Species diversity and dominance-richness relationships for ground and arboreal ant (Hymenoptera: Formicidae) assemblages in Namibian desert, saltpan, and savannah

Article

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Species diversity and dominance-richness relationships for ground and arboreal ant (Hymenoptera: Formicidae) assemblages in Namibian desert, saltpan, and savannah

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Abstract

Namibia has high levels of invertebrate endemism, but biodiversity research has been geographically and taxonomically restricted. In South African savannah, species richness of ground-foraging ant assemblages is regulated by dominant ant species. However, this pattern has not been tested in other arid regions. In this study, we provide a description of ant diversity at baits in three different Namibian habitats (savannah, saltpan, and desert), and we test the relationship between ant dominance and richness for ground-foraging and arboreal species.

Forty-two ant species were collected in this study, with species richness being highest in the saltpan, followed by savannah and then desert. Due to shared arboreal species, ant assemblages were most similar between the savannah and desert, whereas similarity between savannah and saltpan ant assemblages was due to an overlap in ground-foraging species. Ground ants were more diverse than arboreal ants, and several species were observed at baits for both strata, although the degree of overlap varied with habitat type.

The dominance-richness relationship varied with habitat type and sampling strata. We found a unimodal relationship in the saltpan but not in the savannah. In the desert, low ant abundance meant that we were unable to assign species dominance, possibly due to reduced foraging activity caused by high temperatures. For ground ants alone, the dominance-richness relationship was logarithmic, with increasing abundance of dominants leading to decreasing overall species richness. However, no trend was observed for the arboreal ant assemblage. The lack of a consistent trend across assemblages may be the result of varying degrees of environmental stress or competition. We hope that this preliminary description of diversity and dominance in Namibia stimulates further research on ant assemblages in other arid regions of the Afrotropics.

Key words: Competition, dominance, diversity, Formicidae, Namibia, species richness.

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Introduction

Understanding the patterns and processes of species abundance and diversity is at the core of ecology; however, not all regions are equally represented in the scientific literature, with the Afrotropics receiving relatively little attention. Southern Africa contains unique biomes; in the east, it is dominated by montane grasslands and shrublands, and in the west by deserts and xeric shrublands (OLSON & al. 2001). The arid and semi-arid tree savannahs in this region are considered a "keystone structure ecosystem" (TEWS & al. 2004). The region is renowned for its endemic plants and animals (for review, see SIMMONS & al. 1998) and, in the few places where they have been sampled, especially for invertebrates (GRIFFIN 1998, SOLE & al. 2005, WASSENAAR & al. 2013). Compared with other continents, African ants are poorly represented in ecological research (CAMPBELL 2013). Most studies of ants in the Afrotropics discover new species or species records, but the lack of existing taxonomic and ecological information is an obstacle for scientists (KOCH & VOHLAND 2004, DUNN & al. 2007). Although interest in Afrotropical ants is growing, extreme arid regions such as Namibia remain neglected. Much of what is known about Namibian ants is based on the work of MARSH (1986a, b) in the Namib Desert. He emphasised that, despite the importance of ants in arid ecosystems, they are virtually unstudied. Nearly thirty years later, this situation remains largely unchanged with the exception of pilot studies and research confined to the grey literature, including thesis and consultancy work (KOCH & VOHLAND 2004, THERON 2010, HAWKES & FISHER 2011).

The role of competition in structuring ant assemblages is widely debated (HÖLLDOBLER & WILSON 1990, CERDÁ & al. 2013). At baits, dominant ants can regulate species richness (PARR & GIBB 2009, WITTMAN & al. 2010), although it is unclear if the relationship consistently scales up to the assemblage level (PARR 2008, BACCARO & al. 2012). The dominance-species richness relationship at baits is typically unimodal (humped), due to the combined effects of environmental stress, abundance-frequency distributions and interspecific competition (PARR & al. 2005). In extreme environments or periods of unfavourable abiotic conditions, stress leads to low numbers of both dominant ants and total species richness. With increasing habitat favourability stress is reduced, and abundance of dominants and overall richness increases; this represents the ascending portion of the unimodal distribution. Additionally, this pattern is influenced by the shape of the abundance-frequency distributions (ANDERSEN 1992, PARR & al. 2005). Dominant ant species may increase richness by moderating the effect that subdominants have on subordinate species. This "competition cascade" is comparable to food web trophic cascades (ARNAN & al. 2011) that are observed when the top trophic level (predators) positively influences the bottom level (i.e., plants or small prey) by suppressing the intermediate level (i.e., herbivores or mesopredators) (SCHMITZ & al. 2000, HALAJ & WISE 2001, SHURIN & al. 2002). The descending part of the dominance-richness curve is observed as a result of competitive interactions. When the abundance of dominant ants is high enough then subordinate ants are excluded and overall species richness decreases (ANDERSEN 1992, PARR & al. 2005).

In this study we describe the diversity of ground and arboreal ants at baits in Namibian savannah, saltpan and desert habitats. The inclusion of arboreal diversity is particularly important as there are so few studies investigating ant diversity on vegetation in arid areas. Many of these studies are not published in peer-reviewed literature and none make comparisons with ground-foraging ant assemblages (KRÜGER & MCGAVIN 1998, THERON 2010; B. Taylor & G. McGavin, unpubl.). Ant species richness is higher for ground-foraging ants than arboreal ants in Australian and Brazilian savannahs (VASCONCELOS & al. 2008, CAMPOS & al. 2011). Therefore, we predict that ant species richness will also follow this pattern in Namibian savannah, and that this will extend to the other habitats sampled in this study. The unimodal dominance-richness relationship has been demonstrated across numerous habitat types (SAVOLAINEN & VEPSÄLÄINEN 1988, ANDERSEN 1992, VASCONCELOS & al. 2008, ARNAN & al. 2011, JANDA & KONECNA 2011), however, these studies have been largely restricted to areas of intermediate to high rainfall (mean annual rainfall of 1400 mm to 3558 mm). In desert regions, levels of precipitation can influence ant species composition, and many ant species are locally restricted according to habitat type (PAKNIA & PFEIFFER 2014). Highly arid habitats often exhibit low ant abundance. In these extreme conditions dominance-richness patterns are unknown but may only represent a portion of the unimodal relationship. Under extreme temperatures and aridity, there may be an increase of the effects of environmental stress and a reduced influence of interspecific competition. We test whether the full unimodal dominance-richness relationship is observed for ants at baits in Namibian savannah, saltpan and desert.

Materials and methods

Study sites

This study was carried out at two locations in Namibia approximately 345 km apart: Kuzikus Wildlife Reserve (Kuzikus) and Gobabeb Training and Research Centre (Gobabeb). Gobabeb is 120 km south east of Walvis Bay, in the Namib-Naukluft Park in the Namib Desert (23° 34' S, 15° 03' E). At Gobabeb, mean annual rainfall is between 19 and 25 mm (SOUTHGATE & al. 1996, ECKARDT & al. 2013). Mean annual fog is 37 mm, resulting in mean annual precipitation of 56 mm, ranging between 18 and 127 mm (SOUTHGATE & al. 1996). Mean annual temperature at Gobabeb is 21.1°C, and during November, the month of our sampling, the daily temperature can range from 11.8 to 31.2°C (LANCASTER & al. 1984). Kuzikus is approximately 180 km south east of Windhoek, situated in the Namibian Central Kalahari (23° 13' S, 18° 24' E). It is difficult to obtain detailed, long term weather data for such remote sites as there are few meteorological stations. The nearest weather station with data available is Sandveld, which recorded 441.3 mm total annual rainfall for 2011, but 0 mm monthly rainfall for October 2011 when our sampling took place. For October 2011 the mean monthly temperature was 20.6°C with a range of 1.8 to 36.7°C (SASSCAL 2014).

