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Elevation–diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa

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ABSTRACT

Aim Patterns of biological diversity are often investigated across space but little work has attempted to explore the consistency of such observations through time. Here, our aim was to understand the patterns of diversity for a functionally critical taxon, the ants (Hymenoptera: Formicidae), through space and time using an extensive dataset collected across an elevational gradient. In addition, we evaluated the importance of two key postulated drivers of elevational diversity patterns: temperature and available area.

Location The Maloti-Drakensberg Mountains of southern Africa.

Methods We sampled epigaeic ant communities biannually for 7 years (2006–2012) at eight different elevational sites. We then used an information theoretic approach combined with generalized linear mixed models to: (1) describe diversity patterns through space and time; (2) assess the importance of different abiotic drivers; and (3) understand how much spatio-temporal variation can be explained by these drivers. Simple regression approaches were also used to test for differences in seasonal variation along the elevational gradient.

Results We found clear mid-elevational peaks of species density and evenness measures. Abundance patterns were complex. The spatial distributions of all three metrics changed across seasons and years. Temperature variables had important roles in explaining both species density and abundance patterns, whilst species density was also influenced by available area. In conjunction, we found much greater seasonal variability in species density at low elevations. This variation was independent of differences in species pool size.

Main conclusions We found patterns of ant diversity that are strongly modulated by temporal change. There was a consistent and strong signature of seasonality on the elevation–diversity patterns of the ants, whilst annual changes throughout the study period had a weaker influence. We conclude that both spatial and temporal patterns are driven primarily by temperature, with only a weak influence of available elevational area. This study is the first to describe the spatio-temporal distribution of a suite of community-level metrics along an elevational gradient and implies that temporal variation should be considered more carefully in studies of invertebrate diversity, particularly with respect to elevation and the mechanisms that may be maintaining diversity patterns.

Keywords

Ant, elevational gradient, evenness, Formicidae, mid-domain peak, seasonality, southern Africa, spatio-temporal variability, species diversity, species richness.

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INTRODUCTION

Describing patterns of biodiversity and revealing the factors that are driving them has long been a central research theme in ecology (Pianka, 1966; Rohde, 1992; Gaston, 2000). Such a goal not only allows ecologists to gain a better understanding of the diversity of life on Earth, but also provides information typically needed for decision-making in conservation science (Myers et al., 2000; Samways, 2005). Elevational gradients provide useful natural experiments when investigating the distribution of biodiversity (Körner, 2007; Sundqvist et al., 2013). They condense a large amount of environmental variation into a small geographical space (Körner, 2007), allowing us to more easily test patterns and processes that occur on larger scales (Sanders et al., 2007; Sundqvist et al., 2013). Elevational gradients are also of interest in their own right, particularly given that species distributions are expected to shift into higher elevations as well as higher latitudes following global climate change (Wilson et al., 2005; Parmesan, 2006; Colwell et al., 2008). An understanding of the patterns of biodiversity across elevation can therefore contribute towards basic and applied ecological goals.

Whilst much emphasis has been placed on describing and explaining spatial patterns, few studies have investigated how elevational diversity and its explanatory factors may vary through time. This is despite the potential importance of a temporal component in allowing us to fully understand diversity patterns and tease apart the mechanisms generating them (Willis & Whittaker, 2002; White et al., 2010). Can the patterns and drivers of diversity across space be generalized through inter- and intra-annual time-scales?

With respect to space, unimodal peaks and monotonic declines of species density (the number of species per unit area, i.e. Gotelli & Colwell, 2001) with elevation are the most commonly reported patterns (Rahbek, 1995, 2005). Many proposed explanations for these diversity patterns concern elevational clines in variables such as temperature, precipitation and available area. Here, species density is predicted to peak at elevations that offer an optimal set of environmental conditions. The role of area in this context is analogous to a species–area effect: elevational bands with the most available area will have a larger number of individuals, and therefore likelihood of a larger species pool with which to supply local communities (Lomolino, 2001; Romdal & Grytnes, 2007). Other explanations for elevational diversity patterns rely on the geometric constraints of mountain topology. For example, the mid-domain effect model predicts peaks in diversity at mid-elevations as a result of the random overlap of species ranges placed between the hard bounds of the base (i.e. sea level) and peak of an elevational gradient (Colwell & Lees, 2000; Dunn et al., 2007).

Few studies have investigated potential temporal changes in these diversity measures and their putative drivers. Beck et al. (2010) found a linear decline in moth species number with elevation during spring and autumn, which changed to a unimodal pattern in the summer. McCain (2004) reported that the mid-elevational peak in diversity of non-volant Neotropical mammals shifted to higher elevations between the dry and wet seasons. These results suggest that there is more to learn about the distribution and drivers of elevational diversity through time. Many studies do sample elevational gradients over multiple seasons or years, yet this temporal variation is often pooled or averaged away for analysis (Axmacher et al., 2004; Naniwadekar & Vasudevan, 2007; Wu et al., 2013). The lack of interest in, or availability of, time-series data means that we are likely to be underestimating the true range of elevational diversity patterns and the extent to which these patterns are related to potential explanatory variables. Here, we address this significant gap by presenting the first results from a long-term monitoring scheme of ants (Hymenoptera: Formicidae) along an elevational gradient in southern Africa.

Ants are a globally important and abundant taxonomic group (Hölldobler & Wilson, 1990; Ness et al., 2010; Del Toro et al., 2012). Linear declines (Brühl et al., 1999; Robertson, 2002; Yusah et al., 2012) and mid-elevational peaks (Fisher, 1999; Sanders, 2002; Sanders et al., 2003; Bharti et al., 2013) of ant species density have been reported. Reports of ant abundance patterns are also mixed, with examples of declines with elevation, mid-elevation peaks, and some examples of no significant change in abundance with elevation (Sabu et al., 2008; Munyai & Foord, 2012; Yusah et al., 2012). Temperature and available land area have been cited as being important factors governing the distribution of ant diversity across elevation (Sanders, 2002; Botes et al., 2006; Sanders et al., 2007; Machac et al., 2011; Chaladze, 2012; Munyai & Foord, 2012).

