Buffer zones maximize invertebrate conservation in a Biosphere Reserve

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Abstract
Recent declines in invertebrates are linked to anthropogenic global change drivers thus land use planning that considers invertebrate conservation is necessary. Although most animals are invertebrates, conservation initiatives largely ignore these groups in part because of a paucity of studies addressing their diversity patterns. Biosphere Reserves provide an holistic approach to conservation planning. Here we explore the covariates that underlie beetle and spider diversity across the largest Biosphere Reserve in South Africa and use this model to predict compositional turnover across the reserve using Generalized Dissimilarity Modelling (GDM). We then use these patterns to assess the proportion of the ecological environments, scaled using beetle and spider assemblages, that is included in either core or buffer zones. The GDM model explained 53% of the variation in observed compositional turnover. Important local-scale drivers of turnover were leaf litter and organic content of the soil, while broad-scale co-variables were isothermality and mean diurnal range. Buffer zones increased conservation coverage by between 50 and 100%, depending on the planning scenario involved and complimented regional conservation plans. However, local conservation practices rarely reflect that of regional planning exercises, and initiatives should focus on monitoring compliance that considers both landscape and local processes.

Implications for insect conservation
Conservation efforts should not only focus on core areas in Biosphere Reserves. Managing buffer zones must receive similar if not more attention due to the larger anthropogenic footprint.

Keywords
Epigeic · Coleoptera · Araneae · Vhembe Biosphere Reserve · Bioregions · Limpopo

Introduction
Humans are precipitating the 6th mass extinction on earth (Bellard et al. 2012; Díaz et al. 2020) and the global biodiversity crisis is one of the most pervasive concerns of contemporary life. Concerns have mostly centred around habitat loss, plant and vertebrate extinctions, and often ignores invertebrates (Samways et al. 2010). However, observed declines of invertebrates is a well-documented phenomenon (Leather 2017; Sánchez-Bayo and Wyckhuys 2019; Cardoso et al. 2020) with severe declines recorded for flying insects in Germany (Hallmann et al. 2017) and even for common and widely distributed moths in Britain (Fox 2013).

A predicted invertebrate Armageddon calls for conservation initiatives that adequately consider the impacts of habitat loss, destruction and homogenization on biodiversity (Samways et al. 2020).

The current biodiversity crisis calls for the establishment of more protected areas (Kremen and Merenlender 2018), while mapped biodiversity provides the framework on which effective conservation plans are developed. This is mostly done using surrogates such as mammals, birds, and plants (Ferrier et al. 2004; Mittermeier et al. 2011). However, invertebrate diversity patterns do not always mirror well-known, and taxonomically well-defined groups (Oliver et al. 1998; Su et al. 2004; Schoeman et al. 2019a) and better results are obtained when several more taxa are included (Sauberer et al. 2004). Furthermore, invertebrate turnover occurs at smaller scales while mapping based on a large-scale, coarse filter data might not predict insect diversity across space (Su et al. 2004). Identifying covariates that vary with invertebrate α-diversity and β-diversity across landscapes is therefore essential (Gering and Crist 2002).
This would allow for predictions across both space and time. Alpha-diversity helps to identify hotspots (Mittermeier et al. 2011) but compositional turnover captures complementarity between assemblages and is probably much more appropriate for conservation efforts at regional scales (Reyers et al. 2000; Kati et al. 2004).

Although reserves promote strict protection, edge effects can threaten biodiversity within areas of conservation (Woodroffe and Ginsberg 1998). The severity of edge effects depend however on the size of the conservation area, and must take into consideration other factors such as location and management (Constant and Bell 2017). Strict reserves should as a precaution be complemented with protected areas outside them (Gove et al. 2005). Biosphere reserves promote this holistic approach by circumscribing areas within them as core, buffer, and transitional zones (Ishwaran et al. 2008). Core areas comprise strictly protected reserves; buffer zones surrounding the core areas are important conservation areas but might not be formally designated as reserves; transition zones are areas of sustainable ecological practices and include human habitation.

