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# Moving from representation to persistence: The capacity of Australia's National Reserve System to support viable populations of mammals

Hayley S. Clements[1] | Stephen G. Kearney[2] | Carly N. Cook[1]

[1]School of Biological Sciences, Monash University, Melbourne, Vic., Australia

[2]School of Earth and Environmental Sciences, University of Queensland, Brisbane, Qld, Australia

**Correspondence**
Hayley S. Clements, Centre for Complex Systems in Transition, Stellenbosch University, Stellenbosch, South Africa.
Email: clementshayley@gmail.com

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## Abstract

**Aim**: Species require sufficiently large and connected areas of suitable habitat to support populations that can persist through change. With extensive alteration of unprotected natural habitat, there is increasing risk that protected areas (PAs) will be too small and isolated to support viable populations in the long term. Consequently, this study addresses the urgent need to assess the capacity of PA estates to facilitate species persistence.

**Location**: Australia.

**Methods**: We undertake the first assessment of the capacity of the Australian National Reserve System (NRS) to protect 90 mammal species in the long term, given the size and distribution of individual PAs across the landscape relative to species' habitat and minimum viable area (MVA) requirements and dispersal capabilities.

**Results**: While all mammal ranges are represented within the NRS, the conservation capacity declined notably when we refined measures of representation within PAs to include species' habitat and area requirements. The NRS could not support any viable populations for between three and seven species, depending on the MVA threshold used, and could support less than 10 viable populations for up to a third of the species. Planning and managing PAs for persistence emerged as most important for species with large MVA requirements and limited dispersal capabilities.

**Main conclusions**: The key species characteristics we identify can help managers recognize species at risk within the current PA estate and guide the types of strategies that would best reduce this risk. We reveal that current representation-based assessments of PA progress are likely to overestimate the long-term success of PA estates, obscuring vulnerabilities for many species. It is important that conservation planners and managers are realistic and explicit regarding the role played by different sizes and distributions of PAs, and careful in assuming that the representation of a species within a PA equates to its long-term conservation.

KEYWORDS

Australia, connectivity, conservation planning, conservation targets, habitat suitability, minimum viable population, species persistence, terrestrial mammals

  

# 1 | INTRODUCTION

In the current biodiversity extinction crisis, emphasis is being placed on the establishment of a global portfolio of protected areas (PAs) that maximizes the number of species and habitats represented, given land availability and budgetary constraints (UNEP-WCMC & IUCN, 2016). Catalysed by international targets within the Convention on Biological Diversity (CBD; Aichi Targets 11&12), the terrestrial land area under protection has doubled in the past 20 years (UNEP-WCMC & IUCN, 2016), improving the representation of species' ranges and ecoregions within PAs (Kuempel, Chauvenet, & Possingham, 2016; Venter et al., 2017). It is readily acknowledged; however, that the representation of species within PAs does not necessarily ensure their persistence (Gaston, Jackson, Cantú-Salazar, & Cruz-Piñón, 2008; Watson et al., 2016). There is growing evidence of population declines and extinctions within PAs around the world (Geldmann et al., 2013). Many PAs are believed to be subject to an extinction debt, whereby extensive alteration of unprotected natural habitat results in PAs that are too small and isolated to support viable populations in the long term (Newmark, 2008; Woodroffe & Ginsberg, 1998). These extinction debts suggest that PAs may become increasingly ineffective over time, and there is therefore an urgent need to assess the capacity of PA estates to facilitate species persistence. Such assessments could provide PA planners and policymakers with: (1) an understanding of the extent to which current investments in PAs are likely to be successful in the long term, and (2) guidance regarding strategic PA establishment and management going forward.

Assessing the capacity of current PA estates to conserve biodiversity in future requires an understanding of the processes that facilitate species persistence and the ability of PAs to support these processes in the long term. Ecological theory and evolutionary theory provide a wealth of guidance regarding the determinants of species extinction (Caughley, 1994; Lacy, 1997), which has informed principles for optimal PA design (Crooks & Sanjayan, 2006; Diamond, 1975; Frankham, Ballou, & Briscoe, 2010; Margules & Pressey, 2000). At a minimum, species require sufficiently large and connected areas of suitable habitat to support viable populations that can persist through demographic, environmental and genetic stochasticity, disturbance and change (Caughley, 1994). They further require ongoing threat management to protect those populations in to the future (Caughley, 1994). Species persistence within PAs is therefore influenced by processes occurring at multiple spatial scales, from suitable habitat patches within individual PAs to the spatial configuration and connectivity of PAs across the landscape and the extent of threats within this landscape (Gaston et al., 2008). Assessments of the capacity of large-scale (national or continental) PA estates to support viable populations of the diverse species they represent are rare (Di Marco et al., 2016; Gaston et al., 2008). Recent studies of the European and Canadian PA estates illustrate, however, that such assessments are now possible for some taxa (Santini, Di Marco, Boitani, Maiorano, & Rondinini, 2014; Wiersma & Nudds, 2009) given improvements in available data with which to predict species' habitat suitability and ecological attributes (e.g., minimum viable area requirements and dispersal capabilities; Rondinini et al., 2011a; Whitmee & Orme, 2013; Hilbers et al., 2017). This study makes use of these advances to undertake the first assessment of the capacity of the Australian PA estate to protect mammal species in the long term, given the size and distribution of individual PAs across the landscape.

