

Topographic ruggedness and rainfall mediate geographic range contraction of a threatened marsupial predator

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Abstract

Aim: Species range contractions are increasingly common globally. The niche reduction hypothesis posits that geographic range contractions are often patterned across space owing to heterogeneity in threat impacts and tolerance. We applied the niche reduction hypothesis to the decline of a threatened marsupial predator across northern Australia, the northern quoll (*Dasyurus hallucatus*).

Location: Northern Australia.

Methods: We assembled a database containing 3,178 historic and contemporary records for northern quolls across the extent of their distribution dating between 1778 and 2019. Based on these records, we estimated changes in the geographic range of the northern quoll using α -hulls across four main populations. We then examined how range contractions related to factors likely to mediate the exposure, susceptibility, or tolerance of northern quolls to threats.

Result: The extent of range contractions showed an east–west gradient, most likely reflecting the timing of spread of introduced cane toads (*Rhinella marina*). There were clear changes in environmental characteristics within the contemporary compared to the historic geographic range, with the most substantial occurring in populations that have suffered the greatest range contractions. The contemporary range is comprised of higher quality habitats (measured using environmental niche models), characterized by higher topographical ruggedness and annual rainfall, and reduced distance to water, compared to the historic range.

Main conclusions: Changes to range and niche likely reflect the capacity of complex habitats to ameliorate threats (namely predation and altered fire regimes), and access to resources that increase threat tolerance. This study highlights the multi-variate nature of ecological refuges and the importance of high-quality habitats for the persistence of species exposed to multiple threats. Our methods provide a useful framework which can be applied across taxa in providing valuable insight to management.

KEYWORDS

introduced species, niche decline, range contraction, refuge, threatened species

1 | INTRODUCTION

The contraction of species' geographic ranges is the result of population decline and local extinction, and a stark, prominent manifestation of adverse anthropogenic environmental change (Hobbs, Valentine, Standish, & Jackson, 2017). Range contractions are increasingly common across the globe (Thomas, Franco, & Hill, 2006)—for instance, 40% of 177 mammal species studied by Ceballos, Ehrlich, and Dirzo (2017) have experienced range contractions of >80%. As range contractions increase extinction risk (Purvis, Gittleman, Cowlshaw, & Mace, 2000), the extent of a species' geographic range, as well as its population size, are considered key elements by the International Union for Conservation of Nature (IUCN) in determining a species' global conservation status (IUCN, 2006). Range contractions entrain a raft of changes that occur when species are in decline, such as changes to species' niches (Breiner, Guisan, Nobis, & Bergamini, 2017). Small changes in a species' geographic range size can correspond to substantial reductions in its niche breadth, and *vice versa*, due to local extinctions occurring in distinct environments (Breiner et al., 2017), leading to spatial patterning in range declines (McDonald, Luck, Dickman, Ward, & Crowther, 2015).

To integrate the concepts of range decline and niche reduction, Scheele, Foster, Banks, and Lindenmayer (2017) introduce the 'niche reduction hypothesis'. This hypothesis distinguishes between a species' 'historical niche'—defined as the realized niche of a species prior to decline—and the 'contemporary niche', a subset of the historical niche after a reduction in niche breadth due to novel threats (e.g. introduced species, habitat loss, disease). Three factors that shape the contemporary niche of species are (a) *threat occurrence*, which, when a threat operates variably across different populations or parts of a species' range, may cause species to persist only in environmental refugia, (b) a species' *threat tolerance*, the ability to persist despite

threats, which can be increased within a subset of environmental conditions due to, for example, larger populations sizes, and (c) *geographic barriers* that exclude threats from a part of a species range (Scheele et al., 2017). Understanding how threats shape species' niches, and geographic ranges, is critical to conservation, as it can assist in identifying ecological refuges (Reside et al., 2019). Further, basing conservation on the contemporary niche can lead to a narrow understanding of a species' potential habitat, thereby limiting the range of options available for conservation, translocation and restoration (Scheele et al., 2017).

Here, we apply Scheele et al. (2017) niche reduction hypothesis by quantifying changes in the historical and contemporary range and niche of four populations of a marsupial predator—the northern quoll (*Dasyurus hallucatus*). The northern quoll is the smallest of four *Dasyurus* species found in Australia, ranging from 300 to 1,200 g, and males within the species often exhibit a semelparous life history, surviving for only a single breeding season (Oakwood & Cockburn, 2001). The geographic range of northern quolls spans much of northern Australia (Figure 1), but is suspected to have declined considerably since European colonization of Australia (1788), and particularly in the past 50 years (Braithwaite & Griffiths, 1994). Consequently, the northern quoll is classified as 'endangered' by the IUCN, with a 'declining' population trend (IUCN, 2016). The main threats to northern quolls are predation by introduced animals such as feral cats, poisoning by the introduced cane toads (*Rhinella marina*), and habitat degradation caused by altered fire regimes and grazing by introduced herbivores (IUCN, 2016).

The northern quoll offers an excellent case study of range contraction and niche reduction in a declining species for three reasons. First, declines in northern quoll range have occurred relatively recently (i.e. from the mid to late 20th century to the present day), and so, an extensive catalogue of species records exists from within both

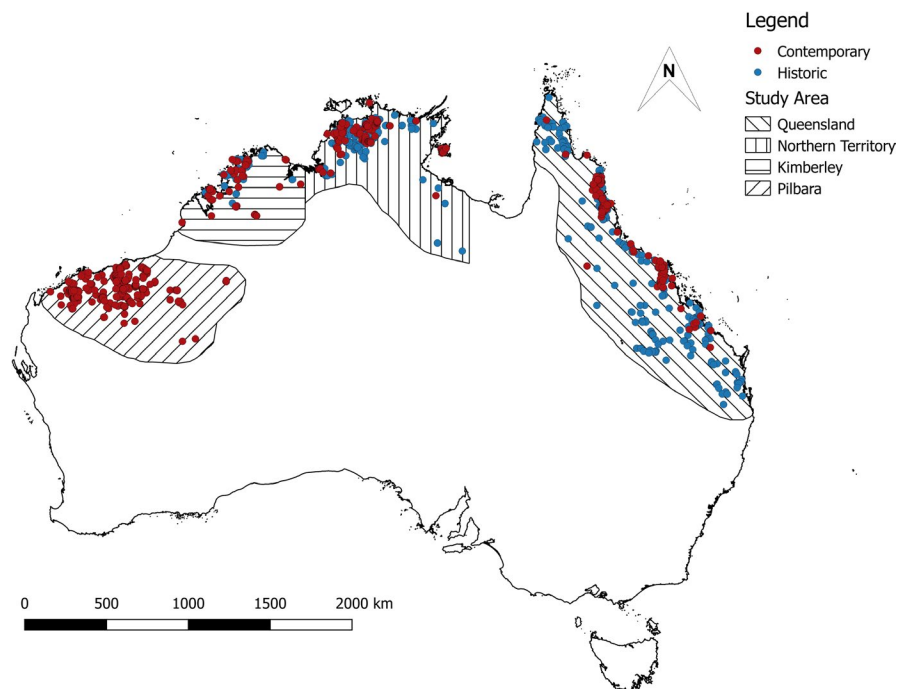


FIGURE 1 Northern quoll presence records across each of the four populations. Blue markers represent historic presence records, and maroon markers represent contemporary presence records (>2,000). Populations are represented by varying line patterns