Three habitat types were sampled: savannah and saltpan at Kuzikus (CAMPBELL & al. 2013b), and desert at Gobabeb (see Appendix S1, published together with Appendices S2-S4 as digital supplementary material to this article, at the journal's web pages). The savannah is dominated by the camelthorn acacia *Vachellia erioloba*, with a small number of other tree species (CAMPBELL & al. 2013a). The saltpan is the site of an ephemeral lake with the margins covered in scrub vegetation and small trees. *Vachellia hebeclada* is the dominant plant species with some *Senegalia mellifera* and *V. karroo*. The desert site is comprised of three habitats including gravel plains, dune fields, and the dry Kuiseb riverbed. Our sampling was restricted to sections of the riverbed with bare sand and isolated *V. erioloba* trees.

Diversity

Ants were sampled using observations at meat baits in each of the three habitats in October and November 2011. For each habitat, a 1 ha plot was established and within a plot baiting was carried out six times (three mornings and three afternoons). This resulted in a total of 18 separate baiting sessions for this study (three habitat plots × six baiting sessions). Baiting was conducted on the ground and on trees. For each session of ground sampling, 15 bait stations total were set out at 5 m intervals along a 70 m transect. The location and direction of ground transects were haphazard within a plot and were different for each baiting session. The sparse distribution of trees within each plot, as is typical of arid environments, affected the sampling strategy for the baiting in trees. It was not possible to sample 15 trees in order to match the sampling effort for ground baiting and for the same reason it was also not possible to sample unique trees for each bait session. Ten bait stations total, one per tree, were set out within a plot. The placement of the bait square was changed to a new location within a tree for each baiting session in order to increase sampling coverage. As many of the trees were very large,

sampling on branches at varying heights and along different parts of the branch and trunk attracted ants that were utilising different parts of the tree. Sampling different locations on trees therefore captured multiple aspects of ant diversity, abundance and dominance compared with consistently sampling the same section of the tree.

A teaspoon of corned meat (Eloolo) was used as bait and placed on a small piece of white card (60 mm × 50 mm). For ground baits, the card was placed directly on the ground surface. For tree baits, the card was placed on the branch or trunk, and, if necessary, was held in place with masking tape (see Appendix S1). All species present on the bait square after 60 minutes of setting the bait were recorded. Ant abundance was scored for each individual species on a six-point scale: 1 = 1 ant, 2 = 2 - 5 ants, 3 = 6 - 10 ants, 4 = 11 - 20 ants, 5 = 21 - 50 ants, 6 = > 50 ants (ANDERSEN 1997, PARR & al. 2005, PARR 2008). The abundance per baiting session for each species is calculated as the total of the species' abundance scores summed across the 15 baits. Total abundance of dominant ants during a baiting session is the sum of each dominant species' total abundance for each bait station. Total maximum abundance for any ant species per baiting session is 90 for ground baits (maximum abundance score of 6 × 15 baits) and 60 for tree baits (maximum abundance score of 6 × 10 baits). The bait sampling methods have been adapted from PARR (2008).

A pilot experiment in the savannah habitat showed that pitfall trapping was not effective due to the presence of mammals that destroyed over 50% of traps. To add to the species inventory, we carried out hand collecting within each habitat to search for ants that were not attracted to baits. Searching for ants was conducted in the time available between observing interactions at baits. Ants were collected that were found along ground transects and on trees being sampled. The hand-collected species are not included in the analysis of numerical and behavioural dominance because they were not observed at baits, but they are analysed in the diversity results.

Samples of each species were collected to verify identifications in the laboratory at the University of Reading, UK. Specimens were identified to genus level (B. Bolton & B.L. Fisher, unpubl.) and then to species level using the most recent keys available (for full list see FISHER 2012). Due to the lack of taxonomic information, for many genera only morphospecies designations were available. Mr Peter Hawkes (AfriBugs CC, Pretoria) provided confirmation of species identifications (see Appendix S4). Voucher specimens were deposited in the State Museum of Namibia and the Oxford University Museum of Natural History, UK.

Dominance

We categorised ants as dominants or subordinates using a combination of numerical and behavioural dominance criteria, using the measures defined by PARR (2008) and based on other previous studies (DAVIDSON 1998, PARR & al. 2005). Numerical dominance is based on the abundance data described previously and has three components: occurrence at a large number of baits, percentage of baits monopolised, and high mean abundance score (see Appendix S3a, S3b). The percentage of baits monopolised is usually defined as baits with more than 20 individuals of a species present (ANDERSEN 1997, PARR & al. 2005, PARR 2008). At Kuzikus and Gobabeb, there were few ants recruiting to baits and rarely > 20 individuals monopolising a bait. For this reason, we used percentage of baits monopolised to indicate that this was the only species present at the bait, although the number of individuals may have been less than 20 (see Appendix S3a).

Behavioural dominance was measured by observing interspecific interactions at baits (see, FELLERS 1987, BESTELMEYER 2000, RETANA & CERDÁ 2000). Dominant behaviour was defined as an ant exhibiting aggression that displaced another species from the bait. This may have been achieved through biting, charging, or use of chemical secretions. For each of the baits, species interactions were observed at 15, 30 and 60 minutes for 30 seconds. The behavioural dominance score for a species is the number of encounters in which its behaviour was dominant, as a percentage of all its interspecific encounters at baits (see Appendix S3c and FELLERS 1987). Overall dominance in our study was classified using these combined measures of numerical and behavioural dominance as follows: percentage of baits monopolised > 50%, mean abundance score > 3, and dominance score > 50% (PARR 2008).

Statistical analyses

Ant species richness was estimated using rarefaction techniques in EstimatesS (COLWELL 2013). We used three non-parametric, asymptotic species richness estimators: Chao2, ICE (Incidence Coverage-based Estimator), and the first-order Jackknife. Extrapolation of MaoTau values was used to estimate additional sampling effort required to collect all species in a habitat. To assess the overlap of species between habitats, and between ground and arboreal strata, we used the incidence-based classic Sørensen similarity index (CHAO & al. 2005). The richness estimators and Sørensen index are all based on incidence (presence / absence) data. This allowed us to incorporate records of species found during hand collecting and from baiting, whereas abundance-based measures would only be valid for baiting data. To test the nature of the dominance-diversity relationship we performed least-squares regressions of species richness at baits against abundance of dominant ant species for linear, logarithmic and quadratic models (following PARR 2008). If more than one model was statistically significant we compared the AIC value to select the best-fitting model for the data (CRAWLEY 2005). For each habitat, we performed regressions for the entire ant assemblage. Additionally, we conducted separate analyses for ground and arboreal ant assemblages. Regression analyses were performed in R, version 2.15.2 (R CORE DEVELOPMENT TEAM 2012).

