ORIGINAL ARTICLE

Savanna ant species richness is maintained along a bioclimatic gradient of increasing latitude and decreasing rainfall in northern Australia

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ABSTRACT

Aim Using a standardized sampling protocol along a 600-km transect in northern Australia, we tested whether ant diversity within a single biome, tropical savanna, decreases with increasing latitude (as a surrogate of temperature) and decreasing rainfall, as is expected for biodiversity in general.

Location Northern Australia.

Methods Ants were sampled using pitfall traps on three occasions at 1-ha sand, loam and clay sites at each of five locations along the Northern Australian Tropical Transect (NATT), from 12°50′ S (1400 mm mean annual rainfall) to 17°21′ S (650 mm).

Results We recorded a total of 246 species from 37 genera. Mean observed species richness pooled across sampling periods was similar at sand (85.4) and loam (82.2) sites, but was less than half this at clay sites (40.0). Ant communities were also compositionally distinct on clay soils compared with sands and loams. Individual genera showed variable diversity patterns, ranging from a linear increase to a linear decrease in species richness along the NATT. However, total species richness was relatively uniform along the gradient. Patterns of ant species turnover were consistent with previously recognized biogeographical boundaries, with a primary disjunction between the arid and monsoonal zones in the south, and a secondary disjunction between the semi-arid and mesic zones in the north.

Main conclusions Patterns of ant diversity in Australian savannas do not conform to global patterns of biodiversity declines with increasing latitude and decreasing rainfall. We believe this is due to a lack of significant temperature change across the latitudinal gradient, and, in particular, to the fauna's evolutionary history in association with aridification, which makes it unusually resilient to increasing aridity. The diversity of other important faunal groups such as termites and lizards is also exceptionally high in arid Australia and is likewise not closely linked to rainfall in Australian savannas. We predict that these taxa are far more sensitive to increasing aridity in savannas elsewhere in the world, and especially in the Neotropics, where savannas have an evolutionary association with humid rain forest rather than desert.

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INTRODUCTION

Rainfall and temperature are major predictors of local diversity for a wide range of taxa (Hawkins *et al.*, 2003; Currie *et al.*, 2004; Field *et al.*, 2009; Cancello *et al.*, 2014). In particular, there are widespread patterns of decreasing diversity with increasing latitude (from the tropics to temperate regions) as a surrogate of temperature (Gaston, 2000; Hillebrand, 2004; Bannister *et al.*, 2012; Mannion *et al.*, 2014) and with decreasing rainfall (Sommer *et al.*, 2010; Liberal *et al.*, 2011) for both plants and animals.

Ants are an ecologically dominant faunal group (Hölldobler & Wilson, 1990; Folgarait, 1998; Del Toro *et al.*, 2012) that have well-documented global diversity patterns in relation to climate (Dunn *et al.*, 2009; Jenkins *et al.*, 2011). Temperature is a key factor controlling ant distributions (Andersen, 1995; Kaspari *et al.*, 2004; Chaladze, 2012; Diamond *et al.*, 2012; Bishop *et al.*, 2014), and ant diversity declines with increasing latitude (Dunn *et al.*, 2009). At a global scale, ant diversity has only a weakly negative relationship with rainfall (Dunn *et al.*, 2009). However, within any particular biome ant diversity tends to increase with rainfall (Fisher, 1999; Paknia & Pfeiffer, 2012; Pérez-Sánchez *et al.*, 2013), unless increases in rainfall are counterbalanced by decreases in temperature (Pfeiffer *et al.*, 2003; Chaladze, 2012).

A confluence of latitudinal and rainfall gradients occurs in the vast savanna landscapes of northern Australia, where rainfall declines markedly with increasing latitude from the northern coast (> 1500 mm mean annual rainfall) south to the fringe of the central arid zone (600 mm) over a distance of about 1000 km (Hutley *et al.*, 2011). Local diversity likewise declines markedly over this gradient for a wide range of plant and animal taxa (Whitehead *et al.*, 1992; Bowman, 1996; Williams *et al.*, 1996; Barrett *et al.*, 2003). Ant diversity is strongly related to rainfall in tropical savannas of southern Africa (Parr *et al.*, 2004), and one might therefore expect a particularly marked gradient of decreasing ant species richness with increasing latitude and decreasing rainfall in Australian savannas. Local ant diversity is known to be extremely high in the high rainfall zone, with up to 100 or more species often recorded within a single hectare (Andersen, 1992; Arnan *et al.*, 2011), but it is not known how such diversity changes with increasing latitude and decreasing rainfall.

The use of bioclimatic gradients to understand the degree to which climate drives patterns of species diversity can help inform the extent to which such patterns might be influenced over coming decades by global climate change (Koch *et al.*, 1995; Canadell *et al.*, 2002; Werneck *et al.*, 2012; de Frenne *et al.*, 2013). Bioclimatic gradients are especially valuable for identifying regions where rates of compositional change are particularly high, making them highly sensitive to climate change (Williams *et al.*, 1995).

Here, we use results from standardized sampling to describe variation in ant species richness and composition along the Northern Australian Tropical Transect (NATT), a bioclimatic gradient that captures the full variation in latitude and rainfall within Australia's tropical savanna biome (Hutley *et al.*, 2011). We address two key questions. First, to what extent does ant species richness decline along the gradient of increasing latitude and decreasing rainfall? Second, can zones of high rates of change in species richness or composition be identified that are likely to be particularly sensitive to climate change?

MATERIALS AND METHODS

Study sites

The study region experiences a monsoonal climate, with rainfall heavily concentrated in a summer wet season, and maximum daily temperatures high throughout the year. The dominant vegetation throughout is eucalypt-dominated savanna woodland. Details of variation in climate and vegetation along the gradient are provided in Hutley *et al.* (2011). The latest (2013) climate-change projections (http://www.climatechange2013.org/images/report/WG1AR5_ALL_FINAL.pdf; http://www.climatechangeinaustralia.gov.au/en) are for a 2–5% decrease in rainfall by 2070, with the greatest changes expected in the southern part of the NATT. A 5% decrease would equate to the 1000 mm zone occurring 50–75 km further north than its current location. Mean annual temperature is predicted to increase by 0.5–1.3 °C by 2030.

