

Mammalian herbivore movement into drought refugia has cascading effects on savanna insect communities

Matthew O. Trisos¹, Catherine L. Parr^{2,3,4}, Andrew B. Davies^{3,5}, Monica Leitner³,
Edmund C. February^{1,*}

¹Department of Biological Sciences, University of Cape Town, Cape Town, South Africa

²School of Environmental Sciences, University of Liverpool, Liverpool, UK

³Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

⁴School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Wits, South Africa

⁵Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA

*Correspondence to: Edmund C. February, Email: edmund.february@uct.ac.za

Abstract

1. Global climate change is predicted to increase the frequency of droughts, with major impacts on tropical savannas. It has been suggested that during drought, increased soil moisture and nutrients on termite mounds could benefit plants but it is unclear how such benefits could cascade to affect insect communities.
2. Here, we describe the effects of drought on vegetation structure, the cascading implications for invertebrates and how termite mounds influence such effects. We compared how changes in grass biomass affected grasshopper and ant diversity on and off *Macrotermes* mounds before (2012) and during a drought (2016) at two locations that experienced large variation in drought severity (Skukuza and Pretoriuskop) in the Kruger National Park, South Africa.
3. The 2013–2016 drought was not ubiquitous across the study site, with rainfall decreasing at Skukuza and being above average at Pretoriuskop. However, grass biomass declined at both locations. Grasshopper abundance decreased at droughted Skukuza both on and off mounds but decreased on mounds and increased off mounds at non-droughted Pretoriuskop. Ant abundance and species richness increased at Skukuza but remained the same on mounds and decreased off mounds at Pretoriuskop.
4. Our results demonstrate the spatially extensive effects of drought. Despite above average rainfall in 2016 at Pretoriuskop, grass biomass decreased, likely due to an influx of large mammalian herbivores from drought-affected areas. This decrease in grass biomass cascaded to affect grasshoppers and ants, further illustrating the effects of drought on invertebrates in adjoining areas with higher rainfall. Our grasshopper results also suggest that increased drought in savannas will contribute to overall declines in insect abundance. Moreover, our recorded increase in ant abundance was primarily in the form of increases in dominant species, illustrating how drought-induced shifts in relative abundance will likely influence ecosystem structure and function.
5. Our study highlights the phenomenon of spill-over drought effects and suggests rather than mitigating drought, termite mounds can instead become the focus for more intense grazing, with important consequences for insect communities.

KEYWORDS: ants, drought, grasshoppers, rainfall, savanna, termite mounds

1 INTRODUCTION

Drought frequency and intensity has increased in many regions globally with consequences for the structure and function of ecosystems (Bailing et al., 2018; Spinoni et al., 2014). Drought may, however, vary both spatially and temporally across the landscape with consequent differential effects. For example, animals can move from areas where rainfall is low to drought refugia with higher rainfall and therefore more resources (Roshier et al., 2002). The movement of animals to drought refugia has been documented for species as diverse as small mammals moving relatively large distances (Dickman et al., 1995; Letnic, 2003) to water birds responding to changes in the extent and condition of wetlands (Roshier et al., 2002; Wen et al., 2016).

In Africa, the effects of drought on savanna vegetation structure and large mammalian herbivores have been well documented (Knight, 1995; Staver et al., 2019; Thornley et al., 2020), but few studies have investigated how drought-induced changes in savanna vegetation structure might cascade to affect other groups, including insects (Deacon et al., 2019; Huberty & Denno, 2004). As herbaceous biomass in grassy ecosystems decreases with drought (Augustine, 2003; February et al., 2013), insect abundance is thought to decline (Bell, 1985; Hawkins & Holyoak, 1998; Prather et al., 2020; Wagner, 2020), although some groups have been shown to increase in abundance, such as the Banded Achaea *Achaea catella* moth, certain groups of wood borers (Anderegg et al., 2013; Smit & Bond, 2020) and termites (Ashton et al., 2019; Braack, 1995).

The potentially variable responses to environmental change for grasshoppers and ants motivate these as ideal candidates for investigating drought responses among savanna insect groups. With drought, grasshopper abundance and species richness can decrease because of increasing soil surface temperature (Prather et al., 2020) and reductions in grass and forb biomass (particularly affecting grass and mixed feeders; Lenhart et al., 2015). Post-diapause development in grasshoppers is directly related to soil surface temperatures with any changes in temperature affecting breeding success while reductions in grass and forb biomass result in reductions in available food and shelter (Lenhart et al., 2015; Prather et al., 2020; Van Wingerden et al., 1991). Decreases in grasshopper abundance and species richness during drought could, however, also reflect survival mechanisms; for example, drought-resistant egg pods could result in grasshopper generations skipping drought years by prolonging initial diapause (Ingrisch, 1986; Matthée, 1951). Ant responses to drought could be very different from other insect groups because ant colonies are comparatively sessile and movement tends to be local once nests are established (Banschbach & Herbers, 1999; McGlynn et al., 2004; Underwood & Fisher, 2006). Additionally, ants as a group are considered thermophilic (Kaspari et al., 2000) and may therefore be able to take advantage of the altered conditions. At our study site, ant species richness has been shown to decrease with decreasing grass biomass and rainfall (Parr et al., 2004). However, abundance, species richness and composition of ant communities are also strongly influenced by habitat openness (Gibb et al., 2019). With drought, where rainfall is below average and temperature above average, ground cover should decline well below what would normally be expected with low but average rainfall (Andersen, 2019; Staver et al., 2019; Wigley-Coetsee & Staver, 2020). Therefore, while predictions based on rainfall amount would suggest a decrease in ant

abundance and species richness, local changes to habitat openness and microclimate during drought could result in an overall increase in abundance and species richness.

In African savannas, the large epigeal mounds constructed by the termite genus *Macrotermes* are associated with increased quantities of organic and inorganic materials relative to the savanna matrix (Seymour et al., 2014; Turner, 2019) and are considered nutrient and moisture hotspots (Erpenbach et al., 2013; Erpenbach & Wittig, 2016; Gosling et al., 2012). The increase in nutrients and water availability on mounds results in distinct floral communities (Davies, Robertson, et al., 2014; Moe et al., 2009), that also have higher nutrient concentrations (Davies, Levick, et al., 2016; Grant & Scholes, 2006) and consequently are attractive to both insect and mammalian herbivores (Davies, Levick, et al., 2016; Davies, Van Rensburg, et al., 2016). Moreover, termite mounds have also been proposed to increase ecosystem resistance to drought through benefits to plants from enhanced soil moisture and nutrient enrichment (Ashton et al., 2019; Bonachela et al., 2015). Using a theoretical modelling approach for a semi-arid savanna similar to our study site, Bonachela et al. (2015) showed that the higher soil moisture on mounds could increase vegetation resistance to drought, providing islands of refugia for the revegetation of the surrounding matrix after drought. There has, however, been little empirical testing of this phenomenon overall, and no assessment related to termite mounds acting as drought refugia for insect communities specifically.

Despite several studies demonstrating the high abundance and diversity of insects in savanna systems, faunal research on termite mounds has largely focused on large mammals rather than insects (Braack & Kryger, 2003; Davies, Levick, et al., 2016; Gandar, 1982). Recent research has, however, shown that there is greater insect abundance and species diversity on mounds relative to the savanna matrix (Leitner et al., 2020), and that during the wet season (when insects are most active), insects can consume more mound vegetation biomass than large mammalian herbivores (Davies, Van Rensburg, et al., 2016). However, while grasshoppers are more abundant on nutrient-rich mounds than in the savanna matrix, species richness and assemblage composition between mounds and the matrix does not differ (Leitner et al., 2020). In contrast, ant assemblage composition does vary between mounds and the matrix possibly because of an increase in mammalian herbivory on mounds (Leitner et al., 2020).

