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The contribution of land tenure diversity to the spatial resilience of protected area networks

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Abstract

1. The relationship between diversity and resilience is relatively well-established for ecological systems, but remains much less explored for socio-economic systems. Institutional diversity can have particular relevance for protected areas, whose managerial responses to environmental change depend on their legal basis, ability to make and enforce rules and socio-political acceptance and endorsement.
2. Protected area expansion strategies are increasingly turning to private land conservation to increase the configuration and connectivity of national protected area networks. Yet, we know little about the relative role of privately owned protected areas in protecting threatened and poorly protected (under-represented) habitats, and in the overall connectivity of the national protected area network.
3. We present an empirical assessment of protected area tenure diversity across South Africa.
4. Privately owned protected areas comprise 25.58% (2,878,422.26 ha) of the area of the total protected area estate.
5. Private nature reserves emerged as the dominant protected area type in under-represented and threatened habitats, protecting, on average, 32%, 38% and 41%, respectively, of poorly protected, threatened and endangered vegetation classes.
6. Private nature reserves had the largest overall effect, compared to other protected area types, on connectivity within the national network. A spatially randomized comparison showed that privately owned protected areas are overdispersed and more strategically positioned to connect other types of protected areas than would be expected by chance from their extent and abundance.
7. Our results suggest that privately owned protected areas enhance the resilience of the national protected area network, making it more extensive and better-connected, with greater levels of habitat redundancy. More generally, our analysis highlights the potentially valuable role of institutional diversity in building resilient habitat networks for biodiversity conservation.

KEYWORDS
composition, configuration, diversity, network analysis, private land conservation, social–ecological, South Africa

1 | INTRODUCTION

A growing body of theory in ecology and social–ecological systems research suggests that in complex systems, there is a predictable and generally positive relationship between diversity and resilience (Folke et al., 2004). With a few exceptions (Bellwood, Hoey, & Choat, 2003), this relationship is well-established in ecology and grounded in evolutionary theory (Tilman, 1999). In more diverse systems, it is less likely that environmental change that leads to the loss of some species will also result in the loss of entire functional groups and the collapse of entire ecosystems (Bernhardt & Leslie, 2013; Oliver et al., 2015; Yachi & Loreau, 1999). The likelihood that natural selection will identify one or more successful solutions to a given environmental problem, in the form of persistent species and functions, is strongly related to the range and nature of options (species) in the system (Elmqvist et al., 2003; Nash, Graham, Jennings, Wilson, & Bellwood, 2016; Walker, Kinzig, & Langridge, 1999). Natural selection can also make ecological communities more resilient by selectively removing individuals that are poorly suited to their environment (Moseby, Blumstein, & Letnic, 2016). For example, removal by predators of individuals that are more vulnerable to pathogens which may act as spreaders of disease, can improve the health of animal populations.

Diversity–resilience relationships are thought to exist, but are less clear, in socio-economic systems (Norberg, Wilson, Walker, & Ostrom, 2008). The sociocultural systems of people (and indeed other social animals) are under a different kind of selective pressure because the traits that determine survival and adaptive capacity can be learned or copied and are strongly influenced by social rather than biophysical dynamics. Strong parallels between ecological and socioeconomic selection pressures nonetheless exist (Bruderer & Singh, 1996; Hannan & Freeman, 1989), and there is growing evidence that social systems with a diversity of personality types, cultures, roles, institutions and/or economic models (for example) may be more effective at responding to environmental change through the effects of these traits on processes of innovation, adaptation and resistance (Abernethy, Bodin, Olsson, Hilly, & Schwarz, 2014; Clements, Baum, & Cumming, 2016; Evans, 2004; Leslie & McCabe, 2013; Ostrom, 2009; Phelps & Parsons, 2003). For example, in Wisconsin (U.S.A.), the existence of two different tenure systems (specifically, the presence of lakes that were owned and managed by first nation people and others managed by the Wisconsin Department of Natural Resources) made it easier for new management strategies for in-demand Walleye fish populations to be tested in lakes with restricted access (Westley, Carpenter, Brock, Holling, & Gunderson, 2002); and in Zimbabwe, during ZANU-PF's controversial resettlement program, nature conservancies that were co-managed with local communities proved harder than private game reserves for corrupt elites to take ownership of (e.g. see Kreuter, Peel, & Warner, 2010; Child, Musengezi, Parent, & Child, 2012). Norberg et al. (2008) have argued that since many management situations involve processes of learning by experimentation, an important component of successful adaptive management is to have 'a rich reservoir of options, i.e., institutional diversity' in the sense of a range of operational and collective choice rules that can be tried out in different circumstances.

Diversity in socio-economic systems may also be costly or inefficient to maintain, or may create problems, particularly in situations in which the environment is relatively constant. It can lead to social fragmentation and related problems of marginalization and inequity (Bolay, Pedrazzini, Rabinovich, Catenazzi, & García, 2005; Cumming, 2011a; Wacquant, 1996). In political systems, the additional transaction costs involved in incorporating diverse opinions into decision-making processes can lead to a failure of the processes themselves; and economic experiments that fail (e.g. Samsung's Galaxy Note 7; Yun et al., 2018) can be costly. Similarly, businesses that can coexist during periods of economic growth may enter more directly into competition with each other during periods of economic decline, when selective processes remove those that are inefficient at an individual level (Martin, 2012).

The presence of diverse institutions and organizations in conservation and other sectors leaves a physical footprint on the landscape (Poiani, Richter, Anderson, & Richter, 2000). Landscape ecology has demonstrated that landscape heterogeneity—or more specifically, the composition and configuration of habitat types and land uses across a landscape that may result, in part from decisions made by institutions on the landscape—has strong relevance for ecosystem processes (Lovett, Jones, Turner, & Weathers, 2005) and ultimately for social–ecological resilience (Cumming, 2011b). Anthropogenic habitat types, such as farmland and cities, have well-documented negative impacts on species diversity, not only because they reduce the number and extent of habitats available to different species (Newbold, 2016), but also because of the ways that they interrupt connectivity between these habitats (Crook, 2015).

Protected areas, which are social–ecological systems with explicit ecological goals (Cumming et al., 2015), offer a useful arena within which to investigate the relevance of institutional diversity for spatial patterns at broad scales, and to better understand the interactions between institutional diversity, ecological diversity and resilience. Tenure diversity has mostly been considered in terms of its relevance inside versus outside protected areas (Bruner, Gullison, Rice, & da Fonseca, 2001; Geldmann et al., 2013). Although conservation planning, in particular, has long considered the link between biological diversity, spatial arrangement and ecological resilience (Gaston, Pressey, & Margules, 2002; Margules & Pressey, 2000), relatively little attention has been paid to differences in protected area tenure types as structuring influences on ecological and social–ecological processes (Aswani, Albert, & Love, 2017). Most conservation planning exercises, for example, disregard protected area tenure diversity or management heterogeneity and consider planning units from the perspective of animal and plant populations as either 'conserved' or 'not conserved.'

At the same time as community management or co-management of protected areas appears to be expanding (Aswani et al., 2017), privately owned protected areas are increasingly being considered for achieving conservation targets in a difficult economic climate (Bingham et al., 2017; Mitchell et al., 2018; Stolton et al., 2014).