Ants were sampled at five locations along the NATT, ranging from Annaburro Station (approximately 1400 mm mean annual rainfall) in the north to the Kalkarindji region (650 mm) in the south, a distance of approximately 600 km (Fig. 1). Mean annual rainfall at the other locations is: Douglas Daly – 1200 mm; Willeroo – 900 mm; Kidman Springs – 750 mm. Mean annual temperature is remarkably constant across the locations (approximately 28 °C), but both maximum and minimum temperatures are more extreme with increasing latitude (see Hutley *et al.*, 2011).

Three 1-ha sites were established at each location, one each on sand, loam and clay soil (see Appendix S1 in Supporting Information for grid coordinates). Sites within a location were separated by at least 5 km. Canopy cover and height tended to be highest on sand, where it ranged from 68% and 17.6 m respectively at Annaburroo to 7% and 6.2 m at Kalkarindji (see Appendix S2). Canopy cover was always low (0–12%) on clay, where it did not vary systematically with rainfall.

Sampling

Ants were sampled using two 5×3 grids of pitfall traps located at opposite corners of each site, with 10 m spacing between traps. Traps were plastic containers 8.5 cm in diameter, partly filled with a 70% ethanol/glycol mixture as a preservative, and operated for a 48-h period on three occasions covering a range of seasonal conditions: July (mid dry

Figure 1 Map of the Northern Territory showing the five study locations along the Northern Australian Tropical Transect (NATT) in the Northern Territory. The NATT covers Australia's monsoonal zone, where rainfall is heavily concentrated into a summer wet season, and ranges from > 1500 mm annually in the north to about 600 mm in the south. A, Annaburroo; DD, Douglas Daly; W, Willeroo; KS, Kidman Springs; Ka, Kalkarindji.
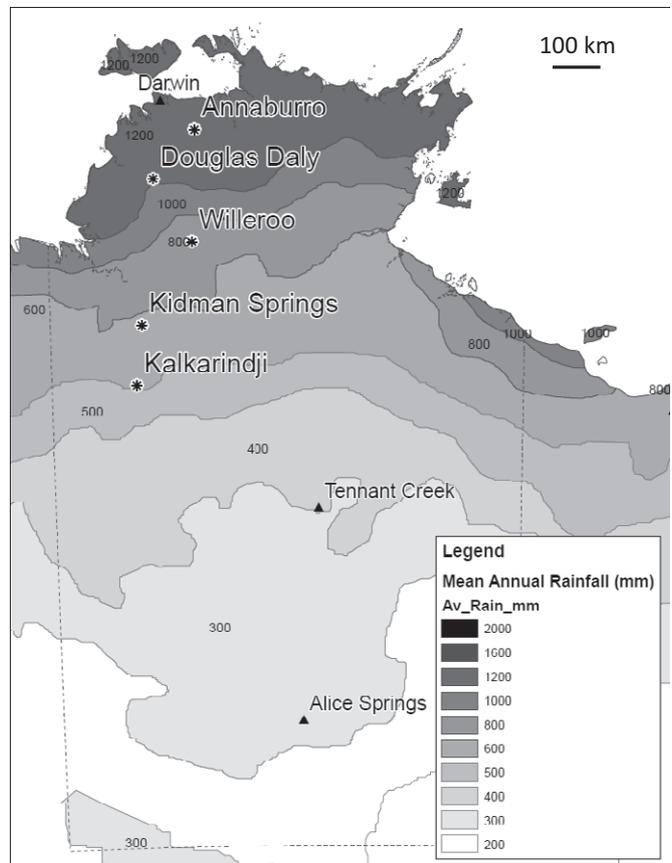
season) 1996; April (end of wet season) 1997; and October (late dry season) 1997. The arid-adapted nature of Australia's savanna ant fauna means that it includes very few specialist cryptobiotic or arboreal species (Andersen, 2000), and sampling by pitfall traps has been shown to provide a reliable representation of ant diversity and composition (Andersen, 1991).

Analysis

Ants were sorted to species, and given species names where possible, with species nomenclature following Shattuck (1999). Unidentified species were identified to species group following Andersen (2000) and assigned code numbers (sp. 1, etc.) following those of previous ant studies in the Northern Territory (e.g. Andersen, 1992; Andersen *et al.*, 2006; Arnan *et al.*, 2011; Campos *et al.*, 2011). All unidentified species without previous number codes were assigned letter codes (sp. A, etc.) that apply only to this study. Genetic analysis has consistently verified the accuracy of these species demarcations (Andersen *et al.*, 2013a,b). A full collection of voucher specimens is held at the CSIRO Tropical Ecosystems Research Centre in Darwin.

In order to reduce the possibility of serious data distortions caused by very large numbers in few traps, which can compromise the reliability of abundance data, species abundances in individual traps were transformed according to a 10-point score (Andersen, 1991): 1 = 1, 2 = 2; 3 = 3–5; 4 = 6–10; 5 = 11–15; 6 = 16–25; 7 = 26–50; 8 = 51–100; 9 = 101–200; 10 = > 200. A species total abundance at a site was defined by the sum of its abundance scores across the 30 traps (i.e. maximum of 300, where all traps had > 200 individuals). The transformed abundances were used in all analyses involving abundance.

Our focus was on ant diversity patterns at the 1-ha scale rather than on how sample diversity varied seasonally or within a 1-ha site, and so data were pooled across the two plots and three sampling periods to provide a single ant species × abundance matrix for each of the 15 sites. We estimated site species richness based on presence–absence data using the Chao2 and ICE metrics in EstimateS version 8.2.0 (Colwell, 1997). Relationships between species richness and latitude were examined for the richest genera (those with > 15 species) and for total observed richness by fitting both linear and quadratic equations using R version 2.15.2 (R Core Team, 2013). These regressions were intended only to describe pattern rather than as rigorous tests of relationships given that sample sizes were small. Changes in biogeographical profiles of local faunas were examined by classifying species into one of four categories according to the distribution within Australia of the species-group to which they belong, following Andersen (2000): Eyrean (arid), Torresian (tropical), Bassian (cool-temperate) and widespread. Patterns of species composition were explored using non-metric multidi-

mensional scaling (NMDS) of site species abundance data, based on Bray–Curtis dissimilarity. This analysis was conducted using the 'vegan' package in R, with the 'metaMDS' function (Oksanen *et al.*, 2013). The Jaccard index based on species presence/absence data was used to analyse species turnover between each pair of sites (beta diversity), using the 'beta.pair' function of the BetaSim package in R (Baselga & Orme, 2012) with the specified 'index.family' set to 'jaccard'. The 'beta.pair' function computes three distance matrices that account for the spatial turnover and nestedness components of beta diversity.

