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Over what timeframes do desert ants respond to variation in climate and resources?

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ABSTRACT

In hot deserts, low, but highly variable precipitation drives resource availability, resulting in dramatic fluctuations of many consumer populations. However, the timeframes over which species respond to resource influxes are poorly understood. We pitfall-trapped ants in winter and spring over a twenty-two year period (1992-2013) in the Simpson Desert, central Australia. We asked: over what time-scale does ant activity (abundance and species richness) respond to climate (temperature and precipitation) and vegetation (plant species richness, cover and plant resources: flowering and seeding)? We considered both 'standard lags', i.e., the conditions at time *i* prior to sampling, and 'cumulative lags', i.e., the conditions prevailing over the entire period since time *i*. Ant species richness in samples responded positively to high winter temperatures, but negatively to high summer temperatures during the year prior to sampling. Short-term responses to precipitation were idiosyncratic, but longer-term responses were positive, peaking at fourteen months and probably driven indirectly through precipitation impacts on plant production. Responses to resource availability over long time frames (cumulative lags) were relatively stable, while short-term responses (standard lags) were stronger, but highly idiosyncratic, indicating that high cumulative resource availability promotes ant abundance and diversity, while short-term pulses in resource availability have less predictable impacts. The social structure of ants may allow greater flexibility in short-term responses to resource fluctuations, imparting greater long-term stability than non-social species.

Key words: abundance, Formicidae, long-term, precipitation, Simpson Desert, species richness, temperature, time lag, vegetation.

Introduction

The abundance and diversity of organisms usually fluctuate through time and space due to a variety of biotic and abiotic factors (Andrewartha and Birch 1984). The drivers of spatial variation in abundance at local to global scales are relatively well known (e.g., temperature) but temporal variation is less well understood (Rull 2014). The need for long-term studies to identify and understand the temporal drivers of abundance has become increasingly obvious as ecologists have begun to recognize the importance of natural and anthropogenic changes in ecosystems that occur over temporal scales from days (e.g., daily fluctuations in temperature) to months (e.g., seasonal variation), to years (e.g., cyclical events occurring over periods of several years). Further, changes in the abundances of species often lag behind changes in their environment, but few studies have investigated the importance of lag times, or the cumulative impact of environmental conditions on animal abundances (but see Monger, Sala *et al.* 2015 for a review of legacy effects in drylands). This gap in knowledge impedes our ability to predict responses to disturbances such as extreme weather events, which are expected to increase in frequency under climate change (Greenville, Wardle *et al.* 2012).

In many hot deserts, year-to-year variation in precipitation is immense, varying up to ten-fold (Morton, Smith *et al.* 2011; Schwinning and Sala 2004; Van Etten 2009). Water is the key limiting resource for most species in deserts (e.g., Dickman, Mahon *et al.* 1999; Greenville, Wardle *et al.* 2014; Pavey and Nano 2013; Whitford 2002), but for terrestrial consumers, precipitation also acts indirectly by limiting the availability of plant resources. Vegetation cover (e.g., spinifex, Nano, Clarke *et al.* 2012; Nguyen, Greenville *et al.* 2015) expands and populations of a range of vertebrate taxa, including rodents (Dickman, Greenville *et al.* 2010) and birds (Tischler, Dickman *et al.* 2013), irrupt at distinct lags ranging from two to ten months following heavy precipitation. However, other taxa, such as dasyurid marsupials (Dickman, Haythornthwaite *et al.* 2001; Greenville, Wardle *et al.* 2016) and dragon

lizards (Dickman, Letnic *et al.* 1999), show more muted responses. Studies investigating the responses of desert invertebrates to resource pulses suggest that the variety of responses reflects their taxonomic diversity, with both short and long-term responses evident (e.g., Kwok, Wardle *et al.* 2016; Langlands, Brennan *et al.* 2006; Palmer 2010; Popic and Wardle 2012).

Ants (Hymenoptera: Formicidae) are amongst the most abundant of animals, making up a large fraction of animal biomass in most terrestrial communities (King, Warren *et al.* 2013). Most ant species are ground-nesting and species inhabiting the soil are particularly important in arid ecosystems (Whitford 1996). Ants also perform a range of important ecosystem functions and represent an important food resource for a variety of vertebrates and invertebrates (Andersen 1995; Del Toro, Ribbons *et al.* 2012; Folgarait 1998). Pulses in the abundances of ants and other invertebrates might therefore drive fluctuations in populations of their predators (Kwok, Wardle *et al.* 2016). However, few studies have examined long-term changes in ant populations. Over a six-year sampling period, Kwok *et al.* (2016) showed that ant activity in the Simpson Desert was most strongly related to long-term rainfall (14 month lag) and temperature (11 month lag), increasing with rainfall and decreasing with temperature. Here, we examine lags in ant activity in the Simpson Desert at five sites over a much longer period: 22-years. The twenty-two year timeframe of this work, comparison of cumulative and standard lags (described below) and consideration of both climate and vegetation lags make this work unique from Kwok *et al.* (2016). We ask: over what time scale is the response of ant activity to climate (temperature and precipitation) and vegetation (plant species richness, cover and plant resources: flowering and seeding) strongest? We considered both 'standard lags', i.e., the conditions prevailing at time *i* prior to sampling, and 'cumulative lags', i.e., the conditions occurring over the entire period since time *i*. In the short term, ants may respond to environmental favourability by increasing activity; over longer time periods, worker numbers within existing nests may increase or the number of nests may increase. Correlations with short-term lags thus reflect changes in activity, while those over the longer term reflect changes in worker populations or increases in the abundance of nests.

