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The South African National Red List of spiders: patterns, threats, and conservation

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Abstract. Triage in conservation biology necessitates the prioritization of species and ecosystems for conservation. Although highly diverse, ecologically important, and charismatic, spiders are rarely considered. With 2,253 known species, South Africa's spider diversity is among the highest in the world. A 22-year initiative culminating in a national assessment of all the South African species saw a 33% increase in described species and a 350% rise in specimen accessions of the national collection annually. Endemism is high, at 60% of all South African species. Levels of endemicity are particularly high in Fynbos, Succulent Karroo and Forests. Relative to its area, Forests have three times more endemics than any of the other biomes, followed by the Indian Ocean Coastal Belt. A total of 127 species (5.7%) are either rare or endangered. Threats to these species are largely linked to habitat destruction in the form of urbanization and agriculture. The bulk (62.8%) of taxa are of least concern, but many species are data deficient (27%). Predicted large-scale diversity patterns are confounded by the localised nature of distribution records. Best estimates of compositional turnover point to an east-west bias in our understanding and conservation of spiders in the country, a bias that is most acute in the north-western parts of the country because this region has seen less collecting and has fewer conservation estates. In general, rare and threatened species are mainly ground-dwelling taxa that are either relictual or have poor dispersal abilities. Complemented with long-term surveys that will provide insights into population dynamics of spiders, exploring the use of species traits in predicting extinction probability could provide additional criteria for conservation prioritization. Based on these assessments, targeted species-level interventions might provide a platform for more public awareness and institutional involvement.

Key words: Araneae, biomes, endemism, provinces, SANSA

With their discipline in crisis, conservation biologists have to prioritize their efforts. Limited funds, manpower, and time necessitates the identification of hotspots for conservation (Myers et al. 2000). Mapping patterns of endemism, rarity and threats across the landscape is the starting point for such a process (Burlakova et al. 2011), while Red List assessments provide the framework for evaluating these criteria at species level, linking them to extinction risk and guiding conservation initiatives.

Turnover, or understanding how assemblages differ from each other, provides another important criterion for prioritizing conservation efforts. Compared to species richness, turnover, measured as β-diversity, is probably a more meaningful way to describe macroecological patterns (Mammola et al. 2019), and prioritize conservation efforts (Ferrier et al. 1999). In spite of the constraints in distribution data, current analytical frameworks allow for integration of biological and environmental data, using predictive modelling, and incorporating remotely sensed data that would allow for extrapolating patterns across landscapes (Ferrier 2002; Engelbrecht et al. 2016).

South Africa has produced Red List assessments for a range of animal taxa. Although these assessments include reptiles (Bates et al. 2014), mammals (Child et al. 2016), Odonata (Samways 2006) and butterflies (Mecenero 2013), none exits for any of the mega-diverse taxa in South Africa (but see Cardoso et al. 2019).

Spiders are one of the most important groups of terrestrial predators (Dippenaar-Schoeman et al. 2013; Nyffeler & Birkhofer 2017), with a strong but ambiguous imprint in human consciousness (New 1999), and a remarkable diversity (World Spider Catalog 2019). Conservation assessments of this group therefore provide an opportunity to incorporate "the little things that run the world" into conservation efforts (Wilson 1987). However, the initial requirements for such an assessment include positive determinations and accurate distribution records (Cardoso et al. 2011); information that is particularly scarce in developing countries. In an attempt to address these constraints, the South African National Survey of Arachnida (SANSA) was initiated in 1997 (Dippenaar-Schoeman et al. 2015). The project had a range of objectives, but the main goal was to discover and describe the non-acarine arachnids of South Africa.

One of the key accomplishments of SANSA was the First Atlas of South African Spiders (Dippenaar-Schoeman et al. 2010), which served as the basis for a national Red List assessment of South African spiders. This was largely made possible through the digitization of species-level specimen records in collections and records from taxonomic publications into the SANSA database (Dippenaar-Schoeman et al. 2012). This database is now central in addressing questions around patterns of species richness and endemism (Ball-Damerow et al. 2019), and also provided the basis for initial analyses of South African spider biodiversity more generally (Foord et al. 2011a), and diversity patterns in the savanna (Foord et al. 2011b) and grassland biomes (Haddad et al. 2013).

South Africa has now finalized the first ever national Red List assessment of spiders. This milestone provides an opportunity to identify national patterns in spider diversity, summarize threats, and suggest avenues of research that would optimize the relevance of data collected for spider conservation. This paper aims to accomplish that by: (1) summarizing patterns in data, rarity and endemism across South Africa; (2) modelling and predicting complementarity between spider communities; (3) assessing threats and whether these vary across lineages; (4) quantifying constraints to our assessments; and finally, (5) identifying strategic objectives and possible avenues for future research that will address these constraints.