In African savannas, however, drought is rarely ubiquitous across the landscape and several recent studies have shown that large mammalian grazers will move from droughted areas with decreased herbaceous biomass to areas where rainfall and grass biomass are higher (Abraham et al., 2019; Staver et al., 2019). In contrast to Bonachela et al.'s (2015) suggestion that mounds create refugia for vegetation during and after drought, we test an alternative hypothesis: during drought, preferential heavy grazing by large mammals intensifies on mounds (Davies, Levick, et al., 2016), thereby exacerbating the effects of drought, resulting in an overall greater decrease in grass biomass on mounds relative to the savanna matrix. However, we predicted declines in grass biomass on and off termite mounds at both droughted areas and drought refugia in response to declining rainfall and increased mammalian herbivory, respectively (Abraham et al., 2019; Staver et al., 2019). Declines in grass biomass were predicted to have consequences for insects with grasshopper abundance decreasing and ant abundance increasing. Here, we evaluate these hypotheses in a large African national park after 4 years of above average rainfall, in 2012, and after 4 years of drought, in 2016.

2 MATERIALS AND METHODS

2.1 Description of the study site

The study took place at two locations in the southern region of the Kruger National Park, South Africa in January 2012 and February 2016. The first of these locations was 12 km southwest of Skukuza village (-25.045417, 31.509533) and the second approximately 4.5 km southeast of Pretoriuskop rest camp (-25.207050, 31.281683). Mean annual rainfall at Skukuza is 588 mm and at Pretoriuskop is 707 mm, although interannual variation is significant (SANParks Scientific Services). Rainfall for 2012 was higher than average for both Skukuza (847 mm) and Pretoriuskop (852 mm). The 4-year MAP from 2013 to 2016 was below average at Skukuza (349 mm) and Pretoriuskop (649 mm). Drought in tropical savanna is, however, often not ubiquitous across the landscape and in 2016, rainfall was the lowest since 1985 for Skukuza (228 mm) and just above average for Pretoriuskop (753 mm). The consistently low, and below average, rainfall for the region over several years (2013–2016) makes this a drought period for the entire region.

At both locations, the soils are nutrient-poor granite or gneiss derived, typically shallow, acid sands (Venter et al., 2003). Grass assemblages on mounds are distinct both taxonomically and functionally, being more palatable to grazers than savanna matrix grasses while also having higher nutritional value and significantly lower C:N ratios (Davies, Robertson, et al., 2014). The vegetation at Skukuza is categorised as Granite Lowveld, with dominant woody species *Senegalia nigrescens* and *Combretum apiculatum* (Rutherford et al., 2006). The dominant grasses on mounds are *Panicum maximum* and *Urochloa mosambicensis* while *P. maximum*, *Pogonarthria squarrosa*, *Digitaria eriantha* and *Brachiaria nigropedata* dominate the matrix (Davies, Robertson, et al., 2014). The vegetation at Pretoriuskop is classified as Pretoriuskop Sour Bushveld, with woody species dominated by *Terminalia sericea* and *Dichrostachys cinerea* (Rutherford et al., 2006). Dominant grasses on mounds are *Cynodon dactylon* and *P. maximum* while dominant grasses in the matrix are *Setaria sphacelata*, *Loudetia simplex*, *P. squarrosa* and *Schizachyrium sanguineum* (Davies, Robertson, et al., 2014).

Both locations occur in an undulating landscape with distinct uplands and bottomlands where *Macrotermes* mounds are associated with hillcrests and upper sections of hillslopes (Davies, Levick, et al., 2014; Levick et al., 2010; Venter et al., 2003). The dominant *Macrotermes* species were *M. flaciger* and *M. natalensis* with mound densities ≥ 1 mound/ha (Davies, Levick, et al., 2014; Davies, Robertson, et al., 2014). Skukuza mound height and diameter were $2.31 \text{ m} \pm 0.15$ (mean and *SE*) and $10.73 \text{ m} \pm 0.42$, respectively, while Pretoriuskop was $1.57 \text{ m} \pm 0.07$ and $8.62 \text{ m} \pm 0.74$, respectively. Mammalian herbivore biomass on average is greater at Skukuza (1568 kg/km^2) than Pretoriuskop (838 kg/km^2 ; Davies, Levick, et al., 2016).

2.2 Grass biomass sampling

In all, 10 termite mounds spaced at least 50 m apart, and often over 100 m apart, were sampled at each of the two locations in January 2012 and February 2016. As both active and inactive mounds are vegetated at the study sites, and because the effects of mounds on soil properties are long lasting (Darlington, 1985; Erens et al., 2015), we did not discriminate between these two mound classes. Grass biomass was determined non-destructively using a Disc Pasture Meter (DPM; Bransby & Tainton, 1977). The DPM was dropped six times on the upper sections and 10 times on the lower sections of each mound. Sampling was stratified

by aspect, with eight drops on the north and eight on the south side of each mound. For each termite mound, a paired matrix plot (5 × 5 m) situated 30 m from the edge of the mound, and at least 30 m away from any neighbouring mounds, was also sampled by taking another 16 stratified DPM measurements, with each measurement at least 1 m apart. A calibration curve established for KNP was used to convert DPM settling height to above-ground grass biomass for both the 2012 and 2016 sampling periods:

$$(\sqrt{x} \times 2,260) - 3,019 = \text{kg} \cdot \text{ha}^{-1},$$

where x is the DPM settling height in cm (Trollope & Potgieter, 1986).

2.3 Insect sampling

Grasshoppers were sampled in January 2012 and February 2016 with 24 sweeps of a 40-cm diameter sweep net on mounds for both years and off mounds at 20 m from the base around the periphery of the mounds in 2012 and at the paired matrix plot in 2016. All life stages of grasshoppers were used for abundance scores, but only adults were used for species assemblage analyses because of taxonomic uncertainty in nymph identification (Leitner et al., 2020).

Epigeaic ants were sampled using pitfall traps containing a 50% water–dipropylene glycol solution. Ant sampling differed slightly between locations and years. In both 2012 and 2016, 10 mounds were sampled at Pretoriuskop and 6 mounds at Skukuza. In 2012, six evenly spaced traps were placed on the upper sections of each mound and six around the base with a further six traps equally spaced around the periphery at a distance of 20 m away from the mound. In 2016, five evenly spaced traps were placed on the upper sections of the mound and five around the base with a further 10 traps on the paired savanna matrix plot. Relative to the surrounding matrix, the entire termite mound from the centre to the base has higher nutrient levels that corresponds with unique vegetation assemblages (Davies, Robertson, et al., 2014). All the samples from both upper section and base traps were therefore pooled per mound, as in Leitner et al. (2020) to derive a single value per mound. The 2016 savanna matrix plot traps were arranged in two transects (spaced 4 m apart), each consisting of five traps spaced 2 m apart. The traps were left open for 5 days in 2012 and for 3 days in 2016. Species accumulation curves for both mound and matrix show no difference in sampling adequacy for the different number of trap days in the 2 years (60 trap days in 2012 and 30 in 2016, Figure S1). Despite the fewer sampling days in 2016, more species were sampled in 2016 than in 2012 and the comparable species accumulation curves (i.e. Skukuza mounds in 2012 vs. 2016) had similar slopes (Figure S1). Ants were identified to morphospecies for each genus with species names assigned where possible, and the number of individuals counted for each species. Army ants (*Aenictus* spp.) and Driver ants (*Dorylus* spp.) were not included in the analysis as these are nomadic with no fixed nesting sites and were therefore not deemed representative of the resident ant community. Voucher ant specimens are held at the Biological Sciences Department, University of Cape Town and the Zoology and Entomology Department, University of Pretoria.

2.4 Data analysis

Drought severity differed between Skukuza and Pretoriuskop and as a result statistical analyses were conducted for each location separately. Grass biomass at Skukuza was compared between the time periods using two-way analysis of variance (ANOVA) after data

were log-transformed to satisfy assumptions of normality and homogeneity of variance. At Pretoriuskop, grass biomass was compared using the Aligned Rank Transform (ART) for nonparametric factorial analysis of variance (Kay & Wobbrock, 2019). The predictor variables for both the ANOVA and ART grass biomass models included treatment (mound or matrix) and year (2012 or 2016), as well as the interactions between these variables.