its historic and contemporary range. This is not the case for many of the Australian mammals that declined earlier following European colonization (Woinarski, Burbidge, & Harrison, 2015).

Second, in addition to range contractions, northern quolls are thought to have suffered a reduction in niche breadth, due to the disproportionate loss of local populations from particular environments, such as lowland savanna and the arid fringe of their range (Braithwaite & Griffiths, 1994; McKenzie, 1981; Oakwood, 2000). Consistent with the niche reduction hypothesis, local extinctions are thought to have related to both threat occurrence and threat tolerance. For instance, topographically rugged areas (e.g. rocky outcrops) are considered to offer fixed refuges (*sensu* Reside et al., 2019) from predation, grazing and fire (Burnett, 1997), increasing the likelihood of persistence of northern quolls (Begg, 1981). In addition, local extinctions are hypothesized to have occurred more often in marginal habitats (i.e. low rainfall and lower population size) that predispose populations to a lower threat tolerance due to smaller population sizes (Burnett, 1997).

Third, range contractions of northern quolls likely differ across its four main populations (Queensland, Northern Territory, Kimberley and Pilbara), due to geographic barriers that have so far prevented one primary threat—the cane toad (*R. marina*)—from reaching parts of the northern quoll's geographic range. Cane toads were introduced to Queensland in 1935 and spread westwards across the northern third of Australia, reaching the Northern Territory during the early 1970s (Urban, Phillips, Skelly, & Shine, 2008), and the Kimberley in 2010 (Doody et al., 2018; although they have not yet colonized that region entirely), but have not yet reached the Pilbara (Appendix S3). The primary mechanism by which northern quolls are impacted by cane toads is through lethal ingestion (Shine, 2010). While there have been a number of reports documenting local northern quoll extinctions in Queensland (Burnett, 1997; Burnett & Zwar, 2009; Woinarski et al., 2008) and the Northern Territory (Braithwaite & Griffiths, 1994; Oakwood, 2004; Woinarski et al., 2010; Ziembicki, Woinarski, & Mackey, 2013), fewer extirpations have been recorded in the Kimberley (Hohnen et al., 2016; Start, Burbidge, McKenzie, & Palmer, 2007), and none have been documented in the Pilbara (Cramer et al., 2016), a pattern of loss consistent with the sequential spread of toads.

We quantify and compare environmental conditions within the historic and contemporary geographic range of the northern quoll across its four major populations, compare range declines with niche reductions (i.e. declines in niche volume), and compare environmental conditions within the contemporary niche to those within the historic niche. We predicted that range size and niche volume would be most reduced in Queensland and the Northern Territory, due to their long-term exposure to cane toads. Consistent with the niche reduction hypothesis, we predicted that range declines within each population would relate to environmental variables that buffer (due to reduced co-occurrence) or increase the threat tolerance of quolls. Specifically, contemporary ranges would trend towards more topographically rugged areas with higher rainfall and greater protection from fire when compared to historic ranges due to extinctions

occurring more often in more open, topographically simple and marginal habitats.

2 | METHODS

2.1 | Study area

The region over which northern quolls are believed to have occurred is ~2,634,641 km² and stretches from south of Brisbane on Australia's east coast, along northern Australia, to the Pilbara region in Western Australia. This region includes four discrete populations of northern quolls: in Queensland, the Northern Territory (including several islands), the Kimberley (including several islands) and the Pilbara (Figure 1). We used previous estimates of northern quoll range to guide the placement of population boundaries (Braithwaite & Griffiths, 1994; Oakwood, Woinarski, & Burnett, 2016). Recent analysis suggests each of these populations function as distinct evolutionally significant units, and thus in the interests of genetic conservation, they should be considered separately (How, Spencer, & Schmitt, 2009).

The Queensland population spans substantial climatic variation with northern areas characterized by monsoonal wet seasons (December–March), while southern coastal areas receive rainfall that is less seasonal, and the western extent exhibits semi-arid conditions (BOM, 2019; Table 1). Vegetation varies significantly ranging from monsoonal rain forests to mixed eucalypt woodlands and tropical savannas (NVIS, 2019). The Northern Territory population experiences a monsoonal tropical climate, with rainfall falling mainly in the period December–March (BOM, 2019; Table 1). Vegetation is mostly characterized by eucalypt open woodlands and forests, spinifex grasslands and tropical savannas (NVIS, 2019). The Kimberley population also experiences a tropical monsoonal climate (Table 1). Vegetation is characterized by desert grasslands in the southern interior and tropical savanna in the north (DPIRD, 2017). Climate in the Pilbara is characterized by extremely hot summers, mild winters and low rates of sporadic rainfall (BOM, 2019; Table 1). Vegetation is dominated by *Acacia* and *Eucalyptus* low woodlands and hummock grasslands (NVIS, 2019).

2.2 | Data collection

A database containing 6,391 northern quoll records was collected from national and state/territory fauna databases, museum records, past publications, trap records as well as mining and government agencies, dated between 1788 and January 2019. The majority of records were sourced from online databases the Atlas of Living Australia (ALA, 2019), NatureMap (NatureMap, 2019) and Wildnet (Wildnet, 2019) as well as a 2008 Australian government report investigating northern quoll decline in northern Australia (Woinarski et al., 2008). Duplicates were identified and removed. Records missing information or with high locational inaccuracy were also removed. In the interest of controlling for threat absences on islands, all island records were removed from our analysis. To minimize the effect of

TABLE 1 Study area size and climatic variability in terms of mean coldest and warmest quarter temperature, as well as annual precipitation

Population	Study area (km ²)	Mean coldest quarter temp range (°C)	Mean warmest quarter temp range (°C)	Annual precipitation range (mm)
Queensland	989,833	8.6–25.4	19.9–30.4	407–3,945
Northern Territory	619,058	17.9–24.3	28.2–31.6	340–1,834
Kimberley	362,014	19.1–25.6	27.6–33.0	419–1,453
Pilbara	663,736	13.2–21.9	28.6–33.3	216–465

localized survey effort on analysis, all records collected within the same year in the same 1 km × 1 km grid cell were condensed to one.

