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Stability of Afromontane ant diversity decreases across an elevation gradient

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ABSTRACT

As the need to better understand the ecology of hotspots of endemism intensifies, the insurance hypothesis is drawing increasing attention from policy-makers and scenario-planners. The hypothesis states that biodiversity increases ecosystem stability. When species numbers fluctuate, there is potential for further perturbation, loss of function and increased opportunity for invasive species to fill vacated niches. Southern Africa is predicted to be disproportionately impacted by global change, and high altitude systems as foci of endemism are particularly vulnerable to warming. Using ants, a group key to ecosystem function, we assess effects of temperature, season, aspect, vegetation and soil conditions on montane ant species richness, stability of ant community composition, and stability of ant species richness across an altitude gradient. Over six consecutive years of bi-annual sampling, we gathered one of the largest standardized data sets to date. We showed for the first time that stability of ant species richness decreases with increasing altitude, whilst compositional similarity of ant communities is higher with increasing altitude. Findings reveal more similar, species-poor, less stable ant communities at high altitude at the same sites over time.

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1. Introduction

Global anthropogenic change is shifting distributions of vertebrate and invertebrate assemblages at a range of scales, and the final outcome is likely to be deleterious to biodiversity and ecosystem function (Joseph et al., 2018a., Davis and Vincent,

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2017; Duffy et al., 2015; García-Palacios et al., 2018). Ecological stability is therefore important, and has become a focal topic in ecological circles, as the impacts of global change to ecosystem stability through altered species richness and composition patterns become better appreciated (García-Palacios et al., 2018; Hautier et al., 2015).

The insurance hypothesis postulates that species richness can increase ecosystem stability. The hypothesis has received wide research attention (Doak et al., 1998; García-Palacios et al., 2018; Isbell et al., 2009; Lehman and Tilman, 2000; Loreau et al., 2001; Pennekamp et al., 2018; Yachi and Loreau, 1999), and is emerging as a key issue politically, as impacts to biodiversity threaten ecosystem services and mutualistic networks (e.g., Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services; Isbell et al., 2017; Simba et al., 2018). Stability, the inverse of variation over time, has long been recognised as a fundamental ecosystem property that offers insights into biodiversity and ecosystem processes (Doak et al., 1998). The insurance hypothesis posits that species respond to environmental perturbations in different ways, fluctuating in their abundance and contribution to ecosystem functioning under different conditions. In a system with high species richness, these different species responses are more likely to complement each other, conferring overall stability, than in a low species richness system. Species richness thus acts as a buffer against environmental perturbation (García-Palacios et al., 2018; Loreau et al., 2001; Tilman, 1999).

Mountain-inhabiting ectotherm assemblages across elevational gradients can be particularly vulnerable (García-Robledo et al., 2016), as the flexibility of adaptive traits that influence organism fitness and ecosystem function become tested by the rapid changes in thermal regimes that are predicted to occur in these regions (Modiba et al., 2017; Petchey and Gaston, 2006; Salas-Lopez et al., 2017). Mountain-dwelling communities need to adapt to specific temperature niches, microhabitats and soils. Furthermore, landscape heterogeneity means that montane assemblages can be effectively isolated and surrounded by an ecological matrix to which they are not well adapted (Bishop et al., 2017; Suggitt et al., 2011). The modification of cooler microclimates (which can enhance ectotherm persistence; Duffy et al., 2015; G. S. Joseph et al., 2016), and microhabitat loss (e.g. loss of shade provided by vegetation through herbivory; G. Joseph et al., 2018b; Minor et al., 2016; Suggitt et al., 2011) are anticipated to impact community composition, species richness, and increase the likelihood of localised extinctions (Stocker et al., 2013; Thomas et al., 2004).

As anthropogenic impacts to ecological systems intensify, identifying patterns and conditions that affect biodiversity over time become increasingly relevant. Research in arid systems has revealed that climate can modulate the relationships between diversity and ecosystem stability, leading to climate dependency of the biodiversity–ecosystem stability relationship, and that species richness can play an important stabilizing role with increasing aridity (García-Palacios et al., 2018; Pennekamp et al., 2018). Despite ample evidence of the biodiversity–stability relationship (García-Palacios et al., 2018; Loreau et al., 2001; Pennekamp et al., 2018), and that global change is impacting ecosystem stability (Donohue et al., 2016), predictive modelling efforts addressing ecosystem stability at regional and global scales require studies conducted over protracted timescales (García-Palacios et al., 2018). For the most part, such studies do not exist.