Results

Diversity

A total of 42 ant species were collected: 23 in the saltpan, 15 in the savannah, and 9 in the desert (Fig. 1). Of these, 29 were found exclusively on the ground and 17 exclusively on trees. In the saltpan (Sørensen = 0.231) and in the desert (Sørensen = 0.20), there were ant species present at baits both on the ground and on trees. Based on abundance data, four species were found on the ground and on trees, although an additional species occurred briefly at one bait, bringing the total number of overlapping

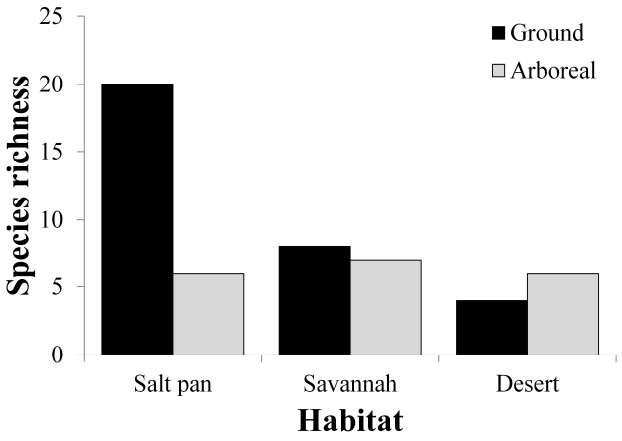

Fig. 1: Total species richness across three habitats for ground and arboreal ant assemblages in Namibia.

species to five (see Appendix S2). In the savannah, the ground-foraging and arboreal assemblages were unique with no shared ant species.

There was a small amount of overlap (0 - 3 species) in ants collected in multiple habitats. The savannah ant assemblage was more similar to the desert (Sørensen = 0.25) than to the saltpan (Sørensen = 0.105). The savannah and desert shared more arboreal species (Sørensen = 0.308) than ground-foraging species (Sørensen = 0.167). In contrast, the savannah and saltpan shared no arboreal species. Assemblage similarity between these habitats was due to the overlap in ground-foraging species, although the overlap was still lower than between the savannah and desert (Sørensen = 0.143). The saltpan and desert shared no common ant species.

Based on richness estimators, total ant species richness in the savannah is predicted to be 19 - 26 species (Fig. 2), so we sampled c. 68% of the ant species present. Sampling at the saltpan captured c. 79% of the ant assemblage, with total species richness predicted to be 28 - 30 species. Total ant species richness in the desert is estimated to be 12 - 17 species, so we sampled c. 64% of the ant assemblage. Extrapolation from a logarithmic curve fit to Mao Tau values indicated that if sampling effort was doubled in each habitat (extended to 300 ant-occupied sites), then we could expect to find an additional three, five and three species for the savannah, saltpan and desert, respectively. This would lead to collection of c. 82% for savannah, c. 97% for saltpan and c. 85% for desert, of the total ant assemblage.

Dominance

The dominant ant species in the savannah were *Monomorium rufulum* on the ground and *Crematogaster* sp. A on trees (Fig. 3, Tab. 1). At the saltpan, *Crematogaster* sp. C was dominant on trees. *Monomorium rufulum* was behaviourally dominant on the ground, but was only recorded at a small percentage of baits (3.3%), and did not monopolise any; therefore we do not consider it a dominant species in the saltpan. *Ocymyrmex micans*, *Pheidole tenuinodis* and *Tetramorium* sp. A all scored highly across measures of numerical and behavioural dominance and we consider these three species to be co-dominant at the saltpan on the ground. For both the saltpan and savannah many of the subordinate ants were species of *Camponotus* (Tab. 1).

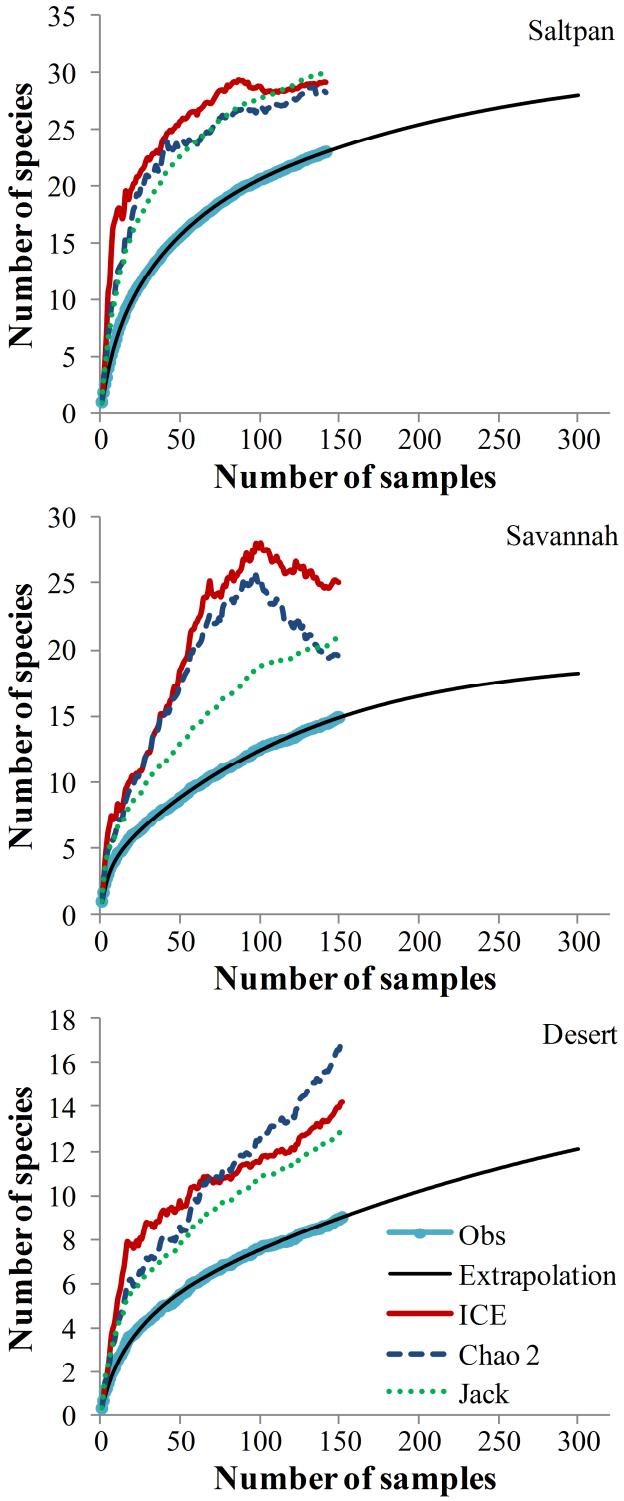

Fig. 2: Species accumulation and extrapolation curves based on 100 randomised iterations of data for ant assemblages in savannah, saltpan and desert sites. Species accumulation curves show observed data (Obs) and a logarithmic curve fit to Mao Tau values (Extrapolation), which estimates species richness if sampling effort was doubled. Richness estimators for observed data are; ICE (Incidence Coverage-based Estimator), Chao2, and the first-order Jackknife.