Methods

Study site

The study was conducted at five sites within 10 km of "Main Camp" on Ethabuka Reserve (23°46'S, 138°28'E) in the Simpson Desert, central Australia (Fig. 1). The landscape is dominated by parallel sand dunes up to 10 m in height and separated by 0.6 – 1 km that run in a north-north-west to south-south-easterly direction (Purdie 1984). Each site included a crest and swale sampling point to account for the gradient in cover of the dominant spinifex hummock grass, *Triodia basedowii* E. Pritz., and the

associated compositional differences in vegetation. While relatively open, dune crests have low, but variable, cover of grasses, ephemeral herbaceous plants, subshrubs and characteristically patchy cover of shrubs including *Acacia ligulata*, *Dodonaea viscosa*, *Crotalaria eremaea* and *Grevillea stenobotrya*. Dune swales have higher cover of spinifex, up to 60%, along with similar composition of grasses, forbs and scattered shrubs. Distinct patches of Georgina gidgee *Acacia georginae* woodlands ranging from 0.5 ha to 10 ha and lie on heavier clay soils (Wardle, Greenville *et al.* 2015). Daily temperatures in summer usually exceed 40°C; winter minima fall below 5°C (Purdie 1984). Rainfall in the region is highly variable in time and space (Greenville, Wardle *et al.* 2012), but average annual precipitation was 217 mm during the period of the study (range: 79 – 570 mm.yr^{-1}).

Ant sampling

Ants were collected over a twenty-two year period during the course of vertebrate trapping surveys between August 1992 and August 2013. For this study, we included sampling sessions carried out in spring (September, October or November) and winter (June, July or August) each year, where possible. This is a significant advance on Kwok *et al.* (2016), which examined different samples from the same sites collected over a six year period between 1999 and 2005 because the longer time period encompasses much greater variation in precipitation. Vertebrate pitfall traps were set in grids of 36 traps, each trap separated by 20 m, with the first line of six traps set along a dune crest and the sixth line set 100 m distant in the corresponding swale. A set of six invertebrate (wet) pitfall traps was placed in a grid of 2 × 3 (each trap separated by ~3 m) around one vertebrate trap on the dune crest and around another one, 100 m away in the swale (on the sixth line). Invertebrate pitfall traps were 40 mm diameter and 90 cm deep and collected surface-active species. They were filled with 3% formalin solution, then buried flush with the ground and generally left open for three consecutive days. On return to the laboratory, trap contents were transferred to 80% ethanol and ants were separated from other taxa, identified to morphospecies and counted under a dissecting microscope. A reference collection of morphospecies (Oliver and Beattie 1996) was identified to species by Alan Andersen (Charles Darwin University, Darwin). Because some traps were disturbed, abundance and species richness data were converted to individuals or species per trap for analysis.

Vegetation data

Vegetation cover and composition were sampled at six vertebrate trap locations, one per trap-line, distributed over the 1 ha vertebrate trapping grids. In a 5 m circular plot, centred on the trap, each plant species was identified and visual estimates of cover were recorded to the nearest 5%. To track changes in plant resources, flowering and seeding were scored on a scale of 1 – low to 5 - high, for each species. For each sampling location, plant species richness, total plant cover, total seed index, and total flowering index were calculated.
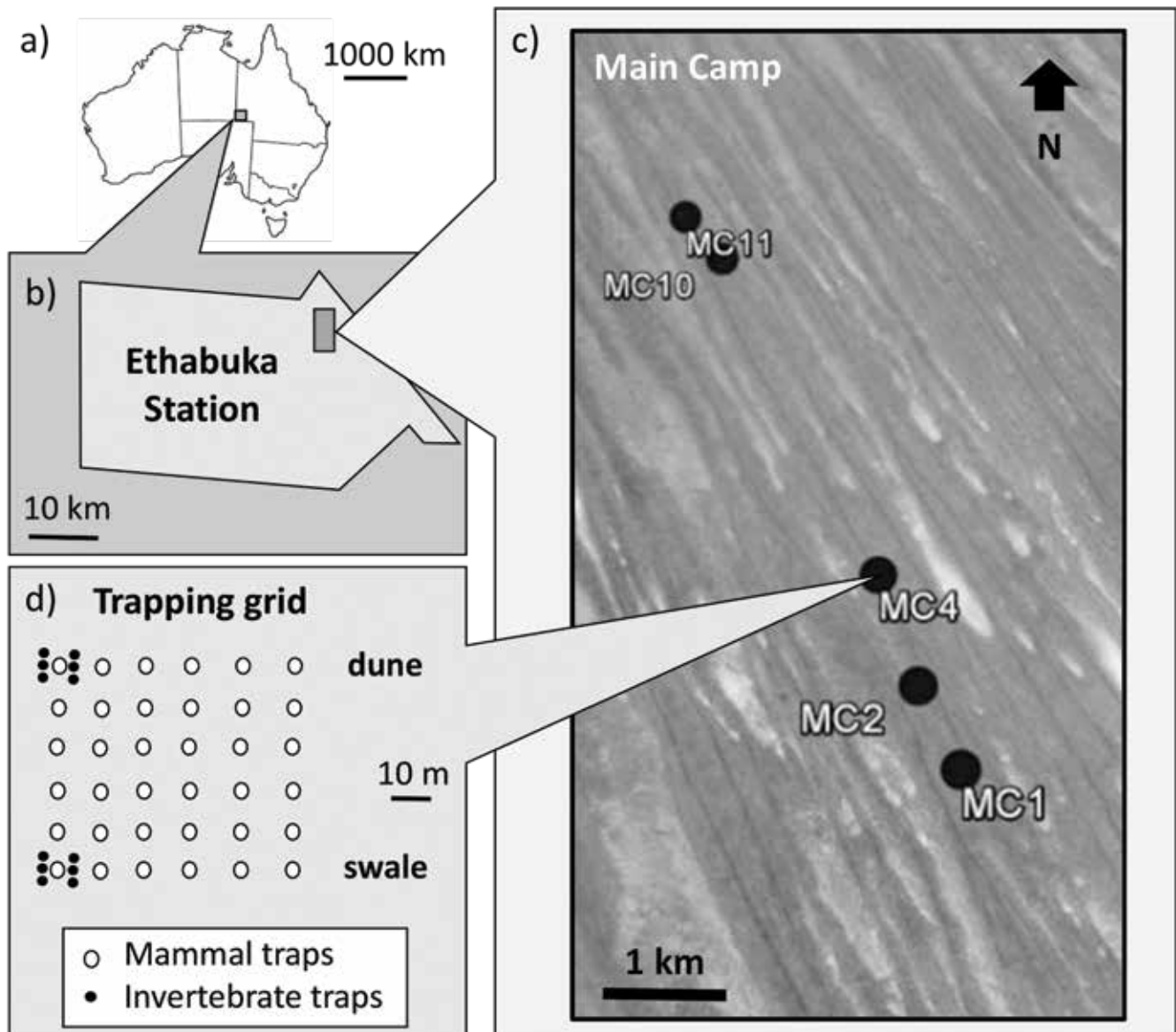
Figure 1: Location of study sites and layout of trapping grids: a) location of Ethabuka Reserve in Australia; b) location of "Main Camp" in Ethabuka; c) location of the five trapping grids near Main Camp, showing lines of dunes from GoogleEarth; and d) layout of the trapping grids in each site, showing mammal and invertebrate pitfall traps in dune and swale habitats.