Australia has the worst record for mammal conservation of any country or continent; fifty percentage of all mammal species that went extinct worldwide in the past 200 years were lost from the Australian continent (Short & Smith, 1994). The Australian government has actively sought to halt these losses (Commonwealth of Australia, 2009) by doubling the National Reserve System (NRS) in the past two decades to improve representation of bioregions and threatened species, albeit suboptimally (Barr, Watson, Possingham, Iwamura, & Fuller, 2016; Watson et al., 2011). Assessments of progress in protecting biodiversity have been based on the extent to which the NRS covers species' geographic ranges or areas of likely occurrence (Barr et al., 2016; Watson et al., 2011). They do not account for the fact that species require the protection of sufficiently large and connected areas of suitable habitat to persist within their ranges, reflecting a prevailing gap in global mammal conservation strategies (Rondinini, Rodrigues, & Boitani, 2011b). The capacity of a protected habitat patch to support a viable population will be dependent on the species' minimum viable area requirements (a function of its minimum viable population size and population density), as well as the capacity of individuals to move between habitat patches (Hanski, 1998). In this study, we used the distribution of suitable habitats, together with species-specific dispersal abilities and minimum area requirements, to assess the extent to which the NRS protects viable populations of species. We provide a notable step forward from current assessments of progress towards PA targets, by accounting not only for the representation of species within a national PA estate, but also the likelihood that they persist in that estate over time. By exploring how differences between predicted species representation and persistence within PAs relate to species characteristics (area requirements, population densities, dispersal abilities, range sizes, suitable habitat extents and PA coverage), we identify targeted conservation strategies to improve PA efficacy.

# 2 | METHODS

## 2.1 | Species data

This study included 90 extant, terrestrial indigenous mammal species (see Appendix S1) for which the necessary data were available (e.g., habitat suitability, life history), providing the most comprehensive assessment of PA coverage for Australian mammals. These species belong to four mammalian orders, which cover a wide range of habitats, area requirements and dispersal abilities. We followed the method outlined by Santini et al. (2014) to assess the extent to which the NRS covered each species' geographic range (Assessment A), suitable habitat within the geographic range (Assessment B) and viable habitat within the geographic range (Assessment C). Viable habitat was defined as suitable habitat large enough to support the minimum viable population (MVP) size to ensure a 95% probability of persistence over 100 years, despite environmental and demographic stochasticity (Hilbers et al., 2017; Pe'er et al., 2014; Shaffer, 1981). Assessments of viable habitat coverage therefore account for processes of importance for species persistence (e.g., Di Marco et al., 2016; Kerley, Pressey, Cowling, Boshoff, & Sims-Castley, 2003; Santini et al., 2014). Estimates of viable habitat require both an understanding of species' MVP requirements and their capacity to move through the landscape, as several patches of habitat may collectively support a viable metapopulation provided the species can move between patches. Assessing the capacity of PAs to support viable populations therefore required the following data for each species: (1) the distribution of suitable habitat within the PA estate; (2) minimum viable area (MVA) estimates, determined by dividing MVP size by population density; and (3) dispersal distance capabilities (Santini et al., 2014).

Following the methods outlined in Rondinini et al. (2011a), we developed models that predict suitable habitat for each mammal species at 300-m resolution according to: (1) spatial land cover data (ESA 2010) and species' geographic ranges (IUCN, 2016), and (2) descriptions of species' preferences for land cover and elevation, as well as dependence on water and tolerance to human presence (IUCN, 2016). Based on descriptions of species' habitat preferences, we assigned each species to one or more broad habitat type (forest, shrubland, grassland, bare and artificial) and intersected this information with the suitability of flooded habitat and to the level of tolerance to human-impacted (degraded or mosaic) natural habitat types, to select appropriate land cover types within each species' geographic range (Rondinini et al., 2011a). When an elevation range was documented for a species (IUCN, 2016), we further limited the suitability model to habitat within this range. An elevation map was produced by resampling (averaging) to 300-m the Shuttle Radar Topography Mission elevation map (Geoscience Australia, 2017), originally at 1 arcsecond resolution (approximately 90-m at the equator). Rondinini et al. (2011a) further limited species' habitat suitability to within a small distance of water bodies if water dependence was noted in the IUCN (2016) data. For the 90 Australian species considered here, no mention of water dependence was made in the IUCN data, and this step was thus excluded. We validated these models with occurrence data from the Atlas of Living Australia (ALA, 2017) for a subsample of 20 randomly selected species, following the method described by Rondinini et al. (2011a). The models were found to correctly predict 82.0% (SD 21.0%) of species occurrences on average, a slightly higher success rate than that recorded by Rondinini et al. (2011a) (see Appendix S2 for full model evaluation).

A new approach for generating meaningful species-specific estimates of MVP avoids the intensive data requirements and site specificity of conventional population viability analyses by applying allometric scaling relationships in models of population dynamics. Hilbers et al. (2017) used models of population dynamics across a range of life history traits related to body mass to estimate MVP thresholds for the world's mammal species and found their estimates to be a reasonable approximation of those from species- and site-specific studies. A range of estimates were provided for each species, which vary according to assumptions about growth rate and parameter uncertainty (Hilbers et al., 2017). To account for a range of potential environmental conditions and to assess the sensitivity of our results to MVP estimates, we made use of four estimates that assume populations grow at a rate ($r_m$) of 0.4 (conservative), 0.6, 0.8 or 1.0 (non-conservative), and account for uncertainty by increasing estimates by two standard deviations. The masses used by Hilbers et al. (2017) were validated using those provided by Van Dyck and Strahan (2008) for Australian mammals. For two species (*Dasyurus maculatus* and *Lasiorhinus krefftii*), masses used by Hilbers and colleagues were incorrect, and we adjusted MVP estimates accordingly. For each species, the range and mean MVA requirement were determined by dividing MVP estimates by mean population density, following Santini et al. (2014). Mean population densities were obtained from the PanTHERIA database (Jones et al., 2009). Following Santini et al. (2014), species' median dispersal distance capabilities were predicted according to allometric equations (Santini et al., 2013) based on body mass (herbivores and omnivores; data from Van Dyck & Strahan, 2008) and home range area (carnivores; data from Cronin, 2008; Van Dyck & Strahan, 2008; Jones et al., 2009; IUCN, 2016). These predictions were found to be reasonable approximations of reality for species for which independent empirical dispersal data were available (see Appendix S3 for dispersal model evaluation).

