatzoglou & Williams, 2016; Lindenmayer, Hobbs, Likens, Krebs, & Banks, 2011), studies such as ours can assist policymakers and land managers to plan and improve conservation management actions, even when ultimate or proximate causes of declines are not yet fully elucidated.

#### 4.1 | The relationship between range reduction and niche decline

The niche reduction hypothesis suggests that contraction of the realized niche is likely to be a common phenomenon as species decline, because the intensity of threats and/or the capacity to tolerate threats varies across niche space (Scheele et al., 2017). Here, we provide the first quantification of this hypothesis using a taxonomically diverse, declining mammal assemblage in northern Australia, and report that in six of nine species the contraction of the realized niche was greater than reduction of the EOO.

Broadly, our results corroborate simulation predictions that change in niche breadth will poorly reflect change in range size in declining species (Breiner, Guisan, Nobis, & Bergamini, 2017). Differences between these response parameters can be quite stark in some cases. For example, one of our target species, I. macrourus, experienced a decline in EOO of just 1.8% and a decline in niche hypervolume of 34.9%. While there is some evidence that range size and niche breadth tend to be moderately correlated (Slatyer et al., 2013), our results suggest that there is a high level of variation in the response of these two parameters to declines, and correlations can be weak across an assemblage. Further, while other studies have reported that the historical niche breadth of species appears to predict extent of range reductions (i.e. species with a narrow niche are more likely to experience a reduction in range) (Botts et al., 2013), we found no correlation between these two measures for our mammal assemblage.

We argue that species experiencing a greater reduction in the breadth of the realized niche than the EOO may be at greater risk of extinction than appreciated by evaluation under IUCN criteria, which often rely heavily on declines in EOO for assessment (IUCN, 2006, 2012). This increased risk is the result of the species inhabiting a narrower set of environmental conditions, making them more vulnerable to changing environments and threatening processes. The

| TABLE 3 | Permutation importance values for contemporary ecological niche models for nine species of mammals in northern Australia |
|-----------------------------------------------|-----------------------------------------------|
| Antechinus bellus                             | 10.33                                        |
| Conilurus penicillatus                       | 14.25                                        |
| Dasyurus hallucatus                          | 27.07                                        |
| Isoodon macrourus                            | 13.09                                        |
| Mesembrionys gouldii                         | 30.17                                        |
| Petaurus breviceps                           | 11.88                                        |
| Pseudomys nanus                              | 11.90                                        |
| Rattus tunneyi                               | 13.17                                        |
| Trichosurus vulpecula                         | 51.37                                        |
| Rainfall                                     | Elevation                                    |
| Rainfall                                     | 5.50                                         |
| Rainfall                                     | 8.08                                         |
| Rainfall                                     | 15.44                                        |
| Rainfall                                     | 27.75                                        |
| Rainfall                                     | 17.24                                        |
| Rainfall                                     | 24.20                                        |
| Rainfall                                     | 34.43                                        |
| Rainfall                                     | 9.58                                         |
| Rainfall                                     | 10.87                                        |
| FireFreq                                     | 0.72                                         |
| FireFreq                                     | 2.12                                         |
| FireFreq                                     | 8.08                                         |
| FireFreq                                     | 15.94                                        |
| FireFreq                                     | 19.75                                        |
| FireFreq                                     | 7.67                                         |
| FireFreq                                     | 19.85                                        |
| FireFreq                                     | 3.63                                         |
| FireFreq                                     | 8.36                                         |
| FireFreq                                     | 5.42                                         |
| FireFreq                                     | 4.55                                         |
| FireFreq                                     | 5.42                                         |
| FireFreq                                     | 4.55                                         |
| FireFreq                                     | 5.42                                         |
| FireFreq                                     | 4.55                                         |
| FireFreq                                     | 5.42                                         |
| FireFreq                                     | 5.42                                         |
| FireFreq                                     | 5.42                                         |
| MaxTemp                                      | 40.48                                        |
| MaxTemp                                      | 33.02                                        |
| MaxTemp                                      | 10.20                                        |
| MaxTemp                                      | 12.52                                        |
| MaxTemp                                      | 12.52                                        |
| MaxTemp                                      | 12.52                                        |
| MaxTemp                                      | 12.52                                        |
| MaxTemp                                      | 12.52                                        |
| MinTemp                                      | 35.27                                        |
| MinTemp                                      | 33.43                                        |
| MinTemp                                      | 12.18                                        |
| MinTemp                                      | 8.67                                         |
| MinTemp                                      | 8.67                                         |
| MinTemp                                      | 8.67                                         |
| MinTemp                                      | 8.67                                         |
| TRI                                          | 1.91                                         |
| TRI                                          | 3.63                                         |
| TRI                                          | 16.46                                        |
| TRI                                          | 0.83                                         |
| TRI                                          | 0.83                                         |
| TRI                                          | 7.00                                         |
| TRI                                          | 4.95                                         |
| TRI                                          | 7.00                                         |
| TRI                                          | 7.00                                         |
| TWI                                          | 2.66                                         |
| TWI                                          | 1.66                                         |
| TWI                                          | 4.95                                         |
| TWI                                          | 7.00                                         |
| TWI                                          | 4.95                                         |
| TWI                                          | 7.00                                         |
| VegCover                                     | 3.13                                         |
| VegCover                                     | 3.81                                         |
| VegCover                                     | 5.62                                         |
| VegCover                                     | 5.62                                         |
| VegCover                                     | 5.62                                         |
| VegCover                                     | 5.62                                         |
| VegCover                                     | 5.62                                         |
| VegCover                                     | 5.62                                         |
| VegCover                                     | 5.62                                         |
| VegCover                                     | 5.62                                         |
| VegCover                                     | 5.62                                         |
| VegCover                                     | 5.62                                         |