In terms of diversity, epigeal fauna is often dominated by ground-dwelling beetles and spiders. Beetles are particularly species rich and locally abundant. The bulk of epigeal beetle diversity in Africa consists of three taxa, Carabidae, Tenebrionidae, and Scarabaeinae. Carabids are important predators of arthropods, with a few important seed feeders in the Harpalinae and Chlaeniinae. Over 960 species of Carabidae are known to occur in South Africa (Picker et al. 2004). Tenebrionidae and Scarabaeinae are significant detritivores, with the latter specializing on the dung of large herbivores (Picker et al. 2004). In fact, beetles can be regarded as biodiversity surrogates (Gerlach et al. 2013). Hutcheson (1990) considered them to be representative of insect diversity in general, as they include widespread and specialized species. They are rarely used however because of the taxonomic challenge of identifying them to genus and species, with only a few well-known beetle taxa used regularly, such as Scarabaeinae and Cicindelinae. Spiders can also act as surrogates (Sauberer et al. 2004; Foord and Dippenaar-Schoeman, 2016), because they are major predators of other invertebrates (Dippenaar-Schoeman et al. 2012) and consume an estimated 400–800 million tons of insect prey annually (Nyffeler and Birkhofer 2017). More than 2200 spider species are known from South Africa (Dippenaar-Schoeman 2014), and >90% of all endemic spiders in South Africa are epigeic (Foord et al. 2020).

Overall, temperature and rainfall are the most significant predictors of biodiversity (Gaston 2000). However, local variation in climate and other environmental features such as vegetation cover, rocks, leaf litter, and the soil associated with microhabitats might also be important (Gough et al. 1994; Schoeman and Samways 2011; Gaigher and Samways 2014). These predictors often act as ‘drivers’ of diversity, not only local or alpha diversity, but also compositional change or beta diversity (Koleff et al. 2003). Large-scale selection of conservation units has been found to be remarkably effective in conserving regional biodiversity (Rouget 2003; Schaffers et al. 2008; Ramos et al. 2018). However, species may be distributed in patches, and preserving only part of a vegetation unit may miss an important component of the unit’s species. Coarse-scale conservation strategies should be complemented with fine-scale data on patterns of invertebrate diversity (Lombard et al. 2003; Barton et al. 2011).

There are at present 714 biosphere reserves in 129 countries, including 21 transboundary sites (UNESCO 2021). Africa accomplishes 85 biosphere reserves and is the continent with the fewest. (Ten new biosphere reserves have been proclaimed since 2017.) Furthermore, very few studies measuring the effectiveness of core and buffer zones in protecting invertebrate biodiversity within biosphere reserves in Africa are available (but see Van Schalkwyk et al. 2019). Herein we use a dataset of epigeal spiders and beetles collected across the largest Biosphere Reserve in South Africa and ask the following questions. What are the relative roles of fine and large-scale variables in predicting invertebrate diversity? Furthermore, can we use these scaled environmental variables to predict richness and turnover across the Biosphere Reserve and evaluate the effectiveness of buffer and core zones in conserving two major groups of invertebrates?

Methods and materials

Study site

The Vhembe Biosphere Reserve (VBR) was inscribed in 2009 (Pool-Stanvliet 2013). It is situated in the northernmost region of Limpopo Province of South Africa (coordinates: 22°49′31.5″ S 29°53′46.5″ E). 3 037 590 ha encompassing a diverse array of biomes and habitats, including mist-belt forest, mountainous flora, arid bushveld and moist savanna (Mucina and Rutherford 2006). The Soutpansberg mountains are the dominant geographic feature of the VBR and drives much of its environmental variation (Fig. 1, Appendix 1a). The VBR also contains important rivers and catchment areas, including the Limpopo and Luvuvhu Rivers (Modiba et al. 2017). The region has been identified as a centre for plant endemism (Hahn 2017), and several recent studies have highlighted the significance of its invertebrate diversity (Foord et al. 2002; Schönhofer 2008; Haddad 2009; Foord et al. 2015; Munyai and Foord 2015) with more than 700 spider species (Foord et al. 2002; Foord et al. 2019). A Strategic Environmental Management Plan (SEMP) was...
completed in 2016 and proposes revised core and buffer zones based on a more detailed analysis of biodiversity information (Strategic Environmental Focus 2016). This SEMP complements the existing bioregional plan (Vhembe District Municipality 2017) and the Limpopo Conservation Plan (Desmet et al. 2013).

The climate at VBR is highly seasonal with a warm wet period from October to April (16–40 °C) and a cool dry period from May to September (12–22 °C). Seasonality is characterized by summer drenching and winter desiccation, particularly of the higher ridges of the Soutpansberg dominated by lithosols (Mostert et al. 2008). Entabeni Forest, situated at the intersection of the Soutpansberg Mountains (Fig. 1, Appendix 1a) and the northern escarpment has an average annual rainfall of 1 874 mm, diminishing eastwards with Punda Malia receiving 545 mm. The rain shadow of the escarpment causes Louis Trichardt’s rainfall to drop to 618 mm while the combined rain shadows of the escarpment and Soutpansberg cause Waterpoort settlement (Appendix 1a) to have the lowest recorded rainfall of 367 mm.