Private lands have the potential to increase the resilience of protected area networks. They may contribute to increasing redundancy (both in terms of adding more areas to the protected area network and buffering of public protected lands), and connectivity (Fitzsimons & Wescott, 2008; Mitchell et al., 2018; Wallace, Theobald, Ernst, & King, 2008). They may also offer complementarity to state-owned protected areas by protecting areas with high agricultural potential that may be less easily protected by state-owned parks, such as riparian (Wallace et al., 2008) and low-lying areas (Gallo, Pasquini, Reyers, & Cowling, 2009). Despite evidence that different types of protected area tenure have different consequences for the resilience of protected area networks (Clements, Kerley, Cumming, De Vos, & Cook, 2018; De Vos, Clements, Biggs, & Cumming, 2019; Stolton et al., 2014), the importance of tenure diversity of protected areas for biodiversity conservation remains largely unexplored.

We assessed the relevance of the tenure diversity of protected areas in South Africa for conservation. South Africa offers a unique opportunity to understand tenure diversity at a national scale, thanks to its long history and record of privately owned protected area gazettement (De Vos et al., 2019), as well as well-developed institutional framework encompassing a broad diversity of protected area types (DEA, 2013). We expected that the spatial footprint of privately ownedprotected areas (in South Africa, private nature reserves, contractual national parks and stewardship nature reserves, Appendix S1) would differ from that of state-owned areas (in South Africa, national parks and provincial-, forest-, local-, and development nature reserves) because privately owned areas are created under different socio-economic incentives and constraints, and often with different objectives (Cumming & Daniels, 2014; Mitchell et al., 2018). Resilience theory suggests that privately owned protected areas will improve the resilience of the reserve network by increasing its area (number of species is a function of area), redundancy (adding more examples of habitat types that are also represented in the state-owned network while also offering a wider range of management strategies), and connectivity, facilitating the regenerative ecological processes of dispersal, gene flow and propagation as well as providing a form of ecological memory (Bengtsson et al., 2003).

Many of these consequences are obvious, resulting inevitably from the addition of natural land to the reserve network, and have been already been demonstrated at a regional scale (Gallo et al., 2009). The more interesting question is whether the private reserve network (or some element of it) punches above its weight; and in particular, whether it disproportionately conserves and connects habitat and ecosystem types that are under-represented in the state-owned network, resulting in greater landscape heterogeneity than what could have resulted from a system with only state-owned tenure.

We thus focused our analysis on two important questions that link tenure diversity and ecological resilience: (a) Do privately owned protected areas disproportionally add novel or under-conserved habitats to the reserve network, or do they simply add further redundancy of already-conserved habitat types? and (b) At a national extent, does the addition of privately owned protected areas have a disproportionate impact on the overall connectivity of the reserve network?

2 | MATERIALS AND METHODS

2.1 | Protected area data

South African Protected areas are gazetted under the National Environmental Management: Protected Areas Act (2003). We included national parks, nature reserves, local nature reserves and forest nature reserves in our analysis. Protected environments and mountain catchment areas are two additional protected area types that exist on private land. Along with world heritage sites, those areas were not included in this study on account of their overlap with other protected areas, ambiguity in accounting for these areas in national targets and their relative high susceptibility to human pressures. All types of protected areas can exist on private land (Cumming & Daniels, 2014).

We compiled a complete protected area spatial and gazettement dataset, consolidated using ArcGIS 10.5, with Albers equal area projection (ESRI, 2017). Data were obtained from the national protected area register (Department of Environmental Affairs, 2017), provincial conservation authorities and national gazettes, as described in Appendix S1. There were 1,462 protected area entries in total (Table 1). Of these, 1,018 (35.76% of the total official estate, by area) were privately owned (this estimate counts world heritage sites as state-owned).

Different investigators have defined South Africa's private conservation estate in different ways, leading to a wide array of different estimates for the actual coverage of private land that is in the conservation estate (Gallo et al., 2009). Taylor, Lindsey, and Davies-Mostert (2015) provide an estimate of 17,419 km^2, or 14% of the country's surface area, for the country's informal wildlife ranching estate. Here, we include only areas that are considered to be part of the country's formal protected area estate, by virtue of having been officially gazetted (DEA, 2013; Driver, 2016). No areas that form part of the 'informal conservation estate' (which includes Ramsar sites and Biosphere reserves) were thus included in our study. Our definition of what constitutes a protected area is in alignment with its official national use (DEA, 2013), and not the broader IUCN definition that includes 'other effective means'. Additionally, we only included non-overlapping protected area types were tenure was clearly demarcated. Thus, we excluded IUCN category V and VI protected areas (in South Africa, protected environments, world heritage sites and mountain catchment areas) from all but the initial accounting analysis. We simplified the tenure subtype classification by reclassifying tenure types with low abundance with similar subtypes (see Appendix S1).

2.2 | Contribution to conservation outcomes

We used ArcGIS 10.5 (ESRI, 2017) to calculate the total spatial footprints of different protected area categories. We addressed

TABLE 1 A summary of South Africa's protected area estate

Tenure type	Owner	Total area (ha)	No	Per cent of estate	Mean area (ha)	*SD*
Contractual park	Private	172,373.33	10	1.53	5,069.80	11,375.14
National park	State	3,811,643.13	20	33.91	53,685.11	247,129.71
Development areas reserve	State	87,742.74	41	0.78	3,249.73	5,907.98
Forest nature reserve	State	90,253.40	32	0.80	2,820.42	4,430.65
Local nature reserve	State	79,886.49	109	0.71	566.57	1,231.41
Stewardship nature reserve	Private	204,070.87	80	1.82	2,125.74	6,150.68
Private nature reserve	Private	2,501,978.06	888	22.26	2,587.36	5,509.29
Provincial nature reserve	State	1,674,897.56	209	14.90	6,491.85	16,410.30
Forest wilderness area[a]	State	164,891.11 (274,489.89)	12	1.47	274,489.89	16,835
Mountain catchment area[a]	Private	563,334.05 (624,566.67)	16	5.01	624,566.67	26,713
World heritage site[a]	State and private	1,311,643.28 (2,027,066.08)	21	11.67	2,027,066.08	110,557
Protected environment[a]	Private	577,951.10 (593,216.10)	24	5.14	593,216.10	52,163
Total estate		11,240,665.12	1,462		5,303.10 (7,146,67)	52,981.15 (54,794.41)

[a]Areas that were not included in this study and overlap with other protected area tenure types. Numbers reported for these areas indicate the non-overlapping area (ha) added to the conservation estate. The total areas for these tenure types are indicated in brackets.

the question of whether privately owned protected areas add additional value, apart from increasing redundancy, from the standard landscape ecology perspectives of composition (focusing on habitat amount) and configuration (focusing on habitat arrangement, and particularly on connectivity, Gergel & Turner, 2017). All comparisons were undertaken relative to the reference point provided by existing state-owned areas. Since state-owned areas are generally older, larger and accepted as public rather than private goods (Langholz & Lassoie, 2001), we treated them as fixed elements of the landscape.