Note: Cells have been coloured according to the level of importance of the variable (darker = more important). Values represent the normalized importance (as a percentage) of each variable’s contribution to the model.
degree to which range decline correlates with a reduction in EOO may depend on the spatial distribution (patchiness and geographic extent) of refuge habitats where threats are either reduced or are more tolerable (Channell & Lomolino, 2000a). The distribution of refuge habitats is also likely to depend on the specific threatening processes impacting a species. In the case of *I. macrourus* and *T. vulpecula*, fire frequency is associated with decline patterns and fire-related refuge habitats are patchily but broadly distributed across the landscape. Under such circumstances, it should be noted that a small decline in the EOO may potentially mask a substantial decline in the extent of suitable environmental conditions within the EOO. In contrast to this, the primary threat for *D. hallucatus* (i.e. introduced cane toads) is effectively ubiquitous across the landscape, resulting in a large geographic decline and a relatively small niche breadth decline, with refuge habitats not as broadly available.

### 4.2 Causes of niche contractions—variability in threat intensity or mediation of threat impact?

The niche reduction hypothesis proposes that species are able to persist under certain environmental conditions because those...
conditions either mediate the threatening process or enable a species to tolerate the threat impact (Scheele et al., 2017). It is likely that both of these situations are at play in our study system. While there were differences among species in the environmental dimensions of niche declines, there was a common set of niche dimensions (high vegetation cover, high rainfall, low fire frequency and mild temperatures) associated with species persistence.

In the context of understanding conditions associated with species persistence, some background on the threat posed to northern Australian mammals through predation by feral cats and inappropriate fire regimes is needed. Feral cats are highly successful predators after fire events, so our results may reflect fire as a process that influences the susceptibility of native mammals to the threat of predation by an exotic species (Carwardine et al., 2012; McGregor, Legge, Jones, & Johnson, 2014, 2015). Higher vegetation cover and mid-storey complexity might also mediate the impacts of feral cats, by limiting cat densities and/or reducing their hunting efficiency (McGregor, Legge, Jones, & Johnson, 2014, 2015). On the other hand, niche contraction to areas of high rainfall is likely to be an example of environmental conditions enabling species to tolerate threatening processes. High rainfall can strongly modify demographic parameters such as survival, growth and recruitment (Nouvellet, Newman, Buesching, & Macdonald, 2013), thereby buffering populations against threats related to fire frequency and feral predators. We suggest that demographic buffering due to these factors is likely to be a common feature of contemporary niches when species declines are driven by biotic threats (Scheele et al., 2016).

Broadly, the environmental dimensions that we identified as being most important align with species-specific research conducted in the study region, yet the niche focus offers new insights. For example, fire frequency has been documented as an important driver of habitat suitability for many species. High fire frequency can lower vegetation cover and reduce mid-storey vegetation complexity (Russell-Smith, Price, & Murphy, 2010; Woinarski, Risler, & Kean, 2004), factors that are thought to be important components of habitat quality for C. penicillatus and T. vulpecula (Davies et al., 2017; Geyle et al., 2019; Stobbe-Wilson et al., 2019). Similarly, research has also demonstrated that simplification of understorey vegetation by large exotic herbivores and frequent high-intensity fire increases the density of feral cats (Davies et al., 2020), while at the same time reducing the ability of small mammals to avoid predators (Legge et al., 2019). Applying a niche lens does not specifically identify threatening processes, but can illustrate how the breadth of conditions (e.g. fire frequency and vegetation structure) occupied by each species has changed (rather than simply a reduction in the geographic extent of those same conditions), thus improving our understanding of interactions between threatening processes and niche dimensions.