**Sampling**

We sampled sites within the core, buffer and transition zones of the Vhembe Biosphere Reserve (Fig. 1). Sampling was stratified across the five major vegetation types of the VBR (Fig. 1, Appendix 1b) and included three sites within the existing core areas, four sites within buffer zones, and 13 sites within the transition zones. Elevation, precipitation and temperature interact to produce distinct vegetation types in the region. These vegetation units occur in longitudinal east-to-west bands across the Biosphere Reserve (Appendix 1b). The Polokwane Plain and Eastern Limpopo Flats harbour geographically large, and continuous plant communities. We stratified 20 sampling sites across the major vegetation units (Mucina and Rutherford 2006) and longitudinal extent that the vegetation type covers in the Biosphere Reserve (Fig. 1). These were: Makhado Sweet Bushveld (3 sites), Soutpansberg Summit Sourveld (4 sites), Northern Mistbelt Forest (4 sites), Roodeberg Bushveld (2 sites), Soutpansberg Mountain Bushveld (4 sites), Musina Mopane Bushveld (2 sites), and Limpopo Ridge Bushveld (1 site). In each site, eight sampling units were selected. Sampling units were selected to be as representative of the vegetation unit as possible. Sampling effort was focussed on least anthropogenically disturbed habitats. Sampling units were a minimum of 300 m apart to avoid pseudoreplication (Samways et al., 2010). A sampling unit consisted of five pitfalls (Ø= 100 mm, height = 150 mm), arranged in a pentagon spaced 10 m apart and filled with 100 ml propylene glycol. The pitfalls of each SU were too close to each other to be considered independent and were therefore pooled in the analysis. The unit for data analysis is therefore the SU, for a total of eight SU’s per site ･ 20 sites = 160 assemblages. The following small-scale environmental variables were collected at each sampling unit: leaf litter cover, vegetation complexity, organic content of soil and canopy cover. The 1 m² area...
around each pitfall was imaged and the following variables estimated as such: percentage leaf litter cover; canopy cover (estimated from shade); habitat complexity (scored from 1 (bare ground), 2 (grass cover), 3 (grass cover, and small bushes), 4 (grass cover, large bushes) to 5 (thicket, forest); organic content was estimated from substrate or soil type (scored as 0: gravel, 1: sand; 2: loam, 3: clay, 4: mulch).

Sampling was conducted in November-December 2012. This period corresponds with the start of the wet and hot summer period. Pitfalls were left open for seven days, contents were washed in the laboratory using a micro net and clean water and stored in 96% ethanol. Spiders were identified to species or morpho-species. Tenebrionidae and Carabidae were identified to species and Scarabaeidae to species and morphospecies. Spider specimens were deposited in the National Collection of Arachnida (NCA) of the Plant Protection Research Institute, Agricultural Research Council, Pretoria while beetle specimens were deposited in the Ditsong National Museum of Natural History and the University of Venda Sarchi Chair Biodiversity Collection.

Data analysis

Catches from a sampling unit were pooled resulting in eight assemblages per site × 20 sites = 160 assemblages. Sample coverage (Chao and Jost 2012) was calculated for observed richness at each sampling unit using the function ‘iNEXT’ in the iNEXT package (Sieh et al. 2014). Gridded climatic (Fick and Hijmans 2017) and land cover (Tuanmu and Jetz 2014) data at a resolution of 1km2 were used to derive covariates at point localities. As there is considerable topographic variation in the VBR, slope, aspect (north-to-south and east-to-west orientation) and the Topographic Position Index were also calculated using Digital Elevation Models for the region. Models also included small-scale variables measured at each sampling unit. Collinearity between these predictors were explored using variance inflation factors (VIF). Variables that had VIF > 3 were excluded from the analysis. Collinearity was further explored using Pearson product moment correlations between predictors.