## 2.2 | Protected area coverage of species' geographic ranges and viable habitats

The Collaborative Australian PA Database (CAPAD) contains spatially explicit data on every PA in the NRS, last updated at the end of 2016 (DEE, 2016). We conducted a comprehensive range of checks on the database to identify and correct errors and inconsistencies (e.g., overlapping PAs) following the methods described in Cook, Valkan, Mascia, and McGeoch (2017). For each species, we first determined the size of its geographic range and the extent covered by PAs (Assessment A). We then calculated the area of suitable habitat within the species' range and the extent covered by PAs (Assessment B). Finally, we used the species' median dispersal distance to identify clusters of suitable habitat within the NRS that could be assumed to be connected (Santini et al., 2014). We excluded clusters with an aggregate area less than the species' MVA and then summed the remaining habitat area to assess the extent of viable habitat within the PA estate (Assessment C) (Santini et al., 2014). This was done for each of the four MVA estimates ($r_m$ = 0.4, 0.6, 0.8, 1.0), resulting in four estimates of protected viable habitat area. We calculated the number of protected viable habitat clusters for each species (both the mean and range) to represent the number of potential populations. Median dispersal distance was used to identify habitat clusters because Santini et al. (2014) found viable habitat extent estimates to be insensitive to the use of median versus maximum dispersal distance. To enable comparison between estimates of protected range, habitat and viable habitat areas, we divided these estimates by the geographic range extent (Santini et al., 2014).

We assessed whether percentage coverage of species' geographic ranges by PAs met conservation targets for each species, based on coverage estimates from the three assessment methods (A to C). These targets were set using the commonly applied approach for large-scale conservation assessments, which inversely scales targets to the species' range size (Rodrigues et al., 2004; Santini et al., 2014; Venter et al., 2017). This approach has been used to assess representation of threatened species in the Australian NRS (Polak et al., 2016; Watson et al., 2011). Targets were set as 100% of the range for species with a narrow range (<1,000 km$^2$) and 10% of the range for widespread species (>10,000 km$^2$). Where range size was intermediate between these extremes, the target was linearly interpolated (Polak et al., 2016).

## 2.3 | Trends in conservation progress according to species characteristics

The difference between the percentages of species' geographic ranges covered by PAs estimated using habitat (Assessment B) versus mean viable habitat (Assessment C) extent was related to dispersal ability and mean MVA using linear regressions. Plots of fitted and observed values and residuals were examined for deviations from the assumptions of homogeneity and normality, and all variables were log-transformed to meet these assumptions. The adjusted coefficients of determination were used to assess model fit (Zar, 2010).

To assess whether species could be categorized into unique groups sharing similar combinations of the characteristics that influence the capacity to conserve viable habitat and achieve targets, we performed a principal component analysis followed by a hierarchical agglomerative cluster analysis of species characteristics. Characteristics included geographic range area, suitable habitat area, percentage PA coverage of range and of mean habitat in viable clusters, mean MVA, population density and dispersal ability (R package: vegan; function: rda) (Oksanen et al., 2015). Prior to performing the analysis, range and habitat area, MVA, population density and dispersal distance were log-transformed to meet the assumptions of normality and all data were scaled. The cluster analysis employed Euclidean distance and Ward linkages (R packages: vegan and stats; functions: vegdist and hclust) (Oksanen et al., 2015; Ward, 1963). We used a Mantel-based comparison as well as mean silhouette width to identify the number of distinct clusters (R package: cluster; functions: daisy and silhouette) (Maechler et al., 2015).

Differences between the distinct species groups identified by the cluster analysis were described according to their location on a biplot of the first two principal components and the mean values of species characteristics within each group. We then compared between groups: (1) the proportion of species currently considered threatened (listed under Australia's Environment Protection and Biodiversity Conservation Act 1999 as critically endangered, endangered or vulnerable) (DEE, 2017), and (2) the proportion of species for which representation (geographic range protected) and persistence (mean viable habitat within geographic range protected) targets were met, using Fisher's exact tests. The (log-transformed) mean number of populations of each species that could be supported within the NRS was compared between groups using an ANOVA, followed by a post hoc Tukey test.

We determined the theoretical maximum number of populations that could be supported on the total viable habitat extent within the NRS by dividing this habitat extent by the species' MVA (i.e., we assessed the maximum number of populations that could be supported if the total viable habitat extent was fragmented into equal areas, each the size of the species' MVA) (Santini et al., 2014). By then dividing the actual number of potential populations by this theoretical maximum, we could gain insight into the distribution of viable habitat across the NRS. A maximum score of 1 would indicate that viable habitat was maximally fragmented, with lower scores indicating more aggregated viable habitat. We thus refer to this as the 'fragmentation index' and compare the (log-transformed) index between species groups using an ANOVA followed by a Tukey post hoc test. Mean maximum and actual population estimates based on the four MVA thresholds for each species were used for this analysis. The three species with mean viable population estimates of zero (*Lagorchestes hirsutus*, *Lagostrophus fasciatus*, *Perameles bougainville*; Appendix S1) were excluded.

Finally, our identification of viable habitat patches for each species was based on the assumption that individuals can move between PAs located within their dispersal distance, irrespective of the land use in between. This assumption is likely to become less valid with increasing transformation of unprotected habitat in future, and we thus assessed the sensitivity of our findings to this assumption by rerunning Assessment C for each species based on the assumption that individuals can only move across protected land within their dispersal distance. We refer to this as the 'scorched-earth' analysis. For each species, we compared mean estimates for protected viable habitat area (across the four MVA thresholds) between the scorched-earth analysis and the original analysis, excluding the three species with no predicted viable habitat in the NRS (Appendix S1). Spatial analyses were performed in ArcGIS 10.4, with an Albers Equal Area Projection for Australia and the Geocentric Datum of Australia 1994. Statistical analyses were performed in R (R Development Core Team, 2016) at a significance level of $\alpha = 0.05$.