2.3 | Composition analyses

In this context, composition describes the amounts and kinds of habitat occurring within privately owned protected areas. We asked whether privately owned protected areas disproportionally conserve either (a) unique habitats; or (b) different proportions of particular habitats relative to the areas of habitats contained within state-owned areas. To do this, we used a national map of vegetation classes (Mucina & Rutherford, 2006), which was also used in the development of the national biodiversity assessment (2011), and protected area expansion strategy (2010). The dataset maps 440 vegetation classes, spread across 43, 646 polygons. It classifies each according to its threat level ('least threatened', 'vulnerable', 'endangered' and 'critically endangered') and level of protection ('not protected', 'hardly protected', 'poorly protected', 'moderately protected', 'well protected'). We used these protection and threat statuses to understand the contribution of different protected area tenure types to the composition of the national protected area estate.

We used ArcGIS to calculate areas (hectares) for each vegetation class, and cross-tabulated the overlapping areas of each protected area tenure type with that of different vegetation classes. We were interested in understanding the proportion of unique (i.e. threatened or poorly protected) habitats (vegetation classes) that would not otherwise be protected by other tenure classes. We, therefore, calculated the proportion of total protection, for each tenure type, in each vegetation class. Given that the data were not normally distributed, we used a nonparametric Kruskal–Wallis one-way ANOVA on ranks to detect significant differences between tenure types. If the Kruskal–Wallis test is significant, a post hoc analysis can be performed to determine which levels of the independent variable differ from each other level. We used the Dunn test (Dunn, 1961), performed in R with the Dunn test function in the FSA package (Ogle, Wheeler, & Dinno, 2018). The Dunn test is appropriate for groups with unequal numbers of observations (Zar, 2010). All statistics were performed in the statistical R programme.

2.4 | Configuration analyses

Configuration describes the spatial arrangement of privately owned protected areas and their spatial relationships to state-owned areas. Adding more patches to a network will almost inevitably increase its overall connectivity, but this observation does not resolve the following questions: (a) do privately owned protected areas contribute to connectivity in the same way as state-owned areas, and what is the proportion of total connectivity within the network that is due to privately owned protected areas (i.e. does the private network increase connectivity by 5, 20 or 50 per cent)? (b) Do the locations of privately owned protected areas increase the connectivity of the reserve network more or less than might be expected by chance?

We dealt with these questions through analysis of either the entire network, or subsets of the network, using the igraph package in R (Csardi & Nepusz, 2006). Vertex lengths (i.e. inter-protected area distances) were measured in km, using the *gDistance* command in the *gdistance* package (Van Etten, 2017), as the great-circle distance between the nearest edges of individual polygons.

We measured the contributions of individual nodes to connectivity using betweenness centrality (hereafter, 'BC'), which is a well-accepted and widely used measure of the contribution of an individual node to overall network connectivity. BC measures the number of shortest paths across a network that goes through a given node (Newman, Barabási, & Watts, 2006). In an ecological and biogeographical setting, nodes with a high BC are located along multiple potential movement routes and hence, can be interpreted as being more important for spatial connectivity than those with a low BC (Borgatti, 2005; 2012; Maciejewski & Cumming, 2016).

2.5 | Relative connectivity of privately owned protected areas

Ecological connectivity depends on movement capability. For example, a rodent that will only disperse up to 1 km away from a grassland patch will regard patches 2 km apart as being disconnected, whereas a raptor that flies tens of kilometres in a day may regard patches of grassland 10 km apart as being connected. To evaluate ecological connectivity across a range of scales, we thus defined a threshold distance for connectivity across a range of scales from 100 to 1,000 km, and quantified BC at each scale. These data were either summed for analysis over all scales, or compared at each individual scale.

We used the BC data to compare the connectivity of different kinds of protected area in both relative and absolute terms. For clarity, we have given each set of analyses a unique label that we will use throughout the manuscript.

2.5.1 | Whole-network comparison by protected area type

We first estimated BC for each protected area in the entire protected area network, treating all protected areas as potentially connected and calculated mean BC and its variance for all nodes of each protected area type within the network. BC values were log-normally distributed. We tested for differences between protected area types using a nonparametric Kruskal–Wallis test on the logs of BC values, followed by a post hoc, nonparametric Dunn's test with Benjamini–Hochberg correction. We did not use a Tukey's honestly significant difference test for these data because Levene's test indicated that their variances were not homoscedastic.

2.5.2 | Comparison within protected area type

Second, we estimated BC and minimum inter-patch distance across all protected areas of each different protected area type (i.e. treating each different tenure type as its own network) to test how the mean and variance in the BC metric varied within protected area types. We ran this analysis only for the more abundant protected area types in the data set.

2.5.3 | Whole-network exclusion comparison by protected area type

Third, since the changes in connectivity that result from adding nodes are nonlinear and synergistic, calculating BC or minimum inter-patch distances for each individual protected area type and comparing these results can be misleading. For example, widely dispersed nodes might nonetheless act as critical stepping stones between other protected area types by virtue of their location. To explore interaction effects, we thus ran a third series of analyses in which we systematically removed each protected area type in turn from the full network to explore how this affected the mean BC (and its variance).

These analyses gave us estimates of the means and variances in (a) the individual contributions from each protected area type to connectivity and dispersal distances within the full existing network; (b) the connectivity within each different protected area type, as though it was a stand-alone network; and (c) the relative effect on mean protected area contributions to connectivity of removing all protected areas of a particular type. We used the results to triangulate to general inferences about the relevance of different protected area types for network configuration. Since these analyses were intended to explore absolute effect sizes, rather than proportional effect sizes, we did not undertake additional randomizations to test for the influence of protected area or number on our results.

Randomization analysis: We also wanted to know whether there was something 'special' about the placing of privately owned protected areas, as might for example occur if they were strongly clustered around state-owned areas, that led to a higher or lower influence on connectivity. As a control, we generated 20 randomized maps in which the same privately owned protected area polygons were moved at random to new locations on the landscape. We used a python script in the ArcPy library to generate a new random centroid for each privately owned protected area polygon (private nature reserves, stewardship nature reserves and contractual national parks), around which the polygon shape was then redrawn. If there were any overlaps between polygons, the script would rerun until a map of non-overlapping protected areas could be drawn. We then ran an analysis of configuration metrics for privately owned protected areas for each randomized map and compared the results to those for the existing protected area network.

3 | RESULTS

3.1 | Composition analyses

3.1.1 | Overall footprint

Privately owned areas (nature reserves and national parks) make up 25.58% of South Africa's conservation estate, compared to 51.11% of state-owned areas (Table 1, Figure 1). Protected environments and mountain catchment areas (which are also both private) add an additional 10.14%, whilst world heritage sites (mostly state-owned) and forest wilderness areas (state-owned) add 13.12%. The total area under protection by our calculations (11,240,665.12 ha, 9.2% of South Africa's land area) is slightly higher than reported by state agencies (DEA, 2013; Mitchell et al., 2018). This is probably a result of additional private nature reserves identified in our study that are not currently captured by official datasets.