METHODS

Data used for this analysis were derived from two sources. The first is the National Collection of Arachnida (NCA) at the Agricultural Research Council – Plant Health and Protection in Roodeplaat, Pretoria (Dippenaar-Schoeman et al. 2010). The collection is the largest in Africa, with more than 60,000 records, the bulk of which were accessioned over the last 22 years as part of SANSA (see Fig. S1 in supplemental materials, online at http://dx.doi.org/10.1636/JoA-S-20-011.s1). Additional records included in this analysis were restricted to those included in published revisions and descriptions of taxa housed in 17 museum collections. Distribution records of all known South African species were extracted from original descriptions, re-descriptions and revisionary work, as well as species newly recorded during ecological surveys (Dippenaar-Schoeman et al. 2010). All records that fell outside the borders of South Africa, Lesotho and Swaziland were excluded, duplicates of localities removed, and maps of species inspected for outliers. All the data used in this analysis are available in the First Atlas of South African Spiders (Dippenaar-Schoeman et al. 2010), which will be updated in 2020.

The distribution of occurrence records across South Africa, Lesotho and Swaziland was visualized using quarter degree, degree square and density kernel plots for all the records (76,069). Records in the NCA that were not identified up to species level were excluded from data used for Red List assessments. A total of 23,827 records were therefore used for the assessments. Analysis for Red List assessments used the package red (Cardoso 2017). We performed spatial analysis on observed occurrences using functions for Extent of Occurrence (EOO), Area of Occupancy (AOO), and elevational range. We assumed knowledge of the full range for all species based on their observed occurrences, and EOO was calculated as the minimum convex polygon around all occurrences, and the 2 km^2 cells occupied were used to calculate AOO. EOOs smaller than the AOO were made equal. The distribution of threats across lineages were visualized using a mosaic plot, with the size of rectangles representing the proportion of species in a specific family represented within four categories: data deficient, least concern, rare and threatened.

Generalized difference models (GDM) were used to model compositional similarity at a resolution of 10 km^2 across South Africa. GDM is a nonlinear extension of matrix regression that uses a traditional distance approach, flexible splines and a GLM to accommodate two types of nonlinearity common in ecological datasets (Ferrier et al. 2007). The function ‘gdm’ fits generalized dissimilarity models, after biological and predictor data have been formatted to a site-pair table (Van Schalkwyk et al. 2019). The maximum height of each spline indicates the magnitude of total biological change along that gradient, and represents the relative importance of that predictor in contributing to biological turnover while holding all other variables constant, and therefore represents partial ecological distance. Predictors included were climatic (Fick & Hijmans 2017) and land cover (Tuanmu & Jetz 2014) datasets, at an approximate resolution of 10 km^2. Predictors that had Pearson’s correlations larger than 0.7 were excluded. Models were weighted by species richness and grids that had fewer than 10 species were removed (Mammola et al. 2019). Output of the GDM model was used to predict compositional turnover across South Africa. The proportional representation of ecological environment (scaled using spider data) in conservation areas and the sample coverage of these environments by the database were quantified as a continuous fraction of the entirety of South Africa (Pennifold et al. 2017). Lesotho and Swaziland were excluded from this analysis as layers for conserved areas in these countries were not available. K-means clustering was used to identify regions that were largely homogenous in species composition, and the optimum number of groups was chosen by using the silhouette coefficient (Kaufman & Rousseeuw 2009).

RESULTS

Database growth and properties.—Descriptions of South African spider species experienced two periods of rapid growth, the first at the start of the previous century and the second at the start of this century, which corresponds with the initiation of SANSA in 1997 (Fig. S1a). The latter period of activity has resulted in a 33% increase in newly described species, while the number of accessions in the NCA increased by 350% since SANSA phase two was initiated in 2006 (Fig. S1b). However, records are very localised and largely restricted to the northern parts of the Limpopo, Gauteng and KwaZulu-Natal provinces, respectively, and the Cederberg Mountains in the Western Cape Province (Fig. 1a). This bias is less pronounced when only those records with species level determinations are considered (Figs. 1b, S2 in supplemental materials), and had a larger extent expanding to include large parts of the Free State, KwaZulu-Natal, and isolated areas of the Eastern Cape Province (Figs. 1b, S2). The North-West and Northern Cape provinces have remained largely under-sampled (Fig. 1b).

Almost 60% of all species are endemic to South Africa and another 18% are endemic to southern Africa (Fig. 2a). The southern African endemics were concentrated in the north-eastern parts of the country (Fig. 1c), while the south-western parts of the Western Cape province had conspicuously more South African endemics (Fig. 1d). In terms of biomes, Fynbos, Succulent Karoo and forests have more South African endemic species than extralimital species, whose distributions extend beyond the South African borders (Fig. 2a). As expected, the two largest biomes in South Africa in terms of area, savannas and grasslands, have the most endemics (Fig. 2a). Correcting for area though, highlights the significance of forests and the Indian Ocean Coastal Belt as hotspots of endemicity (Fig. 2b).