No studies have investigated temporal variation in ant elevational diversity. Ant species density and abundance, however, are known to shift with season in a range of habitats (Andersen, 1983; Kaspari & Weiser, 2000; Deblauwe & Dekoninck, 2007). Typically, greater species density and abundance are observed at the time of year which has greater humidity, temperatures or forage availability (Whitford, 1978; Andersen, 1983; Kaspari & Weiser, 2000). In addition, this seasonal flux of diversity may be modulated by other environmental factors. For example, the response of ant communities to different seasons can depend on the vegetation type sampled (Deblauwe & Dekoninck, 2007; Barrow & Parr, 2008).

Here, we tested previously reported relationships of ant diversity with elevation, temperature and available area. Crucially, we incorporated a temporal component into our analyses in order to assess the inter- and intra-annual generality of both the patterns and the potential drivers of ant diversity. We also investigated the relatively unknown relationship of species evenness with elevation. Evenness provides information of the equitability of abundances of species in a given community and is likely to be important in fully understanding the structure and function of biological communities. We investigated these relationships using an extensive dataset from a region previously unexplored in

detail for ants: the Sani Pass of the Maloti-Drakensberg Mountains, southern Africa. Our dataset ranges from 900 to 3000 m a.s.l. and encompasses seven consecutive years of biannual sampling, making it one of the largest standardized, spatio-temporal invertebrate community datasets available. We did not directly investigate hypotheses of geometric constraints because we lacked a hard lower elevational boundary (Colwell & Lees, 2000; Sanders *et al.*, 2003) and were more interested in effects driving relatively small and local-scale diversity, for which mid-domain effect predictions have been shown to be inappropriate (Dunn *et al.*, 2007).

We asked the following questions: (1) How does ant diversity vary in space and time within the Sani Pass? (2) Does ant diversity respond positively to the drivers of temperature and available area? (3) How much of the spatio-temporal variation in ant diversity can be explained by these drivers? In line with previous work, we predicted that species density, the abundance of individuals and evenness would decline with increasing elevation. In addition, we expected that departures from a monotonic decline in these metrics across elevation would be explained by variation in temperature or available area (Sanders, 2002; Sanders *et al.*, 2007). We expected no systematic trend in any of our diversity metrics across years but anticipated reduced species density, abundance and evenness in the harsher dry season. Finally, we expected that the form of the diversity–elevation relationship would change between the seasons, in line with previous work (McCain, 2004; Beck *et al.*, 2010).

MATERIALS AND METHODS

Study site

We sampled ants in the Maloti-Drakensberg Transfrontier Conservation Area of South Africa and Lesotho. This area forms part of the grassland biome (Cowling *et al.*, 1997) and is recognized as a centre of endemism within southern Africa (Carbutt & Edwards, 2006; Kuhlmann, 2009). We sampled along an elevational transect located in the southern region of the Maloti-Drakensberg which runs from near the village of Ixopo at 900 m a.s.l. (30°09′ S 30°03′ E) to a point above the top of the Sani Pass at 3000 m a.s.l. (29°35′ S 29°17′ E). Eight sampling sites were placed at increasing elevations of 300 m. The transect is 104 km long; however, the majority of the sampling sites were located in the final 7 km of the Sani Pass (1800–3000 m a.s.l.). All sampling sites were placed in natural vegetation. Mean annual rainfall between 2002 and 2005 along the transect ranged from 793 to 861 mm (Nel & Sumner, 2008). Annual rainfall increases with elevation with the exception of the very highest elevations, where rainfall is reduced (Nel & Sumner, 2008). The majority of the rainfall occurs during the summer (October–March) with as much as 19% occurring in January. In contrast, only 5% of the annual rainfall occurs in September (Nel & Sumner, 2006). Mean ground temperatures vary strongly between seasons and tend to decline with increasing elevation. Mean ground temperatures range from 13.1 to 22.1 °C in January, and from 9.2 to 15.2 °C in September (M.P.R., unpublished data). Snowfall is common during the winter, particularly at high elevations.

Ant sampling

Epigaeic (ground-dwelling) ant sampling took place during January (wet season) and September (dry season) for the years 2006–2012 inclusive (7 years in total). We established four replicate blocks, spaced at least 300 m apart, at each elevational site. We consider each block to be an independent ecological community. Within each block, 10 pitfall traps were dug in two parallel lines, with 10 m spacing between traps. This design mirrors that used in sister sampling schemes throughout South Africa (Botes *et al.*, 2006; Munyai & Foord, 2012). Pitfall traps were 150 ml in volume with a diameter of 55 mm and a depth of 70 mm. Rain guards of 220 mm diameter, supported on wire legs 100 mm above the traps, were used to prevent flooding. Traps contained a 50% ethylene glycol solution to preserve ant specimens. Traps were left out for five trapping nights in total but were replaced after 2 or 3 days to prevent overfilling. Ants were later transferred to 70% alcohol in the laboratory and were identified to morphospecies, and species level where possible.

Environmental variables

Thermocron iButtons (DS1921G, Semiconductor Corporation, Dallas/Maxim, TX, USA) were buried 10 mm below the soil surface at two replicates at each elevational site. These iButtons were replaced each sampling period. Temperature was recorded every 1.5 hours. Hourly readings were taken from January 2010 as higher capacity iButtons (DS1922L) were phased into use. Mean, minimum and maximum temperatures were calculated for January and September for each year of the study for each elevational band. Plots of temperature through time were inspected for each iButton and instances where recording had malfunctioned or where the iButton had clearly been exposed were excluded from analysis.

Available area was calculated for each elevational site. Vertical bands ± 150 m of the focal elevations were set. Then, the available area of each of these elevational bands in a 40-km buffer around the sampling sites was determined using ArcMap GIS 9.3.1 (ESRI, Redlands, CA, USA).

Statistical methods

For each of the 440 ant communities in the dataset, i.e. replicated blocks (4 blocks per sampling site × 8 sites × 7 years × 2 seasons = 440 following the removal of those eight communities without valid temperature data), species density (Gotelli & Colwell, 2001), total abundance and evenness were calculated. Species density and abundance are

counts of the number of species and the number of individuals, respectively, in each standardized replicate block. The probability of interspecific encounter (PIE) was used as a measure of evenness and was calculated as:

$$PIE = 1 - \sum_{i=1}^{S} p_i^2,$$

where S is the number of species and p is their relative abundance within a community. This represents the probability of interspecific encounter within a community (Hurlbert, 1971). Strictly, this is the probability that two individuals drawn at random from a given community will represent different species. To assess spatial independence between communities, Moran's I was used to test for spatial autocorrelation of species density, abundance and evenness values at each elevational band for each year and season.