3.1.2 | Protection of threatened habitats

There were significant differences in mean proportion of total protected areas conserved by different tenure types in vegetation classes classified as 'least threatened' (Kruskal–Wallis

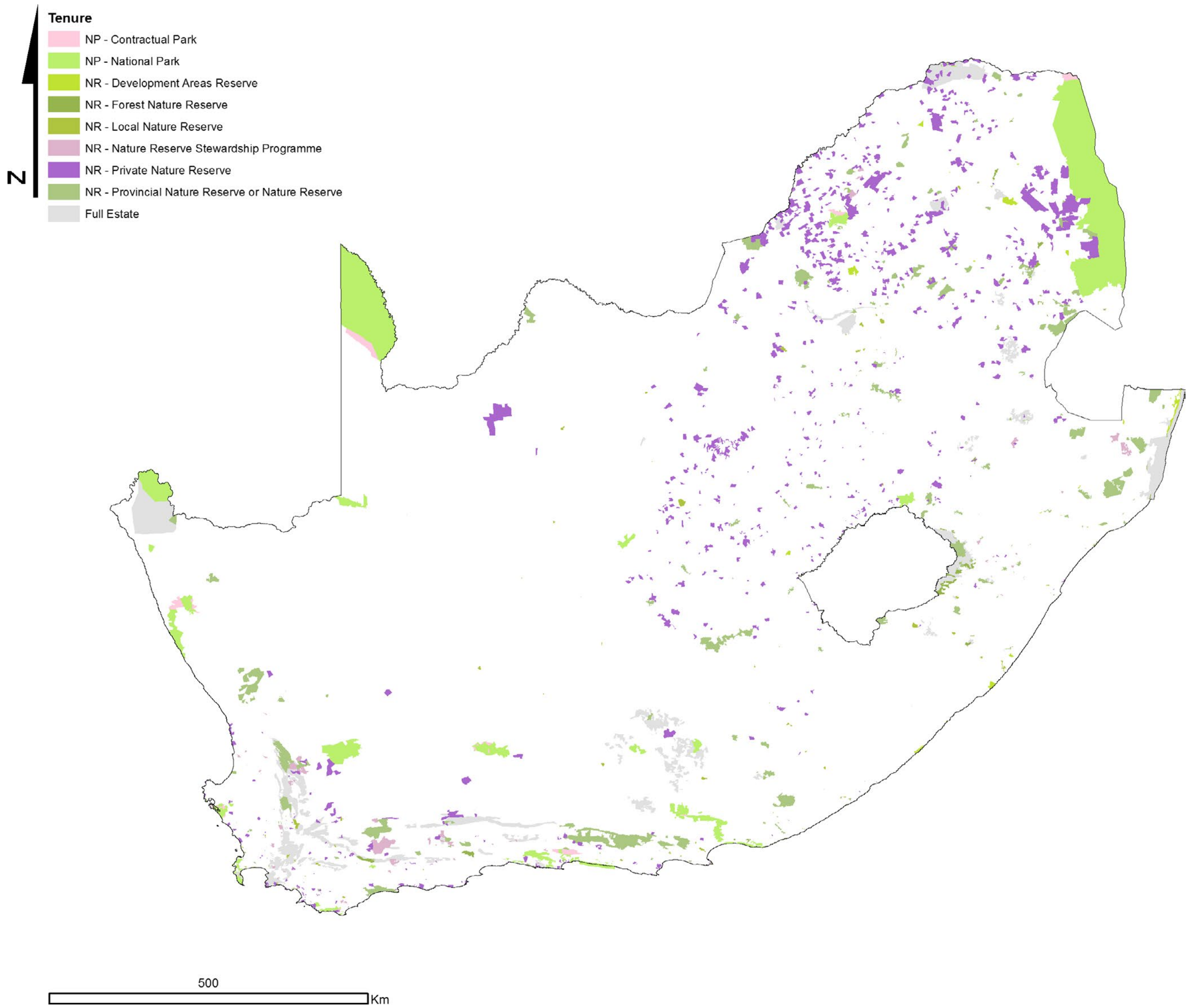

FIGURE 1 South Africa's official protected area estate. Privately-owned protected areas are indicated in purple hues, whilst state-owned areas are indicated in greens. Grey-coloured areas show non-overlapping portions of protected environments, mountain catchment areas, forest wilderness areas, and world heritage sites (because of their higher tolerance of human impacts and ambiguous contribution to protected area targets , these four tenure types were not included in analyses)

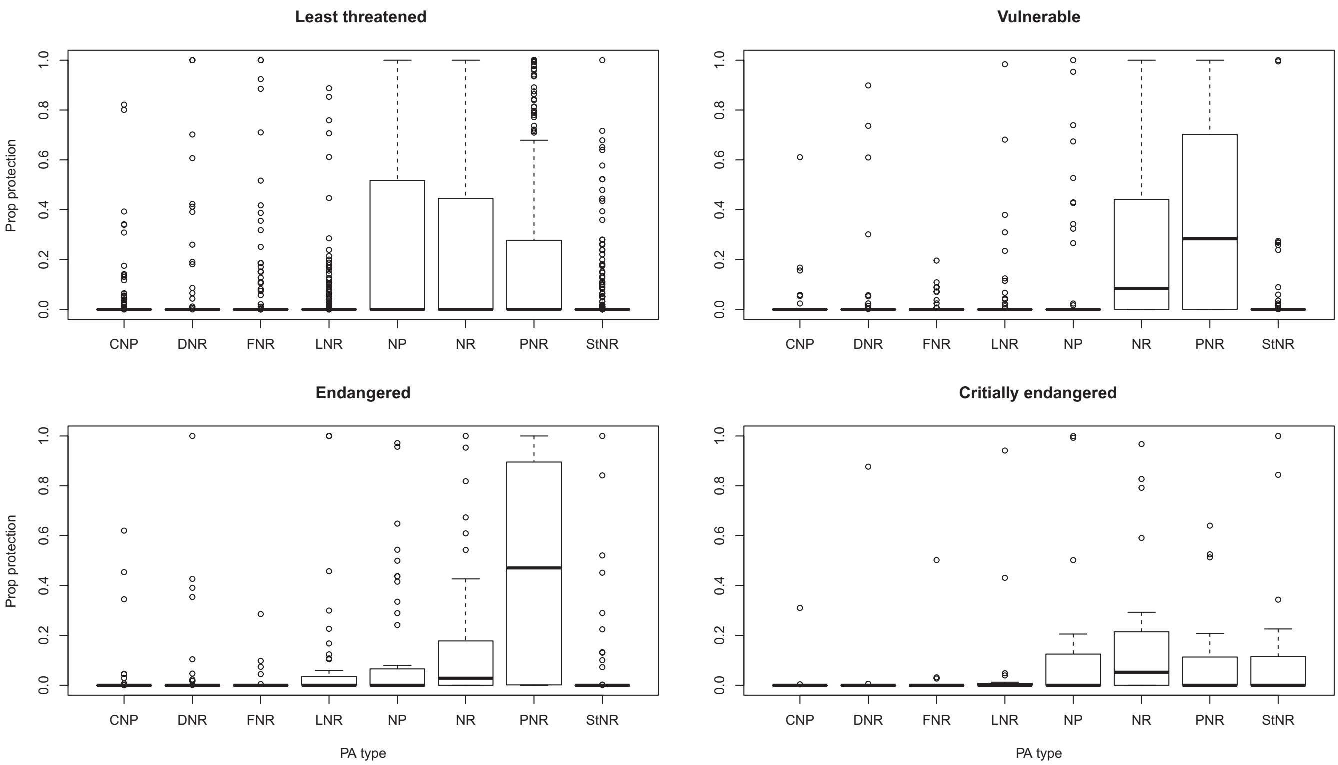

FIGURE 2 The mean proportion (±SD) of total protection of least threatened (n = 294), vulnerable (n = 68), endangered (n = 58), and critically endangered (n = 20) vegetation classes represented by contractual national Parks (CNP), development nature reserves (DNR), forest nature reserves (FNR), local nature reserves (LNR), national parks (NP), provincial nature reserves (NR), private nature reserves (PNR) and stewardship nature reserves (StNR)