Observed richness were modelled using Generalized Linear Mixed Models (GLMM) with a loglink function and Poission error distribution using the function ‘lmer’ in the lmer package (De Boeck et al. 2011). Fixed factors included both broad-scale climatic and landcover variables as well as finer scale predictors measured at each sampling unit. Site was included as a random factor to account for spatial autocorrelation between replicates within a site. Variograms of the residuals of the GLMM’s were used to identify any spatial correlation between sites. Prior weights were given to observed richness variables based on their coverage. Better estimates of richness therefore contributed more to the model construction. Models were compared using the Akaike information criterion and the best models those that had ΔAIC < 2 compared to the model with the lowest AIC (Burnham and Anderson 2004). Marginal R² (R²m, due to fixed effects only) and conditional R² (R²c, due to fixed and random effects) were calculated for the best model to determine how much of the variation is explained by fixed and random effects respectively (Nakagawa and Schielzeth 2010).

The compositional similarity was modelled using generalized dissimilarity models (GDM) at a resolution of 1 and 10 km2 across the VBR. GDM extends the traditional distance approach of matrix regression to include nonlinear relationships as well as flexible splines and a GLM that deals with two kinds of nonlinearity common in ecological data (Ferrier et al. 2007). It allows for the quantification of varying compositional turnover along a gradient. Patterns in turnover can be analysed as well as how different sites are in terms of environmental and geographic variables. The function ‘gdm’ in the package gdm was used to fit generalized dissimilarity models based on Bray-Curtis dissimilarities, after biological and predictor data have been formatted to a site-pair table (Fitzpatrick and Lisk 2016) in R (R core team 2021). Each assemblage in the model was weighted sample coverage for that assemblage (Mammola et al. 2019). Spline heights represent the total biological change along that gradient, and relative importance of that predictor in contributing to biological turnover while holding all other variables constant (partial ecological distance). Variable importance were quantified using matrix permutation that tests the variable and model significance and estimate variable importance. Fifty permutations were done to estimate p-values (Ferrier et al. 2007). Output of the GDM model was used to predict compositional turnover across the VBR.

The proportional representation of ecological environments (scaled using spider and beetle data) in core and buffer zones, and the proportional sampling of these environments by the database were quantified as a continuous fraction of the entire biosphere reserve (Pennifold et al. 2017). We also assessed this representation for the Critical Biodiversity Areas 1 and CBA 2 used for regional conservation planning by the Limpopo Department of Economic Development, Environment and Tourism (Desmet et al. 2013). K-means clustering based on pair-wise Manhattan distances was used to identify regions that are largely homogenous in species composition, and the optimum number of groups was chosen by using the silhouette coefficient (Kaufman and Rousseeuw 2009).
Results

A total of 2624 spiders, representing 217 species and 47 families were sampled; Gnaphosidae (39 species), Lycosidae (28 species), Zodariidae (23 species), and Salticidae (22 species) were the most diverse families. These four families represent 57% of all spiders caught. There were 260 beetle species in the three families, and altogether 14,109 individuals were sampled: 59 carabid, 119 scarabaeid, and 82 tenebrionid species. Scarabaeidae was the most abundant beetle family (9567 individuals), followed by Tenebrionidae (3885 individuals) and Carabidae (657 individuals).

On average, much more beetles (93) than spiders (19) were caught in a sampling unit. Coverage was also higher. Predictably average coverage was also higher for beetles (0.9) compared to the spiders (0.69). However, only slightly more beetle species (9.1) than spider species (7.3). Mean diurnal range in temperature was an important predictor of both beetles and spiders richness which increased with increasing diurnal range (Table 1). Beetle richness was negatively associated with isothermality in the best model (Table 1), while spider richness decreased towards lower latitudes and in association with mixed/other trees. There was a significant relationship between predicted species richness at a sampling unit and the observed species richness for beetles (R^2 = 0.604, p < 0.001, Fig. 2) and spiders (R^2 = 0.56, p < 0.001, Fig. 2) Fixed effects in the best model for beetle richness explained 52% of the variance while fixed and random effects explained 80%. Fixed effects in the best model for spider richness explained 28% of the variance while fixed and random effects explained 58%. Variograms of the residuals of both models were not correlated with distance and suggesting that there was no spatial autocorrelation between sites (Fig. S1).

Models of compositional similarity that included local-scale variables (leaf litter, canopy cover, vegetation type and organic content of soil) explained 46% of the variation compared to 43% when only broad-scale variables were included. Therefore, including these finer scale variables improved our ability to predict compositional turnover in assemblages. Important local-scale variables were leaf litter, where turnover increased with leaf litter cover (Fig. 3d), and the organic content of the soil (Table 2), which suggests that these act as filters at a finer scale. Leaf litter cover between 50 and 100% was particularly important in explaining turnover.