Three sets of generalized linear mixed models (GLMMs) and an information theoretic approach based on the bias-corrected Akaike's information criterion (AIC_c) were used to examine the extent to which ant species density, abundance and evenness is related to temperature and available area across a spatio-temporal scale. The first set of models aimed only to describe the pattern of the spatio-temporal distribution of the response variables, namely ant species density, abundance and evenness. Elevation, elevation^2, season, year and various two-way and three-way interactions were used as explanatory variables in these models. A polynomial term of elevation was included in order to detect potential hump shapes in the relationships between elevation and the response variables. Sixteen plausible models combining these variables were constructed for this first set of models. The second set of models examined the extent to which ant diversity is related to temperature and available area. Area, the mean and standard deviation in temperature and their two-way interactions were used as explanatory variables. These variables were chosen because of their lack of collinearity. The third set investigated the spatio-temporal patterns of the residuals of the second set. This procedure would reveal whether any spatio-temporal patterning remained after removing the effect of the most important drivers. For example, a model of the residuals that included only the intercept would indicate that the best model of the drivers could account for all previously observed spatio-temporal patterns.

A Poisson error structure was used for models of species density and abundance. For models of evenness, a logit transformation on the response variable, to meet model assumptions, and Gaussian errors were used. Models of residuals used a Gaussian error structure. All numeric explanatory variables were centred around the mean and standardized to allow for greater interpretability of coefficients (Schielzeth, 2010). Season was coded as a binary variable. Replicate was included as a random effect to account for temporal pseudoreplication. Maximum likelihood estimation was used and AIC_c values compared to choose the best model for each response variable in each set of models. Modelling was performed using the LME4 package in R (Bates *et al.*, 2013; R Core Team, 2013). Marginal R^2 (R^2_m,

due to fixed effects only) and conditional R^2 (R^2_c, due to fixed effects and random effects) were calculated for each model (Nakagawa & Schielzeth, 2013). Conditional R^2 cannot yet be computed for models using a Poisson error structure (Bartoń, 2013).

Following the results of the modelling, we tested the hypothesis that communities at lower elevations had greater seasonal fluctuations in species density than communities at high elevations. For each replicate, we calculated the seasonal component of variation in species density values. This was performed by treating individual replicates as time series with 14 data points (seven years and two seasons). From these time series, the seasonal component was extracted by classical decomposition using moving averages (Kendall & Stuart, 1976). This quantifies the seasonal variation in species density values, for each of the 32 replicates, across the entire 7 years of sampling. These values were then regressed against elevation. A negative relationship would indicate that the seasonal variation is greater at lower elevations. To account for species pool effects, the same analysis was performed twice again on species density values that had been corrected for differences in species pool sizes. This was performed by expressing species density values as a proportion of (1) the total number of species seen at that given replicate across the 7 years, and (2) the total number of species seen at all four replicates within that elevational band across the 7 years.

RESULTS

We collected 60,236 individuals from 92 ant species in 28 genera and seven subfamilies throughout the study period. Our assumption that the communities were spatially independent was confirmed by non-significant results of the Moran I tests for each response variable in each year and season. All coefficients are reported on the standardized scale as phenotypic standard deviations with their associated standard errors and consequently do not have units (Schielzeth, 2010).

Species density

Spatio-temporal patterns

Species density was best modelled by elevation, elevation^2, season, year and interactions between both elevational terms and both temporal terms, as well as an interaction between season and year (Table 1). The form of this model describes a hump-shaped relationship of species density with elevation that changes depending on the season (Fig. 1, Table 2). The hump shape is more pronounced, and peaks at a higher elevations, in the dry season. Overall, species density also tends to be lower in the dry season. The interaction between the elevational terms and year describes a situation where the hump shape becomes increasingly linear through time. Fewer species are found in later years and this effect is greatest in

Table 1 Summaries of generalized linear mixed models linking ant species density, abundance and evenness to (1) spatio-temporal explanatory variables, (2) environmental drivers and (3) residual spatio-temporal variables with the effect of the drivers removed, along an elevational gradient within the Sani Pass, southern Africa. The best models, according to the bias-corrected Akaike information criterion (AIC_c) are reported. The change in AIC_c between the best model and the next best and worst are also given. Marginal R^2 (R^2_m), measuring variation explained by fixed effects only, and conditional R^2 (R^2_c), measuring variation explained by both fixed and random effects, are given.

Response	Model	AIC_c	ΔAIC_c (next best)	ΔAIC_c (worst)	R^2_m	R^2_c
Ant species density						
Spatio-temporal patterns	~ elevation + elevation^2 + season + year + elevation:season + elevation:year + elevation^2:season + elevation^2:year + year:season	683.96	3.07	356.29	0.68	NA
Drivers	~ mean temperature + area	774.85	0.53	262.45	0.43	NA
Residual analysis	~ elevation + elevation^2 + season + year + elevation:season + elevation:year + elevation^2:season + elevation^2:year + year:season	1348.77	4.13	23.89	0.08	0.08
Ant abundance						
Spatio-temporal patterns	~ elevation + elevation^2 + season + year + elevation:season + elevation:year + elevation^2:season + elevation^2:year + year:season + season:year:elevation + season:year:elevation^2	20599.09	5.75	9889.83	0.67	NA
Drivers	~ mean temperature + SD temperature	19551.81	224.52	10938.31	0.7	NA
Residual analysis	~ Intercept	2939.08	1.84	7.27	0	0
Ant community evenness						
Spatio-temporal patterns	~ elevation + elevation^2 + season + year	1174.77	0.53	37.12	0.32	0.46
Drivers	~ mean temperature	1211.43	0.19	1.47	0.006	0.43
Residual analysis	~ elevation + year	1094.38	1.02	14.19	0.03	0.03

the wet season due to the inclusion of the season + year interaction. The fixed effects explained a large amount of variation in species density ($R^2_m = 0.68$).

Drivers

The best model of the drivers of species density included mean temperature and area. Positive estimates were found for both of these variables, indicating that species density increases with increasing mean temperature (0.32 ± 0.02) and area (0.08 ± 0.05). The influence of area, however, was weak, with the next best model including only mean temperature ($\Delta AIC_c = 0.53$). The best model explained a relatively large amount of variation with an R^2_m of 0.43. The relationship of species density with mean temperature is displayed in Fig. 2a.