Insects, amongst the most species-rich and functionally important of animals, have evolved specific traits and thermal tolerances to suit their habitat, impacting distribution, fitness and ultimately functioning of ecosystems dependent on their services (Wilson, 1987). Amongst insects, ants (Hymenoptera: Formicidae) are critical to ecosystem processes at a range of scales, and are indicators of environmental change (Tiede et al., 2017). Recent studies highlight that ant species richness can decrease linearly, or with mid-elevational peaks, as altitude increases and temperatures decrease (Bishop et al., 2014; Yusah et al., 2012). Despite the central role of ants to ecological systems, and the vulnerability of isolated montane communities to environmental perturbation, few studies examine temporal trends in biodiversity, and to our knowledge no study has to date addressed the stability of invertebrate diversity over time across an elevation gradient.

As maintaining species number can buffer and modulate an ecosystem's response to change, preventing niches from becoming available to invasive species and restructuring communities (García-Palacios et al., 2018; Yachi and Loreau, 1999), we test the implications of an altitudinal gradient for stability of ant species richness ($\text{stability}_{\text{asr}}$) and ant community composition over time. We sampled ant communities in an Afrotropical mountain range recognised for its high endemism of several taxa, the Soutpansberg, in southern Africa. The Vhembe biosphere planning group has recently proposed that all areas in the Soutpansberg be proclaimed core conservation areas, prompting the South African government's Department of Environmental Affairs, and the South African National Spatial Biodiversity Assessment (NSBA) to include the Soutpansberg complex as a national priority area for conservation action (Department of Environmental Affairs, 2018). We used an extensive dataset collected biannually for six consecutive years, making it amongst the largest standardized, spatio-temporal invertebrate community datasets in existence.

To date, research confirms the negative relationship between ant species richness and increasing altitude (Bishop et al., 2017; Munyai and Foord, 2012; Szweczyk and McCain, 2016). Given that the presence of more species enhances stability, we predicted decreased $\text{stability}_{\text{asr}}$ at altitude. In the knowledge that endemic, altitude-adapted taxa often occur at higher elevations, and that this holds for the Soutpansberg (Munyai and Foord, 2015), we expected increasing altitude to impact community similarity through time, with community composition being more variable between years. As ant diversity decreases with altitude, we anticipated that species-poor communities at high altitude might be dominated by a small number of similar species able to survive the environmental filtering of high altitude. To test these hypotheses, we asked:

- (1) does species richness of ants vary with altitude, aspect and with variables of habitat structure and soils?
- (2) does $\text{stability}_{\text{asr}}$ change across altitude?

- (3) is similarity of composition of ant communities constant across an altitudinal gradient?
 (4) are there elevational thresholds that influence occurrence of ant taxa across an altitudinal gradient?

2. Methods

2.1. Study site

Ants were sampled in a recognised southern African centre of endemism (Van Wyk and Smith, 2001), the Soutpansberg Mountains within the Vhembe Biosphere Reserve. We sampled along an elevational transect beginning at 23°02'16.91"S, 29°26'34.22"E, running in a north-south direction, starting at 800 m above sea level (a.s.l.) on the southern aspect, and climbing to 1700 m a.s.l., before descending to 800 m a.s.l. on the northern aspect. The transect is characterised by sandstone, erosion-resistant quartzite, conglomerate, basalt, and shale rocks (Mostert et al., 2008), experiencing summer rainfall, dry winters and mean annual precipitation of about 450 mm (Mucina and Rutherford, 2006).

2.2. Ant sampling

Epigeaic ant sampling took place biannually for 6 years, from 2009 to 2015. Given that sampling can vary even at the same time of year through fluctuating environmental variables (e.g. rainfall events, fires, temperature variability), we mitigated against short-term temporal variation in foraging activity by (1) sampling at the same time each year, during January (wet season) and September (dry season), (2) ensuring that sampling was not coupled to rainfall events, (3) only sampling on sites not impacted by fire, (4) sampling during 5 day periods in which full sun (no cloud) was present for an average of over 6 h per day. Sampling was done at eleven sites, spaced 200 vertical metres apart, for each elevational band. Each site contained four replicates, spaced at least 300 horizontal metres apart to avoid pseudo-replication (McKillup, 2011). At each replicate, ten pitfall traps (each \varnothing 62 mm) were laid out in a grid composed of two parallel lines (2×5) with 10 m spacing between traps, following Munyai and Foord (2012) and Bishop et al. (2014). Traps contained a 50% solution of propylene glycol and were left open for five days during each survey. Ants were identified to morphospecies or species when possible.