RESULTS

We recorded a total of 246 species from 37 genera, including the two introduced species *Tetramorium simillimum* and *Paratrechina longicornis* (see Appendix S3). The richest genera were *Melophorus* (35 species), *Monomorium* (22), *Camponotus* (21), *Rhytidoponera* (20), *Meranoplus* (20), *Polyrhachis* (19), *Pheidole* (17) and *Iridomyrmex* (16) (Appendix S3). Four of these genera showed clear patterns of total richness at a location in relation to latitude: *Melophorus* (Fig. 2a) and *Monomorium* (Fig. 2b) both increased markedly in richness with latitude (adjusted $R^2 = 0.987$, $P = 0.006$; and adjusted $R^2 = 0.863$, $P = 0.014$), *Pheidole* showed a linear decline in richness with latitude (Fig. 2c; adjusted $R^2 = 0.998$, $P < 0.001$) and *Meranoplus* showed a unimodal pattern of richness, which was highest at mid-latitude (Fig. 2d, adjusted $R^2 = 0.95$, $P = 0.03$). These high R^2 values and associated P-values should be interpreted with caution given the low sample sizes.

Total observed site richness ranged from 19 (Annaburroo clay) to 97 (Kidman Springs loam). Observed species richness at sand and loam sites had similar overall means (85.4 and 82.2 respectively) and showed no systematic variation ($P > 0.10$) with latitude (Fig. 3a). Chao2 and ICE estimators indicated that total richness at these sites ranged from about 100–150 species and was bimodal, with lowest richness at mid-latitudes (Fig. 3a). Observed richness was substantially lower at clay sites (mean of 40.0), where all richness measurements showed a strongly unimodal pattern of highest values at mid-latitude (Fig. 3a). Total ant abundance scores increased with latitude on loams (best-fit regression adjusted $R^2 = 0.30$, $P = 0.012$) and clays ($R^2 = 0.12$, $P = 0.036$), but did not vary systematically with latitude on sands ($R^2 = 0.01$, $P = 0.565$; Fig. 3b).

The biogeographical profiles of local faunas varied systematically along the rainfall gradient. The proportion of species with Eyrean affinities increased linearly from 32% at Annaburro in the north to 43% at Kidman Springs, but then jumped markedly to 58% at Kalkarindji. The proportion of species with Torresian affinities correspondingly decreased from 51% at Annaburroo to 28% at Kalkarindji (Fig. 4). The proportion of species belonging to widespread taxa was relatively uniform at about 25%, and species from Bassian taxa represented < 1% of the fauna throughout.

NMDS revealed that sand and loam sites had strongly overlapping ant species compositions that were distinct from those of clay sites (Fig. 5). BetaSim analysis of sand and loam sites indicated that there were two major zones of species compositional change, the first between the four more northerly locations and Kalkarindji, and the second between Douglas Daly and Annaburroo at lowest latitudes on one hand, and Kidman Springs and Willeroo at mid-latitudes on the other (Fig. 6).

DISCUSSION

Contrary to expectations based on global biodiversity patterns in relation to latitude and rainfall, high ant diversity was maintained all along the NATT, without any decrease with increasing latitude and decreasing rainfall. Observed species richness was particularly high at sand and loam sites, averaging 84. Richness estimators indicated peaks of 120–150 species at the top (Annaburro) and lower middle (Kidman Springs) of the gradient. Such high figures are not inconsistent with those documented by intensive studies of local faunas; for example, 147 savanna species have been recorded from a site near Darwin (Andersen *et al.*, 2007). Notably, estimated richness at Kalkarindji (650 mm mean annual rainfall) exceeded 100, and was similar to that at Douglas Daly (1200 mm) and Willeroo (950 mm). We are unaware of any other study that has documented the maintenance of such high ant diversity over such a large latitudinal and rainfall gradient. Despite a lack of pattern overall, individual genera showed a wide range of diversity patterns, including a linear increase (*Melophorus*) and decrease (*Pheidole*) in species richness with latitude, and peak richness at mid-latitudes (*Meranoplus*).

Ant communities on clay soils were far less diverse than, and compositionally distinct from, those on sands and loams. This is unsurprising given that the clay soils represent extremely challenging environments for soil-nesting animals, alternating between heavily waterlogged during the wet season and deeply cracking during the dry season. Cracking clays are known to support compositionally distinct ant faunas with relatively low diversity throughout northern Australia (Andersen, 1993, 2003), and soil type is known to be a key driver of variation in ant diversity and composition more generally (Andersen, 1995; Castracani *et al.*, 2010; Delsinne *et al.*, 2010; Hoffmann & James, 2011). Clay soils support low tree density (< 15% canopy cover at our sites), and the reduced availability of tree-associated resources is also likely to have contributed to the relatively low ant diversity on clay soils in our study. It is unclear why the unimodal pattern of ant diversity on clay soils was so different from that on sands and loams.