Residual analysis

The best model of the residuals obtained from the drivers model (immediately above) included the same explanatory variables as that for the spatio-temporal patterns, namely elevation, elevation^2, season, year and their two-way interactions. This model explained very little variation with an R^2_m of 0.08. This indicates that the residuals are modelled very poorly by the spatio-temporal variables. There is little to no interpretable pattern across space or time; in other words, the drivers of available area and temperature explain the patterns of species density.

Abundance

Spatio-temporal patterns

The best model for abundance was the most complicated one included in the candidate list. Elevation, elevation^2, season, year, their two-way interactions and the three-way interactions between season, year and each elevational term were included (Table 1). Abundance displays a mild hump-shaped relationship with elevation, which differs with the season (Fig. 3, Table 2). The hump is more pronounced in the dry season. Essentially, however, this hump is nearly flat as the estimates for elevation (0.45 ± 0.44) and elevation^2 (-0.7 ± 0.44) are close to 0. Abundance is lower in the dry season and also decreases through time, but more so in the wet season and at lower elevations. This is indicated by the three-way interactions between elevation:season:year and elevation^2:season:year. The interactions of the elevation terms with year show that the abundance–elevation relationship has become less pronounced through time. This model of abundance has an R^2_m of 0.67.

Drivers

Mean temperature (0.63 ± 0.01) and the standard deviation in temperature (0.08 ± 0.01) were both included in the best model of abundance. Both had positive estimates, indicating that abundance increases with increasing mean (Fig. 2b) and standard deviation of temperature. This model has an R^2_m of 0.7.
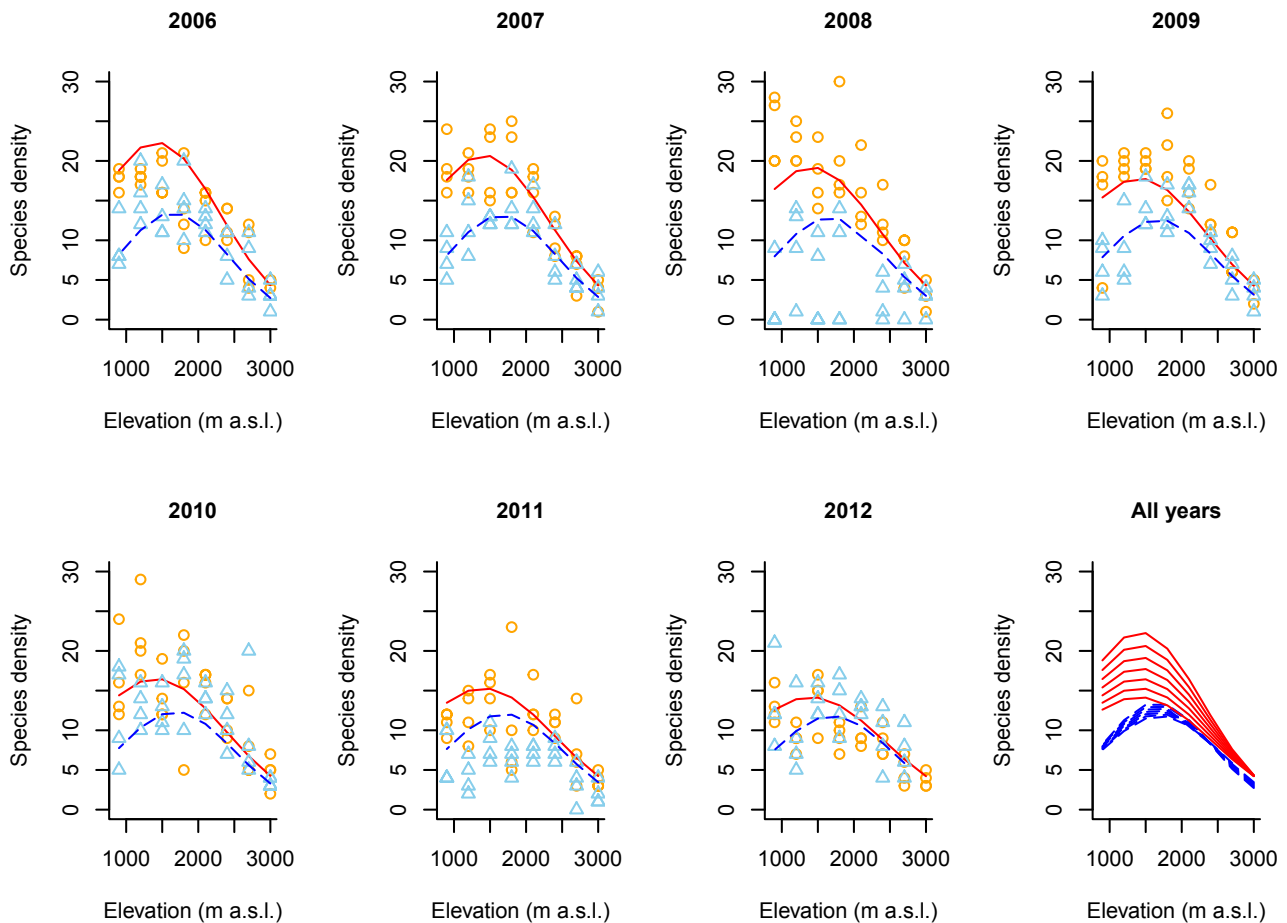
Figure 1 Plots of ant species density against elevation in the Sani Pass, southern Africa, for consecutive years and for all years combined. Red solid lines indicate predicted values from generalized linear mixed modelling for January (wet season; circles) and blue dashed lines for September (dry season; triangles). Each point represents a sampled community. Marginal R^2 (due to fixed effects only) = 0.68.

Residual analysis

The model including only the intercept was the best (Table 1). Consequently, patterns of abundance are entirely explained by variation in the mean and standard deviation in temperature.

Evenness

Spatio-temporal patterns

The best model for evenness included the main effects of elevation, elevation^2, season and year. This model describes a hump-shaped relationship between evenness and elevation (Table 2). Evenness is lower in the dry season and also decreases across years (Fig. 4). The ant communities are more even in the wet season and in early years. This is the poorest fitting of the spatio-temporal models with an R^2_m of 0.32.