Climate data

Climate data for the period of the study were taken from the Bureau of Meteorology weather stations at Glenormiston, Boulia, Birdsville, Marion Downs, Sandringham and Bedourie (BOM 2016). Data were extracted in lags of 1 to 18 days and 1 to 18 months prior to sampling, i.e., the four month precipitation lag data included the sum of precipitation in the four months prior to sampling. We extracted the following climate data: maximum daily (1 - 18 days) and monthly (1 – 18 months) temperature and minimum daily and monthly temperature and daily and monthly precipitation (also see Kwok, Wardle *et al.* 2016).

Statistical analyses

Relationships between ant variables (i.e., abundance and species richness of ants in pitfall traps) and lag variables for climate (precipitation and minimum and maximum temperature) and vegetation (plant species richness,

Triodia basedowii and other (non-*Triodia*) cover, flowering index and seeding index) were explored using Pearson's correlations. We tested both cumulative (i.e., sum(x_1:x_i)/count(x_1:x_i), where x_i is the climate or vegetation variable at lag time i) and non-cumulative (i.e., x_i; henceforth "standard") lags. Cumulative lags accounted for the average conditions in the time prior to sampling, while standard lags considered long-term responses to short-term events. Correlation rs for lags of between 1 day and 18 months were plotted.

Results

Correlations with climate lags

Relationships for standard lags were generally more idiosyncratic than those with cumulative lags. Abundance of ants in pitfall traps was not correlated with either

mean daily minimum or maximum temperatures at any cumulative or standard lag time (Figs 2a, b, c, d). Species richness was positively correlated with mean daily maximum temperature at standard lag times of up to three months and cumulative lag times of up to four months (Figs 2a, b), possibly reflecting the importance of winter temperatures, as sampling was conducted in winter and spring. At cumulative lag times of between five and twelve months and greater than 16 months, the correlation was negative, which may indicate a lasting negative impact of extreme summer temperatures. For standard lag times, correlations were again positive around a year prior to sampling, which may reflect long-term benefits of warmer winters. However, summer or winter temperatures are correlated among years, so correlations over time frames longer than one year may be an artefact of responses to short-term temperatures and should be interpreted with caution. Trends were similar for correlations between species richness and mean daily minimum temperatures for both standard and cumulative lags (Figs 2c, d).

Abundance was correlated with mean monthly precipitation at standard lag times of 2, 4, 8 and 9 months. For cumulative lag time, abundance was most strongly correlated at 9 months, although all correlations were significant between 4 and 18 months lag (Figs 2e, f). Species richness showed idiosyncratic correlations with precipitation at standard lags, being positive at 1, 2, 4, 7, 8 and 13 months and negative at 3, 6 and 18 months (Fig. 2e). Species richness was most strongly correlated with mean monthly precipitation with a cumulative lag time of 13 months, with positive correlations mostly above 9 months (Fig. 2f).

Correlations with vegetation lags

For standard lags, ant species richness was positively correlated with plant species richness at 3 and 6 months and negatively correlated at 12 and 13 months, while abundance was not correlated at any standard lag time (Fig. 2g). Both abundance and species richness of ants were positively correlated with plant species richness at cumulative lag times between approximately 2 and 13 months, with correlation coefficients peaking at 5 months for abundance and 6 months for species richness (Fig 2h).