We provide two explanations for why high ant diversity was maintained along our latitude/rainfall gradient. First, although latitudinal variation is typically a surrogate for variation in mean annual temperature, this is not the case along the NATT, where mean annual temperature is highly uniform. Such uniformity is in contrast to comparable latitudi-

Figure 2 Relationship between site (1 ha) species richness and latitude for the eight richest ant genera at 15 sites representing three soil types at each of five locations along the Northern Australian Tropical Transect. Ants were sampled using two 5 × 3 grids of pitfall traps (10 m spacing between traps) located at opposite corners of each site, and operated for a 48 h period on each of three occasions. Data are given for sand (open circles), loam (triangles) and clay (squares) soils, as well as for all soil types combined (closed circles; $n = 5$ in all cases). Statistically significant best-fit regression curves are shown (dashed lines: clay soils for *Melphorus* and *Polyrhachis*, sand for *Monomorium*; solid lines = combined across soil types) A, Annaburroo; DD, Douglas Daly; W, Willeroo; KS, Kidman Springs; Ka, Kalkarindji.
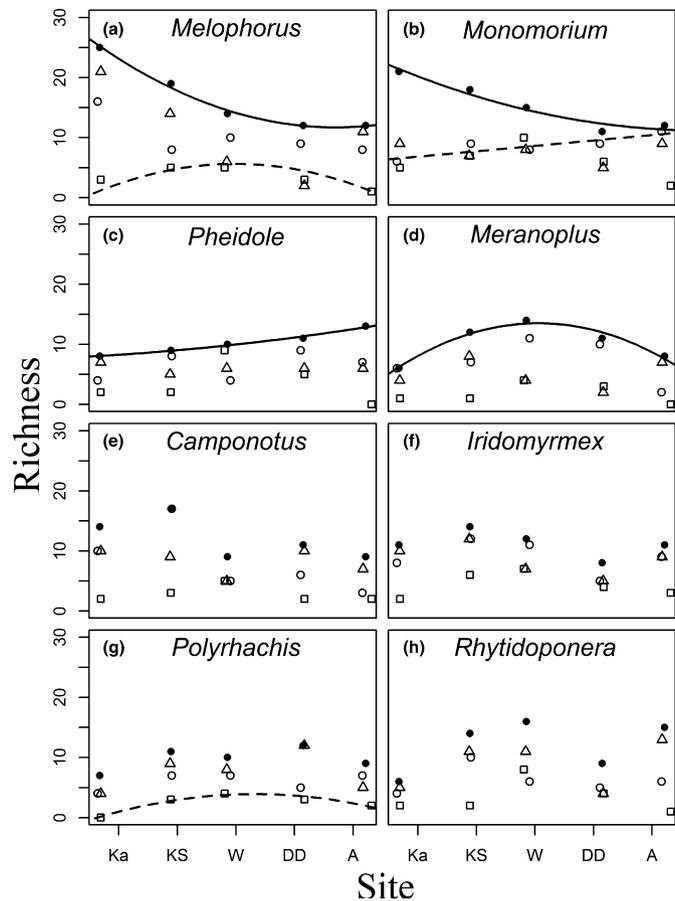
nal changes in more temperate parts of the world, such as in Europe where ant species richness declines markedly with increasing latitude (Cushman *et al.*, 1993; Kumschick *et al.*, 2009). Although mean annual temperature was highly uniform along the NATT, the ranges in daily and seasonal temperature increased with increasing latitude. Such variation is potentially important for thermal control of ant distributions (Diamond *et al.*, 2012), but showed no relationship with species richness in our study.

Second, the peculiar evolutionary history of Australia's savanna ant fauna makes it unusually resilient in relation to decreasing rainfall. Australian savannas occur on the fringes of its vast arid zone, and evolved during the aridification of the Australian continent (Byrne *et al.*, 2008). Arid Australia supports an exceptionally rich ant fauna (Andersen, 2003), and the savanna fauna is dominated by these arid-adapted taxa (Andersen, 2000). The proportion of species with Eyrean (arid) affinities increased from 32% at Annaburoo in the north to 58% at Kalkarindji in the south, and this increased representation of arid-adapted taxa explains why overall diversity was maintained with decreasing rainfall. Such dominance by arid-adapted taxa does not occur in savanna ant faunas elsewhere in the world. In particular, Neotropical savannas have an evolutionary history embedded in expanding and contracting rain forest, such that its ant fauna is dominated by taxa with forest origins, as illustrated by an exceptionally high diversity of

arboreal species (Campos *et al.*, 2011). The ant fauna of southern African savannas is dominated by highly generalized taxa (such as *Pheidole* and *Tetramorium*), and similarly lacks a diverse arid element (Parr & Chown, 2001; Parr *et al.*, 2004; Parr, 2008). Interestingly, extremely high ant diversity is maintained along a 400 mm (460–887 mm) rainfall gradient in semi-arid Chaco of Paraguay (Delsinne *et al.*, 2010), which suggests that the ant fauna of Paraguayan Chaco likewise has a long evolutionary history in association with aridity.

The NATT considers only the monsoonal zone of northern Australia, and the question arises: to what extent is exceptionally high ant diversity maintained further along the rainfall gradient into the central arid zone, where mean annual rainfall is typically only 200 mm? Unfortunately, comparable data are not available for the rest of the gradient. Local ant diversity in semi-arid (350 mm mean annual rainfall) southern Australia is exceptionally high, with well over 100 species recorded within 1 ha (Andersen, 1983), which indicates that the high diversity along the NATT might be maintained substantially further along the gradient. We would expect that diversity would be substantially lower in the most-arid zone, and our unpublished observations support this. However, there are no published studies quantifying local ant richness in this region.