In the desert, no ants fitted the definition of dominant species using the combined measures of numerical and behavioural dominance. The distribution of ants was patchy

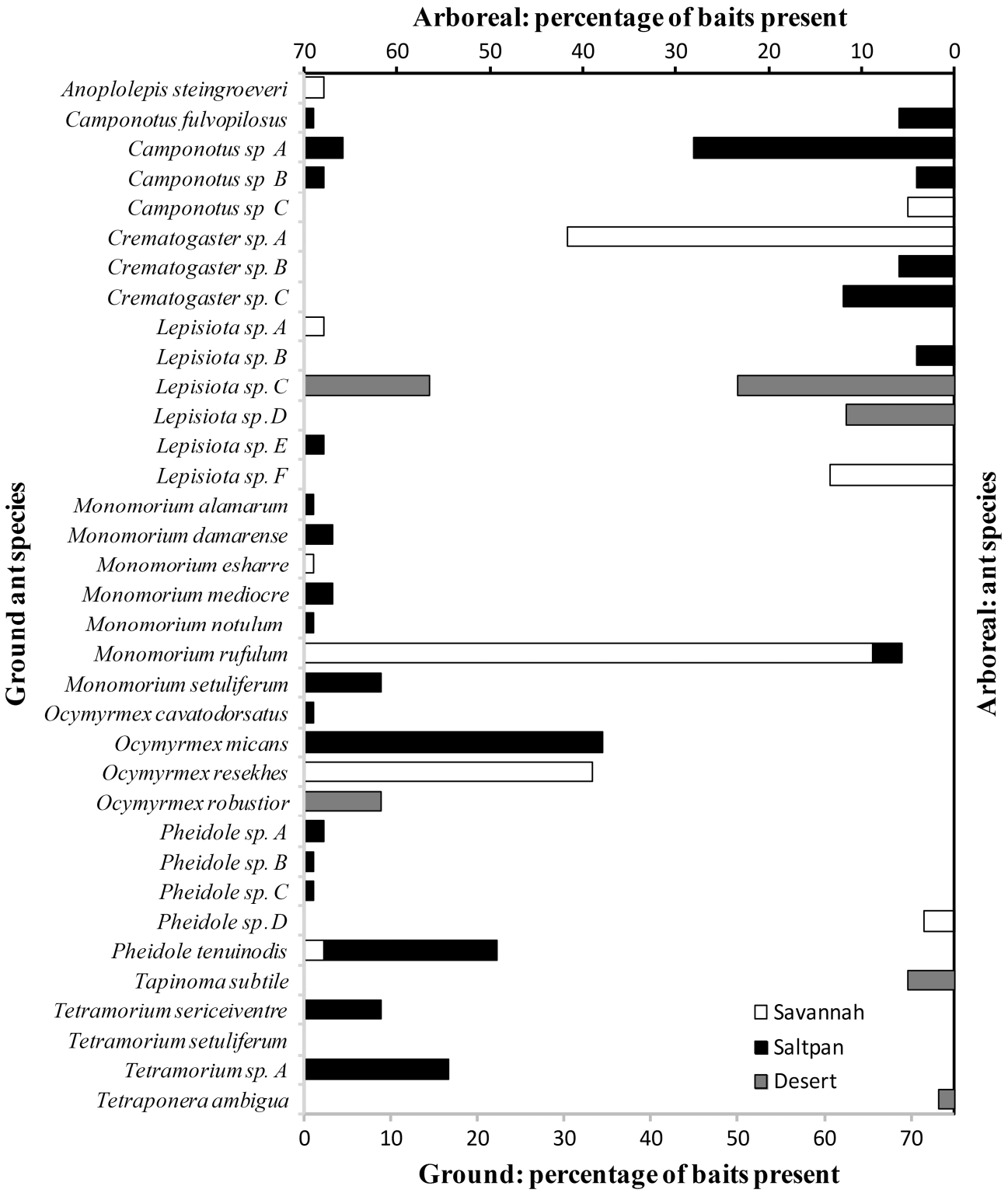

Fig. 3: Occupancy of baits across three habitats in Namibia for ground-foraging (left axis) and arboreal (right axis) ants. Where a species was found in multiple habitats, the percentages are stacked.

at this site: 70% of baits were empty in the desert, compared with 20.7% in the saltpan and 22.7% in the savannah. This resulted in no interspecific encounters at baits and we were unable to assign behavioural dominance scores to any of the species. Based only on numerical measures of dominance, we can consider *Lepisiota* sp. C as the dominant species in the desert because it was present at and monopolised most baits.

Dominance-richness relationships

As no true dominant species could be assigned for desert ants, the dominance-richness analyses were restricted to the savannah and saltpan habitats. For both habitats combined and for the savannah only, there was no relationship between abundance of dominant ants and total species richness at baits. At the saltpan the relationship was unimo-

Tab. 1: Summary of behavioural and numerical dominance analyses of ants occurring at baits at Kuzikus and Gobabeb. Classification as a dominant species requires three of these behavioural and numerical dominance measures to be met. Species highlighted in bold are those which meet the following dominance criteria: a score > 50% for baits monopolised, a score of > 3 for mean abundance, and a score of > 50% for dominance.

Habitat Species	Baits present (%)	Baits monopolised (%)	Mean abundance score	Behavioural dominance score
Savannah				
Ground				
Anoplolepis steingroeveri	2.2	100.0	4.5	0.0
Lepisiota sp. A	2.2	100.0	3.0	10.0
Monomorium esharre	1.1	0.0	2.0	0.0
Monomorium rufulum	65.6	**79.7**	**4.2**	**71.0**
Ocymyrmex resekhes	33.3	63.3	3.1	39.3
Pheidole tenuinodis	2.2	0.0	3.5	50.0
Tree				
Camponotus sp. C	5.0	0.0	1.3	16.7
***Crematogaster* sp. A**	41.7	**88.0**	**4.9**	**83.3**
Lepisiota sp. F	13.3	87.5	1.6	0.0
Pheidole sp. D	3.3	50.0	5.5	0.0
Saltpan				
Ground				
Camponotus fulvopilosus	1.1	0.0	2.0	0.0
Camponotus sp. A	4.4	50.0	3.3	0.0
Camponotus sp. B	2.2	0.0	1.5	0.0
Lepisiota sp. E	2.2	50.0	3.0	50.0
Monomorium alamarum	1.1	100.0	5.0	0.0
Monomorium damarense	3.3	100.0	5.0	0.0
Monomorium mediocre	3.3	33.3	2.3	50.0
Monomorium notulum	1.1	100.0	6.0	0.0
Monomorium rufulum	3.3	0.0	3.3	100.0
Monomorium setuliferum	8.9	87.5	3.4	33.3
Ocymyrmex cavatodorsatus	1.1	0.0	4.0	0.0
Ocymyrmex micans	34.4	**87.1**	**3.5**	**72.7**
Pheidole sp. A	2.2	0.0	1.5	0.0
Pheidole sp. B	1.1	100.0	4.0	50.0
Pheidole sp. C	1.1	0.0	2.0	0.0
Pheidole tenuinodis	20.0	**72.2**	**3.8**	**100.0**
Tetramorium sericeiventre	8.9	42.9	0.0	40.0
***Tetramorium* sp. A**	16.7	**66.7**	**3.7**	**72.7**
Tree				
Camponotus fulvopilosus	6.0	100.0	1.0	0.0
Camponotus sp. A	28.0	71.4	3.1	0.0
Camponotus sp. B	4.0	50.0	1.0	0.0
Crematogaster sp. B	6.0	66.7	4.0	0.0
***Crematogaster* sp. C**	12.0	**33.3**	**5.0**	**100.0**
Lepisiota sp. B	4.0	100.0	3.0	0.0
Pheidole tenuinodis	0.0	0.0	0.0	100.0
Desert				
Ground				
Lepisiota sp. C	14.4	100.0	2.3	0.0
Ocymyrmex robustior	8.9	100.0	2.0	0.0
Tree				
Lepisiota sp. C	23.3	100.0	2.1	0.0
Lepisiota sp. D	11.7	85.7	2.1	0.0
Tapinoma subtile	5.0	100.0	2.0	0.0
Tetraponera ambigua	1.7	0.0	1.0	0.0