Drivers

PIE was best modelled by mean temperature only (0.09 ± 0.05). Mean temperature had a positive effect on evenness. However, this model actually explained very little variation ($R^2_\mathrm{m} = 0.006$, $R^2_\mathrm{c} = 0.43$). The next best model included the mean and standard deviation of temperature ($\Delta\mathrm{AIC_c} = 0.19$).

Residual analysis

The best model for the residuals obtained from the drivers model (immediately above) included elevation and year as main effects (Table 1). Both had negative estimates, indicating that the residuals decrease with elevation and across time. The result from this model indicates that the curvature in the pattern of evenness distribution (elevation^2) and the seasonal effect are explained by differences in mean temperature. This model explains very little variation ($R^2_\mathrm{m} = 0.03$, $R^2_\mathrm{c} = 0.03$).

Seasonal fluctuation

There was a significant decline in the seasonal component with elevation for all three levels of analysis: raw species density ($b = -0.002$, d.f. = 30, $P < 0.01$, Fig. 5a), controlling for

Table 2 Parameter estimates from generalized linear mixed models linking ant species density, abundance and evenness to spatio-temporal explanatory variables, along an elevational gradient within the Sani Pass, southern Africa. Estimates are on the standardized scale ± standard error. Empty cells indicate terms not included in the best model for a given response variable.

Term	Estimates		
	Species density	Abundance	Evenness
Elevation	2.42 ± 0.03	0.45 ± 0.44	2.24 ± 0.59
Elevation^2	-1.46 ± 0.22	-0.70 ± 0.44	-2.77 ± 0.59
Season	-0.39 ± 0.03	-0.75 ± 0.01	-0.13 ± 0.08
Year	-0.13 ± 0.02	-0.08 ± 0.01	-0.14 ± 0.04
Elevation:Season	0.76 ± 0.22	2.71 ± 0.07	
Elevation^2:Season	-0.63 ± 0.23	-2.43 ± 0.07	
Elevation:Year	-0.17 ± 0.10	0.08 ± 0.03	
Elevation^2:Year	0.20 ± 0.11	0.01 ± 0.04	
Season:Year	0.09 ± 0.03	0.11 ± 0.01	
Season:Year: Elevation		-0.15 ± 0.07	
Season:Year: Elevation^2		0.12 ± 0.07	

the replicate species pool ($b = -2.98^{-5}$, d.f. = 30, $P < 0.01$, Fig. 5b) and controlling for the elevational species pool ($b = -2.33^{-5}$, d.f. = 30, $P < 0.01$, Fig. 5c). The seasonal variation of species density is greater at lower elevations than at higher elevations and is independent of the differing sizes of the available species pools at different elevations.

DISCUSSION

Whilst many patterns of elevational diversity have been documented from various taxa and regions, the time dependence of these relationships has rarely been investigated (but see McCain, 2004; Beck *et al.*, 2010). Here, we found that the spatial distribution of ant species density, abundance and evenness depends on both inter- and intra-annual time. The drivers of this variation, however, appear to be consistent across time as they are able to account for the spatio-temporal patterns observed. These results suggest that environmental factors, rather than geometric constraints, control the diversity of ants within the Maloti-Drakensberg.

We found a mid-elevational peak of species density that differs in both size and shape depending on the season and year (Fig. 1). A number of studies have found mid-elevational peaks of ant species density (e.g. Fisher, 1999; Sanders, 2002; Bharti *et al.*, 2013). This pattern is the most common across a range of taxa and regions (Rahbek, 1995, 2005). Whereas Beck *et al.* (2010) found that the elevational diversity pattern of European moths changed from a monotonic decline to a mid-elevational peak with the onset of summer, we found a mid-elevational peak throughout our study period. This peak was found to change in magnitude and position depending on the season. Fewer species and a more
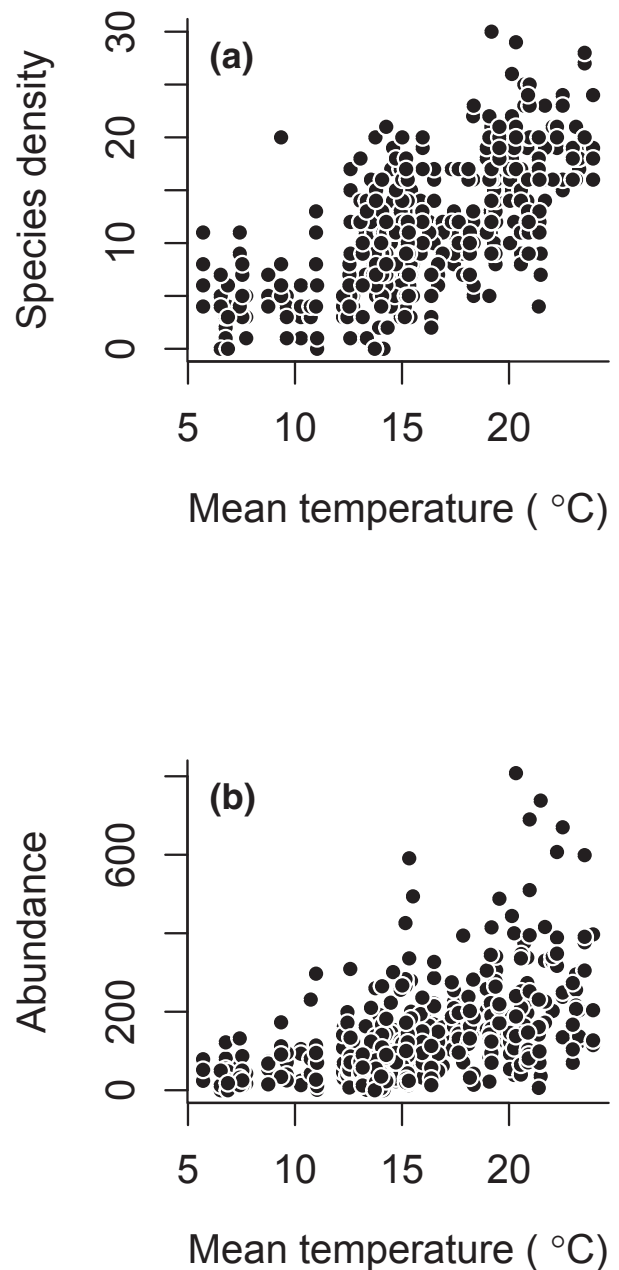
Figure 2 Plots of (a) ant species density and (b) ant abundance against mean temperature within the Sani Pass, southern Africa. All data across the elevational gradient and time series are plotted.

pronounced hump shape were observed in the dry season than in the wet season (Fig. 1). This is comparable to the findings of McCain (2004) where the mid-elevational peak of small mammal density shifts between two of the seasonal replicates sampled. Our dataset extends this result as we found consistent seasonal shifts in each year against a backdrop of annual change. We recorded an annual decline in species density, although this was a relatively weak effect (-0.13 ± 0.02, Table 2).