Several other Australian taxa are also atypical compared with other continents in showing no consistent change in
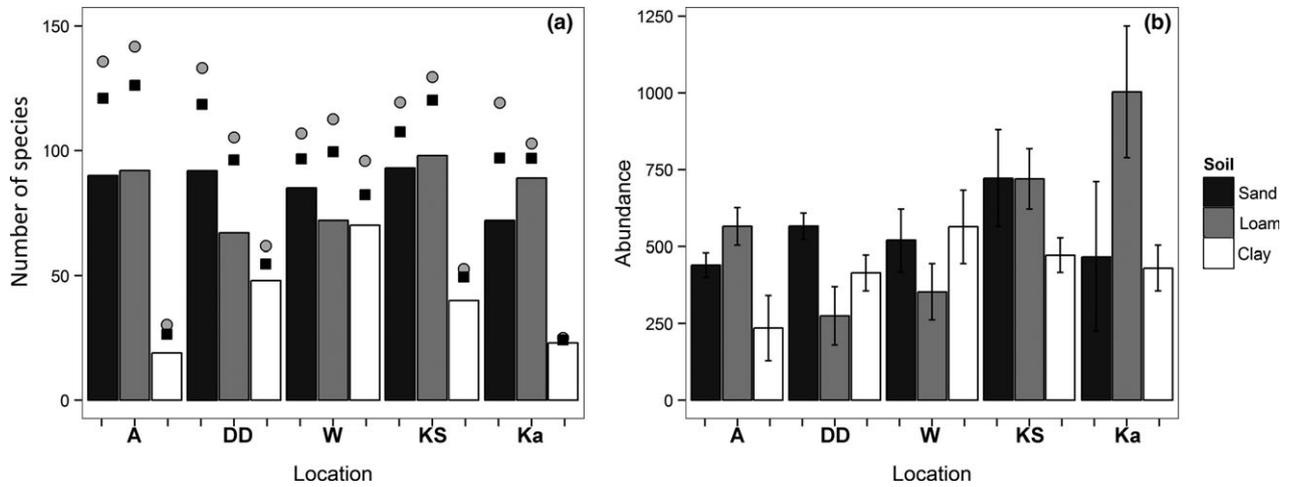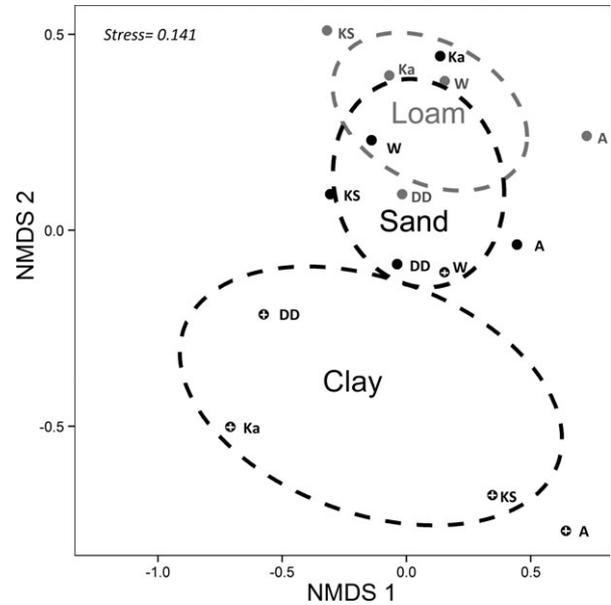
Figure 3 Patterns of local ant richness and abundance at 15 1-ha sites representing three soil types at each of five locations along the Northern Australia Tropical Transect. (a) Observed (bars) and estimated (grey circles – Chao2; black square – ICE) richness at the 15 1-ha study sites. (b) Mean ($\pm$ standard error) total ant abundance scores per sampling event per sampling grid ($n = 6$). A, Annaburroo; DD, Douglas Daly; W, Willeroo; KS, Kidman Springs; Ka, Kalkarindji.
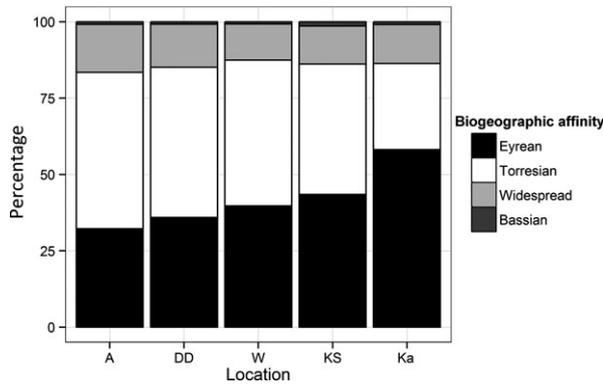

Figure 4 Biogeographical profiles of local ant faunas along the Northern Australian Tropical Transect, showing changes in percentage contributions to total species richness of species belonging to groups with Eyrean (arid), Torresian (tropical), Bassian (cool-temperate) and widespread distributions. Data have been combined across 1-ha sand, loam and clay soils at each of the five locations. A, Annaburroo; DD, Douglas Daly; W, Willeroo; KS, Kidman Springs; Ka, Kalkarindji.

Figure 5 Non-metric multi-dimensional scaling plot (stress = 0.141) of site similarity based on ant species composition at 15 1-ha sites representing three soil types at each of five locations along the Northern Australian Tropical Transect. Dashed ellipses represent the 95% confidence intervals about the distribution of points representing different soil types. A, Annaburroo; DD, Douglas Daly; W, Willeroo; KS, Kidman Springs; Ka, Kalkarindji.

diversity with latitude and rainfall. For example, the species richness of termites (Blattodea: Termitoidae) in semi-arid Australia is comparable to that in the tropics (Watson & Abbey, 1993; Abensperg-Traun & Steven, 1997), and Australian mammals do not show a clear decline in diversity with latitude (Schall & Pianka, 1978). Lizard diversity shows no systematic relationship with rainfall, having peaks in both the wet tropics and central arid zone (Powney *et al.*, 2010). It is likely that these patterns reflect more broadly the long history of aridity in Australia and its highly diverse arid-adapted biota (Byrne *et al.*, 2008). For example, arid Australia has an exceptionally rich lizard fauna, with extreme diversification in all five Australian families (Scincidae, Varanidae, Agamidae, Gekkonidae and Pygopodidae) (Pianka,

1986; Morton & James, 1988). The scincid genus *Ctenotus* has 100 or more Australian species, with most occurring in the arid zone (Wilson & Swan, 2003). The diversification is found in families of both Gondwanan (e.g. Pygopodidae) and Asian (e.g. Varanidae) origin, and has occurred primarily over the past 23 million years in association with increased aridity (Jennings *et al.*, 2003).
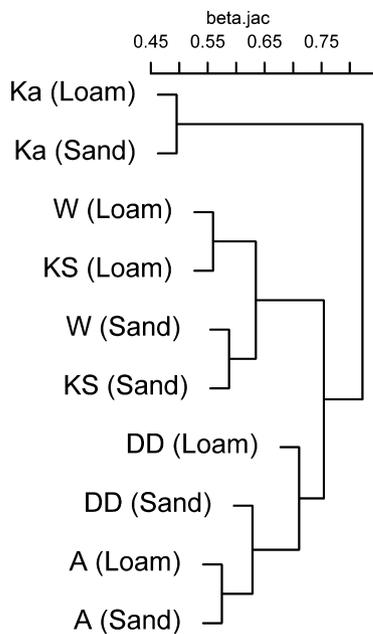
Figure 6 Species turnover across 1-ha sand and loam sites at each of five locations along the Northern Australian Tropical Transect, based on BetaSim values. Data from clay sites are not included because they support a distinctly different fauna. A, Annaburroo; DD, Douglas Daly; W, Willeroo; KS, Kidman Springs; Ka, Kalkarindji.