Grasshopper and ant abundance (number of individuals) at Skukuza and ant abundance at Pretoriuskop were compared using generalised linear models (GLMs). The models were fitted using quasi-Poisson error distributions because the response variables were overdispersed count data (O'Hara & Kotze, 2010). Grasshopper abundance at Pretoriuskop and ant species richness at Skukuza and Pretoriuskop were compared using two-way ANOVA. Treatment (mound or matrix) and year (2012 or 2016), and the interactions between them, were predictor variables for all insect models. Model simplification, for all grass and insect models, was performed using backward step selection, with the highest-order non-significant interaction removed until the minimal adequate model was determined. For all grass and insect models, the year 2012 and mound were used as the baselines for the temporal (2012–2016) and treatment (mound–matrix) contrasts, respectively.

Both the 2012 and 2016 grasshopper species data were used to analyse species composition between the mound and matrix communities. However, because of the large proportion of nymphs sampled (81%) in 2012, for which absolute identifications were difficult, the 2012 and 2016 grasshopper data could not be collated and were instead analysed separately. At both Skukuza and Pretoriuskop, the effect of treatment (mound vs. matrix) during the drought year (2016) on the grasshopper species assemblage, and the effect of treatment (mound vs. matrix) interacting with year (2012 vs. 2016) on the ant species assemblages were evaluated using semi-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) with 1,000 permutations and using the Bray–Curtis dissimilarity index. To aid the interpretation of the ant PERMANOVA, canonical analysis of principal coordinates (CAP) ordination was also performed (Anderson & Willis, 2003). The canonical correlations were tested using 1,000 permutations. Similarity percentage (SIMPER) values, using the Bray–Curtis dissimilarity index, were calculated to evaluate the relative contributions of individual species to the discrimination between mound and matrix as well as between years. All statistical analyses were carried out in R version 3.3.3 (R Core Team, 2017), using the packages `ARTOOL`, `EMMEANS`, `GGPLOT2`, `HH` and `VEGAN`.

3 RESULTS

3.1 Effects at the high drought severity location, Skukuza

Grass biomass declined substantially at this location, with a fourfold decline observed on mounds and 3.5-fold decline in the matrix from 2012 to 2016 (two-way ANOVA, $F = 103.95$, $p < 0.001$). There was no clear difference in biomass between the mound and matrix plots in either year (Figure 1a).

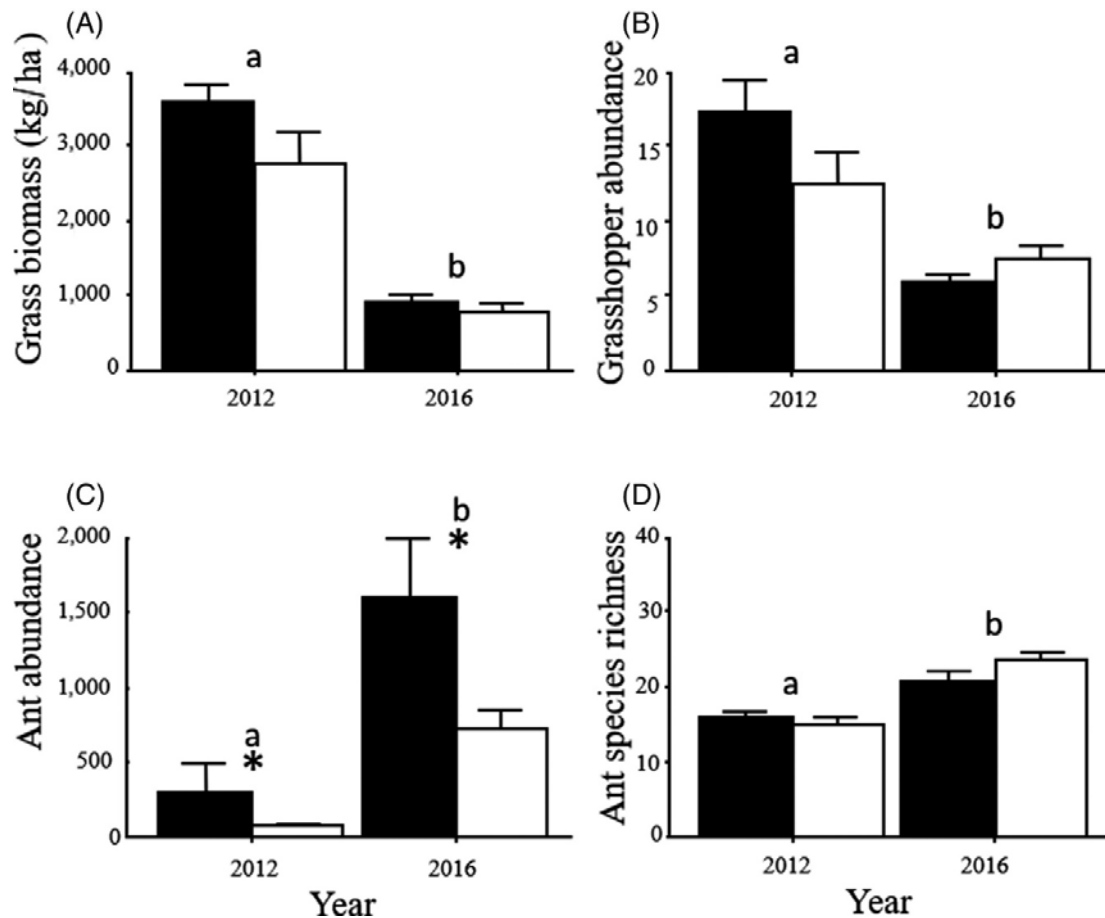


FIGURE 1. Means and standard error for (A) grass biomass, (B) grasshopper, (C) ant abundance and (D) ant species richness per mound and in the comparative matrix in 2012 and during the drought in 2016 at the high drought severity site, Skukuza. Letters indicate significant differences between sampling years while asterisks denote significant differences between mound (black bars) and matrix (white bars)

There was a 3.4-fold decrease in grasshopper abundance on the mounds and a 1.9-fold decrease in the matrix (GLM, $\beta = -1.15$, $t = -4.96$, $p < 0.001$), but there was no clear difference in grasshopper abundance between mound and matrix plots in either year (Figure 1b). There also was no clear difference in grasshopper assemblage composition between mound and matrix plots in 2012 (Leitner et al., 2020) or in 2016.

In contrast, there was a clear 5.7-fold increase in ant abundance per mound and a 10.9-fold increase in the matrix from 2012 to 2016 (GLM: year, $\beta = 1.85$, $t = 4.05$, $p = 0.001$; treatment, $\beta = -0.87$, $t = -2.54$, $p = 0.02$; Figure 1c). There was also a 1.3-fold increase in ant species richness per mound and a 1.6-fold increase in the matrix between 2012 and 2016 (two-way ANOVA, $F = 35.72$, $p < 0.001$; Figure 1d). There was, however, no clear difference in ant species richness on and off mounds in either year. Ant assemblage composition differed between years (2012 and 2016) and treatments (mound vs. matrix), with distinct mound and matrix assemblages sampled in each year (PERMANOVA: year, $F = 9.58$, $p = 0.001$; treatment, $F = 4.67$, $p = 0.001$). The interaction between year and treatment was also clear ($F = 2.23$, $p = 0.04$). The CAP analysis revealed that ant assemblages between treatments (mounds and matrix plots) were separated by the first CAP axis, and assemblage differences between 2012 and 2016 were separated by the second CAP axis ($F = 5.49$, $p = 0.001$; Figure 2a).