2.3. Environmental variables

Temperature was recorded in two replicates at each site. Within each replicate, one Thermocron iButton (Semiconductor Corporation, Dallas/Maxin/Texas) was buried 1 cm below the soil to record temperature at hourly intervals. Mean, minimum and maximum temperatures were calculated for wet and dry season for each year at each elevational band.

Vertical and horizontal habitats were quantified. During each survey, a 1 m² grid was placed over each pitfall trap, and imaged to establish horizontal habitat structure by estimating percentage area covered by bare ground, vegetation, rock and leaf litter. For vertical structure, a 1.5 m measuring rod was placed at four corners of the grid, 1.5 m from the pitfall trap. The number of vegetation contacts on the rod was recorded along 25 cm intervals (0–25 cm, 25–50 cm, 50–75 cm, 75–100 cm, 100–125 cm, 125–150 cm, >150 cm).

In January 2010, ten soil samples were taken randomly from each replicate using a soil auger, and analysed for particle size composition (clay, sand, rock and silt), pH, conductivity, Carbon (C), Potassium (K), Sodium (Na), Calcium (Ca), Magnesium (Mg), Phosphorus (P), and Nitrate (NO₃) by BemLab, South Africa.

Principal component analysis (PCA) was performed to summarize the variation for vertical and horizontal habitat structure respectively. The first two principal coordinates explained 37% and 24% of variation for vertical (cumulative variation = 61%) and 41% and 30% (cumulative variation = 71%) for horizontal habitat structure. The first principal component axis for vertical habitat structure (PC1_{intermediate.vertical.habitat}) was positively correlated with sites harbouring intermediately tall vegetation structure (50–75 cm, 75–100 cm, 100–125 cm), and negatively with habitats lacking vertical structure. The second principal component (PC2_{canopy.vertical.habitat}) was positively correlated with tall canopy cover (125–150 cm, 150+) and negatively with vertical vegetation below 25 cm and no canopy cover. The first principal component axis for horizontal habitat structure (PC1_{bare.ground.horizontal.habitat}) was positively correlated with bare ground and negatively correlated with vegetation cover. The second principal component (PC2_{leaf.litter.horizontal.habitat}) was positively correlated with leaf litter presence and negatively to exposed rock.

For soil characteristics the first two axes explained 46% and 15% of the variation. The first principal component axis (PC1_{acid.soils}) was positively correlated with acidic soil and negatively with basic soils. The second principal component axis (PC2_{sandy.soils}) was positively correlated with sandy soil and negatively with clay soil.

2.3.1. Statistical analysis

For each of the 528 ant communities in the dataset [i.e. 4 replicates per sampling site \times 11 sites \times 6 years \times 2 seasons = 528], we calculated species richness. Species richness was modelled using linear mixed effect models with Gaussian distribution and replicates specified as random intercept to account for temporal pseudo-replication while all predictor variables were included as fixed effects, with various subsets of variables and in various combinations. Certain variables

(altitude, mean temperature, minimum temperature, and maximum temperature) were collinear, therefore none of the candidate models contained more than one of these as the explanatory variable. For measures of vertical (vegetation height, canopy cover) and horizontal (percentage bare ground, vegetation, rock, leaf litter) vegetation structure, and soil parameters (particle size, pH, conductivity, and chemical composition), we used the values generated by the principal correspondence analyses. Along with these, other predictor variables used in the model were aspect, year and season. The best model was chosen using Akaike information criterion (AIC). Marginal R^2_m (variation explained by effects only) and conditional R^2_c (variation explained by fixed and random effects) were calculated for the best random-intercept model (Nakagawa and Schielzeth, 2013) in R programming environment version 3.5.0 (R Core Team, 2017).

Next we calculated stability_{asr} over time using mean species richness and its standard deviation, using each replicate set of traps at each site ($n = 4$ replicate \times 11 sites = 44). These were used to calculate the coefficient of variation, the inverse of which yielded a measure of stability, following various authors (Isbell et al., 2009; Lehman and Tilman, 2000). Thus stability was calculated as:

$$CV^{-1} = \frac{\text{mean}(\bar{X})}{\text{standard deviation}} \times 100$$

We calculated community similarity using two methods, Bray-Curtis similarity (1 minus the Bray-Curtis dissimilarity, which quantifies compositional similarity between different sites, based on abundance at each site), and Sorensen's index (which uses presence and absence to discriminate as to whether a species is common at a site or not, giving greater emphasis to species common to sites than to those found at only one site). Replicates from each site were lumped to yield the total community caught at each site. We compared the similarity of community composition for each site from each year and season with the composition of the community at that site for every other year and season, using the Vegan package in R (Oksanen et al., 2016). We then assessed these similarity values for each of the sites with the similarity values for sites at other altitudes and aspects, using a multiple linear regression.