Species richness was negatively correlated with *Triodia* cover at standard lags of 3 and 13 months, but not at any cumulative lag time (Figs 3a, b). Abundance was not correlated with *Triodia* cover at any time (Figs 3a, b). For standard lags, correlations between the cover of plants other than *Triodia* and ant abundance were negative at 11 months and for ant species richness, they were positive at 3 and 4 months (Fig. 4a). For cumulative lags, correlations between ant abundance and species richness and cover of other (non-*Triodia*) plants were weak and only significant for species richness at 5 and 6 months (Fig. 4b).

For standard lag times, ant abundance was positively correlated with *Triodia* flowering index at 1, 3 and 4 months, while species richness was positively correlated

at 6 and 8 months (Fig. 3c). Ant abundance was positively correlated with the flowering index of *Triodia* (Fig. 3d) at all cumulative lags, peaking at 6 months, while species richness was only correlated from around 10 months. For other plants, standard lag correlations with flowering index were significant for ant abundance at 2 months and species richness at 6 months (Fig. 4c). Correlations between flowering index and ant species richness were positive at all cumulative lag times, while ant abundance was correlated with other plant cover at cumulative lags up to 6 months (Fig. 4d).

Ant abundance was correlated positively with *Triodia* seeding index, peaking at 9 month cumulative lags and significant at 1, 4 and 6 month standard lags (Figs 3f, e). Although species richness was correlated with *Triodia* seeding index at 8 and 15 month standard lags, correlations were not significant at any cumulative lag (Figs 3e, f). Abundance responded positively to the seeding index of other plants at 5 and 17 months standard lags, while species richness showed positive correlations at 1, 3 and 6 month standard lags (Fig. 4e). Abundance and species richness responded very similarly to the seeding index of other plants, with positive correlations at lags between 1 and 7 months and *r* values highest at 4 month lags (Fig. 4f).

Discussion

To study the impact of changes in the environment on species, it is important that we test impacts over appropriate temporal and spatial scales. Here, we identify the temporal scales at which the activity of ants, a key component of animal biomass in most terrestrial communities, responds most strongly to climate and vegetation. We consider the influence of time lags in terms of both precipitation events (standard lags) and cumulative conditions (cumulative lags). We also identify differences and similarities in timeframes over which key measures of ant diversity - abundance and species richness in pitfall traps - respond to environmental fluctuations in a desert ecosystem.

Ant abundance showed little response to temperature, with correlations generally negative, but non-significant. Different ant species are active at different temperatures (Briese and Macauley 1981; Cros, Cerdá *et al.* 1997; Retana and Cerda 2000), but activity periods may shift through the day, rather than being significantly reduced under higher temperatures. This could result in abundances in pitfall traps (collected over a three day period) appearing similar despite differences in minimum or maximum temperatures. Although temperature also influences larval development rates, and thus might be expected to affect abundance within nests, ants can compensate for temperature changes by moving larvae to thermally suitable chambers (e.g., Roces and Núñez 1989). In contrast to abundance, ant species richness responded at both short and long lags, displaying a cyclical response to seasons. For shorter lag times (less than three months), species richness increased with
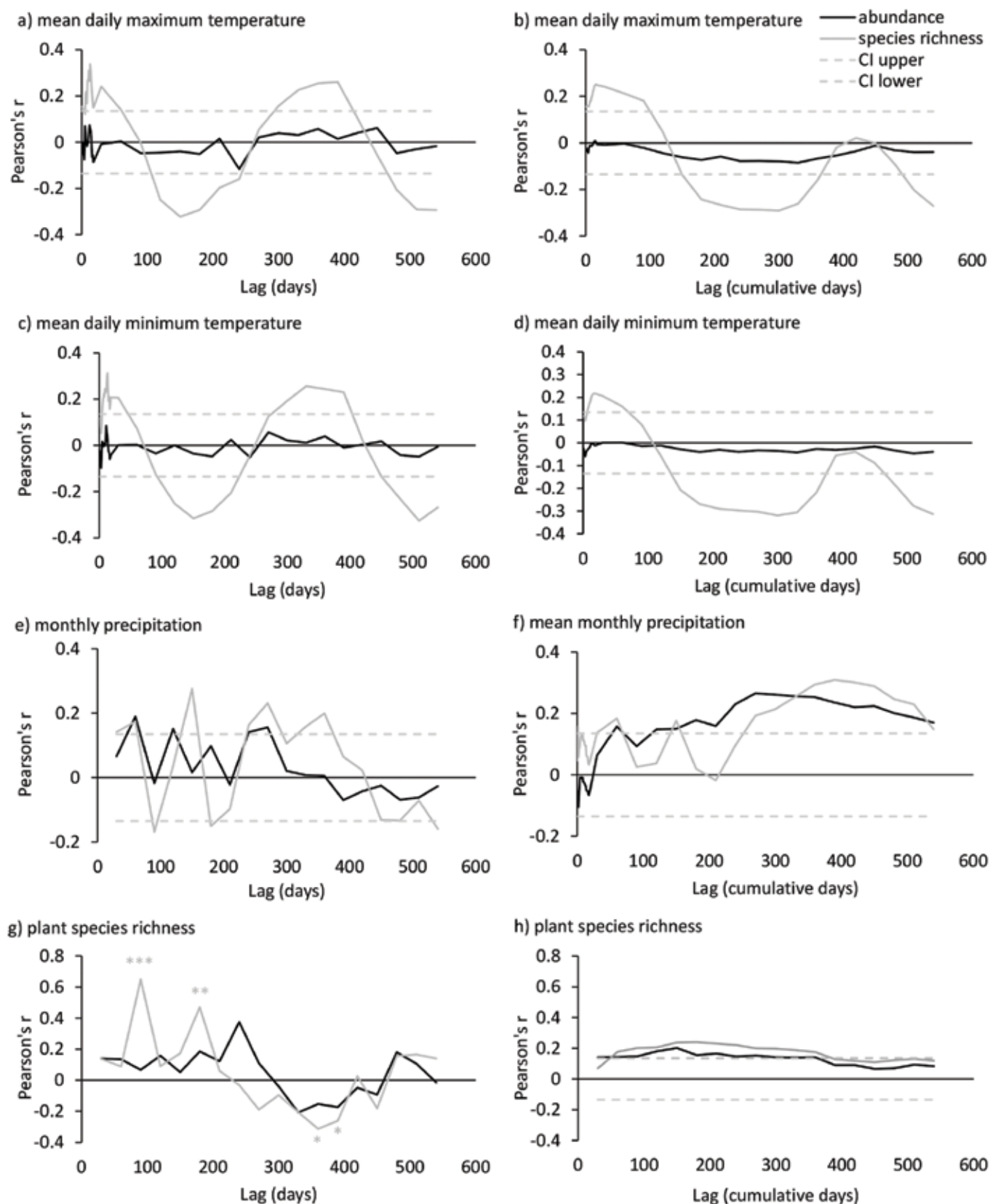
Figure 2: Pearson's *r* for correlations between species richness and abundance of ants in pitfall traps and standard (a,c,e,g) and cumulative (b,d,f,h) lags for mean daily maximum temperature (a,b), mean daily minimum temperature (c,d), monthly precipitation (e,f) and plant species richness (g,h). Values above the upper dotted line or below the lower dotted line are significant. Asterisks indicate significant *r* values where sample sizes varied (* p < 0.05; ** p < 0.01; *** p < 0.001).