dal (quadratic model: $F_{2,8} = 0.73$, $R^2 = 0.67$, $P = 0.005$, Fig. 4).

Considering ground-foraging and arboreal assemblages separately, the dominance-richness relationship for ground-foraging ants was significant for all models, but was best described as logarithmic ($F_{1,10} = 19.4$, $R^2 = 0.66$, $P = 0.001$). However, no significant relationship was detected for arboreal ants (Fig. 4).

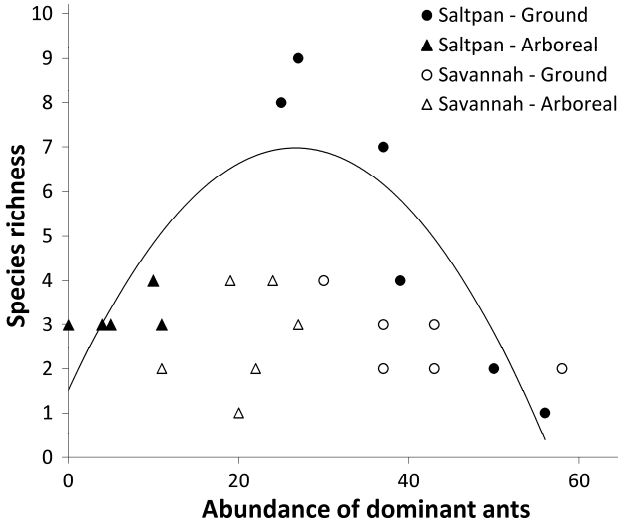

Fig. 4: Relationship between the abundance of dominant ants and total species richness (including dominant ant species) across saltpan and savannah habitats at Kuzikus Wildlife Reserve for ground and arboreal ants. Each data point represents total species richness and total abundance of dominant ants per baiting session (total of 15 baits for ground and 10 baits for arboreal). At the saltpan, this total includes a number of co-dominant species for ground ants. Regression line shows the quadratic relationship for the saltpan data only ($y = -0.008x^2 + 0.41x + 1.52$). Regressions of species richness at baits against abundance of dominant ant species showed no relationship for the total ant assemblage (ground and arboreal) for both habitats together (linear; $F_{1,21} = 0.33$, $R^2 = 0.02$, $P = 0.57$, logarithmic; $F_{1,21} = 1.13$, $R^2 = 0.05$, $P = 0.30$, quadratic; $F_{2,20} = 2.35$, $R^2 = 0.19$, $P = 0.12$) or for the savannah assemblage (linear; $F_{1,10} = 0.10$, $R^2 = 0.01$, $P = 0.76$, logarithmic; $F_{1,10} = 0.00$, $R^2 = 0.00$, $P = 0.99$, quadratic; $F_{2,9} = 0.66$, $R^2 = 0.13$, $P = 0.53$), however, the saltpan assemblage was significant under a quadratic model (linear; $F_{1,9} = 0.01$, $R^2 = 0.00$, $P = 0.94$, logarithmic; $F_{1,9} = 0.56$, $R^2 = 0.06$, $P = 0.47$, quadratic; $F_{2,8} = 0.73$, $R^2 = 0.67$, $P = 0.005$). Regressions of dominance-richness relationships performed separately on either the ground or arboreal assemblages showed a logarithmic relationship for the ground assemblage (linear; $F_{1,10} = 15.19$, $R^2 = 0.60$, $P = 0.003$, AIC = 51.26, quadratic; $F_{2,9} = 10.65$, $R^2 = 0.70$, $P = 0.004$, AIC = 49.78, logarithmic; $F_{1,10} = 19.4$, $R^2 = 0.66$, $P = 0.001$, AIC = 49.41), but no significant relationship for the arboreal assemblage (linear; $F_{1,9} = 0.05$, $R^2 = 0.01$, $P = 0.83$, logarithmic; $F_{1,9} = 0.21$, $R^2 = 0.02$, $P = 0.66$, quadratic; $F_{2,8} = 0.07$, $R^2 = 0.02$, $P = 0.93$).

Discussion

Ant species richness across three Namibian habitats was broadly similar to the diversity found by other researchers, although due to the use of different sampling methods there are no directly comparable studies for this region or for analogous habitats elsewhere (however, see Tab. 2). The diversity trends are consistent with the moderate ant diversity usually found in savannahs and grasslands, and the lower diversity in deserts (Tab. 2). We do not know if the species richness at the Kuzikus saltpan (23 spp.) is representative of similar habitats because most studies of saltpan nesting ants focus on the ecology of individual species (WHITFORD & al. 1981, DILLIER & WEHNER 2004, STECK & al. 2009) rather than overall diversity. Given that this was the most diverse habitat, it may be that saltpans represent a source of biodiversity in extreme arid environments, and should be made a priority habitat for ant sampling in future studies.

The species inventory presented here is likely to be incomplete due to the employment of a single sampling methodology. Extrapolation showed that our collecting captured between c. 64 - 79% of the ant species and doubling our sampling effort for baiting would have found between three to five additional species, taking a further nine days. Pitfall traps are a standard ant sampling method (CAMPOS & al. 2011), but mammals dug up traps in our sites so alternative strategies are required for future collecting. Direct hand searching is known to be a time-efficient and reliable technique for sampling savannah and desert ants (ROMERO & JAFFE 1989, HAWKES & FISHER 2011) and we predict more time spent using this method would yield an accurate assessment of total species richness (BESTELMEYER & al. 2000).