However, predictors that summarize aspects of temperature variability dominated both broad and fine-scale models (Table 2), isothermality (Fig. 3a), and mean diurnal range (Fig. 3c). The distribution of deciduous broad-leaved trees was the only land cover variable that was important

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![Fig. 2 The relationship between predicted (GLMM) and observed spider species richness in the VBR](image)

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![Fig. 4a](image)
Table 1 Summary of the best models predicting species richness for beetles and spiders

| Model | Log likelihood | AIC | ΔAIC |
|-------|----------------|-----|------|
| Beetles | | | |
| Mean diurnal range + isothermality | −394.1 | 796.2 | 0 |
| Mean diurnal range + isothermality + precipitation seasonality | −393.9 | 797.7 | 1.5 |
| Best model | $S_{obs} = e^{1.99 (0.11) + 0.41 (0.09) \text{mean diurnal range} - 0.33 (0.09) \text{isothermality}}$. | $R^2_m = 0.52$, $R^2_c = 0.8$ |
| Spiders | | | |
| Mean diurnal range + mixed/other trees | −255.8 | 521.5 | 0 |
| Mean diurnal range + latitude + mixed/other trees | −255 | 521.7 | 0.2 |
| Best model | $S_{obs} = e^{1.85 (0.09) + 0.27 (0.09) \text{mean diurnal range} - 0.14 (0.06) \text{Mixed/Other trees}}$. | $R^2_m = 0.26$, $R^2_c = 0.6$ |

Fig. 3 Generalized dissimilarity model fitted I-splines (partial regression fits) of selected environmental predictors, significantly associated with compositional turnover of spiders and beetles in the VBR. The total β-diversity explained by a variable is given by the maximum height reached by a curve and reflects the total amount of compositional turnover explained by that variable when all other variables held constant. The rate and change of compositional turnover is reflected in the shape of the curve.
1 3

CBA 2 (Fig. S2).

The fact that temperature co-vary with a range of other variables precludes the identification of any causal relationship for a 50% increase in area, while the proposed buffer zone and that of the gazetted Limpopo conservation plan almost conserved all (100%) of the ecological environments identified. Provincial conservation efforts complement the proposed zonation.

The most important broad-scale variables affecting the distribution of biodiversity over the region were related to temperature: isothermality and mean diurnal range. These are important bioclimatic predictors related to species physiology, showing that temperature fluctuations and extremes are key to assembling species over larger areas (O’Donnell and Ignizio 2012). In our analysis these co-varied with elevation and precipitation, acting as appropriate proxies (Gaston 2000; Willig et al. 2003). Deciduous broad-leaved trees were the only important large-scale land cover variable, linking plant functional traits with herbivory (Njovu et al. 2019).

Geographic distance is known to have an important impact on community assembly (Schoeman and Foord 2012). Soininen (2016) showed that dispersal ability is limited for spiders over large areas. This may be explained by highly localized availability of resources (Wise 2006; Saxer et al. 2009) with the resultant observation of distinct communities. The evolutionary history of invertebrate distribution over distance is an acknowledged phenomenon, although it cannot be isolated from the effect of habitat and vegetation type (Qian and Ricklefs 2012). Here we do not attempt to disentangle the relationship between geographic distance and environmental distance. Carvalho et al. (2011) found that broad-scale environmental gradients drove Mediterranean spider species richness. In general, large-scale selection of conservation units is effective in conserving regional biodiversity (Rouget 2003; Schaffers et al. 2008; Ramos et al. 2018).

Fine scale variables, such as leaf litter and organic content, were also important drivers especially for invertebrates which are small and often associated with micro-habitats. Barton et al. (2011) found that beetles in grassy Australian woodland were more strongly affected by micro-habitat elements such as logs than macro-habitat elements. MacLeod et al. (2004) have also shown that fine scale refuges and shelters are essential for the maintenance of carabid assemblages. Similarly, Barton et al. (2010) found that two different species of co-occurring eucalyptus supported different assemblages of litter-dwelling beetles. Some of the species in the VBR are very dependent on micro-habitat elements as logs and fine scale refuges and shelters are essential for the maintenance of carabid assemblages. Similarity, Barton et al. (2010) found that two different species of co-occurring eucalyptus supported different assemblages of litter-dwelling beetles. Some of the species in the VBR are very dependent on micro-scale elements especially in forests. For instance, a carabid endemic from afro-montane forests, Wahlbergiana alternans, is found predominantly under rocks in areas of densely compacted leaf litter. The importance of leaf litter could be related to the sampling method used in this study. Pitfall traps capture more active invertebrates and not sample less active litter dwelling species, such as Collembola and Staphylinidae, which are normally abundant faunas associated with leaf litter (Gerlach et al. 2013; Janion-Scheepers et al. 2016). A study by Maudsley et al. (2002) found high numbers of Carabidae in leaf litter in hedgerows in England. Speciose