To better understand which species drive community similarity at altitude, we used community abundance data, exploring the directionality, magnitude and uncertainty of individual taxa threshold responses and community threshold responses to an altitudinal gradient for each year separately using Threshold Indicator Taxa Analysis in TITAN2 package in R (Baker et al., 2015; Baker and King, 2010). Z scores are standardized against the mean and standard deviation of permuted samples, and so emphasise degree of change, thus prioritising taxa with infrequent occurrence. We used untransformed abundances on taxa occurring three or more times in the different sites over the entire period (2009–2015), with all partitions having at least three observations on both sides. TITAN also identifies taxon-specific community thresholds. Bootstrapping is used to estimate indicator reliability and purity as well as uncertainty around the location of individual taxa and community change points. Standardized taxa responses increasing at the change point ($z+$) are distinguished from those that decrease ($z-$).

3. Results

3.1. Patterns of species richness

Our traps contained a total of 102496 ants representing 35 genera from 128 species. Altitude and mean temperature were correlated ($t = -8.8$, $n = 438$, $p < 0.001$). We therefore ran two sets of models, one using altitude, and the other using mean temperature as one of a number of explanatory variables. We adopted an information theoretic approach, based on the bias-corrected Akaike information criterion (AIC_c) to choose the best model. The fit of altitude ($AIC_c = 2377$; variation explained 42%) to the data was better than mean temperature ($AIC_c = 2378$; variation explained 39%). Species richness (1) declined significantly with increasing altitude and was lower (2) on south-facing slopes (3) at the end of the dry season, and (4) in 2009 than in other years. The decrease in richness with increasing altitude was more marked on northern aspects. Species richness was significantly greater for sites with sandy soils with low clay content (Table 1a; Fig. 1.). An interaction between altitude and southern aspect was observed, with richness declining with altitude on the northern aspect, but remaining almost constant across altitudes on southern slopes.

3.2. Patterns of stability

Overall, stability_{asr} declined significantly with altitude, and was significantly lower on south-facing aspects. There was an interaction between altitude and aspect, such that stability_{asr} decreased with increasing altitude on northern slopes, but increased slightly on southern slopes (Fig. 2.).

Stability_{asr} also varied with vegetation, increasing with both axis 1 (more bare ground and little live vegetation cover) and 2 (increasing leaf litter with minimal exposed rock) of the PCA for horizontal vegetation structure, and with the second axis for soils (sandy soils with low clay content; Table 1b).

Table 1

Summary of the AIC_c-based model selection for variables explaining ant species richness (a), stability of ant species richness (b), compositional similarity of ant communities using Bray-Curtis (c) and Sorensen's (d) indices. The change in AIC_c between the best model, the next best, and worst are reported. Marginal R² (R²_m), measuring variation explained by fixed effects only, and conditional R² (R²_c), measuring variation explained by both fixed and random effects, are given.