Following Martínez-Freiría, Tarroso, Rebelo, & Brito, 2016), we separated our data set for each population into two: a historical data set, which sought to describe ranges prior to the year 2001, and a contemporary data set, which sought to describe the range of populations from 2001 onwards. Also following Martínez-Freiría et al. (2016), the historical data set included the contemporary observations (i.e. was 'nested'), so that it included all populations that have likely been present (but may not have been detected) since European colonization. This approach was justified given the relatively sparse sampling effort in the historical period. To test the effect that nesting contemporary records within historic records had on our results, we ran a series of analyses (methods below) on both nested and un-nested data sets and compared the results. In Queensland and the Northern Territory, we found nesting had little impact on range contraction, niche volume or habitat suitability predictor importance (Appendix S2). Conversely, in the Kimberley and the Pilbara, where historical sampling was less thorough, we found range size and niche volume increased through time in un-nested data sets—trends with no supporting evidence. Based on this comparison, we elected to only use nested data in further analysis.

We chose the year 2000 as the separation point between historic and contemporary data sets as it allowed us to have a large number of presences both before and after this point, facilitating the development of separate range estimates for each population during each of the two time periods (historic and contemporary). While separating the data into more than two time periods would have been preferable, the amount of presences within finer temporal windows did not allow for the development of reliable models. Further, while we note that local extinctions have occurred post-2000 (Oakwood, 2004), these are likely minor compared to the reductions that occurred in the 20th century when cane toads and invasive predators spread across a large proportion of the quoll's range (Braithwaite & Griffiths, 1994).

2.3 | Range contractions

We measured change in geographic range using α -hulls, a standard IUCN measure representing a generalization of convex polygons that accounts for breaks in a species range (IUCN, 2006). Breiner et al. (2017) found α -hulls closely tracked simulated extinctions and outperformed a range of alternative range quantification metrics

(e.g. ENMs, convex polygons). Following IUCN recommendations (IUCN, 2006), we used an α value of two when calculating α -hulls for all data sets. α -hulls were created using 'alphahull' package in R (Pateiro-López & Rodríguez-Casal, 2009).

2.4 | Niche change

We quantified niche volume (the space defined within the bounds of n independent environmental axes) for each population in each time period. To do this, we used niche hypervolumes generated by a one-class support vector machine method (SVM), as described by Blonder et al. (2019). Hypervolumes were defined by the bounds of the five environmental variables (Table 2) and were scaled prior to analysis (following Tingley, Vallinoto, Sequeira, & Kearney, 2014). The SVM was used as it is insensitive to outliers and generates a smooth boundary around the data, yielding binary predictions of niche volume, facilitating comparisons between data subsets. Once all n -dimensional hypervolumes had been assembled, niche volume was calculated and compared within populations to assess niche reduction. Hypervolumes were calculated in the R package 'hypervolume' (Blonder, Lamanna, Violle, & Enquist, 2014).

We created a layer of habitat quality for northern quolls across study populations using ecological niche models (ENMs). Ecological niche models combine presence records with environmental data to predict habitat that is most likely to support populations of a given species (Guisan & Thuiller, 2005). Ecological niche models were developed using the MaxEnt algorithm (Elith et al., 2011). MaxEnt default output consists of a map with every cell assigned a log value representing relative probability of occurrence, ranging from 0 to 1. Cell size for all ENMs in this study was 1 km² (1 km × 1 km). To quantify habitat quality within the range of northern quolls, we incorporated five ecogeographical layers based on evidence within the literature supporting their relevance to northern quoll ecology (Table 2). As presence-only data are often subject to selection bias, we included a bias grid within MaxEnt models, indicating sample biases across the study area (Kramer-Schadt et al., 2013). We used a 'target group' background sampling approach to generate the bias layers (Phillips et al., 2009). We defined our target group as all critical weight range (CWR) mammals (including northern quoll) within the study area (following Molloy, Davis, Dunlop, & van Etten, 2017). These species were selected as survey methods used to detect them would also detect the northern quoll (following Molloy et al., 2017)—typically

TABLE 2 Variables included in northern quoll ecological niche model and hypervolume analysis accompanied by justification for inclusion and source

Variable	Description	Justification	Source
Topographical ruggedness	Calculated from the difference in elevation between a cell and the eight cells surrounding it (following Riley, 1999)	Studies suggest quality northern quoll habitat is often associated with rocky rugged areas (Braithwaite & Griffiths, 1994; Burnett, 1997; Hernandez-Satin, 2016; Schmitt et al., 1989)	Calculated according to Riley (1999) Geoscience Australia (2018)
Elevation	Metres above average sea level	Pollack 1999 found northern quolls in central Queensland were typically found at lower elevation. Molloy et al. (2017) found elevation was a strong contributor to MAXENT modelling for northern quolls in the Pilbara	Geoscience Australia (2018)
Annual precipitation	Derived from spatially interpolated monthly climate database based on averages between 1950 and 2000	Increased productivity as a result of high annual precipitation may boost the capacity of northern quolls to tolerate threats (Burnett, 1997; Hohnen et al., 2016; McKenzie et al., 2007)	WorldClim (2019)
Precipitation seasonality	Average monthly variation in rainfall (1950–2000) expressed as a percentage ratio of the mean monthly precipitation total and the standard deviation of the monthly precipitation	Northern quoll records in Queensland associated with higher levels of rainfall seasonality (Woinarski et al., 2008)	WorldClim (2019)
Distance to water	Distance to permanent water measured in decimal degrees	Studies suggest areas proximate to permanent water are more likely to provide high quality for northern quolls (Begg, 1981; Braithwaite & Griffiths, 1994; Burnett, 1997; Molloy et al., 2017)	Derived from 1:100,000 water-course mapping provided by Geoscience Australia (2018)

a highly detectable species (Austin, Tuft, Ramp, Cremona, & Webb, 2017)—thus ensuring both northern quoll presence data and model background data were drawn from a comparable sampling intensity. Target group species records were subjected to point density analysis (PDA), masked to a 1 km² grid layer using ArcGIS 10.3, creating a layer with cell values that accurately represent survey effort in relation to location. This layer was included as a bias grid in all MaxEnt models. The contribution of variables to each model was assessed using permutation importance values. Permutation importance is calculated by alternating the predictor values between presence and background points and recording the effect this has on model AUC (Phillips, 2011).