Threat status and current conservation.—Of the 2,253 species known from South Africa, approximately two-thirds (62.8%) of species are of least concern, while 80 (3.6%) have some

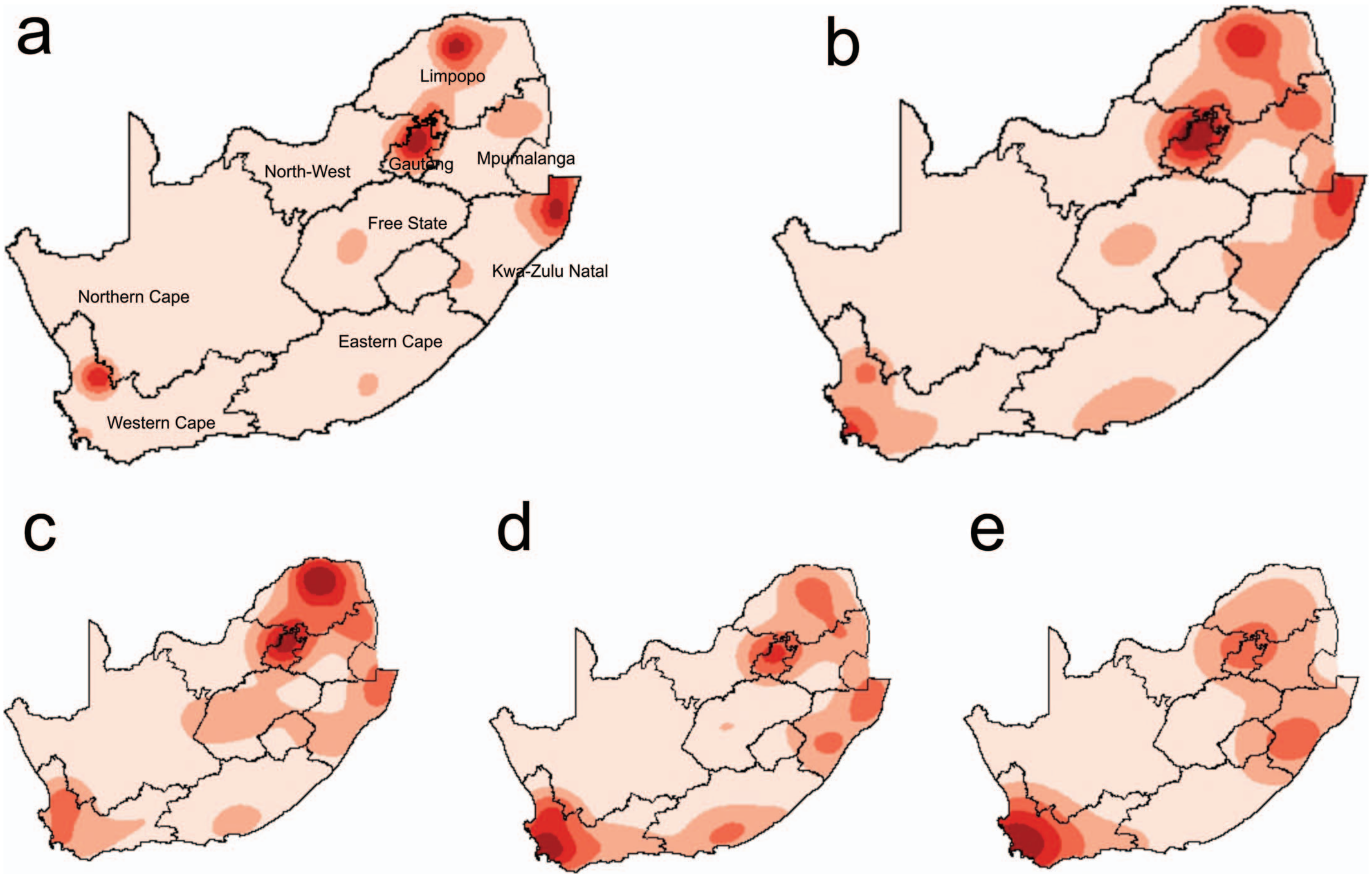

Figure 1.—Kernel density plots for: (a) published records and all specimens accessioned at the National Collection of Arachnida; (b) all the records that had species level determinations and that were used for the South African National Red List assessment; (c) southern African endemics; (d) South African endemics; and (e) rare and endangered species.

threat status (CR, VU, EN) and 47 (2.1%) were rare, the latter categories accounting for approximately 5.7% of the known species (Fig. 3, Table S1 in supplemental materials). A large proportion of the species (ca. 27%) are data deficient, primarily for taxonomic reasons, with figures only available for one sex, which makes them difficult to identify with a high level of accuracy.

An examination of the distribution of threat and rarity across families (Fig. 4) suggests that Pholcidae, Trachelidae and Corinnidae, in particular, have more rare species than would be expected by chance (Fig. 4), while Zodariidae and Zoropsidae had more Red Listed species. Several archaeid species are either rare or threatened. Araneidae, Thomisidae, Philodromidae and Pisauridae had more least concern species than expected, while a large proportion of species in the families Cyrtaucheniidae, Ctenizidae, Agelenidae, Idiopidae and Nemesiidae were data deficient, primarily due to a lack of taxonomic revisions (Fig. 4). Habitat loss, mainly through urbanization and agriculture, represents the biggest threat to spiders (Table 1). No species have been listed as vulnerable to climate change so far (Table S1).