Response variable	Model	AIC _c	ΔAIC _c (next best)	ΔAIC _{cnull}	R ² _m	R ² _c
(a) ant species richness	~ elevation x aspect + season + PC2 _{sandy.soils} + year	2377.4	3.2	101.4	0.30	0.42
<i>Best Model:</i>						
North aspect: $y = 16.2 (\pm 1.7) - 0.004 (\pm 0.001)\text{elevation} - 1.5 (\pm 0.4)\text{wet} + 8.0 (\pm 1.8)\text{PC2}_{\text{sandy.soils}} + 1.6 (\pm 0.6)\text{year}_{2010} + 3.3 (\pm 0.6)\text{year}_{2011} + 2.4 (\pm 0.6)\text{year}_{2012} + 4.5 (\pm 0.6)\text{year}_{2013} + 3.1 (\pm 0.8)$						
South aspect: $y = 7.5 (\pm 1.7) + 0.001 (\pm 0.001)\text{elevation} - 1.5 (\pm 0.4)\text{wet} + 8.0 (\pm 1.8)\text{PC2}_{\text{sandy.soils}} + 1.6 (\pm 0.6)\text{year}_{2010} + 3.3 (\pm 0.6)\text{year}_{2011} + 2.4 (\pm 0.6)\text{year}_{2012} + 4.5 (\pm 0.6)\text{year}_{2013} + 3.1 (\pm 0.8)$						
(b) stability of ant species richness	~ elevation x aspect + PC1 _{bare.ground.horizontal.habitat} + PChor2 + PC2 _{sandy.soils}	115.5	2.6	12.2	0.47	–
<i>Best Model</i>						
$y = 7.7 (\pm 1.0) - 0.003 (\pm 0.001)\text{elevation} - 6.7 (\pm 1.3)\text{aspect} + 39.5 (\pm 17.0)\text{PC1}_{\text{bare.ground.horizontal.habitat}} + 42.2 (\pm 13.7)\text{PC2}_{\text{leaf.litter.horizontal.habitat}} + 1.9 (\pm 0.9)\text{PC2}_{\text{sandy.soils}}$						
(c) similarity: Bray-Curtis	~ elevation x aspect	-694.9	25.3	187.3	0.23	–
<i>Best Model:</i>						
North aspect: $y = 0.23 (\pm 0.03) + 1.9 \times 10^{-4} (\pm 2.6 \times 10^{-5})\text{elevation}$						
South aspect: $y = -0.08 (\pm 0.03) + 4.1 \times 10^{-4} (\pm 2.6 \times 10^{-5})\text{elevation}$						
(d) similarity: Sorensen's	~ elevation x aspect	-1691.1	32.2	214.5	0.21	–
<i>Best Model:</i>						
North aspect: $y = 0.73 (\pm 0.02) - 8.3 \times 10^{-4} (\pm 2.2 \times 10^{-5})\text{elevation}$						
South aspect: $y = 0.44 (\pm 0.02) - 6.7 \times 10^{-4} (\pm 2.2 \times 10^{-5})\text{elevation}$						

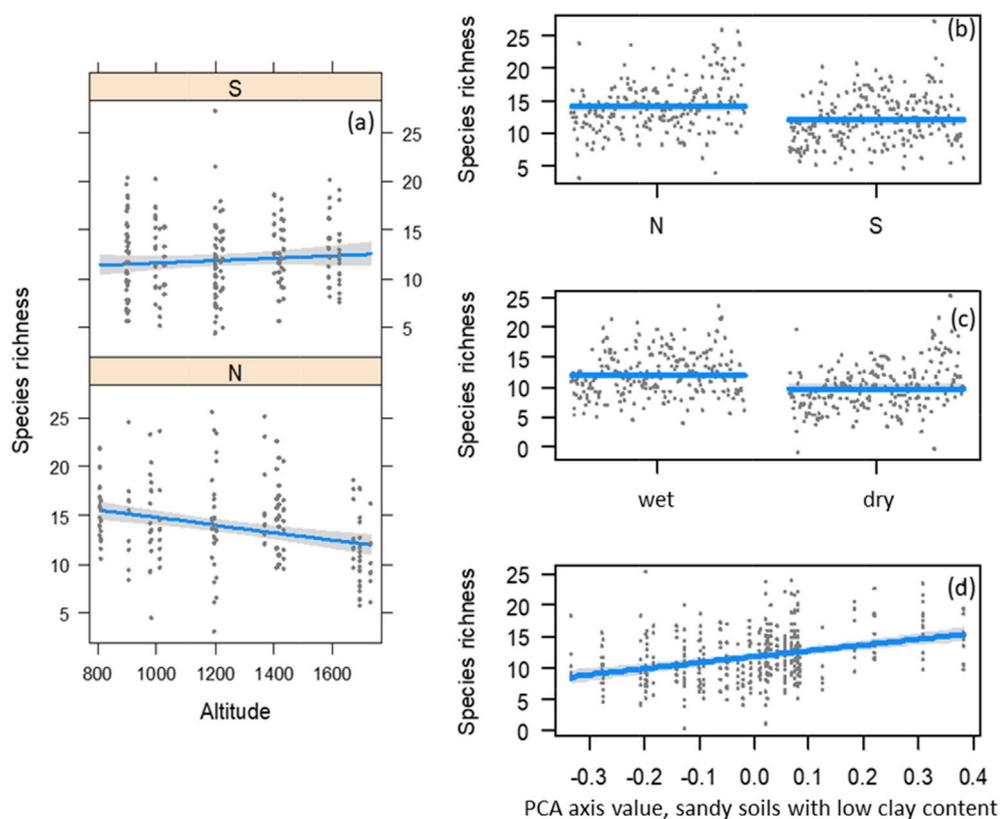


Fig. 1. Ant species richness as a function of aspect and increasing altitude (a), aspect alone (b), season (c), sandy soils low in clay content (d).