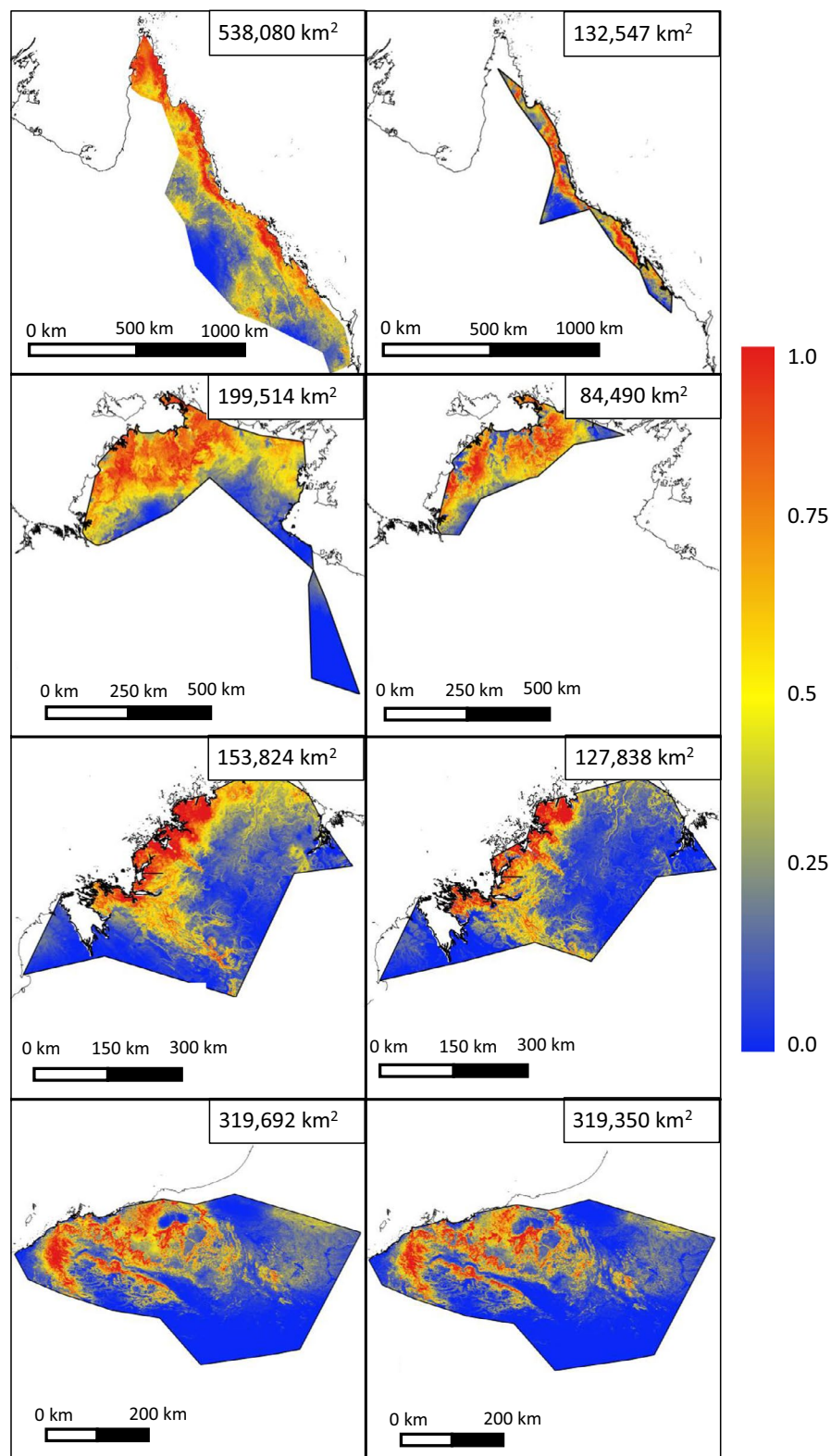
To quantify changes in the environmental conditions within the contemporary range of quolls, we sampled each of our five environmental predictors 10,000 times within historic and contemporary α -hulls, across all populations. Finally, to quantify changes in habitat quality over time, we sampled the MaxEnt habitat quality layer within both historic and contemporary α -hulls. We used generalized linear models (GLMs) to compare the average values of the five environmental predictors between the two time periods, using the historic period as the reference category. We considered there to be significant difference between time periods when the 95% confidence interval of the regression coefficients did not overlap zero.

Violin plots were generated to visualize these data using the 'plotly' package in R (Sievert et al., 2017).

3 | RESULTS

The total historic database consisted of 2025 historic records and 1,153 contemporary records (Appendix S1). Range size, as estimated by α -hulls, declined across all populations except for the Pilbara. Consistent with predictions, the largest absolute and proportional declines occurred in Queensland (areal reduction of 405,533 km², 75.4% of the historic range), followed by the Northern Territory (115,024 km², 57.7%) and the Kimberley (25,986 km², 16.9%; Figure 2). Range declines in the Northern Territory were dominated by the loss of record outliers from the semi-arid gulf region in the south-east of their range. Total loss in range size across all populations was 546,886 km² (45.2%; Figure 2). In Queensland, the vast majority of persisting northern quoll populations are present on the Central Mackay Coast bioregion, the northern extent of the Northern Brigalow Belt, the Wet Tropics region (Cooktown, Cairns and Atherton Tablelands areas) and near Weipa on the Cape York Peninsula (Figure 2). In the Northern Territory, persisting populations are mostly found in the Darwin Coastal bioregion, the northern

FIGURE 2 Northern quoll historic and contemporary predicted range across four study populations using α -hulls. Colouring within ranges represents outputs from MaxEnt ecological niche models. Values in the right-hand corner of plots represents α -hull area



extent of the Pine Creek bioregion, and the Tiwi Cobourg peninsula and the Victoria Bonaparte bioregion between the Victoria and Fitzmaurice rivers. For the Kimberley, contemporary records were mostly found in the King Leopold Ranges north of Derby as well as the Mitchell Plateau region, particularly between the Mitchell and Lawley River National Parks. Northern quolls are still distributed

across the entire Pilbara bioregion and also enter the southern extent of the Great Sandy Desert and western extent of the Little Sandy Desert around Karlamilyi National Park.