In our dataset, the seasonal change in the elevation–species density relationship is due to greater seasonal fluctuation at
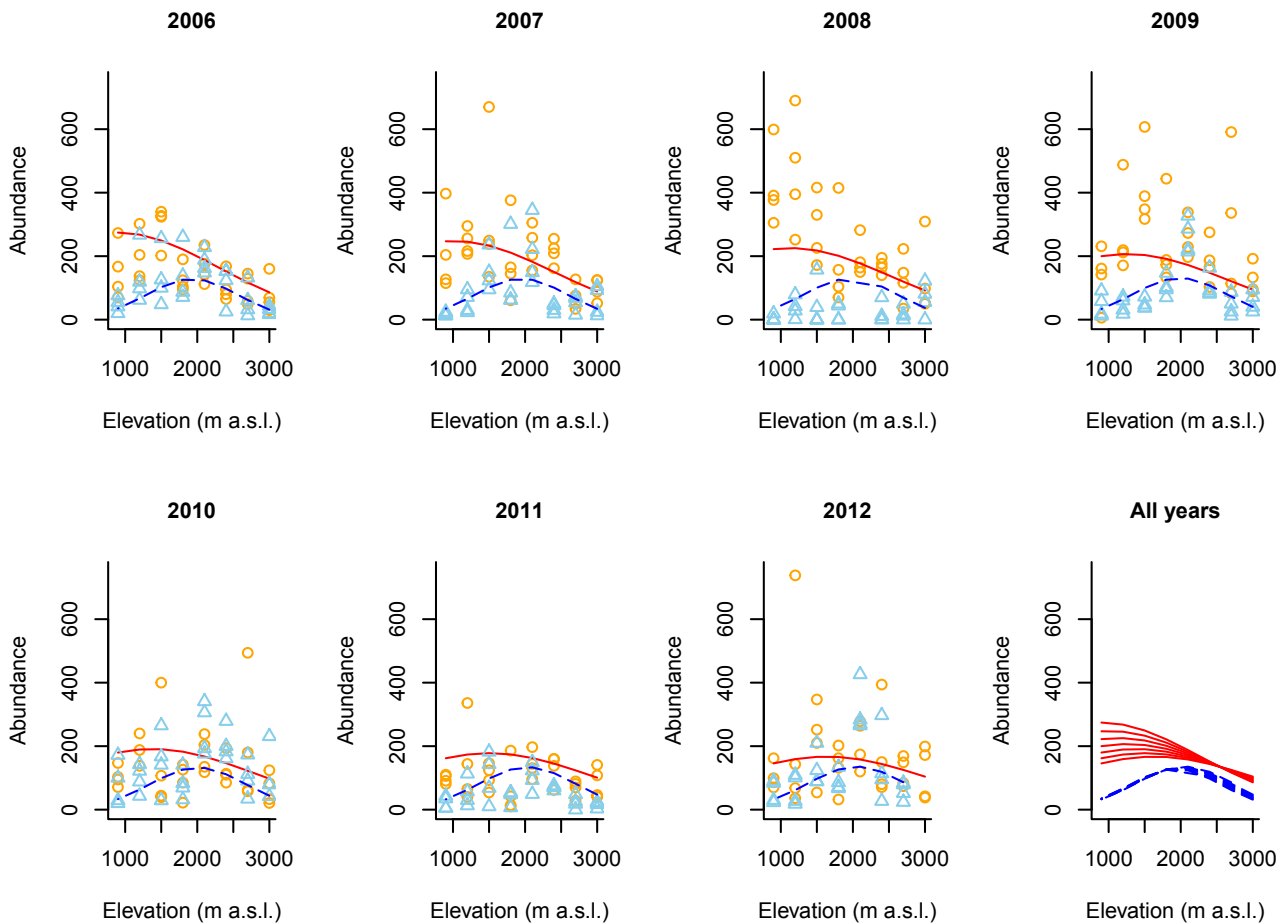
Figure 3 Plots of ant abundance against elevation in the Sani Pass, southern Africa, for consecutive years and for all years combined. Red solid lines indicate predicted values from generalized linear mixed modelling for January (wet season; circles) and blue dashed lines for September (dry season; triangles). Each point represents a sampled community. Marginal R^2 (due to fixed effects only) = 0.67.

low elevations. As the species pool is larger at lower elevations there is inherently more opportunity for variation at these sites. Consequently, the greater variation at low elevations could be a mathematical artefact. This is not the case, however, as we controlled for the size of the available species pools (Fig. 5). This distinction is important as it confirms the dependence of the seasonal effect on elevation, as found in our spatio-temporal model (Table 2). Species density fluctuates more at lower elevations.

These patterns of species density appear to be entirely explained by the effects of mean temperature and available area. The residual model of species density had poor explanatory power, indicating that after removing the effects of these two variables there is no spatio-temporal patterning remaining (R^2_m = 0.08, Table 1). Many studies have stressed the importance of temperature in promoting ant diversity at both local and global scales (Botes *et al.*, 2006; Sanders *et al.*, 2007; Jenkins *et al.*, 2011). The effect of temperature has also been cited to be responsible for seasonal changes in ant diversity (Andersen, 1983). Low temperatures are likely to limit ant foraging, resulting in fewer species being active at particular elevations or time periods.

The ubiquitous role of temperature across a range of habitats and scales implies that it is a general mechanism controlling ant diversity (Kaspari *et al.*, 2004; Sanders *et al.*, 2007; Jenkins *et al.*, 2011). By describing ant species density patterns across consecutive seasons and years, we are able to further strengthen this view. We found cooler temperatures in both the dry season and in later years (Appendices S1 & S2).