In contrast to diversity, there were clear patterns of ant compositional change along the NATT. The primary zone of species turnover was between Kalkarindji at the low rainfall end of the NATT and all other sites. This zone also had a particularly high rate of increase in the proportion of Eyrean taxa; the increase from Kidman Springs (43%) to Kalkaringji (58%) was greater than the increase along the entire remainder of the gradient, from Annaburro (32%) to Kidman Springs. Kalkarindji is at the southerly limit of monsoonal influence, occurring at the transition between the semi-arid monsoonal tropics and the northern arid zone (Burbidge, 1960). The secondary peak in estimated ant species richness at Kidman Springs can be attributed to 'biogeographical enrichment' due to the overlap of faunas from adjacent biogeographical zones (Segev, 2010). Such enrichment also occurs at the southern fringe of the Australian arid zone, where the arid and cool-temperate faunas overlap (Andersen, 2003). The arid-monsoonal transition represents a well-known biogeographical boundary in northern Australia (Bowman *et al.*, 1988; Williams *et al.*, 1995; Egan & Williams, 1996), and is where the primary division of the regional avifauna occurs (Whitehead *et al.*, 1992). We found a secondary zone of species turnover between Douglas Daly and Willeroo, and this represents the transition between semi-arid and mesic regions. It is a major phytogeographical boundary (Bowman *et al.*, 1988), and is another important avifaunal division (Whitehead *et al.*, 1992). These biogeographical boundaries are likely to be especially sensitive to species compositional change in response to a changing climate (Botkin *et al.*, 2007; Bellard *et al.*, 2012), and might be expected to move northwards, given the projected decreases in rainfall. They represent priority locations for monitoring climate-change impacts.

In conclusion, we have shown that patterns of ant diversity in Australian savannas do not conform to global trends of biodiversity declines with increasing latitude and decreasing rainfall. We believe that the lack of response to rainfall is primarily due to the peculiar evolutionary history and therefore functional composition of the Australian savanna ant fauna that makes it unusually resilient to increasing aridity. The diversity of other important faunal groups such as termites and lizards is also exceptionally high in arid Australia and is likewise not closely linked to rainfall in Australian savannas. The historical association of Australian savannas with aridity contrasts strikingly with the historical association of Neotropical savannas with rain forest. We predict that patterns of savanna biodiversity in the Neotropics would show similarly striking contrasts in terms of sensitivity to gradients of decreasing rainfall for a range of faunal groups, but especially ants, termites and lizards.

ACKNOWLEDGEMENTS

REFERENCES

Abensperg-Traun, M. & Steven, D. (1997) Latitudinal gradients in the species richness of Australian termites (Isoptera). *Australian Journal of Ecology*, **22**, 471–476.

Andersen, A.N. (1983) Species diversity and temporal distribution of ants in the semi-arid mallee region of northwestern Victoria. *Australian Journal of Ecology*, **8**, 127–137.

Andersen, A.N. (1991) Sampling communities of ground-foraging ants: pitfall catches compared with quadrat counts in an Australian tropical savanna. *Australian Journal of Ecology*, **16**, 273–279.

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. (1993) Ant communities in the Gulf region of Australia's semi-arid tropics: species composition, patterns of organization, and biogeography. *Australian Journal of Zoology*, **41**, 399–414.

Andersen, A.N. (1995) A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography*, **22**, 15–29.

Andersen, A.N. (2000) *The ants of northern Australia: a guide to the monsoonal fauna.* CSIRO Publishing, Collingwood.

Andersen, A.N. (2003) Ant biodiversity in arid Australia: productivity, species richness and community organization. *Records of the South Australian Museum Monograph Series*, **7**, 79–92.

Andersen, A.N., Hertog, T. & Woinarski, J.C.Z. (2006) Long-term fire exclusion and ant community structure in an Australian tropical savanna: congruence with vegetation succession. *Journal of Biogeography*, **33**, 823–832.

Andersen, A.N., van Ingen, L.T. & Campos, R.I. (2007) Contrasting rain forest and savanna ant faunas in monsoonal northern Australia: a rain forest patch in a tropical savanna landscape. *Australian Journal of Zoology*, **55**, 363–369.

Andersen, A.N., Arnan, X. & Sparks, K. (2013a) Limited niche differentiation within remarkable co-occurrences of congeneric species: *Monomorium* ants in the Australian seasonal tropics. *Austral Ecology*, **38**, 557–567.

Andersen, A.N., Hoffmann, B.D. & Berman, M. (2013b) Diversity in the Australian ant genus *Iridomyrmex* MAYR, 1862 (Hymenoptera: Formicidae): a critique of Heterick & Shattuck (2011), with particular reference to *I. coeruleus* Heterick & Shattuck, 2011. *Myrmecological News*, **18**, 103–111.

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 competition cascade. *Oecologia*, **166**, 283–294.

Bannister, J.R., Vidal, O.J., Teneb, E. & Sandoval, V. (2012) Latitudinal patterns and regionalization of plant diversity along a 4270-km gradient in continental Chile. *Austral Ecology*, **37**, 500–509.

Barrett, G., Silcocks, A., Barry, S., Cunningham, R. & Poulter, R. (2003) *The new atlas of Australian birds*. Birds Australia, Melbourne.

Baselga, A. & Orme, C.D.L. (2012) Betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, **3**, 808–812.

Bellard, C., Bertelsmeier, C., Leadley, P., Thuiller, W. & Courchamp, F. (2012) Impacts of climate change on the future of biodiversity. *Ecology Letters*, **15**, 365–377.