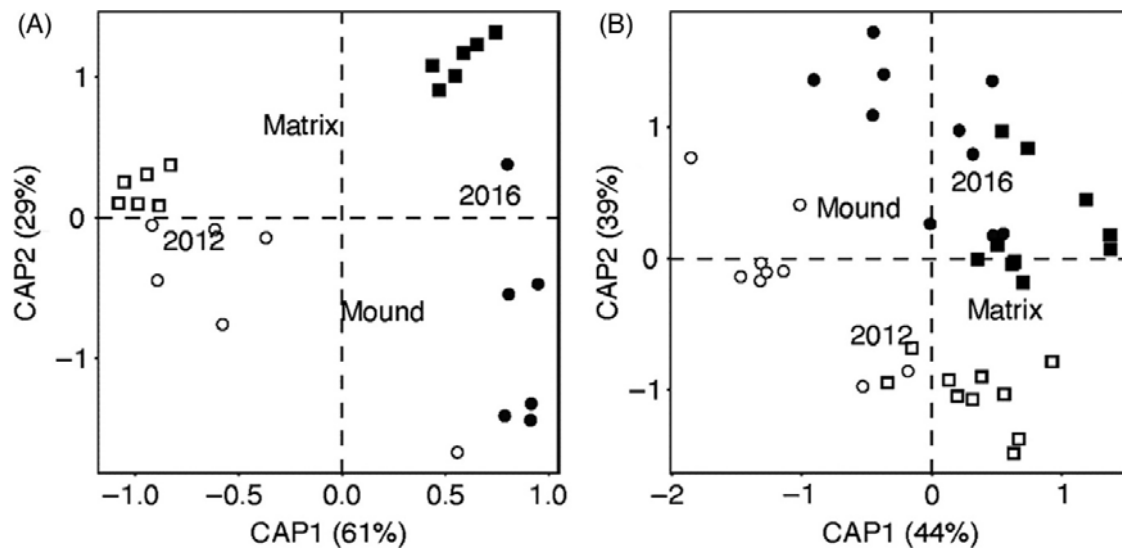


FIGURE 2. Constrained canonical analysis of principal coordinates (CAP) ordination of the ant species assemblage per mound and in the comparative matrix in 2012 and 2016 at (A) Skukuza and (B) Pretoriuskop. Treatment (Matrix and Mound) and year (2012 and 2016) centroids are shown. Percentages are the percentage variation explained by each axis. Mound samples, open circles 2012, solid circles 2016. Matrix samples, open squares 2012 solid squares 2016

Similarity percentage (SIMPER) results revealed that seven ant species in 2012 and four in 2016 accounted for 70% of the discrimination in ant assemblages between mound and matrix plots (Table 1). In both years, *Monomorium junodi* dominated mound assemblages, contributing to roughly half of the discrimination (Table 1). There was a 4.3-fold increase in *M. junodi* individuals per mound from 2012 to 2016, while a *Pheidole* spp. (*Pheidole* MOT-ZA03) increased 56-fold per mound from 2012 to 2016. Both these species occurred much less frequently off termite mounds, with a mean of <10 individuals per matrix plot in both years for both these species. Combined, *M. junodi* and the *Pheidole* spp. accounted for 54% of the cumulative change in 2016 (Table 1).

TABLE 1. Similarity percentage (SIMPER) results for the Skukuza ant assemblage per mound and comparative matrix for 2012 and 2016 including mean abundance and cumulative percentage of the species contribution to assemblage differences in community assembly

Species	Abundance mounds	Abundance matrix	Cumulative (%)
2012			
<i>Monomorium junodi</i>	214.17	0.34	34
<i>Monomorium</i> MOT-ZA04	11.83	21.67	43
<i>Pheidole</i> MOT-ZA07	9	2.33	49
<i>Ocymyrmex</i> MOT-ZA01	9	4.83	56
<i>Pheidole</i> MOT-ZA03	5.33	0.17	61
<i>Monomorium damarensis</i>	8.33	3.67	65
<i>Tapinoma</i> MOT-ZA01	0.5	5.17	69
<i>Pheidole</i> MOT-ZA02	2.33	3.67	72
2016			
<i>Monomorium junodi</i>	916.83	0	39
<i>Pheidole</i> MOT-ZA03	279.5	9.17	54
<i>Pheidole</i> MOT-ZA14	79	57.17	63
<i>Anoplolepis custodiens</i>	1.17	146.17	69
<i>Tapinoma</i> MOT-ZA01	6.83	74.83	74

3.2 Effects at the low drought severity location, Pretoriuskop

Grass biomass decreased to a lesser extent at this location, with a twofold decrease on the mounds and a 1.4-fold decrease in the matrix plots from 2012 to 2016 (two-way ART, $F = 19.17$, $p < 0.001$; Figure 3a). Again, there was no clear difference between mound and matrix plot biomass in either year.

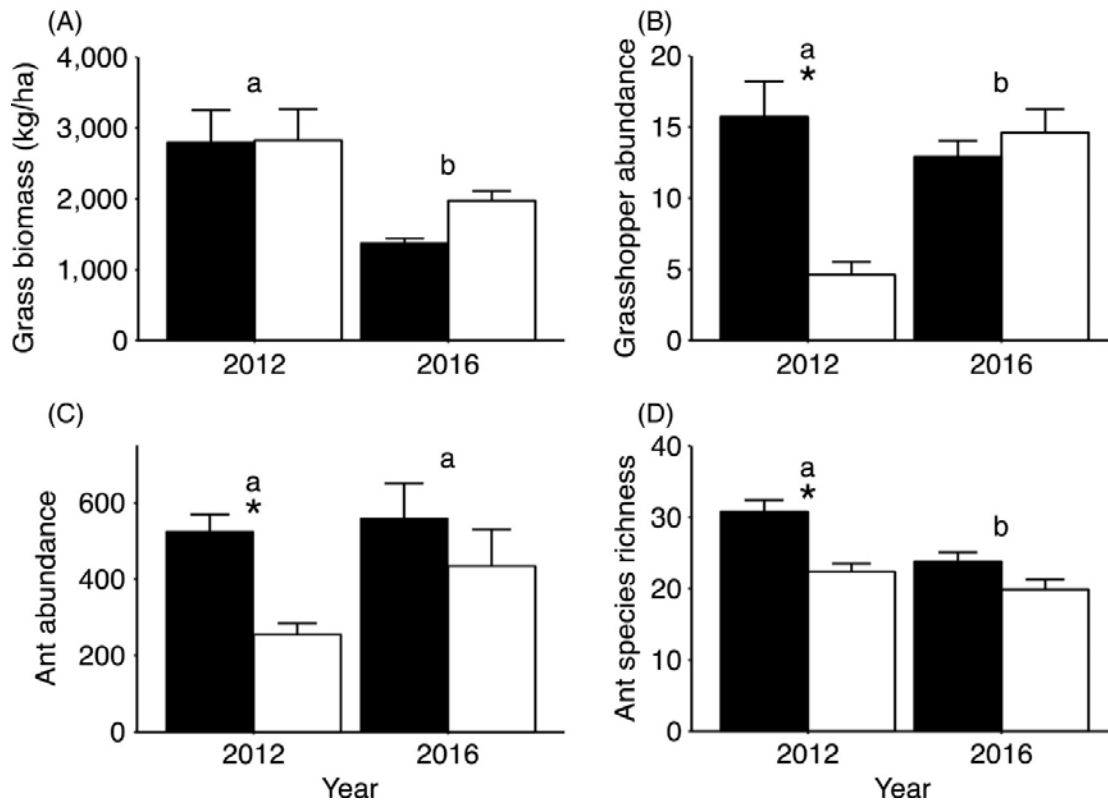


FIGURE 3. Means and standard error for (A) grass biomass, (B) grasshopper, (C) ant abundance and (D) ant species richness per mound and in the comparative matrix before (2012) and during the drought (2016) at the low drought severity site, Pretoriuskop. Letters indicate significant differences between sampling years while asterisks denote significant differences between mound (black bars) and matrix (white bars)

In 2012, termite mounds showed a 3.2-fold increase in grasshopper abundance compared to the savanna matrix; however, in 2016, there was no clear difference between mound and matrix plots (two-way ANOVA: treatment \times year, $F = 14.75$, $p < 0.001$, Figure 3b). The clear interaction between treatment and year was due to an increase in grasshopper abundance in the matrix and a decrease on the mounds from 2012 to 2016 (two-way ANOVA: treatment, $F = 7.95$, $p = 0.008$; year, $F = 4.67$, $p = 0.04$, Figure 3b). There was, however, no clear difference in mean species richness between the mounds (3 ± 0.56 species) and the matrix (3 ± 0.49 species) in 2016. While there was no difference in grasshopper assemblage composition between mound and matrix communities in 2012 (Leitner et al., 2020), a clear difference was observed in 2016 (PERMANOVA: $F = 2.46$, $p = 0.008$).