Area has also previously been linked to ant diversity across elevation. Sanders (2002) found mid-elevational peaks in ant species richness that were largely explained by the amount of available area within elevational bands. This effect is variable, however, as area had no role in a separate mountain range (Sanders *et al.*, 2003). In our case, a weak indirect area effect (Romdal & Grytnes, 2007) may be in operation: the number of species found in a local community was correlated with the available area within that elevational band. The larger available area could result in a larger species pool which feeds into local communities. This is the indirect elevational area effect (Romdal & Grytnes, 2007). We emphasize the weakness of the area effect in this instance, as the next best model included only temperature (Table 1).
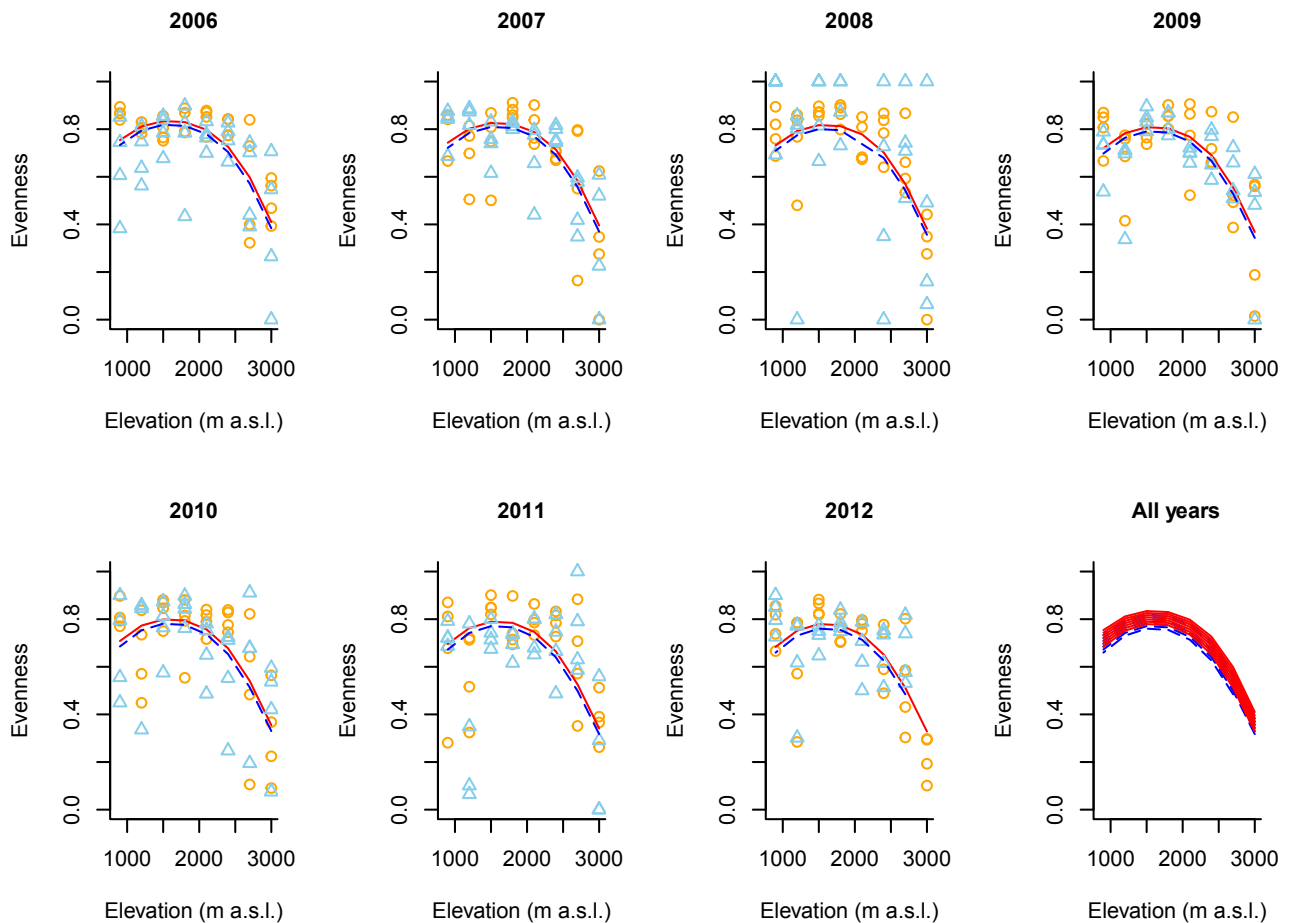
Figure 4 Plots of ant community evenness against elevation in the Sani Pass, southern Africa, for consecutive years and for all years combined. Red solid lines indicate predicted values from generalized linear mixed modelling for January (wet season; circles) and blue dashed lines for September (dry season; triangles). Predicted values have been back transformed onto the original scale. Each point represents a sampled community. Marginal R^2 (due to fixed effects only) = 0.32.

Sanders (2002) also found that geometric constraints, in the form of the mid-domain effect model, explained large portions of variation in species richness values. Although we did not directly test for such an effect it is unlikely to be responsible for generating the mid-elevational peaks we observe here. This is because the shape of the species density–elevation relationship changes both between seasons and across years. As highlighted by Beck *et al.* (2010), mechanisms that do not accommodate a temporal component cannot be primary drivers of time dependent elevational diversity patterns. There are no temporal predictions in the mid-domain effect model. It must also be noted that the same reasoning could be applied to the effect of available area. Consequently, we interpret the relatively weak influence of area in our models of species density (0.08 ± 0.05, Table 2) as driving spatial patterns only. Mean temperature (0.32 ± 0.02) was the primary observed driver of species density through both space and time.

In general, a weak linear decline in abundance across elevation was seen in the wet season and a bell-shaped curve in the dry season (Fig. 3). These patterns are largely consistent through time, with the exception of a gradual decline in abundance at low elevations in the wet season across years. Mean temperature and the standard deviation in temperature were completely able to explain these patterns of abundance (Table 1). The relationship between mean temperature and abundance has previously been described (Kaspari *et al.*, 2000; Munyai & Foord, 2012): ants are thermophilic and consequently more individuals are found where temperatures are higher.