We attempted to determine the effectiveness of South Africa's network of protected areas to conserve spider species by identifying which spiders are presently conserved in conservation estates. A total 1,533 species have distributions that either overlap with or fall within protected areas, while 603 have no formal protection. Of these species that have no formal protection, 24 species are critically rare, vulnerable or endangered (Table S1).

Faunistic turnover.—The Generalized Dissimilarity Model (GDM) included 11 predictor variables (Table 2) and explained 10% of spider compositional turnover, with an intercept of 2.6. The most important variable in this model was mean temperature of the warmest month, followed by the presence of evergreen/deciduous needleleaf trees, and then geographic distance. Barren and cultivated landscapes were also important predictors of turnover. A map of compositional turnover highlights the distinct communities found in the Western Cape (primarily fynbos), as well as those of the Succulent Karoo. The Eastern Cape and Free State comprise transitional communities (Fig. 5a), which is evidenced by the large number of biogeographic groups found in these provinces (Fig. 5b). Proportional sampling of ecological environments suggests that even the most surveyed sites only represent around 12% of these habitats. There is a clear east-west gradient across the country, with the northern parts of the Northern Cape representing the largest gap in terms of survey effort (Fig. 6a). A similar pattern can be observed for ecological environments that are conserved. The north-eastern part of the country is well represented, while ecological

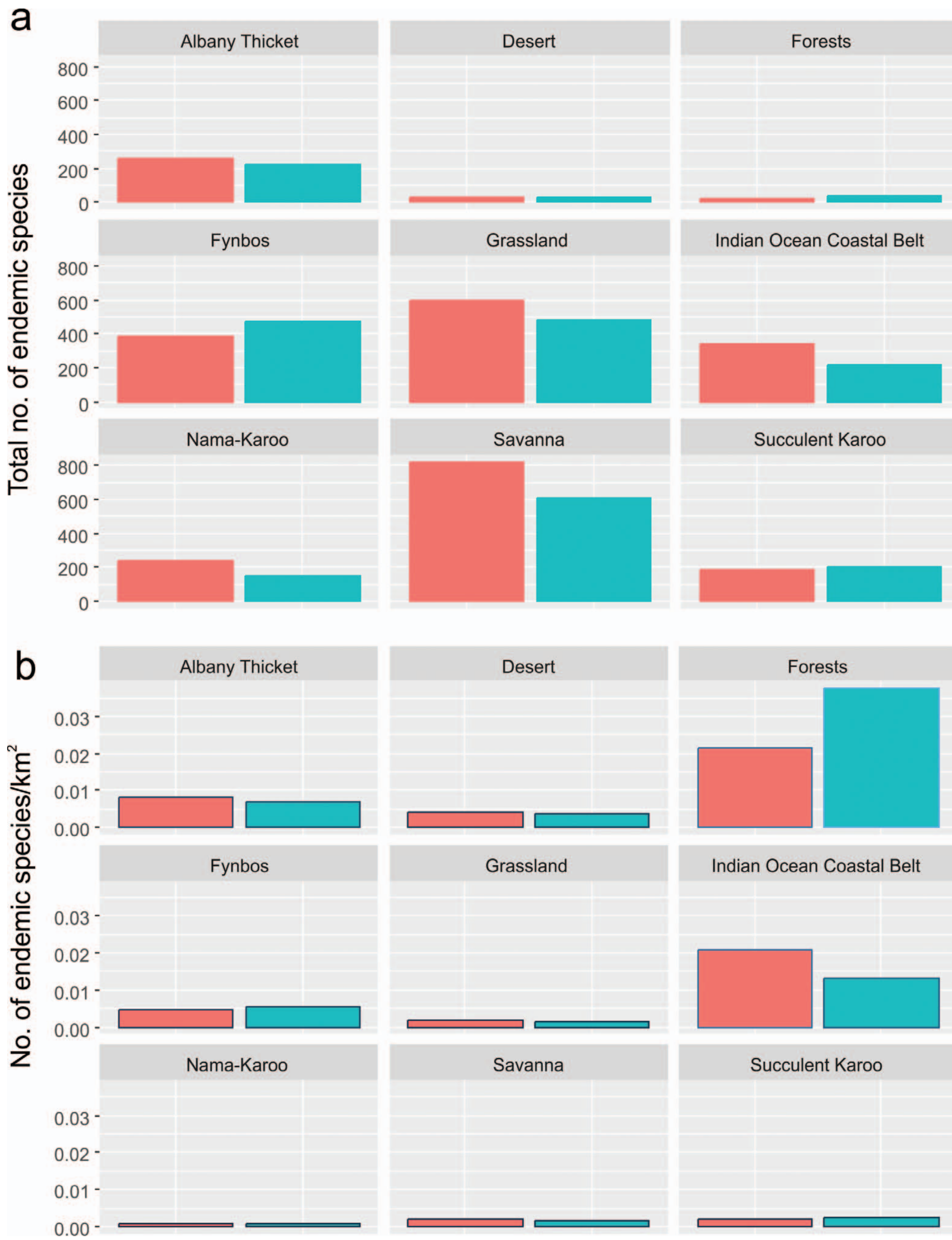

Figure 2.—Bar plots of: (a) the number of extralimital (red) and South African endemics (green) in each of the South African biomes; and (b) the density of extralimital (red) and South African endemics (green) in each of the South African biomes.

environments in the north-western parts are poorly conserved (Fig. 6b).