Mean ant abundance increased twofold on mounds relative to the matrix in 2012, but not in 2016 where no differences were observed (GLM: treatment, $\beta = -0.72$, $t = -2.88$, $p = 0.007$, Figure 3c). There was also no clear difference in mean ant abundance between years (Figure 3c). There was also an overall decrease in mean ant species richness from 2012 to

2016, primarily driven by a 1.3-fold decrease in species richness on mounds (two-way ANOVA: year, $F = 11.42$, $p = 0.002$; Figure 3d). More species were sampled on mounds than in matrix plots in 2012 (two-way ANOVA: treatment, $F = 19.14$, $p < 0.001$; Figure 3d), but not in 2016.

There was a significant difference in ant assemblage composition between mound and matrix plots and years (PERMANOVA: treatment, $F = 4.90$, $p = 0.001$; year, $F = 4.79$, $p = 0.001$). The interaction between year and treatment for ant species assemblage was also significant with distinct mound and matrix assemblages maintained across years ($F = 2.09$, $p = 0.02$). Mound and matrix species assemblages were separated by the first CAP axis, whereas the 2012 and 2016 assemblages were separated by the second CAP axis ($F = 3.92$, $p = 0.001$), with little change between mound and matrix assemblages between years (Figure 2b). Results of the SIMPER analysis showed that nine ant species in 2012 and eight in 2016 contributed at least 70% of the discrimination in ant species assemblage differences between mound and matrix plots (Table 2). These results also reveal a more even distribution of ant species at Pretoriuskop where three ant species accounted for the same amount of discrimination (39%) as a single species, *M. junodi*, did at Skukuza in both sampling years (Table 2). In contrast, the mean abundance of *M. junodi* on mounds at Pretoriuskop contributed only 16% and 11% to the cumulative change in 2012 and 2016, respectively (Table 2).

TABLE 2. Similarity percentage (SIMPER) results for the Pretoriuskop ant assemblage per mound and comparative matrix for 2012 and 2016 including mean abundance and cumulative percentage of the species contribution to assemblage differences in community assembly

Species	Abundance mounds	Abundance matrix	Cumulative (%)
2012			
<i>Monomorium junodi</i>	85	0	16
<i>Crematogaster</i> MOT-ZA04	84.7	15.3	29
<i>Monomorium</i> MOT-ZA04	79.1	76.4	39
<i>Pheidole</i> MOT-ZA11	39.4	3.5	47
<i>Pheidole</i> MOT-ZA08	31.2	5.1	53
<i>Anoplolepis custodiens</i>	23.3	5.4	58
<i>Pheidole</i> MOT-ZA07	26.4	8.1	62
<i>Monomorium albopilosum</i>	24.6	27	66
<i>Tapinoma</i> MOT-ZA01	15.4	25.4	70
2016			
<i>Anoplolepis custodiens</i>	111.9	105.9	18
<i>Monomorium</i> MOT-ZA04	95.9	91	30
<i>Monomorium junodi</i>	84.3	1	41
<i>Pheidole</i> MOT-ZA03	72.9	5.6	51
<i>Crematogaster</i> MOT-ZA03	2.7	43.8	57
<i>Tetramorium baufra</i>	13.2	39.5	63
<i>Crematogaster</i> MOT-ZA04	12.9	29.3	67
<i>Tapinoma</i> MOT-ZA01	20.1	22.1	70

4 DISCUSSION

Globally, climate model predictions suggest an increase in the frequency and intensity of droughts (Cai et al., 2014; Dai, 2013; Fauchereau et al., 2003). Drought has been shown to alter ecosystem functioning by changing vegetation structure and/or plant and animal

community assembly (Hawkins & Holyoak, 1998; Wagner, 2020), but effects on insect communities are almost entirely unknown. Termite mounds have been suggested to confer resistance to drought for vegetation Bonachela et al. (2015) and are central to savanna insect diversity because they create fine-scale environmental resource partitioning and host distinct communities of insects relative to matrix habitats (Davies, Levick, et al., 2014; Leitner et al., 2020). It is therefore pertinent to develop an understanding of how droughts might alter insect communities and whether termite mounds mitigate drought impacts for insects and other taxa.

In 2016, the drought in Kruger National Park was heterogeneous across the landscape, with some areas experiencing >50% rainfall reduction (e.g. Skukuza) while other areas received above average rainfall (e.g. Pretoriuskop). As forage quantity declined with a decrease in rainfall at locations such as Skukuza, bulk grazers, including zebra *Equus quagga*, wildebeest *Connochaetes taurinus* and buffalo *Syncerus caffer caffer*, migrated to areas where forage was more abundant, such as at Pretoriuskop (Abraham et al., 2019; Smit & Bond, 2020; Staver et al., 2019; Swemmer et al., 2018). As a result, buffalo density increased by ± 4.5 animals per square kilometre at the higher rainfall Pretoriuskop and decreased by ± 1.5 animals per square kilometre at the lower rainfall Skukuza (Staver et al., 2019). Despite no reduction in rainfall, our results indicate that the consequence of this increase in herbivory at Pretoriuskop was a significant decrease in grass biomass, with a proportionally greater decrease on mounds (51%) than in the savanna matrix (29%). The greater biomass decline on mounds corresponded with the higher nutritional value of mound grasses, which leads to mounds being preferred grazing patches, particularly in nutrient-poor savannas such as Pretoriuskop (Davies, Levick, et al., 2016; Davies, Robertson, et al., 2014).

Our results suggest that these patterns of mammalian herbivore movement and consequent grazing patterns during the drought cascaded to affect grasshopper and ant communities. The observed reduction in grass biomass in 2016 at the higher rainfall Pretoriuskop, combined with the decrease in grasshopper abundance on mounds and significant increase off mounds, suggests that grasshoppers moved away from mounds and into the matrix during the drought year as grass biomass decreased on the mounds with the increased mammalian herbivory. While we did not find any significant difference in the number of grasshopper species between the mound and matrix plots in 2016, contrary to the findings of Leitner et al. (2020), we did record different assemblages of grasshoppers between the two suggesting that some species were not able to move off the mounds. However, we were only able to identify a small proportion of the grasshoppers, due to the predominance of nymphs (61%), and therefore grasshopper species richness and composition require further investigation (Leitner et al., 2020).

For above-ground herbivorous insects, nutrient availability is a key driver of foraging decisions (Behmer, 2009; Lenhart et al., 2015), and mean annual precipitation (MAP) is an important determinant of forage quality (Branson, 2014; de Wysiecki et al., 2011). The lower MAP at Skukuza results in less leaching of soil nutrients and higher quality vegetation relative to Pretoriuskop (Davies, Robertson, et al., 2014; Leitner et al., 2020). Differences between mound and matrix soils at Skukuza are therefore not as pronounced as at higher rainfall Pretoriuskop, where matrix soils have lower nutrient concentrations than mounds (Davies, Robertson, et al., 2014). As a result, there was little difference between mound and matrix plots for grasshopper species richness and abundance at Skukuza either in 2012 (Leitner et al., 2020) or in 2016. Grasshopper abundance on and off mounds at Skukuza did, however, significantly decrease from 2012 to 2016 as grass biomass declined during the

drought, likely due to decreased rainfall and increased mammalian herbivory (Staver et al., 2019).

At higher rainfall Pretoriuskop in 2012, there was no significant difference in grass biomass between the mound and matrix plots, but there were significantly more grasshoppers on the nutrient-rich termite mounds than in the matrix, likely reflecting the preference of grasshoppers for the higher nutrient quality of grass species on mounds (Davies, Robertson, et al., 2014; Leitner et al., 2020). Grasshopper abundance, however, is not only positively correlated with grass nutrient quality but also with grass biomass due to increased food availability (resulting in more opportunities to forage and decreased searching time; Prendini et al., 1996; Zhu et al., 2020) and a reduction in predation pressure due to the increased aerial cover (Prendini et al., 1996; Zhu et al., 2020). Our results for grasshoppers are more complex than expected as we did not record a ubiquitous decline in grasshopper biomass with declining grass biomass during the drought, possibly because increases in soil nutrients also play a role in grasshopper distributions.