A few common ant species were found in multiple habitats. Despite being widely geographically separated the savannah and desert had the most similar ant assemblages, and although there were shared species for both strata there was more overlap in ants found on trees than on the ground. In contrast, similarity between ant assemblages in savannah and saltpan was accounted for by shared ground-foraging species. The saltpan and savannah sites were located close together within the same reserve, which may account for their shared ground species. The vegetation differed between these sites; the savannah had larger trees, mainly *Vachellia erioloba*, whereas the saltpan had smaller scrub vegetation, primarily *V. hebeclada*. The attributes of plant communities are known to influence associated ant species richness (RIBAS & al. 2003, BOULTON & al. 2005) as vegetation can regulate microclimate and other microhabitat characteristics (LONGINO & NADKARNI 1990, VASCONCELOS & al. 2008). The differences in vegetation could account for the distinction in the arboreal ant species between these two habitats. For the same reason, similarity of vegetation may also account for the shared arboreal species in the desert and savannah where *V. erioloba* was the most common tree species used for arboreal baits. Given the limitations of the data we cannot say with certainty that vegetation type and corresponding microhabitat differences drives assemblage similarity in these habitats. Other possible explanations for differences in ant diversity across these habitats include the effects of fire, grazing, precipitation, or substrate type (ANDERSEN 1991, BESTELMEYER & WIENS 2001, BOULTON & al. 2005, PAKNIA & PFEIFFER 2014).

Tab. 2: Ant species richness for Southern Africa and for comparable habitat types in other regions. Richness is ant species richness as reported by the study; numbers in parentheses are extrapolated estimates of species richness.

Country	Richness	Sampling Method	Reference
Multiple habitats			
Namibia	42 (59 - 73)	Baits and hand collecting	Figures 1 - 2
Namibia	44	Hand collecting	(HAWKES & FISHER 2011)
Namibia	36	Baits, hand collecting and pitfalls	(MARSH 1986b)
Namibia and South Africa	24	Pitfalls	(KOCH & VOHLAND 2004)
South Africa	45	Pitfalls, dig-sampling and quadrats	(LINDSEY & SKINNER 2001)
Saltpan / biological soil crusts			
Namibia	23 (28 - 30)	Baits and hand collecting	Figures 1 - 2
China	7	Quadrats	(LI & al. 2011)
Savannah / grassland			
Namibia	15 (19 - 26)	Baits and hand collecting	Figures 1 - 2
South Africa	69	Baits	(PARR 2008)
South Africa	164	Pitfalls	(PARR 2008)
South Africa	92	Pitfalls	(BISHOP & al. 2014)
South Africa	41 (39.71)	Pitfalls, dig-sampling and quadrats	(LINDSEY & SKINNER 2001)
Brazil	64 (62.5)	Baits	(VASCONCELOS & VILHENA 2006)
Brazil	84	Baits and hand collecting	(VASCONCELOS & al. 2008)
Australia	81	Pitfalls	(ANDERSEN 1991)
Desert			
Namibia (Riverbed and dune fields)	9 (12 - 17)	Baits and hand collecting	Figures 1 - 2
Namibia (Riverbed and dune fields)	15	Hand collecting	(HAWKES & FISHER 2011)
Namibia (Dune fields)	13	Baits, hand collecting and pitfalls	(MARSH 1986b)
Mongolia (Desert and steppe)	26	Baits and hand collecting	(PFEIFFER & al. 2003)
USA (Desert scrub and grassland)	32	Hand collecting and pitfalls	(ROJAS & FRAGOSO 2000)

The dominant and subordinate species in this study belong to the same genera as those in South African (PARR 2008) but not Australian (ANDERSEN 1992) savannah, indicating taxonomic consistency at a regional rather than cross-continental level. In the desert, the combined dominance criteria were not appropriate due to the patchy distribution of desert ants. Numerical criteria alone could provide a sufficient measure of dominance in deserts and do not require interspecific behavioural encounters to occur. There is a precedent for this approach, in North America species of *Monomorium*, *Pheidole* and *Crematogaster* are classified as dominants based solely on numerical criteria (ANDERSEN 1997). However, before changing the criteria, the underlying reasons for the failure to define dominant ants should be given consideration. Either the methods of sampling or criteria for defining dominance are not applicable to all habitats, or there are no true dominant species in deserts. Foraging activity of ground ants is strongly influenced by temperature and spatial heterogeneity (CROS & al. 1997). In open habitats like deserts there is low heterogeneity due to a lack of vegetation. This also causes high temperatures that may restrict ant foraging activity (PARR 2008) and could lead to the large number of empty baits in the desert. Additionally, ant species dominance corresponds with thermal tolerance (CROS & al. 1997, CERDÁ & al. 1998) so if dominant ants were foraging at night then they would not be detected by baiting carried out during the day. Rather than a failure to detect dominants the lack of aggressive interactions at baits could also be caused by the absence of true dominant ants from the desert habitat, as has been suggested by ARNAN & al. (2011) in reference to South African savannah ant assemblages (PARR 2008).

The relationship between the abundance of dominant ants and total species richness varied with habitat and strata. In the savannah there was no relationship, whereas in the saltpan dominant ants controlled species richness at baits. Previous studies have shown that the full unimodal relationship is only observed across a range of environments and sampling approaches (ANDERSEN 1992, PARR & al. 2005, PARR 2008, BACCARO & al. 2010). At the saltpan, the unimodal relationship exists due to the combined influence of arboreal and ground assemblages, which each occupy a different portion of the full relationship. At ar-

boreal baits there is a low abundance of dominants and low species richness (the ascending portion of the curve), while at ground baits there is a high abundance of dominant ants that show a negative relationship with species richness (the decreasing portion of the curve). This finding may be because arboreal habitats genuinely support fewer ant species (VASCONCELOS & al. 2008, CAMPOS & al. 2011) or may be an artefact of lower sampling intensity on trees than on the ground. Generally, in a diversity-dominance relationship the ascending portion of the curve corresponds with environmental stress and the descending part of the curve is attributed to competition (PARR & al. 2005, PARR 2008). Based on our results this suggests that low dominance levels in arboreal assemblages are linked to low habitat favourability. Species richness only appeared to be regulated by dominant ants at ground baits, where the relationship was logarithmic and could be because competition is more important in ground-foraging than arboreal ant assemblages. This contrasts with research in tropical forest that found competition was more intense between canopy ants than leaf-litter ants (YANOVIAK & KASPARI 2000). Competition is not the only factor in structuring local ant assemblages, which can be influenced by predators, parasitoids, habitat complexity and levels of disturbance, as well as trade-offs of dominance against thermal tolerance or food discovery (for review see CERDÁ & al. 2013). Finally, bait studies reflect only "momentary diversity" and may not represent assemblage or population level effects (ANDERSEN 1992, BACCARO & al. 2012). Significant further research is required to fully elucidate the factors influencing species richness and dominance in Namibian ant assemblages.

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References

ANDERSEN, A.N. 1991: Responses of ground-foraging ant communities to three experimental fire regimes in a savanna forest of tropical Australia. – Biotropica 23: 575-585.

ANDERSEN, A.N. 1992: Regulation of "momentary" diversity by dominant species in exceptionally rich ant communities of the Australian seasonal tropics. – The American Naturalist 140: 401-420.

ANDERSEN, A.N. 1997: Functional groups and patterns of organization in North American ant communities: a comparison with Australia. – Journal of Biogeography 24: 433-460.

ARNAN, X., GAUCHEREL, C. & ANDERSEN, A.N. 2011: Dominance and species co-occurrence in highly diverse ant communities: a test of the interstitial hypothesis and discovery of a three-tiered competition cascade. – Oecologia 166: 783-794.