DISCUSSION

It is clear that SANSA has facilitated a considerable increase in our understanding of spider diversity. SANSA I (1997-2005) and SANSA II (2006 onwards) are associated with inflection points that transition into rapid growth in new species descriptions and accessions. Even so, the large numbers of spider species and the limited distribution records, evidenced by the presence of species that are data deficient (27%), remains the biggest obstacle to meaningful assessments. In general, research projects have been fine grained, localized and, focused on a particular site and limited in extent, e.g., Cederberg (Foord & Dippenaar-Schoeman 2016), Soutpansberg (Foord et al. 2008), Ndumo (Haddad et al. 2006) and iSimangaliso Wetland Park (Dippenaar-Schoeman & Wassenaar 2006). Our understanding of species distributions and community turnover would benefit from surveys that have a larger geographical extent and target ecological environments that have received less research interest, particularly those in the northern-western parts of South Africa. Environmental concerns in general could provide resources for these future

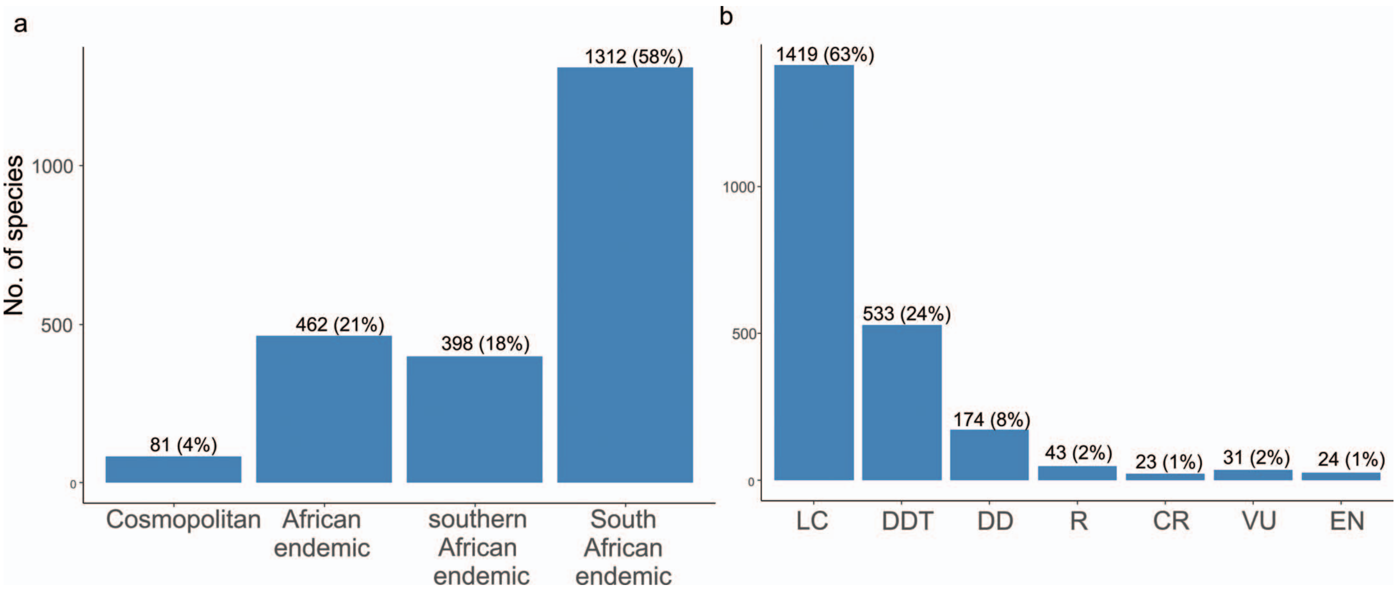

Figure 3.—Barplot of: (a) the global distribution of South African species; and (b) the number of South African species in each of the IUCN red list categories.