Grass biomass decreased most notably at the lower rainfall Skukuza in 2016 as a result of both drought and mammalian herbivory relative to higher rainfall Pretoriuskop, where there was no drought but an increase in mammalian herbivory (Abraham et al., 2019; Staver et al., 2019). The consequent change in vegetation structure at Skukuza resulted in ant species richness and abundance significantly increasing on mounds, likely as a result of the drought-induced reduction in grass biomass and increased bare ground (see Andersen, 2019). There was, however, no indication that either mound or matrix ant species extended their range with more bare ground, as the ant species assemblages did not homogenise between the mound and matrix plots. Overall, the positive response of mound and matrix ants to the drought suggests remarkable resilience and resistance akin to their resistance to other natural disturbances, such as fire and grazing (Andersen, 2019; Engle et al., 2008). At Pretoriuskop, ant abundance did not increase with the decrease in grass biomass either on the mounds or in the matrix in 2016. This suggests that the decrease in mound and matrix grass biomass at Pretoriuskop was not substantial enough to alter habitat structure to affect ant diversity as was the case at Skukuza. Moreover, distinct mound and matrix ant communities were maintained across years, suggesting that the reduction in biomass from the influx of large herbivores to Pretoriuskop during the drought had little influence on the ant communities.

While there was a general decrease in grasshopper abundance with a decline in grass biomass at lower rainfall Skukuza, ant abundance increased with the drought as the amount of bare ground increased. The increase in ants was, however, largely due to increases in *Anopolepis custodiens* and *Monomorium junodi*. Both *A. custodiens* and *M. junodi* have been shown to be behaviourally dominant at our study site (Parr, 2008; Sithole et al., 2010). Dominant ants behave aggressively to other ants when competing for food and may have outcompeted other species for resources (Parr, 2008). While ant abundance did not increase significantly at Pretoriuskop, there is an increase in dominant ants at both locations. The increase in dominance of aggressive ants at both high rainfall Pretoriuskop and low rainfall Skukuza suggests that the predicted increase in drought frequency may have negative effects on savanna insect diversity more broadly as ants have been shown to structure the broader invertebrate community via predation and competition (Parr et al., 2016).

5 CONCLUSIONS

Global change, especially in land use and cover, has been associated with a concerning decline in insect abundance and diversity (Cardoso et al., 2020). Our results show that predicted increases in drought frequency associated with anthropogenic change may well contribute to these declines in tropical savanna systems. Our results do, however, suggest different drought responses for two key invertebrate groups, with overall declines in grasshoppers and increases in ant abundance. While ant abundance may indeed increase with drought, our results indicate that this is primarily driven by dominant and aggressive species, which not only results in shifts in species composition but will have consequences for trophic interactions, ecosystem services and biodiversity. Our findings of contrasting ant and grasshopper assemblages on and off mounds across years reaffirm the importance of termite mounds as key resources for maintaining and contributing to insect diversity and abundance in nutrient-poor savannas.

Our study further illustrates the indirect influence of drought beyond the immediate area affected by a reduction in rainfall. While drought in tropical savannas is often not ubiquitous across landscapes, a key finding of our study is that the effects of drought on insect community structure can manifest in areas where drought did not occur (i.e. rainfall did not decrease) because of the movement of large mammalian herbivores into drought refugia. Moreover, rather than mitigating drought effects as suggested by Bonachela et al. (2015), our results suggest that termite mounds experience increased mammalian herbivory during drought that results in decreases in grass biomass with cascading effects on insect assemblages. The importance of examining the effects of global change on insect diversity, and the need for more research on changing insect communities beyond temperate northern latitudes cannot be overemphasised.

ACKNOWLEDGEMENTS

We thank South African National Parks for logistical support and permission to work in the Kruger National Park. Happy Mangena, Khensani Mkhonto and Velly Ndlovu helped with collecting data in the field. Mike Picker commented on earlier drafts. Funding was provided by the National Research Foundation Freestanding Innovation and Scarce Skills Development Fund (to M.O.T.), the Andrew W. Mellon Foundation and the DST-NRF Centre of Excellence for Invasion Biology.

AUTHORS' CONTRIBUTIONS

All authors conceived the ideas and designed the methodology; M.O.T., A.B.D. and M.L. collected the data; M.O.T. and E.C.F. analysed the data; E.C.F. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

REFERENCES

Abraham, J. O., Hempsen, G. P., & Staver, A. C. (2019). Drought-response strategies of savanna herbivores. *Ecology and Evolution*, 9, 7047– 7056.
<https://doi.org/10.1002/ece3.5270>

- Anderegg, W. R., Kane, J. M., & Anderegg, L. D. (2013). Consequences of widespread tree mortality triggered by drought and temperature stress. *Nature Climate Change*, 3, 30–36. <https://doi.org/10.1038/nclimate1635>
- Andersen, A. N. (2019). Responses of ant communities to disturbance: Five principles for understanding the disturbance dynamics of a globally dominant faunal group. *Journal of Animal Ecology*, 88, 350–362. <https://doi.org/10.1111/1365-2656.12907>
- Anderson, M. J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32–46.
- Anderson, M. J., & Willis, T. J. (2003). Canonical analysis of principal coordinates: A useful method of constrained ordination for ecology. *Ecology*, 84, 511–525. [https://doi.org/10.1890/0012-9658\(2003\)084\[0511:CAOPCA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2003)084[0511:CAOPCA]2.0.CO;2)
- Ashton, L. A., Griffiths, H. M., Parr, C. L., Evans, T. A., Didham, R. K., Hasan, F., Teh, Y. A., Tin, H. S., Vairappan, C. S., & Eggleton, P. (2019). Termites mitigate the effects of drought in tropical rainforest. *Science*, 363, 174. <https://doi.org/10.1126/science.aau9565>
- Augustine, D. J. (2003). Long-term, livestock-mediated redistribution of nitrogen and phosphorus in an East African savanna. *Journal of Applied Ecology*, 40, 137–149. <https://doi.org/10.1046/j.1365-2664.2003.00778.x>
- Bailing, M., Zhiyong, L., Cunzhu, L., Lixin, W., Chengzhen, J., Fuxiang, B., & Chao, J. (2018). Temporal and spatial heterogeneity of drought impact on vegetation growth on the Inner Mongolian Plateau. *The Rangeland Journal*, 40, 113–128. <https://doi.org/10.1071/RJ16097>
- Banschbach, V. S., & Herbers, J. M. (1999). Nest movements and population spatial structure of the forest ant *Myrmica punctiventris* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America*, 92, 414–423. <https://doi.org/10.1093/aesa/92.3.414>
- Behmer, S. T. (2009). Insect herbivore nutrient regulation. *Annual Review of Entomology*, 54, 165–187. <https://doi.org/10.1146/annurev.ento.54.110807.090537>
- Bell, H. (1985). Seasonal variation and the effects of drought on the abundance of arthropods in savanna woodland on the Northern Tablelands of New South Wales. *Australian Journal of Ecology*, 10, 207–221. <https://doi.org/10.1111/j.1442-9993.1985.tb00884.x>
- Bonachela, J. A., Pringle, R. M., Sheffer, E., Coverdale, T. C., Guyton, J. A., Caylor, K. K., Levin, S. A., & Tarnita, C. E. (2015). Termite mounds can increase the robustness of dryland ecosystems to climatic change. *Science*, 347, 651. <https://doi.org/10.1126/science.1261487>
- Braack, L. (1995). Seasonal activity of savanna termites during and after severe drought. *Koedoe*, 38, 73–82. <https://doi.org/10.4102/koedoe.v38i1.307>
- Braack, L., & Kryger, P. (2003). Insects and savanna heterogeneity. In J. T. Du Toit, K. H. Rogers, & H. C. Biggs (Eds.), *The kruger experience: Ecology and management of savanna heterogeneity* (pp. 263–275). Island Press.