BACCARO, F.B., DE SOUZA, J.L.P., FRANKLIN, E., LANDEIRO, V.L. & MAGNUSSON, W.E. 2012: Limited effects of dominant ants on assemblage species richness in three Amazon forests. – Ecological Entomology 37: 1-12.

BACCARO, F.B., KETELHUT, S. & DE MORAIS, J.W. 2010: Resource distribution and soil moisture content can regulate bait control in an ant assemblage in Central Amazonian forest. – Austral Ecology 35: 274-281.

BESTELMEYER, B.T. 2000: The trade-off between thermal tolerance and behavioural dominance in a subtropical South American ant community. – Journal of Animal Ecology 69: 998-1009.

BESTELMEYER, B.T., AGOSTI, D., ALONSO, L.E., BRANDAO, C., BROWN, W., DELABIE, J.H. & SILVESTRE, R. 2000: Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation. In: AGOSTI, D., MAJER, J.D., ALONSO, L.E. & SCHULTZ, T.R. (Eds.): Ants: standard methods for measuring and monitoring biodiversity. – Smithsonian Institution Press, Washington and London, pp. 122-144.

BESTELMEYER, B.T. & WIENS, J.A. 2001: Ant biodiversity in semiarid landscape mosaics: the consequences of grazing vs. natural heterogeneity. – Ecological Applications 11: 1123-1140.

BISHOP, T.R., ROBERTSON, M.P., VAN RENSBURG, B.J. & PARR, C.L. 2014: Elevation – diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa. – Journal of Biogeography: DOI: 10.1111/jbi.12368.

BOULTON, A.M., DAVIES, K.F. & WARD, P.S. 2005: Species richness, abundance, and composition of ground-dwelling ants in northern California grasslands: role of plants, soil, and grazing. – Environmental Entomology 34: 96-104.

CAMPBELL, H. 2013: Ant diversity, coexistence and myrmecophyte interactions in Namibia. – PhD Thesis, University of Reading, Reading, UK, 186 pp.

CAMPBELL, H., FELLOWES, M.D.E. & COOK, J.M. 2013a: Arboreal thorn-dwelling ants coexisting on the savannah ant-plant, *Vachellia erioloba*, use domatia morphology to select nest sites. – Insectes Sociaux 60: 373-382.

CAMPBELL, H., TOWNSEND, I., FELLOWES, M.D.E. & COOK, J.M. 2013b: Thorn-dwelling ants provide antiherbivore defence for camelthorn trees, *Vachellia erioloba*, in Namibia. – African Journal of Ecology 51: 590-598.

CAMPOS, R.I., VASCONCELOS, H.L., ANDERSEN, A.N., FRIZZO, T.L.M. & SPENA, K.C. 2011: Multi-scale ant diversity in savanna woodlands: an intercontinental comparison. – Austral Ecology 36: 983-992.

CERDÁ, X., ARNAN, X. & RETANA, J. 2013: Is competition a significant hallmark of ant (Hymenoptera: Formicidae) ecology? – Myrmecological News 18: 131-147.

CERDÁ, X., RETANA, J. & CROS, S. 1998: Critical thermal limits in Mediterranean ant species: trade-off between mortality risk and foraging performance. – Functional Ecology 12: 45-55.

CHAO, A., CHAZDON, R.L., COLWELL, R.K. & SHEN, T.-J. 2005: A new statistical approach for assessing similarity of species composition with incidence and abundance data. – Ecology Letters 8: 148-159.

COLWELL, R.K. 2013: EstimateS: statistical estimation of species richness and shared species from samples. Version 9. – <http://purl.oclc.org/estimates>, retrieved on 11 March 2013.

CRAWLEY, M.J. 2005: Statistics: an introduction using R. 2nd edition. – John Wiley & Sons Ltd, Chichester, UK, 342 pp.

CROS, S., CERDA, X. & RETANA, J. 1997: Spatial and temporal variations in the activity patterns of Mediterranean ant communities. – Ecoscience 4: 269-278.

DAVIDSON, D.W. 1998: Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. – Ecological Entomology 23: 484-490.

DILLIER, F.X. & WEHNER, R. 2004: Spatio-temporal patterns of colony distribution in monodomous and polydomous species of North African desert ants, genus *Cataglyphis*. – Insectes Sociaux 51: 186-196.

DUNN, R.R., SANDERS, N.J., FITZPATRICK, M.C., LAURENT, E., LESSARD, J.P., AGOSTI, D., ANDERSEN, A.N., BRUHL, C., CERDÁ, X., ELLISON, A.M., FISHER, B.L., GIBB, H., GOTELLI, N.J., GOVE, A.D., GUENARD, B., JANDA, M., KASPARI, M., LONGINO, J.T., MAJER, J.D., MCGLYNN, T.P., MENKE, S., PARR, C.L., PHILPOTT, S., PFEIFFER, M., RETANA, J., SUAREZ, A.V. & VASCONCELOS, H.L. 2007: Global ant (Hymenoptera: Formicidae) biodiversity and biogeography – a new database and its possibilities. – Myrmecological News 10: 77-83.

ECKARDT, F.D., SODERBERG, K., COOP, L.J., MULLER, A.A., VICKERY, K.J., GRANDIN, R.D., JACK, C., KAPALANGA, T.S. & HENSCHEL, J. 2013: The nature of moisture at Gobabeb, in the central Namib Desert. – Journal of Arid Environments 93: 7-19.

FELLERS, J.H. 1987: Interference and exploitation in a guild of woodland ants. – Ecology 68: 1466-1478.

FISHER, B.L. 2012: Ant genera of the Afrotropical region. Ant Course 2012. – Blurb, San Francisco, CA, USA, 40 pp.

GRIFFIN, R.E. 1998: Species richness and biogeography of non-acarine arachnids in Namibia. – Biodiversity & Conservation 7: 467-481.

HALAJ, J. & WISE, D.H. 2001: Terrestrial trophic cascades: How much do they trickle? – The American Naturalist 157: 262-281.

HAWKES, P.G. & FISHER, J.N. 2011: The distribution of ants in the Central Namib Desert. First edition. – AfriBUGS CC, Pretoria, South Africa, 58 pp.

HÖLLDOBLER, B. & WILSON, E.O. 1990: The ants. 1st edition. – Harvard University Press, Cambridge, MA, USA, 732 pp.

JANDA, M. & KONECNA, M. 2011: Canopy assemblages of ants in a New Guinea rain forest. – Journal of Tropical Ecology 27: 83-91.

KOCH, F. & VOHLAND, K. 2004: Ants along a southern African transect – a basis for biodiversity change monitoring (Insecta: Hymenoptera: Formicidae). – Zoosystematics and Evolution 80: 261-273.

KRÜGER, O. & MCGAVIN, G. 1998: The influence of ants on the guild structure of *Acacia* insect communities in Mkomazi Game Reserve, north-east Tanzania. – African Journal of Ecology 36: 213-220.

LANCASTER, J., LANCASTER, N. & SEELY, M. 1984: Climate of the central Namib Desert. – Madoqua 14: 5-61.