# 3 | RESULTS

All 90 mammal species had a portion of their geographic range and suitable habitat included in the NRS (median 24.2%, minimum 4.1%, maximum 95.4% of the range covered by PAs and median 14.3%, minimum 0.03%, maximum 81.7% of the range covered by suitable habitat within PAs; Appendix S1). On average across species, 30.0% to 54.0% of protected habitat clusters were large enough to support a viable population (depending on the MVA threshold used), although this ranged substantially between species (SD 28.3% and

28.4%, respectively). Between three and seven species had no suitable habitat of a viable size included within the PA system (depending on the MVA threshold used; Appendix S1). The current system of PAs achieved representation targets for 66% of species based on geographic range coverage, but this dropped to 41% of species once range coverage by PAs was limited to viable habitat areas (irrespective of the MVA threshold used). These 'persistence targets' were not met for 25 (68%) of the 37 species that are currently considered to be threatened in Australia, while they were not met for 28 (53%) of the 53 species that are currently considered non-threatened (Appendix S1).

The percentage of species' geographic ranges covered by protected but non-viable habitat was positively related to species' mean MVA requirements ($r^2 = .53$, $F_{1, 86} = 99.66$, $p < .001$) and negatively related to species' dispersal abilities ($r^2 = .38$, $F_{1, 86} = 53.59$, $p < .001$). Four clusters of species were evident with distinct combinations of area requirements, population densities, dispersal capabilities, range sizes, suitable habitat extents and PA coverage (Mantel $r = .48$; Figure 1). These four groups differed in their proportions of threatened versus non-threatened species (Fisher's $p < .001$), and the proportion of species for which representation targets had been met versus not been met (Fisher's $p < .001$; Figure 2).

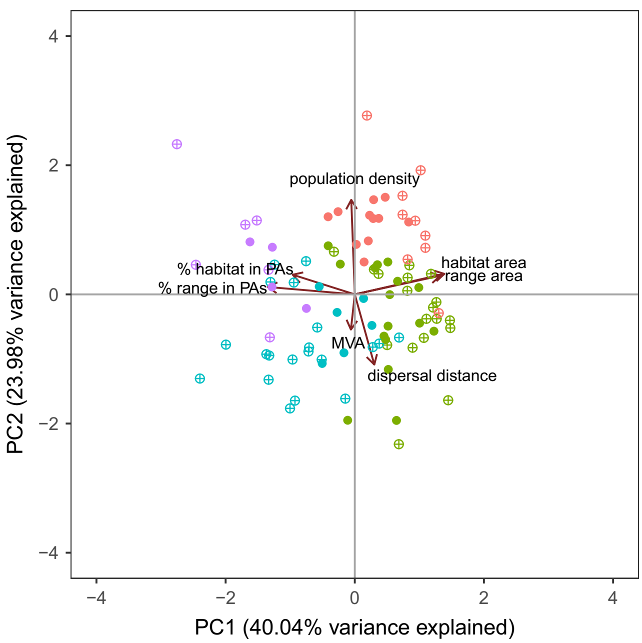


**FIGURE 1** Biplot depicting the relative scores of seven species characteristics on the first two principal components (PC). Data points indicate the scores of 90 Australian mammal species, with colours corresponding to the four identified clusters. Solid and crossed points indicate species for which persistence targets are currently met and not met, respectively. Table 1 provides average values of each characteristic in each species cluster [Colour figure can be viewed at wileyonlinelibrary.com]

The first group (pink cluster) was characterized by species with intermediate MVA requirements, high population densities and very limited dispersal abilities (Figure 1, Table 1). PAs covered, on average, a fifth of these species' large geographic ranges and a quarter of their large habitat extents. Just one species (5%) is currently threatened, and representation and persistence targets were met for a relatively large number of species (85% and 55%, respectively; Figure 2). All rodent species (family Muridae) considered fell within this group, as did all dunnarts (genus *Sminthopsis*) and almost two-thirds of antechinus (genus *Antechinus*; Appendix S1). This group can be thought of as mostly small-bodied omnivores.

The second group (green cluster) had relatively small MVA requirements and low population densities, as well as the highest dispersal abilities of the four groups (Figure 1, Table 1). PAs covered around a fifth of these species' large ranges and habitat extents. Threatened species comprised 38% of this group, and representation and persistence targets were met for a relatively large number of species (82% and 47%, respectively; Figure 2). Almost three-quarters of the macropods (family Macropodidae) fell within this group, including 91% of species in the genus *Macropus* (kangaroos and wallabies) and all pademelons (genus *Thylogale*; Appendix S1). Three-quarters of quolls (genus *Dasyurus*) also fell within this group. This group can be thought of as predominantly larger-bodied species.