3.2.1. Patterns of similarity

Using the Bray-Curtis index, overall for the system similarity increased with altitude and this was the case for both northern and southern aspects. There was an interaction between aspect and altitude, with a more rapid increase in similarity

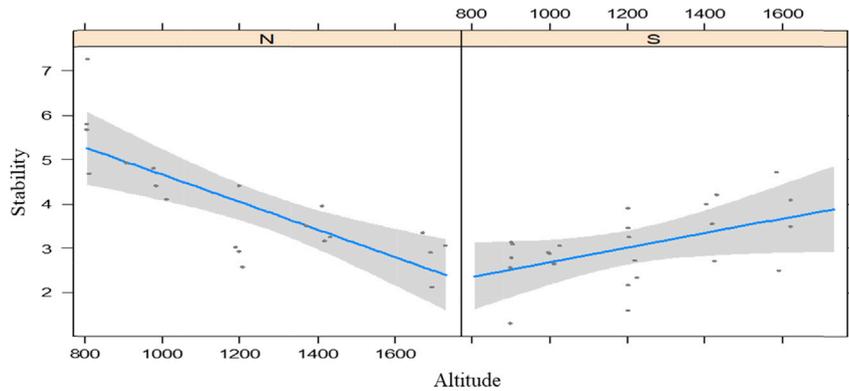


Fig. 2. Stability of ant species richness decreased significantly with increasing altitude on northern slopes, yet increased negligibly on southern slopes.

on southern aspects. However, it is notable that at low elevations of 800 m similarity between communities was lower on the southern than on the northern aspect (Table 1c; Fig. 3a). With Sorensen's index, overall, similarity also increased with altitude, but similarity underwent a slight decrease on the northern aspect with increasing altitude (Table 1d; Fig. 3b).

3.2.2. Threshold Indicator Taxa Analysis

Threshold Indicator Taxa Analysis cumulatively identified 37 individual ant taxa that declined in response to increasing altitude, with an observed environmental change point occurring around 1200 m. For 20 species, a positive change point was observed at 1400 m, and these species increased in response to increasing altitude (Fig. 4).

4. Discussion

We found that the stability of invertebrate richness, using Afrotropical montane ants as an example, decreased with increasing altitude. This study is the first to evaluate stability of species richness and composition along an elevational gradient over time. Unsurprisingly, patterns of ant species richness echo previous studies (decreasing with higher altitude, cooler south-facing slopes, and the dry season, conditions with lower forage availability, temperatures and humidity; Bishop et al., 2014; Mauda et al., 2018; Yusah et al., 2012), emphasising that broad changes in temperature are a strong driver of ant richness patterns (Bishop et al., 2017; Hölldobler and Wilson, 1994; Sanders et al., 2007).

In general, the presence of many species increases stability (García-Palacios et al., 2018; Loreau et al., 2001), and the finding that stability_{asr} displayed a strong elevational pattern, with species number fluctuating increasingly with altitude, supported our hypothesis of decreasing stability_{asr} at higher elevations, in line with a decrease in ant species richness at altitude (Bishop et al., 2014; Munyai and Foord, 2015). Stability_{asr} was lower on southern slopes, which are colder across seasons, and receive less exposure to sunlight in the southern hemisphere. Although stability_{asr} remained lower than on northern slopes, it increased marginally on southern slopes with increasing elevation. Vegetation structure was not shown to

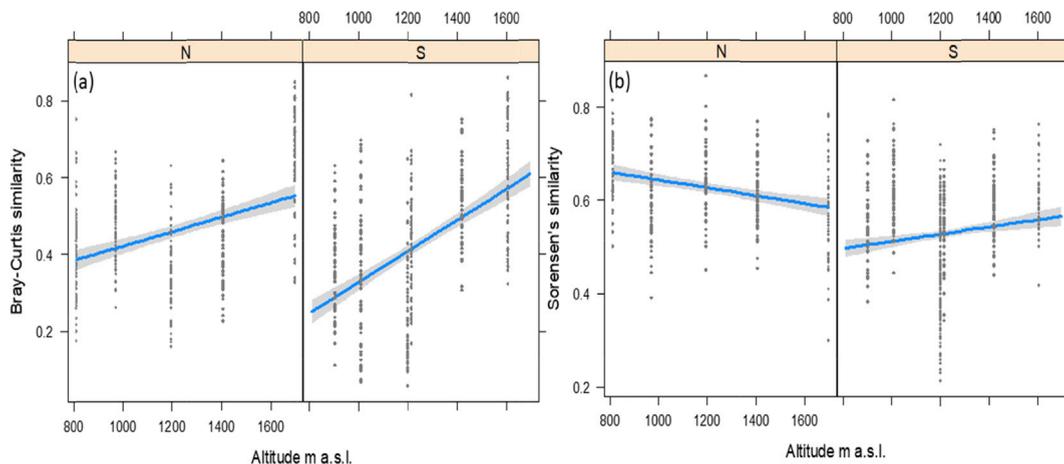


Fig. 3. The relationship between ant community similarity and altitude using Bray-Curtis (a) and Sorensen's (b) similarity indices.