temperature, suggesting that higher winter and spring temperatures facilitated the activity of a greater diversity of species. This might reflect increased activity of species in the thermophilic genus *Melophorus* (19 morphospecies collected), which require high temperatures (e.g., 44°C and 35°C at the soil surface for *M. bagoti* and *M. aeneovirens*, respectively, Christian and Morton 1992; Hoffmann 1998) to commence aboveground activity. The positive correlation between ant species richness and temperature was repeated for standard time lags of around one year, suggesting that higher winter temperatures of the previous year had a lasting positive impact on richness. Over time lags of greater than four months (but less than one year), correlations between species richness and temperature were negative, indicating that fewer species thrived when temperatures from the previous summer were high. Temperature may have acted directly on ant activity: extreme heat on summer days might negatively affect some species by causing direct

mortality to workers or colonising queens or by decreasing the number of days a colony might be active (Cerda, Retana *et al.* 1998). Although ants shift their activity to suitable foraging temperatures, those temperatures must coincide with appropriate light conditions for their visual systems (c.f., Greiner, Narendra *et al.* 2007), so activity times may be less plastic during the hotter months. Alternatively, high temperatures over extended periods may reduce the availability of plant resources, shutting down photosynthesis and delaying flowering (Reynolds, Virginia *et al.* 1999), thus affecting ant activity indirectly.

Unlike temperature, responses to precipitation were not linked to season, probably because precipitation is not strongly seasonal in the Simpson Desert (Nano and Pavey 2013). Although short-term responses to precipitation were weak for cumulative lags and idiosyncratic for standard lags, both abundance and species richness responded strongly to precipitation at
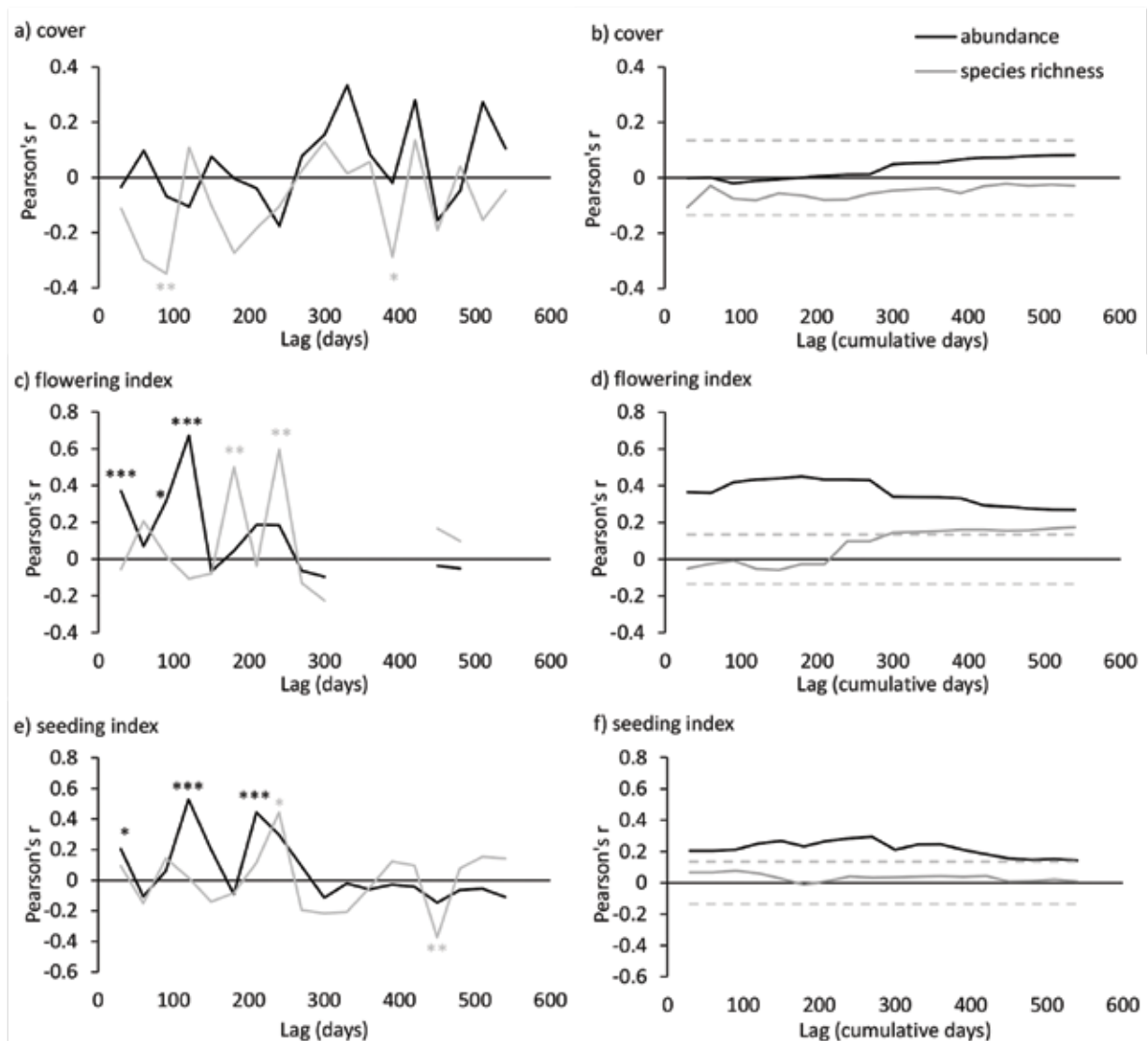