The third group of species (blue cluster) were characterized by the largest MVA requirements, lowest population densities and intermediate dispersal abilities (Figure 1, Table 1). These species have small geographic ranges and habitat extents. While PAs covered 37% of their ranges on average (nearly double the previous two groups), only 28% of their habitat was protected in viably sized clusters. Representation and persistence targets were met for only 35% and 23% of species, respectively, and 81% are currently threatened (Figure 2). This group included two-thirds of the Petauridae family

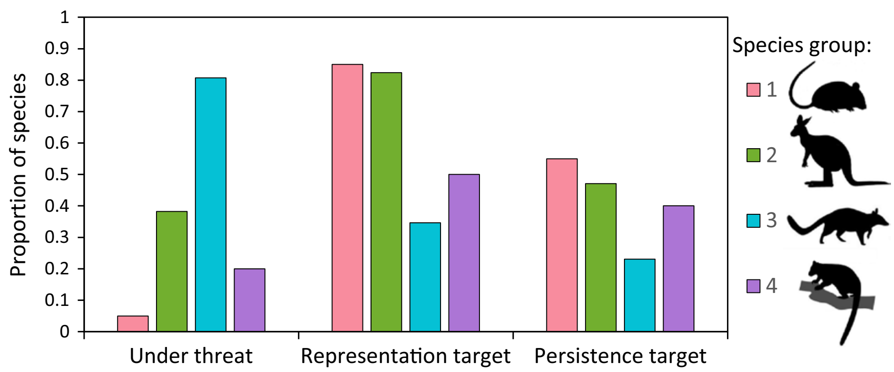


**FIGURE 2** Proportion of 90 Australian mammal species in each of four species groups, which are currently considered to be threatened, and for which representation and persistence targets were met by the Australian National Reserve System (See Table 1 for characteristics of each group with corresponding colours) [Colour figure can be viewed at wileyonlinelibrary.com]

**TABLE 1** Characteristics (mean ± *SE*) of 90 Australian mammal species falling within four groups. Colours refer to group differentiation in Figure 1

| | Species group | | | |
|---|---|---|---|---|
| **Characteristic** | **1 (Pink)** | **2 (Green)** | **3 (Blue)** | **4 (Purple)** |
| Group description | Small-bodied omnivores | Larger-bodied species | Medium-sized omnivores | Arboreal folivores |
| Example species | Rodents, antechinus | Quolls, kangaroos, wallabies | Bettongs, numbat | Tree kangaroos, ringtail possums |
| Number of species | 20 | 34 | 26 | 10 |
| PC 1 | 0.27 (±0.06) | 0.37 (±0.05) | −0.37 (±0.08) | −0.85 (±0.10) |
| PC 2 | 0.60 (±0.07) | −0.17 (±0.07) | −0.37 (±0.07) | 0.33 (±0.14) |
| MVA ($km^2$) | 35.55 (±22.11) | 6.92 (±3.11) | 49.56 (±22.01) | 1.28 (±0.27) |
| Density (no. per $km^2$) | 2,241.85 (±1,451.03) | 123.40 (±23.95) | 66.73 (±24.39) | 864.57 (±591.52) |
| Dispersal distance (km) | 0.42 (±0.05) | 4.83 (±0.89) | 1.58 (±0.30) | 1.92 (±0.61) |
| Range (1,000 $km^2$) | 851.29 (±220.84) | 942.22 (±242.74) | 71.80 (±42.05) | 12.38 (±6.46) |
| Range in PAs (%) | 20.08 (± 2.10) | 18.38 (±1.73) | 37.42 (±3.88) | 69.34 (±4.32) |
| Suitable habitat (1,000 $km^2$) | 384.77 (±97.96) | 479.69 (±112.57) | 28.71 (±10.47) | 6.49 (±2.03) |
| Suitable habitat in viable clusters in PAs (%) | 24.48 (±2.58) | 22.17 (±2.05) | 28.13 (±3.04) | 73.28 (±3.76) |

PC, principal component; MVA, minimum viable area; PA, protected area.

(e.g., striped possums) and 86% of the Potoroidae family, including all bettongs (genus *Bettongia*; Appendix S1). This group can be thought of as largely medium-sized omnivores.

The fourth and smallest group of species (purple cluster) had the lowest MVA requirements, as well as relatively high population densities and intermediate dispersal abilities (Figure 1, Table 1). PAs covered over two-thirds of these species' extremely limited range and habitat extents, on average. Representation and persistence targets were met for 50% and 40% of these species, and a fifth are currently threatened (Figure 2). This group included two-thirds of the ringtail possum species (family Pseudocheiridae), as well as both tree kangaroos (genus *Dendrolagus*; Appendix S1). This group comprises predominantly arboreal folivores.

The NRS could support a greater number of populations of species in the first (Pink cluster—small omnivores) and second (Green cluster—larger-bodied species) groups, compared with the third (Blue cluster—medium-sized omnivores) and fourth (Purple cluster—arboreal folivores) groups ($F_{3, 83}$ = 36.23, $p$ < .001; Figure 3a). The extent to which viable habitat was fragmented also differed between species groups ($F_{3, 83}$ = 22.00, $p$ < .001; Figure 3b). Fragmentation was highest for species in the third group, although there was considerable variation among species within this group.

Under a scorched-earth scenario, just 0.5% of the protected habitat area considered viable in the previous analyses became unviable on average across species, although this ranged from 0% to 14.7%. This range depicted species' differences in the size and distribution of suitable habitat patches within PAs (Figure 4). The predicted loss in protected viable habitat area under a scorched-earth scenario varied between species groups ($H$ = 15.31, $p$ = .002); higher in the second group (Green cluster—larger-bodied species) than in the first and fourth groups (Pink and Purple clusters—small omnivores and arboreal folivores, respectively) (Figure 3c). The third group of species (Blue cluster—medium-sized omnivores) depicted high interspecies variability in predicted losses.

## 4 | DISCUSSION

The process of setting PA targets, assessing progress towards achieving these targets and establishing new PAs that maximize progress requires a means of assessing how effectively PAs both represent biodiversity and ensure its persistence (Gaston et al., 2008; Margules & Pressey, 2000). While the conservation capacity of the Australian NRS according to representation of mammal species' ranges within PAs was relatively high (all assessed mammal species had a portion of their range covered by PAs), it declined notably when we moved to viewing progress based on species' habitat requirements. Once habitat patches that were too small to support a viable population were excluded from the analysis, the NRS was found to be incapable of supporting a single population of up to 8% of species (Appendix S1). Protection was insufficient for up to a third of species based on a threshold of 10 viable, protected populations as reasonable insurance against stochastic processes (although there is a notable knowledge gap regarding appropriate targets for protected population number; Rondinini et al., 2011b; Di Marco et al., 2016). Current representation-based assessments of national and global PA progress (e.g., Barr et al., 2016; Venter et al., 2017) are therefore likely to overestimate the long-term success of PA estates, obscuring vulnerabilities for many species.