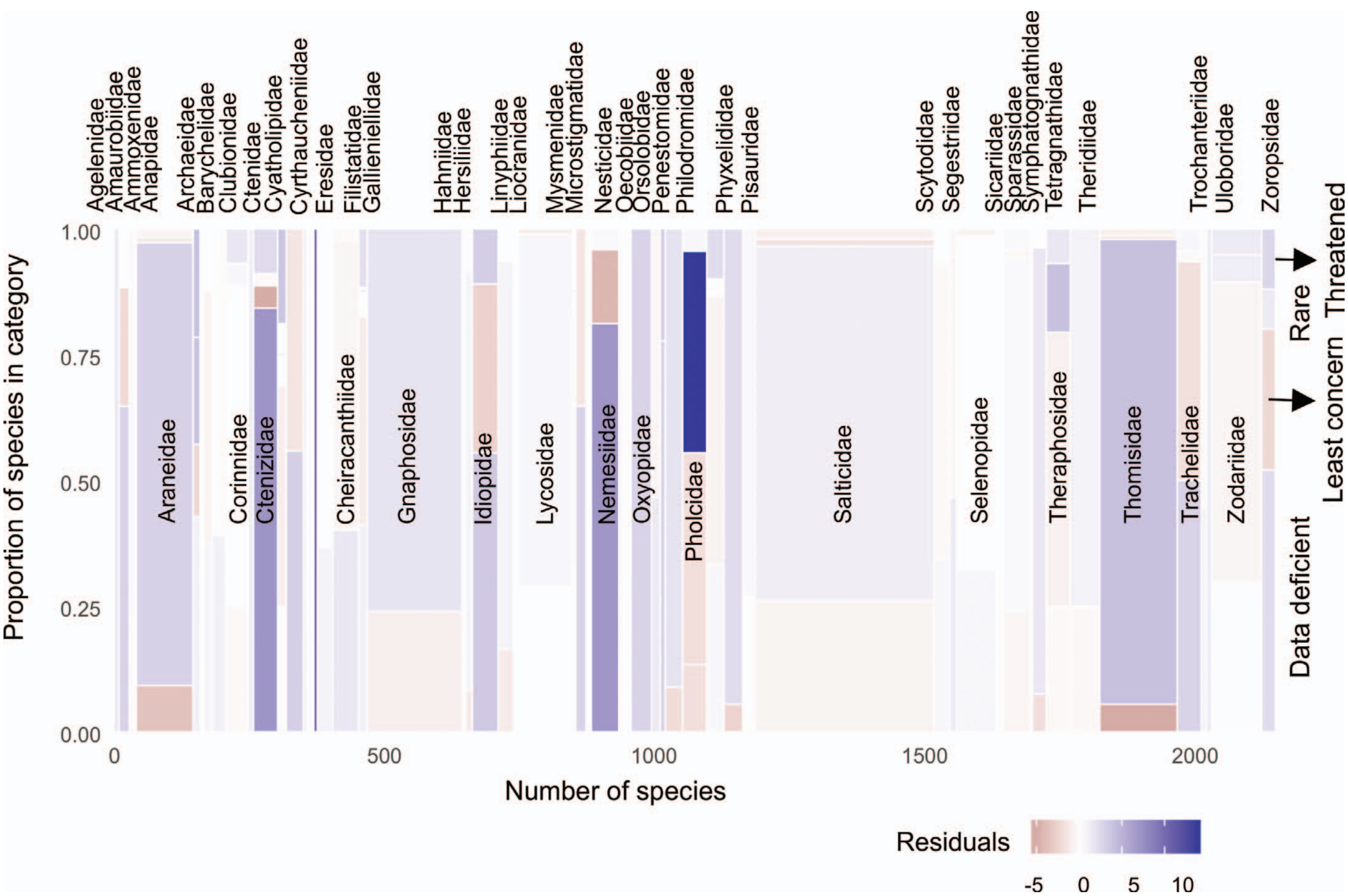

Figure 4.—Mosaic plot of families and their proportional representation in for categories of the IUCN Red List. Residuals represent the under (red) or over (blue) representation of a family within a category.

Table 1.—Threats identified and their prevalence among threatened species

Threat		No. of species
Habitat loss	Crops	26
	Agroforestry	10
	Urban and infrastructure developments	32
	Cave disturbance	1
Grazing		2
Mining		3
Catastrophic events		1
Invasive alien species		2

surveys, e.g., public concern surrounding Shale Gas Fracking in parts of the Karoo provided the impetus for the Karoo BioGap project, a project that will provide baseline data from areas that are known to be under-sampled and understudied.

Relative to other South African taxa that have been assessed, e.g., amphibians, for which 131 species are known and 23% have some threat status (Measey et al. 2019), a considerably smaller proportion of spiders have some threat status (3.6%) and a large number of species are of least concern (63%). However, hotspots (areas with high levels of endemism and experiencing exceptional habitat loss (Myers et al. (2000)) are evident from this analysis. The Cape Floristic Region is a particularly important hotspot, and patterns of spider endemism and threat also seem to conform to the east-west gradient observed for plants of this region (Cowling & Lombard 2002). Large parts of Gauteng and central KwaZulu-Natal also represent hotspots of rare and endangered species. A reasonable explanation for this could be that these regions largely overlap with the Grassland Biome, the most threatened biome in South Africa (O'Connor & Kuyler 2005).

Table 2.—List of significant variables selected for model 1 (spatial and site measured variables) with variable importance based on 500 permutations for each. Relative variable importance was determined by summing the I-spline coefficients.