Figure 3: Pearson's *r* for correlations between species richness and abundance of ants in pitfall traps and standard (a,c,e,g) and cumulative (b,d,f,h) lags for cover (a,b), flowering (c,d), and seeding (e,f) of *Triodia*. Values above the upper dotted line or below the lower dotted line are significant. Asterisks indicate significant *r* values where sample sizes varied (* p < 0.05; ** p < 0.01; *** p < 0.001).

cumulative time lags of around one year. Long term impacts of precipitation on ants might be direct, e.g., higher precipitation may improve soil moisture and reduce physiological stress (Johnson 2006). However, they are most likely to result from the effects of precipitation on plant resources. In particular, the correlation between plant seeding and flowering and precipitation peaked at a five month cumulative lag (Appendix I) and ants responded to seeding and flowering index over up to a seven month lag, which corresponds well with the one year lag effect of precipitation on ant abundance and species richness. Previous studies suggest that lag times for responses of other animals to rainfall in the Simpson Desert are shorter or of similar duration: introduced house mice (*Mus musculus*) erupted within two months of a significant rainfall event, while native rodents responded 3-10 months after rain (Dickman, Mahon *et al.* 1999), mulgaras (*Dasycercus cristicauda*) responded

at 7-9 months (Dickman, Haythornthwaite *et al.* 2001), dragon lizards at nine months (Dickman, Letnic *et al.* 1999), while a succession of bird functional groups follows precipitation (Tischler, Dickman *et al.* 2013).