The identification of groups of species with distinct combinations of characteristics and current levels of protection proved useful in recognizing species for which considerations of persistence are most

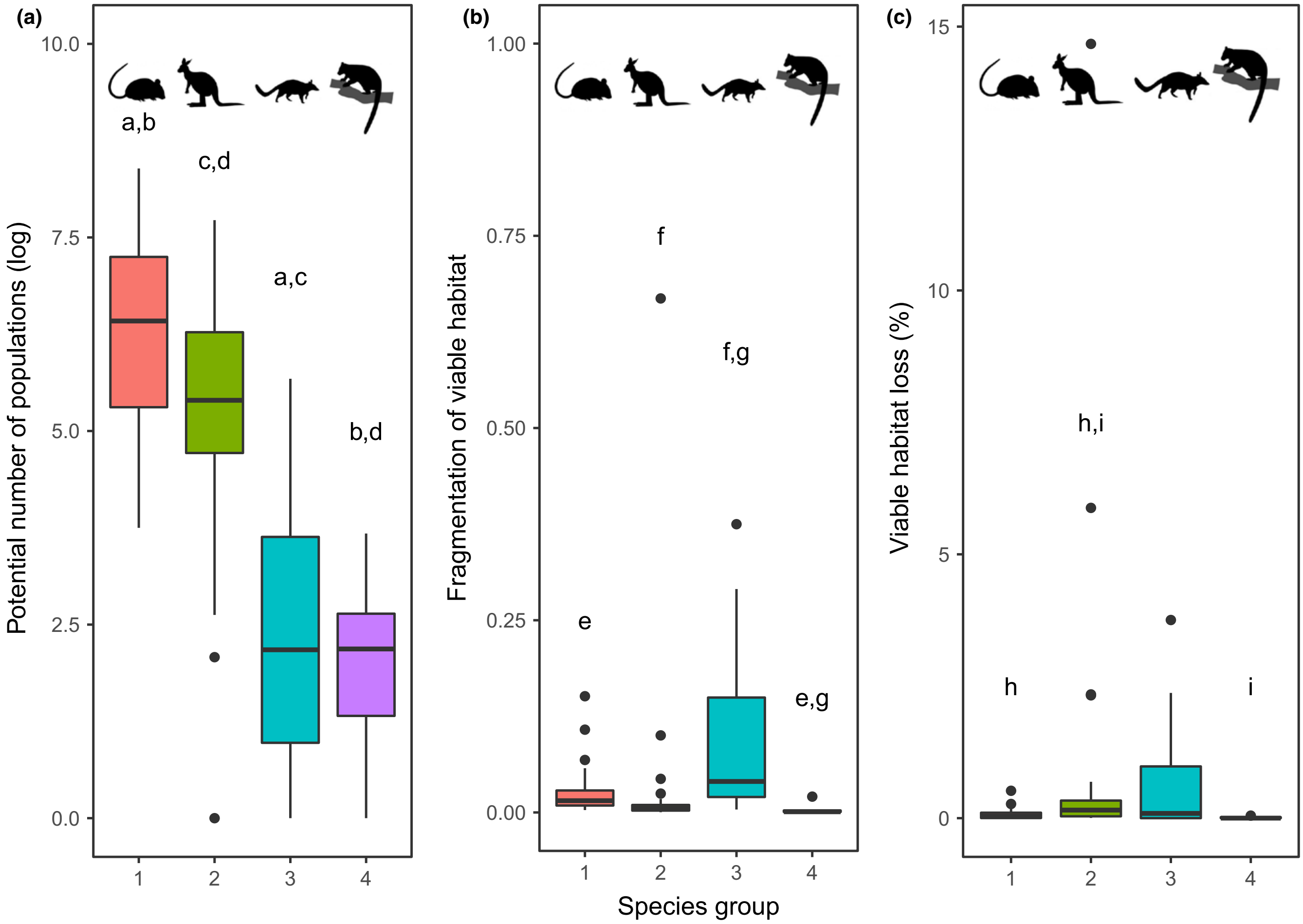


**FIGURE 3** For four mammal species groups with distinct combinations of characteristics, (a) the potential number of populations that can be supported within the Australian National Reserve System according to the distribution of viable habitat clusters; (b) the extent to which viable habitat is fragmented (1—maximally fragmented); and (c) the percentage of viable protected habitat that is lost under a scorched-earth scenario analysis. (See Table 1 for characteristics of each group with corresponding colours). Letters indicate significant difference between groups ($p < .006$) [Colour figure can be viewed at wileyonlinelibrary.com]

important for conservation planning and management. The species falling in groups one and three (Pink and Blue clusters—small- and medium-sized omnivores, respectively; Figure 1) possess both relatively large MVA requirements (because of their high MVP values and low population densities, respectively) and limited dispersal capabilities. This combination flags the importance of ensuring that individual PAs conserve sufficiently large habitat patches to facilitate population persistence, as there is a low probability of individuals moving between PAs. The medium-sized omnivores (Blue cluster) tend to have much smaller range and habitat extents than the small-bodied omnivores (Pink cluster) and their protected habitat is often highly fragmented (Table 1, Figure 3), suggesting that planning for persistence is of greater priority for this group. In support of these findings, the Blue cluster comprises predominantly threatened species and has the poorest rates of target achievement. Given the low coverage of these species' habitats by PAs (28% on average), considerations of persistence could be made through protecting new or adding to existing habitat patches to ensure they are larger than the species' MVA requirements.