Variables	Percent deviance explained
Full model	10.29%
Environmental variable	**Relative importance**
Mean Temperature of Warmest Quarter	1.7
Evergreen/Deciduous Needleleaf Trees	1.65
Geographic distance	1.26
Barren	0.96
Precipitation of Warmest Quarter	0.85
Herbaceous Vegetation	0.84
Cultivated and Managed Vegetation	0.65
Shrubs	0.6
Max Temperature of Warmest Month	0.54
Isothermality (Mean Diurnal Temperature Range/ Annual Temperature Range) (* 100)	0.5

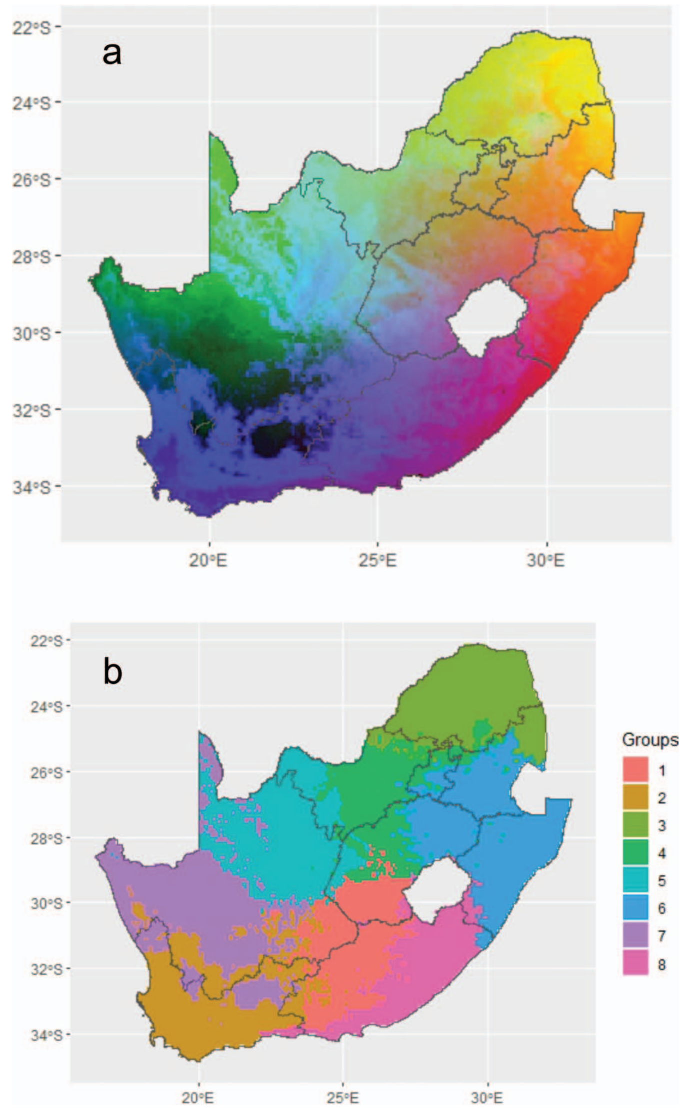

Figure 5.—(a) Predicted compositional turnover of spider communities in South Africa, with areas that have similar colours predicted to have similar spider assemblages; (b) eight optimal groups of spider assemblages identified using the silhouette coefficient.

In contrast to the threat status of species in this group, a remarkable 60% of spider species are endemic to South Africa. Compared to 20% of Odonates (Dijkstra 2007), 37% of all butterflies (Edge & Mecenero 2015), and just over half of all plant species, this is extraordinary. This high level of endemism could be partly explained by the differences in research and taxonomic expertise between African countries (Piel 2018). However, future research throughout Africa will largely affect the endemicity of spiders from savanna in particular.

Fynbos, forests, and Succulent Karoo endemism would probably be unaffected by work further north in Africa. Conservation of these areas would benefit from an understanding of the origins of this endemism, and related theories, such as the very old, climatically buffered, infertile landscapes (OCBIL) theory (Hopper 2009), and the ancient nature of