- Bransby, D. I., & Tainton, N. M. (1977). The disc pasture meter: Possible applications in grazing management. *Proceedings of the Annual Congresses of the Grassland Society of Southern Africa*, 12, 115– 118. <https://doi.org/10.1080/00725560.1977.9648818>
- Branson, D. H. (2014). Influence of a large late summer precipitation event on food limitation and grasshopper population dynamics in a northern Great Plains grassland. *Environmental Entomology*, 37, 686– 695. [https://doi.org/10.1603/0046-225X\(2008\)37\[686:IOALLS\]2.0.CO;2](https://doi.org/10.1603/0046-225X(2008)37[686:IOALLS]2.0.CO;2)
- Cai, W., Borlace, S., Lengaigne, M., van Rensch, P., Collins, M., Vecchi, G., Timmermann, A., Santoso, A., McPhaden, M. J., Wu, L., England, M. H., Wang, G., Guilyardi, E., & Jin, F.-F. (2014). Increasing frequency of extreme El Niño events due to greenhouse warming. *Nature Climate Change*, 4, 111. <https://doi.org/10.1038/nclimate2100>
- Cardoso, P., Barton, P. S., Birkhofer, K., Chichorro, F., Deacon, C., Fartmann, T., Fukushima, C. S., Gaigher, R., Habel, J. C., Hallmann, C. A., Hill, M. J., Hochkirch, A., Kwak, M. L., Mammola, S., Ari Noriega, J., Orfinger, A. B., Pedraza, F., Pryke, J. S., Roque, F. O., ... Samways, M. J. (2020). Scientists' warning to humanity on insect extinctions. *Biological Conservation*, 242, 108426. <https://doi.org/10.1016/j.biocon.2020.108426>
- Dai, A. (2013). Increasing drought under global warming in observations and models. *Nature Climate Change*, 3, 52– 58. <https://doi.org/10.1038/nclimate1633>
- Darlington, J. P. E. C. (1985). Lenticular soil mounds in the Kenya highlands. *Oecologia*, 66, 116– 121. <https://doi.org/10.1007/BF00378562>
- Davies, A. B., Levick, S. R., Asner, G. P., Robertson, M. P., van Rensburg, B. J., & Parr, C. L. (2014). Spatial variability and abiotic determinants of termite mounds throughout a savanna catchment. *Ecography*, 37, 852– 862. <https://doi.org/10.1111/ecog.00532>
- Davies, A. B., Levick, S. R., Robertson, M. P., van Rensburg, B. J., Asner, G. P., & Parr, C. L. (2016). Termite mounds differ in their importance for herbivores across savanna types, seasons and spatial scales. *Oikos*, 125, 726– 734. <https://doi.org/10.1111/oik.02742>
- Davies, A. B., Robertson, M. P., Levick, S. R., Asner, G. P., van Rensburg, B. J., & Parr, C. L. (2014). Variable effects of termite mounds on African savanna grass communities across a rainfall gradient. *Journal of Vegetation Science*, 25, 1405– 1416. <https://doi.org/10.1111/jvs.12200>
- Davies, A. B., Van Rensburg, B. J., Robertson, M. P., Levick, S. R., Asner, G. P., & Parr, C. L. (2016). Seasonal variation in the relative dominance of herbivore guilds in an African savanna. *Ecology*, 97, 1618– 1624. <https://doi.org/10.1890/15-1905.1>
- de Wysiecki, M. L., Arturi, M., Torrusio, S., & Cigliano, M. M. (2011). Influence of weather variables and plant communities on grasshopper density in the Southern Pampas, Argentina. *Journal of Insect Science*, 11, 1– 14. <https://doi.org/10.1673/031.011.10901>
- Deacon, C., Samways, M. J., & Pryke, J. S. (2019). Aquatic insects decline in abundance and occupy low-quality artificial habitats to survive hydrological droughts. *Freshwater Biology*, 64, 1643– 1654. <https://doi.org/10.1111/fwb.13360>

- Dickman, C., Predavec, M., & Downey, F. (1995). Long-range movements of small mammals in arid Australia: Implications for land management. *Journal of Arid Environments*, 31, 441– 452. [https://doi.org/10.1016/S0140-1963\(05\)80127-2](https://doi.org/10.1016/S0140-1963(05)80127-2)
- Engle, D. M., Fuhlendorf, S. D., Roper, A., & Leslie Jr., D. M. (2008). Invertebrate community response to a shifting mosaic of habitat. *Rangeland Ecology & Management*, 61, 55– 62. <https://doi.org/10.2111/06-149R2.1>
- Erens, H., Boudin, M., Mees, F., Mujinya, B. B., Baert, G., Van Strydonck, M., Boeckx, P., & Van Ranst, E. (2015). The age of large termite mounds—radiocarbon dating of *Macrotermes falciger* mounds of the Miombo woodland of Katanga, DR Congo. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 435, 265– 271. <https://doi.org/10.1016/j.palaeo.2015.06.017>
- Erpenbach, A., Bernhardt-Römermann, M., Wittig, R., Thiombiano, A., & Hahn, K. (2013). The influence of termite-induced heterogeneity on savanna vegetation along a climatic gradient in West Africa. *Journal of Tropical Ecology*, 29, 11– 23. <https://doi.org/10.1017/S0266467412000703>
- Erpenbach, A., & Wittig, R. (2016). Termites and savannas—an overview on history and recent scientific progress with particular respect to West Africa and to the genus *Macrotermes*. *Flora Vegetatio Sudano-Sambesica*, 19, 35– 51. <https://doi.org/10.21248/fvss.19.34>
- Fauchereau, N., Trzaska, S., Rouault, M., & Richard, Y. (2003). Rainfall variability and changes in Southern Africa during the 20th century in the global warming context. *Natural Hazards*, 29, 139– 154.
- February, E. C., Higgins, S. I., Bond, W. J., & Swemmer, L. (2013). Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology*, 94, 1155– 1164. <https://doi.org/10.1890/12-0540.1>
- Gandar, M. (1982). The dynamics and trophic ecology of grasshoppers (Acridoidea) in a South African savanna. *Oecologia*, 54, 370– 378. <https://doi.org/10.1007/BF00380006>
- Gibb, H., Grossman, B. F., Dickman, C. R., Decker, O., & Wardle, G. M. (2019). Long-term responses of desert ant assemblages to climate. *Journal of Animal Ecology*, 88, 1549– 1563. <https://doi.org/10.1111/1365-2656.13052>
- Gosling, C. M., Cromsigt, J. P. G. M., Mpanza, N., & Olf, H. (2012). Effects of erosion from mounds of different termite genera on distinct functional grassland types in an African Savannah. *Ecosystems*, 15, 128– 139. <https://doi.org/10.1007/s10021-011-9497-8>
- Grant, C. C., & Scholes, M. C. (2006). The importance of nutrient hot-spots in the conservation and management of large wild mammalian herbivores in semi-arid savannas. *Biological Conservation*, 130, 426– 437. <https://doi.org/10.1016/j.biocon.2006.01.004>
- Hawkins, B. A., & Holyoak, M. (1998). Transcontinental crashes of insect populations? *The American Naturalist*, 152, 480– 484. <https://doi.org/10.1086/286184>

- Huberty, A. F., & Denno, R. F. (2004). Plant water stress and its consequences for herbivorous insects: A new synthesis. *Ecology*, 85, 1383– 1398. <https://doi.org/10.1890/03-0352>
- Ingrisch, S. (1986). The plurennial life cycles of the European Tettigoniidae (Insecta: Orthoptera). 3. The effect of drought and the variable duration of the initial diapause. *Oecologia*, 70, 624– 630. <https://doi.org/10.1007/BF00379915>
- Kaspari, M., Alonso, L., & O'Donnell, S. (2000). Three energy variables predict ant abundance at a geographical scale. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267, 485– 489.
- Kay, M., & Wobbrock, J. O. (2019). ARTool: Aligned rank transform for nonparametric factorial ANOVAs. R package version 0.10.6. <https://doi.org/10.5281/zenodo.594511>
- Knight, M. H. (1995). Drought-related mortality of wildlife in the southern Kalahari and the role of man. *African Journal of Ecology*, 33, 377– 394. <https://doi.org/10.1111/j.1365-2028.1995.tb01047.x>
- Leitner, M., Davies, A. B., Robertson, M. P., Parr, C. L., & van Rensburg, B. J. (2020). Termite mounds create heterogeneity in invertebrate communities across a savanna rainfall gradient. *Biodiversity and Conservation*, 29, 1427– 1441. <https://doi.org/10.1007/s10531-020-01943-5>
- Lenhart, P. A., Eubanks, M. D., & Behmer, S. T. (2015). Water stress in grasslands: Dynamic responses of plants and insect herbivores. *Oikos*, 124, 381– 390. <https://doi.org/10.1111/oik.01370>
- Letnic, M. (2003). The effects of experimental patch burning and rainfall on small mammals in the Simpson Desert, Queensland. *Wildlife Research*, 30, 547– 563. <https://doi.org/10.1071/WR02093>
- Levick, S. R., Asner, G. P., Chadwick, O. A., Khomo, L. M., Rogers, K. H., Hartshorn, A. S., Kennedy-Bowdoin, T., & Knapp, D. E. (2010). Regional insight into savanna hydrogeomorphology from termite mounds. *Nature Communications*, 1, 65. <https://doi.org/10.1038/ncomms1066>
- Matthée, J. J. (1951). The structure and physiology of the egg of *Locustana pardalina* (Walk.).
- McGlynn, T. P., Carr, R. A., Carson, J. H., & Buma, J. (2004). Frequent nest relocation in the ant *Aphaenogaster araneoides*: Resources, competition, and natural enemies. *Oikos*, 106, 611– 621.
- Moe, S. R., Mobæk, R., & Narmo, A. K. (2009). Mound building termites contribute to savanna vegetation heterogeneity. *Plant Ecology*, 202, 31. <https://doi.org/10.1007/s11258-009-9575-6>
- O'Hara, R. B., & Kotze, D. J. (2010). Do not log-transform count data. *Methods in Ecology and Evolution*, 1, 118– 122. <https://doi.org/10.1111/j.2041-210X.2010.00021.x>