By contrast, species in the Green and Purple clusters (larger-bodied species and arboreal folivores, respectively) are able to benefit from the protection of smaller habitat patches, because they have smaller MVA requirements (particularly the Purple group) and are more capable of moving between habitat patches (particularly the Green group). These species are therefore more likely to benefit from conservation actions that focus on maximizing representation within PAs, as well as those that build landscape connectivity between PAs. Achieving targets will be challenging for the arboreal folivores however, given that their small habitat extents are already well-covered by PAs (73% on average). Restoration may therefore be the only option for increasing the number of protected populations of these species, along with strict protection of any remaining habitat outside PAs. The categorization of 90 species into four groups means that variability exists within these groups. We therefore do not intend our insights to serve as blanket recommendations for all species, but rather to illustrate how an understanding of drivers of persistence, together with species characteristics, can enable a transition from assessments of PA representation to

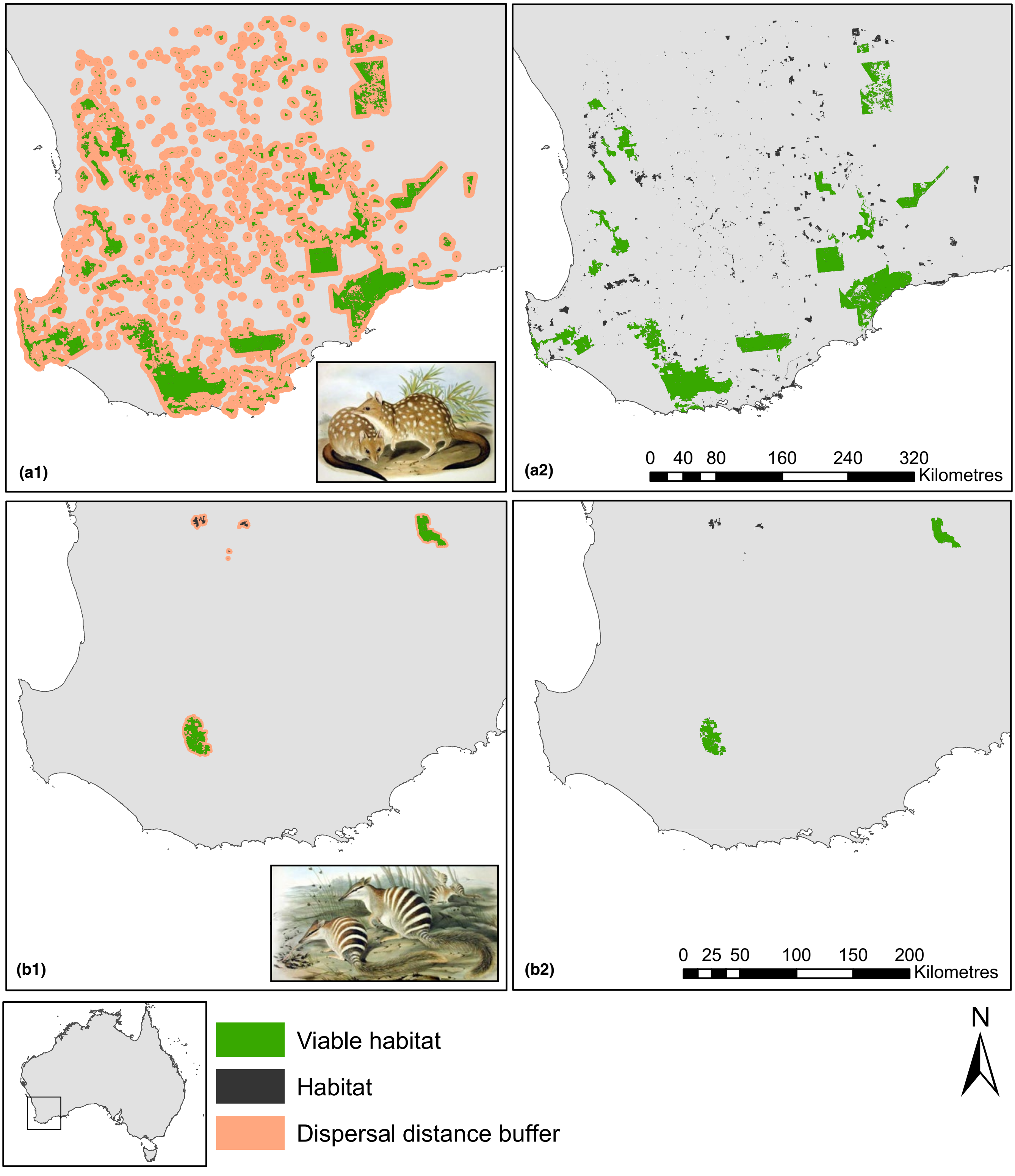


**FIGURE 4** Distributions of habitat and viable habitat within Australian protected areas (PAs) for two species: (a) western quoll *Dasyurus geoffroii* and (b) numbat *Myrmecobius fasciatus*. Buffers around suitable habitat patches (1) represent half the species' dispersal distance, with adjoining buffers thus depicting PAs that are considered to be connected for that species. During the scorched-earth analysis (2), these buffers were removed and all non-adjacent PAs were assumed to be disconnected, resulting in predicted reductions in total viable habitat area of 14.7% (a) and 2.2% (b) [Colour figure can be viewed at wileyonlinelibrary.com]

persistence at large scales for multiple, diverse species. Such an approach can provide managers with starting parameters to identify species that are at risk in the longer term within the PA estate, and guidance on the types of strategies that would reduce this risk.