4.3 Improving conservation through the characterization of niche declines

The most intuitive conservation outcome of niche modelling is the identification of conditions under which species can persist in the context of contemporary threats, and the geographic locations of those conditions. While we acknowledge that field-based validation is important, using a contemporary niche modelling approach may be more informative than mapping distributions from known records when survey intensity is low or study areas are large, remote and difficult to access. Our models identified environmental characteristics of different geographic areas that may be informative in planning conservation actions. Formal spatial prioritization of management actions can integrate a number of evolutionary considerations into the process of conservation planning, which may include ensuring that a representative sample of niche conditions is conserved (Faith & Walker, 1996), or through the generation of prioritizations for evolutionary lineages or ecotypes (Carvalho, Brito, Crespo, & Possingham, 2011). Native mammal declines in northern Australia are occurring across land tenures including World Heritage-listed national parks, and the regions we identified where contemporary niche conditions occur, or have been more stable, could be considered areas of conservation value in the absence of further effective management of threatening processes. If conservation management is to sustain species within landscapes, it is vital that resilience to the impacts of threatening processes in such refuge habitats is promoted, and the availability of these refuges is increased or maintained (Reside et al., 2019).

Focussing on the environmental dimensions of niche declines, the niche modelling approach enables identification of habitat variables that can potentially be managed to expand the geographic extent of the realized niche. For example, understorey and shrub-level vegetation structure can be improved through management of fire regimes and density of large exotic herbivores, with cost-benefit analyses suggesting high feasibility in this regard (Carwardine et al., 2012). A strategic and adaptive implementation of actions to manage these environmental dimensions is thus likely to be the most tractable approach to large-scale conservation of critical weight range mammals in the study area. Existing systematic conservation planning tools, such as Marxan with Zones (Watts et al., 2009), can be used to achieve this through the development of a spatially explicit multi-zone prioritization framework. While there is strong evidence that a range of native mammals decline more severely in areas subject to frequent fires (Griffiths, Garnett, & Brook, 2015; Lawes et al., 2015; Legge et al., 2019), fire managers have a much greater capacity to reduce fire intensity than frequency, by burning early in the dry season (Russell-Smith et al., 2013). Thus, critical avenues of further research should include investigating meta-population persistence of declining species under economically and logistically feasible landscape fire management strategies, relating to the amount of long-unburnt habitat within the landscape and the different impacts of early versus late dry season fires.

4.4 Secondary consequences of reduced niche breadth

When declining species experience reductions in realized niche breadth, there is potential for declines in the fundamental niche
if there is a loss of adaptive genetic diversity associated with environmental conditions that no longer occur in the realized niche. It is well established that range declines can lead to losses of genetic diversity, through selectively neutral processes associated with low population sizes and reduced gene flow (Andersen, Fog, & Damgaard, 2004; Hague & Routman, 2016). However, under the scenario of a substantial reduction in niche breadth, even with a relatively small reduction in EOO (e.g. the pattern we observed for L. macrourus and T. vulpecula), it is possible that a substantial loss of genetic diversity could occur without a noticeable contraction of the EOO (Willoughby et al., 2015). While a quantitative comparison of genetic parameters among species with varying levels of niche contraction and EOO reduction has not been conducted, we suggest that this would be an important avenue of future research. In an applied context, a key question for conservation management agencies is whether individuals from refuge habitats are genetically and phenotypically capable of recolonizing environmental space from which the species was extirpated. This is pertinent in light of strong differences between intraspecific lineages in responses to threats (Levin, 2019), as well as genetic evidence of local adaptation (Anderson, Perera, Chowdhury, & Mitchell-Olds, 2015), particularly on the margin of species’ geographic distributions (Kawecki, 2008).

5 | CONCLUSION

The niche reduction hypothesis provides a powerful lens for examining factors influencing patterns of species decline across landscapes. Importantly, a niche perspective can inform conservation management by identifying environmental conditions under which threatening processes are either mediated or tolerated, which can guide the development of management activities that maximize protection of refuges and increase population persistence. We suggest that utilizing and building upon approaches such as the method presented here provides an opportunity for pre-emptive conservation action, rather than acting on species declines when extinction risk is high and genetic diversity and adaptive potential are much reduced.

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PEER REVIEW

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DATA AVAILABILITY STATEMENT

All scripts and data used in this study have been deposited to the Dryad Digital Repository.

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BIOSKETCH

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Author contributions: BvT and SB conceived the ideas; BvT conducted the data collection and analysis with input from all co-authors; BvT led the writing with assistance from BS, SB, BM and HM; all authors contributed to framing and intellectual content.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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