Parr, C. L. (2008). Dominant ants can control assemblage species richness in a South African savanna. *Journal of Animal Ecology*, 77, 1191– 1198. <https://doi.org/10.1111/j.1365-2656.2008.01450.x>

Parr, C., Eggleton, P., Davies, A., Evans, T. A., & Holdsworth, S. (2016). Suppression of savanna ants alters invertebrate composition and influences key ecosystem processes. *Ecology*, 97, 1611– 1617. <https://doi.org/10.1890/15-1713.1>

Parr, C. L., Robertson, H. G., Biggs, H. C., & Chown, S. L. (2004). Response of African savanna ants to long-term fire regimes. *Journal of Applied Ecology*, 41, 630– 642. <https://doi.org/10.1111/j.0021-8901.2004.00920.x>

Prather, R. M., Castillioni, K., Welti, E. A., Kaspari, M., & Souza, L. (2020). Abiotic factors and plant biomass, not plant diversity, strongly shape grassland arthropods under drought conditions. Wiley Online Library.

Prendini, L., Theron, L.-J., Van der Merwe, K., & Owen-Smith, N. (1996). Abundance and guild structure of grasshoppers (Orthoptera: Acridoidea) in communally grazed and protected savanna. *African Zoology*, 31, 120– 130. <https://doi.org/10.1080/02541858.1996.11448403>

R Core Team. (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Retrieved from <https://www.R-project.org/>

Roshier, D., Robertson, A., & Kingsford, R. (2002). Responses of waterbirds to flooding in an arid region of Australia and implications for conservation. *Biological Conservation*, 106, 399– 411. [https://doi.org/10.1016/S0006-3207\(01\)00268-3](https://doi.org/10.1016/S0006-3207(01)00268-3)

Rutherford, M. C., Mucina, L., Lötter, M. C., Bredenkamp, G. J., Smit, J. H. L., Scott-Shaw, C. R., Hoare, D. B., Goodman, P. S., Bezuidenhout, H., Scott, L., Ellis, F., Powrie, L. W., Siebert, F., Mostert, T. H., Henning, B. J., Venter, C. E., Camp, K. G. T., Siebert, S. J., Matthews, W. S., ... Hurter, P. J. H. (2006). Savanna biome. In L. Mucina & M. C. Rutherford (Eds.), *The vegetation of South Africa, Lesotho and Swaziland* (pp. 439– 539). South African National Biodiversity Institute.

Seymour, C., Milewski, A., Mills, A., Joseph, G., Cumming, G., Cumming, D., & Mahlangu, Z. (2014). Do the large termite mounds of *Macrotermes* concentrate micronutrients in addition to macronutrients in nutrient-poor African savannas? *Soil Biology and Biochemistry*, 68, 95– 105. <https://doi.org/10.1016/j.soilbio.2013.09.022>

Sithole, H., Smit, I. P., & Parr, C. L. (2010). Preliminary investigations into a potential ant invader in Kruger National Park, South Africa. *African Journal of Ecology*, 48, 736– 743.

Smit, I. P., & Bond, W. J. (2020). Observations on the natural history of a savanna drought. *African Journal of Range & Forage Science*, 37, 119– 136. <https://doi.org/10.2989/10220119.2020.1723695>

Spinoni, J., Naumann, G., Carrao, H., Barbosa, P., & Vogt, J. (2014). World drought frequency, duration, and severity for 1951–2010. *International Journal of Climatology*, 34, 2792– 2804. <https://doi.org/10.1002/joc.3875>

- Staver, A. C., Wigley-Coetsee, C., & Botha, J. (2019). Grazer movements exacerbate grass declines during drought in an African savanna. *Journal of Ecology*, 107, 1482– 1491. <https://doi.org/10.1111/1365-2745.13106>
- Swemmer, A. M., Bond, W. J., Donaldson, J., Hempson, G. P., Malherbe, J., & Smit, I. P. (2018). The ecology of drought-a workshop report. *South African Journal of Science*, 114, 1– 3. <https://doi.org/10.17159/sajs.2018/5098>
- Thornley, R., Spencer, M., Zitzer, H. R., & Parr, C. L. (2020). Woody vegetation damage by the African elephant during severe drought at Pongola Game Reserve, South Africa. *African Journal of Ecology*, 58(4), 658– 673. <https://doi.org/10.1111/aje.12736>
- Trisos, M., Parr, C., Davies, A., Leitner, M., & February, E. (2021). Data from: Mammalian herbivore movement into drought refugia has cascading effects on savanna insect communities [Dataset]. *University of Cape Town*, <https://doi.org/10.25375/uct.1282653>
- Trollope, W., & Potgieter, A. (1986). Estimating grass fuel loads with a disc pasture meter in the Kruger National Park. *Journal of the Grassland Society of Southern Africa*, 3, 148– 152. <https://doi.org/10.1080/02566702.1986.9648053>
- Turner, J. S. (2019). Termites as mediators of the water economy of arid savanna ecosystems. P. D'Odorico, A. Porporato, & C. Wilkinson Runyan (Eds.), *Dryland ecohydrology* (pp. 401– 414). Springer International Publishing.
- Underwood, E. C., & Fisher, B. L. (2006). The role of ants in conservation monitoring: If, when, and how. *Biological Conservation*, 132, 166– 182. <https://doi.org/10.1016/j.biocon.2006.03.022>
- Van Wingerden, W., Musters, J., & Maaskamp, F. (1991). The influence of temperature on the duration of egg development in West European grasshoppers (Orthoptera: Acrididae). *Oecologia*, 87, 417– 423. <https://doi.org/10.1007/BF00634600>
- Venter, F. J., Scholes, R. J., & Eckhardt, H. C. (2003). The abiotic template and its associated vegetation pattern. In J. T. DuToit, K. H. Rogers, & H. C. Biggs (Eds.), *The Kruger Experience. Ecology and Management of savanna heterogeneity* (p. 519). Island Press.
- Wagner, D. L. (2020). Insect declines in the Anthropocene. *Annual Review of Entomology*, 65, 457– 480. <https://doi.org/10.1146/annurev-ento-011019-025151>
- Wen, L., Saintilan, N., Reid, J. R., & Colloff, M. J. (2016). Changes in distribution of waterbirds following prolonged drought reflect habitat availability in coastal and inland regions. *Ecology and Evolution*, 6, 6672– 6689. <https://doi.org/10.1002/ece3.2091>
- Wigley-Coetsee, C., & Staver, A. (2020). Grass community responses to drought in an African savanna. *African Journal of Range & Forage Science*, 37, 43– 52. <https://doi.org/10.2989/10220119.2020.1716072>
- Zhu, H., Nkurunziza, V., Wang, J., Guo, Q., Ruan, H., & Wang, D. (2020). Effects of large herbivore grazing on grasshopper behaviour and abundance in a meadow steppe. *Ecological Entomology*. <https://doi.org/10.1111/een.12919>