Populations of protected species not only need to be large enough to be resilient to natural environmental, demographic and genetic stochasticity, they also need to be resilient to threats within PAs and the surrounding landscape that erode the capacity of PAs to support species and influence the ability of individuals to move between PAs (Newmark, 2008; Woodroffe & Ginsberg, 1998). Our scorched-earth analysis shows that, on average across species, the predicted extent of protected habitat in viably sized patches is insensitive to the assumption that species can move across the unprotected landscape between PAs. Meeting species' MVA requirements through habitat protection therefore appears to rarely be dependent on multiple nearby (but non-adjacent) PAs functioning collectively. This is likely because of the limited MVA requirements (e.g., arboreal folivores) and dispersal capabilities (e.g., small-bodied omnivores) of many Australian mammals, which respectively enable small PAs to be viable regardless of connectivity and limit the ability of PAs to function as a network between-which species can move. Differences between species are notable, however, ranging from species that are completely insensitive to connectivity assumptions, to those for which the capacity to move between PAs accounts for 15% of all viable habitat. The western quoll *Dasyurus geoffroii* (a threatened, larger-bodied species in the Green group) has intermediate MVA requirements and high dispersal capabilities, but also highly fragmented protected habitat spanning multiple small PAs that fall within the quoll's dispersal capabilities (Figure 4a). Many of these small PAs could in theory collectively provide habitat of a viable size, but only if the quoll can move between habitat patches across the unprotected landscape. The transformation of habitats between PAs therefore has the potential to significantly impede the capacity of the PA estate to conserve western quolls. By contrast, the numbat *Myrmecobius fasciatus* (median-sized omnivore; Blue group) occurs in a few highly isolated PAs, with viable protected habitat estimates thereby largely unaffected by the suitability of the matrix habitat for dispersal (Figure 4b). The Australian mammal assemblage is relatively small in body size, with more limited dispersal capabilities than many of the large- and medium-sized mammals occurring in other countries. For larger mammal species, assumptions around PA connectivity become more important (Santini, Saura, & Rondinini, 2016; Santini et al., 2014).

An assessment of the capacity of the European PA estate to conserve 27 mammal species found the estate to achieve representation targets for all species, but persistence targets for just 7.4 to 18.5% of species (depending on the MVP threshold used) (Santini et al., 2014). While the European PA estate therefore appears to have a greater capacity than the Australian estate to represent mammals, it has a lower capacity to facilitate the persistence of these species. These differences are likely to be partially the result of differences in species characteristics (e.g., European mammals, such as grey wolf *Canis lupus* and European bison *Bison bonasus*, have lower population densities and greater dispersal capabilities than many Australian mammals). Differences in PA capacity to facilitate persistence are likely to be further influenced by differences in the size and distribution of the two PA estates (e.g., Australia is estimated to have higher intra-PA connectivity than Europe, based on models that use a range of mammal dispersal distances) (Santini et al., 2016). Taxa such as amphibians and reptiles will tend to have smaller MVA requirements than mammals, but also more limited dispersal capabilities. The protection of smaller patches of suitable habitat is therefore likely to better support these species than many of the Australian mammals. Furthermore, small PAs can be imperative for ensuring the persistence of fragmented vegetation communities (Tulloch, Barnes, Ringma, Fuller, & Watson, 2016). It is therefore important that conservation planners are realistic and explicit regarding the intended role of different sizes and distributions of PAs, and careful in assuming that the presence of suitable habitat for a species within a PA constitutes meaningful progress towards species conservation targets.

We assess the potential capacity of the Australian NRS to protect mammal species in the long term. The translation of this capacity into conservation outcomes depends on effective management practices. Numerous threats continue to operate within some Australian PAs, with effective management, thus, imperative to ensuring species persistence (Evans et al., 2011). For example, severe declines of a number of mammal populations have recently been recorded in Kakadu National Park—one of Australia's largest PAs—likely as a result of an altered fire regime, feral stock and invasive species (Woinarski et al., 2011). These threats require intensive and effective management to mitigate their impacts on species. Furthermore, the NRS includes a large number of very small PAs (Cook et al., 2017), which are highly susceptible to degradation through edge effects (Laurance, 1991). While our assessment is thus a best-case scenario for the NRS, capacity is nevertheless a critical consideration, enabling systematic expansion of the existing PA estate and strategic identification of where to focus management efforts (Margules & Pressey, 2000). Finally, it is important to note the limitations on the availability, accuracy and generalizability of species data. Assessments of progress towards the long-term conservation of species are never absolute or complete; they must continue to integrate more and better ecological data as it becomes available.

## 5 | CONCLUSION

In the first assessment of the capacity of Australia's NRS to meet the habitat and area requirements of 90 mammal species, we provide managers with an approach to identify species whose long-term persistence within the PA estate is vulnerable and guide possible management strategies to enhance this capacity. While planning for species representation within the PA estate is likely to be sufficient for some species, planning for persistence is of particular importance for species with large MVA requirements and limited dispersal abilities. Acknowledging that many recommendations will need to be species-specific, our study demonstrates that we can and should be moving towards considerations of persistence in national PA planning and management.

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## DATA ACCESSIBILITY

All models are based on freely available online data, see in-text references.

## ORCID

*Hayley S. Clements* http://orcid.org/0000-0002-7015-6532

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

## BIOSKETCHES

**Hayley S. Clements** is a conservation scientist with interests in protected areas, private land conservation, large predator ecology and social–ecological systems.

**Stephen Kearney** is a conservation scientist interested in understanding the pressures affecting biodiversity and how to mitigate them effectively.

**Carly N. Cook** is a conservation biologist interested in evidence-based conservation and the development of decision tools that integrate the best available science into conservation management.

Author contributions:

HC, SK and CC contributed to paper conceptualization, HC undertook analyses and wrote the paper, SG and CC provided input on the written manuscript.

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