Bishop, T.R., Robertson, M.P., van Rensburg, B.J. & Parr, C.L. (2014) Exploring variation in ant diversity through space and time: an elevational study in the Maloti-Drakensberg Mountains of South Africa. *Journal of Biogeography*, **41**, 2256–2268.

Botkin, D.B., Saxe, H., Araújo, M.B. *et al.* (2007) Forecasting the effects of global warming on biodiversity. *BioScience*, **57**, 227–236.

Bowman, D. (1996) Diversity patterns of woody species on a latitudinal transect from the monsoon tropics to desert in the Northern Territory, Australia. *Australian Journal of Botany*, **44**, 571–580.

Bowman, D.M.J.S., Wilson, B.A. & Dunlop, C.R. (1988) Preliminary biogeographic analysis of the Northern Territory vascular flora. *Australian Journal of Botany*, **36**, 503–517.

Burbidge, N.T. (1960) The phytogeography of the Australian region. *Australian Journal of Botany*, **8**, 387–392.

Byrne, M., Yeates, D.K., Joseph, L., Kearney, M., Bowler, J., Williams, M.A., Cooper, S., Donnellan, S.C., Keogh, J.S., Leys, R., Melville, J., Murphy, D.J., Porch, N. & Wyroll, K.H. (2008) Birth of a biome: insights into the assembly and maintenance of the Australian arid zone biota. *Molecular Ecology*, **17**, 4398–4417.

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 inter-continental comparison. *Austral Ecology*, **36**, 983–992.

Canadell, J.G., Steffen, W.L. & White, P.S. (2002) IGBP/GCTE terrestrial transects: dynamics of terrestrial ecosystems under environmental change – Introduction. *Journal of Vegetation Science*, **13**, 298–300.

Cancello, E.M., Silva, R.R., Vasconcellos, A., Reis, Y.T. & Oliveira, L.M. (2014) Latitudinal variation in termite species richness and abundance along the Brazilian Atlantic forest hotspot. *Biotropica*, **46**, 441–450.

Castracani, C., Grasso, D.A., Fanfani, A. & Mori, A. (2010) The ant fauna of Castelporziano Presidential Reserve (Rome, Italy) as a model for the analysis of ant community structure in relation to environmental variation in Mediterranean ecosystems. *Journal of Insect Conservation*, **14**, 585–594.

Chaladze, G. (2012) Climate-based model of spatial pattern of the species richness of ants in Georgia. *Journal of Insect Conservation*, **16**, 791–800.

Colwell, R.K. (1997) *EstimateS: statistical estimation of species richness and shared species from samples.* Version 8.2.0. Available at: http://viceroy.eeb.uconn.edu/estimates/

Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, **7**, 1121–1134.

Cushman, J.H., Lawton, J.H. & Manly, B.F.J. (1993) Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia*, **95**, 30–37.

De Frenne, P., Graae, B.J., Rodríguez-Sanchez, F., Kolb, A., Chabrerie, O., Decocq, G., De Kort, H., De Schrijver, A., Diekmann, M., Eriksson, O., Gruwez, R., Hermy, M., Lenoir, J., Plue, J., Coomes, D.A. & Verheyen, K. (2013) Latitudinal gradients as natural laboratories to infer species' responses to temperature. *Journal of Ecology*, **101**, 784–795.

Del Toro, I., Ribbons, R.R. & Pelini, S.L. (2012) The little things that run the world revisited: a review of ant-mediated ecosystem services and disservices (Hymenoptera: Formicidae). *Myrmecological News*, **17**, 133–146.

Delsinne, T., Roisin, Y., Herbauts, J. & Leponce, M. (2010) Ant diversity along a wide rainfall gradient in the Paraguayan dry Chaco. *Journal of Arid Environments*, **74**, 1149–1155.

Diamond, S.E., Sorger, D.M., Hulcr, J., Pelini, S.L., Del Toro, I., Hirsch, C., Oberg, E. & Dunn, R.R. (2012) Who likes it

hot? A global analysis of the climatic, ecological, and evolutionary determinants of warming tolerance in ants. *Global Change Biology*, **18**, 448–456.

Dunn, R.R., Agosti, D., Andersen, A.N. *et al.* (2009) Climatic drivers of hemispheric asymmetry in global patterns of ant species richness. *Ecology Letters*, **12**, 324–333.

Egan, J.L. & Williams, R.J. (1996) Lifeform distributions of woodland plant species along a moisture availability gradient in Australia's monsoonal tropics. *Australian Systematic Botany*, **9**, 205–217.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M. & Turner, J.R.G.. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, **36**, 132–147.

Fisher, B.L. (1999) Ant diversity patterns along an elevational gradient in the reserve Naturelle Integrale d'Andohahela, Madagascar. *Fieldiana Zoology*, **94**, 129–147.

Folgarait, P.J. (1998) Ant biodiversity and its relationship to ecosystem functioning: a review. *Biodiversity and Conservation*, **7**, 1221–1244.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.

Hawkins, B.A., Field, R., Cornell, H.V., Currie, D.J., Guégan, J.-F., Kaufman, D.M., Kerr, J.T., Mittelbach, G.G., Oberdorff, T., O'Brien, E.M., Porter, E.E. & Turner, J.R.G. (2003) Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, **84**, 3105–3117.

Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *The American Naturalist*, **163**, 192–211.

Hoffmann, B.D. & James, C.D. (2011) Using ants to manage sustainable grazing: dynamics of ant faunas along sheep grazing gradients conform to four global patterns. *Austral Ecology*, **36**, 698–708.

Hölldobler, B. & Wilson, E.O. (1990) *The ants*. The Belknap Press of Harvard University Press, Cambridge, MA.

Hutley, L.B., Beringer, J., Isaac, P.R., Hacker, J.M. & Cernusak, L.A. (2011) A sub-continental scale living laboratory: spatial patterns of savanna vegetation over a rainfall gradient in northern Australia. *Agricultural and Forest Meteorology*, **151**, 1417–1428.