Higher plant species richness was associated with higher abundance and species richness of ants, with a peak cumulative lag time of five to six months before sampling (standard lag correlations were positive and significant at three and six months for species richness; surprisingly, they were negative at one year). An association between plant and animal species richness has been reported for a range of systems previously (e.g., Haddad, Crutsinger *et al.* 2009) and may reflect the greater number of diet niches presented by diverse plant resources. Higher plant diversity is generally associated with greater plant production, up to a point (Fraser, Pither *et al.* 2015). Greater plant production is, in turn, associated with increased consumer production, i.e., higher abundances (Borer, Seabloom
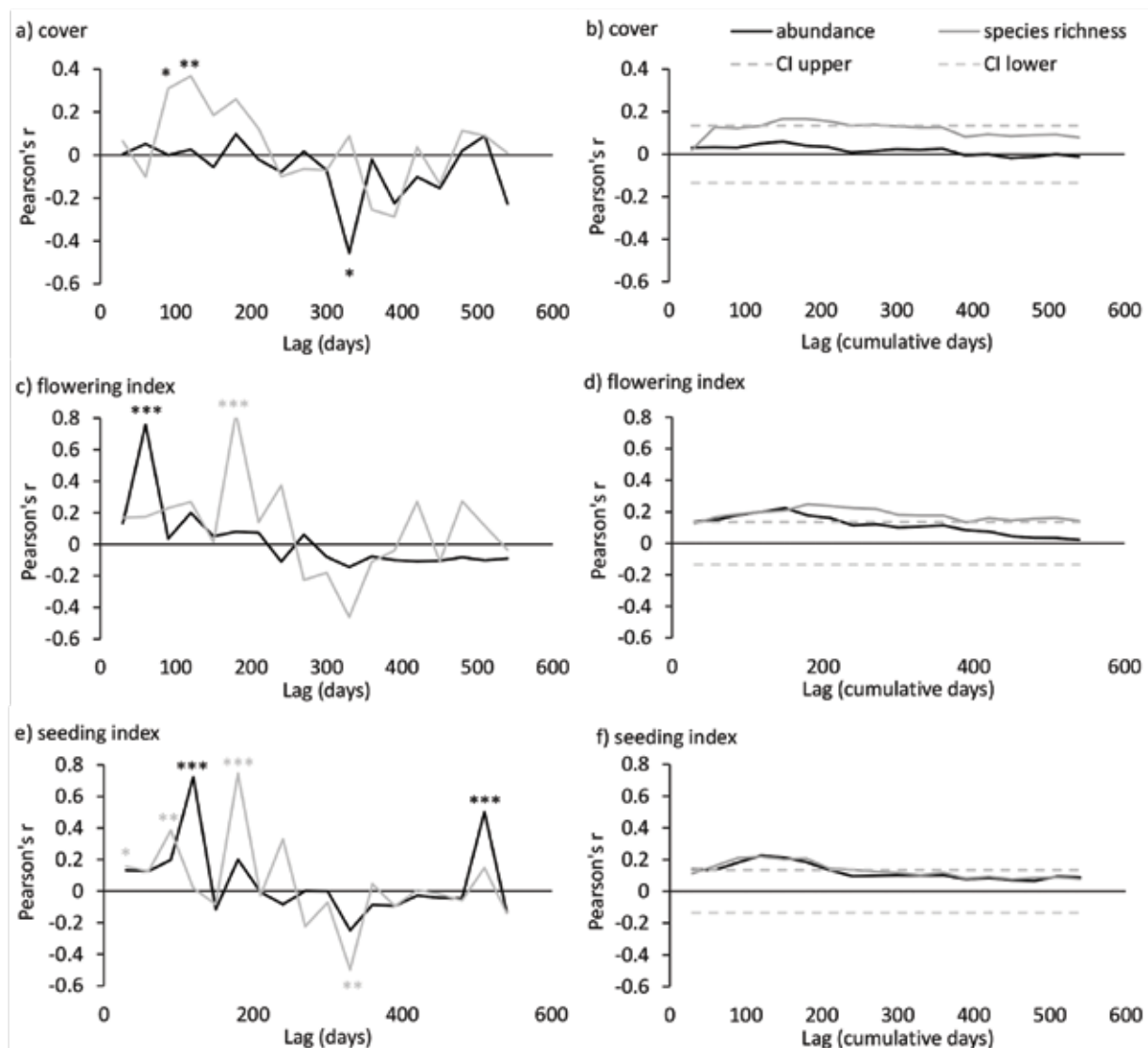

Figure 4: Pearson's *r* for correlations between species richness and abundance of ants in pitfall traps and standard (a,c,e,g) and cumulative (b,d,f,h) lags for cover (a,b), flowering (c,d), and seeding (e,f) of other (non-*Triodia*) plants. Values above the upper dotted line or below the lower dotted line are significant. Asterisks indicate significant *r* values where sample sizes varied (* p < 0.05; ** p < 0.01; *** p < 0.001).

et al. 2012). Further, the more individuals an ecosystem can support, the more species it is likely to contain (the More Individuals Hypothesis, Hurlbert 2006; Srivastava and Lawton 1998). While it seems plausible that this is the mechanism responsible for the positive association between ant abundance and species richness and plant diversity, plant cover - a measure of plant production - had little effect on ant abundance and is therefore unlikely to have driven species richness. Increased plant cover is likely associated with increased shading, but in Australia, numerically dominant ants are favoured by warm, open habitats (Andersen 1995). The trade-off between the beneficial increases in plant production and disadvantageous decline in open habitats may explain why increases in vegetation cover were not associated with changes in ant abundance. Further, increases in the cover of dominant *Triodia* may decrease habitat heterogeneity, reducing opportunities for ant species coexistence and thus constraining species richness (Reid 1995).

In contrast to plant cover, the abundance and richness of ants was clearly correlated with measures of plant resource availability: the flowering and seeding indices. Flowers of many plants (but not *Triodia*) provide nectar to ants, fuelling activity over the short term (Cook and Davidson 2006), while seeds can be consumed *in situ* or cached in nests for future use (Briese and Macauley 1981; Hughes and Westoby 1992). Ant abundance was associated positively with *Triodia* resources, with responses strongest at short standard lag times and all cumulative lag times; species richness responded at longer standard lag times of six to eight months, but cumulative lags were not significant. Increased availability of a single resource (*Triodia* seeds) might particularly favour those species best adapted to utilise it, thus increasing ant abundance more than richness. The long lag times over which abundance increases with *Triodia* seed availability may reflect the ability of some ants to cache seeds and use them over longer periods of time (Briese and Macauley 1981). Both abundance and richness of ants increased with other plant resources, with relationships most pronounced between one and six month standard lags. The similarity in responses to these two different resource types was unexpected: nectar was predicted to be most important at short lags and to increase activity, but not necessarily abundance; seeds were expected be important over longer lag times as they provide resources for larvae and are stored by some species, thus increasing worker abundance over a longer timeframe. Although some ants are able to store nectar resources using a specialised replete caste; of the sampled species, only *Melophorus bagoti* is known to have repletes (Schultheiss, Schwarz *et al.* 2010). The energy from nectar might therefore be expected to be used by most species shortly after collection. However, if increased nectar availability drives foraging, increased collection of resources such as insect carcasses and seeds may support greater larval production. The longer term outcome of greater nectar availability might therefore be greater abundance within nests and potentially greater reproductive output.