χ^2 = 387.62, df = 7, p < 0.001, n = 294), 'vulnerable' (Kruskal–Wallis χ^2 = 147.82, df = 7, p < 0.001, n = 68), 'endangered' (Kruskal–Wallis χ^2 = 104.81, df = 7, p < 0.001, n = 58), and 'critically endangered' (Kruskal–Wallis χ^2 = 19,987, df = 7, p = 0.06, n = 20) (Figure 2). In 'least threatened', 'vulnerable' and 'endangered' habitats, a post hoc Dunn test revealed significant differences (p < 0.001) between the mean total proportion of all tenure types. In 'least threatened' vegetation types, national parks (pp = 0.25, SD = 0.39), nature reserves (pp = 0.25, SD = 0.35) and private nature reserves (pp = 0.2, SD = 0.32) conserved the largest proportion, on average, of all tenure types. In 'vulnerable' habitats, nature reserves (pp = 0.27, SD = 0.33) and private nature reserves (pp = 0.38, SD = 0.38) protected the largest mean proportion, and in 'endangered' habitats, private nature reserves (pp = 0.46, SD = 0.41) were significantly more dominant than nature reserves (pp = 0.16, SD = 0.26) and national parks (pp = 0.11 SD = 0.24). In 'critically endangered' habitats, national parks (pp = 0.15, SD = 0.31), state-owned nature reserves (pp = 0.2, SD = 0.32), stewardship nature reserves (pp = 0.13, SD = 0.29) and private nature reserves (pp = 0.11, SD = 0.21), protected the largest proportions of vegetation classes. A post hoc Dunn test (Appendix S2) revealed significant differences only between state-owned nature reserves and contractual national parks (Z = −3.54, p = 0.01), development nature reserves (Z = −3.48, p = 0.01) and forest nature reserves (Z = −3.20, p = 0.04).

3.1.3 | Protection of under-protected habitats

There were significant differences in mean proportions of total protected areas conserved by different tenure types in vegetation classes classified as 'well protected' (Kruskal–Wallis χ^2 = 149.71, df = 7, p < 0.000,1, n = 108), 'moderately protected" (Kruskal–Wallis χ^2 = 106.82, df = 7, p < 0.001), 'endangered' (Kruskal–Wallis χ^2 = 421.7, df = 7, p < 0.001) (Figure 3). In all three classes of protection levels, a post hoc Dunn Test revealed significant differences (p < 0.001) between the mean total proportion protected by different tenure types. In 'well protected' vegetation types, national parks (pp = 0.44, SD = 0.45) and state-owned nature reserves (pp = 0.24, SD = 0.35), on average, represented the largest proportion of protected areas. In moderately protected areas (n = 57), national parks (pp = 0.26, SD = 0.39), state-owned nature reserves (pp = 0.35, SD = 0.38) and private nature reserves (pp = 0.23, SD = 0.31) protected the largest shares of vegetation classes. In poorly protected vegetation classes (n = 275), private nature reserves (0.32, SD = 0.39), and to a lesser extent, state-owned nature reserves (0.21, SD = 0.32) represented the largest proportion of protection (Figure 3).

The spatial distribution of the proportion of state-owned and privately owned protected (Figure 4) reveals state-owned areas to represent the largest proportion of the protected estate in coastal and desert biomes, whilst privately owned protected areas protected

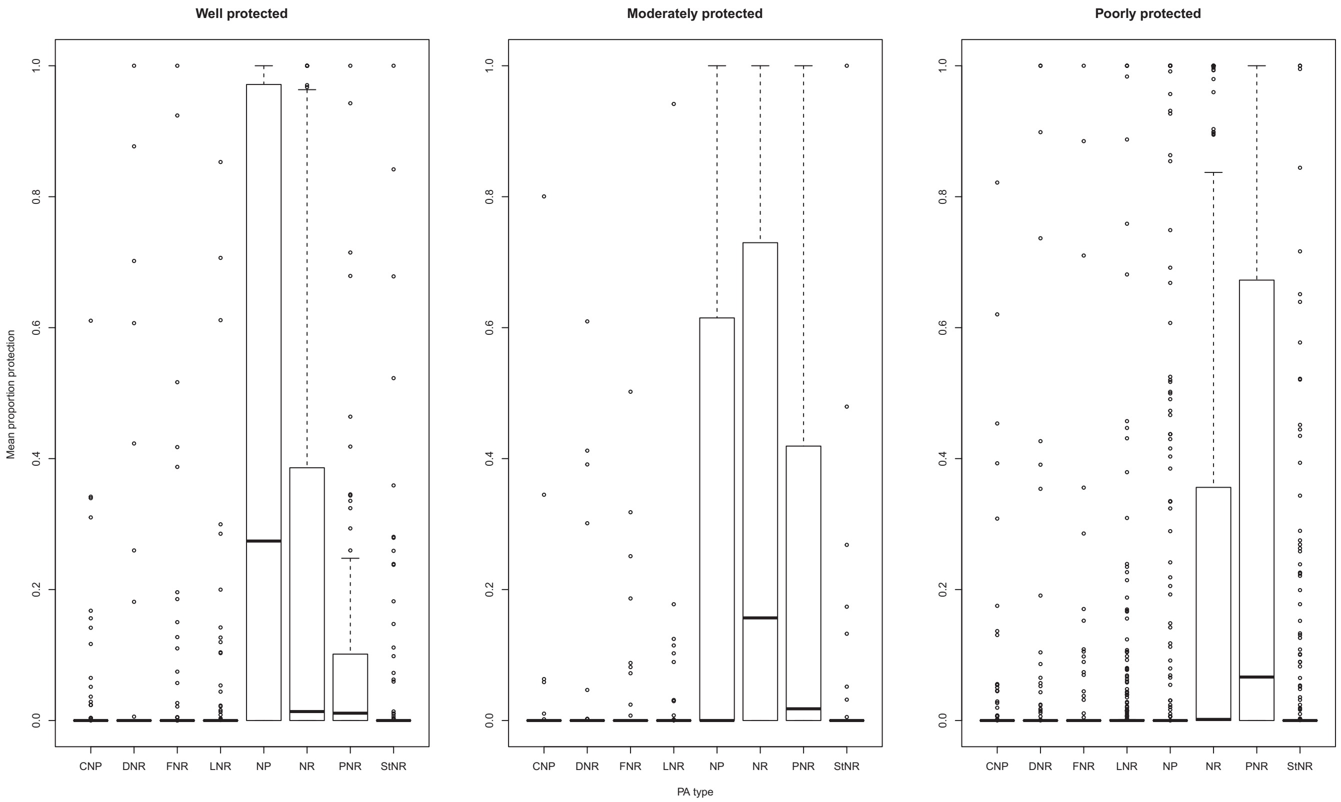

FIGURE 3 The mean proportion (±SD) of total protection of vegetation types that have been classified as poorly protected (n = 275), moderately protected (n = 57) and well protected (n = 108), that are protected by contractual national parks (CNP), development nature reserves (DNR), forest nature reserves (FNR), local nature reserves (LNR), national parks (NP), provincial nature reserves (NR), private nature reserves (PNR) and stewardship nature reserves (StNR)

a larger proportion of the grassland biome and inland vegetation types.