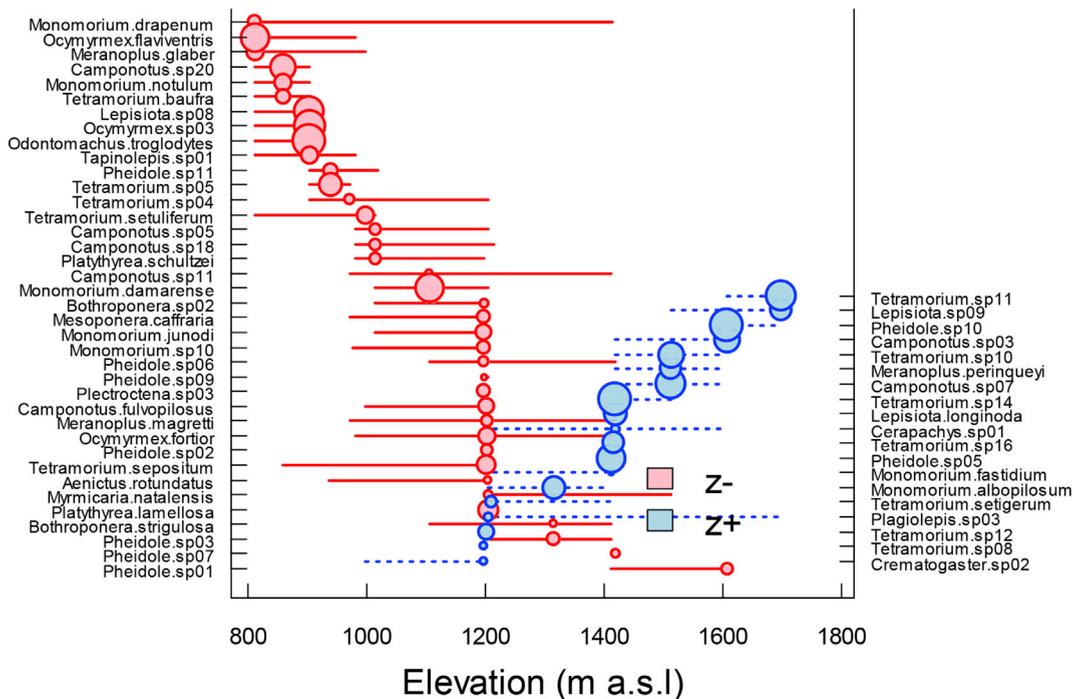


Fig. 4. Significant ant indicator taxa identified in threshold indicator taxa analysis (TITAN), across an altitudinal gradient. Red symbols correspond to negative (z^-) indicator taxa, and denote taxa that decrease with increasing elevation, and blue correspond to positive (z^+) taxa, namely those that increase as altitude increase. Symbols are in size proportional to z scores. Horizontal lines show 5th and 95th percentiles among 500 bootstrap replicates. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

be a driver of stability_{ASR} in our study, but these southern slopes are known to receive more precipitation, and are characterised by more woody vegetation, resulting in shading and cooler microclimates (Munyai and Foord, 2015). This in turn may influence stability_{ASR} on southern slopes, but remains untested. It is more likely that species richness, which did not decrease on southern slopes (also perhaps due to the vegetation and precipitation properties of this southern aspect; Fig. 3), exerts a modulating effect, given the expectation that presence of more species can enhance stability (García-Palacios et al., 2018; Loreau et al., 2001).

Bare ground with little intermediate vegetation structure increased stability_{ASR}, as did increased leaf litter with minimal exposed rock, perhaps as a consequence of additional habitat complexity minimising variation of species richness over time (Mauda et al., 2018; Tiede et al., 2017). Stability_{ASR} also increased with sandy soils with low clay content, a substrate known to favour ant species richness (Mauda et al., 2018). Stability_{ASR}, lower in the first year, is interpreted in the context of both mean annual temperature, which was lower in 2009 than in all other years (by at least 1 °C), and minimum annual temperature, which was >1 °C higher in 2010, but 5 °C higher by 2014–2015 (Appendix Fig.S1; Sanders et al., 2007).