Niche reduction, measured as hypervolumes, occurred differentially across all populations, closely matching range declines in the Northern Territory (60.8%) and the Kimberley (16.9%). Marginal

declines occurred in the Pilbara (0.1%). While substantial niche reduction was also observed in Queensland (49.2%), it was a proportionally smaller reduction compared to range declines (Figure 3).

The performance of MaxEnt models was high across each of the four data sets, with AUC values averaging 0.92 (SD 0.02; Appendix S2). Little change was observed in variable permutation importance between time periods, except for distance to water in the Northern Territory, which increased by 22 percentage points between historic and contemporary periods (Figure 4). Annual precipitation was the most important predictor in 6 of the 8 ENMs. Precipitation seasonality also contributed highly in Queensland (Figure 4).

There were clear differences between time periods in the average values of environmental variables within the geographic ranges of all four populations (Figure 5), and in habitat quality as measured by MaxEnt, as indicated by 95% confidence intervals of coefficients not overlapping zero (Figure 5). The largest changes occurred in Queensland and the Northern Territory, and smaller changes occurred in the Kimberley and the Pilbara (Figure 6). Consistent with predictions, values for topographic ruggedness and annual precipitation increased in the contemporary range compared to the historic range in Queensland, the Northern Territory and the Kimberley. A large positive shift in precipitation seasonality was also recorded for Queensland. Finally, consistent with predictions, habitat quality (as measured by the historic MaxEnt model) was higher in the contemporary range, suggesting a loss of lower quality habitats (Figures 5 and 6).

4 | DISCUSSION

We applied the niche reduction hypothesis (Scheele et al., 2017) to quantify changes in the geographic range and ecological niche of a declining marsupial predator through time, across multiple populations. Our results confirm a contraction in geographic range and niche volume for northern quolls in Queensland, the Northern Territory and the Kimberley (Braithwaite & Griffiths, 1994; Woinarski et al., 2008). As predicted, range declines have been most severe in Queensland

and the Northern Territory, less severe in the Kimberley, and negligible in the Pilbara. These findings are consistent with localized declines in each of these regions (Braithwaite & Griffiths, 1994; Burnett, 1997; McKenzie, 1981) and at least partly reflect the incremental spread of toxic cane toads across the species' range (Urban et al., 2008). Reductions in the northern quoll's niche volume were >20% in all populations other than the Pilbara, and, consistent with the niche reduction hypothesis, we found evidence of environmental variables mediating niche reduction, potentially due to threat occurrence, species' tolerances and geographic barriers.

Niche volume—the array of environmental conditions within a species' realized niche—is a predictor of extinction risk both now and over geological time-scales (Saupe et al., 2015). Reductions in niche volume were largely proportionate to range contractions, except in Queensland, where proportional range declines exceeded proportional reductions in niche volume. This result aligns with theory suggesting species range and niche should be correlated for the most part (Slatyer, Hirst, & Sexton, 2013); for example, a recent analysis of 148 species using simulated data found niche volume and range size were mostly similar, although considerable residual variation did exist (Breiner et al., 2017). This variation was also detected in our analysis with range decline exceeding niche decline by 29% in Queensland, reaffirming that while a consistent relationship between niche volume and range size holds for the most part, one is not always fully reciprocal of the other (Colwell & Rangel, 2009). Niche may provide a poor surrogate for range in Queensland given quolls have declined from large swathes of flatter, more open (and relatively homogeneous) country, characterized by open savanna woodland vegetation and acacia forests, similar to declines from grasslands and savanna habitat observed in the Northern Territory (Oakwood, 2000). While less diverse in terms of topography and vegetation than coastal habitats, this habitat accounted for the majority of Queensland northern quoll historic range, and thus in disappearing from these areas, range size was reduced to a larger extent than niche volume.

Our finding that the Pilbara population has experienced less range contraction and niche reduction compared to other regions is consistent with expert opinion and the literature—the Pilbara is generally regarded as a stronghold for the northern quoll, due largely to the (current) absence of cane toads and abundance of topographically complex rocky outcrops (Cramer et al., 2016). However, we recognize that a smaller range contraction in the Pilbara may also be an artefact of low historic record availability. Our final database for this region contained 66 unique northern quoll records collected before 2001, and 740 unique records from 2001 onward—an 11-fold increase. The difference in sample size is due to a massive increase in survey effort as part of impact assessments and offsets related to a boom in iron ore exploration between 2002 and 2015 (ABS, 2018). However, our findings are supported to some extent by genetic data from the Pilbara, which shows no signs of substantial range contraction (Spencer et al., 2013).

By comparing the average values of environmental variables that shape northern quoll distributions within the historic and contemporary niches, we assessed a series of hypotheses regarding the

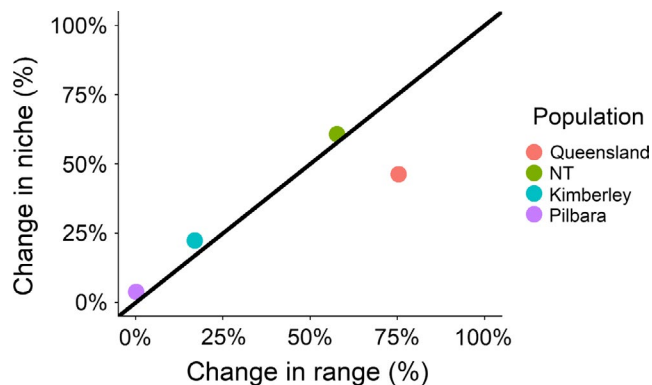


FIGURE 3 Change in northern quoll range (α -hull), and niche volume (hypervolume) plotted against one another. Queensland (purple), Northern Territory (blue), Kimberley (green), Pilbara (red). The solid line shows where a 1:1 correspondence between range decline and niche decline would fall