3.2 | Configuration analyses

3.2.1 | Whole-network comparison by protected area type

Comparing BC by protected area type for the entire network identified significant differences in contributions to network connectivity between types (Kruskal–Wallis χ^2 = 37.66; df = 7; p < 0.001, Figure 5). Dunn's test comparisons between protected area types (Appendix S2) indicated that these differences were mainly associated with contractual parks and local nature reserves.

3.2.2 | Comparison within protected area type

Comparisons of network measures within protected area types (Table 2) showed that the configuration of private nature reserves displayed similar properties to other kinds of protected area, although being more abundant they contributed to many more edges and displayed a much higher *SD* in BC. The mean edge length and mean nearest neighbour distance between private protected areas was lower than that of either National or Provincial Parks, the primary state-owned protected areas, although the total network diameter for both state-owned reserves was higher (indicating a slightly wider coverage). Private areas thus appear to be more numerous and more connected, but slightly less widespread than the two state-owned reserves.

3.2.3 | Whole-network exclusion comparison by protected area type

The exclusion analysis (Table 3) showed that leaving out private nature reserves would have the largest single effect of any protected area type on both mean edge length and mean nearest neighbour distance (increasing both), offering further evidence that private reserves make a key contribution to the overall network connectivity in South Africa's protected area estate. Interestingly, leaving out Private Nature Reserves also had the largest single (increasing) effect on network diameter.

3.2.4 | Randomisation analysis

Comparison of configuration metrics for the private nature reserves within the actual versus random protected area networks (Appendix S4) showed that the mean BC of Private Areas within the actual network was 3.6 times higher than within the random network (141,577,

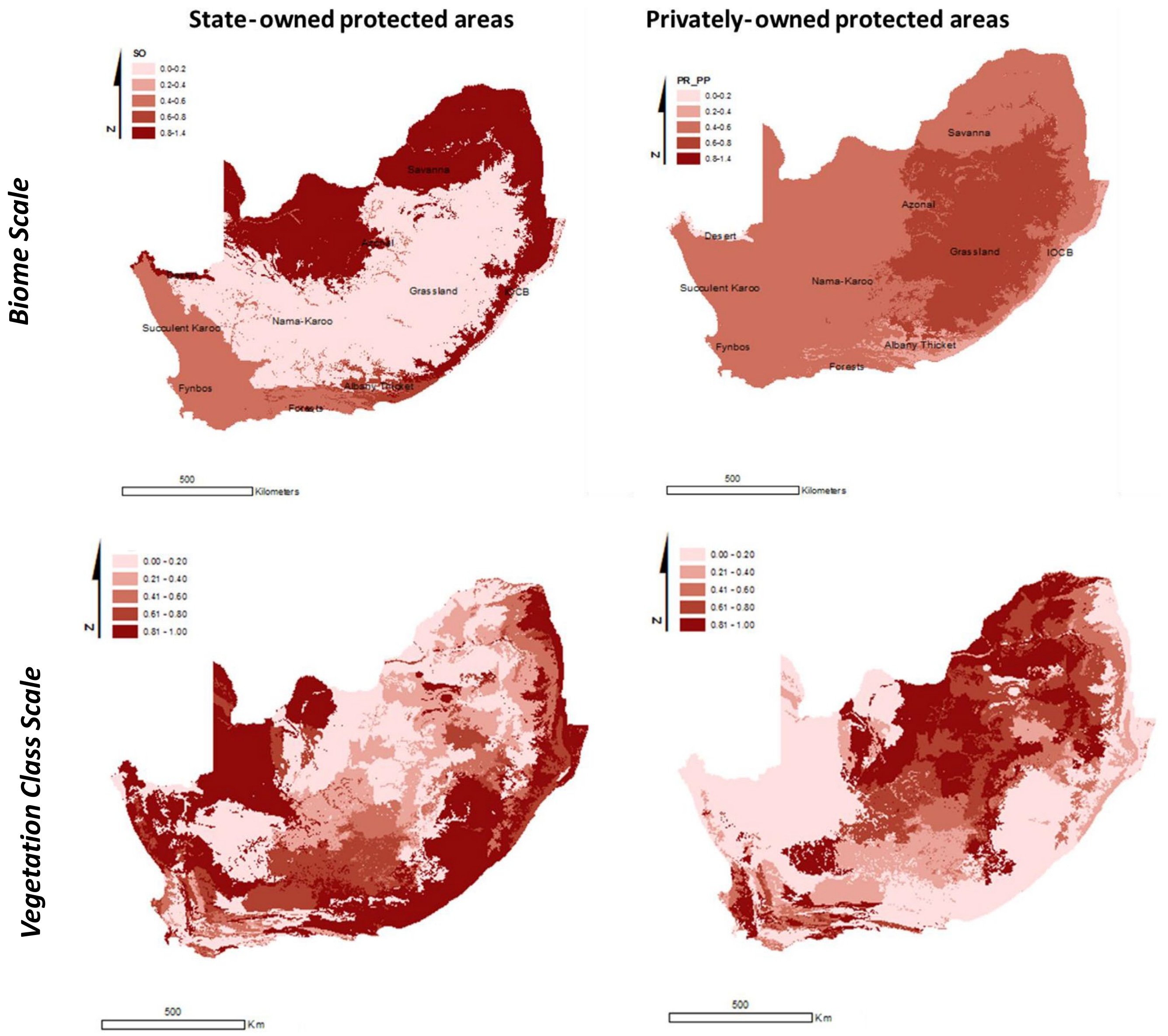

FIGURE 4 The spatial distribution of state-owned and privately-owned protection in South Africa. The top maps show the proportion of different biomes that are protected by (left) state-owned, and (right) privatelyowned protected areas. The lower maps show the proportion of protection of each vegetation classes

SD 271,610 for the actual data, vs. 38,981, *SD* 141,577 for the randomized data). The network diameter for the actual network was more than twice that of the randomized network (1,356 and 608 respectively) and the mean distance between protected areas was again much higher for the actual networks (448.6 km vs. 244.4 km). Private nature reserves in South Africa were thus both more spread out (overdispersed) and more strategically positioned to connect other types of protected areas than expected by chance from their extents and abundance.

4 | DISCUSSION

Our results show that privately owned protected areas increased the area, redundancy and connectivity of the officially recognised South African protected area network. Importantly, the conservation value added to the protected area network by privately owned areas is not the equivalent of adding the same area of state-owned protected areas. Privately owned protected areas conserve complementary vegetation types to state-owned areas, playing a particularly important role in protecting poorly protected, vulnerable and endangered vegetation classes. The loss of private nature reserves would also have a greater negative impact, compared to other tenure types, on the overall connectivity of the protected area estate. Having a diversity of tenure types within the protected area network thus contributed positively to both the amount and representation of different habitats within the network (improved composition) and the overall connectivity between ecologically intact habitat patches (improved configuration).