Conclusions

Our twenty-two year data set relating ant abundance and richness to lags in climate and resources showed that responses to resource availability over long time frames (cumulative lags) are relatively stable, while responses to short-term weather events (standard lags) are stronger, but highly idiosyncratic. This suggests that high cumulative resource availability promotes ant abundance and diversity, while the impacts of short-term pulses in resource availability are less determinate. The colonial nature of ants likely imbues them with a high degree of flexibility in their responses to changes in climate and plant resources. The timeframes over which resources could be used (either fresh, cached or distributed among colony members) may explain both the idiosyncratic nature of short-term responses and the stability of longer term responses. Other studies suggest that lag times vary among invertebrate groups (Kwok, Wardle *et al.* 2016), and ants are unlikely to be representative of other invertebrate groups because of their social nature. However, their large contribution to invertebrate biomass, ecosystem function and vertebrate diets makes a thorough understanding of the temporal scales over which they respond to climate critical to understanding the ecology of temporally variable desert ecosystems.

Acknowledgements

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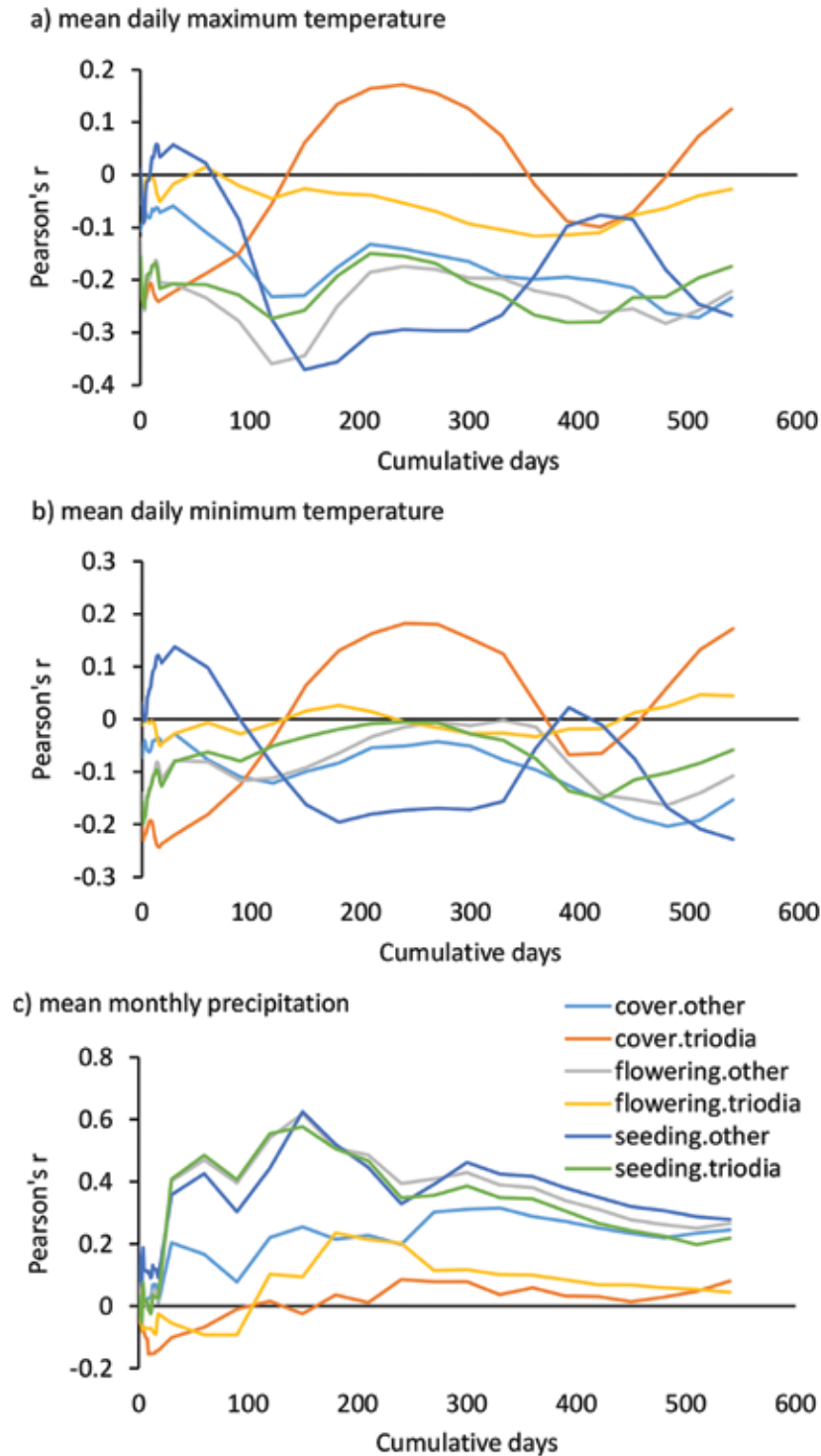
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APPENDIX I

Pearson's *r* for correlations between species plant cover, flowering and seeding and cumulative lags for: a) mean daily maximum temperature richness; b) mean daily minimum temperature; and c) mean monthly precipitation.

a) mean daily maximum temperature

b) mean daily minimum temperature

c) mean monthly precipitation

cover.other
cover.triodia
flowering.other
flowering.triodia
seeding.other
seeding.triodia

APPENDIX 2

Dune crest with rattle-pod grevillea, *Grevillea stenobotrya*. Location: near Main Camp, Ethabuka Station, Simpson Desert. Photo credit: H. Gibb.

Dune swale with Georgina gidgee, *Acacia georginae*, woodlands. Location: near Main Camp, Ethabuka Station, Simpson Desert. Photo credit: H. Gibb.