### Table 2: Significance and importance of variables for VBR beetle and spider β-diversity based on 50 permutations of the generalized dissimilarity models

| Variable                  | Scale | Large-scale only | Large and fine-scale |
|---------------------------|-------|------------------|----------------------|
| Geographic                | Large | 2.2*             | 1.83*                |
| Slope                     | Large | 0.7*             | 0.46*                |
| East–West                 | Large | 0.5              | 0.53*                |
| North–South               | Large | 2.9*             | 2.38*                |
| Topographic Position index| Large | 0.2              | 0.18                 |
| Mean diurnal range        | Large | 5.6*             | 4.42*                |
| Isothermality             | Large | 9.9*             | 5.36*                |
| Precipitation seasonality | Large | 2.7*             | 2.02*                |
| Deciduous broadleaf trees | Large | 5.6*             | 4.81*                |
| Mixed/other trees         | Large | –                | –                    |
| Shrubs                    | Large | –                | –                    |
| Herbaceous vegetation     | Large | 0.03             | –                    |
| Leaf litter               | Fine  | NA               | 2.25*                |
| Canopy cover              | Fine  | NA               | 0.78                 |
| Organic content           | Fine  | NA               | 2.17*                |
| Vegetation complexity     | Fine  | NA               | 0.09                 |

An n-dash indicates variables which explained no model variance (*p < 0.05)

50% of the VBR but includes 75% of the scaled ecological environments, while including the proposed buffer zones (Fig. 5d) increases this proportion to almost 100% (97%) but cover 75% of the VBR (Fig. 5f). Similar results were obtained using LEDET’s Critical Biodiversity Areas 1 and CBA 2 (Fig. S2).

### Discussion

Compositional turnover of the invertebrates in this study was mainly the result of variability in temperature and vegetation cover (deciduous broadleaved forests). Although local-scale variables increased the amount of variation explained by 24% (Table 2), the importance of temperature is evident. Future changes in land cover and climate would therefore have important implications for community composition. The fact that temperature co-vary with a range of other variables precludes the identification of any causal relationships, but temperature and vegetation certainly provide some explanatory power within this context. The ability to predict these changes are confounded by the low sample coverage across the biome as invertebrate communities at VBR are largely unknown. Current buffer zones double conservation for a 50% increase in area, while the proposed buffer zone and that of the gazetted Limpopo conservation plan almost conserved all (100%) of the ecological environments identified. Provincial conservation efforts complement the proposed zonation.

The most important broad-scale variables affecting the distribution of biodiversity over the region were related to temperature: isothermality and mean diurnal range. These are important bioclimatic predictors related to species physiology, showing that temperature fluctuations and extremes are key to assembling species over larger areas (O’Donnell and Ignizio 2012). In our analysis these co-varied with elevation and precipitation, acting as appropriate proxies (Gaston 2000; Willig et al. 2003). Deciduous broad-leaved trees were the only important large-scale land cover variable, linking plant functional traits with herbivory (Njovu et al. 2019).

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carabid taxa associated with leaf litter and recorded from the region (Harpaolinae, Chleiniinae, and Pterostichinae) were very poorly represented in our samples.

We found a strong east-to-west gradient in richness among Tenebrionidae, observing that the decline in richness towards the east reflected movement away from the southwest African centre of tenebrionid diversity. However, the Soutpansberg harbours a unique community. The change in composition may be driven by a decrease in temperature, which lowers the activity of ectotherms at higher elevations, reduction in possible habitat (e.g., mountain tops), and a decrease in resource abundance associated with reduced habitat size (Classen et al. 2015). Although richness often decreases with elevation, there is also a definite increase in complementarity with elevation, so that sites on the mountain are distinct, harbouring a considerable number of endemics (Munyai and Foord 2015). Assemblages north and south of the Soutpansberg mountain are also distinct, emphasizing the importance of beta diversity studies that focus on complementarity.