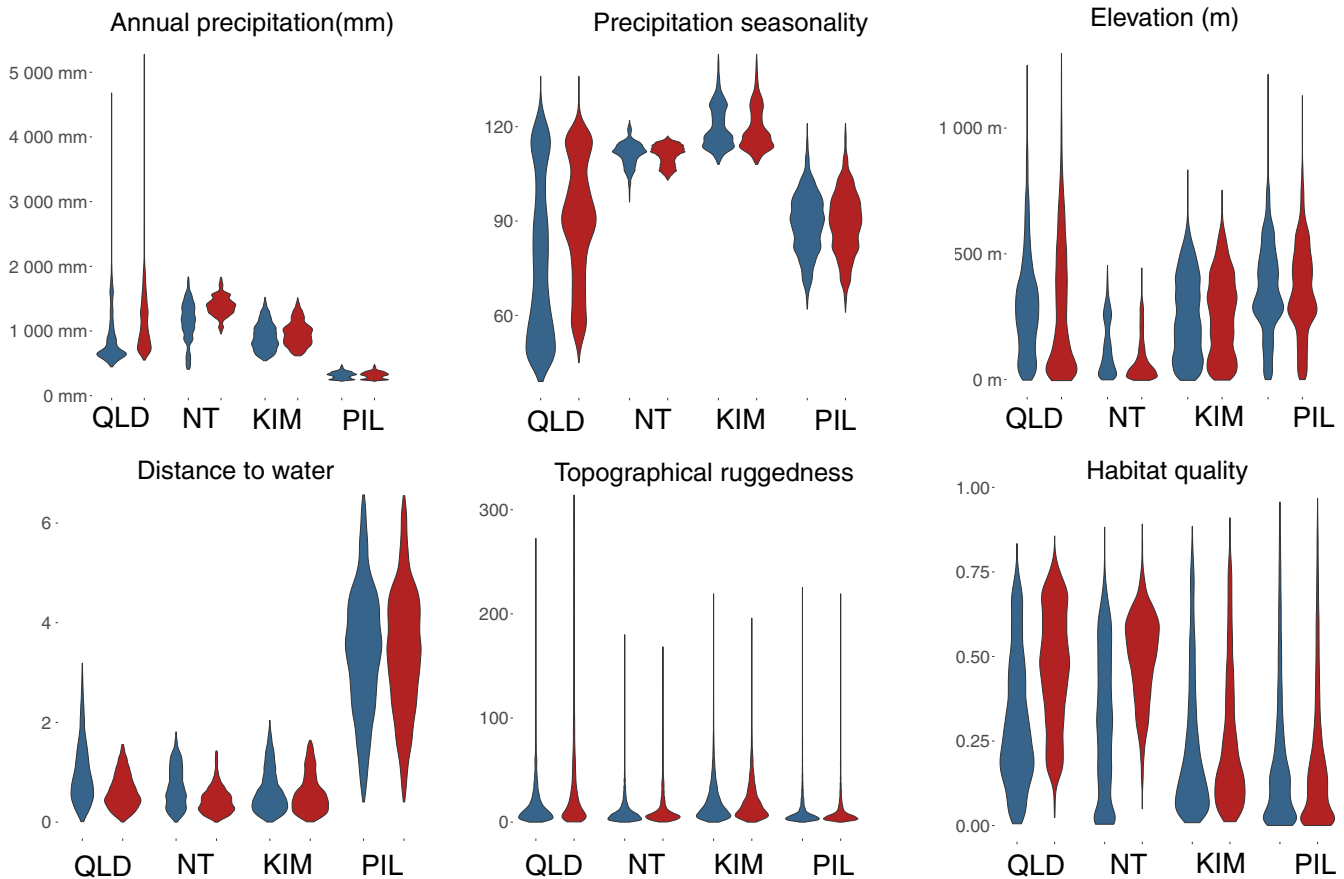


FIGURE 4 Permutation importance of variables included in northern quoll MAXENT ecological niche models. Permutation importance is calculated by alternating the predictor values between presence and background points and recording the effect this has on model AUC

types of environments that would favour northern quoll persistence. We found that the contemporary niche quolls is characterized by more topographically rugged areas, supporting the hypothesis that complex landscapes increase the resistance of northern quolls to threats (or because in such areas the threats are absent or of lower intensity) by acting as fixed refuges (Reside et al., 2019). We found support for this hypothesis in all populations other than the Pilbara, with the greatest increase observed in the Queensland population. The increase in ruggedness within the Queensland contemporary range likely reflects the loss of populations that previously occupied highly flammable, topographically simple landscapes, thought to have been more exposed to the threats of livestock grazing, altered fire regimes (more frequent and intense fires) and invasive predators (Hernandez-Satin, 2016; Oakwood, 2000). Similarly, central rock rats (*Zyomys pedunculatus*) have contracted from more simple to more complex rugged habitat where the impact of their primary threat, the feral cat, is reduced (McDonald, Stewart, & Dickman, 2018). Rocky habitats are also important to northern quolls because they provide highly suitable areas within which females are able to establish maternal denning sites (Oakwood, 1997)—critical features in providing developing offspring with protection from predators (Oakwood, 2000). The importance of suitable denning habitat is further compounded when considering the unusually

short, semelparous life history of northern quolls, which makes population persistence particularly reliant on recruitment (Moro, Dunlop, & Williams, 2019), and thus the effectiveness of dens in providing young with protection. While there is no evidence that rugged habitats reduce the direct impacts of cane toads, it has been suggested that, by limiting the impacts of grazing, fire and invasive predators, rocky habitats may indirectly buffer against toads by increasing population sizes that can offset mortality due to toads (Burnett, 1997). And then this finding is consistent with previous work showing that northern quolls are found at higher densities and that individuals live longer, in rocky habitats (Begg, 1981; Schmitt et al., 1989). A similar mechanism might explain why northern quoll contemporary range is characterized by a decreasing distance to permanent water when compared to the historic range, as northern quolls have been found in better reproductive condition closer to creek lines—a habitat associated with free-standing water (Braithwaite & Griffiths, 1994). The authors of that study suggest quolls closer to water are likely to engage in increased rates of reproduction, presumably because of an increased availability of resources, leading to increased recruitment and overall population size (Braithwaite & Griffiths, 1994). This finding is also consistent with Reside et al. (2019), who identified water sources as important fixed refuges for threatened species.