The role of the standard deviation in temperature in driving abundance is less clear. Higher abundances are seen with greater variation in temperature. One explanation for this may be the thermal partitioning of the day by the ants. Ant species can partition foraging times during the day based on temperature. This can be a mechanism of avoiding competition (Cerda *et al.*, 1997; Stuble *et al.*, 2013). If in operation, we would have expected to see greater abundances of ants at sites where there is a greater variation in temperature. A wider range of temperatures could allow species with high abundance to be active at all time of the day. The same prediction applies to species density but the standard deviation
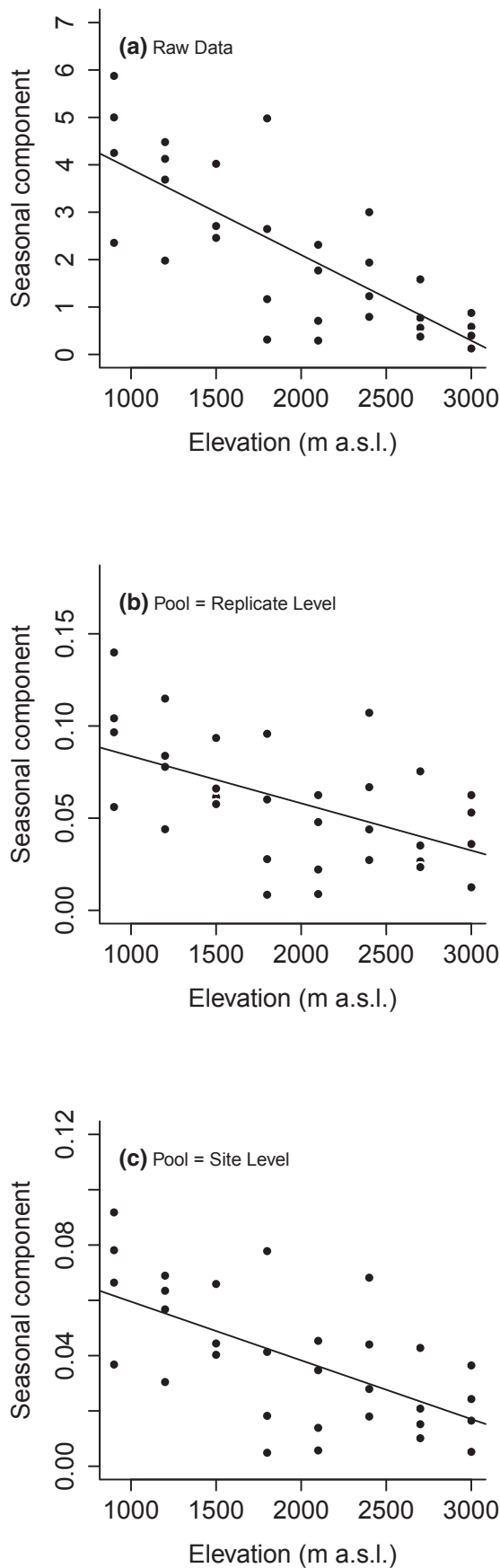
(a) Raw Data

(b) Pool = Replicate Level

(c) Pool = Site Level

Figure 5 Plots of the seasonal component of temporal variation in ant species density against elevation within the Sani Pass, southern Africa, for (a) raw species density values (seasonal component = $6.23 - 0.002 \times$ elevation), (b) species density controlled by the replicate level species pool (seasonal component = $0.124 - 2.98^{-5} \times$ elevation), and (c) species density controlled by the site level species pool (seasonal component = $0.89 - 2.33^{-5} \times$ elevation).

in temperature is not important in explaining this variable. This disparity may be caused by the weak effect of standard deviation in temperature on abundance (0.08 ± 0.01). Such a small effect may not be strong enough to also influence species density.

Evenness displayed a mid-elevational peak. Season and year were included in the spatio-temporal model of evenness, yet both of these had relatively weak effects (Table 2). Evenness was marginally lower in the dry season and decreased across years. Consequently, evenness displays a strong elevational pattern, which is largely unaffected by time. To our knowledge, this is the first time that mid-elevational peaks in evenness have been found. Previously, evenness measures have been reported to decline with elevation in northern temperate litter-dwelling arthropods (Lessard et al., 2011) and to have shown no systematic variation with elevation in the Costa Rican herpetofauna (Fauth et al., 1989). Whilst mean temperature was found to be the single best driver of evenness in our study, it explained only a tiny proportion of the existing variation ($R^2_m = 0.006$, Table 1). Therefore, it is not clear which variables are driving changes in evenness. Broadly speaking, evenness appears to correlate with species density (Pearson's $r = 0.5$). This is compatible with an assemblage level dominance-impoverishment rule (Parr, 2008). This rule predicts lower species density with low evenness or high dominance – the conceptual inverse of evenness. Two mechanisms may account for this pattern. First, the superior competitive and resource monopolization abilities of dominant ant species could reduce species density (Andersen, 1992; Parr et al., 2005). Dominant ant species may not be present at mid-elevational sites, leading to the pattern we observe here. Second, it may be that only a small number of species are able to thrive, and dominate, in the harsh conditions (cool temperatures) at high elevations. Further studies investigating the functional traits and ecologies of high-elevation ants may resolve which of these mechanisms is responsible for generating the pattern of evenness across elevation.

This is the first analysis of ant diversity within an extensive, combined spatial and temporal context and one of only a few studies to explicitly investigate the temporal variation that is associated with elevational diversity patterns. We found that species density, abundance and evenness vary through time, although to different extents. Time strongly influences patterns of species density whilst evenness is only mildly affected. For species density and abundance, elevational patterns show a strong seasonal signature. This temporal variation is largely explained by variation in mean

temperature. More ant individuals and species are found in the hotter parts of the elevational gradient and at warmer time periods. These results suggest a strong environmental, rather than geometrical, control on ant diversity patterns within the Maloti-Drakensberg. Such a conclusion was only possible with the availability of time-series data. This highlights the importance of monitoring ecological communities at multiple points in time if we are to properly understand the factors generating them.

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SUPPORTING INFORMATION

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

Appendix S1 Generalized linear mixed models of spatio-temporal patterns of mean temperature.
Appendix S2 Figure displaying spatio-temporal patterns of mean temperature.

BIOSKETCH

Tom R. Bishop is a PhD student at the University of Liverpool. He is interested in understanding the structure of ecological communities and the distribution of ant diversity.

Author contributions: M.P.R. and B.J.V.R. designed the sampling protocol and oversaw all data collection. T.R.B. and C.L.P. developed the research questions. T.R.B. analysed the data and led the writing of the paper. M.P.R., B.J.V.R., and C.L.P. all contributed to the final draft of the paper.

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