In the current zonation, topographically complex sites such as the western Soutpansberg and Blouberg were included in the core and buffer zones as they have low human population density on unproductive quartzitic derived soils (Hahn 2018). These two mountains can also represent old, climatically buffered, infertile landscapes (OCBIL) within the VBR (Hopper 2009). Like the Cape Floristic Region, the above-mentioned mountains are characterized by high levels of diversity and endemism. The narrow distribution ranges and limited dispersal capabilities of taxa coupled with strong environmental gradients and relative climatic stability on these mountains could account for the high richness patterns we observed in the core areas. For instance, species of the darkling beetle *Anaxius* (Kamiński and Schoeman 2018) are limited to elevations higher than 900 m.a.s.l. across the bushveld of southern Africa, with endemic species limited to particular ranges. Most rare and endemic species of spiders are also mainly found in the Soutpansberg and Blouberg and their surrounding foothills (Foord et al. 2002; Foord et al. 2019).

We found that the proposed zonation which encompasses significantly large tracts of land conserves almost all species. The coverage results highlight the importance of large conservation areas (e.g., Kruger National Park) in regional conservation efforts. We found that the KNP’s conservation footprint extends well beyond its border in terms of ecological environments conserved. However, both current and proposed zonation reflect the priorities of humans with infertile arid land (the OCBILS) comprising most of the core areas and buffer zones (Hopper et al. 2016).

Both the Biosphere and provincial zonation effectively represented invertebrate diversity in the VBR and suggest that...
planning based on vertebrates and plants might be successful in conserving invertebrates (Mittermeier et al. 2011). However, the current zonation only represents 50% of that diversity and it assumes that real world land use reflects that of the planned zonation. Although large scale covariates drive invertebrate distribution, local-scale processes played a significant role in maintaining invertebrate diversity in those areas identified as core and buffer zones. Broader scale changes in climate could be mitigated by focusing on microhabitats and microclimates at smaller scales, managing for fine-scale covariates (e.g., leaving logs in the veld, simulating natural disturbance regimes). Providing suitable microhabitats could allow for behavioural rescue (Scheffers et al. 2014). Rewilding the proposed core areas by reintroducing ungulate browsers will also help stay bush encroachment and natural trampling optimizing epigaeic faunal diversity (Pryke et al. 2016). Buffer zones in this study were highly complementary and would allow for an almost complete coverage of spider and beetle ecological environments. However, it assumes that land use activities falls within those described for each of the zonation categories.

**Appendix**

Map showing (a) localities referred to in text including the Soutpansberg mountain range and the Limpopo Valley, and (b) sites (black dots) within vegetation units (illustrated in different colours) in the Vhembe Biosphere Reserve. Boxplot (c) of changes in proportional representation of ecological environments for these four scenarios and the (f) percentage area of the VBR falling within these four scenarios.
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Declarations

Ethical approval Specimens were collected on permit no. CPM-005-00005, provided by Limpopo Department of Economic Development, Environment and Tourism. The research leading to these results received funding from the University of Venda Research and Publications Committee under grant no P109. The authors declare they have no financial interests.

References

Barton PS, Manning AD, Gibb H, Lindenmayer DB, Cunningham SA (2010) Fine-scale heterogeneity in beetle assemblages under co-occurring Eucalyptus in the same subgenus. J Biogeogr 37(10):1927–1937. https://doi.org/https://onlinelibrary.wiley.com/doi/full/https://doi.org/10.1111/j.1365-2699.2010.02349.x

Barton PS, Manning AD, Gibb H, Wood JT, Lindenmayer DB, Cunningham SA (2011) Experimental reduction of native vertebrate grazing and addition of logs benefit beetle diversity at multiple scales. J Appl Ecol 48(4): 943–951. https://doi.org/https://besjournals.onlinelibrary.wiley.com/doi/https://doi.org/10.1111/j.1365-2664.2011.01994.x

Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F (2012) Impacts of climate change on the future of biodiversity. Ecol Lett 15(4):365–377. https://doi.org/https://onlinelibrary.wiley.com/doi/https://doi.org/10.1111/j.1461-0248.2011.01736.x

Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC model selection. Social Methods Res 37:261–304. https://doi.org/10.1177/0049124104268644