Jenkins, C.N., Sanders, N.J., Andersen, A.N., Arnan, X., Brühl, C.A., Cerda, X., Ellison, A.M., Fisher, B.L., Fitzpatrick, M.C., Gotelli, N.J., Gove, A.D., Lattke, J.E., Lessard, J.-P., McGlynn, T.P., Menke, S.B., Parr, C.L., Philpott, S.M., Weiser, M.D. & Dunn, R.R. (2011) Global diversity in light of climate change: the case of ants. *Diversity and Distributions*, **17**, 652–662.

Jennings, W.B., Pianka, E.R. & Donnellan, S. (2003) Systematics of the lizard family Pygopodidae with implications for the diversification of Australian temperate biotas. *Systematic Biology*, **52**, 757–780.

Kaspari, M., Ward, P.S. & Yuan, M. (2004) Energy gradients and the geographic distribution of local ant diversity. *Oecologia*, **140**, 407–413.

Koch, G.W., Vitousek, P.M., Steffen, W.L. & Walker, B.H. (1995) Terrestrial transects for global change research. *Vegetatio*, **121**, 53–65.

Kumschick, S., Schmidt-Entling, M.H., Bacher, S., Hickler, T., Espadaler, X. & Nentwig, W. (2009) Determinants of local ant (Hymenoptera: Formicidae) species richness and activity density across Europe. *Ecological Entomology*, **34**, 748–754.

Liberal, C.N., Isidro de Farias, A.M., Meiado, M.V., Filgueiras, B.K.C. & Iannuzzi, L. (2011) How habitat change and rainfall affect dung beetle diversity in Caatinga, a Brazilian semi-arid ecosystem. *Journal of Insect Science*, **11**, 1–11.

Mannion, P.D., Upchurch, P., Benson, R.B.J. & Goswami, A. (2014) The latitudinal biodiversity gradient through deep time. *Trends in Ecology and Evolution*, **29**, 42–50.

Morton, S.R. & James, C.D. (1988) The diversity and abundance of lizards in arid Australia: a new hypothesis. *The American Naturalist*, **132**, 237–256.

Oksanen, J., Guillaume Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) *vegan: Community Ecology Package.* 2.0-7. Available at: https://github.com/vegandevs/vegan.

Paknia, O. & Pfeiffer, M. (2012) Productivity alone does not explain species richness of ants – An example from Central Persian deserts. *Journal of Arid Environments*, **85**, 86–92.

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. & Chown, S.L. (2001) Inventory and bioindicator sampling: testing pitfall and Winkler methods with ants in a South African savanna. *Journal of Insect Conservation*, **5**, 27–36.

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.

Pérez-Sánchez, A.J., Lattke, J.E. & Viloria, A.L. (2013) Patterns of ant (Hymenoptera: Formicidae) richness and relative abundance along an aridity gradient in western Venezuela. *Neotropical Entomology*, **42**, 128–136.

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.

Pianka, E.R. (1986) *Ecology and natural history of desert lizards: analyses of the ecological niche and community structure*. Princeton University Press, Princeton, NJ.

Powney, G.D., Grenyer, R., Orme, C.D.L., Owens, I.P.F. & Meiri, S. (2010) Hot, dry and different: Australian lizard richness is unlike that of mammals, amphibians and birds. *Global Ecology and Biogeography*, **19**, 386–396.

Schall, J.J. & Pianka, E.R. (1978) Geographic trends in numbers of species. *Science*, **201**, 679–686.

Segev, U. (2010) Regional patterns of ant-species richness in an arid region: the importance of climate and biogeography. *Journal of Arid Environments*, **74**, 646–652.

Shattuck, S.O. (1999) *Australian ants: their biology and identification*. CSIRO Publishing, Melbourne.

Sommer, J.H., Kreft, H., Kier, G., Jetz, W., Mutke, J. & Barthlott, W. (2010) Projected impacts of climate change on regional capacities for global plant species richness. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2271–2280.

R Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org/

Watson, J.A.L. & Abbey, H.M. (1993) *Atlas of Australian termites*. Division of Entomology, CSIRO, Canberra.

Werneck, F.P., Nogueira, C., Colli, G.R., Sites, J.W., Jr & Costa, G.C. (2012) Climatic stability in the Brazilian Cerrado: implications for biogeographical connections of South American savannas, species richness and conservation in a biodiversity hotspot. *Journal of Biogeography*, **39**, 1695–1706.

Whitehead, P.J., Bowman, D.M.J.S. & Tidemann, S.C. (1992) Biogeographic patterns, environmental correlates and conservation of avifauna in the Northern Territory, Australia. *Journal of Biogeography*, **19**, 151–161.

Williams, R.J., Cook, G.D., Braithwaite, R.W., Andersen, A.N. & Corbett, L.K. (1995) Australia's wet-dry tropics: identifying the sensitive zones. *The impact of climate change on ecosystems and species: terrestrial ecosystems* (ed. by J. Pernetta, R. Leemans, D. Elder and S. Humphrey), pp. 39–65. IUCN, Gland, Switzerland.

Williams, R.J., Duff, G.A., Bowman, D.M.J.S. & Cook, G.D. (1996) Variation in the composition and structure of tropical savannas as a function of rainfall and soil texture along a large-scale climatic gradient in the Northern Territory, Australia. *Journal of Biogeography*, **23**, 747–756.

Wilson, S. & Swan, G. (2003) *A complete guide to reptiles of Australia*. Reed New Holland, Sydney.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Latitude and longitude of study sites.

Appendix S2 Percentage canopy cover and height at study sites.

Appendix S3 Ant species list and distribution across study sites.

DATA ACCESSIBILITY

The abundances of all ant species recorded in pitfall traps in each plot during each of the three sampling periods are available via ÆKOS Data Portal (www.aekos.org.au/home).

BIOSKETCH

Alan Andersen is a Chief Research Scientist with the CSIRO Land & Water Flagship. He leads CSIRO's tropical savannas research in Darwin, which aims to provide the scientific basis for delivering environmental, social and economic benefits to northern Australia. His main research interest is the biogeography and global ecology of ant communities.

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Author contributions: A.N.A. designed the project, identified the ants and drafted the manuscript. I.D.T. analysed the data and contributed to the writing. C.L.P. contributed to the writing.

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