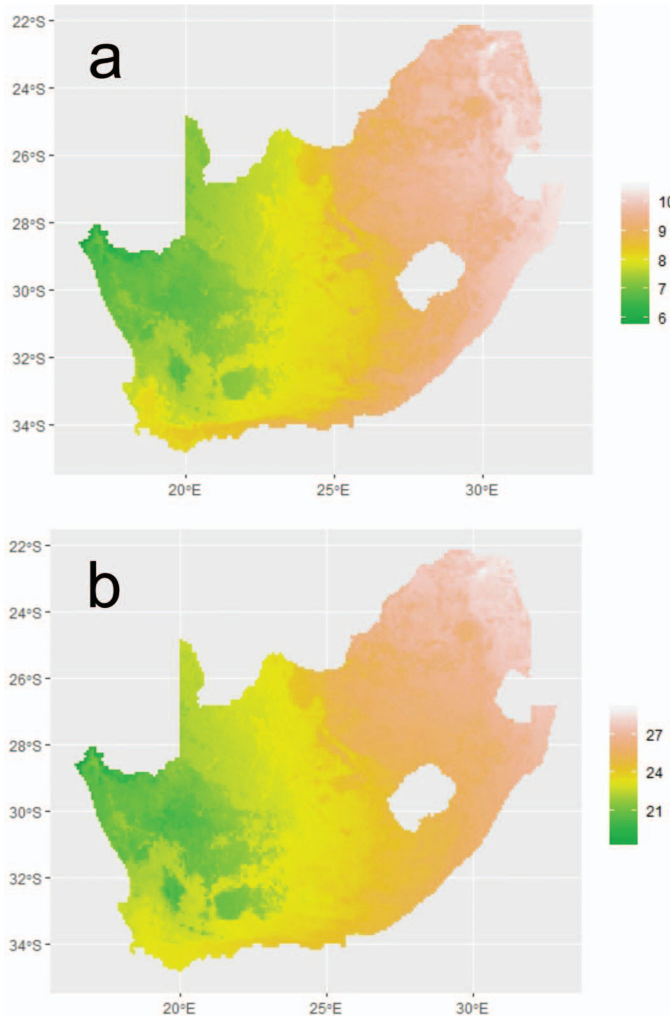

Figure 6.—(a) Proportional (%) sampling of ecological environments (scaled by spider species) by the survey sites; (b) Proportional (%) representation of ecological environments (scaled by spider species) within conservation areas in South Africa.

large parts of the South African landscape (Jocqué 2008), which can provide a framework for the conservation of these unique taxa (Harms 2018).

Rarity in this study was often a function of whether a group has been the subject of recent major revisions, e.g., Cheiracanthiidae (Lotz 2002), Pholcidae (Huber 2003), and Trachelidae (Haddad 2006; Haddad & Lyle 2008; Lyle & Haddad 2009, 2010; Haddad et al. 2011; Lyle 2011, 2013, 2015; Khoza & Lyle 2019). Data deficient taxa such as Ctenizidae and Idiopidae formed part of *ad hoc* descriptive work at the beginning of the last century and would probably have to be prioritized from a taxonomic point of view. Families with a preponderance of threatened and rare species have a limited dispersal ability, e.g. Zodariidae (Jocqué 2013; Jocqué & Henrard 2015) or are cryptic taxa mostly restricted to leaf litter, e.g., Zoropsidae and Archaeidae (Lotz 2003).

Temperature, and particularly mean temperature in the warmest quarter of the year, are very important in driving spider turnover. The inclusion of evergreen needleleaf forests seems to be quite an anomaly (Fig. S5 in supplemental materials), as all the needleleaf forests in South Africa are exotic. However, it is probably not the commercial forests themselves that are driving turnover in spider assemblages, but the remnants of indigenous forests that are often associated with these forestry areas. These forests are rich in endemic and ancient taxa that are distinct from taxa found in the surrounding matrix (Griswold 1991). The forestry industry established plantations in grasslands and shrubland surrounding forests. Forests themselves have benefited from silviculture in various ways, not least of which includes reduced pressure for timber-wood (Geldenhuys et al. 1986). Although most of these forests enjoy protection by public authorities, there is noticeable legal and illegal exploitation of forest resources, chief among which include fuel-wood collecting, cattle grazing, traditional medicines and food sources (Mucina et al. 2006). Land use around State forests is mainly in the form of commercial plantations, and although there is a mandate to protect indigenous forest, conservation is not a core function in these landscapes. Some species in State forests were therefore listed as threatened (Table S1), particularly when the historical grassland forest matrix is highly transformed and further transformation is expected. The inclusion of barren land and cultivated landscapes probably points to the impact of agriculture and urban development in driving not just threats to spider species, but also having a contemporary impact on spider community composition (Dippenaar-Schoeman et al. 2013).

In addition to the Linnean and Wallacean shortfall, the recent decrease in insect abundances and the need to understand population trends, generally known as the Prestonian shortfall, is particularly acute (Cardoso & Leather 2019). All the Red List assessments were done using either criteria B or D, which mainly concentrate on area occupied and inferred threats, while the other categories A, C and E require empirical evidence of population dynamics and trends. Long-term monitoring of spider abundance (Foord & Dippenaar-Schoeman 2016) in habitats that differ in their scaled ecological environments would provide the necessary understanding of spider demographics required for more informed assessments, while a sampled approach to Red List Indices is a cost effective approach to monitor national trends as long as it is done at appropriate time scales (Henriques et al. 2020).

As found for so many other taxa, South Africa has a remarkable diversity of spiders. The majority of species are of least concern, a small percentage are threatened and a large percentage are found in conserved areas. Threats are mainly linked to agriculture and urbanization, but as suggested by the importance of temperature in driving turnover, future climate change will become more important. Impacts such as these can be mitigated through a better understanding of the role temperature plays in spider biology, monitoring spider populations along elevations and identifying future refugia for conservation (Keppel & Wardell-Johnson 2012).

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