Compositional similarity of ant communities was higher overall with increasing altitude regardless of the index used, but the findings for aspect were more complex. On both northern and southern slopes, the Bray-Cutis index showed that on both northern and southern slopes, ant communities become more similar with higher altitude. As this index determines similarity by using species abundance, findings suggests that species that are common (altitude-adapted) at high elevations, remain common as altitude increases, and that ant taxa poorly adapted to altitude disappear, or become less common with increasing elevation. Sorensen's index revealed the same pattern for the southern slope, but that communities were slightly less similar with increasing altitude on northern slopes. Given that Sorensen's index uses presence-absence, it is sensitive to the appearance or disappearance of a given species, and results may reflect a lower degree of environmental filtering on the relatively warmer, more hospitable northern slopes. Furthermore, within the context of there being fewer species at elevation, Sorensen's index can be expected to be sensitive to adding or taking away species, because the number of species at altitude is low to start off with.

Given the thermophilic nature of ants (Bishop et al., 2017; Hölldobler and Wilson, 1994; Sanders et al., 2007), and studies confirming that ability to tolerate cold temperatures at altitude can be important for ant distribution (Bishop et al., 2017), it is likely that at higher altitude, the limited species that are best adapted to elevation come to dominate high altitude communities, which gradually become more similar with increasing elevation. In summary, findings reveal that there are few species at higher relative to lower altitudes, and that these few species tend to be dominant at higher altitudes as only they can persist in such conditions. Conversely, at lower altitudes, more species are able to persist in the relatively benign low-elevation conditions, limiting opportunities for specific species to emerge as dominant over the protracted period of six years.

Threshold Indicator Taxa Analysis confirmed that there were 85% more indicator species that decreased with increasing altitude, nearly double the small number of indicator species that increased with increasing altitude (Fig. 4). This facilitates interpretation of similarity indices (which increased with increasing altitude), and stability_{asr} measures, if one considers that not only do the threshold indicator taxa reveal a smaller species pool at altitude, but also reveal a threshold altitude, above which the majority of indicator species are poorly represented. The majority of indicator ant taxa decrease consistently as elevation increases to 1200 m. The small number of altitude-adapted indicator species dominate at altitudes above 1420 m, and as altitudes declines below 1420 m, such species no longer dominate as they did at higher altitudes. Findings reveal that these high altitude ant communities are (1) species poor (2) have lower stability_{asr} (and with low-species numbers, even alteration of a few species can cause fluctuation to richness over time), and are (3) more similar to one another by virtue of there being only a limited suite of ant species able to tolerate high altitude (and the variables correlated with elevation, e.g. lower minimum, mean and maximum temperatures, decreased humidity, differing soils and vegetation structure).

At a regional scale, currently within the Soutpansberg, a few altitude-adapted species appear to be 'holding the fort' at high elevation, living in communities that increasingly resemble one another as altitude increases. The new Vhembe biosphere reserve zonation proposes that all areas above 1200 m in the Soutpansberg be proclaimed core conservation areas, and our findings identify 1200 m as the change point where the lower elevation species start falling out of assemblages, whilst altitudes approaching 1400 m become important for the high altitude species. At the scale of the Soutpansberg complex itself, 1200 m also coincides with the appearance of Afromontane forests on southern aspects, and 1400 m corresponds with a switch to more open, Soutpansberg Mountain Sourveld habitat (Department of Environmental Affairs, 2018; Mucina and Rutherford, 2006).

Given that montane assemblages across elevational gradients are often dominated by rare or endemic species, they can be particularly vulnerable to temperature changes (García-Robledo et al., 2016), so at the broadest scales, fluctuation of species numbers at higher elevations disproportionality places them at risk from global change. In southern Africa, temperatures are anticipated to rise by up to 2.5 °C over three decades (Davis and Vincent, 2017), potentially opening niches to thermophilic, heat-adapted invertebrates. Although this study does not address the impact of global change, it can be speculated that with the buffer that stability of species richness can confer already compromised at altitude, communities at higher elevation may be at increased risk of invasion and restructuring as new niches form. Suitable microclimates and microhabitats may modulate this (Duffy et al., 2015; G. S. Joseph et al., 2016), as was the case with e.g. sandy soils and leaf litter in this study, but further research will be needed to determine whether the lowered stability_{asr} will allow thermophilic, low-altitude ants and invasive species to restructure communities at high altitudes.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2019.e00596>.

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