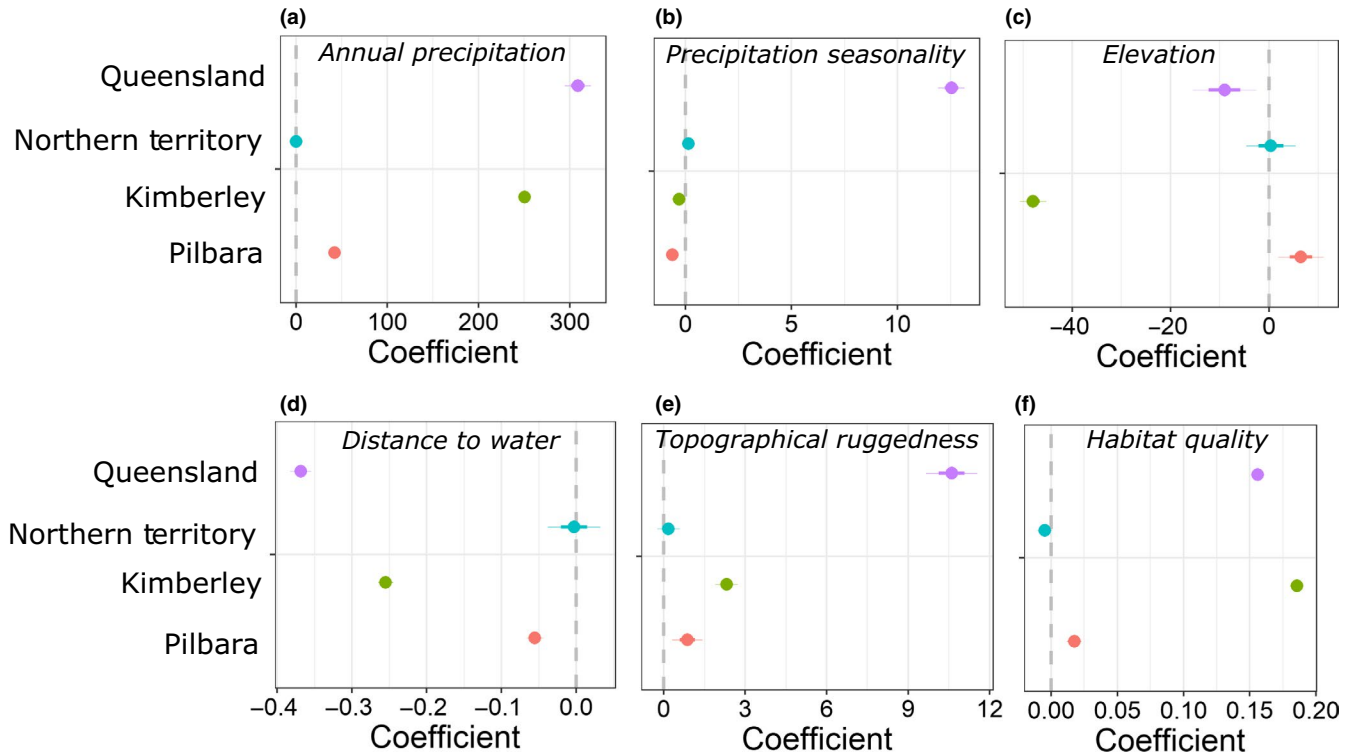


FIGURE 5 Violin plots comparing 10,000 random samples of habitat variables within the historic (blue) and contemporary (maroon) range of northern quolls: (a) annual precipitation, (b) precipitation seasonality, (c) elevation, (d) distance to water, (e) topographical ruggedness and (f) habitat quality derived from the MaxEnt model

Some of the largest changes in environmental values between the historic and contemporary niche were for annual rainfall, which was also the most important variable driving quoll distributions in three of the four regions. The contemporary niche is characterized by much higher average annual rainfall compared to the historic niche, particularly in the two regions that have experienced the greatest range declines (Queensland and the Northern Territory). The most likely explanation for this shift is that rainfall increases primary productivity (Pianka, 2017), and food resources (Dickman, Mahon, Masters, & Gibson, 1999), leading to improved body condition, increased offspring survivorship and population size (Meserve, Gutiérrez, Yunker, Contreras, & Jaksic, 1996), thereby offsetting increased mortality due to threats. Support for this hypothesis in northern Australia is strong, with native mammals typically persisting longer in areas that receive higher annual rainfall (Fisher et al., 2014; Start, Burbidge, McDowell, & McKenzie, 2012). Northern quolls also persist more in higher rainfall areas (Radford et al., 2014; Woinarski et al., 2008; Ziembicki et al., 2013), even though threats such as grazing, predation and intense fire are present across both the arid and mesic extents of their range. Hohnen et al. (2016) suggested one reason northern quoll populations may be more stable in high rainfall areas is because genetic connectivity is greater. They supported this hypothesis by showing quolls in wetter habitats were more closely related than quolls in drier habitats (Hohnen et al., 2016). Here, it is important to note that our analysis did not account for changes in rainfall patterns over time, a factor which has

the potential to drive shifts in species range (Davis & Shaw, 2001) and niche (Broennimann et al., 2007). While the inclusion of such analysis was outside the scope of this study, we strongly suggest this topic be addressed in future studies as it has been in other species of quoll (Fancourt et al., 2015), particularly in the context of the earth's rapidly changing climate (Urban, 2015).

We also observed a substantial increase in rainfall seasonality within the contemporary niche in Queensland. As with the previous two examples, we suggest that this shift most likely reflects increased population size and output related to the timing in quoll breeding activity, where offspring dispersal (November–February; Oakwood, 2000) coincides with a boom in resource availability brought by summer monsoonal systems in northern Australia (Oakwood, 2000). By synchronizing their reproductive time line with highly seasonal rainfall patterns, northern quolls are likely able to increase offspring survivorship, allowing populations to be more likely to persist despite increased mortality due to threats (e.g. cane toads, invasive predators).

By comparing habitat quality derived from MaxEnt models within the historic and contemporary niche, we found that the contemporary geographic range of northern quolls comprises a subset of the historical niche that is of higher predicted habitat quality, highlighting the importance of high-quality habitats for providing refuge from stressors. Here, it is important to recognize that refuges, like niches (Guisan & Thuiller, 2005), are multivariate and can be defined by the bounds of more than one environmental