Cardoso P, Barton PS, Birkhofer K, Chichorro F, Deacon C, Fartmann T, Fukushima CS, Gaigher R, Habel JC, Hallmann CA, Hill MJ, Hochkirch A, Kwak ML, Mammola S et al (2020)
landscapes of eastern Austria. Biol Conserv 117(2):181–190. https://doi.org/10.1016/S0006-3207(03)00291-X
Saxer G, Doebeli M, Travisano M (2009) Spatial structure leads to ecological breakdown and loss of diversity. Proc R Soc Lond [Biol] 276:2065–2070. https://doi.org/10.1098/rspb.2008.1827
Schaffers AP, Raemakers IP, Šykora KV, Ter Braak CJ (2008) Arthropod assemblages are best predicted by plant species composition. Ecology 89(3):782–794. https://doi.org/10.1890/07-0361.1
Scheffers BR, Evans TA, Williams SE, Edwards DP (2014) Microhabitats in the tropics buffer temperature in a globally coherent manner. Biol Lett 10(12):20140819. https://doi.org/10.1098/rsbl.2014.0819
Schoeman CS, Samways MJ (2011) Synergisms between Alien Trees and the Argentine Ant on Indigenous Ant Species in the Cape Floristic Region, South Africa. Afr Entomol 19(1):96–105. https://doi.org/10.4001/003.019.0117
Schoeman CS, Foord SH (2012) Deciding on an appropriate scale for conservation activities: partitioning alpha and beta ant diversity in North-West Province, South Africa (Formicidae: Hymenoptera). Trans R Soc S Afr 67(1):1–10. https://doi.org/10.1080/0035919X.2011.641690
Schoeman CS, Tshililo P, Foord SH, Hamer M (2018) Annotated checklist of Carabidae (Insecta: Coleoptera) of the Vhembe Biosphere Reserve, South Africa. https://doi.org/10.13140/RG.2.2.33610.06089
Schoeman CS, Hahn N, Hamer M, Foord SH (2019a) Regional invertebrate cross-and within-taxon surrogacy are scale and taxon dependent. Trans R Soc S Afr 75(1):23–32. https://doi.org/10.1080/03403919.X.2019.1658656
Schoeman CS, Cory Toussaint D, Tshililo P, Foord SH, Hamer M (2019b) Darkling beetles of the bushveld: an annotated checklist of the Tenebrionidae of the Vhembe Biosphere Reserve, South Africa (Coleoptera). https://doi.org/10.13140/RG.2.2.29054.33604
Schönhofe AL (2008) On harvestmen from the Soutpansberg, South Africa, with description of a new species of Monomontia (Arachnida: Opiliones). Afr Invertebr 49(2):109–126. https://doi.org/10.5733/afin.049.0206
Sieh T, Ma K, Chao A (2014) iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0. https://doi.org/10.13140/RG.2.2.29054.33604
Soininen J (2016) Spatial structure in ecological communities–a quantitative analysis. Oikos 125(2):160–166. https://doi.org/10.1111/oik.02241
Su JC, Debinski DM, Jakubauskas ME, Kingscher K (2004) Beyond species richness: community similarity as a measure of cross-taxon congruence for coarse-filter conservation. Conserv Biol 18(1):167–173. https://doi.org/10.1111/j.1523-1739.2004.00337.x
Tuanmu MN, Jetz W (2014) A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. Glob Ecol Biogeogr 23(9):1031–1045. https://doi.org/10.1111/geb.12182
UNESCO (2021) Biosphere Reserves in Africa. https://doi.org/https://en.unesco.org/biosphere/africa/. Accessed 1 May 2021
Van Schalkwyk J, Pryke JS, Samways MJ, Gaigher R (2019) Complementary and protection value of a Biosphere Reserve buffer zone for increasing local representativeness of ground-living arthropods. Biol Conserv 239:108292. https://doi.org/10.1016/j.biocon.2019.108292
Vhembe DM (2017) Vhembe District Bioregional Plan. Compiled by: Limpopo Department of Economic Development, Environment and Tourism (LEDET). http://www.nuleafs.co.za/wp-content/uploads/2018/01/Vhembe-Bioregional-Plan_rev4_Dec-2017_name-changes.pdf. Accessed 1 May 2021
Willig MR, Kaufman DM, Stevens RD (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. Annu Rev Ecol Ecol Syst 34(1):273–309. https://doi.org/10.1146/annurev.ecolsys.34.012103.144032
Wise DH (2006) Cannibalism, food limitation, intraspecific competition, and the regulation of spider populations. Annu Rev Entomol 51:441–465. https://doi.org/10.1146/annurev.ento.51.110104.150947
Woodroffe R, Ginsberg JR (1998) Edge effects and the extinction of populations inside protected areas. Science 280(5372):2126–2128. https://doi.org/10.1126/science.280.5372.2126

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