LI, X.R., JIA, R.L., CHEN, Y.W., HUANG, L. & ZHANG, P. 2011: Association of ant nests with successional stages of biological soil crusts in the Tengger Desert, Northern China. – Applied Soil Ecology 47: 59-66.

LINDSEY, P.A. & SKINNER, J.D. 2001: Ant composition and activity patterns as determined by pitfall trapping and other methods in three habitats in the semi-arid Karoo. – Journal of Arid Environments 48: 551-568.

LONGINO, J.T. & NADKARNI, N.M. 1990: A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a Neotropical montane forest. – Psyche 97: 81-94.

MARSH, A.C. 1986a: Ant species richness along a climatic gradient in the Namib Desert. – Journal of Arid Environments 11: 235-241.

MARSH, A.C. 1986b: Checklist, biological notes and distribution of ants in the central Namib Desert. – Madoqua 14: 333-344.

OLSON, D.M., DINERSTEIN, E., WIKRAMANAYAKE, E.D., BURGESS, N.D., POWELL, G.V.N., UNDERWOOD, E.C., D'AMICO, J.A., ITOUA, I., STRAND, H.E. & MORRISON, J.C. 2001: Terrestrial ecoregions of the world: a new map of life on earth. – BioScience 51: 933-938.

PAKNIA, O. & PFEIFFER, M. 2014: Niche-based processes and temporal variation of environment drive beta diversity of ants (Hymenoptera: Formicidae) in dryland ecosystems of Iran. – Myrmecological News 20: 15-23.

PARR, C.L. 2008: Dominant ants can control assemblage species richness in a South African savanna. – Journal of Animal Ecology 77: 1191-1198.

PARR, C.L. & GIBB, H. 2009 [2010]: Competition and the role of dominant ants. In: LACH, L., PARR, C.L. & ABBOTT, K.L. (Eds.): Ant ecology. – Oxford University Press, Oxford, UK, pp. 77-96.

PARR, C.L., SINCLAIR, B.J., ANDERSEN, A.N., GASTON, K.J. & CHOWN, S.L. 2005: Constraint and competition in assemblages: a cross-continental and modeling approach for ants. – The American Naturalist 165: 481-494.

PFEIFFER, M., CHIMEDREGZEN, L. & ULYKPAN, K. 2003: Community organization and species richness of ants (Hymenoptera: Formicidae) in Mongolia along an ecological gradient from steppe to Gobi desert. – Journal of Biogeography 30: 1921-1935.

R CORE DEVELOPMENT TEAM 2012: R: A language and environment for statistical computing. R Foundation for Statistical Computing. R Version 2.15.0. <http://www.R-project.org/>, retrieved on 26 September 2012.

RETANA, J. & CERDÁ, X. 2000: Patterns of diversity and composition of Mediterranean ground ant communities tracking spatial and temporal variability in the thermal environment. – Oecologia 123: 436-444.

RIBAS, C.R., SCHOEREDER, J.H., PIC, M. & SOARES, S.M. 2003: Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. – Austral Ecology 28: 305-314.

ROJAS, P. & FRAGOSO, C. 2000: Composition, diversity, and distribution of a Chihuahuan Desert ant community (Mapimi, Mexico). – Journal of Arid Environments 44: 213-227.

ROMERO, H. & JAFFE, K. 1989: A comparison of methods for sampling ants (Hymenoptera: Formicidae) in savannas. – Biotropica 21: 348-352.

SASSCAL 2014: Southern African Science Service Centre for Climate Change and Adaptive Land Management (SASSCAL) WeatherNet. – <http://www.biota-africa.org/weather/index.php>, retrieved on 12 June 2014.

SAVOLAINEN, R. & VEPSÄLÄINEN, K. 1988: A competition hierarchy among boreal ants: impact on resource partitioning and community structure. – Oikos 51: 135-155.

SCHMITZ, O.J., HAMBÄCK, P.A. & BECKERMAN, A.P. 2000: Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. – The American Naturalist 155: 141-153.

SHURIN, J.B., BORER, E.T., SEABLOOM, E.W., ANDERSON, K., BLANCHETTE, C.A., BROITMAN, B., COOPER, S.D. & HALPERN, B.S. 2002: A cross-ecosystem comparison of the strength of trophic cascades. – Ecology Letters 5: 785-791.

SIMMONS, R.E., GRIFFIN, M., GRIFFIN, R.E., MARAIS, E. & KOLBERG, H. 1998: Endemism in Namibia: patterns, processes and predictions. – Biodiversity & Conservation 7: 513-530.

SOLE, C.L., SCHOLTZ, C.H. & BASTOS, A.D.S. 2005: Phylogeography of the Namib Desert dung beetles *Scarabaeus* (*Pachysoma*) MACLEAY (Coleoptera: Scarabaeidae). – Journal of Biogeography 32: 75-84.

SOUTHGATE, R.I., MASTERS, P. & SEELY, M.K. 1996: Precipitation and biomass changes in the Namib Desert dune ecosystem. – Journal of Arid Environments 33: 267-280.

STECK, K., HANSSON, B.S. & KNADEN, M. 2009: Smells like home: desert ants, *Cataglyphis fortis*, use olfactory landmarks to pinpoint the nest. – Frontiers in Zoology 6: 1-8.

TEWS, J., BROSE, U., GRIMM, V., TIELBÖRGER, K., WICHMANN, M.C., SCHWAGER, M. & JELTSCH, F. 2004: Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. – Journal of Biogeography 31: 79-92.

THERON, L. 2010: Temporal and spatial composition of arboreal insects along the Omaruru River, Namibia. – Magister Scientiae Thesis, University of the Free State, Bloemfontein, South Africa, 119 pp.

VASCONCELOS, H.L., LEITE, M.F., VILHENA, J.M.S., LIMA, A.P. & MAGNUSSON, W.E. 2008: Ant diversity in an Amazonian savanna: relationship with vegetation structure, disturbance by fire, and dominant ants. – Austral Ecology 33: 221-231.

VASCONCELOS, H.L. & VILHENA, J.M.S. 2006: Species turnover and vertical partitioning of ant assemblages in the Brazilian Amazon: a comparison of forests and savannas. – Biotropica 38: 100-106.

WASSENAAR, T.D., HENSCHEL, J.R., PFAFFENTHALER, M.M., MUTOTA, E.N., SEELY, M.K. & PALLETT, J. 2013: Ensuring the future of the Namib's biodiversity: ecological restoration as a key management response to a mining boom. – Journal of Arid Environments 93: 126-135.

WHITFORD, W.G., DEPREE, D.J., HAMILTON, P. & ETTERSHANK, G. 1981: Foraging ecology of seed-harvesting ants, *Pheidole* spp. in a Chihuahuan Desert ecosystem. – The American Midland Naturalist 105: 159-167.

WITTMAN, S.E., SANDERS, N.J., ELLISON, A.M., JULES, E.S., RATCHFORD, J.S. & GOTELLI, N.J. 2010: Species interactions and thermal constraints on ant community structure. – Oikos 119: 551-559.

YANOVIAK, S.P. & KASPARI, M. 2000: Community structure and the habitat templet: ants in the tropical forest canopy and litter. – Oikos 89: 259-266.