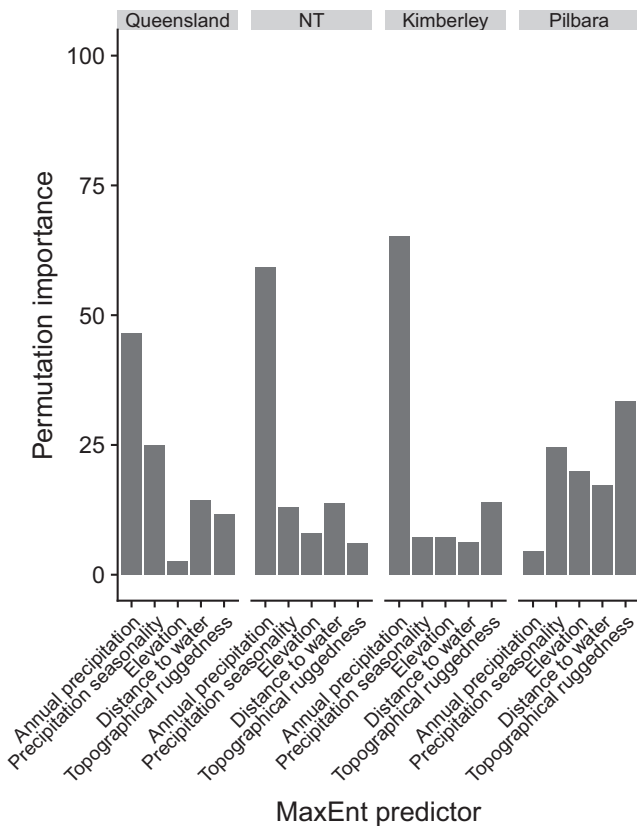


FIGURE 6 Generalized linear model coefficients comparing 10,000 random samples of habitat variables from within the historic and contemporary ranges of northern quolls: (a) annual precipitation, (b) precipitation seasonality, (c) elevation, (d) distance to water, (e) topographical ruggedness and (f) habitat quality derived from the historical MaxEnt model. Positive coefficients depict an increase in average values of the variable in the contemporary (cf historic) range. Negative coefficients depict a decrease in average values of the variable in the contemporary (cf historic) range

parameter (Keppel et al., 2012). The most effective refuges should occur on the environmental continuum where resource availability and buffering from threats permit the greatest chance of persistence (Keppel et al., 2012). In Queensland and the Northern Territory, where shifts to high-quality habitat were greatest, habitat quality was best predicted by annual precipitation, distance to water and precipitation seasonality. This result conforms with research showing mammal attrition in Australia has been greatest in resource-poor arid and semi-arid landscapes (Johnson, 2006). Topographical ruggedness was also an important predictor for habitat quality in Queensland and the Kimberley, suggesting a combination of complex and high-resource habitats may in some cases act as more effective refuge habitat than habitat that is simply high in resources.

While effective refuge habitat is clearly critical to the persistence of species in the short term, it can also be important at an evolutionary scale as refugium—a space within a species niche that can support populations over evolutionary time-scales (Keppel et al., 2012; Reside et al., 2019). In the case of the northern quoll,

habitat that limits but not fully eliminates exposure to key threats such as cane toads and feral predators may facilitate the development of both behavioural and phenotypic traits through behavioural learning or evolution that could potentially allow re-expansion into their historic niche. Previous studies have found the timeframe for such changes to occur in response to threats (including cane toads) can be surprisingly short (<70 years; Hudgens & Garcelon, 2011; Phillips & Shine, 2006). Further, recent studies have found that not only can northern quolls be trained to avoid cane toads in a single generation, but that the trained quolls offspring also avoided eating toads, suggesting quolls have the capacity to rapidly learn behaviour and distribute the information to their young (Cremona, Spencer, Shine, & Webb, 2017; Webb, Legge, Tuft, Cremona, & Austin, 2015). These results suggest investment in protecting refuges (and populations within them) over a relatively short period of time has the potential to yield important conservation outcomes.

An important caveat of our study was that we did not explicitly account for threats such as cane toads, feral predators or fire, in any of our models. While including threats as predictors would likely aid in determination of their relative influence in shaping the northern quoll's contemporary range and niche, the scale and resolution of spatial layers required for this analysis do not currently exist and creating them was beyond the scope of our study. It may be possible to explicitly test the effect of threats on quoll populations in future studies by limiting the scale of analysis to a regional level and linking changes in northern quoll occupancy with threat distributions (Hernandez-Satin, 2016). For example, by measuring declines in range and niche in relation to fire, it may be possible to elucidate the value of logs and tree hollows—important refuge features for many northern boreal and arboreal mammal species (Goldingay, 2012)—as quoll habitat.

4.1 | Management implications

Previous research suggests cane toads have immediate and lasting detrimental impacts on northern quoll populations (Shine, 2010). It is therefore likely that cane toads are a key culprit responsible for larger range and niche contractions in Queensland and the Northern Territory (Burnett, 1997; Woinarski et al., 2008), given that cane toads have only very recently arrived in Western Australia and are yet to reach the Pilbara (Pizzatto, Both, Brown, & Shine, 2017). Cane toads are expected to colonize the remainder of the Kimberley within the next 5–10 years (Doody et al., 2018) and the Pilbara by 2037–2046 (Southwell, Tingley, Bode, Nicholson, & Phillips, 2017). In the light of these predictions, several strategies have been developed to halt or slow the spread of cane toads from the Kimberley to the Pilbara (Phillips, Shine, & Tingley, 2016; Tingley et al., 2013). These include closing off water bodies (Tingley et al., 2013), as well as introducing toads with 'less dispersive' genes to the front of the invasion line to impede the progress of toads carrying 'highly dispersive' genes (Phillips, 2016; Phillips et al., 2016). We suggest these strategies be given full consideration.

As with the northern quoll, previous studies show topographically rugged and high rainfall habitats also provide important refuge for a range of other threatened species of mammal (Southgate, Paltridge, Masters, & Carthew, 2007) and as such should form areas of focus for management (Reside et al., 2019). A first step in protecting refuge habitats is recognizing where they are located, a process that has been enhanced by remote sensing technologies (Allan et al., 2018). Once a refuge is located, a management priority should be to ameliorate any existing or emerging stressors to ensure they remain functional in facilitating species persistence (Reside et al., 2019). In the case of northern quolls, these may include limiting extensive grazing and burning, as well as implementing feral predator control programmes (Hill & Ward, 2010), and potentially applying cane toad aversion techniques (O'Donnell, Webb, & Shine, 2010). Although we excluded islands from considerations in our analyses, the marked contractions in range and niche for mainland quolls reinforce the importance of island populations and the need to maintain biosecurity for these islands to reduce the likelihood of toad or predator invasion. Finally, effective management of refuge systems requires high-quality ecological data collected over biologically meaningful timeframes (Lindenmayer et al., 2012). Therefore, the implementation of sustained and effective monitoring programmes inside and outside refuge habitats is highly recommended.

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DATA AVAILABILITY STATEMENT

Study data are publicly available via data sharing platform Dryad.

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BIOSKETCH

Harry Moore is a PhD student interested in how predators interact with biotic and abiotic factors within their environment, and how these shape their spatial ecology and behaviour. The researchers involved in this publication have broad expertise in mammal conservation, applied ecology, field ecology and ecological modelling.

Author contributions: H.A.M. and D.G.N. conceived the ideas; H.A.M. collected the data; H.A.M. and D.G.N. analysed the data with input from J.A.D. and J.C.Z.W.; and H.A.M. and D.G.N. led the writing with input from J.C.Z.W., J.A.D., E.G.R., D.M.W. and L.E.V.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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