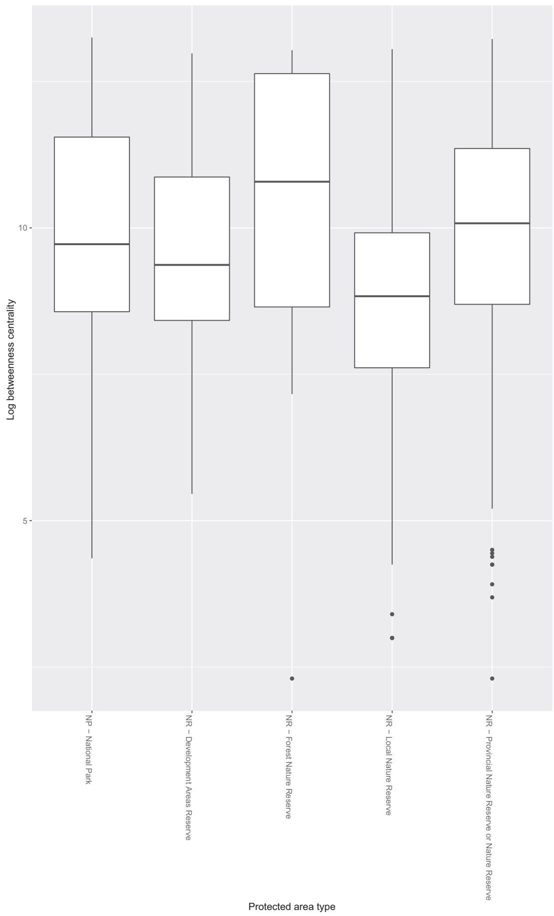

FIGURE 5 Boxplot of the log of betweenness centrality by protected area type

These results have important implications for our understanding of interactions between institutional diversity, ecological diversity and resilience, as well as for the governance and management of protected area networks. Our results support the general proposition that institutional diversity (at relatively small numbers of institutional types) improves social–ecological resilience. Although we did not measure resilience directly, theory suggests that the increases in total conserved area, network connectivity and increased redundancy within the system observed in our study—plus the much lower administrative cost of private lands to the national government—will make the full protected area network more resilient to both ecological shocks and socio-economic change (Folke et al., 2004).

We also identified an interesting interaction between redundancy and diversity. In adding 2,878,422 hectares to the total estate, spread across the country, privately owned protected areas contributed significantly to redundancy of protected lands. Private nature reserves are comparatively small and disproportionately numerous. Their small size may have negative ecological implications (Hansen & DeFries, 2007; Langholz & Lassoie, 2001), but it also means that they can be dispersed across landscapes in which conservation is not a dominant land use, better connecting larger PAs. Their ability to add this redundancy is a function of their identity and the different political and economic parameters under which they operate. Similarly, since private nature reserves are more diverse in ownership and management strategies than state-owned areas (Raymond & Brown, 2011; Stolton et al., 2014) their abundance on the landscape creates a much greater variety of management approaches for protected lands and potentially the creation of suitable habitat for a larger range of species. We have treated private nature reserves as a single tenure type, but in reality there is a diversity of business models, motivations, goals and conservation strategies that shape different private land conservation identities (Clements & Cumming, 2017). Additionally, there are many private land 'conservation' areas that are not explicitly recognized; by some estimates these far exceed the land under formal conservation (Gallo et al., 2009). Such areas may potentially play important roles in both ecological and social connectivity. Since these areas are not formally recorded, their extent, value and functional role in protected area resilience remain largely unknown.

TABLE 2 Network measures for different PA tenure types

Only included PA type	Number of vertices	Number of edges	Mean BC	*SE* of BC	Mean edge length	Mean distance (km)	Network diameter
(All PA types included—baseline)	1627	1,322,751	327,340.70	661,217.10	694.59	458.15	1,210.62
Private NR	968	468,028	141,577.68	271,610.58	578.43	448.57	1,356.86
NR Stewardship Programme	96	4,560	1,871.79	2,588.27	451.68	422.20	1,452.76
Local NR	141	9,870	2,914.62	3,779.01	635.65	619.10	1,550.59
Contractual Park	34	561	307.09	291.88	511.12	483.69	1,793.90
National Park	71	2,485	1,670.46	2051.13	630.08	534.55	1,567.21
Provincial NR or NR	258	33,153	14,195.40	19,168.15	655.63	559.74	1,636.13
Forest NR	32	496	593.88	658.03	535.22	498.32	1,554.05
Development areas reserve	27	351	203.48	194.83	409.05	384.30	971.63

Note: BC measures the number of shortest paths across a network that goes through a given node.
Abbreviations: BC, betweenness centrality; PA, protected area; NR, nature reserve; *SE*, standard error.

TABLE 3 Network measures reflecting the impact of leaving out all PA of the given type

Left-out PA type	Number of vertices	Number of edges	Mean BC	*SD* of BC	Mean edge length	Mean distance (km)	Network diameter	Number of vertices
(all PA types included - baseline)	1,627	1,322,751	327,340.70	661,217.10	694.59	1,212,792,743	458.15	1,210.62
Private NR	659	216,811	101,371	212,023.50	735.64	221,964,567	511.11	1,347.52
NR Stewardship Programme	1,531	1,171,215	298,863.20	564,387.20	673.95	1,056,938,821	450.92	1,244.53
Local NR	1,486	1,103,355	283,095.10	563,390.80	679.79	995,031,335	450.61	1,238.26
Contractual park	1,593	1,268,028	319,518	642,409.70	687.11	1,153,101,441	454.40	1,227.84
National park	1,556	1,209,790	284,592.80	514,900.90	681.75	1,177,631,934	486.40	1,305.29
Provincial NR or NR	1,369	936,396	235,081.20	499,730.10	692.98	951,716,108	507.81	1,352.08
Forest NR	1,595	1,271,215	311,819.10	640,888.30	695.24	1,175,826,820	462.19	1,214.83
Development areas reserve	1,600	1,279,200	312,387.30	641,465.20	694.22	1,178,266,132	460.26	1,242.66

Note: BC measures the number of shortest paths across a network that goes through a given node.
Abbreviations: BC, betweenness centrality; PA, protected area; NR, nature reserve.

In many countries, conservation agencies are moving away from models under which any willing land owner can gazette their land as a private protected area (FitzGibbon, 1993; Miranda, Corral, Blackman, Asner, & Lima, 2016; Stolton et al., 2014). South African conservation authorities have been focusing their private-land strategy on stewardship (contractual) nature reserves (Cumming & Daniels, 2014), which are actively sought out by provincial planning authorities in priority conservation areas. Land owners and agencies engage over the terms of the contract, management plans and the gazettement process, as well as audited management systems (Cumming & Daniels, 2014; Rawat, 2017). Land owners have to commit their land to the programme for at least 30 years, but around 40% have chosen to contract their land into perpetuity (Rawat, 2017). Rawat (2017) provides a useful overview of the terms and benefits of different contracts within the stewardship programme.

There are good reasons for such a strategy: under a conservation free-for-all, the protection of land may not be informed by any national and regional conservation priorities (Langholz & Lassoie, 2001), and thus could easily be adding suboptimal land to the conservation estate. Additionally, without strong legal contracts and monitoring programmes, privately protected areas could easily be degazetted when a landowner changes his/her mind about the goals of the property (Hardy, Fitzsimons, Bekessy, & Gordon, 2017), or even if they remain protected, change the land use of the property. There is good sense in investing in quality conservation over quantity (Kareiva, 2010), and there is some evidence that stewardship contractual reserves (and other areas like them in, for example, the United States and Australia) are effective conservation instruments (Farmer, Knapp, Meretsky, Chancellor, & Fischer, 2011; Hardy et al., 2017; Merenlender, Huntsinger, Guthey, & Fairfax, 2004; Rissman et al., 2007) in critical habitats. However, in writing off private nature reserves as a conservation strategy altogether (SANBI, 2017), conservation authorities are ignoring a potential source of resilience in the protected area network.

There has been much discussion in the literature around the reliability and persistence of privately owned protected areas (Hardy et al., 2017; Kamal, Grodzińska-Jurczak, & Brown, 2015; Stolton et al., 2014), and their ability to contribute novel land to the protected area network over long time horizons (Gallo et al., 2009; Kamal et al., 2015). Recent evidence suggests that privately owned protected areas may be more resistant to protected area downgrading, downsizing and degazettement (PADDD) than previous feared (De Vos et al., 2019; Hardy et al., 2017). Private land conservation instruments, such as covenants and easements, aim to conserve complementary habitats to state-owned areas (Farmer et al., 2011; Hardy et al., 2017; Rissman et al., 2007). In some countries with similar 'voluntary conservation' systems, however, privately owned protected areas have been shown to have similar biases in the habitats they protect relative to state-owned areas (Schutz, 2018). Our results show that private nature reserves are the biggest contributors to the protection of threatened and under-protected habits in South Africa. This finding lends support to the idea that privately owned protected area types are more likely to occur in areas that were previously used as farmland (Gallo et al., 2009), and in transformed landscapes, coupled with the notion that privately owned protected areas can protect areas that state-owned areas cannot (Stolton et al., 2014).

Although we found strong support for the proposition that tenure type diversity improves protected area network resilience, our analysis also highlights many knowledge gaps. First, whilst we can show that privately owned areas contribute significantly to ecological connectivity, it is unclear how well they are socially and economically connected. Indeed, Maciejewski and Cumming (2016) found little social connectivity in the private conservation network of South Africa's Cape Floristic Region. In their study, private land conservation areas showed little overall coordination in their management objectives, and little sharing of resources (Maciejewski & Cumming, 2016). Thus, unlike in state-owned protected areas, privately owned protected areas may not able to buffer underperforming or under-stress protected areas elsewhere in the network by, for example, spreading funding within the network (Biggs, 2004). Conversely, the existence of protected areas with different management approaches may also be a source of resilience if a particular management is flawed or ineffective at managing a particular perturbation or species (e.g. variance in fire regimes and ungulate densities between similar managed habitats may facilitate the persistence of higher beta and gamma diversity). In either case, a deliberate fostering of focused socio-economic institutions may be necessary to make protected areas more resilient to perturbations (Maciejewski & Cumming, 2016). Stewardship reserves improve connections between the state and private conservation (Cumming et al., 2017), but existing institutions around the translocation of animals, fencing, hunting and sharing of ecotourists, could similarly be leveraged to better link private nature reserves with each other.

Second, although there is some evidence that privately conserved areas are resilient to change in tenure (De Vos et al. 2019; Hardy et al., 2017), there is very little evidence for how effectively these areas are managed, or how good they are at conserving biodiversity (but see Merenlender et al., 2004; Horton, Knight, Galvin, Goldstein, & Herrington, 2017), particularly at regional and national scales. Increasingly available high resolution remote-sensing imagery (Gorelick et al., 2017) may help improve our understanding of conservation effectiveness as measured through land change metrics, but such assessments should also be accompanied by studies that investigate management effectiveness across tenure types, and the factors that shape it. Manager motivations vary between and within tenure types (Clements et al., 2016; Clements & Cumming, 2017; Goodman, 2003; Selinske, Coetzee, Purnell, & Knight, 2015; Selinske et al., 2019), and these motivations (e.g. managing land primarily for protection of biodiversity (Selinske et al., 2015) versus managing land for profit derived from a conservation land use (Clements et al., 2016) may have a significant impact on both the conservation effectiveness of protected areas, and their resilience to different perturbations.

The societal benefits of South Africa's protected area estate, as for those of other African countries, are intimately related to its faunal diversity. A third major gap is that most studies, including ours, focus almost exclusively on floral diversity. Given the importance of wildlife ecotourism for the economic sustainability of private nature reserves (Baum, Cumming, & De Vos, 2017; Clements & Cumming, 2017), it is particularly important to understand the role they play in protecting vertebrates. In a recent study that modelled the ability of privately owned protected areas to contribute the persistence of large- and medium-sized mammals in the Cape Floristic regions, Clements et al. (2018) found that the potential mammal species diversity and richness that could persist within a protected area increased more rapidly with protected area size on privately owned than on state-owned protected areas, but also that their greatest absolute contribution was in areas where private areas adjoined, and thus, expanded, state-owned protected areas.

Our analysis suggests that privately owned protected areas are important contributors to conservation initiatives in South Africa. They provide additional area, connectivity and redundancy, while conserving habitats that may be difficult to conserve using other kinds of institutions. Private lands also offer a relatively efficient, low-cost strategy for South Africa to meet its commitments under the Convention on Biodiversity (and other agreements such as the Ramsar Convention, the Convention on Migratory Species and the Africa-Eurasia Waterbird Agreement), and may buffer the network from some of the effects of climate change. Although there are still large gaps in our knowledge of how private land conservation contribute to protected area network resilience, our discussion here suggests several ways in which governments can support privately owned conservation land to enhance the resilience of their national networks. These include better support for privately owned protected area managers, a greater diversity of recognized and supported instruments through which landowners can protect their land, better monitoring and reporting frameworks for areas that are not proclaimed via formal stewardship agreements. We also need more research on the contribution of informal private land conservation areas to protected area resilience. Finally, it is worth noting that the persistence of protected areas are, at least partially, dependent on the resolution of long-standing political concerns around land ownership and the rights of rural farming communities. Private areas make a clear contribution to ecological resilience; time will tell whether the diversity of tenure types and arrangements currently found in the private conservation sector makes private protected areas more or less resilient to social, political and economic change.

5 | SUPPORTING INFORMATION

A description of protected area categories, and a summary of their policy context (Appendix S1), a Dunn's test comparison of betweenness centrality between different pairs of protected area types (Appendix S2), and the Python script used in our randomized analysis (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

Both authors contributed to the design, analysis and writing of the manuscript. A.D.V. performed data collection.

DATA AVAILABILITY STATEMENT

The dataset on which our analysis was based is archived in the Dryad Digital Repository https://doi.org/10.5061/dryad.474hv77 (De Vos & Cumming, 2019). Publicly available datasets which informed our dataset are explained and referenced in Appendix S1

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